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Swarnendu Roy · Piyush Mathur · Arka Pratim Chakraborty ·
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Plant Stress: Challenges and Management in the New Decade

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Editors
Swarnendu Roy
Department of Botany
University of North Bengal
Siliguri, India

Piyush Mathur
Department of Botany
University of North Bengal
Siliguri, India

Arka Pratim Chakraborty
Department of Botany
Raiganj University
Raiganj, India

Shyama Prasad Saha
Department of Microbiology
University of North Bengal
Siliguri, India

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Preface

Plant stress management is an amalgamation of various conventional and advanced techniques that can help immensely in the augmentation of crop productivity in the presence of stress. Plants are continuously exposed to different abiotic (salinity, drought, temperature, heavy metal, ultraviolet, ozone, etc.) and biotic (bacteria, fungi, viruses, etc.) stresses which exerts utmost damage to their growth, development, and productivity. In the present scenario of climate change, scientists all over the world are engrossed with strategizing the management of plant stresses with new and improved techniques. The book has been designed in such a way so that a complete understanding of the plant responses to different abiotic and biotic stresses can be portrayed. The book will deliver the recent advances in the field of plant biology, viz., microbiology, pathology, physiology, molecular biology, biotechnology, plant breeding, and allied fields such as agroecology, nanobiotechnology, sustainable agriculture, climate-resilient agriculture, etc., for enhancing plant productivity and crop protection. The mechanisms at the genomic, proteomic, and metabolomic levels will also be described to facilitate the development of climate-resilient crop plants. An important section of the book will also focus on the role of different microbes in the mitigation of various abiotic and biotic stresses. Additionally, the book attempts to describe new-age techniques like nanotechnology, OMICS, metabolite engineering, and remote-sensing for the management and detection of plant stresses to achieve the goal of sustainable development in the new decade.

Siliguri, India Swarnendu Roy
Siliguri, India Piyush Mathur
Raiganj, India Arka Pratim Chakraborty
Siliguri, India Shyama Prasad Saha

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About the Editors

Dr. Swarnendu Roy is presently working as an Assistant Professor at the University of North Bengal, West Bengal, India. He has more than 11 years of teaching experience. His doctoral thesis involved understanding the mechanism of salinity stress tolerance in grasses mainly *Cynodon dactylon* and *Imperata cylindric*a by comparative evaluation with the model grass rice. He has published many articles in reputed journals and book chapters in edited volumes to date. He has submitted cDNA sequences of NHX and SOS1 genes of *Cynodon dactylon* for the first time to NCBI. Presently, he is actively engaged in research topics encompassing the mechanism of salinity and drought stress, stress management by engineered nanoparticles, and bioinformatics study of stress-related transcription factors. He is presently supervising 4 research scholars including 3 UGC-JRFs. He has published a number of Reviews and Research papers in journals of international repute. Also, he has recently received International Travel Support (ITS) from DST, Govt. of India, to present his research paper at International Conference on Integrative Plant Physiology at Sitges, Spain (27–29 October 2019). He is a life member of prestigious societies like 'The Indian Science Congress Association' and Association of Food Scientists and Technologist (India)'.

Dr. Piyush Mathur is presently working as an Assistant Professor in the Department of Botany, University of North Bengal, West Bengal, India. He has been teaching for the past 6 years and has also taught at the undergraduate level in the Department of Botany, Zakir Husain Delhi College, and Sri Guru Tegh Bahadur Khalsa College, University of Delhi. He has done his Ph.D. in Botany with a specialization in Mycology and Plant Pathology. His Ph.D. research dealt with the effect of elevated carbon dioxide on plant–pathogen interactions. Presently, he is working on microbial diversity, bioprospecting, and plant disease management. He has actively participated in both National and International conferences held in India and abroad and received a travel grant from CSIR and SERB, DST, Govt of India. He has published quite a number of research and review papers in well-known international journals of good repute. He has also contributed articles as book chapters in International and National books. Dr. Mathur is an active member of the Society of Rapeseed Mustard Research (SRMR), Bharatpur, and Delhi University Botanical Society (DUBS) Delhi, India.

Dr. Arka Pratim Chakraborty is currently working as an Assistant Professor in the Department of Botany, Raiganj University, Raiganj. He graduated and obtained his Master's degree from the University of North Bengal, Siliguri, India. He has been a recipient of the University Gold medal for securing 1st position at M.Sc. level. He has about 9 years of research experience in various research projects (funded by DBT, CSIR, and NBAIM-ICAR) and has 36 peer-reviewed International and National publications (International Journals = 14 and National Journals = 22), 04 research articles in proceeding volumes, 12 articles as a book chapter, and 07 books till date. He has also delivered numerous oral and poster presentations in numerous International and National symposia/conferences. He is interested in the field of research related to plant–microbe interactions, host–pathogen interactions, plant disease management through plant growth promoting rhizobacteria, biotic and abiotic stresses. Dr. Chakraborty is actively associated with scientific societies as a life member of the Asian PGPR Society, Association of Microbiologists of India (AMI), Indian Mycological Society (IMS), and Indian Phytopathological Society (IPS).

Dr. Shyama Prasad Saha is presently working as an Assistant Professor in the Department of Microbiology, University of North Bengal, West Bengal, India. He has been teaching for the past 10 years and has also taught at the Post Graduate level in the Department of Tea Science, Department of Food Technology, University of North Bengal. He has done his Ph.D. in Biotechnology with a specialization in Microbial Biotechnology and Enzymology. His Ph.D. research dealt with the production of microbial xylanase and its role in xylitol production. Presently, he is working on carbohydrate-active enzymes (Cazymes), antibiotic producing microbes, plant growth promoting bacteria, and probiotic bacteria. He has actively participated in both National and International conferences held in India. He has published quite a number of research and review papers in well-known international journals of good repute. He has contributed articles as book chapters in National books. He is also an active member of the Microbiological Society of India (MSI), India.

Contributors

Lokesh Kumar Agarwal Department of Chemistry, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Meenakshi Arya Rani Lakshmi Bai Central Agricultural University, Jhansi, India

Kavya Bakka Department of Microbiology, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu, India

Kuntal Bera Department of Seed Science and Technology, Pundibari, Cooch Behar, West Bengal, India;
Plant Molecular Biology Laboratory, Department of Botany, Raiganj University, Uttar Dinajpur, Raiganj, West Bengal, India

Nabanita Bhattacharyya Department of Botany, Gauhati University, Guwahati, Assam, India

Basanta Kumar Borah Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, India

Arka Pratim Chakraborty Department of Botany, Raiganj University, Raiganj, Uttar Dinajpur, West Bengal, India

Rakhi Chakraborty Department of Botany, Acharya Prafulla Chandra Roy Government College, Himachal Vihar, Matigara, Siliguri, West Bengal, India

Dinakar Challabathula Department of Life Sciences, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu, India

Soumya Chatterjee Microbiology and Microbial Biotechnology Laboratory, Department of Botany, University of Gour Banga, Malda, West Bengal, India

Sushil Kumar Chaturvedi Rani Lakshmi Bai Central Agricultural University, Jhansi, India

Siva P. K. Chetri Department of Botany, Dimoria College, Kamrup Metro, Assam, India

Papan Chowhan Department of Botany, Raiganj University, Raiganj, Uttar Dinajpur, West Bengal, India

Mrittika Datta Department of Botany, Zakir Husain Delhi College, University of Delhi, New Delhi, India

Puspendu Dutta Department of Seed Science and Technology, Pundibari, Cooch Behar, West Bengal, India

Namrata Farwaha Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, India

Prasanta Kumar Ghosh S.B.S. Government College, Hili, Dakshin Dinajpur, West Bengal, India;
Microbiology and Microbial Biotechnology Laboratory, Department of Botany, University of Gour Banga, Malda, West Bengal, India

Rupeet Gill Department of Vegetable Science, Punjab Agricultural University, Ludhiana, India

Lina Gogoi Department of Energy, Tezpur University, Assam, India

Nirmali Gogoi Department of Environmental Science, Tezpur University, Assam, India

P. V. Gopika Department of Microbiology, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu, India

Tripti Gour Department of Botany, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Anshul Gupta Department of Agriculture, Rajasthan Govt, Jaipur, Rajasthan, India

Astha Gupta School of Agricultural Sciences, Sharda University, Greater Noida, Uttar Pradesh, India

Monika Heikrujam Department of Botany, Maitreyi College, University of Delhi, Delhi, India

Somveer Jakhar Plant Physiology and Biochemistry Laboratory, Department of Botany, Kurukshetra University, Kurukshetra, Haryana, India

Mukul Joshi Department of Biological Sciences, Birla Institute of Technology and Science (BITS), Pilani, Rajasthan, India

Rupam Kataki Department of Energy, Tezpur University, Assam, India

Sukhjeet Kaur Department of Vegetable Science, Punjab Agricultural University, Ludhiana, India

Namrata Konwar Microbiology & Molecular Systematics (MMS) Laboratory, Department of Botany, Gauhati University, Guwahati, Assam, India

Koppolu Raja Rajesh Kumar Department of Biotechnology, IGNTU, Amarkantak, Madhya Pradesh, India

Rajesh Kumar Department of Botany, Hindu College, University of Delhi, Delhi, India

Savindra Kumar Department of Botany, Zakir Husain Delhi College, University of Delhi, New Delhi, India

Sarita Kumari Department of Botany, Maitreyi College, University of Delhi, New Delhi, India

Sukanta Majumdar Microbiology and Microbial Biotechnology Laboratory, Department of Botany, University of Gour Banga, Malda, West Bengal, India;
Department of Botany, School of Life Sciences, Mahatma Gandhi Central University, Motihari, Bihar, India

Shahana Majumder Department of Botany, School of Life Sciences, Mahatma Gandhi Central University, Motihari, Bihar, India

Mamun Mandal Microbiology and Microbial Biotechnology Laboratory, Department of Botany, University of Gour Banga, Malda, West Bengal, India

Parimal Mandal Mycology and Plant Pathology Laboratory, Department of Botany, Raiganj University, Raiganj, West Bengal, India

Vivekananda Mandal Plant and Microbial Physiology and Biochemistry Laboratory, Department of Botany, University of Gour Banga, Malda, WB, India

Piyush Mathur Microbiology Laboratory, Department of Botany, University of North Bengal, Rajarammohunpur, Darjeeling, West Bengal, India

Deepika Mazumdar Department of Microbiology, North Bengal St. Xaviers College, Jalpaiguri, West Bengal, India

Prashanta Kumar Mitra Department of Botany, University of Kalyani, Nadia, WB, India

Soumya Mukherjee Department of Botany, Jangipur College, University of Kalyani, Kalyani, West Bengal, India

Diganta Narzary Microbiology and Molecular Systematics (MMS) Laboratory, Department of Botany, Gauhati University, Guwahati, Assam, India

Ricky Raj Paswan Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, India

Kavita Rani Plant Tissue Culture Laboratory, Department of Botany, Kurukshetra University, Kurukshetra, Haryana, India

Ratan Lal Department of Botany, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Swarnendu Roy Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Raja Rammohunpur, Darjeeling, India

Sanjoy Sadhukhan Plant Molecular Biology Laboratory, Department of Botany, Raiganj University, Raiganj, Uttar Dinajpur, West Bengal, India

Shyama Prasad Saha Department of Microbiology, University of North Bengal, Siliguri, West Bengal, India

Richita Saikia Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, India

Anup Kumar Sarkar Department of Botany, Dukhulal Nibaran Chandra College, Aurangabad, Murshidabad, West Bengal, India;
Plant Molecular Biology Laboratory, Department of Botany, Raiganj University, Raiganj, Uttar Dinajpur, West Bengal, India

Ashis Sarkar Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Raja Rammohunpur, Darjeeling, India

Mahima Misti Sarkar Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Raja Rammohunpur, Darjeeling, India

Banashree Sarma Department of Environmental Science, Tezpur University, Assam, India

Srota Satapathy Department of Botany, Zakir Husain Delhi College, University of Delhi, New Delhi, India

Gurumayum Suraj Sharma Department of Botany, Bhaskaracharya College of Applied Sciences, University of Delhi, Delhi, India

Kuldeep Sharma Department of Botany, Mohanlal Sukhadia University, Udaipur, Rajasthan, India

Rita Sharma Department of Biological Sciences, Birla Institute of Technology and Science (BITS), Pilani, Rajasthan, India

Tripti Sharma School of Agricultural Sciences, Sharda University, Greater Noida, Uttar Pradesh, India

Khomdram Niren Singh Microbiology and Molecular Systematics (MMS) Laboratory, Department of Botany, Gauhati University, Guwahati, Assam, India

Sombir Singh P.T.C.L.S. Govt. College Karnal, Karnal, Haryana, India

Vibhuti Singh Department of Botany, Swami Shraddhanand College, University of Delhi, Delhi, India

Shubham Kumar Sinha Department of Biotechnology, IGNTU, Amarkantak, Madhya Pradesh, India

Haresh Sreelakshmi Department of Microbiology, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu, India

Zerald Tiru Department of Botany, Raiganj University, Raiganj, West Bengal, India

Prabha Toppo Microbiology Laboratory, Department of Botany, University of North Bengal, Rajarammohunpur, Darjeeling, West Bengal, India

Akanksha Vashishtha Department of Botany, Department of Plant Protection, C. C. S. University, Meerut, India

Vikrant Department of Botany, School of Life Sciences, Mahatma Gandhi Central University, Motihari, Bihar, India

Understanding and Management of Abiotic and Biotic Stress in Plants

Plant Responses Under Abiotic Stress and Mitigation Options Towards Agricultural Sustainability

Kuntal Bera, Puspendu Dutta, and Sanjoy Sadhukhan

Abstract

Plants are continually exposed to various environmental extremities during their growing period. As such, plants have to constantly struggle with different abiotic and biotic factors. Biotic factors can be controlled to a certain extent through the application of pesticides or by adopting various crop protection techniques. But the adverse impacts of abiotic stress elements such as drought, high temperature, salinity, heavy rainfall, snowfall, UV radiations, hazardous chemicals, air pollutants, etc., are very difficult to manage. Plants usually adopt various mechanisms involving alteration in anatomical, physiological, biochemical functions, or regulation of different stress-responsive genes, signaling pathways, etc. Abiotic stresses cause modifications in plant metabolism that leads to enhanced production of different secondary metabolites like polyamines, phenol, proline, etc., which, in turn, act directly or indirectly to build up abiotic stress tolerance by activating different stress response systems. Starch, the major reserve material of plants plays a key role in stress mitigation. Plants remobilize their reserve starch during stress conditions to provide energy. This chapter aims to discuss briefly how plants perceive different kinds of stresses, transduce early signals within their system, elicit different types of responses, or how these stress responses are determined genetically. Attempts have also been made to illustrate what options would be helpful to attain agricultural sustainability through the mitigation of stresses.

Keywords

Abiotic stress • Mitigation • Molecular response • PGPR • PGPF • Phytohormones • Signaling pathway

Abbreviations

ABA	Abscisic acid
ABF	Abscisic acid-Responsive Transcription Factors
AHL	N-acyl homoserine lactone
AMF	Arbuscular mycorrhizal fungi
AP2	Apetala 2
APX	Ascorbate peroxidase
AsA	Acetylsalicylic acid
ATP	Adenosine triphosphate
BAP1	BRCA1-Associated Protein 1
BR	Brassinosteroid
bZIP	Basic Leucine Zipper
CAM	Crassulacean acid metabolism
CAT	Catalase
CEF	Cyclic electron flow
CFC	Chlorofluorocarbon
CK	Cytokinin;
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
CRISPR-Cas9	CRISPR associated protein 9
CRY1	Cryptochrome Circadian Regulator 1
DAO	Diamine oxidase
DHAR	Dehydroascorbate reductase
EIN3/4	Ethylene Insensitive ¾
ELIP1/2	Early Light-induced Protein ½
ERF	Ethylene Responsive Factor
ET	Ethylene
ETR1/2	Ethylene Response ½
Fv/Fm	Chlorophyll fluorescence parameter
GA	Gibberellic acid
GPX	Guaiacol peroxidase
GR	Glutathione reductase

K. Bera · P. Dutta
Department of Seed Science and Technology, Uttar Banga Krishi Viswavidyalaya, Pundibari, Cooch Behar, 736165, West Bengal, India

K. Bera · S. Sadhukhan (✉)
Plant Molecular Biology Laboratory, Department of Botany, Raiganj University, Uttar Dinajpur, Raiganj, 733134, West Bengal, India

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GS	Genome Selection
GSH	Glutathione
GST	Glutathione s-transferase
H_2O_2	Hydrogen peroxide
HSP	Heat shock protein
HY5	Elongated Hypocotyl 5
IAA	Indole acetic acid
JA	Jasmonic acid
KNO3	Potassium nitrate
MAS	Marker Assisted Selection
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
miRNA	Micro RNA
NaCl	Sodium chloride
NaOCl	Sodium hypochlorite
NADP	Nicotinamide adenine dinucleotide phosphate
NADPH–NPQ	Non-photochemical quenching
NOX	NADPH-dependent-oxidases
PAO	Polyamine oxidase
PAP1/2	Anthocyanin Pigment ½
PCD	Programmed cell death
PGPF	Plant Growth-Promoting Fungi
PGPR	Plant growth-promoting rhizobacteria
PIP	Plant incorporated protectants
POD	Peroxidase
PP2C	Protein Phosphatase 2C
PPFD	Photosynthetic photon flux density
PPO	Polyphenol oxidase
PS-I	Photosystem I
PS-II	Photosystem II
PYR	Pyrabactin Resistance Protein
PYL	PYR1 like Protein
QS	Quorum sensing
QTL	Quantitative Trait Locus
RBOH	Rubidium hydroxide
RCAR	Regulatory Components of ABA Receptor
RNS	Reactive nitrogen species
ROL	Radial oxygen loss
ROS	Reactive oxygen species
RuBPC	Ribulose bisphosphate carboxylase
RuBisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
SA	Salicylic acid
SL	Strigolacton
SNF1	Sucrose Non-Fermenting 1
SnRK2	SNF1-related Protein Kinase 2
SOD	Superoxide dismutase
UV	Ultraviolet
VAZ	Violaxanthin antheraxanthin zeaxanthin cycle
WUE	Water use efficiency
ZAT12	Zinc Finger Protein

1 Introduction

Any kind of environmental factor that adversely affects plant growth and productivity are considered abiotic stress. Abiotic stresses are the environmental extremities that mostly include drought, salinity, high or low temperatures, UV radiations, hazardous chemicals, air pollutants, etc., leading to huge yield loss every year. Abiotic stress is not always a true natural phenomenon, rather anthropogenic influences such as long-term indiscriminate use of natural resources by humans also result in the generation of specific abiotic stress in a particular region. For example, over lifting of groundwater for agricultural uses, deforestation of large areas can lead to extreme drought or high-temperature stress in near future. Further, heavy metals and other toxic chemicals as emitted from rapidly growing chemical-based industries lead to an increase in heavy metals and other toxic compounds to the soil and that results in deterioration of soil health or thus adversely affects the crop stand. As the emissions of greenhouse gases (mainly CO_2, CH_4, and N_2O) are the main causes of global warming, that is, resulting in the rise of seawater level by melting the ice reservoirs. A meta-analysis study indicates that the average global temperature will increase 2.0–4.9 °C by the end of 2100 (Raza et al. 2019). Though there are many reasons behind global climate change, it is thought that the consolidated reason behind the global climatic change is the revolution in industrialization (Dutta et al. 2020). Mainly the anthropogenic causes including extensive use of fossil fuels to support the rapid industrialization, urbanization, deforestation, burning of agricultural wastes, excessive use of non-biodegradable commodities, etc., play a major role in changing the climate. Moreover, climate change is also being induced due to a break in hydrological cycles that causes alteration in atmospheric behaviour. Consequently, this leads to exposing plants to severe and extreme climatic situations that adversely affect the morphological, developmental, cellular, and molecular processes in plants (Chaudhry and Sidhu 2021).

Out of the total arable land of the world, which is about 24.2% of the total geographical land of the world, only 10.6% is potentially cultivated and the rest is not practicable for farming due to abiotic stresses (Das and Tzudir 2021). Worldwide about 42% of yield loss is accounted for every year due to several abiotic stresses. Only the drought stress leads to about 27% yield loss per year in the tropical regions of the world. Further, it has been estimated that 50% of the world's arable land will be damaged due to high-level salinity by the year 2050 (Hasanuzzaman et al. 2014). The biggest challenge is to ensure feed for the rapidly increasing global population. The global population is predicted about 9 billion by 2050 and the food requirements are expected to rise about 85% of total present needs (FAOSTAT 2017). But the global food security is under severe threat as different abiotic stresses can cause up to 70% annual yield loss of major food crops worldwide (Waqas et al. 2019).

Plants usually adopt two major strategies to combat these abiotic stresses. These strategies include stress avoidance and stress tolerance or acclimation (Kosová et al. 2011). The stress acclimation by the plants is chiefly facilitated through the changes in gene expression, alterations in the transcriptome, proteome, and metabolome of the plant (Koyro et al. 2012). Researchers are focussed on understanding different components involved in the molecular excitation and expression of different pathways under different abiotic stresses (Haak et al. 2017). Elucidation of the exact mechanisms behind the plant's acclimation to abiotic stresses would lead us to achieve sustainability in agricultural production as the main challenges in sustainable agriculture practices are the development of crops with desired agronomical traits and stress-resilient capabilities. Further, to develop stress-resistant high-yielding crop varieties, it is essential to have better insight into different aspects of plant systems such as physiological, biochemical, and molecular changes during stress and also about the regulatory network of gene expression (Yadav et al. 2020).

With this perspective, the present chapter aims to categorize different abiotic stresses and the plant responses under such stress conditions. Further, attempts have been taken to illustrate the mechanisms or strategies adopted by plants towards mitigation of abiotic stresses.

2 Definition and Classification of Abiotic Stresses

The environment is made of both living and non-living components. The interaction between these two components and the negative impacts of these interactions on any living component can be defined as stress. The abiotic stress only relates the negative impacts of some non-living components of the environment on the living components and in the context of abiotic stress, these non-living components are often known as abiotic factors such as temperature, salt, water, light, radiation, chemicals, and heavy metals and these factors responsible for related stresses (Fig. 1).

2.1 Nature of Stress Factors

Worldwide agriculture is greatly affected by the three major abiotic factors, viz., high temperature, salinity, and water scarcity or drought. All these stresses have a wide geographical distribution and they limit the crop yield and thus cause a serious threat to the food security of the ever-growing global population (Fedoroff et al. 2010). At the average rate of temperature anomaly of 0.2 °C per year, it is predicted that the global average temperature will be increased by 1.8–4 °C at the end of 2100 (Hasanuzzaman et al. 2013). Heat stress or high-temperature stress is initiated

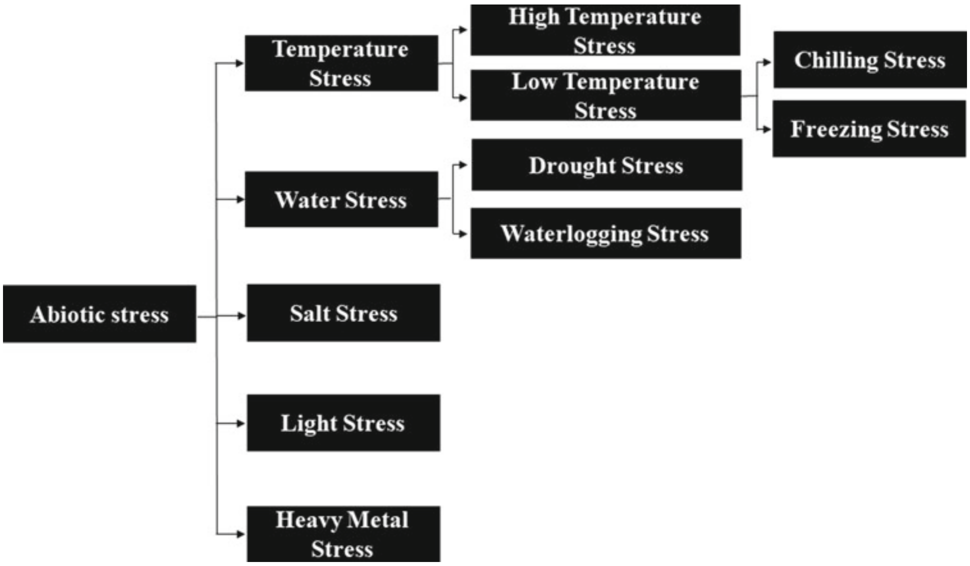

Fig. 1 Different abiotic stress factors

when the environmental temperature increases above the optimal temperature for the plant. The regulating factors of heat stress include the quality, intensity, and duration of light exposed to the plant. On contrary, low temperature is also abiotic stress faced by higher plants and it affects normal growth and development by altering the functions of cellular components or their metabolism on plants. Thus, low-temperature stress has also a huge impact on impeding the geographical distribution of plant species. It can be classified into two types, viz., chilling (0–15 °C) and freezing (<0 °C) stress (Fig. 1) (Ritonga and Chen 2020). Plants acclimatize with low temperature through very complex mechanisms that include the accumulation of cryoprotectant compounds such as soluble sugars, prolines, types of flavonoids and anthocyanins, changes in the composition of cellular membranes such as lipid and protein, and also changes in the plant's transcriptomic and proteomic status (Leuendorf et al. 2020).

Drought, on the other hand, is described as a lack of water over an extended period. It may occur due to several reasons like low rainfall, accumulation of excessive salts into the rhizospheric region, extreme temperature fluctuation, and high intensity of light. Due to the complex multidimensional nature of drought, it can be classified into four categories, these are (1) meteorological drought, which is the consequence of dry weather and very low or no precipitation, (2) hydrological drought represent by the low and restricted supply of surface and ground waters which come across after a prolonged meteorological drought, (3) agricultural drought can be defined as a decrease in soil water levels and crop failures, which relentlessly affects the worldwide crop production and food security, and (4) socio-economic drought, that is, the ultimate consequences of other three droughts as it restricts the supply and demand chain of our everyday needs and huge monetary losses (Ahluwalia et al. 2021; Wojtyla et al. 2020; Zia et al. 2020). Currently, more than 55 million people worldwide are being affected by drought and this number may be about 700 million by 2030 as predicted in the United Nations World Water Development Report, 2018 (UNESCO World Water Assessment Programme 2018). In terms of land affected by drought, only in India, about 42% of arable land facing drought (Gogoi and Tripathi 2019) out of 159.7 million hectares of agricultural land (Himani 2014). Further, waterlogging is emerging as major abiotic stress due to drastic changes in the current climatic scenario. As such increase in the intensity and frequency of flood occurrence make the situation worse (Kaur et al. 2021). About 16% of irrigated arable lands all over the world are affected by waterlogging caused either by natural or anthropological means (Zheng et al. 2021). The regions of the world such as Southeast Asia, East Africa, and the northern part of South America are expected to be affected by waterlogging more frequently (Voesenek and Bailey-Serres 2015; Zheng et al. 2021). As a result of waterlogging conditions, primarily roots are affected with severe hypoxia due to slowing down of oxygen diffusion rate by nearly 104 times than that in the air (Panozzo et al. 2019; Kaur et al. 2021).

Soil salinity is another major threat to crop production worldwide. Salinity affects about 900 million hectares of land which is nearly 20% of the total land on Earth, and also covers about half of the total irrigated land worldwide (Velmurugan et al. 2020). The accumulation of salts into the soil can be a result of natural phenomena like the physical and chemical weathering of rocks. This is because weathering leads to the formation of soluble salts such as chlorides (Cl^-), sulphates (SO_4^{2-}), and carbonates (HCO_3^-) of sodium, calcium or magnesium. Further, the movement of soluble salts through the rivers and other water channels, and then using this salt contaminated water for irrigation purposes causes salt deposition in soil (Sharma et al. 2016). Salt accumulation may also be due to high evaporation, lack of sufficient precipitation, and intrusion of seawater into the coastal lands (Kumar and Sharma 2020). The anthropogenic reasons for soil salinity include an unplanned restricted drainage system, use of low depth groundwater during irrigation, inappropriate or poor irrigation practices in low rainfall areas, excessive use of chemical-based fertilizers, and soil amendments like lime and gypsum, dumping of industrial as well as domestic sewage sludge onto the soil (Bui 2017; Kumar and Sharma 2020).

Further, the energy sources such as light are an important developmental signal that can also negatively affect the plant's growth and also act as a modulator for respective stress responses. Both the quality and the quantity of light (the intensities of light exceeded over light saturation point (PPFD) are the two main aspects of light stress. These two factors are being constantly changed due to sunny or cloudy skies and seasonal shifts like spring with canopy closure due to the sun's inclination (Casal 2013; Kozai 2016; Roeber et al. 2021). Another cause of light stress is photoperiodism, that is, the period of light exposure received by plants in the ratio of day and night (Thoma et al. 2020). UV-B and UV-A, an integral part of the light spectrum reaching the earth's surface, also cause severe damages that include damage to DNA and protein, excessive production of reactive oxygen species (ROS), and other changes in the cellular functioning of a plant (Müller-Xing et al. 2014).

Heavy metals are the transition metals characteristics with an atomic mass higher than 0.002 kg with approximate molecular weight and density of 5 N/m^3 and 5 ^{g}/cm^3, respectively (Rascio and Navari-Izzo 2011; Singh et al. 2020). There are two main sources of heavy metals, viz., natural resources such as weathering of rocks, mineral ores, volcanic ashes or lava deposition and anthropological influence such as urban development, rapid industrialization, waste of electricity generation plants, sewages from mining or refinery industries (Singh et al. 2020). There are two categories of these metals that induce stress to the plants either due to deficiency or abundance. Some of these are metals such as Cu, Zn, Mn, Ni, Fe, Co, Mo, Se, etc., are essential but others such as Cd, As, Pb, Cr, Hg, Al, etc., are the nonessential metals. The major events of metal toxicity in agriculture are observed for Cd, As, Pb, Cr, and Cu (Singh et al. 2020). The essential metals take part in several biochemical reactions like transfer of electrons in different pathways, activation of enzymes, synthesis of different pigments, and also in the redox reactions (Fageria et al. 2009; Chaffai and Koyama 2011), whereas the nonessential metals don't have any role in the biological reactions or plants growth, rather they are the toxic for the plants even at low concentration as they compete with the essential metals for the same protein binding sites (Torres et al. 2008). The deficiency in the required concentration of essential metals to carry out normal cellular functioning of plants is known as nutrient deficiency. Although at higher concentrations some essential metals may also cause serious damage to the plants. Generally, an increased concentration of the nonessential metals over the toxic limit is referred to as heavy metal stress.

3 Effects of Abiotic Stresses

3.1 Heat Stress

Overexploitation of fossil fuels to meet the demand of the ever-increasing population is the major cause of global warming and associated climate change. Heat stress has recently been come up as a major factor that contributes to a significant reduction of crop yield every year (Zhou et al. 2016; Shukla et al. 2019; Hassan et al. 2021). Heat stress leads to oxidative stress in plants through the overproduction of ROS in plants. The main effects of ROS under heat stress include disruption of membrane stability by promoting peroxidation of lipid constituents of the membrane, and thereby leads to the disintegration of membrane or increases membrane leakage (Balal et al. 2016). The disintegration of the cell membrane has been reported to promote the passive efflux of ions from the cytosol. Further, membrane disintegration is considered to be irreversible, and that ultimately leads to plant death (Ilík et al. 2018). Heat stress also limits the overall plant growth and crop yield as the rate of photosynthesis is severely affected due to reduced chlorophyll biosynthesis or Rubisco activity under heat stress (Balal et al. 2016; Zhou et al. 2016; Masouleh and Sassine 2020). It has also been reported that continuous exposure of plants to a fairly high temperature or for a shorter time with extremely high temperature lead to denaturation of proteins and inactivation of different enzymes along with a loss of membrane integrity. Moreover, continuous heat stress also alters the anatomical structures of various subcellular organelles including changes in the shape of chloroplasts, bulging of stomatal lamellae, changes in structural organizations of thylakoids, and these changes resulted in downward functioning of photosynthesis and respiratory activities (Lipiec et al. 2013). Heat stress also alters ion and osmotic homeostasis at the cellular level as it eventually interrupts the pool of molecular chaperones that are involved in sustaining protein homeostasis as well as in DNA stabilization (Rai et al. 2020). Heat stress may also cause to increase in the soil temperature and this situation is accompanied by a scarcity of soil water content or drought. The occurrence of such a situation magnifies the stress effects on plants. Pollen sterility and damage in female reproductive organs have been reported under the combined effect of heat and drought due to alterations in the phenology and viability of pollens, changing morphology and anatomical construction of pistils. For example, the combined effect of these stress intensify intensifying lipid peroxidation and/or decreasing nitrogen oxide production in stigmatic papilla cells of wheat (Fábián et al. 2019). Further, the concurrent effects of these two stresses in terms of biosynthesis of photosynthetic pigments, accumulation of osmolytes like soluble sugars and free prolines, enzymatic and non-enzymatic antioxidants, and the nutrient uptake have been reported to be more intense than individual effects in maize (Hussain et al. 2019).

3.2 Low-Temperature Stress

Similar to heat stress, cold stress also causes huge crop loss every year mainly in the subtropical and temperate regions of the world. Field crops like *Oryza sativa*, *Zea mays*, *Solanum lycopersicum*, *Glycine max*, *Gossypium hirsutum* cannot acclimatize with cold stress. The growth and development of these species are severely affected under cold stress, and this limits the geographical distribution of these plant species only within tropical or subtropical regions (Ding et al. 2019). Cold stress causes severe disturbances at the morphological, cellular, and/or molecular levels. Low temperature below the optimal level (15 °C) causes lower germination along with stunted seedlings, chlorosis and necrosis and wilting of leaves, membrane damage due to acute dehydration associated with freezing, altered viscosity of cytoplasm, disrupted integrity of intracellular organelles, loss of organelle compartmentalization, disruption of normal flow of photosynthesis, reduced enzymatic activities, destabilization of protein complexes, disruption of DNA strands and secondary structure of RNA, accumulation of ROS, and ultimately may lead to death. Furthermore, cold stress during anthesis causes severe damages to the reproductive organs of the plants including increased pollen sterility, distortion of pollen tubes, ovule abortion or flower dropping (Yadav 2010; Thakur and Nayyar 2013; Atayee and Noori 2020).

Freezing stress refers to the type of cold stress when the temperature drops below 0 °C. It leads to the formation of ice crystals in the intracellular fluid and ultimately causes severe damages to the membrane integrity as well as metabolic processes (Atayee and Noori 2020).

3.3 Drought Stress

Drought or water deficit stress is one of the major abiotic stresses that also adversely affect crop production worldwide. Primarily drought affects the normal growth of plants by changing their water retention capacity and water use efficiency. Such alterations cause to decrease in water pressure within the leaves and finally result in wilting of leaves as the first recognized symptom (Zeppel et al. 2015; Fathi and Tari 2016). Generally, drought induces changes in various aspects of plants including morphological, anatomical, phenological, physio-biochemical, and molecular changes. Water is known as the most essential component for every living things on the Earth. Thus, the scarcity of water can also cause several negative effects on plants including reduced seed germination, prolonged or absolute dormancy, root proliferation at early growth stages, wilting of leaves, and reduced the size of leaves and/or stems. Water stress also causes to loss of turgor pressure in leaves and reduces stomatal conductance. Further, it reduces the rate of photosynthesis and transpiration by affecting the electron transport chain. Drought stress also enhances the generation of ROS that leads to the disintegration of chloroplast and damages the thylakoid structure. Drought is generally concurrent with heat stress and soil salinity, and the combined effects of these stresses amplify the negative impacts on the plant's growth and development. Drought together with heat shows a similar type of effects but with a greater magnitude of injuries including damage of PS-II, reduce the activity of RuBisCO, significantly increase of leaf temperature, decrease stomatal conductance, and reducing the concentration of photosynthetic pigments (Ahluwalia et al. 2021). Exposure of *Solanum lycopersicum* to both drought and heat stress has been reported to reduce the concentration of chlorophyll and carotenoids by 80% and 57%, respectively (Raja et al. 2020). The reproductive stage is greatly affected by the combined effect of both as these stresses negatively affect the pollen and pistil development, disrupt ovule functions, and ultimately resulted in low grain weight (Prasad et al. 2011). The combined effects of drought and heat lead to an increase in the generation of ROS and malondialdehyde accumulation, downregulating the activities of antioxidant enzymes like CAT and APX in maize (Hussain et al. 2019). Proline acts as the major osmoprotectant under drought stress. But excessive proline exhibits toxicity, whereas sucrose acts as the main osmoprotectant when the plants are exposed to the combined stresses (Cohen et al. 2021). Though there are several similarities in the adverse impact of drought and salinity stress, they differ in their manifestations. For example, roots elongation to the deeper level of soil in search of water is the natural adaptation by plants under severe drought, but roots become thicker and accumulate more ions like Na^+ and Cl^- under salinity stress (Lee et al. 2004; Sahin et al. 2018). Excessive production of reactive oxygen species (ROS) is another effect under the combined stress of drought and salinity that leads to a higher degree of lipid peroxidation, a mutation in DNA strands, and obvious cell damage (Kumar et al. 2019). The combined stress of drought and salinity has been reported to increase abscission of leaves and flowers, early senescence, and premature cell death (Ahmed et al. 2015; Sahin et al. 2018).

3.4 Waterlogging Stress

Waterlogging poses a serious threat to sustainable agriculture particularly in the region where heavy rainfall is quite frequent. In the agricultural aspect, flooding is the result of either intensive and/or extensive rainfall over a period or overflowing of water from the small to large water bodies like rivers. Waterlogging not only causes crop losses, rather its effect encompasses economic and social aspects as floods cause heavy loss to livestock and seed stocks, spreading of diseases, destruction of infrastructures, agricultural yield loss, and obvious food shortage (Fukao et al. 2019). The crop loss by waterlogging during 2006–2016 has been estimated to the tune of billions of dollars (FAO 2017). Several alterations as takes place in soil during flooding include disruption of soil properties like pH, redox potential, and the soil O_2 level. Waterlogging stresses are classified into two categories depending on the O_2 availability, and these are (i) hypoxia (refers to a deficiency of O_2) and (ii) anoxia (refers to the complete absence of O_2). It has been reported that there is a metabolic shift from aerobic to anaerobic fermentation to supply the ATP required for sustaining the metabolic processes of the plant particularly when it undergoes oxygen restrictions (Ashraf 2012). Further, waterlogging or flooding conditions can be classified into two groups depending on the water depth over the land in respect to plant height. These are either complete submergence or superficial that covers only the root to the middle part of a plant. However, both types of flooding cause hypoxia ($<21\%$ O_2) by reducing the flow of oxygen from the air to the plants (Lee et al. 2011; Sasidharan et al. 2017). Several negative impacts of flooding include increasing the vulnerability of plants to pathogen attack, hindering exposure of plants to light, and causing disturbances in stomatal conductance. It also leads to a decrease in net CO_2 assimilation rate, hydraulic conductivity of roots, which affects adversely the translocation of carbohydrates. It has also been reported that waterlogging decreases PS-II efficiency by disrupting the chloroplast membrane, limits the activity of RuBPC (ribulose bisphosphate carboxylase), leads to reduce the rate of photosynthesis, and that are ultimately reflected in crop losses (Ashraf 2012; Hsu et al. 2013; Tsai et al. 2016; Yeung et al. 2018; Fukao et al. 2019). Further, it generates nutrient deficiencies in the plant and causes damage to the cell membrane integrity by enhancing the production of ROS. It is also evident that waterlogging would initiate autophagy or adaptive mechanisms of sequestrating the damaged cellular components to the vacuoles to prevent programmed cell death (PCD) as found in several plants like *Triticum aestivum* Arabidopsis, *Zea mays* (Zhou et al. 2021).

3.5 Salinity Stress

Like other stresses, salinity is also considered major stress that poses a severe threat to global crop production and food security. Salinity has several negative impacts on the physiological and biochemical functioning of plants including germination of seeds or prolonging seed dormancy (Zhang and Dai 2019). It has been reported that salt stress decreases water potential, as well as reduces food reserve in germinating seeds, which, in turn, restricts effective seed germination of broccoli and cauliflower (Wu et al. 2019). Salinity enhances the dormancy in seeds of Arabidopsis thaliana by masking phosphatase activity in seeds (Nasri et al. 2016). Germination rates are reduced under salt stress due to increased accumulation of soluble carbohydrates, starch, and abscisic acid content but reduced levels of GA_3 (Arif et al. 2020). Plants exposed to high soil salinity disrupt the structural integrity of stomata and chloroplasts so decreases photosynthetic pigment concentrations and ultimately lead to a fall in photosynthetic rate. It has been reported that salt stress reduces net photosynthesis, Fv/Fm ratio, stomatal conductance, and transpiration rate in rocket plants (Hniličková et al. 2017). Salt stress has also been reported to significantly reduce gaseous exchange, the efficiency of PS-II, stomatal conductance, water potential of soil and leaf. Salinity also leads to osmotic stress in plants as it prevents ascent of sap by lowering turgor pressure. Ionic imbalances within the cell are the major consequences of salt stress. The toxicity by ions of Na^+ and Cl^- creates a physiological drought by reducing the osmotic potential of soil water and it leads to induce a nutrient deficiency in plants (Khan et al. 2019). Deposition of Na^+ causes to reduce the life span of leaves and creates necrosis (Khan and Bano 2016). The cytoplasmic composition and its viscosity are also altered by salt stress (Ali and Xie 2020). The detrimental effects of salt stress are often observed in leguminous plants. Salinity reduces the size and volume of nodules per plant and also hampers the nodulation as it lowers the pressure of the peripheral cells of the nodules or leads to a very low release of bacteria due to the enlargement of infection thread and/or, stimulated accumulation of phenolic compounds (Shahid et al. 2020).

3.6 Light Stress

Sunlight is one of the major inputs for plant growth as it provides the necessary energy for the metabolic functionality of plants by photosynthesis. But sometimes sun energy, particularly when it comes in the form of high-intensity light along with the integral ultraviolet (UV) rays, can cause potential damage to DNA, protein, and other cellular components. Solar UV rays are composed of UV-A (315–400 nm), UV-B (280–315 nm), and UV-C (<280 nm). But it is only UV-A and part of UV-B reaching the earth's surface as the total UV-C plus most of the UV-B are absorbed by the stratospheric ozone layer (McKenzie et al. 2011). But the hazardous effects of UV-B have increased significantly in recent decades as more amounts of UV-B are now reaching the earth due to the excessive release of chlorofluorocarbon (CFC) in the atmosphere that results in depletion of the ozone layer (Müller-Xing et al. 2014). The high-intensity light over the photosynthetic requirement disturbs photosynthetic processes, particularly PS-II that leads to photoinhibition. Photoinhibition is a state where light reduces the photosynthetic efficiency either by decreasing the rate of O_2 evolution or CO_2 assimilation. But photoinhibition represents a complex mechanism at the molecular level, and it involves the degradation of D1 protein which is a part of the reaction centre of PS-II (Takahashi and Badger 2011; Vass 2012; Tyystjärvi 2013). It has been reported that the entire process of photoinhibition, as well as its repair mechanism, depends on the membrane fluidity of the thylakoid membrane (Yamamoto 2016). Excessive light may also cause oxidative damage by increasing ROS accumulation (Roeber et al. 2021). Some specific and dynamic transcriptional changes during expression of certain genes such as CRY1, HY5, PAP1/PAP2, ELIP1/ELIP2 have been reported under extreme light stress (Consentino et al. 2015; Jourdan et al. 2015; Maier and Hoecker 2015; Li et al. 2018; Huang et al. 2019; Brelsford et al. 2019). Further, photoperiod is a state where plants are exposed to a longer period of light and it can also cause photoperiod stress or circadian stress (Nitschke et al. 2016; Nitschke 2017). Some specific genes such as ZAT12 and BAP1 have been reported to be expressed with induction of oxidative stress specifically at night after a long period of light exposure. A reduction in the maximum quantum efficiency of PS-II has been observed on the very next day of photoperiod stress. Further, a repeated happening of this event has been reported to cause PCD (Abuelsoud et al. 2020).

3.7 Heavy Metal Stress

Heavy metal stress is also a major hazard as it hinders the growth and development of crop plants. Heavy metal induces excessive accumulation of ROS in plant cells, and then it leads to cellular apoptosis associated with membrane peroxidation severe damage to nucleic acids, oxidation of proteins, or inhibition of key enzymes required for several metabolic processes (Flora 2011; Shahid et al. 2014). Acute heavy metal stress has been reported to cause nutrient deficiency by restricting nutrient uptake through roots due to overproduction of ROS or RNS burst, and it ultimately results in accelerated senescence in leaves, and/or cell death (Gallego and Benavides 2019). Few effects under cadmium (Cd) stress are chlorosis of leaf, rolling of leaf lamina, stunted growth, hindrance in the stomatal opening, increased membrane permeability, limited absorption, and its mobilization of nitrate from root to shoot by decreasing the activity of nitrate reductase (Singh et al. 2020). A higher concentration of arsenic (As) interacts with several metabolic processes. The two forms of arsenic, i.e., arsenate (AsV) and arsenite (AsIII) can easily be absorbed by the plants, and AsV is then converted into AsIII within the cell. Arsenic damages the photosynthetic system by disrupting the chloroplast membrane and also inhibits nutrient homeostasis by competing with essential metals. Arsenic also disturbs the carbohydrate, lipid, protein, and sulphur metabolisms of plants. Moreover, arsenic induces the accumulation of ROS, which, in turn, causes membrane damage through lipid peroxidation (Finnegan and Chen 2012; Wei et al. 2020; Singh et al. 2020; Zhang et al. 2021).

Lead toxicity to plants includes chlorosis of leaves, restricted growth, blackening of the root system, reduced mineral nutrition (N, P, and K) and water balance, damaged membrane structure, increased electrolyte leakage, and accumulation of MDA. Lead also disrupts the ultrastructure of chloroplast, interrupts with electron transport or Calvin cycle by inhibiting the activities of associated enzymes, causes deficiency in the content of CO_2 by inducing stomatal closure, reduces several parameters associated with seed germination in various crops. It also restricts the activity of –SH containing enzymes and inhibits the cell division at the meristematic region of the root tip (Singh et al. 2020; Sofy et al. 2020; Wei et al. 2020). Another heavy metal, chromium is easily absorbed by the plants due to high solubility particularly of chromium-IV (Cr(IV)). After entering into the plant system, Cr(IV) is converted into less soluble but highly toxic Cr(III). Apart from reducing growth, wilting of leaves, or lowering vigour index, the major toxicity of chromium includes overproduction of ROS that leads to oxidative stress, damage DNA and protein structures, induce lipid peroxidation, alters ultrastructure of thylakoids, inhibits δ-aminolevulinic acid dehydratase that involves in chlorophyll biosynthesis, and ultimately limits photosynthetic activity (Singh et al. 2020; Sharma et al. 2020).

Another heavy metal, copper is an essential mineral associated with several cellular constituents and metabolic processes including mitochondrial respiration, electron transport during photosynthesis. It also acts as a responder to oxidative stress, synthesis of proteins, used in various hormone signaling cascades, cell wall metabolism, a cofactor in numerous enzymes such as cytochrome c oxidase, polyphenol oxidase, Cu/Zn superoxide dismutase, amino oxidase, plastocyanin, and laccase (Nazir et al. 2019; Zhang et al. 2019). However, excessive uptake of Cu can cause serious hazards to the plants including reduced growth of plants, barred uptake of essential nutrition leading to nutrient deficiency in plants, reduced pigment concentration, decreased photosynthetic rate, hampered root development, halted leaf expansion. Moreover, copper accumulation in the plant has been reported to generate ROS that leads to damage the key constituents of the cell-like nucleic acid, proteins, lipids, and enzymes (Lillo et al. 2019; Zhang et al. 2019; Ameh and Sayes 2019, Jaime-Pérez et al. 2019).

4 Plant Responses to Stress Factors

Being sessile, plants are always being exposed to this constantly changing environment. Such environmental changes have often been proved as stressful to the plants. However, plants adapt various mechanisms to sensing stress, and such adaptation techniques have always been fundamental questions to the scholars of the respective field. Generally, plants adapt multiple strategies ranging from morpho-physiological to biochemical or molecular levels to survive against different stresses. Scientists have divided the stress responses of plants into two main categories, viz., stress avoidance and stress tolerance or known as stress acclimation. Stress avoidance is the adaptation taken by the plants for a limited period mostly until the stress condition remains and these adaptations mainly involve morpho-physiological alterations. But stress tolerance is physiologically active and mediated through distinct changes in the biochemical or even at the genetic level by changing the expression of different genes and these finally lead to the changes of plant's transcriptome, proteome, and metabolome (Chaudhry and Sidhu 2021; Marothia et al. 2020). It is noteworthy that plants undergo stress escape through morphological adaptations under major environmental stresses like heat, drought, waterlogging, salinity, and high light. But the adaptations involve physio-biochemical changes like modifying molecular signaling cascade and expression of several genes have been found under low temperature and heavy metal stress.

4.1 Morpho-Physiological Responses

Morpho-physiological adaptations are mainly involved either for stress avoidance or stress escaping for a certain period. These responses include stunted growth, several changes in shape and size of leaves, structural changes of the cell membrane, changes in stomatal appearance, rate of transpiration, water relation, water use efficiency, changes in ionic imbalance, and structural disintegration of cell organelles like chloroplast or thylakoid. The morpho-physiological responses of plants under various stresses have been described below.

4.1.1 Heat

Heat stress induces several morpho-physiological alterations in plants. One of the very common responses under intense heat is the curling and rolling of leaf blades parallel to sunrays to check the excessive absorption of solar light. Other strategies adopted by plants under prolonged heat stress include intensive transpiration to lower the leaf temperature, increase the number of trichomatous of stomata, induce stomatal closure, dense hairs are observed on leaves and/or stems, large vessels are formed within leaves' cells, reduce leaf size to minimize light or heat absorption. Further, it induces changes in the leaf orientation against light, deposition of silicon compounds, cuticle or waxy substances on leaf epidermis to restrict water loss. Prolonged heat stress also causes to increase in xylem vessels in the vascular bundle of the root as well as of shoot and root length. Although some plants undergo early heading to check the heavy yield loss under heat stress through enhanced retention of green leaves at anthesis. But this adaptation depends on the genotypes, accumulation of different osmolytes, and enhanced photosynthesis (Srivastava et al. 2012; Hasanuzzaman et al. 2013; Tiwari et al. 2020; Hassan et al. 2021).

4.1.2 Drought

Plants can escape drought by modulating vegetative or reproductive growth in two different ways. One of these mechanisms is rapid phonological development that involves the reduced duration of crop growth with minimum seed production before soil water depletes. As such these plants don't reveal any special modification in terms of morphology, physiology, or biochemical responses. Whereas the other strategy is developmental plasticity when the plants show reduced growth with a little number of flowers and seeds under a dry spell, but with the onset of wet seasons, extensive growth and increased seed yield is observed. Several adaptation mechanisms like increased root number increase, enhanced root length improved hydraulic conductance, and minimized rate of transpiration rate are very common under drought stress to maintain higher water content within the tissues either by minimizing water loss or maximizing water uptake. Higher water content in plant tissues induces several positive responses such as maintenance of turgor pressure and elasticity of cells, as well as enhancement of protoplasmic resistance. Further, the accumulation of ABA content in the mesophyll cell as well as in the guard cell of stomata leads to stomatal closure under drought stress. Another adaptation to protect photosynthetic apparatus from severe damage involves the restricted generation of ROS as achieved either through stomatal closure, or reduced metabolic activities (Ahluwalia et al. 2021; Basu et al. 2016; Chun et al. 2021; Fathi and Tari 2016; Zia et al. 2020).

4.1.3 Waterlogging

Several morpho-physiological adaptations to escape waterlogging conditions include the emergence of adventitious roots that help the plant stick to the surface or enhance the water and nutrient uptake, anatomical changes such as the formation of aerenchyma cells in the root tissues to facilitate transportation of various gases from the aboveground plant parts to the root system. The appearance of floating adventitious roots helps in maintaining the balance between O_2 and CO_2 levels within plants during waterlogging conditions. The formation of aerenchyma cells also helps to connect the adventitious roots to the stem and facilitate diffusion of O_2 from surrounding water to aerial shoots. Moreover, the formation of aerial roots in some species has been found as an important adaptation by plants to maintain metabolic balance under submergence. Further, it has been found that waterlogging leads to the formation of structural barriers in the root to prevent oxygen loss from the root apices that are termed a barrier to radial oxygen loss (ROL). ROL has also been observed to inhibit the invasion of phytotoxins in the root meristems. The floral development gets delayed under waterlogging to save a lot of energy. Accumulation of ethylene to the roots under hypoxic conditions is another very common mechanism of adaptation since it is associated with the development of adventitious roots and the formation of aerenchymatous tissues (Sauter 2013; Voesenek and Bailey-Serres 2015; Ayi et al. 2016; Rodríguez et al. 2018; Fukao et al. 2019; Ejiri and Shiono 2019; Eysholdt-Derzsó and Sauter 2019, Li et al. 2019; Garcia et al. 2020, Pedersen et al. 2021, Sharma et al. 2021).

4.1.4 Salinity

Plants tend to adapt themselves through several morpho-physiological alterations to maintain normal water potential during salinity stress conditions. The carbon dioxide fixation mechanism is shifted from C_3 to C_4 or CAM in certain plants, viz., *Mesembryanthemum crystallinum* and *Atriplex lentiformis* since such shifting in CO_2 metabolism allow these plants to reduce water losses through transpiration as well as to tolerate long-term salinity. Apart from their succulence nature, changes in root architecture are another adaptive response by salt-tolerant plants under salinity. A rapid reduction in root length, root diameter, or mean surface area helps the plants to maintain water status by regulating the uptake of water and ions. Further, the development of many small stomata under salt stress is another adaptive mechanism under salt stress. Moreover, prompt accumulation of ABA in photosynthetic tissues has been reported to stabilize the stomatal conductance under high salinity. The role of the vacuole is also very important under salinity stress as excess sodium is transported by H^+/Na^+ antiporter present in cellular membrane and tonoplast and finally stored into the vacuole. Such accumulation of Na^+ in vacuoles helps in maintaining Na homeostasis (Carillo et al. 2019; Ijaz et al. 2019; Zhao et al. 2020; Ayub et al. 2020; Guan et al. 2020).

4.1.5 Light

Plants employ several adaptation mechanisms to escape from both high and low light stress conditions. Some morpho-physiological responses under high light stress include modified leaf orientations, reduced rosette diameters, changed leaf angle against the direction of light exposure, altered leaf reflectance, lowering light exposure of leaf through downward bending of leaf lamina to minimize excessive light absorption and development of air-filled hairs in leaf surfaces. Further, increasing stomatal as well as hydraulic conductance, deposition of inorganic materials on leaf surfaces important physiological adaptation mechanisms under high light stress. Moreover, changes in the chloroplast positioning are yet another strategy to combat high light stress where chloroplasts move towards the sidewalls of the cell from the surface of the cell to avoid excessive absorption of light. It has also been observed that prolonged high light with or without enough groundwater can cause heat and/or drought stress, respectively. In such conditions, plants' morpho-physiological responses vary accordingly to the specific stress. However, plants respond in opposite ways during low light stress. So the chloroplast moves from the side-wall of the cell surface to a strategic spreading throughout the cell surface that leads to absorb more light. By and large, the adaptation techniques of plants to light stress have been explored at the biochemical and transcriptomic levels, and these have been discussed in later parts of this chapter. Apart from high and low light stress, the UV-B spectrum is another component of solar radiation that has been reported to cause severe damages to plants. Although the adaptation against UV-B radiation is mostly achieved through alterations at the molecular level, a few morpho-physiological responses such as a reduced expansion of cells at the epidermis, shortened inflorescence stem, the reduced diameter of leaf rosette, increased the number of flowering stems, and accumulation of flavonoids in the epidermal and sub-epidermal cells have also been observed under UV-B stress (Christie et al. 2015; Ghorbanzadeh et al. 2020; Hectors et al. 2014; Müller-Xing et al. 2014; Suetsugu et al. 2016; Yang et al. 2019).

4.1.6 Heavy Metal Toxicity

Plants' responses to overcome heavy metals stress are broadly divided into two groups such as extracellular defence and intracellular scavenging or detoxification to heavy metals. The extracellular defence strategies include secretion of inorganic ions, water, metal-binding amino acids, sugars, bicarbonates, protons, CO_2, mucilage substances, siderophores, allelopathic compounds, etc., as root exudates. Then the root exudates form several stable ligand complexes to reduce metal toxicity, make redox barriers, and also alter the pH of the rhizosphere. Further, root exudates facilitate ectomycorrhizal and arbuscular mycorrhizal association with plants, and it then prevents the uptake of heavy metals by plant roots as heavy metals get absorbed, adsorbed, or chelated within the mycorrhizal cell. But the scavenging and detoxification mechanisms get started only when the heavy metals enter into the cells. The scavenging mechanisms involve the production of stable ligand compounds like carboxylic acids (citrate, malate, etc.), amino acids (histidine, glutamate, proline, etc.), nicotinamide, and phytate that reduce the toxicity level of heavy metals by binding them into complex compounds and sequestrating them into the apoplastic spaces, cell wall, plasma membrane, vacuoles, and other organelles (Arif et al. 2019; Choppala et al. 2014; Dalvi and Bhalerao 2013; Hossain et al. 2012; Iqbal et al. 2020; Singh et al. 2020).

4.2 Biochemical Responses

Biochemical responses of plants under stress exposure have mostly involved the formation of ROS or induction of oxidative stresses, and scavenging of ROS. ROS are mainly generated in chloroplasts, mitochondria, apoplasts, peroxisomes, or several other sites having high redox potentiality to provide electrons to the atmospheric O_2 under different abiotic stresses (Rodríguez-Serrano et al. 2016; Takagi et al. 2016; Vaahtera et al. 2014). Various ROS derivatives generated during stress include singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), superoxide radical (O_2^-), hydroxyl radical ($OH\cdot$), alkoxy radicals ($RO\cdot$), and peroxy radicals ($ROO\cdot$), which have been known to create oxidative stress and found to be highly toxic to the cellular components (Gilroy et al.

2016; Liu and Yang 2020). The ROS play dual roles within the cell. However, the negative (*toxic*) or positive (*signal transduction*) role of ROS depend on the balance between the ROS generation and its scavenging, and such equilibrium is most often disturbed by the prevailing stress conditions like high temperature, drought, salinity, high light and heavy metal toxicity (Baxter et al. 2014; Zhu 2016). The stability of the equilibrium state of ROS depends on the proper stress signaling towards ROS formation, the reactivity of its diffusion, the baseline of ROS metabolism, and the effective recognition of ROS signaling in different cell organelles (Mittler 2017). The toxicity of ROS is neutralized by membrane-bound NADPH oxidases including both rubidium hydroxides (RBOHs) and NADPH-dependent-oxidases (NOXs), or also by several enzymatic and non-enzymatic antioxidants. Enzymatic antioxidants include APX, CAT, SOD, DHAR, GPX, GR, GST, MDHAR, and PPO while non-enzymatic antioxidants include AsA, flavonoids, reduced GSH, tocopherols (α, β, γ, and δ), carotenoids, phenolics, free amino acids like arginine, histidine or proline (Liu and Yang 2020). Similar to the ROS, the above antioxidants also have various subcellular localizations such as in cytoplasm, chloroplast, mitochondria, peroxisome, apoplasts, endoplasmic reticulum, plasma membrane, or other non-green plastids (Liu and Yang 2020).

The temperature-sensitiveness of enzymatic antioxidants has been studied and it has been reported that the accumulations of APX, CAT, and SOD are accelerated at the initial stage of high temperature (50 °C) exposure, but these enzymes get declined under prolonged exposure to high temperature. Further, POD and GR have also been reported to witness a declining trend under exposure between 20 °C and 50 °C temperatures. The average temperature at which the antioxidant status is between 35 °C and 40 °C in heat tolerance species while in heat-sensitive species this temperature is 30 °C (Chakraborty and Pradhan 2011). Superoxide is continually formed in chloroplast and mitochondria because of electron leakage, but at the same time, SOD acts as a first-line defence to protect the cell from superoxide toxicity or superoxide-mediated damages under heat stress. SOD converts superoxides into H_2O_2 and then the enzymes such as APX, CAT, and POD regulate the scavenging of H_2O_2. In the presence of Fe^{2+} and Fe^{3+}, H_2O_2 forms OH· (hydroxyl radical) by Haber–Weiss reaction and the OH· radicals are extremely dangerous for membranes, proteins, lipids, DNA, and other macromolecules of the cell. But several antioxidants like flavonoids, proline, sugars, GR, GSH, etc., can effectively scavenge hydroxyl radicals (Tiwari et al. 2020; Liu and Yang 2020). An increased accumulation of H_2O_2 and MDA has been reported in tomato plants under individual heat, drought, and/or combined stress. Accumulation of MDA under these stresses is an indicator of membrane injury since MDA is formed by the lipid peroxidation of bio-membranes (Zandalinas et al. 2018). The accumulation of prolines also gets enhanced under the same stress combinations. Prolines help to tolerate heat and drought stress by stabilizing subcellular components, scavenging free radicals, and maintaining the redox balance of cellular buffer (Nurdiani et al. 2018). In moth beans, heat stress has been reported to cause increased accumulation of GPOX, SOD, and CAT along with non-enzymatic antioxidants as proline and sugars (Harsh et al. 2016).

ROS are generated in plants as an inexorable consequence of drought stress. While in low concentration, ROS act as secondary messengers to initiate several metabolic pathways, but excessive accumulation of ROS induces oxidative damage to the cellular components. The various damaging roles of ROS include lipid peroxidation at the cell membrane, disruption of membrane integrity, fragmentation of peptide chains, altering protein structure and functions, rupturing of DNA strands, removal of nucleotides from the DNA strand, inducing PCD, etc. (Sharma et al. 2012). Further, one of the primary responses under drought conditions is the closing of stomata to restrict water loss through transpiration. But gaseous exchange through stomata is also hampered as a definite consequence of early closure of stomata under drought stress. It, therefore, leads to a decrease in the rate of photosynthesis and also affects the Calvin cycle, and causes to decrease in the regeneration of electron acceptors through feedback inhibition or due to low consumption of NADPH or ATP. These events, in turn, promote higher production and accumulation of ROS within cellular compartments (Chiappero et al. 2019). However, different enzymatic (APX, CAT, SOD, POD, etc.) and non-enzymatic antioxidants (proline, soluble sugars, carotenoids, etc.) come into action to cope with such overproduction of ROS and damage caused by them (Etesami and Maheshwari 2018; Chiappero et al. 2019; Zia et al. 2020). It is worthy to mention that C_4 and CAM plants have better tolerance against drought as compared to C_3 plants. C_4 plants possess a special 'Kranz wreath structure' which helps to improve water use efficiency (WUE) in C_4 plants than C3 plants. Further, this special anatomical feature helps to assimilate more CO_2 that results in higher production of organic matter, and this, in turn, saves the C_4 plants from early death under drought conditions. On the other hand, CAM plants adapt a unique mechanism to reduce water loss from the plants. These plants absorb CO_2 and fix it into malic acid at night since the stomata of CAM plants remain open during the night. However, decarboxylation of malic acid provides CO_2 for the Calvin cycle to operate in the daytime when stomata remain closed, and as such transpiration loss during the day can be avoided successfully (Yang et al. 2021).

Similarly, the other abiotic stresses like salinity also induce generations of ROS due to stomatal closure. It, therefore, leads to a higher accumulation of Na^+ as well as disruption of photosynthesis, and consequently, the surplus of absorbed light promotes ROS production. ROS production in apoplast is facilitated by several genes encoding enzymes such as plasma membrane-bound respiratory burst oxidase homologs (AtRbohD and AtRbohF), apoplastic DAO, POD, and PAO (Miller et al. 2010b). The genes like AtRbohD and AtRbohF get upregulated under salt stress and provide hypersensitive responses to salinity. Further, AtRbohD/AtRbohF induced production of ROS has been reported to enhance the movement of K^+ into the cytosol and that, in turn, decreases the Na^+/K^+ ratio (Ma et al. 2012). AtRbohD facilitates the long-distance signal transport upon exposure to various environmental stimuli whereas AtRbohF has been found to decrease the transport of Na^+ from root to shoot as it limits the distribution of Na^+ in xylem sap (Miller et al. 2009; Jiang et al. 2012). Apart from the usual oxidative damage to the cellular components, ROS can also interrupt the ionic homeostasis within the cell under salt stress. Moreover, it activates different ROS susceptible ion channels such as Ca^{2+}, K^+, Na^+, GORK like K^+ efflux, annexin mediated conductance, Ca^{2+} pump ion channels, and these result in altered functions of several organelles like chloroplast. However, some enzymes such as CAT, SOD, APX or GR, and some non-enzymatic antioxidants like ascorbate, glutathione, and tocopherols have also been reported to be accumulated for scavenging the ROS (Bose 2014, Hanin et al. 2016; Demidchik 2018; Zhao et al. 2020).

Both the quality and quantity of light are important as any imbalance can induce severe damage to PS-I or PS-II. As a consequence, it can create energy discrepancy between photosystems and also trigger stoichiometric adjustments of photosynthetic complexes which may lead to generating reactive oxygen species (Tikkanen and Aro 2014; Zavafer et al. 2015). The generation of excessive ROS is directly related to oxidative damage of chloroplast and also to photoinhibition in photosystems which ultimately results in reduced growth and yield of the crop plants. However, plants activate buffering mechanisms to maintain the balance between light-induced ROS accumulation and scavenging, as well as to improve photosynthetic efficiency by inducing cyclic photosynthetic electron flow (CEF) and non-photochemical quenching (NPQ) (Murchie 2017; Yang et al. 2018). The mechanism of CEF is related to the absorption of excess light energy around the PS-I and also the re-utilization of reducing equivalents produced by PS-I with the generation of ATPs but without accumulation of NADPH (Shikanai 2014). Whereas, NPQ helps to effectively eliminate surplus light energy from PS-II involving associated chlorophyll-bound quenching process, zeaxanthin formation by VAZ cycle, state transition or photoinhibition quenching (Kulasek et al. 2016; Ruban 2016).

ROS generation is also the primary indicator of heavy metal stress. ROS particularly at low concentrations acts as signaling molecules to induce an antioxidant system while excessive production leads to cellular damage as happened in other stresses (Gokul et al. 2016). The signaling system mediated by ROS has been found to upregulate antioxidant enzymes to scavenge the reactive oxygen species under heavy metal stress. H_2O_2 has often been observed as a signal amplifier in plants as it has the longest life span among the reactive oxygen species. Glutathione is a small non-enzymatic antioxidant that serves as a substrate of glutathione-dependent enzymes including glutathione peroxidase (GPOX) and glutathione S-transferase (GST). Both GPOX and GST play vital roles in the successful scavenging of ROS (Ding et al. 2017). Another aspect of glutathione-mediated tolerance to heavy metal stress involves the transportation and storage of the reduced sulfurs derived from cysteine. These reduced sulfurs then bind directly to the heavy metals or induce indirect synthesis of phytochelatins from glutathione by phytochelatin synthases. Phytochelatins have a higher degree of affinity to heavy metals, and thus these can effectively bind with heavy metals and then transport them to the vacuole (Hasanuzzaman et al. 2017; Jacquart et al. 2017). It is now well studied that glutathione can induce heavy metal tolerance by alleviating the oxidative stress and scavenging ROS through glutathione S-transferase and glutathione peroxidase or inducing synthesis of phytochelatins (Keyster et al. 2020).

Waterlogging or flooding also leads to oxidative stress by generating ROS. However, plants induce antioxidant-mediated defence mechanisms including both enzymatic and non-enzymatic systems to cope with the damage as made by ROS under waterlogging. It has also been reported that enzymatic antioxidants such as CAT, POD, POX, SOD, APX, and GR as well as non-enzymatic antioxidants such as AsA, reduced GSH, proline, carotenoids, and xanthophylls are involved to scavenge ROS under waterlogged conditions (Amador et al. 2012; Arbona et al. 2008; Ashraf 2012; Gomathi et al. 2015; Ou et al. 2011).

4.3 Molecular Responses

Plants can quickly sense the type and intensity of the stress, and then they try to escape from the stress effects through some alterations at the molecular level. By sensing the characteristics of various stresses, plants initiate several kinds of changes through molecular networks including signaling, initiation or termination of different pathways to develop short or long-term tolerance. Some common responses including phytohormonal modulation, generation or scavenging of ROS, changes in protein framework, expression or depression of several transcription factors, miRNA mediated response, etc., are associated with the development of abiotic stress tolerance so that plants can acclimatize according to the surrounding stress condition and continue its growth and development.

Phytohormones which are involved in stress responses are often known as stress hormones, and major stress hormones include abscisic acid (ABA), ethylene (ET), and salicylic acid (SA) (Tiwari et al. 2017). Out of these stress hormones, abscisic acid has an exclusive role in interplaying with other stress hormones (Fig. 2).

Abiotic stresses enhance the accumulation of ABA which ultimately leads to the expression of several genes encoding different proteins (Xiong et al. 2014). These proteins, in turn, play an important role as enzymes to lower oxidative damage, transduce different signals, or as transcription factors like AP2/ERF, bZIP, MYB, NAC, and WRKY which act as early responders in the perception of stress signals and rapidly enhance the activation of ABA inducing genes and build ABA-dependent framework in tolerance against respective abiotic stresses (Xiong et al. 2014; Basu and Rabara 2017). ABA signaling is associated with three classes of proteins, viz., (1) pyrabactin resistance/ pyrabactin resistance like PYR/PYL/RCARs that act as receptors, while (2) PP2Cs negatively and (3) SNF1-related kinase2s or SnRK2s (SRK2D/SnRK2.2, SRK2I/SnRK2.3, and SRK2E/SnRK2.6/OST1) positively regulates ABA transduction pathway (Danquah et al. 2014; Vishwakarma et al. 2017). Further, (Luo et al. 2013) have reported that two proteins from G-protein-coupled plasma membrane receptors (GTG1 and GTG2) interact with GPA1 and involves in ABA signaling. AREB and ABFs are transcription factors of class bZIP present in the promoter region of ABA inducible genes and activated through multi-domain phosphorylation by SNRK2s. Then they promote the expression of ABF2/AREB1, ABF3, and ABF4/AREB2 that act as a positive regulator to ABA signaling (Verma et al. 2013; Yoshida et al. 2014).

Another important stress hormone is ethylene (ET). ET plays important roles such as ripening of fruits, senescence, germination of seed, abscission of leaves and petals, root initiation, epinastic stimulation, gravitropism and it also involves several stress-responsive mechanisms (Gamalero and Glick 2012; Upreti and Sharma 2016). Receptors that involves in ET perception exhibit two types of regulation as one type (ETR1/2, ETS1/2, EIN3, ELI1) involves in positive regulation whereas other receptors (CTR1, EIN4) are associated with negative regulation of ethylene (Qiu et al. 2012). CTR1 involves the degradation of EIN2 in absence in ET. Thus, it involves the downregulation of ET by decreasing

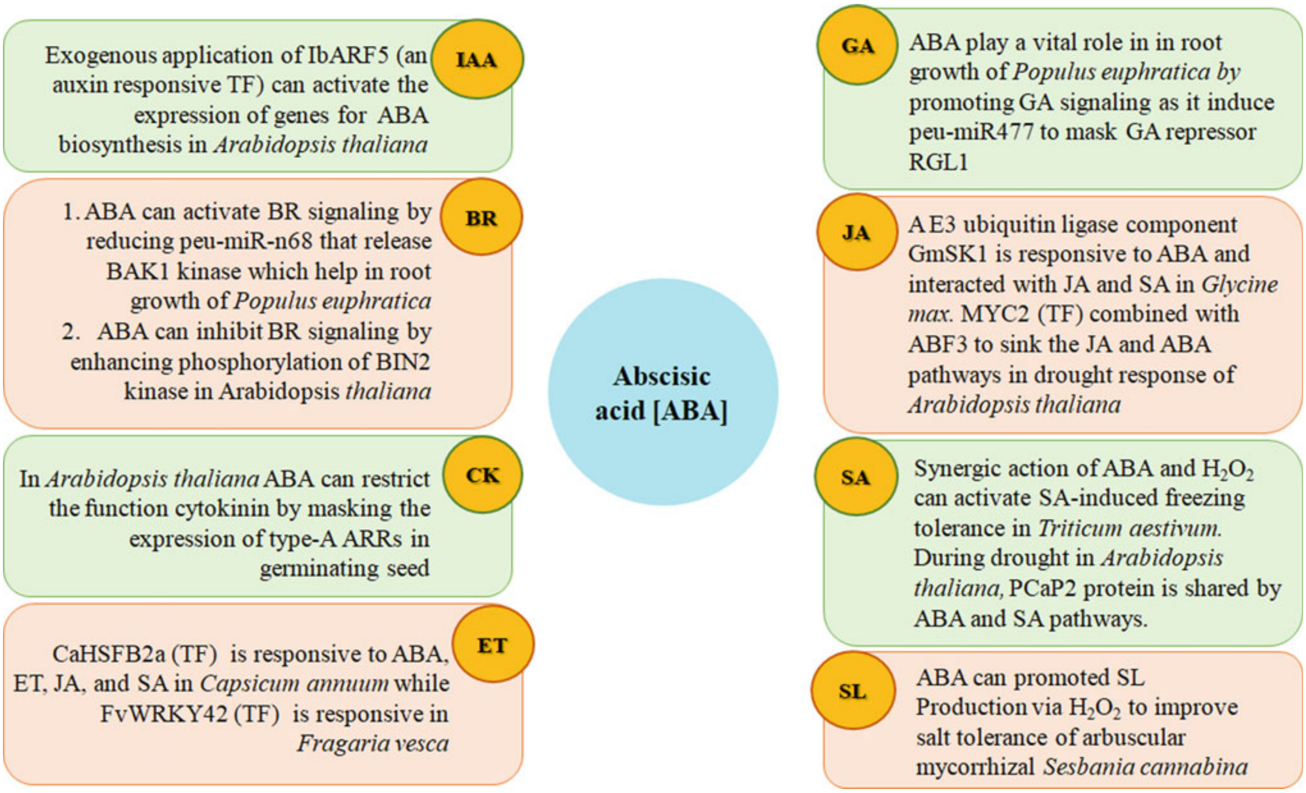

Fig. 2 Crosstalk between ABA and other phytohormones [IAA—Indole acetic acid, BRs—Brassinosteroids, CK—Cytokinin, ET—Ethylene, GA—Gibberellin, JA—Jasmonic acid, SA—Salicylic acid, SL—Strigolactone]

the stability of ET transcription factors (Černý et al. 2016). But EIN2 releases a nuclear localization signal when it undergoes proteolytic cleavage, and then the signal involves the transduction of EIN3 and EIL1 which are the major TFs involved in the early expression of ET genes (Chang et al. 2013; Zhang et al. 2014). Both MPK3 and MPK6 play a crucial role in ET signaling and its response, as stabilization of EIN3 is promoted by them. Further, it has been reported that MPK3 and MPK6 are involved in the phosphorylation of ACS that, in turn, enhance ET signaling and ET production (Hahn and Harter, 2009). EFR1 is important for regulating the expression of ESE1 and building tolerance against salt stress (Zhang et al. 2011; Wang et al. 2013b). Alternatively, expression of ERF can be enhanced by ET under salt stress through the binding with ESE1 to DRE and GCC box found in the promoter region of salt-induced genes such as COR15A, HLS1, P5CS2, and RD29A (Zhang et al. 2011; Wang et al. 2013b). Moreover, Keunen et al. (2016) have observed overexpression of EIN3 during heavy metal stress. EIL1/EIN3 act as a bridge in ET and JA mediated signaling and stress adaptive mechanisms since they can be suppressed by JAZs proteins. It has been reported that JAZs activate histone deacetylases 6 which bind with EIL1 and EIN3 and form a complex that prevents DNA binding of EIN3, and thus it prevents JA induced signaling (Zhu et al. 2011; Wang et al. 2013b).

Salicylic acid (SA) is another very important stress hormone that involves stress signaling and response mechanisms consisting of a complex and well-coordinated pathway under different abiotic stress conditions like heat, drought, salinity, osmotic, and heavy metal stress (Khan et al. 2015). Various developmental processes like seed germination, seedling establishment, nitrogen metabolism, photosynthesis, cellular proliferation, changes in stomatal aperture, respiration, antioxidant defence system, delaying plant senescence, etc., are positively influenced by SA (Khan et al. 2015; Nazar et al. 2015). NPR1 plays a crucial role in salicylic acid-mediated transcriptional reprograming, and it interacts with bZIP transcription factors of the TGA family (An and Mou 2011; Yan and Dong 2014). NPR3 and NPR4 are the two homologues of NPR1 under ubiquitin-induced protein degradation. NPR3 and NPR4 control the activity of NPR1 at high or low SA concentrations, respectively (Fu et al. 2012).

As the by-products of aerobic metabolism, ROS are continuously produced within distinct cellular components such as apoplast, chloroplast, mitochondria, and peroxisomes. Besides toxic effects, ROS works as a valuable signaling molecule in plant defence and is also involved in the regulation of various physiological processes under various abiotic stress conditions (He et al. 2018). For example, apoplastic ROS production depends on various enzymatic stimuli such as RBOHs and plasma membrane-localized NADPH oxidases that are activated after bond establishment between EF-hand motifs in the N-terminal cytosolic region and Ca^{2+} with associated phosphorylation by RLCKs (Kimura et al. 2017). Sometimes two distinct isoforms of RBOH (RBOHD and RBOHF) are present in *Arabidopsis* and they can regulate the ROS production under both abiotic and biotic stress. H_2O_2 influences the MAPK pathways by oxidizing the –SH group of cysteine residues and thus it masks the expression of repressor proteins to MAPKs such as PTPs (Jalmi and Sinha 2015; Liu and He 2017). It has been reported that stress tolerance by GSTs and HSPs is upregulated by MAPK3 and MAPK6 kinases in *Arabidopsis*. Further, H_2O_2 enhances the prompt responses of GSTs and HSPs by mediating several kinase cascades such as ANP1, MAPKKK, and OXI1 involved in MAPK3/6, NDPK2 kinases (Liu and He 2017).

Stress tolerance at the cellular level involves specific proteins function and the associated expression of genes. These proteins can be classified into three groups according to their function (Miller et al. 2010a; Gautam et al. 2020):

(a) Transcription factors involved in signaling cascades and transcriptional regulations

Transcriptional factors like DREB (Wang et al. 2019), WRKY (Banerjee and Roychoudhury 2015), LEA, NAM, ATAF, and CUC (Singh and Laxmi 2015) are mostly involved in the signaling pathway and tolerance response against abiotic and biotic stresses. These transcriptional factors are involved in the biosynthesis of various osmoprotectants, expression and regulation of various genes encoding various proteins, phytohormones, or secondary metabolites (Singh and Laxmi 2015; Banerjee and Roychoudhury 2015; de Zelicourt et al. 2016; Wang et al. 2019).

(b) Proteins associated with defence against membrane damage

Membrane damage is one of the primary phenomena that happen to plant cells under various abiotic stresses (Rawat et al. 2021). Several proteins such as HSPs, LEAs, plasma-membrane proton ATPase, etc., help to maintain membrane stability, fluidity, restore membrane functionality, and also prevent membrane damage during various abiotic stress conditions (Usman et al. 2015; Banerjee and Roychoudhury 2016; Gautam et al. 2020). The expression of ZmLEA3 protein in the tobacco plant is associated with chilling and osmotic stress (Janmohammadi et al. 2015). Rice root cell has been identified with 8 membrane-associated proteins under exposure to salt stress (Duan et al. 2012).

(iii) Proteins involved in the regulation of uptake and transport of ions, and water relation

The ions like Na^+ and Cl^- are generally stored in the vacuole and adjusted by several osmolytes such as proline, sorbitol, mannitol, and glycine betaine (Sharma 2016). But the ionic imbalance is a common phenomenon during salt stress. The vascular sequestration of Na^+ and Cl^- is generally mediated by vacuolar H^+-ATPase and the H^+-pyrophosphatase (Yin et al. 2015). These enzymes prompt electrochemical proton gradients which, in turn, activate the Na^+/H^+ antiporter and lead to Na^+ isolation into vacuoles. It is noteworthy that Na^+ efflux protein in the plasma membrane is the only Na^+/H^+ antiporter in the plasma membrane. It functions in Na^+ sequestration and builds tolerance against negative impact due to over-accumulation of Na^+/Cl^- within the plant system (Yin et al. 2015; Sze and Chanroj 2018). Apart from vacuolar Na^+/H^+ antiporter, AtNHX1 and the K^+/Na^+ symporters are also involved in a similar kind of tolerance mechanism in plants (Zhu et al. 2016; Sze and Chanroj 2018; Al Hassan 2018). Besides, it has also been reported that Cl-sequestration is mediated by voltage-dependent chloride channel proteins and cation chloride co-transporters in rice and *Arabidopsis* (Zhang et al. 2018). Moreover, aquaporins are the important channel proteins that play a crucial role in the transportation of small and uncharged solutes through plasma membranes during heat or drought stress (Gautam et al. 2020). The function of aquaporins is mediated by intrinsic proteins including PIPs, TIPs, small basic intrinsic proteins, Nodulin 26-like intrinsic proteins, and X-intrinsic proteins (Pou et al. 2013; Zargar et al. 2017; Gautam et al. 2020).

Micro-RNAs (miRNAs) are single-stranded noncoding RNA molecules of ~22 nucleotides and are also involved in the regulation of gene expression associated with stress response (Espinoza-Lewis and Wang 2012). They play an important role in many important developmental processes in plants such as the development of roots, leaf morphogenesis, reproductive organ identity, and also actively participate in various signal transduction during various abiotic stresses (Shriram et al. 2016) (Table 1). Wani et al. (2020) have defined the different steps of miRNA-mediated stress response. It has been described that miRNA-mediated stress response is a multistep process that includes the expression of miRNA genes followed by the synthesis of miRNAs and finally miRNA-mediated genetic regulation under influence of various abiotic stresses. The process is initiated with transcription of primary miRNA from miRNA genes and then miRNA precursor is formed from the primary miRNA through cleavage and stem-loop structure formation. The very next step is associated with miRNA duplex formation and this process is controlled by dicer like enzyme present in the nucleus. This miRNA duplex is then transported to the cytoplasm where it gets unwounded and is formed into single-stranded mature miRNA. The newly mature miRNA is then entered in a ribonucleoprotein complex, RNA-induced silencing complex, and participates in gene expression. miRNA regulates target genes positively or negatively gene expression can be regulated by mRNA cleavage or translational repression, and ultimately helps in developing stress tolerance (Fig. 3).

5 Management Strategies Towards Agricultural Sustainability Under Abiotic Stresses

Although the plant has its own strategies to cope with the damaging effects of abiotic stresses sometimes these adaptation or tolerance strategies of plants are not sufficient. In this context, external mitigation options as practised by humans to support the plants against abiotic or biotic stresses or to bypass the stress situation by adopting certain novel strategies are important. Though there are numerous strategies or methods taken in, by humans we have categorized some of the very common mitigation options to minimize agricultural losses. These options have been divided into three board categories:

1. Agro-technological interventions
2. Use of biological remedies
3. Transgenic breeding and/or using biotechnological tools.

5.1 Agro-Technological Interventions to Sustainable Agriculture

Agricultural researchers are always involved in inventing and establishing new technologies and methods to protect plants from the adverse effects of various abiotic stresses. These technologies have provided opportunities to upgrade the existing traditional means of agricultural practices. Some of the agro-technologies or methods which have directed abiotic stress management to a new horizon are discussed below. *Hydroponics and Aeroponics*—In a hydroponic system, plants are grown in a soilless medium particularly in water. Whereas, in aeroponics, plant roots remain naked in the air mostly in a moist environment. Both hydroponic and aeroponic system is not only beneficial for agricultural production, rather it has also been proved to be very effective in terms of stress avoidance. These types of farming are done in a closed and safe environment, and thus plants are not affected by harsh environmental factors. In these farmings, all necessary nutrients are provided and environmental parameters such as humidity, temperature, light source, etc.,

Table 1 Upregulation and downregulation of various miRNAs under various abiotic stresses. (Upregulated: ↑ and Downregulated: ↓)

Kinds of stress	Plant species	miRNA Upregulated/downregulated	References
Salinity	*Zea mays*	miR164↓	Shan et al. (2020)
	Arabidopsis thaliana	microRNA399↑	Pegler et al. (2021)
	Solanum lycopersicum	miR156↑, miR398↑	Çakır et al. (2021)
Heat	*Arabidopsis thaliana*	miR824↑	Szaker et al. (2019)
	Solanum lycopersicum	miR319↑	Shi et al. (2019)
	Populus trichocarpa	miR396↑	Zhao et al. (2021)
UV	*Triticum aestivum*	miR165/166/167↑, miR393↑, miR159↑	Wang et al. (2013a)
	Arabidopsis thaliana	miR398↑	Gao et al. (2016)
	Arabidopsis thaliana	miR158↑, miR165/166/167↑, miR391↑, miR393↑, miR824↑, miR828↑, miR846↑, miR159↓ and miR164↓, miR171↓, miR822↓	Zhou (2020)
Drought	*Solanum lycopersicum*	miR156↑	Visentin et al. (2020)
	Lolium multiflorum	miRNA156i↑, miRNA845a↑, and miRNA2937↓, miRNA3980b↓	Demirkol (2021)
	Zea mays	miR159/160↑, miR167↑, miR389a↑, miR393↑, miR397b↑, miR402↑	Das and Mondal (2021)
Cold	*Manihot esculenta*	miR159↑, miR164↑, miR396↑	Li et al. (2020)
	Hemerocallis fulva	miR159↑, miR166↑, miR396↑, miR319↑, miR167_1↑, miR167_2↑	Huang et al. (2020)
	Taxillus chinensis	miR408↑	Fu et al. (2021)
Heavy metal	*Oryza sativa*	miR528↑	Liu et al. (2015)
	Arabidopsis thaliana	miR156↑, and miR156↓	Zhang et al. (2020)
	Phaseolus vulgaris	miR1511↑	Ángel Martín-Rodríguez et al. (2021)

are closely monitored so that plants would get a healthy environment for their growth and development.

5.1.1 Seed Priming

The priming of seeds before sowing is an important agro-technological intervention. Pre-sowing soaking of seeds in water is the most primitive form of seed priming which is known as hydropriming. But various priming agents have been identified with the advancement of science. The interests in exploring such seed priming methods are also increasing day by day due to their potentiality towards global food security either through yield improvement or developing stress tolerance in crop plants. Besides hydropriming, some of the important and established agents are phytohormones, different chemicals like KNO_3, NaCl, and NaOCl, priming with PGPRs, PGPF, and AMFs, priming with quorum sensing chemicals, use of metallic solutions like Al, Cd, etc., use of various nanoparticles and various physical agents including some of the extra-terrestrial factors like magnetic field, ultraviolet radiation, gamma radiation, etc. (Bera et al. 2021).

5.1.2 Use of Drones in Agriculture

Plants are often provided with external application of certain chemicals to build tolerance against stress factors. These chemicals mostly act as external stimuli to activate some specific pathways within the plant, and finally help the plants to withstand the stress conditions. Although it is possible to

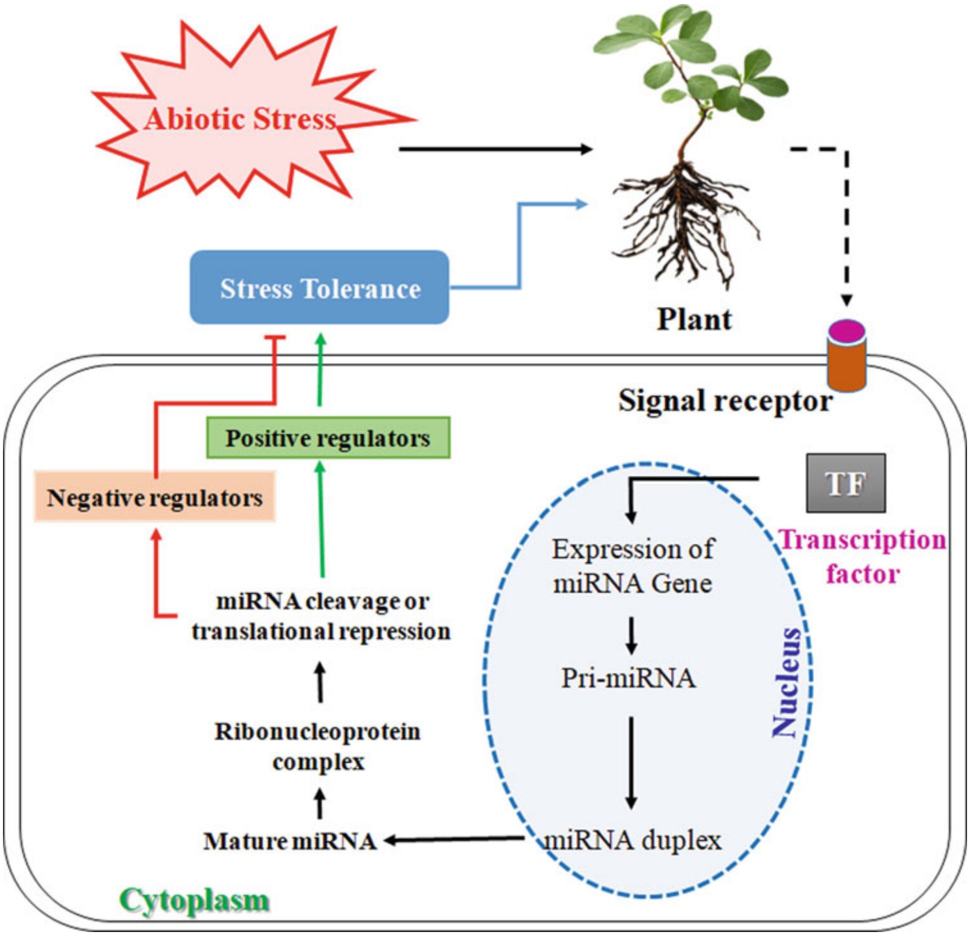

Fig. 3 Schematic representation of miRNA mediated stress response in plants

spray these chemicals manually with the use of manpower in a small area of land, but, it is quite impossible to accomplish this task manually in a vast area of agricultural land. However, the use of drones can make this possible and easy. Heavy carrier drones can carry several litres of these chemicals and can spray over the plants from a very short distance from the plant tops.

5.1.3 Use of Greenhouses

Agricultural practices inside the greenhouses particularly during a moderate or extreme cold can help to bypass the stress environment. It is because greenhouses works on the principle of retaining heat inside, so that the plants can effectively avoid chilling stress or its negative impacts. Greenhouses have also been found to be effective during high temperatures if the required environment and sufficient water are provided. However, this intervention requires some modification and technological support.

5.1.4 Rainwater Management

Effective harvesting and management of rainwater can be very useful in agriculture. Stored rainwater can be used during heavy drought spells in summer or where groundwater is not sufficient to support farming. Rainwater is mainly conserved during the end of summer and monsoon season. There are two major types of storage for rainwater conservation, and they can be either underground storage or aboveground storage.

5.1.5 Shade Tree Plantation

Shade trees are very important for the effective growth and development of various crops like tea, cocoa, coffee, etc. Shading can provide a homologous canopy to these crop plants, protect them from extreme heat or light injuries, and even take part important role in managing pests under field conditions.

5.2 Use of Biological Remedies

5.2.1 Bio-fertilizer

The use of chemical fertilizers and their exploitation would lead to pollution of groundwater by eutrophication of water bodies and also pollute the air. In this regard, organic farming through the use of bio-fertilizers would be a better approach towards agricultural sustainability particularly under changing climate scenarios. Bio-fertilizers do not cause any harm or manipulate soil microflora, rather bio-fertilizers promote the association between soil and arbuscular mycorrhiza fungi (AMF) and plant growth-promoting rhizobacteria (PGPR), It has been proved to be effective in developing tolerance against various abiotic stresses or improving the nutrient cycle in soil, and thus to enhance crop productivity (Bhardwaj et al. 2014). Besides, the use of bio-fertilizers would be helpful to promote plant growth and development even under harsh environmental conditions through maintaining the richness of the soil in terms of micro and macronutrients, facilitating effective nitrogen fixation, solubilizing potassium and phosphate, and releasing plant growth regulating substances, etc. (Bhardwaj et al. 2014; Yimer and Abena 2019).

5.2.2 Bio-accumulators

The process of accumulating different organic and inorganic (particularly toxic heavy metals and trace elements) compounds in the plant body is known as phytoremediation (Yan et al. 2020). Heavy metal toxicity is one of the important abiotic stresses, but several plants can remove these metal compounds from the soil. Such plants are known as 'hyper accumulators', or bio-accumulators (Reeves et al. 2018). Hyperaccumulators are those plants that can accumulate up to 10 to 500 times more metal ions than other plants (Kraj et al. 2021). Some of the hyperaccumulator plants are *Pteris vittata* (threshold value of arsenic accumulation > 1000 $\mu g\ g^{-1}$), *Arabidopsis halleri* (threshold value of cadmium > 100 $\mu g\ g^{-1}$), *Aeolanthus biformifolius* (threshold value of copper > 300 $\mu g\ g^{-1}$), *Noccaea rotundifolia* subsp. *Cepaeifolia* (threshold value of lead > 1000 $\mu g\ g^{-1}$), and *Noccaea caerulescens* (threshold value of zinc > 3000 $\mu g\ g^{-1}$) (Reeves et al. 2018).

5.2.3 Use of PGPR and PGPF

There are some root-associated rhizobacteria and fungi which can enhance tolerance to various biotic and abiotic stress factors. These bacteria are commonly known as plant growth-promoting rhizobacteria (PGPR) and the fungi are called plant growth-promoting fungi (PGPF). Some of the well-known PGPRs like *Glomus mosseae*, *Glomus clarum, Glomus intraradices* BEG 123, *Pseudomonas fluorescens* Aur6, *Chryseobacterium balustinum* Aur9, *Bacillus megaterium, Bacillus cereus, Arthrobacter sp., and Bacillus subtilis* can provide a positive response against salinity stress (Kumar et al. 2019). On the other hand, plant root association with *Arthrobacter brasilense* Sp245, *Bacillus megaterium, Glomus sp., Pseudomonas polymyxa, Rhizobium tropici, Pseudomonas putida* P45, *Pseudomonas putida* H-2-3, and *Achromobacter piechaudii* would build up a strong defence against drought, and with *Azospirillum sp., Azotobacter sp., Klebsiella pneumoniae, Gluconacetobacter diazotrophicus, Thiobacillus thiooxidans, Streptomyces tendae* F4, and *Pseudomonas aeruginosa* BS2 would help to continue natural growth and development of several plants under various heavy metals contaminated soil (Abbaszadeh-Dahaji et al. 2016; Kumar et al. 2019, 2020). Plant growth-promoting fungi (PGPF) are the non-pathogenic fungi that live in a symbiotic association with host plants and play a beneficial role in sustainable agriculture by providing various advantages to the host plant (Govindasamy et al. 2018). Associations between plant roots and PGPF such as *Trichoderma harzianum* TSTh, *Exophiala pisciphila* GM25 (DSE strain), *Cladosporium cladosporioides* E-162, *Rhizophagus irregularis* strain EEZ 58, *Rhizophagus intraradices* and *Funneliformis mosseae,* and *Piriformospora indica* have been proved as successful mitigators of drought stress in various crop species (Pedranzani et al. 2016; Amiri et al. 2017; Repas et al. 2017; Dastogeer et al. 2017; Zhang et al. 2017; Li et al. 2017). Negative impacts of salinity are effectively tolerated by certain crop species after making association with PGPFs such as *Piriformospora indica* (Abdelaziz et al. 2017), *Glomus clarum* (Elhindi et al. 2016), *Funneliformis mosseae* and *Rhizophagus irregularis* (Pollastri et al. 2018), and *Rhizophagus irregularis* strain EEZ 58 (Pedranzani et al. 2016). *Exophiala pisciphila* has been reported to mitigate cadmium-mediated stress (He et al. 2017). Moreover, *Phialophora mustea* Pr27, *Leptodontidium* Pr30, *Cadophora* Fe06 have also been observed with several positive effects on plants under trace elements contaminated soil (Berthelot et al. 2017).

5.2.4 Quorum Sensing Approach

Quorum sensing molecules are the means of interaction between the bacterial community and the host plant. The most extensively studied class of quorum sensing molecule is N-acyl homoserine lactones (AHL) (Shrestha et al. 2020). On the perception of these molecules, several changes occur within bacteria in terms of activation or deactivation of several quorum sensing regulated genes that lead to several effects like alteration in the virulence factors in bacteria, formation of biofilms, chemotaxis movement, etc. (Bellezza et al. 2014). It is now well established that plants' responses to certain QS molecules are very specific and depend on the length of the acyl side-chain which is connected with a homoserine lactone ring (Shrestha et al. 2020). Although some of the responses of certain QS molecules have been studied and established but are not fully explored. The effect of a particular QS molecule may vary across different species. In *Medicago truncatula,* oxo-C14-HSL synthesized by *Ensifer meliloti* induces root nodulation (Veliz-Vallejos et al. 2014), but the effects of the same QS molecule differs in the response in *Arabidopsis sp.* and *Hordeum vulgare* as it promotes resistance against the pathogenic bacteria *Pseudomonas syringae* and a pathogenic fungus *Blumeria* *graminis,* respectively (Shrestha et al. 2019). Priming of *Arabidopsis* seeds with oxo-C14-HSL enhances the accumulation of oxylipin in the distal tissues that leads to stomatal closure, accumulation of callose and phenolic compounds within plants (Schenk and Schikora 2015). Further, it has been reported that oxo-C6-HSL promotes the expression of genes associated with auxin and cytokinin signaling pathways (Zhao et al. 2016). In seedlings of Arabidopsis, oxo-C8-HSL has been reported to enhance the accumulation of proteins associated with several cellular activities like carbon metabolism, biosynthesis of other proteins and plant resistance against various abiotic and biotic stresses (Miao et al. 2012; Ding et al. 2016).

5.3 Transgenic Breeding and/or Using Biotechnological Tools

5.3.1 Transgenic Breeding

Traditional breeding techniques have been practised for a long time to achieve the desired traits of crop plants. But with the technological and scientific up-gradation during the last two decades, traditional breeding merged with transgenic modifications that have led this method to a new height. Transgenic breeding has many advantages over conventional breeding techniques since transgenic breeding offers a great possibility of manipulation of the genes for the introduction of desired traits into the crop plants through QTL mapping (Anwar and Kim 2020; Shen et al. 2018). This method of breeding gives us easy access to identify the desired genes, miRNAs, TFs that are involved in various metabolic activities, signaling pathways, expression of various genes, etc., and also widen our knowledge regarding molecular and physiological mechanisms stress responses or improved crop productivity (Anwar and Kim 2020).

5.3.2 Using Biotechnological Tools

Nowadays, the advancement in several biotechnological tools has led molecular research to a new level. Thus, identification of desired gene and its placement to the new genome with greater accuracy, and also the development of required transgenic lines have been made possible due to the introduction of modern molecular or biotechnological tools such as next-generation sequencing, mapping of quantitative trait loci (QTL) (Anwar and Kim 2020), identification of miRNA and its signaling pathway analysis (Djami-Tchatchou et al. 2017), genome editing with CRISPR-Cas9 (Tang et al. 2017), marker-assisted selection (MAS) (Kumar et al. 2018; Anwar and Kim 2020), genomic selection (GS) (Anwar and Kim 2020).

6 Conclusion

Being incessantly exposed to nature, the plant community as a whole is directly affected by various abiotic stresses. Thus, the adverse impacts like the ecological imbalance, economical loss to a country, area or society as well as global food crisis are of great concern, particularly under the abiotic stresses. The frequent occurrence of abiotic stresses or climatic extremes has become a common phenomenon with the alarmingly increasing rate of temperature anomaly or changing global climates. Though the plants are suffered a lot from abiotic stresses the plants' responses and complex mechanisms of adaptation to abiotic stresses are of interest to the researchers. Plants can easily withstand up to a certain degree of abiotic stress or bypass it through various mechanisms including morpho-physiological modifications, biochemical changes, and/or alterations in the molecular signaling pathway. The effects vary depending on the types and intensity of abiotic stress upon which plants are being exposed and thus, the manifestations of various stresses are also different. But sometimes it needs to provide the external stimuli which we often termed as stress mitigation strategies when the stress environment goes beyond the plant's tolerance level. Thus, the adoption and integration of different technological or other means of stress mitigation strategies would be effective for the sustainability of agricultural production under environmental extremities.

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Plant Viruses: Factors Involved in Emergence and Recent Advances in Their Management

Richita Saikia, Ricky Raj Paswan, Namrata Farwaha,
and Basanta Kumar Borah

Abstract

Plant viruses comprise one of the most important groups of plant pathogens, sometimes causing up to 100% yield loss. Today, nearly 47% of the emerging and re-emerging plant pathogens are viruses. They are more notorious than the other plant pathogens because they can sequester and reprogram the host cellular machinery for their own benefit. This also makes their management a challenge, when compared to other groups of plant pathogens such as bacteria and fungi. A number of plant viruses are transmitted by biotic agents like insects and nematodes; therefore, the management practices of the viruses are often indirect and based on the management of those pests. Nevertheless, recent advances in biotechnology, such as transgenic approaches, RNA interference, and CRISPR/Cas technology, are gaining importance as promising tools for the management of this influential group of pathogens. In this chapter, we discuss some of the important factors involved in the emergence and re-emergence of plant viruses, and the potential of some of the advanced biotechnological tools in their management. We enlist some successful examples too and summarize the relatively old and well-known but proven tools used for the same purpose.

Keywords

Biotechnology tools • Emergence and re-emergence • Factors • Molecular tools • Plant virus management

Abbreviations

AGO	Argonaute
amiRNA	Artificial miRNA
AMV	*Alfalfa mosaic virus*
Avr	Avirulence
BaMV	*Bamboo mosaic virus*
BBTV	*Banana bunchy top virus*
BCTV	*Beet curly top virus*
BDMV	*Bean dwarf mosaic virus*
BeYDV	*Bean yellow dwarf virus*
BnYDV	*Bean yellow disorder virus*
BSCTV	*Beet severe curly top virus*
BSV	*Banana streak virus*
CABYV	*Cucurbit aphid-borne yellows virus*
CBSD	Cassava black streak disease
CBSV	*Cassava brown streak virus*
CC	Coiled coil
CGMMV	*Cucumber green mottle mosaic virus*
ChiVMV	*Chilli veinal mottle virus*
CLCBV	*Cotton leaf curl Burewala virus*
CLCuKoV	*Cotton leaf curl Khokhran virus*
CLCuMB	Cotton leaf curl Multan betasatellite
CLCuRV	*Cotton leaf curl Rajasthan virus*
CMV	*Cucumber mosaic virus*
CP	Coat protein
CPMR	Coat protein-mediated resistance
CRISPR/Cas9	Clustered regularly interspersed palindromic repeats-associated protein9
CTV	*Citrus Tristeza virus*
CVYV	*Cucumber vein yellowing virus*
CYVV	*Clover yellow vein virus*
DCL	Dicer-like protein
DNA	Deoxy ribonucleic acid
eIFs	Eukaryotic translation initiation factors
ER	Extreme resistance
ETI	Effectors-triggered immunity
FnCas9	*Francisellanovicida*
GRSV	*Groundnut ringspot virus*
hp-PTGS	Hairpin RNA-induced PTGS
HR	Hypersensitive response
HV	Helper virus
ihp	Intron hairpin
IMPDH	Inosine monophosphate dehydrogenase

R. Saikia · R. R. Paswan · N. Farwaha · B. K. Borah (✉)
Department of Agricultural Biotechnology, Assam Agricultural University, Jorhat, 785013, India

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JA	Jasmonic acid
kDa	Kilo Dalton
LCV	*Lettuce chlorosis virus*
LMV	*Lettuce mosaic virus*
LRR	Leucine-rich repeat
MAPK	Mitogen-activated protein kinase
MiRNAs	MicroRNAs
miR-mimic	MiRNA mimic technology
MP	Movement protein
MSV	*Maize streak virus*
NA	Neuraminidase
NB	Nucleotide binding
NBS	Nucleotide-Binding Site
NSP	Nuclear Shuttle Protein
ORF	Open reading frame
PDR	Pathogen-Derived Resistance
PDV	*Prune dwarf virus*
PepMV	*Pepino mosaic virus*
PMV	*Peach mosaic virus*
PLRV	*Potato leaf roll virus*
PNRSV	*Prunus necrotic ringspot virus*
PPV	*Plum pox virus*
pri-miRNAs	Primary microRNAs
PR	Pathogenesis-related genes
PRSV	*Papaya ringspot virus*
PTGS	Post-transcriptional gene silencing
PTI	Pathogen molecular pattern (PAMP)-triggered immunity
PVMV	*Pepper veinal mottle virus*
PVX	*Potato virus X*
PVY	*Potato virus Y*
PYVV	*Potato yellow vein virus*
R gene	Resistance gene
RBSDV	*Rice black-streaked dwarf virus*
RBV	Ribavirin
RDRp/RDR	RNA-dependent RNA Polymerase
Rep	Replicase protein
RISC	RNA-induced silencing complex
RNA	Ribonucleic acid
RNAi	RNA interference
ROS	Reactive oxygen species
RSV	*Rice stripe virus*
RTBV	*Rice tungro bacilliform virus*
RTSV	*Rice tungro spherical virus*
SA	Salicylic acid
sat-RNAs	Satellite RNAs
scFv	Single-chain variable fragment
SCMV	*Sugarcane mosaic virus*
SCYLV	*Sugarcane yellow leaf virus*
sgRNA	Single-stranded guided RNA
siRNAs	Small interfering (si)RNAs
S-PTGS	Sense gene-induced post-transcriptional gene silencing
TAS	Trans-acting siRNA
TCV	*Turnip crinkle virus*
TIR	Toll-Interleukin1-like receptor
TLCYnV	*Tomato leaf curl Yunnan virus*
TEV	*Tobacco etch virus*
TMV	*Tobacco mosaic virus*
ToLCNV	*Tomato leaf curl New Delhi virus*
ToMV	*Tomato mosaic virus*
TRV	*Tobacco rattle virus*
TRSV	*Tobacco ringspot virus*
TSV	*Tobacco streak virus*
TSWV	*Tomato spotted wilt virus*
TYLCV	*Tomato yellow leaf curl virus*
TYLCSV	*Tomato yellow leaf curl Sardinia virus*
TuMV	*Turnip mosaic virus;*
TYMV	*Turnip yellow mosaic virus*
VbMS	Virus-based microRNA silencing
WMV-Tr	*Watermelon mosaic virus Turkish isolate*
WMVBV	*Wild melon vein banding virus*
WSMoV	*Watermelon silver mottle virus*
WSMV	*Wheat streak mosaic virus*
ZYMV	*Zucchini yellow mosaic virus*

1 Introduction

Agricultural and horticultural crops are susceptible to a broad set of pathogens like bacteria, fungi, and viruses (Borrelli et al. 2018), and plant viruses account for approximately 30% of plant diseases (Boualem et al. 2016). Viruses are single-stranded or double-stranded DNA or RNA pathogens packed inside a protein coat (capsid) which survive within the host by acquiring host internal machinery and utilizing it for intracellular movement and transmissions (Islam et al. 2017). Viral diseases are a major threat to sustainable and productive agriculture worldwide, resulting in huge yield loss every year (Mumford et al. 2016).

The crucial factors driving virus emergence are (i) their ability to rapidly evolve and adapt in changing environments, (ii) introduction of plant material carrying the virus and their insect vector to a new region and international borders, (iii) global climate change affecting the distribution of host and viral vectors, and (iv) monocropping with low genetic diversity and high plant density, which favours pathogens and pest multiplication (Anderson et al. 2004). Unlike bacteria or fungi that can be treated with antibacterial or antifungal agents, curing virus-infected plants is challenging due to its obligate intracellular parasitic nature.

Disease management strategies require knowledge of plant-virus interactions and effective measures to control viral diseases. It relies on preventing viruses from entering host cells or developing disease resistance through multiple approaches. These include the use of certified planting materials (Novy et al. 2007), controlling vectors population, and implementation of clean agricultural practices (Fereres and Moreno 2009). In addition, the use of attenuated virus strains to increase the resistance responses (Ichiki et al. 2005) and, in some cases, breeding to obtain cultivars with elevated resistance levels act as an alternative strategy to reduce the viral load and prevent crop loss (Ma et al. 2004). Here, the recent advances in the management of plant viruses and the progress of procedures used for virus detection are reviewed. This chapter includes basic concepts of the emergence of new viral diseases in plants along with the important management strategies for disease control aimed to guide plant pathologists to design and apply more accurate detection and efficient management of plant virus diseases.

2 Emerging Plant Viral Diseases and Factors Driving Virus Emergence

The emergence of new viral diseases in plants has gained immense importance in the past few decades. The constant environmental changes, accidental introduction of infected planting materials to new habitats facilitated by global trades, and population expansion of viral vectors provide conditions that permit the emergence of new virus species or strains (Anderson et al. 2004). This results in complexity in plant-virus interactions, which can cause disease outbreaks, and insect carriers may amplify this complexity and the disease severity. Most of the plant viruses imposing threat to global food security fall in seven major genera: Begomoviruses, Carlaviruses, Crinivirus, Ipomoviruses, Potyviruses, Torradoviruses, and Tospoviruses (Ertunc 2020).

Understanding the mechanisms of emergence or re-emergence of plant viruses requires knowledge of host distribution, their spread by various vectors, and the behaviour of the vectors. Several factors drive the emergence of indigenous viruses and enhance disease severity in the introduced cropping environment. Some of the emerging plant viruses, along with their host range, symptoms, geographical distribution, and potential mechanisms of evolution and virulence are enlisted in Table 1.

2.1 Changes in Agricultural Practices

Changes in agricultural practices such as (i) crop intensification and extensification, (ii) loss of genetic diversity through replacement of traditional cultivars and landraces by virus susceptible cultivars, and (iii) the introduction of alternate hosts and excessive use of agrochemicals can facilitate the rate of virus movement or increase potential for viruliferous vectors to migrate from native hosts to the introduced crops (Morales and Anderson 2001; Fargette et al. 2006; Jones 2009).

2.2 Molecular Alterations in Virus Genomes

Molecular alteration of viral genetic components can also drive the evolution of new virus species or virulent strains. These alterations include mutations, recombination, pseudo-recombination, reassortment, evolution, symbiosis or ability to cause mixed infection with other virus species, the genetic drift of virus variants arising from geographical isolation, the introduction of satellite viral components into existing strains, and viral genome integration in host genome causing episomal infection (Gibbs et al. 2008; Jones 2009; Zaidi et al. 2017; Rojas et al. 2018). Other determinants include founder effects and population bottlenecks involved with vector transmission or the spread of the virus within individual plants and genome integration (Jones 2009).

2.3 Altered Biology

The principal factors associated with the crucial alterations in biology include the introduction of new and more efficient virus-vector species, biotypes, or variants of existing vector species, expansion in the natural host range, circumvention of host defences in introduced crops, and infection introduced hosts with more remarkable adaptation (Anderson et al. 2004; Fargette et al. 2006; Gibbs et al. 2008; Jones 2009).

2.4 Climate Change

The changes in climatic conditions can assist in the spread of newly acquainted viruses and their vectors, threatening crop yield both directly and indirectly (Ertunc 2020). Direct consequences like altered rainfall patterns and higher wind speeds and indirect factors like regional alterations greatly influence the dynamics of plant virus epidemics and alter the geographic distribution, rate of evolution, relative abundance, and host adaptation of these viruses. This contributes to a favourable spread of newly introduced viruses and their vectors (Jones 2009). Trebicki (2020) investigated certain factors, such as elevated CO_2, increased temperature, and water availability which either as a single factor or in combination might influence the plant virus epidemiology.

Table 1 Emerging plant viruses, their host range, symptoms, geographical distribution, and potential mechanisms of evolution and virulence

Virus name (Strain)	Host	Symptoms	Vectors	Geographical distribution	Potential mechanisms of evolution and virulence	References
Genus: Badnavirus						
Cacao swollen shoot disease	Cacao	Leaf discolouration, stem/root swelling	Mealybug	South America, West Africa	Recombination events between intergenic region (IR) and open reading frame (ORF2)	Muller (2016)
Genus: Begomovirus						
Tomato yellow leaf curl Mali virus	Tomato, Common bean, *Nicotiana benthamiana*	Upward leaf curling and yellowing in tomato, leaf curl, crumpling with interveinal yellowing in common bean	Whitefly	Mali, West Africa	Recombination between two begomovirus species, *Tomato yellow leaf curl virus*-Mild and *Hollyhock leaf crumple virus*	Chen et al. (2009)
TLCYnV	Tomato, *N. benthamiana, N. tabacum, Petunia hybrida*	Upward leaf curling, vein thickening	Whitefly	Yunnan, China	C4 protein of TLCYnV suppresses post-transcriptional gene silencing or transcriptional gene silencing via inhibiting viral genome methylation	Xie et al. (2013)
ToLCNV	Tomato, Potato, Chilli, Cucurbits (Zucchini, cucumber, and melon), *N. benthamiana*	Leaf curling	Whitefly	Southeast Asia, Southern Europe (Spain and Italy), North Africa (Tunisia), and Iran	Pseudo-recombination of ToLCNV with other begomoviruses and betasatellites	Zaidi et al. (2017)
Tomato yellow leaf curl Sardinia virus (TYLCSV)	Tomato, Potato, Common bean	Leaf curling, mottling, chlorotic leaf margins	Whitefly	Spain	Genetic exchanges achieved through inter-species recombination	Diaz-Pendon et al. (2019)
Tomato curly stunt virus	Tomato	Leaf curling, stunting, foliar chlorosis	Whitefly	South Africa, Mosambique	Intra- or inter-specific recombination with *Replicase* (*Rep*) gene and *Coat protein* (*CP*) gene leading to speciation	Sande et al. (2021)
Genus: Mastrevirus						
Maize streak virus (MSV-A)	Maize (main host); also infects wheat, barley, rye, oats, sugarcane, finger millet, pearl millet, and sorghum	Chlorotic streaks on leaves, stunted growth, and failure to produce cobs or seed	Leafhopper	Different parts of Africa	Probably intra-strain or inter-strain recombination events of MSV-A with ancestral MSV-B variant	Varsani et al. (2008), Shepherd et al. (2010)
Genus: Potyvirus						
PVY Syria (PVY ^{SYR})	Potato, weed, *N. tabacum*	Necrotic ringspot, mosaic patterns	Aphids	Syria	Recombination between PVY^{NTN} and PVY^{NW} strains	Ali et al. (2010)
Watermelon mosaic virus Turkish isolate (WMV-Tr)	Watermelon, melon, zucchini, and squash	Mosaic, mottle, vein banding, and leaf deformation	Aphids	Adana province of Turkey	Recombination	Kamberoglu et al. (2015)

(continued)

Table 1 (continued)

Virus name (Strain)	Host	Symptoms	Vectors	Geographical distribution	Potential mechanisms of evolution and virulence	References
Bean common mosaic virus (BCMV-Az) recombinant isolate	Azuki bean	Mosaic and necrotic symptoms, vain banding	Aphids	China	Recombinant and potential new strain originating from the cowpea isolate R and common bean isolate US10	Li et al. (2016)
PVY isolate (HLJ-C-44)	Potato, *N. tabacum*	Mosaic symptoms	Aphids	Heilongjiang province of China	Recombination between PVY^{N} and PVY^{NW} strains	Han et al. (2017)
Sudan WMV	Cucumber, zucchini, common bean, *N. benthamiana, N. tabacum*	Prominent mosaic and chlorosis on leaf lamina	Aphids	Sudan	Interspecific recombinant between *Moroccan* WMV (MWMV) and *Wild melon vein banding virus* (WMVBV)-like viruses	Desbiez et al. (2017)
New isolates of *Sweet potato feathery mottle virus* and *Sweet potato virus C*	Sweet potato, *Iris setosa*	Mosaic, crinkling, chlorosis, chlorotic blotches, purple ringspot	Aphids	Western and Northern Australia, Southeast Asia (East Timor)	High frequency of intra- and inter-phylogroup recombination	Maina et al. (2018)
ChiVMV-Guangxi and Yunnan isolate	Pepper	Mosaic mottling, twisted or fallen leaves, vein banding, and reduced fruit size	Aphids	Guangxi and Yunnan province of China		Rao et al. (2020)
Genus: Potexvirus						
Pepino mosaic virus (PepMV)	Pepino, tomato	Yellow mosaic, necrotic spots, blotching	Mechanical and seed transmission	Europe, Southern American continent		Martelli and Galitelli (2009), Ertunc (2020)
Genus: Crinivirus						
Potato yellow vein virus	Potato	Yellow spots	Whitefly	South America	Multiple genetic recombinations in the minor capsid protein (CPm) coding region of PYVV	Chaves-Bedoya et al. (2014)
Lettuce chlorosis virus Spain	Lettuce, bean	Yellowing of leaves showing necrosis, chlorotic leaves	Whitefly	Spain	Crossover recombination of intact open reading frames (ORFs) between bean yellow disorder virus (BnYDV) and LCV	Ruiz et al. (2018)
Genus: Polerovirus						
Sugarcane yellow leaf virus (SCYLV)	Sugarcane	Yellow leaf	Aphids	China	Potential recombinant events between genotypes	Lin et al. (2014)
Cucurbit aphid-borne yellows virus (CABYV)	Melon	Yellowing disease	Aphids, whitefly	Brazil	Probably inter- and intraspecific recombination	Costa et al. (2019)
Recombinant CABYV	Melon	Chlorosis and stunting symptoms	Whitefly	Europe, Africa, Asia, and America	Recombination between the common type CABYV and an unknown polerovirus	Costa et al. (2020)

(continued)

Table 1 (continued)

Virus name (Strain)	Host	Symptoms	Vectors	Geographical distribution	Potential mechanisms of evolution and virulence	References
Pod pepper vein yellows virus	Pod pepper plants (*Capsicum frutescens*)	Interveinal leaf yellowing and fruit discolouration	Aphids	Yunnan, China	Single recombination event with *Pepper vein yellows virus* and *Tobacco vein distorting virus*	Zhao et al. (2021)
Genus: Carlavirus						
Potato virus M	Pepino, tomato	Leaf rolling, mosaic patterns	Aphids	China	Recombination in the TGB2-TGB3-CP region	Ge et al. (2014)
Genus: Tobamovirus						
Tomato brown rugose fruit virus	Tomato	Mosaic patterns, necrotic lesions	Mechanical transmission	Middle East, Europe, Mexico, USA, and China	Probably due to recombination among various tomato-infecting tobamoviruses	Salem et al. (2016)
Cucumber green mottle mosaic virus (CGMMV)	Cucurbit *sps*	Leaf mottling, mosaic patterns	No information available	Europe, USA, Canada, and Australia	Recombination	Bertin et al. (2021)
Genus: Tospovirus						
New TSWV isolates (YNta, YNrp, and YNgp)	Tobacco, red pepper, and green pepper	Ringspot, black streak and tip dieback	Thrips	China	Recombination events in the 5′ half of the RNA	Zhang et al. (2016b)

3 Transmission of Plant Viruses

Plant viruses are transmitted majorly by insect vectors. Among them, aphids, whiteflies, and thrips are the most important ones, and all of them are positively affected by global climate change. Other vectors include planthoppers, leafhoppers, and mealybugs (Lv et al. 2017; Ertunc 2020). Aphids are the main transmitting agents in the temperate regions: they transmit more than 275 virus species distributed among 19 genera (Canto et al. 2009). In general, an increase in temperature could make earlier incubation of overwintering eggs of aphids and may catalyze the process of reaching the minimum threshold of population size required for migration (Bell et al. 2015; Wu et al. 2020). This can affect the phenological synchronicity between aphids and host plants (Dewar and Watt 1992). In such a situation, insects that reach adulthood before host plant germination may seek alternate hosts as a means for survival, resulting in expansion of the host range (Paradis et al. 2008). In field-grown vegetables with a temperate climate, the five most economically important plant viruses transmitted by aphids are *Cucumber mosaic virus* (CMV), *Lettuce mosaic virus* (LMV), *Papaya ringspot virus* (PRSV), *Potato virus Y* (PVY), and *Turnip mosaic virus* (TuMV) (Ertunc 2020). Other important aphid-transmitted viruses of horticultural crops include *Banana bunchy top virus* (BBTV), *Bean yellow mosaic virus*, *Chilli veinal mottle virus* (ChiVMV), *Citrus Tristeza virus* (CTV), and *Zucchini yellow mosaic virus* (ZYMV) (Krishnareddy 2013).

Many emerging plant viruses are also transmitted by whiteflies (Hemiptera: Aleyrodidae) belonging to the genera *Bemisia* and *Trialeurodes*. These include tomato-infecting viruses such as *Tomato chlorosis virus*, *Tomato yellow leaf curl virus* (TYLCV), *Tomato leaf curl New Delhi virus* (ToLCNV), and *Tomato leaf curl Yunnan virus* (TLCYnV); *Tobacco curly shoot virus* (Li et al. 2005; Xie et al. 2013; Fiallo-Olive and Navas-Castillo 2019); cassava-infecting *East African cassava mosaic virus* (Zhou et al. 1997); *Sweet potato chlorotic stunt virus* (Gamarra et al. 2010); *Tobacco mosaic virus* (TMV) (Hanssen et al. 2010); and *Bean golden mosaic virus* and *Bean dwarf mosaic virus* (BDMV, Navas-Castillo et al. 2011).

Besides aphids and whiteflies, thrips belonging to the order Thysanoptera are known vectors transmitting several plant viruses (Jones 2005), and several viruses belonging to the genus Tospoviruses (family: Bunyaviridae) are transmitted by thrips (Rojas and Gilbertson 2008). These include *Tomato spotted wilt virus* (TSWV), *Impatiens necrotic spot virus*, and *Iris yellow spot virus* causing a widespread in vegetables, ornamentals, and floral crops (Ertunc 2020).

4 Management Strategies

Management of plant viral diseases is a matter of vital concern and importance as virus-induced diseases are not liable towards direct disease management methods. Several disease management techniques have been applied in the case of diseases caused by plant viruses to minimize their incidence on crop plants. The following section enlists some of such strategies. A schematic representation of different virus resistance strategies developed over the past decades is shown in Fig. 1.

4.1 Cross *Protection*

Cross protection is one of the conventional management strategies to protect plants by inoculating with a mild strain (called the primary virus/strain) of a virus against one or more acute strains (called the secondary virus/strain) of the same virus. The method was first demonstrated in the case of TMV (McKinney 1929). This method of crop protection had been successfully employed to administer many plant viruses, such as ZYMV, PepMV, and CTV (Rast 1972; Müller and Costa 1977; Lin et al. 2007; Aguero et al. 2018; Huang et al. 2019). A recent study showed the utilization of cross-protection by modifying the viral RNA silencing suppressor against the watermelon strain PRSV (Huang et al. 2019). However, the milder strain of the virus protecting one crop variety may sometimes cause severe diseases on other varieties growing elsewhere. This had become a limiting factor for the application of this classical method (Tabassum et al. 2012).

4.2 Pathogen-Derived Resistance

Resistance to viruses has been accomplished in various plants through the usage of genes derived from the virus itself, and this method is known as pathogen-derived resistance (PDR, Sanford and Johnston 1985). The idea of PDR is correlated with cross-protection wherein inoculation of the host with a mild strain can cross-protect the host from infection by severe strains of the same or very closely related viruses (Sanford and Johnston 1985). The concept of PDR is based on the engineering of resistance in susceptible hosts through the use of genetic elements, for example, coding and non-coding sequence elements, from a pathogen's very own genome (Gottula and Fuchs 2009). Common genes utilized to confer viral PDR include coat proteins, replicases, movement proteins, defective interfering RNAs and DNAs, and non-translated RNAs (Beachy 1997). According to Tabassum et al. (2012), as a result of expressing viral genes

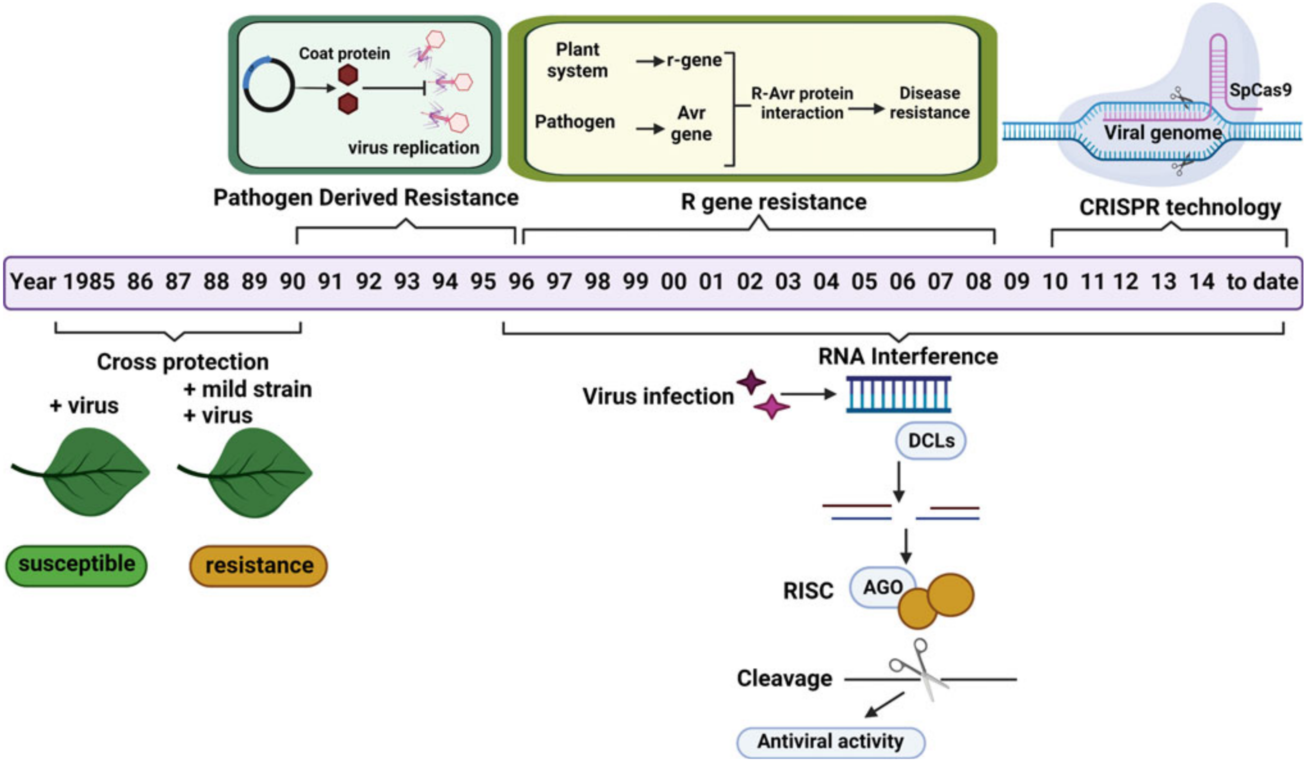

Fig. 1 Schematic illustration of various virus resistance strategies

in plants along such as the *coat protein* (*CP*), *movement protein* (*MP*), and *replicase* (*Rep*) protein genes target a step crucial during viral replication and infection, and thus, virus resistance was achieved. Among all these genes, the *CP* gene is the most widely and commonly used transgene using which virus-resistant transgenic plants have been developed; the *Rep* and the *MP* genes also have been used in several instances (reviewed by Varma et al. 2002).

The efficacy of PDR was first confirmed by expressing the *CP* gene of TMV in transgenic tobacco against TMV infection (Abel et al. 1986). The *CP* gene is associated with viral replication and is also subjected to viral uncoating (Beachy et al. 1990). The *CP*-mediated resistance (CPMR) has been widely used, and so far, several important plant viruses have been targeted utilizing this approach (Galvez et al. 2014). These include CMV, TYLCV, *Potato virus X* (PVX), PVY, *Potato leaf roll virus* (PLRV), *Potato mosaic virus*, ZYMV, WMV, and PRSV (reviewed by Malnoe et al. 1994; Dasgupta et al. 2003; Galvez et al. 2014). Among them, CPMR in PRSV was a major success in the United States when Fitch et al. (1992), by expressing the PRSV *CP* gene, succeeded in producing transgenic papaya showing resistance. Among the others, while Kaniewski et al. (1990) found successful CPMR was achieved against PVY, in squash, success was achieved against CMV, ZYMV as well as WMV using the *CP*s of the cognate viruses (Lindbo and Falk 2017). The use of CPMR is hypothesized to have multiple mechanisms working against different viruses (Beachy 1997; Bendahmane et al. 2007).

The viral *MP* accumulated in the plasmodesmata allows cell-to-cell movement of the virus (Beachy 1997). The first *MP*-mediated resistance was demonstrated in tobacco plants with a defective *MP* through the plasmodesmata (Lapidot et al. 1993; Galvez et al. 2014). Transgenic plants expressing *MP* gene showed resistance against a large number of viruses like *Cowpea mosaic virus*, *Cabbage leaf curl virus*, CMV, PLRV, PVY, PVX, TMV, *Tomato mottle virus*, *Tobacco rattle virus* (TRV), *Tobacco ringspot virus* (TRSV), *Alfalfa mosaic virus* (AMV), *Peanut chlorotic streak virus,* etc. (reviewed by Sudarshana et al. 2007; Cillo and Palukaitis 2014). In DNA viruses belonging to the genus Begomovirus, the truncated *MP* gene also conferred resistance to heterologous and homologous viruses upon transgenic expression (Duan et al. 1997; Hou et al. 2000; Sudarshana et al. 2007). Sudarshana et al. (2007) observed that the viruses of the families Comoviridae and Caulimoviridae encoded a specialized protein that forms a tubule from the infected to adjacent cells allowing the trafficking of virions instead of depending on the plasmodesmata-modifying protein. However, despite providing a broad-spectrum resistance, over-expressed *MP* transgene was also shown to be toxic to plant cells (Khan et al. 2014).

The viral replicase gene (*Rep*) is associated with virus replication and genome integrity (Tabassum et al. 2012). Golemboski and co-workers (1990) first reported engineered viral resistance for TMV by utilizing genes encoding for viral RNA-dependent RNA polymerase (RdRp) (Prins et al. 2008) which consisted of a 54 kDa fragment of the replicase gene (Beachy 1997). According to Galvez and co-workers (2014), resistance achieved by replicase was observed to be durable and significant. Related works were carried out for several other viruses like AMV, PLRV, PVY, CPMV, *Pea early browning virus*, *Rice yellow mottle virus*, TYLCV, *Wheat yellow mosaic virus,* and ZYMV (Dasgupta et al. 2003; Cillo and Palukaitis 2014; Galvez et al. 2014; Khan et al. 2014). Resistance studies in Geminiviruses with viral replication-associated proteins showed that those viral proteins interacted with the host polymerases (Galvez et al. 2014).

Several studies conducted to achieve the *Rep*-mediated resistance showed that different mechanisms function in different viruses (Marano and Baulcombe 1998). Nevertheless, this resistance is generally definite and usually limited to homologous viral strains (Palukaitis and Zaitlin 1997).

4.3 Plantibodies

Plantibodies can be referred to as plant-derived recombinant antibodies to achieve resistance against pathogens (Schots et al. 1992). The concept of plantibody is an animal strategy intended to fight against pathogens in the plant kingdom (Shamim et al. 2013). Hiatt et al. (1989) first demonstrated the expression of recombinant antibodies in transgenic tobacco plants. Initially, the capability of plant-derived antibodies to hinder plant viruses was shown utilizing a single-chain variable fragment (scFv) against *Artichoke mottled crinkle virus* by Tavladoraki et al. (1993). In another study, Jahromi et al. (2009) demonstrated that the *CP21*, the major CP of *Beet necrotic yellow vein virus,* had a higher affinity toscFv; however, there was no further research on this candidate approach. Besides CPs, other structural proteins such as MPs and Rep proteins can also be targeted by recombinant antibodies (Safarnejad et al. 2011). Nine such scFvs having conserved target domains in TSWV MP were created that exhibited antibodies in the cytosol of transgenic tobacco plants upon transgenic production (Zhang et al. 2008). Similarly, Safarnejad et al. (2008) generated two scFvs recognizing distinct epitopes of Rep proteins of TYLCV. Plantibody-mediated resistance has been demonstrated against devastating CTV in citrus, and this approach gave resistance in 40–60% of the plants (Cervera et al. 2010). The most commonly utilized crops for the production of plantibodies include alfalfa, potato, rice, soybean, tobacco, tomato, and wheat (Tilahun et al. 2019). The plantibody approach, therefore, has been concluded to be useful if applied as a substitution or along with classical breeding techniques to manage plant viral diseases; however, several challenges such as optimization of cytosolic antibody accumulation, different patterns of glycosylation, and inadequate expression in some plants limit their wide-scale acceptability (Safarnejad et al. 2011).

4.4 Satellite RNA

Satellite RNAs (sat-RNAs) confers resistance against viruses which relies upon a helper virus (HV) for their replication and invasion in the infected plants (Kong et al. 1997). Lin and Lin (2017) stated that an interesting feature of sat-RNAs is their ability to interfere with the replication of the HV due to their homology with the HV genomes in them at the 5′ and 3′ regions. Reports have demonstrated symptom-attenuating capacity of sat-RNA against AMCV, *Bamboo mosaic virus*, CMV, *Peanut stunt virus*, *Grapevine fanleaf virus, Cymbidium ringspot virus*, TRSV, and *Groundnut rosette virus* that was achieved via transgenic approach (reviewed by Lin and Lin 2017). Varma et al. (2002) had nicely reviewed the successful application of sat-RNAs for establishing resistance against Cucumo- and Nepoviruses by transgenic approaches.

Meanwhile, DNA satellites have been found useful for resistance breeding against geminiviruses too. By exploiting the satellite hairpin construct, Khatoon et al. (2016) reported resistance against *Cotton leaf curl Rajasthan virus* (CLCuRV) in cotton. An intron hairpin (ihp) RNAi construct of *βC1* gene of CLCuMB (Cotton leaf curl Multan betasatellite) was designed and developed in transgenic *N. benthamiana* plants conferring potential resistance against cotton leaf curl disease (Akhtar et al. 2017). However, this strategy cannot fully provide resistance to eradicate the virus and, at times, can also induce minor mutations leading to necrosis (Hussain and Khan 2018).

4.5 Ribozyme

Ribozymes are self-cleaving RNA structures that provide resistance in transgenic plants (Symons and Uhlenbeck 1991). Transgenic tomato plants have been reported to achieve effective resistance against Citrus exocortis viroid using the ribozyme technique (Atkins et al. 1995). De Feyter et al. (1996) demonstrated a hammerhead ribozyme gene to conferred resistance in transgenic tobacco against TMV. In another study, utilization of ribozyme provided resistance against two potyviruses (WMV and ZYMV) in transgenic melon plants (Huttner et al. 2001). Although ribozymes are effective and specific against plant viruses, not much has been explored and achieved with this relatively new technology against plant viruses.

4.6 R Gene-Mediated Resistance and Management

Plant resistance gene (*R*) genes play a critical role in plant immunity through gene-for-gene resistance or race-specific resistance by directly or indirectly recognizing the avirulence (*Avr*) gene encoded by diverse pathogens such as bacteria, fungi, and viruses. The flax/flax rust fungus system was the first experiment to demonstrate gene-for-gene resistance (Flor 1955). The vast majority of *R* genes encode R-proteins which are highly conserved throughout species and also have a high degree of structural similarity. The majority of them are distinguished by the presence of nucleotide-binding (NB) and leucine-rich repeat (LRR) motifs (Takken et al. 2006). Activation of *R* genes is typically associated with programmed cell death response, as evidenced by the rapid formation of necrotic lesions (a hypersensitive response, HR) or, in rare cases, extreme resistance (ER), during which no necrosis is evident. HR leads to pathogen effectors-triggered immunity (ETI) and is considered as an effective way of plants defence against viral infection. The recognition of the pathogen-encoded *Avr* gene by a cognate dominant *R* gene initiates the hypersensitive reactions (Moffett 2009). The Avr/R protein interactions potentially induce a mitogen-activated protein kinase (MAPK) signaling cascade, resulting in the rapid accumulation of reactive oxygen species (ROS) and defence hormones like salicylic acid (SA) and jasmonic acid (JA). HR is coupled with calcium ion influx, callose accumulation at the plasmodesmata, membrane permeability alteration, and a dramatic transcriptional reprogramming that results in the expression of pathogenesis-related (*PR*) genes at the cellular level (Pallas and García 2011; Mandadi and Scholthof 2012).

Through HR, the invading viruses (and other pathogens) are restricted to the point of entry/invasion, where infections are prevented. In contrast to the gradual commencement of antiviral RNA interference (RNAi), the R gene response is often quick and results in virus containment within three to four days (de Ronde et al. 2014).

Dominant *R* genes are divided into two groups: those that encode NB-LRRs and those that do not. The majority of *R* genes are of the NB-LRR type and encode proteins that, regardless of the pathogen they detect, have three domains: (i) the Nucleotide-Binding Site (NBS) in the protein's core, (ii) a Leucine-Rich Repeat (LRR) at the protein's C-terminus, and (iii) a Coiled coil (CC) or Toll-Interleukin 1-like receptor (TIR) domain at the protein's N-terminus (Moffett 2009). The LRR proteins play a critical role in determining the specificity of the target proteins of pathogens and this domain is constantly evolving due to selection pressure to increase its specificity towards new target pathogens (Boualem et al. 2016). After pathogen recognition, NB-LRR proteins serve as molecular switches, switching between a constitutively inactive 'on' conformation and an active 'off' state. Intramolecular interactions occur between the LRR domain which is folded back over the NBS domain and N-terminal dimers, TIR, or CC domain which keeps the NB-LRRs protein in 'off' mode, thus limiting unwanted activation of NB-LRRs-mediated reactions (Takken and Goverse 2012).

Over the past decade, a significant number of *R* genes have been cloned and characterized along with their cognate *Avr* genes. The first viral *R* gene to be cloned and characterized was a tobacco resistance gene (*N*) that encodes a TIRNB-LRR protein that confers resistance to TMV in tobacco (Whitham et al. 1994). The cognate *Avr* gene of TMV was the 50 kDa helicase domain, p50, from the viral replicase complex (Padgett et al. 1997). In the case of TMV resistance, *N* recognizes the p50 helicase domain directly (Ueda et al. 2006). The interaction of the potato *Rx1* and *Rx2* resistance gene (a typical CC-NB-LRR protein) with their cognate *Avr*, i.e., PVX coat protein (*CP*), limits PVX replication independently of the CP-triggered HR cell death (Bendahmane et al. 1995). Few other *R* genes discovered so far in plant viruses are as follows: *Sw5* for TSWV resistance (Brommonschenkel et al. 2000), *tm2* for TMV resistance, *RTM1* for *Tobacco etch virus* (TEV) resistance (Chisholm et al. 2000), *RTM2* for *Plum pox virus* (PPV) resistance (Whitham et al. 2000), *RTM3* for LMV resistance (Decroocq et al. 2009), *HRT* for *Turnip crinkle virus* (TCV) resistance (Cooley et al. 2000), and *RCY1* for resistance against CMV (Takahashi et al. 2001).

Verlaan and colleagues (2013) had lately isolated and characterized an *R* gene (*Ty-1*) that encodes for an RNA-dependent RNA polymerase (RdRp) which is speculated to impart resistance against TYLCV. Three other resistance genes, namely *Tm-1*, *JAX1*, and *Scmv1* have been shown to limit replication of *Tomato mosaic virus* (ToMV), Potexviruses, and *Sugarcane mosaic virus* (SCMV), respectively, at the single-cell level (Ishibashi et al. 2012; Yamaji et al. 2012; Gustafson et al. 2018). Another such *R* gene (*STV11*) has been isolated from rice, which has been reported to protect against the *Rice stripe virus* (RSV) by limiting viral replication (Wang et al. 2014). Some latest examples of such plant *R* genes effective against plant virus along with their *Avr* determinants are enlisted in Table 2.

Table 2 Antiviral *R* genes in plants and their avirulence (*Avr*) determinants

Plant	R gene	Avr	Virus	References
Solanum tuberosum	*Y-1*	Unknown	PVY	Vidal et al. (2002)
S. lycopersicum	*Tm-22*	Movement protein (MP)	ToMV	Lanfermeijer et al. (2005)
Poncirus trifoliata	*Cv* (locus)	Unknown	CTV	Yang et al. (2003)
Phaseolus vulgaris	I locus	Unknown	BCMV, WMV, ZYMV	Vallejos et al. (2006)
P. vulgaris	*PvVTT1*	Nuclear Shuttle Protein (NSP)	BDMV	Zhou et al. (2007), Gururani et al. (2012)
P. vulgaris	*PvCMR1*	*2a* gene	CMV	Seo et al. (2006)
Vigna mungo	*CYR1*	CP	*Mung bean yellow mosaic virus*	Maiti et al. (2012)
Cucumis melo	*Pv1* and *Pv2*	Unknown	PRSV	Anagnostou et al. (2000), Brotman et al. (2013)
Capsicum annuum	*Pvr4*	*Nib* (RNA-dependent RNA polymerase)	PVY, *Pepper mottle virus* (PepMoV)	Kim et al. (2015, 2017)
C. chinense	*Tsw*	RNA silencing suppressor	TSWV	Kim et al. (2017)
N. tabacum	*TPN 1*	Unknown	PVY	Michel et al. (2018)
Arabidopsis spp	*RCY1*	2B	CMV	Ando et al. (2019)
S. lycopersicum	*Sw5a*	AC4	ToLCNV	Sharma et al. (2021)

4.7 Recessive Resistance

Recessive resistance of plants against viruses is based on the finding that viruses require several host factors (also known as susceptibility factors) to infect (Truniger and Aranda 2009). Resistance results from the failure of interaction between such plant factors with the viruses. According to Fraser (1990), susceptibility factors are dominant because of being encoded by dominant susceptibility alleles, and resistance based on the failure of interaction between host factors and a viral component necessitates the presence of all gene copies in the (resistant) recessive form. This is why this type of resistance is referred to as recessive resistance. Many of the recessive virus-resistant genes in plants encode eukaryotic translation initiation factors (eIFs), such as *eIF4E*, *eIF4G*, and similar proteins, and they have been quite well-studied. In addition to its presumed role in viral RNA replication and translation initiation, *eIF4E* is involved in cell-to-cell migration as well (Kang et al. 2005a; Lellis et al. 2002). The number of members of the *eIF4E* family varies by species. For example, the eIF4E family in tomato consists of two eIF4E homologs (*eIF4E1* and *eIF4E2*) and one *eIF* (iso) *4E* homolog (Yoon et al. 2020). The bulk of the recessive resistance genes known for plant viruses has been identified for potyviruses which express translation initiation factors of the 4E or 4G families (*eIF4E/eIF4G*) (Truniger and Aranda 2009). To facilitate translation, the latter proteins must interact with the cap structure on viral transcripts. Viruses that encode their own cap-like structure (such as *VPg* in the case of potyviruses) require interaction with the translation initiation factors *eIF4E/eIF4G* for translation, which causes selection pressure on the host to prevent the interaction between *VPg* and *eIF4E*, resulting in recessive resistance. This interaction is crucial for potyviral infectivity. The *eIF4E1* confers resistance to a variety of potyviruses, including PVY, TEV, and PepMoV (Yoon et al. 2020). Furthermore, mutations in these host factors can prevent them from interacting with the *VPg*, limiting viral replication and infection (de Oliveira et al. 2019). For example, CMV movement is inhibited in Arabidopsis by *cum1* and *cum2* mutations (Yoshii et al. 1998a, b). *CUM1* and *CUM2* encode the eukaryotic translation initiation factors *elf4E* and *eIF4G* (Yoshii et al. 2004). Similar observations have been made in several viruses infecting tobacco, pepper, and pea. The *Pvr1*^{1} (previously known as *pvr2*^{1}) and *sbm1* mutations at a gene expressing *eIF4E* were discovered in pepper and pea (Ruffel et al. 2002; Gao et al. 2004) conferring resistance to PVY and *Pea seed-borne mosaic virus.* Similarly, PVY resistance in tomatoes has also been linked to induced mutations in *eIF4E* (Piron et al. 2010). Besides, knock-out mutation of *eIF4E2* (*Elf4E* homologs) leads to the development of resistance against *Pepper veinal mottle virus* (PVMV) in tomatoes (Moury et al. 2020).

A quicker and more precise way to produce recessive genetic resistance to viral infections is CRISPR/Cas9 (Clustered regularly interspersed palindromic repeats-associated protein 9)-mediated genome editing of host factors. Chandrasekaran et al. (2016), using this approach, found that knocking down the eukaryotic initiation factor, *eIF4E* in cucumber, leads to resistance against several plant viruses, including *Cucumber vein yellowing virus* (CVYV), PRSV-W, and ZYMV. In another study, Pyott et al. (2016) achieved resistance to TuMV by deletion of the gene, *eIF*(iso)*4E*, in *A. thaliana*, using CRISPR/Cas9 approach. Similarly, rice with resistance to *Rice tungro spherical virus* (RTSV) has been established by editing the *elF4G* gene (Macovei et al. 2018), and *Clover yellow vein virus* (CYVV) resistance was established in *A. thaliana* by targeting the *elF4E1* gene (Bastet et al. 2018). Very recently, CRISPR/Cas9-mediated editing in tomato *eIF4E1* successfully created tomato resistance against PepMoV (Yoon et al. 2020). Thus, characterization of host factors in which mutations disrupt viral pathogenesis is a new and emerging avenue for breeding virus resistance.

Research on such so-called recessive *R* genes has primarily concentrated on the Potyviridae family so far. It could be due to their economic relevance, the relative abundance of recessive resistance for potyviruses, and/or the relative simplicity with which these viruses may be experimentally altered (Truniger and Aranda 2009). However, naturally occurring genetic resistance can be difficult to find in some viral families like the Geminiviridae (Kang et al. 2005b).

4.8 RNA Interference

Antiviral RNA silencing {also known as RNA interference (RNAi) and, in the early days, post-transcriptional gene silencing (PTSG)} is one of the first innate immune responses that all plant viruses encounter when infecting a host. In eukaryotes, it's a naturally occurring gene-regulation system (Kuo and Falk 2020). RNAi is a host response triggered by double-stranded RNA (dsRNA), and it entails sequence-specific recognition of mRNAs based on their sequence homology and then suppressing their expression either by ribonuclease-directed destruction or by inhibiting translation (Tabassum et al. 2012). The majority of plant-infecting viruses contain single-stranded RNA as their genetic material and they replicate their genomes in the plant cell cytoplasm through dsRNA intermediates. This dsRNA-triggered RNA silencing is regarded as a pathogen molecular pattern (PAMP)-triggered immunity (PTI) in plants (Ding 2010).

RNA silencing is classified into two major branches: small interfering (si) RNAs, which are generated by long dsRNA and are one of the characteristics of defence through antiviral RNA interference, and (host genome encoded) microRNAs (miRNAs), which play a critical role in gene regulation (Sharma et al. 2013; Lecellier and Voinnet 2004). The antiviral RNAi response acts against all RNA and DNA viruses (Incarbone and Dunoyer 2013). When the plant encounters the virus, the already active RNAi will recognize and eliminate the incoming viral RNA before the virus can multiply and establish itself, although it is a long process that does not result in total viral infection eradication. Plants, fortunately, can be genetically modified to incorporate and express additional genes, allowing plants to be engineered for specialized antiviral RNAi-based resistance.

4.8.1 Small Interfering RNA and MicroRNA-Triggered Gene Silencing/Mechanism of RNAi

The small interfering RNA (siRNA) pathway in plants is triggered by viral dsRNA molecules derived from replicative intermediates or secondary RNA folding structures. These structures are recognized in cell cytoplasm by a Dicer-like (DCL) protein, a host RNase type III-like enzyme, and cleaved into siRNA (Kuo and Falk 2020). Plants, unlike animals, have evolved to use at least four DCLs. In Arabidopsis, four DCLs were reported: DCL 1, 2, 3, and 4 (Gasciolli et al. 2005; Fukudome and Fukuhara 2017). The siRNAs produced are unwound and only one strand, the so-called guide strand, is recruited into a functional protein complex named RNA-induced silencing complex (RISC). RISC is represented by the Argonaute (AGO)/slicer family of proteins. When the RISC containing the guide RNA interacts subsequently with an RNA that has complete homology to the guide RNA (through Watson–Crick base pairing), then the AGO proteins mediate the mRNA cleavage, leading to RNA degradation (Tabassum et al. 2012). In the scenario of incomplete complement, if there are only a few mismatches, translation of target mRNA is blocked by the association of the RISC-guide strand complex and the target mRNA. Another key protein involved in RNAi machinery is RNA-dependent RNA Polymerase (RDR). Its key role is to generate dsRNA from single-stranded RNA which is eventually processed into secondary siRNA by DCL proteins (Csorba et al. 2009). These secondary viral siRNAs enhance antiviral RNA silencing by either targeting viral mRNA in the initially infected cells or alerting neighbouring cells and systemic tissue through plasmodesmata and phloem tissues, respectively. This process is known as transitive silencing, and it is required to establish an RNAi response to combat viruses both locally and systemically (Sijen et al. 2001).

Almost the same mechanism operates in microRNA (miRNA)-triggered gene silencing. miRNAs processed from stem-loop precursors (shRNA and/or hpRNA) are known as primary microRNAs (pri-miRNAs) that are targeted by DCLs in the nucleus, followed by RISC assembly and subsequent degradation of homologous RNA in a sequence-specific manner (Kuo and Falk 2020).

4.8.2 Transgenics Developed by RNAi

Based on the techniques used to activate antiviral silencing, the process underlying can be classified into four categories: (i) sense gene-induced post-transcriptional gene silencing (S-PTGS), (ii) hairpin RNA-induced PTGS (hp-PTGS), (iii) artificial miRNA-induced PTGS (amiRNA), and (iv) trans-acting siRNA generated PTGS (ta-siRNA) (Sanan-Mishra et al. 2021). In a recent report on the case of the *Sri Lankan cassava mosaic virus*, it was demonstrated that antiviral silencing and resistance can be achieved using both sense and antisense approaches (Gogoi et al. 2019). A few examples of transgenically induced RNAi-mediated plant resistance against a few major viral diseases are mentioned below.

Sense and Antisense Induced PTGS

Sense gene-induced PTGS (S-PTGS) was practised in the early 90s and was very successful in the effort of generating viral resistance to viruses like TSWV (Gielen et al. 1991), TEV (Lindbo et al. 1993), and PRSV (Fitch et al. 1992). In S-PTGS, the RDR proteins play a critical role. Transcripts from transgenic loci activate RDR6 to generate complementary RNA strands, which are then processed into siRNA by DCLs from viral dsRNAs, and then degradation of target mRNA through the RISC complex occurs (Singh et al. 2019). This amplifies the antiviral silencing induced by siRNA obtained from viral replication, and silencing can occur either before or after viral infection.

After S-PTGS was tested in the 1990s, antisense RNA expression had also been tested for viral resistance (Khalid et al. 2017). Because the silencing mechanism behind these techniques is similar to that of S-PTGS, it is classified as antisense (AS-PTGS). Even before the discovery of RNA interference (RNAi), the targeted expression of both S-PTGS and AS-PTGS RNA to interfere with a specific target sequence was widely utilized in plants and is still widely utilized till recently, and some of such examples are listed in Table 3.

Table 3 Recent RNAi-based approaches applied for resistance against plant viruses

Crop	Virus(es)	Virus group	Target gene/genomic region	Mechanism	References
N. benthamiana	*Cotton leaf curl Khokhran virus* (CLCuKoV) and *Cotton leaf curl Multan virus*	Geminivirus	*Repsyn130* (*Truncated Rep protein*)	S-PTGS	Yousaf et al. (2013)
N. benthamiana	TSWV	Tospovirus	*CP*	S-PTGS	Jan et al. (2000)
N. benthamiana	TEV	Potyvirus	*CP*	S-PTGS	Voloudakis et al. (2005)
N. benthamiana	PPV	Potyvirus	*Cylindrical Inclusion* (*CI*), *NIa-NIb-CP*, *Hc-Pro*	S-PTGS	Wittner et al. (1998), Guo et al. (1998), Barajas et al. (2004)
N. benthamiana	CTV	Closterovirus	*CP*	hp-PTGS	Roy et al. (2006)
N. benthamiana	*Groundnut ringspot virus*, TSWV, *Tomato chlorotic spot virus*	Tospovirus	*Nucleoprotein* (*N*)	hp-PTGS	Bucher et al. (2006)
N. benthamiana	*Prune dwarf virus, Prunus necrotic ringspot virus* (PNRSV), *Tobacco streak virus* (TSV)	Ilavirus	*CP*	hp-PTGS	Liu et al. (2007)
N. benthamiana	*Peach mosaic virus*	Trichovirus	*CP*	hp-PTGS	Liu et al. (2007)
N. benthamiana	PPV	Potyvirus	*CP*, *P1*, *P3*, *P4*, *Hc-Pro*	hp-PTGS	Liu et al. (2007), Di Nicola-Negri et al. (2005)
N. benthamiana	PVY	Potyvirus	*Nib*, *CP*	hp-PTGS	Xu et al. (2009), Jiang et al. (2011)
N. benthamiana	*Tomato ringspot virus*	Nepovirus	*CP*	hp-PTGS	Liu et al. (2007)
N. benthamiana	*CBSV* and *Cassava brown streak Uganda virus*	ipomovirus	*CP*	hp-PTGS	Patil et al. (2011)
N. benthamiana	CMV	Cucumovirus	*CP* and *2b*	hp-PTGS	Chen et al. (2004), Qu et al. (2007)
N. benthamiana	TSV	Ilarvirus	*CP*	hp-PTGS	Pradeep et al. (2012)
N. benthamiana	CLCBV	Geminivirus	*Pre CP*(*V2*)	amiRNA	Ali et al. (2013)
N. benthamiana	PVY	Potyvirus	*CI*, *NIa*, *Nib*, and *CP*	amiRNA	Song et al. (2014)
N. benthamiana	WSMoV	Tospovirus	*Rep*	amiRNA	Kung et al. (2012)
N. benthamiana	*Cotton leaf curl kokhran virus-Burewala*	Geminivirus (Begomovirus)	*CP*	hp-PTGS	Yasmeen et al. (2016)
N. benthamiana	CLCuKoV and CLCuMB	Geminivirus (Begomovirus)	*βC1*	hp-PTGS	Akhtar et al. (2021)
N. benthamiana	Potato spindle tuber viroid	Pospiviroid	*TAS1c*	TAS	Carbonell and Daròs (2017)
N. benthamiana	TSWV and TuMV	Tospovirus and Potyvirus	*TAS1c*	TAS	Carbonell et al. (2019)

(continued)

Table 3 (continued)

Crop	Virus(es)	Virus group	Target gene/genomic region	Mechanism	References
N. benthamiana	PPV	Potyvirus	*TAS1c*	TAS	Zhao et al. (2015)
N. tabacum	ToLCNV	Geminivirus	–	TAS	Singh et al. (2015)
N. tabacum	CMV	Cucumovirus	*1a*, *Rep*	S-PTGS	Anderson et al. (1992), Canto and Palukaitis (2001)
N. tabacum	CMV	Cucumovirus	*CP*	hp-PTGS	Kalantidis et al. (2002)
N. tabacum	ToLCNV	Geminivirus	*AV1* and *AV2*	amiRNA	Vu et al. (2013)
N. tabacum	*Mungbean yellow mosaic virus-Vigna*	Geminivirus	*CP*, *Rep*, *MP*, *NSP*	S-PTGS	Shivaprasad et al. (2006)
N. tabacum	PVY	Potyvirus	*HC-Pro*	amiRNA	Simon-Mateo and Garcia (2006)
N. tabacum	PVY	Potyvirus	*CP*	S-PTGS	Masmoudi et al. (2002)
N. tabacum	TSWV, TCSV	Tospovirus	*N*	S-PTGS	Gielen et al. (1991), Prins et al. (1995)
N. tabacum	PVY	Potyvirus	*CP*	hp-PTGS	Jiang et al. (2011)
N. tabacum	CMV	Cucumovirus	*2b*	amiRNA	Qu et al. (2007)
A. *thaliana*	CMV, TuMV	Cucumovirus, Potyvirus	*TAS3*	TAS/amiRNA	Chen et al. (2016)
A. thaliana	TuMV	Potyvirus	*CP*	amiRNA	Lafforgue et al. (2013)
A. thaliana	CMV	Cucumovirus	30 UTR (RNA3)	amiRNA	Duan et al. (2008)
A. thaliana	TuMV, *Turnip yellow mosaic virus* (TYMV), TSWV	Potyvirus, Tymovirus, Tospovirus	*HC-Pro*, *P69*, *N*	amiRNA	Niu et al. (2006)
L. esculentum	*Tomato leaf curl Gujarat virus*	Geminivirus	–	TAS	Singh et al. (2015)
L. esculentum	TSWV	Tospovirus	*N*	S-PTGS	Nervo et al. (2003)
L. esculentum	PepMV	Flexiviridae	–	S-PTGS	Leibman et al. (2021)
L. esculentum	TYLCV	Geminivirus	*Rep*	hp-PTGS	Fuentes et al. (2006)
L. esculentum	CMV	Cucumovirus	*2a*, *2b*, 3’ UTR	amiRNA	Zhang et al. (2011a)
L. esculentum	ToLCNV	Geminivirus	*AV1* and *AV2*	amiRNA	Vu et al. (2013)
Oryza sativa	*Rice tungro bacilliform virus* (RTBV) and RTSV	Tungrovirus and Waikavirus	*ORF IV*	S-PTGS	Anand et al. (2021)
O. sativa	*Rice black-streaked dwarf virus* (RBSDV)	Fijivirus	*S1*, *S2*, *S6*, and *S10*	hp-PTGS	Wang et al. (2016a)
O. sativa	RBSDV, *Rice dwarf virus*, *Rice gall dwarf virus*, *Rice grassy stunt virus*, RSV	Fijivirus, Phytoreovirus, Reovirus, Tenuivirus	*P9-1*, *Pns6*, *P8*, *Pns12*, *Pns9*, *pC5*, *pC3*	hp-PTGS	Sasaya et al. (2014)
O. sativa	RTBV and RTSV	Tungrovirus and Waikavirus	*ORF IV*	hp-PTGS	Tyagi et al. (2008), Roy et al. (2012), Valarmathi et al. (2016)

(continued)

Table 3 (continued)

Crop	Virus(es)	Virus group	Target gene/genomic region	Mechanism	References
O. sativa	RBSDV and RSV	Fijivirus and Tenuivirus	*CP*	amiRNA	Sun et al. (2016)
Triticum aestivum	WSMV	Tritimovirus	*CP* and *Nib*	S-PTGS	Sivamani et al. (2000)
T. aestivum	WSMV	Tritimovirus	*Nia* and 5'UTR-*P1-Hc-Pro-P3*	hp-PTGS and amiRNA	Fahim et al. (2010, 2012)
T. aestivum	WSMV	Tritimovirus	*CP*	hp-PTGS	Cruz et al. (2014)
Solanum tuberosum	PVX	Potexvirus	*ORF2*	hp-PTGS	Arif et al. (2012)
S. tuberosum	PVX	Potexvirus	*CP*	S-PTGS	Doreste et al. (2002)
S. tuberosum	PVY	Potyvirus	*CP* and *Hc-Pro*	S-PTGS and hp-PTGS	Arif et al. (2012)
S. tuberosum	PVY	Potyvirus	*CP*	hp-PTGS	Missiou et al. (2004)
Glycine max	AMV	Alfamovirus	*Rep*	hp-PTGS	Zhang et al. (2011b)
G. max	*Bean pod mottle virus*	Comovirus	*Rep*	hp-PTGS	
G. max	*Soybean mosaic virus* (SMV)	Potyvirus	*Rep*	hp-PTGS	
G. max	SMV	Potyvirus	*Hc-Pro*	hp-PTGS	Gao et al. (2015)
Citrullus lanatus	WSMoV, CMV, CGMMV, WMV	Tospovirus, Cucumovirus, Tobamovirus, Potyvirus	*N*, *CP*	S-PTGS	Lin et al. (2012)
Cucumis melo	ZYMV	Potyvirus	*CP*	S-PTGS	Wu et al. (2010)
Zea mays	*Maize dwarf mosaic virus*	Potyvirus	*P1* and *CP*	hp-PTGS	Zhang et al. (2013)
Z. mays	RBSDV	Fijivirus	*P6*	amiRNA	Xuan et al. (2015)
Carica papaya	PRSV	Potyvirus	*CP* and *HC-Pro*	S-PTGS	Fitch et al. (1992), Tennant et al. (2005), Kung et al. (2009), Kung et al. (2015)
Musa paradisiaca	BBTV	Babuvirus	*Rep*	hp-PTGS	Elayabalan et al. (2013), Shekhawat et al. (2012)
Vitis vinifera	GFLV	Nepovirus	*CP*	amiRNA	Jelly et al. (2012)
Arabidopsis	TuMV	Potyvirus	*CP*	amiRNA	Lafforgue et al. (2013)
Arabidopsis	CMV		30 UTR (RNA3)	amiRNA	Duan et al. (2008)
A. thaliana	TuMV, TYMV, TSWV	Potyvirus, Tymovirus, Tospovirus	*HC-Pro*, *P69*, *N*	amiRNA	Niu et al. (2006)

Hairpin RNA-Induced PTGS

In hairpin RNA-induced PTGS (hp-PTGS) technology, silencing vectors are designed using fragments of both the sense and antisense viral DNA/cDNA linked by a non-complementary spacer sequence. When these constructs are heterologously expressed in transgenic plants, they produce transcripts that fold itself into dsRNA due to the self-complementary nature of sense and antisense viral sequences with a single-stranded loop, resulting in hpRNA. The dsRNA is converted into siRNAs, which provide resistance to the associated viruses through the RNAi machinery. Waterhouse et al. (1998) first demonstrated antiviral resistance against PVY in tobacco using this technique. Currently, this technology is used in many crops to combat various viruses (RNA and DNA); in most cases, the level of resistance obtained against target viruses in transgenic plants was reported to be highly efficient (Smith et al. 2000).

Artificial MicroRNA

Another potential tool in functional genomics for RNAi is artificially created miRNAs (amiRNAs). AmiRNAs, like microRNAs, are single-stranded, around 21 nt long, and are created by substituting mature miRNA sequences of duplex within the natural pre-miRNAs. These miRNAs have favourable RISC loading characteristics, allowing the creation of an artificial miRNA gene (Tiwari et al. 2014). This amiRNA, upon plant transformation, can effectively target viral genes with high specificity and prevent viral accumulation and have been adapted to produce virus-resistant plants (Duan et al. 2008). First transgenic plants developed through amiRNA-mediated resistance to TYMV andTuMV was reported in Arabidopsis (Niu et al. 2006). In the same year, Simon-Mateo and Garcia (2006) also reported transgenic tobacco resistant to PPV through transgenically expressed amiRNAs. To date, various transgenic plants were developed and found to be highly resistant to viruses like *Watermelon silver mottle virus*, ToLCNV, *Cotton leaf curl Burewala virus* (CLCBV), and *Wheat streak mosaic virus* (WSMV) (Singh et al. 2019) (Table 3).

Trans-Acting SiRNA

Trans-acting siRNAs (ta-siRNA) are secondary siRNAs that are encoded from TAS genes. TAS transcripts are targeted by miRNAs and processed into dsRNA by RDR6 protein and cleaved into multiple 21 nt ta-siRNAs in a stepwise pattern by DCL (Wu et al. 2012). These generated 21 nt ta-siRNA targets its cognate viruses. A single miRNA target is enough to produce multiple ta-siRNAs, which may then be integrated into a vector to trigger the synthesis of siRNAs and, eventually, gene silencing. Chen et al. (2016) engineered Arabidopsis TAS (*TAS3a*) genes to express artificial ta-siRNAs and established TAS-mediated virus resistance against TuMV and CMV. Various viral resistant plants are developed by exploiting this technology (reviewed by Carbonell 2019).

Multiple Virus Resistance Through RNAi

For the first time, RNAi-based transgenic resistance against multiple viruses at the same time was successfully applied to the commercially cultivated Destiny III yellow crookneck squash, which was designed to exhibit simultaneous RNAi resistance against two potyviruses (ZYMV, WMV) and one cucumovirus (CMV) (Fuchs et al. 1998). A similar strategy was also utilized to give resistance to Cassava black streak disease (CBSD) which is caused by two distinct but related viruses: CBSV and *Ugandan cassava brown streak virus* (Tomlinson et al. 2018). Recently, Kenya Agricultural Research and Livestock Organization have arrived in a stage of open cultivation and marketing of this transgenic CBSD-resistant cassava (https://cassavaplus.org/news/kalro-seeks-approval-to-introduce-disease-resistant-gm-cassava-2/). Gonsalves (2006) reported the adoption of genetically engineered PRSV-resistant papaya, which was produced in Hawaii when there were no other options for managing PRSV.

4.9 MicroRNAs in Plant Virus Resistance

Multiple studies support that plant miRNAs play a critical role in regulating the expression of a family of endogenous plant resistance genes such as NBS-LRR resistance (*R*) genes and affecting RNA silencing factors and hormone signaling (Naqvi et al. 2010; Zhai et al. 2011; Shivaprasad et al. 2012; Li et al. 2012; Zhang et al. 2016a). Antiviral silencing components, such as *AGO* or *RDR/ RdRp* genes, which are involved in the biogenesis and synthesis of siRNA, are natural targets of different plant miRNAs. *MiR444* has been reported to enhance resistance against *rice stripe virus* (RSV) by upregulating the RDR1-mediated RNA silencing pathway, mir444 has been found to interact with RdRp1-inhibiting proteins (Wang et al. 2016b). On the other hand, rice *AGO18* boosts antiviral RNAi against RSV by sequestering *miR168 and miR528*, which suppresses the major antiviral effector *AGO1* expression leading to the inhibition of the formation of RISC. These processes cause the miR528 target *L-ascorbate oxidase* gene to accumulate, which is involved in catalyzing L-Ascorbic acid oxidation and thereby activating ROS-mediated resistance to RSV infection. This results in improved antiviral defence (Wu et al. 2017). Brassica miR1885 was the first plant miRNA to be identified to target an *R* gene (He et al. 2008). Since then, a variety of miRNAs have been demonstrated or predicted to target *R* genes involved in viral resistance. Two tobacco *miRNA*s, *nta-miR6019* and *nta-miR6020*, encoding the resistance TIR-NB-LRR protein have been shown to provide resistance against TMV in transgenic tobacco. Over-expression of these miRNAs reduced TIR-NB-LRR transcript level and weakened *N*-mediated TMV resistance by cleaving the mRNA of the tobacco *N* gene, indicating that *miR6019* and *miR6020* play key roles in viral resistance (Li et al. 2012; Deng et al. 2018). Recently, transgenic over-expression of mutant miR393 in rice was found to give increased vulnerability to RBSDV by inhibiting the auxin receptor TIR1 (Zhang et al. 2019a).

MiRNAs have also been manipulated for virus resistance breeding; an innovative technique is miRNA mimic technology (miR-mimic). MiRNA mimic is dsRNA molecules that have been chemically synthesized to resemble normal miRNA duplexes (Meng et al. 2012). Virus-based microRNA silencing (VbMS) was developed which is an efficient virus-based method for directing the development of miRNA target mimic (TM) molecules that bind to target mRNA molecules and inhibit their production through degradation or translational repression. Using this technology, vectors CMV-based vector system was developed to study miRNA functions in maize (Liu et al. 2019). Zhao and colleagues (2020) developed silenced endogenous miRNAs in *N. benthamiana* and tomato plants using TRV and PVX-based VbMS methods. Thus, VbMS is an effective, robust, and high-throughput approach for screening and examining the role of miRNAs in plants.

4.9.1 CRISPR-Cas System

The concept of genome engineering has recently emerged as a promising tool to confer desirable traits in plants (Zaidi et al. 2016). Among these genome engineering technologies, the CRISPR-Cas system shave recently evolved as one of the most sought-after methods of gene editing because of its specificity, efficiency, and reproducibility (Yin and Qiu 2019). The CRISPR-Cas system depends on the idea of bacterial immunity (adaptive immunity) that acts against invading viruses. Recent advances in CRISPR genome-editing technology expand new opportunities to engineer resistance against plant viral diseases (Borrelli et al. 2018). Plants can achieve viral resistance against various pathogens using CRISPR-Cas systems either through manipulation of plant genome (plant-mediated resistance) or virus genome (virus-mediated resistance) (Fig. 2) (Varanda et al. 2021).

4.9.2 Virus Resistance via CRISPR

Engineered plant viral resistance via CRISPR was first applied against a few geminiviruses by targeting the virus's genome directly inside the plant cell (Baltes et al. 2015; Ji et al. 2015). Zaidi and co-workers (2020) had reviewed the capability of CRISPR to confer resistance in plants by targeting the genomes of both DNA and RNA viruses that was demonstrated by inhibition or impaired accumulation of viruses. Ali et al. (2015) delivered single-stranded guided RNA (sgRNA) molecules via TRV vector into *N. benthamiana* to target coding and non-coding sequences of TYLCV genome and found lesser viral DNA accumulation and reduced symptoms. Resistance could also be obtained against *Beet curly top virus* (BCTV) and *Merremia mosaic virus* (MeMV) following the same approach (Ali et al. 2015). Baltes et al. (2015) and Ji et al. (2015) also could successfully target *Bean yellow dwarf virus* (BeYDV) and *Beet severe curly top virus* (BSCTV) in *N. benthamiana* plants. In another study, Ali et al. (2015) suggested that the CRISPR-Cas9 system with a sgRNA targeting a conserved region can target multiple begomoviruses concurrently. They could successfully confer such concurrent inhibition of CLCuKoV, TYLCV, TYLCSV, MeMV, BCTV-Worland, and BCTV-Logan in *N. benthamiana* plants. Tripathi et al. (2019) utilized a similar concept of the CRISPR-Cas9 mechanism to achieve resistance against banana streak disease by targeting endogenous Banana streak virus (eBSV). In a recent study, a significant reduction in viral DNA accumulation was observed in the case of *Chilli leaf curl virus* which was targeted with CRISPR-Cas9 with multiple sgRNA target sites (Roy et al. 2019).

As the classical SpCas9 from *Streptococcus pyogenes* can only recognize dsDNA, protection against RNA viruses was more challenging to accomplish using the CRISPR-Cas9 system. Nevertheless, further investigation and characterization of related nucleases led to the discovery of enzymes that provided immunity against RNA viruses (Borrelli et al. 2018). Zhang et al. (2018) first reported resistance engineered against RNA viruses, CMV and TMV, in transgenic *N. benthamiana* and *A. thaliana by* expressing FnCas9 (*Francisella novicida*) and a specific RNA-targeting sgRNA, CMV and TMV accumulation was reduced 40–80% in the transgenic plants upon infection (Zhang et al. 2018). One year later, Zhang et al. (2019c) achieved resistance against *Southern rice black-streaked dwarf virus*, an RNA virus targeting rice via CRISPR-Cas13a system. Aman et al. (2018) also exploited a similar approach using the Cas13a system to target the TuMV RNA genome in both *N. benthamiana* and *A. thaliana* plants. Broad-spectrum resistance was obtained against multiple strains of PVY by targeting conserved PVY coding regions in transgenic potato expressing CAS13a/sgRNA constructs (Zhan et al. 2019). Despite the promises of this system, the potential evolution of CRISPR-resistant viruses has been one of the significant concerns with this strategy; however, perhaps this could be, to some extent, addressed by the application of multiplex editing strategies (Zaidi et al. 2020).

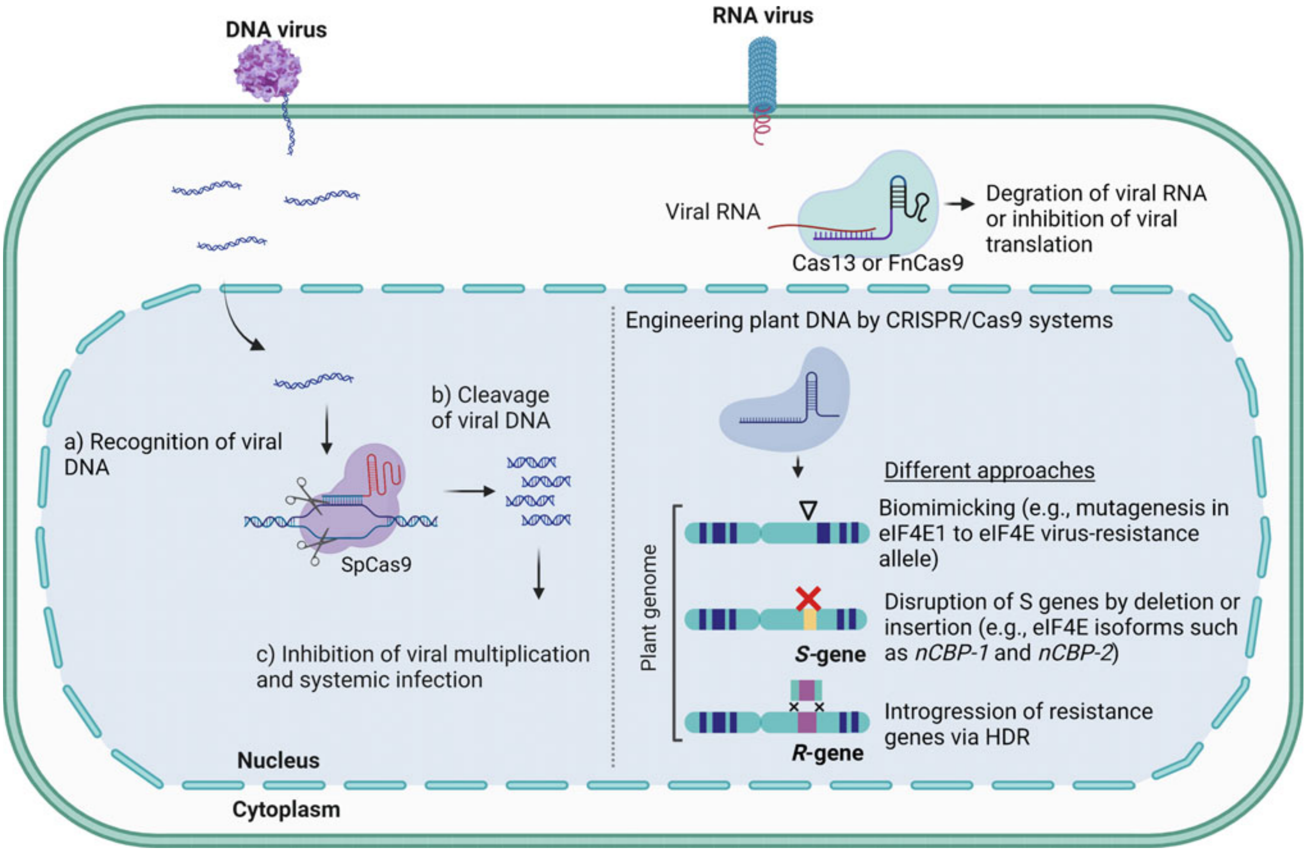

Fig. 2 Illustration of CRISPR-Cas systems conferring resistance to plant viruses. This system can specifically target viral DNA (Cas9 system) or RNA (Cas13/FnCas9 system) genomes for their degradation or translational inhibition. Apart from targeting the viral genome, CRISPR technologies can be utilized by manipulating the plant genome via different approaches, including (i) biomimicking through introducing specific mutations in the plant genome, (ii) disrupting known plant susceptibility genes to avoid viral recognition, and (iii) integration of disease resistance genes by Cas9 via homology-directed repair

4.9.3 CRISPR-Mediated Resistance via Plant Factors

CRISPR-mediated resistance via host factors manipulates susceptibility factors required for a viral infection to enhance plant immunity and restrict viral multiplication. Several studies had reported such resistance against DNA and RNA viruses using CRISPR/Cas9. Translation initiation-like factors, *elF4E*, *elF4G,* and their isoforms, are known to require in the infection process of viruses (Sanfaçon 2015). Chandrasekaran et al. (2016) developed virus-resistant plants by targeting *eIF4E via* the CRISPR-Cas9 system, and resistance was obtained against Potyviruses (ZYMV and PRSV) and Ipomovirus (CVYV) in cucumber. In another study, resistance was achieved against CYVV by targeting the *elF4E1* gene using CRISPR-Cas9 in *A. thaliana* (Bastet et al. 2018). Pyott et al. (2016) utilized a similar approach in Arabidopsis by editing *eIF*(iso)*4E* to obtain resistance against Potyvirus. Double mutations on *nCBP-1* and *nCBP-2*, belonging to the *elF4E* family in cassava, were performed using the CRISPR-Cas9 system, and resistance could be achieved against CBSV (Gomez et al. 2019). As this CRISPR-mediated resistance targeting the host susceptibility genes can be carried out following transgene-free protocols, it has been emerging as a better approach to achieve viral immunity (Zaidi et al. 2020). Various CRISPR-Cas systems targeting the host susceptibility genes have been developed to achieve virus resistance in several crop plants (reviewed by Varanda et al. 2021).

4.10 Other Strategies

4.10.1 Quarantine Measures

Plant quarantine measures limit the dispersal of pathogens (including viruses) and plant products. Regulations for plant quarantine are promoted nationally and internationally to prevent the spread of detrimental pests and pathogens (Chand et al. 2017). Chand et al. (2017) highlighted that the vigilance of pathogens should be a fundamental factor of plant quarantine control. These measure of quarantine control in plants mainly involves evaluating the risk factor (pathogens), preference of clean-planting material, viral examination, micropropagation, and genetic fidelity analysis, and concerning these factors, plants produced according to the directive of the schemes are given corresponding certificates (Kumar et al. 2020). Lee (2020) reported exclusion of plant viruses like citrus canker, CTV, PPV, etc., from California, USA, via various quarantine measures.

4.10.2 Pest Control Monitoring

Transmission of plant viruses occurs via vectors like insects, nematodes, etc. for plant-to-plant spread, and therefore, plant viral diseases can be efficiently administered by restricting the population of their vectors with a suitable pest control measure (Kumar et al. 2020). Bragard et al. (2013) mentioned the utilization of non-host trap plants to draw the attention of vectors to reduce the disease transmission on the crop of interest. The use of insecticides against insect vectors is being used directly as early as the 1930s (Kumar et al. 2020). Other than insecticides, oil sprays, pesticides, viricides, botanicals, etc. are efficient prevention for several viral diseases in plants; however, frequent use of such might be harmful in the long run (Kunkalikar et al. 2006). In recent times, remote sensing technologies, such as visible and near-infrared spectral sensors, fluorescence and thermal sensors, and synthetic aperture radar and light detection and ranging systems, have been applied to monitor plant pathogens and diseases, including viral diseases (Zhang et al. 2019b).

4.10.3 Chemotherapy

Chemotherapy is a preventive measure to control plant viral diseases by delaying the virus multiplication (Matthews 1953). This strategy is based on antiviral drugs used to restrict or interfere with specific steps of the virus life cycle. They include nucleoside analogues inhibiting replication and protease inhibitors preventing protein processing (Rubio et al. 2020). Antiviral drugs like inosine monophosphate dehydrogenase (IMPDH) inhibitors, S-adenosyl homocysteine hydrolase inhibitors, and neuraminidase (NA) inhibitors and chemical compounds such as ribavirin (Virazole), azidothymidine, and 2-thiouracil are primarily used in chemotherapy (Chauhan et al. 2019). The agents of chemotherapy applied in plants have different modes of action; however, they have not been studied in much detail (Panattoni et al. 2013). Therefore, there are not many successful examples of utilization of this approach against plant viruses. Nevertheless, chemotherapy has been a successful and the most frequently used technique in potatoes to eradicate viruses (Panattoni et al. 2013). In a very recent study, Chauhan et al. (2019) reported the application of selective chemotherapy agents like IMPDH, NA inhibitors, or purine biosynthesis inhibitors to be effective against *Grapevine leafroll-associated virus*-1 and -3.

4.10.4 Cryotherapy

Cryotherapy is an approach that utilizes long-term conservation of genetic resources under ultra-low temperature, generally at −196 °C (Engelmann 2004). In this technique, pathogens like viruses can be eradicated when exposed to the lethal effects of low temperatures, producing virus-free plants with greater frequency (Brison et al. 1997). Through shoot tip cryopreservation, successful eradication of BSV in bananas was reported by Helliot et al. (2002). Vieira et al. (2015) mentioned that cryotherapy of shoot tips is an efficient technique to eliminate virus complex from garlic too. Although the method has merits like management of large numbers of plantlets and independence of shoot tip size, extensive consumption of certain gases like Argon and Nitrogen, uninterrupted supply of power, etc. are some of the factors limiting its wide-scale application (Chauhan et al. 2019).

4.10.5 Meristem-Tip Culture

Meristem-tip culture is another widely utilized technique for eliminating viruses (Nehra and Kartha 1994). Lassois et al. (2012) suggested this technique to be the most efficient procedure to eliminate viruses associated with phloem under aseptic conditions and in a suitable nutrient medium. Meristem-tip culture has been shown to be suitable for abolishing plant viruses like *Peanut stripe virus*, SCYLV, and *Piper yellow mottle virus* (Chauhan et al. 2019). Nevertheless, contamination, variability, and high price are some disadvantages of this technique (Chauhan et al. 2019).

4.10.6 Thermotherapy

Plant thermotherapy produces virus-free plants by cleavage of the viral RNA, disrupting the virus particle, inhibiting viral movement, or inactivation of viral replicase (Conci and Nome 1991; Hull 2002; Rubio et al. 2020). Plant thermotherapy can kill the pathogen with limited effect on the host (Chauhan et al. 2019). In this method, the heat can be applied via air, water, or vapour (Grondeau et al. 1994). The temperature required for this method is 52–55 °C for 10–30 min, and it was found that raised temperature fundamentally led to the decrease in viral diseases by disrupting the viral ssRNA and dsRNA synthesis (Chauhan et al. 2019). At first, this technique was implemented in vivo or in vitro in plants but in course of time, it was integrated with the meristem culture method (Lassois et al. 2012). It was observed by Modaressi et al. (2016) that thermotherapy works more efficiently when applied with other methods like chemotherapy, for example, to eradicate *Arabis mosaic virus*, PNRSV from in vitro raised infected plants. In a similar experiment merging thermotherapy and cryotherapy treatments, *Raspberry dwarf virus* could be successfully eliminated from the meristem tips of raspberry plants (Wang et al. 2008). According to Panattoni et al. (2013), plant thermotherapy was the most commonly applied technique in sanitation protocols during 1991–2010.

5 Conclusion

Due to their small genome size, inanimate nature, multi-host life cycle, and relatively frequent occurrence of mutations, recombination, and pseudo-recombination among or within their genomes, the emergence and re-emergence of viruses are becoming a serious threat to human health and well-being. Lately, the global pandemic of COVID-19, caused by a coronavirus, had, at one point in time, brought the entire civilization to a near standstill. Its impact is far from over yet after two years of its emergence. A similar situation is quite common in the case of plant viruses. The emergence and re-emergence of plant viral diseases such as cotton leaf curl disease, tomato yellow leaf curl disease, and cassava mosaic disease had caused havoc to several nations across Asia, Europe, and Africa in the last few decades. However, despite this situation, certain policymakers still do not see plant viruses as important pathogens, and therefore, research on plant viruses is yet to gain the required momentum. Nevertheless, plant scientists, across the world, are putting efforts into harnessing the potential of advanced tools in the management of plant viruses, and commendable success has been achieved too. It is expected that more emphasis will soon be put on this area.

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Crop Plants Under Metal Stress and Its Remediation

Banashree Sarma, Lina Gogoi, Nirmali Gogoi, and Rupam Kataki

Abstract

Soil contamination with heavy metals is a huge concern now. Agricultural soils in the world are slight to moderately affected by heavy metal toxicity. Heavy metals such as cadmium, arsenic, chromium, lead, mercury, and iron are highly toxic and increased accumulation can lead to degradation of the ecosystem. A higher concentration of heavy metals in agricultural soils has tremendous detrimental effects on plant growth and food safety. The primary hazard in plants exposed to these metals lies in oxidative damage due to their ability to produce reactive oxygen species which consequently cause lipid peroxidation, enzyme inactivation, damage to cellular organelles, and DNA. Unfortunately, metals such as mercury, cadmium, lead, iron, etc. are essential for plant growth, but excess of them triggers oxidative damage in the plant. The prime objective of this chapter is to discuss the effects of heavy metals on plant growth, development and yield and to summarize the economical and eco-friendly remediation measures that increase the tolerance of plants to heavy metals.

Keywords

Bioremediation • Heavy metals • Organic amendments • Reactive oxygen species

Abbreviations

APX	Ascorbate peroxidase
CAT	Catalase
CEC	Cation exchange capacity
DAP	Di-ammonium phosphate
DOC	Dissolved organic carbon
DTPA	Diethylenetriamine pentaacetic acid
GR	Glutathione reductase
H_2O_2	Hydrogen peroxide
O_2^-	Superoxide radical
OH^-	Hydroxyl radical
OM	Organic matter
ROS	Reactive oxygen species (ROS)
SOD	Superoxide dismutase (SOD)

1 Introduction

Among the abiotic stresses, heavy metal toxicity has become a major concern due to enhanced environmental pollution. The term “Heavy metal” refers to the group of metal or metalloids with atomic densities five times and greater than water or greater than 4 g cm^{-3} (Gill 2014). However, these metals have become indispensable for life in the course of evolution because of their redox activity under physiological conditions or Lewis acid strength (Palmer and Guerinot 2009). These properties also have been the reason for their toxicity if present in excess, the primary threat being the production of reactive oxygen species (ROS). Heavy metals include lead (Pb), chromium (Cr), arsenic (As), iron (Fe), cadmium (Cd), mercury (Hg), cobalt (Co), copper (Cu), manganese (Mn), silver (Ag), zinc (Zn), and the platinum group elements. Heavy metals give significant toxic effects on ecology, nutrition, and environmental evolutionary processes. Among the heavy metals, As, Cd, Cr, Pb, and Hg are ranked as prior elements due to their high degree of toxicity even at low concentrations. Concentration ranges of some heavy metals in plants are presented in Table 1. Due to their non-decomposable or non-degradable property, heavy metals have a deleterious biological impact (Jaleel et al. 2009). They are bio-accumulative and sometimes biomagnified, and accumulate in the food chain from the producer level and

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B. Sarma · N. Gogoi (✉)
Department of Environmental Science, Tezpur University, Assam, 784028, India

L. Gogoi · R. Kataki
Department of Energy, Tezpur University, Assam, 784028, India

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Table 1 Concentration ranges of some heavy metals in plants (Nagajyoti et al. 2010)

Heavy metal	Range in land plants (μg g^{-1} dry wt.)
Cd	0.1–2.4
As	0.02–7
Cr	0.2–1
Pb	1–13
Hg	0.005–0.02
Fe	140
Co	0.05–0.5
Zn	8–100
Mn	15–100
Mo	1–10

then through uptake at the consumer level (Nagajyoti et al. 2010). Agricultural practices such as long-term use of phosphate fertilizers, pesticides, sewage sludge application, dust from smelters, industrial waste, irrigation with contaminated water, etc. act as the major contributor to heavy metals (Yadav 2010). Plants absorb these metals easily either by roots or sometimes plant leaves act as the entry point of heavy metals when they are deposited from the atmosphere on the leaf surfaces as particulate matter (Nagajyoti et al. 2010). Heavy metals also trigger variation in the cell cycle, apoptosis, or carcinogenesis by disrupting the cellular organelles and components like lysosomes, mitochondria, carbohydrates, proteins, DNA, nuclei, etc. (Beyersmann and Hartwig 2008). Heavy metal toxicity causes disturbances to building blocks of protein structure and commonly forms bonds with the sulfhydryl groups resulting in restricting the activities of vital enzymes, respiration, and photosynthesis (Hall 2002), disrupting the electron transport chain (Qadir et al. 2004) or disturbing the metabolism of essential elements (Yadav 2010). Physiologically, ROS generation, such as hydroxyl free radicles (OH^-), superoxide free radicals (O_2^-), or non-free radicles like hydrogen peroxide (H_2O_2), causes oxidative stress by disturbing the cellular equilibrium (Sytar et al. 2013). However, different physical, chemical, and biological processes at soil media control the fate of the heavy metals in soil. Moreover, the antioxidative system, constituting both enzymes (superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), etc.) and non-antioxidants (glutathione, ascorbate, carotenoids, phenolics, etc.) detoxifies the ROS (Syed et al. 2018). These necessitate the understanding on elevated activities/concentration of the antioxidants support given to the plants to combat oxidative stress induced by heavy metals (Syed et al. 2018).

2 Effects on Crop Growth and Development

2.1 Cadmium

Cadmium (Cd) is usually present in uncontaminated soils at a concentration below 0.5 mg kg^{-1} but depending on parent material, its concentration can reach up to 3.0 $^{mg\ kg-1}$ (Nazar et al. 2012). Human activities have contributed about 13,000 out of the total 30,000 tons of annual addition of Cd to the environment (Gallego et al. 2012) while weathering of rocks, volcanoes, and forest fires naturally release about 25,000 tons of Cd per year into the environment (Shahid et al. 2019). Anthropogenic activities such as industrial processes, application of phosphate fertilizers in agricultural fields, irrigation water, etc. (Du et al. 2013; Kosolsaksakul et al. 2014) along with atmospheric deposition are the major inputs of Cd in agricultural soils.

From soil, plants take up Cd easily, which are transported to the seeds and fruits and consequently enter into the food chain (Rabelo et al. 2017). However, Cd availability is governed by soil characteristics such as soil cation exchange capacity, soil pH, organic matter (OM), soil salinity, and soil texture (Lin et al. 2015). Cadmium, in the form Cd^{2+}, is highly phytotoxic and its detrimental effects on the physiological processes result in growth inhibition. Yang et al. (2010) reported the differential responses of Cd accumulation capacities of 28 species of vegetables of 5 common vegetable species, namely, cowpea (*Vigna sesquipedalis* Koern.), kidney pea (*Phaseolus vulgaris* L.), bitter gourd (*Momordica charantia* L.), cucumber (*Cucumis sativus* L.), and squash (*Cucurbita pepo* L.) and concluded that plant response to Cd stress was a function of genotypic variation. Leaf chlorosis and rolling of the leaves are the primary visible symptoms of Cd stress in the aerial plant parts (Liu et al. 2013). Zhang et al. (2021) reported decreased ratio of green leaves, accelerated leaf senescence, and decreased both upper and lower plant biomass in Cd-treated plants compared to control. Cadmium inhibits the activity of root Fe(III) reductase and affects transporter responsible for Fe (II) uptake resulting in a deficiency of Fe^{2+}, which seriously affects photosynthesis (Chang et al. 2003). In contrast, research also suggested that Cd at a low concentration promoted root growth and is beneficial for nutrient and water absorption. This is due to the stimulation in the exchange in the root cell wall to reject Cd^{2+} and thus is an important means for plants to adapt to adversity (Liu et al. 2013; Zhang et al. 2021). The uptake, transportation, and use of elements such as K, Mg, P, and Ca and water by plants are affected by Cd. Cd inhibits nitrate reductase activity, and thus impedes uptake and transport of nitrate from roots to shoots (He et al.

2017). Balestrasse et al. (2003) reported decreased assimilation of primary ammonia in nodules of soybean plants due to Cd stress. Thus, if it is not rapidly detoxified within a short spell, it triggers secondary metabolism, growth inhibition, and finally cell death (Schutzendubel and Polle 2002). Prolonged exposure to Cd triggers oxidative stress that results in growth inhibition by inducing a transient reduction of growth-stimulating hormones and inhibition of the antioxidative enzymes giving rise to H_2O_2 accumulation. Cadmium toxicity has been found to affect the permeability of plasma membrane resulting in a reduction of water balance (Sidhu et al. 2017). Rupture of the cellular structures in *Sedum alfredii*, a perennial herb, under different levels of Cd concentration, has been reported by Jin et al. (2008). Reduction in photosynthesis due to inhibition of chlorophyll biosynthesis, chloroplast metabolism, and suppression of CO_2 fixing enzyme has been reported by (Raziuddin et al. 2011). The worst effect of Cd toxicity is the effect on the anatomic and structural features of cells (Kupper et al. 2000). Lower mitotic index and chromosomal aberration in various plant species under Cd stress have also been reported (He et al. 2017). Mondal et al. (2020) reported lesser yield in bean in Cd-treated plants compared to the control.

2.2 Arsenic

Arsenic (As), the most toxic metalloid, is ubiquitous in many ecosystems and its distribution is a global concern as it is highly toxic to all life forms. The permissible limit of As in agricultural soils is 20 mg kg^{-1} soil, while a concentration of as low as 5 ppm is reported to be toxic for sensitive crops (Garg and Singla 2011). Arsenic occurs in the soil naturally in two inorganic forms, namely, arsenite [As(III)] and arsenate [As(V)]. Human exposure to As occurs through contaminated drinking water and solid food through the food chain when crops are contaminated with As. The metalloid finds its way into farming systems through natural geochemical processes, application of As-based pesticides, irrigation with As-polluted groundwater, fertilization with As-contaminated solid wastes, mining, etc. (Meharg et al. 2008).

Arsenic is non-essential to plants and roots are usually the foremost part of the plant to get exposed to As where it hinders root extension (Finnegan and Chen 2012). As(V) is absorbed by root through high-affinity phosphate transporters and disrupts the flow of energy in cells. Upon translocation to the shoot, it obstructs normal plant growth by disrupting biomass accumulation and stem expansion (Garg and Singla 2011). Sharma (2012) stated that As(III) can inactivate important enzymes in plants. As(V) has also reported decline in germination rate of Brassica (Srivastava et al. 2009). Decreased plant height with increasing As concentrations and a similar trend in root length, leaf number, and plant biomass of lentils were reported by Ahmed et al. (2006). Several other studies on As toxicity reported loss of root and shoot fresh and dry biomass, cessation of fruit development, and loss of yield (Shaibur et al. 2008; Srivastava et al. 2009). Haque et al (2015) reported a reduction of 6.29%–23.69% in tuber production of potato cultivars in As-contaminated soil compared to controls. Miteva (2002) and Shaibur et al. (2008) reported decreased vegetative growth in tomato and sorghum, respectively, upon exposure to a higher concentration of As. Straight head disease in rice, a physiological disorder characterized by the sterility of the florets/spikelets leading to reduced grain yield, was significantly increased by As contamination (Smith et al. 2010). These detrimental effects of As are due to its reaction with the sulfhydryl (-SH) groups of tissue proteins and enzymes resulting in inhibition of cellular function (Stoeva and Bineva 2003).

Arsenic injures the chloroplast membrane and disrupts the photosynthetic process (Stoeva and Bineva 2003) by significantly decreasing the pigment synthesis. Lack of adaptation to As stress reduces the CO_2 fixation rate and functional activity of photosystem II (Stoeva and Bineva 2003). Arsenic hinders the pathway of oxidative phosphorylation and impedes the mitochondrial enzymes through cellular respiration. Arsenic in excess amount stimulates free radicals and ROS formation resulting in oxidative stress (Srivastava et al. 2005). In the early growth stage of maize, As stimulates lipid peroxidation and increases malondialdehyde accumulation (Stoeva et al. 2004). Increased levels of thiobarbituric acid-reactive substances in the fronds of ferns were reported by Srivastava et al. (2005) as a result of exposure to As(V) indicating As-induced oxidative stress in ferns. However, numerous plant species have developed As tolerance by suppressing the high-affinity P/As uptake system but undergoes detoxification within plant cells to less phytotoxic forms (Finnegan and Chen 2012). Application of arbuscular mycorrhizal fungi is found to be effective against As toxicity in the crop grown in As-contaminated soil (Smith et al. 2010).

2.3 Lead

Erosion and volcanic eruption are natural sources of Pb that adds only a minute fraction of total contamination in the environment (Yokel and Delistraty 2003). While anthropogenic practices like smelting, burning of fossil fuels, electroplating, steel industry, atmospheric deposition, mining, use of pesticides, printing, irrigation, etc. have elevated Pb concentration in the environment (Gottesfeld et al. 2018). Soil pH and texture are the important factors that govern the dynamics and concentration of Pb (Zulfiquar et al. 2019).

WHO (1996) recommended 2 mg kg^{-1} soil as the threshold level of Pb for plants and 50–300 $^{mg\ kg-1}$ for agricultural soils. Lead does not have any beneficial role in the entire biological system but the morpho-physiological and biochemical processes are severely affected if the threshold limits are exceeded (Kushwaha et al. 2018). Lead toxicity has deleterious effects on seed germination of different crop cultivars. Lead markedly impaired the endosperm starch solubilization and hinders α-amylase activity that retards seed germination (Gautam et al. 2010). Deleterious effects of Pb on seed germination have been reported in maize (Hussain et al. 2013), rice (Gautam et al. 2010), and wheat (Yang et al. 2010). Due to the toxic effects of Pb on cell division, chlorophyll synthesis, and transpiration, the seedling growth declined (Hadi 2015). Leaving aside the aerosol exposure of Pb, roots are the first part of exposure and Pb retards root growth at a very faster rate and blackens roots. It is followed by a significant reduction in root volume, lateral root formation, total biomass root length and diameter, and root nutrient uptake (Fahr et al. 2013). The reduced nutrient uptake could be due to the strong interaction with potassium (K) ions because of their similar radii (K^+: 1.33 Å and Pb^{2+}: 1.29 Å), and hence these two ions compete to enter into the plant through the same K^+ channels reducing the overall nutrient uptake (Gopal and Rizvi 2008). The concentration and severity of Pb toxicity decrease with increasing distance of the aerial parts from roots as Pb binds more in lignified tissues rather than non-lignified tissues (Sharma and Dubey 2005). In the aerial parts, the fresh-dry biomass and growth tolerance index of leaves, shoot, and root are negatively correlated to the increasing Pb concentration in many crops such as tomato, pea, beans, maize, etc. (Shua et al. 2002; Jaja and Odoemena 2004). Possibly, the enlarged interphase induced by Pb decreases division leading to stunted plant growth. In leaves, Pb decreases the turgor of guard cells that in turn lessens the cell wall plasticity and closure of the stomata (Sharma and Dubey 2005). The decreased turgor can be attributed to the Pb-induced decrease in the concentration of amino acids, sugar, and other molecules. Similar to other abiotic stress, Pb induces overproduction of ROS in plants that promote oxidative stress and lipid peroxidation in plants. The produced ROS oxidizes the nucleic acids and proteins of the cells (Yadav 2010), and thus the functioning of cellular organelles such as peroxisomes, mitochondria, and chloroplast is significantly disrupted (Malecka et al. 2008). Lead exposure intensifies the activities of antioxidant enzymes like SOD, CAT, APX, glutathione S-transferase, and monodehydroascorbate reductase (Zulfiqar et al. 2019). On the other hand, Pb inactivates more than 100 plant enzymes by replacing the essential metals of metalloenzymes or by interacting with the –SH and –COOH functional groups at the active sites of enzymes (Zulfiqar et al. 2019). Lead concentrations bring down the plant protein pool which was primarily linked with accelerated oxidative damage or due to extensive use of protein to detoxify Pb stress and cessation of N metabolism (Chatterjee et al. 2004). Reduced nutrient and water uptake increased oxidative stress and curtailed C-fixation due to Pb-induced toxicity are the main causes of decreased crop yield. A substantial decline in economic yield of around 25–30% in sugarcane and wheat subjected to Pb was reported by Misra et al. (2010) and Rehman et al. (2017), respectively.

2.4 Chromium

Chromium (Cr), a metal pollutant, is a subject of growing concern for its detrimental effects on the biological system (Srivastava et al 2021). Cr concentration in natural soils ranges between 5 and 1,000 mg kg^{-1} (ATSDR 1998). It naturally occurs in rocks, soil, plants, animals, and volcanic dust and gases (ATSDR 1998) while leather and paint industries are the major anthropogenic contributors. It exists in nature in several oxidation states from +2 to +6. The trivalent [Cr(III)] and hexavalent [Cr(VI)] are the most common forms in the terrestrial environment which interchange and the balance regulated by three reactions, namely, oxidation/reduction, precipitation/dissolution, and adsorption/desorption (Ertani et al. 2017). Cr(VI) predominates in surface waters and aerobic soils and is highly mobile, bioavailable, and toxic. The availability of the forms of Cr is pH dependent and at $pH < 4$, Cr(III) dominates in the environment (Ertani et al. 2017). Seed germination, the first physiological process to be affected by Cr, is a function of the level of tolerance of the species (Srivastava et al. 2021). Cr(III) is reported to inhibit germination in *Glycine max*, *Vigna radiata* (Jun et al. 2009). The reduced seed germination can be ascribed to the suppression of amylase activity resulting in decreased sugar transport toward seed embryo axes and overexpression of the protease activity (Kumar et al. 2016). A decrease of 4–7% was observed in the germination of pigeon pea exposed to 40 to 100 ppm Cr (Dotaniya et al 2014). Roots of seedling and plants, the first plant organ to experience direct exposure, undergo visible decreased root growth and modifications in the root morphology (Zhao et al. 2019). This decreased root growth can arrest cell elongation, and decrease mitotic index and cell division in the root tips (Sundaramoorthy et al. 2010). Arduini et al. (2006) documented the development of light blue deposits on *M. sinensis* roots under Cr(III) exposure. The transport of Cr(III) is a passive-mechanism mediated while that of Cr(VI) is an active process involving sulfate transporters and energy (Srivastava et al. 2021). However, accumulation of Cr is generally higher in roots than shoot which could be attributed to immobilization by cation binding and storage of Cr in the vacuoles of the root cells

(Mangabeira et al. 2014) which acts as a defensive mechanism against Cr toxicity. The lower nutritional flow to the aboveground plant parts consequently results in stunted shoot and leaf growth, reduced plant height, and extension of stem and leaf senescence (Shanker et al. 2005). A significant drop in height in *Helianthus annuus* L. under Cr exposure was documented by Fozia et al. (2008). About 50% reduction in leaf number was documented by Kumar et al. (2016) in wheat plants grown in the 0.5 mM Cr(VI)-contaminated soil.

Chromium toxicity in particular reduces CO_2 fixation, electron transport, suppression of photosynthetic enzymes, and photophosphorylation resulting in reduced photosynthetic efficiency of plants (Shanker et al. 2009). Alterations in chloroplast ultrastructure due to unusual development of lamellar system and inefficiency of the mesophyll cells could be the reasons for lower plant photosynthetic efficiency (Schiavon et al. 2009). Reduction in stomatal transpiration, conductance, and CO_2 assimilation are also reported under Cr toxicity exposed to chromium (Schiavon et al. 2009). This can be attributed to the modification of the spongy parenchyma cellular structure and reduction in the mesophyll stomatal. The decreased level of transpiration is hypothesized to affect the movement of water in the xylem (Ertani et al. 2017). Chromium(VI) also restricts nitrogen (N) assimilation, decreases the levels of nitrate and nitrite reductase, urease, and glutamate dehydrogenase (Shanker et al. 2009). The decrease in the activity of the enzyme as the concentration of the external Cr increased might be because of the inhibitory effect of Cr ions on the enzyme system itself. Furthermore, Cr exposure also triggers the activities of antioxidant enzymes such as SOD, CAT, lipid peroxidase, etc. The activity of SOD was reported to increase by 29% in pea plants Cr(VI) (Dixit et al. 2002). The generation of ROS and lipid peroxidation are higher when plants are exposed to Cr(VI) than that of Cr(III) form of Cr (Scoccianti et al. 2008). Inactivation of electron transport in mitochondria exposed to Cr(VI) results in enhanced O_2^- generation and accumulation of ROS (Dixit et al. 2002). Overall severe effects on the plant biochemical and physiological processes result in a reduction in the yield of crops exposed to Cr. Kumar et al. (2016) reported a total loss of harvestable parts of carrot when exposed to Cr at 270 or 810 kg ha^{-1}. Wyszkowski and Radziemska (2010) reported that the yield of spring grown barley (*Hordeum vulgare*) was significantly decreased upon exposure to Cr.

2.5 Mercury

Mercury (Hg) is the only heavy metal that also exists in liquid form at room conditions and biomagnifies at each trophic level once it enters the food chain. The high solubility of the metal and easiness of the metal to shift to the gaseous phase are the two most important properties for its wide application and usability (Clarkson and Magos 2006). Naturally, Hg is present in the form of ores and mineral-bound forms while emission from coal-burning thermal power plants (TPPs) is the main anthropogenic source. Deposition of the atmospheric Hg into the ground and water due to oxidation is another source of the addition of Hg into the soil (Lindberg et al. 2007). Additionally, the application of Hg-containing fertilizers and pesticides contributes greatly to Hg accumulation in agricultural soil (Han et al. 2002). Hg exists in different forms like Hg, HgS, Hg^{2+}, and methyl-Hg. Among different species, Hg^{2+} is the most available form in agricultural soil that forms organic and inorganic compounds. Moreover, it is easily absorbed while methylmercury (MeHg) is the most hazardous compound of Hg in the environment. However, the uptake of Hg by plants is a function of numerous parameters such as cation exchange capacity, soil pH, soil aeration, and plant species (Patra et al. 2004).

The toxic level of Hg^{2+} can induce visible injuries and physiological disorders in plants. Many Hg forms are related to seed injuries and reduce seed viability. Hg interrelates with the –SH system and forms a complex S–Hg–S bridge which in turn disrupts the stability of the –SH group and drastically reduces the seed's germination and subsequent growth of the young embryo (Patra and Sharma 2000). Hg is imported into the root cells possibly through Cu, Fe, or Zn channels/transporters as these transporters typically have broad substrates (Patra and Sharma 2000; Clemens 2006). In roots, Hg suppresses the differentiation of roots possibly due to the secretion of mucilaginous substance epidermal surface (Patra and Sharma 2000). Du et al. (2005) reported a significant accumulation of Hg on the surfaces of rice roots promoted by the hyper-adsorption due to the presence of arsenate. Thus, the accumulation of Hg is a function of other soil parameters. Approximately, 80% of the Hg absorbed is trapped by the roots by binding it onto the cell wall (Wang and Greger 2004). Although most of the Hg accumulated by plants remains in roots yet a small proportion is translocated to aerial parts/shoots via. xylem uploading (Wang 2004). Hg has been reported to result in stunted aerial growth in tomato (Cho and Park 2000), wheat (Ge et al. 2009), etc. Damage in the ultrastructure could be the direct reason for growth inhibition of plants upon Hg exposure. Binding of Hg with the –SH groups of enzymes upon exposure significantly disrupts the functioning of the metabolic enzymes and cellular functions (Raj and Maiti 2019). Scanning electron microscopy analysis of Indian mustard (*Brassica juncea*) exposed to Hg showed decreased intercellular spaces, deformed cell shape, and abnormality in vacuoles in leaves (Shiyab et al. 2009). Hg exposure also reduces transpiration rate, chlorophyll concentration, photosynthesis, water uptake, and collapses thylakoid (Azevedo and Rodriguez 2012). Hg^{2+} binds to water channel proteins of plants, which induces closure of leaf stomata and obstructs the flow of water in plants (Cargnelutti et al. 2006). High levels of Hg cause loss of K, Mn, Mg, and accumulation of Fe that interfere with the mitochondrial activity resulting in triggering expression of the ROS and oxidative stress (Chen and Yang 2012). Hg encouraged the accumulation of O_2^- and H_2O_2 in alfalfa (*Medicago sativa*) leaves in a dose-dependent manner as reported by Gill and Tuteja (2010). The cumulative effect of Hg on cellular structure, biochemical processes, and production of ROS results in a declined yield in the crops and accumulation in the edible parts of plants. Sheker et al. (2011) reported a decrease in fruit yield in tomato exposed to Hg. Although studies on the effects of Hg genotoxicity are scarce, yet deleterious errors in the genetic materials of crop plants' species have been demonstrated as Hg ions form covalent bonds and easily deform the outer electron shells (Azevedo and Rodriguez 2012). However, thermal treatment, soil washing, and soil amendments are some of the ways to reduce the effects of Hg toxicity in plants (Chen and Yang 2012).

2.6 Iron

Iron (Fe) is one of the most abundant elements in the earth's crust but is the least accessible micronutrient for plants specially grown under oxygen-rich and basic-to-neutral soil conditions. In plants, Fe is usually about 140 μg g^{-1} dry weight (Anjum et al. 2015). Iron is present in the agricultural soil in two forms, viz., Fe^{3+} (insoluble and cannot be taken up by plants) and Fe^{2+} (soluble form for plant uptake) (Becker and Asch 2005). Iron is naturally present in all types of soil while mining, Fe-processing industries, Fe application in agricultural soil in the form of fertilizers, and irrigation with Fe-containing water are the anthropogenic sources of Fe contamination (Gill 2014). Iron is an essential element for the entire biological system as it plays important role in photosynthesis, chloroplast development, and chlorophyll biosynthesis (Rasheed et al. 2020). Iron is a major constituent of all the cell redox systems such as heme proteins including cytochromes, CAT, APX and leghemoglobin and iron-sulfur proteins including ferredoxin, aconitase, and SOD (Filho et al. 2020). Globally, about 18% of soils are suffering either from Fe toxicity or Fe deficiency (Dufey et al. 2015). The toxicity or deficiency is a function of change in soil pH, soil nutrient status, and aerobic/anaerobic condition of the soil (Audebert and Sahrawat 2000). However, the heavy metal toxicity of Fe is dominant in acidic and submerged reduced soil (Mahender et al. 2019). Therefore, worldwide submerged rice, among other crops, is one of the important crops to be worst affected by Fe toxicity (Dufey et al. 2015). Fe toxicity in seed reduces the mitotic activity in the meristem tissue of the embryo, blockage of water transport for soaking and sometimes shows clastogenic effects on chromosomes as described in studies of crops such as papaya (Filho et al. 2020) and sunflower (Chakravarty and Srivastava 1992). Roots affected by Fe toxicity become flimsy, coarse, short, blunted, and develop dark brown color (Fageria et al. 2008). Nevertheless, the roots regain their white color with the withdrawal of Fe toxicity (Sahrawat 2010). The expression of visible symptoms of Fe toxicity under flooded conditions is more prominent in the leaf tissues. With the microbial reduction of insoluble Fe^{3+} to Fe^{2+} under anaerobic conditions (Becker and Asch 2005), Fe^{2+} is absorbed by the root cells and is acropetally translocated via xylem flow and transpiration stream into the leaves. Typically, discoloration of lower leaves from green to reddish-brown occurs as minute spots near or at the tips of the leaves which further disperses toward their bases called “Bronzing”. Further exposure to Fe results in these brown spots growing and coalescing on the leaf intervenes leading to leaf drying and senescence (Nagajyoti et al. 2010). The change in color of leaves and roots is useful visual diagnostic characteristics of Fe stress. Inside the leaves, excess Fe^{2+} triggers Fenton reaction and produces hydroxyl radicals and ROS which cause irreversible damage to the cell structural components like membrane lipid, protein, and genetic materials (DNA) (Arora et al. 2002) and lead to an accumulation of oxidized polyphenols (Yamauchi and Peng 1995). The production of ROS results in oxidization of chlorophyll, chlorosis, and decreases the photosynthesis which consequently acts as a major factor for yield reduction (Onaga et al. 2016). Iron toxicity in tobacco, soybean is accompanied by the reduction of plant photosynthesis and yield and the increase in oxidative stress and APX activity (Nagajyoti et al. 2010). However, Fe toxicity is a complex nutrient disorder associated with the deficiencies of other nutrients, especially P, Ca, Mg, K, and Zn and these nutrients are closely related to the tolerance mechanism against Fe toxicity in plants (Sahrawat 2010). Heavy metal-induced effects on plants have been presented in Table 2.

3 Remediation Strategies

3.1 Bioremediation

Heavy metal pollution is one of the greatest environmental problems today that impacts crop production and food quality due to the excessive use of agricultural inputs like fertilizers, pesticides, and mulches that result in heavy metal contamination of soils (Su 2014). Heavy metals can come from various sources such as natural, agricultural, industrial

Table 2 Effects of heavy metals on different plants

Heavy metals	Plants	Heavy metal-induced effects	References
Cadmium (Cd)	Tobacco (*Lycopersicon esculentum*)	An accumulation of Cd, increased lipid peroxidation, and decreased superoxide dismutase and catalase activity	Islam et al. (2009)
	Brassica sp.	Reduction in photosynthesis due to inhibition of chlorophyll biosynthesis, chloroplast metabolism, and suppression of CO_2 fixing enzyme	Raziuddin et al. (2011)
	Catharanthus roseus	Leaf chlorosis and rolling of the leaves	Liu et al. (2013)
	Canna orchioides	Decreased ratio of green leaves; accelerated leaf senescence; and decreased biomass of stems, leaves, and roots	Zhang et al. (2021)
Arsenic (As)	Lentil (*Lens culinaris*)	Root length, leaf number, and plant biomass	Ahmed et al. (2006)
	Brassica sp.	Declined germination rate	Srivastava et al. (2009)
	Rice (*Oryza sativa*)	Straighthead disease (sterility of the florets/spikelets), reduced grain yield	Smith et al. (2010)
	Carrot (*Daucus carota*), lettuce (*Lactuca sativa*), spinach (*Spinacia olerace*a), sunflower (*Helianthus annuus*)	Decline in growth, photosynthetic pigments, and increased production of stress biomarkers	Bergqvist et al. (2014)
Lead (Pb)	*Spinacea oleracea*	Reduce fresh and dry weight, reduction in chlorophyll, and N and protein concentration affect more in roots than shoots	Kibria et al. (2010)
	Sugarcane (*Saccharum sinense*)	25–30% reduction in yield	Misra et al. (2010)
	Wheat (*Triticum aestivum*)	Reduced yield	Rehman et al. (2017)
	Chickpea (*Cicer arietinum*), horse gram (*Macrotyloma uniflorum*)	Higher activities of antioxidant enzymes like SOD, CAT, APX, glutathione S-transferase, etc	Zulfiqar et al. (2019)
Chromium (Cr)	Tomato (*Lycopersicon esculentum*)	Decreases plant nutrients	Shanker et al. (2005)
	Soybean (*Glycine max*), Mung bean (*Vigna ratiata*)	Inhibit germination	Jun et al. (2009)
	Indian mustard (*Brassica juncea*)	Reduced stomatal transpiration, conductance, and CO_2 assimilation	Schiavon et al. (2009)
Mercury (Hg)	Tomato (*Lycopersicon esculentum*)	Stunted growth of shoot	Cho and Park (2000)
	Rice (*Oryza sativa*)	Hg accumulation on root surfaces	Du et al. (2005)
	Indian mustard (*Brassica juncea*)	Decreased intercellular spaces, deformed cell shape, and abnormality in leaf vacuoles	Shiyab et al. (2009)
	Barley *(Hordeum vulgare)*	Loss/reduction of economic yield	Wyszkowski and Radziemska (2010)
Iron (Fe)	Rice (*Oryza sativa*)	Flimsy, coarse, short, blunted roots with dark brown color, and bronzing of leaves	Fageria et al. (2008)
	Alfalfa (*Medicago sativa*)	Accumulation of O_2^- and H_2O_2	Gill and Tuteja (2010)
	Papaya (*Carica papaya*)	Clastogenic effects on chromosomes	Filho et al. (2020)

solid waste, inland effluent, atmospheric sources, and more. Mines and electroplating, metallurgical smelting as well as agricultural pesticides and fertilizers have affected a great many areas worldwide (Zhang et al. 2011). A few pesticides are organic–inorganic compounds and some contain heavy metals such as Hg, As, Cu, Zn, and other heavy metals as well as pure minerals. Metals, on the other hand, are not degradable and so remain in the environment for long periods; when present at high concentrations, metals have adverse effects on plant metabolism (Ferraz et al. 2012). There is a need for a variety of innovative treatment methods for the removal of heavy metal ions from the soil, water, and wastewater. The removal of heavy metals from soil and water through microbes has been proposed as an efficient and economical alternative (Ahirwar et al. 2016). A variety of microorganisms are capable of degrading, detoxifying, and accumulating various harmful compounds, both organic and inorganic. In the process of bioremediation, the waste is destroyed or rendered harmless by using natural biological activity in the ecosystem (Siddiquee et al. 2015). Degradation or detoxification of hazardous ingredients can be achieved by bacterial, fungal, or plant metabolic processes (Qazilbash 2004). As part of a bioremediation process, several techniques like biofilters, bioventing, biosorption, composting, bioaugmentation, bioreactors, land farming, and biostimulation are used (Qazilbash 2004). Factors that influence the optimization of these methods include available microbial population engaged in degradation of pollutants, type of contaminants, soil pH, presence of oxygen or other electron acceptors, as well as nutritional levels (Khan et al. 1997). It has been shown that some microbes can tolerate heavy metals by removing them from the environment or breaking them down into less toxic or completely benign forms, which then they can metabolize and use for growth (Qazilbash 2004). Microorganisms participate in biosorption by adsorbing metals on the surface of the cell and linking them with extracellular polymers (Gupta and Diwan 2017). An outer cell shield is responsible for the sorption properties of microorganisms. In the surface layers of cellular membranes, active groups of compounds link metals together. Bioaccumulation takes place when the contaminant is absorbed in a faster rate than it is lost. The process of bioaccumulation affects the sensitivity of living organisms to chemicals. Up to a certain point, organisms can tolerate chemicals, but when these levels exceed that point, the chemicals are toxic and pose a threat to the organism. Chemically sensitive organisms differ greatly based on their types and the chemicals they are exposed to (Mishra and Malik 2013). Many environmental bacteria species accumulate metals in their cells, in their cell walls, and areas bordering their cytoplasm. Metals undergo oxidation, reduction, methylation, and demethylation through microbiological reactions. Microorganisms participate in reactions through their enzymatic systems. Some reactions of significantly toxic or valuable metal reduction may be of practical use, such as bacteria isolated from tannery sewers reduced Cr(VI) to less toxic Cr(III), which can be removed from the environment (Kisielowska et al. 2010).

3.1.1 Bacteria

Regardless of their size and ubiquity, bacteria are important biosorbents due to their resilience and ability to grow under controlled conditions under a wide range of environmental conditions (Srivastava et al. 2015). The high surface-to-volume ratio and potential chemisorption sites (teichoic acid) on their cell walls account for their high biosorption capacity (Mosa et al. 2016). Moreover, mixing cultures makes bacteria more stable and allows them to survive longer (Sannasi et al. 2006). Bacterial species such as *Flavobacterium*, *Pseudomonas*, *Enterobacter*, *Bacillus,* and *Micrococcus* are studied on their abilities to bioremediate heavy metals (Igir et al. 2018). The metabolic advantage of consortium cultures, which are appropriate for application in the field, lies in their ability to biosorb metals (Kader et al. 2007). A reduction of 78% in chromium (Cr) was demonstrated using a bacterial consortium of *Acinetobacter* sp. and *Arthrobacter* sp. at 16 mg L^{-1} metal ion concentration (De et al. 2008). An extensive amount of Pb was removed using *Micrococcus luteus*. The elimination ability was 1965 mg/g under ideal conditions (Puyen et al. 2012). The biosorption of Pb, Cr, and Cd in tannery effluent *Bacillus subtilis*, *B. megaterium*, *Aspergillus niger,* and *Penicillium* sp. was studied and *B. megaterium* recorded the highest Pb reduction (2.13–0.03 mg L^{-1}), followed by *B. subtilis* (2.13–0.04 mg L^{-1}) (Abioye et al. 2018). *A. niger* showed the highest ability to reduce the concentration of Cr (1.38–0.08 mg L^{-1}) followed by *Penicillium* sp. (1.38–0.13 mg L^{-1}), while *B. subtilis* exhibited the highest ability to reduce the concentration of Cd (0.4–0.03 mg L^{-1}) followed by *B. megaterium* (0.04–0.06 mg L^{-1}) after 20 days. By using bacterial consortia, Cr, Zn, Cu, Pb, and Co were effectively eliminated within less than 2 h for Pb and Cu (Abbas et al. 2014).

3.1.2 Fungi

As biosorbents, fungi are widely used to remove toxic metals with an excellent capacity for metal adsorption and recovery (Fu et al. 2012). Metal recovery may occur in vacuoles, on the cell surface, and in the extracellular environment (Kisielowska et al. 2010). Through the activity of microorganisms, heavy metal compounds may crystallize or precipitate, which results in the transformation of the metal into forms sparingly, lowering the toxicity of the compounds and may take part in biogeochemical cycles. As a known industrial technology, bioleaching uses the metabolic products of microbes, bacteria, and fungi to extract metals from sulfide materials (Kisielowska et al. 2010). It is primarily connected with two processes: the creation of various organic acids within the living environment (citric acid, gluconic acid, and oxalic acid) and the production of complexion agents that fungi can bioleach (Tarekeng et al. 2020). The following types of fungi may be found under such conditions: *Aspergillus* sp., *Penicillium* sp., *Rhizopus* sp., *Mucor* sp., *Alternaria* sp., and *Cladosporium* sp. owing to their biochemical abilities and high resistance to pH and temperature. Several studies have found that both active and lifeless fungi are essential for the adhesion of inorganic chemicals (Tiwari et al. 2013). Srivastava and Thakur (2006) also investigated the recovery of chromium in tannery wastewaters by using *Aspergillus* sp. In a bioreactor system, 85% of chromium was removed from the synthetic medium, compared to 65% from the tannery effluent which can be attributed to the presence of organic pollutants that hinder the growth of the organism. Bioaccumulation studies on *Coprinopsis atramentaria* tested its ability to bioaccumulate 76% of Cd^{2+} at a 1 mg L^{-1} Cd^{2+} concentration, and 94% of Pb^{2+} at an 800 mg L^{-1} Pb^{2+} concentration. Due to this, it has been proven to be an effective heavy metal accumulator (Lakkireddy and Kues 2017). The method described by Park et al. (2005) provides the possibility of converting toxic Cr (VI) to less toxic or nontoxic Cr(III) by way of dead fungal biomass. Additionally, Luna et al. (2016) stated that *Candida sphaerica* produces biosurfactants that are 90% efficient at removing Fe, 95% efficient at removing Zn, and 79% efficient at removing Pb. The bioconversion of Cr(VI) to Cr (III) has been performed by several yeast strains such as *Hansenula polymorpha*, *Saccharomyces cerevisiae*, *Yarrowia lipolytica*, *Rhodotorula pilimanae*, *Pichia guilliermondii*, and *Rhodotorula mucilage* (Chatterjee et al. 2012). Among microbes, biosorption abilities vary significantly, as do microbial biomasses. Every microbial cell is capable of biosorption in different conditions, depending on how it has been pre-treated and how it is being tested. As physical, chemical, and bioreactor conditions alter, microbes must adapt to facilitate biosorption. Microorganism-mediated heavy metal remediation has been shown in Table 3.

3.2 Soil Amendments

3.2.1 Organic Soil Amendments

In the past, organic soil amendments have been used to immobilize soil heavy metals by changing their speciation from highly bioavailable (i.e., free metal) to much less bioavailable forms (like metal oxides and carbonates) (Walker et al. 2004). A major characteristic of these

Table 3 Remediation of heavy metals by microorganisms

Microbes	Metal	Result	References
Aspergillus sp.	Cr	85% of Cr was removed from the synthetic medium	Srivastava and Thakur (2006)
Acinetobacter sp. *Arthrobacter* sp.	Cr	A reduction of 78% in Cr was demonstrated using bacterial consortium	De et al. (2008)
Micrococcus luteus	Pb	An extensive amount of Pb was removed. The elimination ability was 1965 mg g^{-1} under ideal conditions	Puyen et al. (2012)
Candida sphaerica	Fe Zn Pb	Produces biosurfactants that are 90% efficient at removing Fe, 95% efficient at removing Zn, and 79% efficient at removing Pb	Luna et al. (2016)
Coprinopsis atramentaria	Cd Pb	Bioaccumulate 76% of Cd^{2+} at a 1 mg L^{-1} Cd^{2+} concentration and 94% of Pb^{2+} at an 800 mg/L Pb^{2+} concentration	Lakkireddy and Kues (2017)
Bacillus megaterium *B. subtilis*	Pb	Recorded the highest Pb reduction (2.13 to 0.03 mg L^{-1}) by *B. megaterium*, followed by *B. subtilis* (2.13–0.04 mg/L)	Abioye et al. (2018)
Aspergillus niger *B. subtilis*	Cr Cd	Highest ability to reduce the concentration of Cr (1.38–0.08 mg L^{-1}) Highest ability to reduce the concentration of Cd (0.4–0.03 mg L^{-1})	Abioye et al. (2018)
Hansenula polymorpha, Saccharomyces cerevisiae, Yarrowia lipolytica, Rhodotorula pilimanae, Pichia guilliermondii, Rhodotorula mucilage	Cr	The bioconversion of Cr (VI) to Cr (III)	Tarekeng et al. (2020)
Dead fungal biomass		Convert toxic Cr (VI) to less toxic or nontoxic Cr (III)	Tarekeng et al. (2020)

amendments is their ability to bind with a variety of metal (loid)s, including Pb, Cd, Cr, and Cu (Alvarenga et al. 2009; Walker et al. 2004). For organic soil amendments, the most commonly used ones are biosolids, bark and wood chips, composts from different sources, manures, sawdust, sewage sludge, and wood ash (Karaca 2004; Sabir et al. 2013). Organic amendments are relatively cheap, compared to other soil amendments, and they often facilitate revegetation of contaminated soils. Metal extraction depends on the kind of soil, the initial organic matter (OM) content, and the rate of OM transformation over time. A significant change in metal availability can be attributed to OM decomposition, resulting in an array of organic acids being released over time (Lwin et al. 2018). Increased decomposition of OM is also associated with an increase in dissolved organic carbon (DOC), which contributes to increased metal release (Martinez et al. 2003). Moreover, decomposition of OM can decrease the OM's surface area and decrease its cation exchange capacity (CEC), and ultimately release metals over time (Lwin et al. 2018). Cow, pig, and sheep manure, for example, reduced the amounts of Diethylenetriamine Penta Acetic Acid (DTPA)-extractable Ni in soil because they combined strongly with OM (Lwin et al. 2018). In a sandy loam soil, Alamgir and Islam (2011) showed that applying farmyard manure (FYM) between 10 and 20 tones ha^{-1} significantly reduced Cd and Pb concentrations in the shoots and roots of amaranth. Additionally, Walker et al. (2004) also found that manure application reduced plant tissue concentration of three metals (Cu, Zn, and Pb), compared to plants grown in self-fermented compost, which was most likely due to elevated soil pH from manure application.

Furthermore, application of green waste compost decreased uptake of Cu, Pb, and Zn in Greek Cress by 21, 54, and 16 percent, respectively, in calcareous contaminated soils (Van Herwijnen et al. 2007). Liu et al. (2009) reported that the application of compost effectively decreased Cd toxicity in wheat by more than half, increasing the growth of wheat by decreasing Cd uptake by wheat tissue. Positive impacts of compost application can be accounted for by several factors. These include a high pH, Cd complexion with OM, and co-precipitation with P. The overall retention of metal(loid)s by organic amendments is a consequence of surface charging (Clark et al. 2007) and metal adsorption onto metal-binding compounds such as phosphates and carbonates (Gondar and Bernal 2009). It is also important to note that composted organic amendments affect remediated metal(loid) mobility and bioavailability in soils depending on soil type, metal(loid) specifics, and amendment characteristics (Walker et al. 2004; Bernal et al. 2007). Several studies have suggested that amending contaminated soils with compost may increase metal(loid) mobility, especially As (Cao et al. 2003; Hartley et al. 2010). The use of organic soil amendments improved soil physical characteristics, such as particle size distribution, cracking patterns, and porosity, where the development of better soil structural characteristics may be able to inhibit the dispersion of metal-contaminated particles by the formation of water-stable aggregates. Organic amendments also contain a large amount of N, P, and other essential elements such as Ca, Mg, and Fe which are vital to plant growth (Butler et al. 2008), and which directly improve soil fertility. Long-term use of these amendments bears consideration of the negative environmental impacts. These organic amendments frequently provide pathogens, high salt levels (KCl and NaCl), and can introduce new sources of heavy metals (Nicholson et al. 2003). As a carbonaceous material, biochar has more recently been used to absorb heavy metals from soils and water. Biochars of various sources are known to reduce metal mobility and availability by including plant residues (Dias et al. 2007; Paraskeva et al. 2008) and animal manures (Gercel and Gercel 2007; Lima and Marshall 2005). Biochar often has alkaline properties (which increase soil pH upon application) as well as the release of available P, K, and Ca (resulting from a high CEC) which are associated with soil metal stabilization. Beesley and Marmiroli (2011) concluded that biochar application reduced Cd and Zn leachate concentrations by an additional 300- and 45-fold, respectively. Park et al. (2011) also examined the effect of 5% (w/w) chicken-manure-derived biochar on the concentration of 1 M NH_4NO_3-extractable Cd and Pb, while green waste-derived biochar reduced extractable Cd and Pb by 30 and 37%, respectively. Beesley et al. (2010) applied hardwood-derived biochar to a multi-element (As, Cu, Cd, and Zn)-contaminated soil and found that while Cd and Zn were immobilized, As and Cu were mobilized. In addition to being highly aromatic, the associated functional groups give the biochar particle's surface a negative charge, resulting in higher CEC in soil, enhanced nutrient retention (Cheng et al. 2008; Kammann et al. 2015).

3.2.2 Inorganic Amendments

Liming is primarily intended to buffer soil acidity. However, it has increasingly been used as a method for managing heavy metal toxicity in soils (Kaitibie et al. 2002). Khan and Jones (2008) found that lime applied to an abandoned copper mine tailings site reduced DTPA-extractable metals like Zn, Co, and Fe by 75, 81, and 85%, respectively. Tlustos et al. (2006) also found that the addition of CaO and $CaCO_3$ increased soil pH to 7.3 and reduced $CaCl_2$ extractable Zn, Cd, and Pb by 80, 50, and 20%, respectively. Due to changes in soil pH caused by lime addition, metals can also be hydrolyzed or precipitated with carbonates, thus allowing lime to act as a precipitating agent for metals in soil (Lwin et al. 2018). Among the effects of lime on soil is an increase in Ca saturation and altered particle charge density, which affects the dispersion of soil particles and helps in soil aggregate formation as well as improved soil structure (Lwin et al. 2018). Naturally occurring gypsum (mined as well as industrially produced) and gypsum-like by-products contribute to the treatment of soils contaminated with heavy metals. In a study conducted by Tsunematsu et al. (2012), gypsum powder was found to reduce the concentration of dissolved As released from soils to 0.01 mg dm^{-3}. A study by Vink et al. (2010) also demonstrated that soil sulfide formation was greatly accelerated by the addition of gypsum. As little as 3% of gypsum could significantly decrease Cd and Pb root concentrations in medicinal plants (Kim et al. 2016). Gypsum is widely used in the reclamation of sodic soils to block sodium ions from reaching exchange sites. Despite not being a liming agent, gypsum is an excellent source of calcium and sulfur nutrients for plants. The addition of Ca through gypsum can overcome dispersion and promote flocculation and structural development in heavy metal-contaminated soils. As part of in situ remediation of metal-contaminated soils, phosphorus (P)-containing amendments are commonly applied (Hong et al. 2010). Various P amendments exist, including synthetic and natural apatites, hydroxyl apatites, rock phosphate, phosphate-based salts, and di-ammonium phosphate (DAP) for remediation of metal-contaminated soils. It has been reported that phosphate compounds can immobilize metals like Cd, Cu, Pb, and Zn by reducing their bioavailabilities (Bolan et al. 2014). Bolan et al. (2014) demonstrate that P-based compounds improve metal immobilization via direct metal adsorption or substitution by the phosphate compound, as well as through P anion-induced metal adsorption and precipitation as metal(loid) phosphates. Metal (loid)-P precipitation has been demonstrated to be one of the main mechanisms for immobilizing metals, such as Pb and Zn. Adding phosphate to arsenic-contaminated soil can induce competitive anion exchange, which increases As(VI) leaching from soil (Maier et al. 2019). As and P have very similar chemical characteristics and compete for adsorption sites (e.g., iron hydroxide and OM surfaces); thus, the mobility of As in soil has been greatly enhanced by the addition of P-rich agents (Maier et al. 2019; Cao et al. 2003). Aside from that, P fertilizers (e.g., single superphosphate, triple superphosphate, mono-ammonium phosphate and DAP) may contain elevated levels of Cd. There is extensive evidence that long-term P fertilizers use increased Cd concentration in surface soils and that P fertilizers add to this concentration (Mann et al. 2002).

4 Conclusion

Considerable attention has been paid to understanding heavy metal contamination, its impact on the ecosystem, and possible remediation. Plant's heavy metal uptake and tolerance vary with a variety of factors, which could play a role in how plants survive and grow in contaminated soils. However, despite several findings, the underlying mechanisms of heavy metal stress are still not clearly understood, and more research is needed. Microbial remediation of heavy metal contamination is an economical and eco-friendly solution. Monitoring and managing the heavy metal remediation further requires characterization of its fate and behavior in the environment. The research gap in this area makes it difficult to understand all possible environmental impacts of heavy metals. Therefore, a close link between research and developmental efforts assessing the emerging heavy metal pollutants and the tools, equipment, and know-how that support these challenges is the need of the hour.

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Exploiting Host Resistance in Management of Vascular Wilt in Major Pulses of India

Meenakshi Arya, Vikrant, Shahana Majumder,
and Sushil Kumar Chaturvedi

Abstract

Pulses are one of the most important food crops of the world owing to their 20–25% protein content by weight. India with a large economically weaker section and a major vegetarian population depends on pulses for its protein and food security. Several biotic and abiotic factors are responsible for a poor and unstable yield of pulses. Out of these, biotic stresses caused by *Fusarium oxysporum* the causal organism of vascular wilt is the most destructive causing yield loss of about 20–25%. For the management of fusarium wilt, an integrated management strategy where different practices are included should be used. One of the next most effective strategies for the management of vascular wilt is the use of genetic resistance in host plants. Screening for resistance source, introgression and using resistant cultivar is the most effective, reliable, and safer alternative to chemical treatments that can be combined with other management practices in integrated management strategy.

Keywords

Breeding • *Fusarium* wilt • Integrated breeding • Pulses • Resistance

1 Introduction

The pulses are known to supply dietary protein to the predominantly vegetarian people of the Indian subcontinent as seed protein content in various pulses varies from 20–25% by weight. The amino acids present in pulses complement with cereals and make a perfect blend when consumed as *Dal-Roti*. The tender plant parts and grains form excellent feed and concentrate to improve animal health also. Besides, being the source of vegetarian protein, deep roots of pulse crops are known to open up the soil to the deeper strata and fix atmospheric nitrogen symbiotically through bacteria present which helps in improving soil fertility and texture. The role of pulses in human, animal, and soil health is well known (Stagnari et al. 2017). Therefore, pulses occupy an important position in Indian agriculture. India is one of the largest producers of pulses in the world (FAOSTAT 2019). Major pulses that are grown in India are chickpea (gram), pigeon pea (arhar/tur), lentil (masoor), mungbean, pea, and various other minor pulses. In India, pulses are cultivated on about 29.46 million ha of land with an annual production of 22.95 million tonnes (FAOSTAT 2019). The major pulses growing states are Madhya Pradesh, Maharashtra, Uttar Pradesh, Karnataka, Andhra Pradesh, Rajasthan, Gujarat, Chhattisgarh, Bihar, Orissa, and Jharkhand (Trivedi et al. 2017, Singh et al. 2018) indicating widespread cultivation in India.

Several factors are responsible for the poor and unstable yield of pulse crops, the most important being biotic and abiotic stresses. Yield loss assessment suggests annual yield losses to the tune of 5 to 30% due to various stresses (Table 1). Among various biotic stresses, soil-borne fungal pathogens are major production and productivity constraints limiting higher productivity of pulses in different agro-ecological regions. Soil-borne fungal pathogens of legumes cause seed and seedling blights, root rots, and wilts. Out of these diseases, vascular wilt caused by *Fusarium oxysporum* is the most destructive disease of pulses causing yield loss of about 20-25% (Table 1) and under favourable conditions, it can reach epidemic proportion causing 100% crop loss (Jendoubi et al. 2017; Sinha et al. 2018). Further, *F. oxysporum* is known to cause plant mortality leading to yield loss and reduced seed size (Haware and Nene 1980).

M. Arya · S. K. Chaturvedi
Rani Lakshmi Bai Central Agricultural University, Jhansi, 284003, India

Vikrant · S. Majumder (✉)
Department of Botany, School of Life Sciences, Mahatma Gandhi Central University, Motihari, Bihar, India
e-mail: shahanamajumder@mgcub.ac.in

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Table 1 *Fusarium oxysporum* ff. spp. and its respective races causing *Fusarium* wilt in several legume species (Gaur and Chaturvedi 2004, Jha et al. 2020)

Crop	Causal organism	Races	Growing states	% Yield loss
Chickpea	*Fusarium oxysporum f. sp.ciceri* (Foc)	Eight races (0,1B/C, 1A,2,3,4, and 6)	Eastern U.P., Bihar, Jharkhand, Assam, W.B., Rajasthan, Gujarat, Maharashtra, M.P., Chhattisgarh, Orissa, A.P., Karnataka, and T.N	10–40% and even 100% under favourable condition
Pigeon pea	*Fusarium udum* Butler	–	U.P., Bihar, Jharkhand, W.B., Rajasthan, Gujarat, Maharashtra, M.P., Chhattisgarh, A.P., Karnataka and T.N	10–15% and even up to 100% in favourable condition
Lentil	*Fusarium oxysporum f. sp. Lentis* (Fol)	Eight races/pathotypes	Bundelkhand and Eastern U.P., Haryana and Rajasthan	20–25% and even 100% in favourable condition
Pea	*Fusarium oxysporum* Schl *f. sp. pisi* Snyd and Hans.(Fop)	Four races (1, 2, 5 and 6)	All crop growing areas	30–100%

2 Pathogen Biology and Epidemiology

Fusarium oxysporum Schlecht. emend. Snyder & Hansen (Fo) is a soil-borne fungus found in cultivated and uncultivated soils worldwide. Its phytopathogenic strains are organised into 120 *formae specials* (ff. spp.) i.e., special forms based on host species specificity (Armstrong and Armstrong 1981; Fourie et al. 2011; Leslie and Summerell 2006; Lombard et al. 2019). The *formae specials* infecting the pulses are listed in Table 1.

Butler first recorded wilt on chickpea in India in 1918, but its etiology was not determined properly until 1940. Prasad and Padwick reported its etiology and confirmed that *F. oxysporum* f. sp. *ciceris* is the causal agent of wilt in chickpea (Prasad and Padwick 1939). Lentil wilt causing entity, *F. oxysporum* f. sp. *lentis*, was first time reported by Booth (1971). Similarly, etiology of other *forma specialis* abbreviated f. sp. (plural: *formae specials*, plural ff. spp.) infecting different edible legumes and causing wilt were discovered. Now it is scientifically proven that *F. oxysporum* causes wilt in pulses and is a common factor that limits the quality and yield of edible legumes in all pulse growing areas. The disease is found in most Asian, African, Southern European, and American countries. In India, the disease is widely distributed and known to cause huge yield losses in almost all pulses growing regions however disease severity varies from location to location with the crops (Gaur and Chaturvedi 2004). In addition to *formae specials*, the majority of *Fo* ff. spp. infecting pulses are further categorised in races and pathotypes (Table 1) based on their virulence pattern on different plant genotypes (Sampaio et al. 2020).

Chlamydospores are the primary inoculum for *Fusarium* wilt. They start their germination after being stimulated by germinating seeds and root exudates of host and non-host plants. The chlamydospores can survive in soil and plant debris for more than 5 years (Haware et al. 1996), and so infested soil are the main sources of primary inoculum. Infected seeds are the next source of primary inoculum. *F. oxysporum* f. sp. *cicer* is known to be present in seeds from infected plants. Chlamydospore-like structures have been observed in the hilum region of the seeds, and they co-germinate with the seed and infect the emerging seedling. The infection rate and severity are much higher in plants grown from infected seeds plants raised from healthy seeds grown in sick soil (Haware et al. 1978). The movement of the pathogen is essential for the spread of the pathogen to disease-free soils and geographic areas. Infected seeds having dirt are involved in the long-distance dispersal of the pathogen and its introduction into virgin lands (Pande et al. 2007). Dispersal of infected plant debris and soil through human activity, contaminated machinery, and irrigation water are responsible for the short-distance spread of the pathogen.

3 Symptoms of Wilt Disease

The main symptom of wilt is loss of rigidity and drooping of plant parts including leaves and tender branches in a progressive manner leading to plant death (Agrios 2005, Michielse 2009). Plants infected early during the seedling stage usually show wilting and die quickly. Older plants when infected show varied symptoms like yellowing of leaves, epinasty, defoliation, stunting, and formation of the adventitious roots followed by permanent wilting and death (Table 1). Plants often collapse and lie flat on the ground; necrosis and discolouration could also be observed in the collar region. Often brown discolouration of internal root tissue is visible in infected plants. The infection can occur at any stage of the plant, and affected plants can be found in patches or favourable conditions spread across the whole field (Nene and Reddy 1987; Jiménez-Díaz et al. 2015).

The progression of the disease can be understood very well by taking example of chickpea where clear cut symptoms can be observed at various crop growth stages reflecting disease progression. In the case of chickpea, the disease usually starts appearing after three weeks of sowing. The first symptom appears in form of drooping of leaves and tender stems, later pale coloured leaves, shrunken stems above and below ground followed by plants collapsing flat onto the ground can be seen (Fig. 1a). Upon vertical/longitudinal splitting of infected roots and stem, brown to black coloured vascular tissues can be seen in form of a streak (Fig. 1b). *Fusarium* wilt of chickpea can be confused with other diseases like damping off, dry root rot, *Phoma* blight, *and Phytophthora* root rot but may be distinguished from these based on discolouration of the internal root tissue. Similarly, in chickpea and lentil, the disease in the field can be seen at the seedling stage (early wilting) or in advance crop growth stages (late wilting) showing typical symptoms of sudden drooping and drying of leaves and seedling mortality (Arya et al. 2019). Sometimes apparently healthy-looking roots having reduced proliferation and nodulation with internal discolouration of the vascular system can be seen. Microscopic observation of basal stem/roots of infected plants usually reveals masses of hyphae and conidia in the vascular bundles and discolouration of vascular cells. At an advanced stage, the vasculature is often found to be clogged by fungal mycelium and host defence responses like gels, gums, and tyloses. These structures and exudates prevent the movement of water from the soil thus resulting in wilting (Agrios 2005). Histological distortions occur in the vascular tissues of affected roots and stem as a result of cavity formation between phloem and xylem, xylem and medulla, and phloem and cortical parenchyma, as well as anomalous cellular proliferation in the vascular cambium. This together with the formation of optically dense gels and occlusions in xylem vessels (but not of tyloses), probably contributes to retarded vascular flow of water and nutrients as well as the development of morphological symptoms (Jimenez-Díaz et al. 1989, Jimenez-Díaz et al. 2015).

Fig. 1 Symptom of wilted chickpea plant. **a** Drooping of leaves and **b** Xylem browning in the infected plant

4 Management of Wilt

Fusarium wilt of pulse crops is a monocyclic disease where the pathogen produces only one infection cycle per host cycle. Here disease development is driven by the pathogen's primary inoculums which is usually some resting or surviving structure resistant to desiccation or freezing, such as chlamydospores or mycelium in crop residues. This inoculum is dispersed when the soil is prepared by ploughing and disking the crop residues. When seeds germinate and roots grow in such soils, the seeds come in contact with the resting propagules of the pathogen and become infected. The new inoculum is not dispersed in the soil till the field is prepared again and so cannot initiate a new infection; hence, there is only one complete infection cycle per crop cycle (Arya et al. 2019). As the primary inoculum is a sturdy resting structure like chlamydospore that can withstand unfavourable conditions, therefore exclusion of the pathogen and reduction of the primary inoculum are the main targets of the disease management strategies (Jiménez-Díaz et al. 2015).

The management of *Fusarium* wilt is difficult due to the nature of its primary inoculum. Chemical control is one of the most effective modes of control used by farmers of developed nations to manage soil-borne diseases in crops. Methyl bromide was extensively used as a fumigant in many parts of the world for controlling soil-borne diseases. Conventional synthetic chemical fungicides and fumigants are required to be applied at regular intervals throughout the growing season of the crop to save the crop. However, this approach has numerous disadvantages such as high cost due to which it could not be adopted in developing or underdeveloped countries, human health hazards, damage to the ecosystem, ozone layer depletion, and reduction of non-target beneficial microorganisms in the soil (Panth et al. 2020). The frequent and indiscriminate use of fungicides can lead to fungicide resistance (Panth et al. 2020; Zhao et al. 2017). Therefore, the use of such fungicides is being phased out after the implementation of the Montreal Protocol in 1986. Many different disease control measures were tried in the past which include the following.

4.1 Quarantine and Use of Disease Free Seeds

Wilt disease of pulse crops is responsible for huge loss to the pulse industry and is caused by subspecies of *Fusarium oxysporum* specific to the crop. For example, *F. oxysporum f. sp. pisi* infects pea, *F. oxysporum f. sp. lentis* infects lentil, and *F. oxysporum f. sp. ciceris* infects chickpea. Further, the prevalence of different races within each subspecies makes breeding for resistance more challenging. Though there are resistant sources available to different races of this pathogen still they are few. The pathogen is very long-lived in the soil (as chlamydospores) and can increase in a field each time you replant the susceptible crop. Since resistance breakdown is a reoccurring phenomenon, therefore, the seeds to be used need to be tested for *Fusarium* wilt agents.

4.2 Sowing into Soils with no History

As this pathogen is soil-borne and survives in the soil in form of the resting spores. It is, therefore, necessary that the selection of fields be in such a way that the soil is free of pathogens. For instance, the fields which have not been used for the cultivation of the crops that are prone to *Fusarium* attack can be chosen for cultivation.

4.3 Reduction or Elimination of Inoculum in Soil

This can be achieved by using cultural, chemical, physical, and biological methods. The soil solarisation is the best method as a cultural practice where the heat generated by solarization may not kill a pathogen outright, but the organism may be weakened, resulting in a reduction of its aggressiveness for its host and greater susceptibility to attack by other components of the soil microflora. The other methods include flooding, removal of infected crop debris, burning which can lead to the thermal killing of *Fo* chlamydospores for reducing the risk to subsequent crops.

4.4 Growing of Resistant Cultivars

Many resistant varieties of different pulse crops are now available which contributes to being the most practical and economically efficient control measure for management (Table 2). However, this is a continual activity of the breeding programme to ensure the resistance to the race level and thus the varieties developed can be specifically resistant to a particular race of the pathogen.

4.5 Seed Treatment with Fungicides or Biocontrol Agents

The seed treatment with chemical and biological agents separately or in combination viz. propineb, hexaconazol, zineb, *Pseudomonas fluorescens*, *Trichoderma* spp., *Bacillus* spp., etc., have provided much-needed relief in the management of wilt diseases in pulse crop.

Table 2 List of Resistant/Tolerant/Moderately resistant sources against *Fusarium* wilt in different pulses (Compiled for this study from AICRP reports and DAC data)

Variety	Source	Year	Area of adoption Zone/State of India	Yield (Q/h)	Remarks
Chickpea					
Raj Vijay Gram 121	RVSKVV, Gwalior	2021	CZ	18–20	Resistant
IPCMB19-3	IIPR, Kanpur	2021	CZ	20–21	Resistant
GLK 17301	RVSKVV, Gwalior	2021	CZ	13–14	Resistant
IPK 13-163	RVSKVV, Gwalior	2021	CZ	19.7	Resistant
RSGK 13-414	RVSKVV, Gwalior	2021	CZ	17–18	Resistant
Raj Vijay Gram 210	RVSKVV, Gwalior	2021	CZ	18–21	Resistant
Phule Vikram (Phule G 01808)	MPKV, Rahuri	2020	CZ	22.94	Resistant
SA-1 (Supper Annigeri-1)	ARS, Gulbrga	2020	SZ and CZ	18.35	Highly Resistant
IPC 2005-62	IIPR, Kanpur	2020	CZ	13.5	Moderately Resistant
IPC 2004-98	IIPR, Kanpur	2020	CZ	15–17.5	Moderately Resistant
IPC 2004-01	IIPR, Kanpur	2020	CZ	15–17.5	Moderately Resistant
RLB Chana -1	RLBCAU, Jhansi	2020	SZ	17.18	Resistant
Sabour chana-1	BAU, Sabour	2020	Uttar Pradesh	22–24	Moderately Resistant
BGM 10216	IARI, New Delhi	2020	CZ	13.62	Tolerant
Pusa Parvati (BG 3062)	IARI, New Delhi	2020	CZ	23.62	Tolerant
Haryana Chana No. 7 (H 12-55)	CCSHAU, Hisar	2020	SZ&CZ	18.35	Highly Resistant
RSG 974 (Abhilasha)	RARI, Duragapura	2010	Rajasthan		Moderately resistant
Purva GNG 2299	ARS, Sriganganagar	2019	NEPZ	15	Tolerant
PDKV Kanchan	Dr. PDKV, Akola	2019	Maharashtra	19.35	Resistant
RVS 204	CoA, RVSKVV, Sehore	2019	Madhya pradaesh	20–25	Resistant
RVS 205	CoA, RVSKVV, Sehore	2019	Madhya pradaesh	20–25	Resistant
PDKV Kanchan	Dr. PDKV, Akola	2019	Maharashtra	19.35	Resistant
IPC 2006-77	IIPR, Kanpur	2019	CZ	20–22	Moderately Resistant
RVKG	CoA, RVSKVV, Sehore	2019	Madhya Pradesh	20–22	Moderately Resistant
Pant gram 5	GBPUA&T, Pantnagar	2017	NWPZ	22.15	Tolerant

(continued)

Table 2 (continued)

Variety	Source	Year	Area of adoption Zone/State of India	Yield (Q/h)	Remarks
GNG 2171	ARS, Sriganganagar	2017	NWPZ	20.14	Tolerant
GJG 0809	JAU, Junagarh	2017	NHZ	16	Moderately Resistant
GNG 2144	ARS, Sriganganagar	2016	NWPZ	22	Tolerant
JGK -5	JNKVV, Jabalpur	2016	CZ	15–17	Resistant
CSJ 515	RARI, Durgapura	2016	NWPZ	24	Resistant
JG -36	JNKVV, Jabalpur	2016	CZ	18–20	Tolerant
Vallabh Kabuli Chana-1 (WCGK-2000-16)	SVBPU A&T, Modipuram	2015	NWPZ	23	Moderately resistant
JSC 55 (RVG 202)	CoA, RVSKVV, Sehore	2012	CZ	20	Resistant
JSC 56 (RVG203)	CoA, RVSKVV, Sehore	2012	CZ	19	Moderately resistant
Raj Vijay Kabuli gram 101 (JSC 42)	RVSKVV, Gwalior	2012	Madhya Pradesh	15–20	Resistant
Raj Vijay gram 201 (JSC 40)	CoA, RVSKVV, Sehore	2012	Madhya Pradesh	20–25	Resistant
HK 4 (HK 05-169)	CCSHAU, Hisar	2012	NEPZ	15	Resistant
Surya (MRG-1004)	ARS, Madira	2009	Andhra Pradesh	20–22	Tolerant
JAKI 9218	Dr. PDKV, Akola	2008	Maharashtra	18.65	Resistant
Pigeon Pea					
Warangal Kandi-1 (WRGE-97)	ANGRAU, Hyderabad	2020	Telangana	12–21	Moderately resistant
Raj Vijay Arhar 19 (RVA 19) (RVSA-16-1)	CoA, RVSKVV, Sehore	2020	SZ	12–15	Moderately resistant
Telangana Kandi (WRGE-93)	ANGRAU, Hyderabad	2020	SZ	17	Moderately resistant
Tirupati Kandi 59 (TRG-59)	ANGRAU, RS, Guntur	2020	Andhra Pradesh	16–17	Tolerant
Krishna (LRG 105)	ANGRAU, RS, Guntur	2020	Andhra Pradesh	14.64	Resistant
IPH 15-03	IIPR, Kanpur	2020	Delhi, Haryana, Punjab, Uttar Pradesh	15.95	Resistant
IPA 206	IIPR, Kanpur	2020	Uttar Pradesh	10.63	Resistant
Chhattisgarh Arhar-1 (RPS 2007-10)	IGKV, Raipur	2020	Chhattisgarh	18–20	Moderately resistant
CO 9 (CRG 2012-25)	NPRC, Vamban	2019	SZ	17	Moderately resistant
GT-104 (NPMK-15-05)	NAU, Navsari	2019	Gujarat	18.9	Resistant
DA-2012-1 (Rajendra Arhar-1)	Dr. RPCAU Bihar	2019	Bihar	28–30	Moderately resistant

(continued)

Table 2 (continued)

Variety	Source	Year	Area of adoption Zone/State of India	Yield (Q/h)	Remarks
BDN 716 (BDN 2008-7)	ARS, Badnapur	2017	Maharashtra	21–22	Resistant
Amaravathi (LRG-52)	ANGRAU, RS, Guntur	2017	Andhra Pradesh	14.69	Moderately resistant
GRG 881	ARS, Gulbarga	2016	Karnataka	13–16	Resistant
LRG 52	RARS, Lam	2015	Andhra Pradesh	15–18	Moderately resistant
ICPH 2740	ICRISAT, Hyderabad	2015	Telangana	15–16	Resistant
PKV TARA (TAT—9629)	Dr. PDKV, Akola	2013	CZ		Resistant
Phule T 0012	MPKV, Rahuri	2012	CZ	18–20	Moderately resistant
BDN 711 (BDN2004-3)	ARS, Badanapur	2012	Maharashtra	15–23	Moderately resistant
TS-3R	ARS, Gulbarga	2011	Karnataka	11–17	Resistant in Kharif and late sown cropping system
Lentil					
IPL 329	IIPR, Kanpur	2021	Uttar Pradesh	12–18	Tolerant
IPL 225	IIPR, Kanpur	2021	Uttar Pradesh	10–11	Resistant
Chhattisgarh Masoor -1 (RL 3-5)	IGKV, Raipur	2020	Chhattisgarh	10–11	Resistant
Kota Masoor-4 (RKL 58 F 3715)	AU, Kota	2020	CZ	18.76	Resistant
IPL 534	IIPR, Kanpur	2020	Madhya Pradesh (including other states of CZ)	16–18	Resistant
L-4729	IARI, New Delhi	2020	CZ	17–18	Moderately resistant
VL Masoor-148	VPKAS, Almora	2020	NHZ	11–12	Moderately resistant
LL 1373	PAU, Ludhiana	2020	NWPZ	15–16	Moderately resistant
Raj Vijay Lentil 13-5	CoA, RVSKVV, Sehore	2019	Madhya Pradesh, Chhattisgarh and parts of Rajasthan	12	Moderately resistant
RVL-13-7 (Raj Vijay Lentil 13-7)	CoA, RVSKVV, Sehore	2019	Madhya Pradesh, Chhattisgarh and Rajasthan	12	Resistant
Shekhar 4 (KLB 345)	CSAUA&T, Kanpur	2018	Uttar Pradesh	18–20	Resistant
L 4727	IARI New Delhi	2018	CZ	11–15	Moderately resistant
Shekhar 5 (KLS 122)	CSAUA&T, Kanpur	2018	Uttar Pradesh	16–18	Resistant
IPL 321	IIPR, Kanpur	2018	Uttar Pradesh	9–10	Resistant
RVL 11-6	CoA, RVSKVV, Sehore	2017	CZ	11–12	Tolerant
Pant Lentil–9 (PL 098)	GBPUA&T, Pantnagar	2016	Uttarakhand	13–14	Resistant
L 4717 (Pusa Ageti Masoor)	IARI, New Delhi	2016	CZ	12–13	Resistant
KLB 2008-4 (Krati)	CSAUA&T, Kanpur	2015	Uttar Pradesh	18–20	Resistant

(continued)

Table 2 (continued)

Variety	Source	Year	Area of adoption Zone/State of India	Yield (Q/h)	Remarks
KLS 09-3 (Krish)	CSAUA&T, Kanpur	2015	Uttar Pradesh	18–20	Resistant
IPL 316	IIPR, Kanpur	2013	CZ	14–15	Tolerant
Shalimar Masoor-2	SKUAST-K Srinagar	2013	Kashmir Valley	12.85	Moderately resistant
VL Masoor 133 (VL133)	VPKAS, Almora	2011	Uttarakhand	11	Resistant
VL Masoor 514(VL514)	VPKAS, Almora	2011	Uttarakhand and Hills	9–10	Moderately resistant
VL Masoor 133 (VL 133)	VPKAS, Almora	2010	Uttarakhand	11.25	Resistant
Pant L 8 (Pant L 063)	GBPUA&T, Pantnagar	2010	NWPZ	15–16	Moderately resistant
Pant Lentil 7 (PL 024)	GBPUA&T, Pantnagar	2010	Punjab, Haryana, UP	15	Resistant
Pant Lentil-6 (PL 02)	GBPUA&T, Pantnagar	2010	Uttarakhand	11	Resistant
V L Masoor 129	VPKAS, Almora	2010	Uttarakhand	9	Resistant
Shekhar Masoor 3 (KLB-320)	CSAU&T, Kanpur	2009	Uttar Pradesh	14	Moderately resistant
Shekhar Masoor 2 (KLB-303)	CSAU&T, Kanpur	2009	Uttar Pradesh	14	Moderately resistant
Moitree WBL 77	PORS, Berhampore	2009	East UP, Bihar, Jharkhand, Assam & WB	15	Resistant
Pea					
VL Matar 47 (VL47)	VPKAS, Almora	2011	Uttarakhand	14	Resistant

NHZ (North Hill Zone): Himachal Pradesh, Jammu & Kashmir, Uttarakhand; NWPZ (North West Plain Zone): Punjab, Haryana, Delhi, Rajasthan, Western Uttar Pradesh; NEPZ (North East Plain Zone): Uttar Pradesh, Bihar, Jharkhand, Odisha, Assam, West Bengal; CZ (Central Zone): Madhya Pradesh, Gujarat, Maharashtra, the southern part of Rajasthan and Bundelkhand tracts of Uttar Pradesh; and SZ (South Zone): Andhra Pradesh, Telangana, Karnataka, Tamil Nadu and south-east part of Odisha.

4.6 Good Cultural Practices

Good cultural practices include cultural practices such as intercropping, timely seeding, clean cultivation, and crop rotation. It is well known that early planted pulse crops are usually affected more by disease and delayed planting can be a better alternative to address this issue. Further, the plant spacing is also crucial because the shallow root system in widely spaced crops makes it susceptible to wilt disease when subjected to moisture stress. Similarly, the seeds must be planted at proper depth (10-12 cm) to reduce the disease incidence as the shallow sown crop can be affected by the disease. The other method of good practices includes intercropping. For instance, intercropping of wheat, barley, linseed, and mustard with chickpea has proved to be effective in reducing the wilt incidence and increasing the yield of chickpea (Agarwal et al. 2002). The lowest wilt incidence is reported in chickpea with intercropping and mixed cropping with linseed (Lodhi et al. 2016). Mixed cropping of chickpea with wheat and berseem gives measurable disease control (Hari and Khirbat 2009).

However, none of these measures eliminates the causal agent from the soil due to the nature of the propagule. Moreover, their effects like the conventional fungicides are not instant and total. These measures require persistent efforts over a while to become effective. Therefore, for the management of fusarium wilt, dependence on a single method needs to be avoided (Katan 1999, 2000) and an integrated management strategy whereby different practices are included, should be used (Haware et al. 1990, Jimenez-Díaz and Jimenez-Gasco 2011).

The next most effective strategy to manage vascular wilt diseases next to the use of a synthetic fungicide is the use of genetic resistance in host plants. Breeding and using resistant cultivars is the most effective, reliable, and safe alternative to chemical treatments that can be combined with other management practices in an integrated management strategy. However, as we try to exploit a resistance source meanwhile the pathogen also may evolve to overcome the resistance. So, identifying a novel source of resistance and incorporating it in the breeding programme is a constant process and newer sources are to be identified continually.

5 Genetics of Resistance

Plants show two types of resistance viz., quantitative and qualitative resistance. Genes associated with qualitative resistance (R-genes) usually provides a complete resistance and are therefore also known as major genes. R-genes are most dominant and usually code for pathogen recognition proteins (Nelson et al. 2018). Some of the known R-genes found in major legumes against *Fusarium* wilt are given in Table 3.

On the other hand, quantitative disease resistance (QDR) has a phenotype of incomplete or partial resistance and is controlled by multiple genes. These genes do not show any pronounced effect and are known as minor genes (Nelson et al. 2018). These genomic loci are usually mapped as quantitative trait loci (QTLs). A major resistance quantitative trait locus (QTL) Fnw4.1 (*Fusarium* near wilt) in pea against *Fo* f. sp. race 2 was located in linkage group LG4, as reported by McPhee et al. (2012). Bani et al. (2018) could identify an oligogenic control, with nine SNPs (single-nucleotide polymorphisms) associated with seven candidate resistance genes against *F. oxysporum* f. sp. *phaseoli* on chromosomes 4, 5, 7, and 8 in common bean using genome-wide association studies (GWAS) on a Portuguese accessions collection. Once genes and genomic loci that confer disease resistance are identified they are incorporated in the genome of non-resistant genotypes that are superior in other traits by breeding programmes.

There are two main mechanisms involved in the plant immune response-pathogen associated molecular pattern (PAMP)-triggered immunity (PTI) also known as basal resistance and effector-triggered immunity (ETI). Upon exposure to the wilt pathogen, plants recognize pathogen-associated molecular patterns (PAMPs) through their pathogen pattern-recognition receptors (PRRs) (Nelson et al. 2018). Pathogen-associated molecular pattern (PAMP)-triggered immunity is a broad-spectrum non-host resistance, the phenomenon which makes plants resistant to almost all the microbial pathogens (Lee et al. 2017). PTI is a broad-spectrum resistance that is triggered in response to conserved pathogen features (PAMPs). It can also contribute to quantitative resistance. By contrast, effector-triggered immunity forms the basis of qualitative resistance.

6 Conventional Breeding

The conventional method of breeding has the following steps (i) screening germplasm to identify resistance sources, (ii) hybridization of selected parents, (iii) selection and evaluation of hybrids, and (iv) testing and release of new varieties. Screening of germplasm for identification and characterization of resistant sources is the first step in any classical breeding program for *Fusarium* wilt resistance. It involves mass screenings of large germplasm collections of the same or sometimes related legume species. In search of the resistant donors for *Fusarium* wilt, efficient screening methods are essential. The identification of resistance sources starts normally with mass screenings of large germplasm collections of accessions from the same, or less frequently, related species. The resistance mechanisms of the most promising resistance sources identified through these mass approaches can then be further explored through more detailed screening methods in a smaller number of selected accessions.

Mass screening is performed directly in the sick field (Fig. 2). The sick field could be naturally infested but most often artificially created wilt-sick plots are used where *F. oxysporum* is the only dominant pathogen. Controlled environments, like greenhouse or growth chambers, are used only to optimise disease development conditions or small-scale screening during the non-conducive environment. In this, the parameters are based mainly on whole plant, leaves, or xylem direct observations, and less commonly, on the root aspect. The phenotyping technique allows the screening of a large number of different genetic accessions under natural environmental conditions. For this, a naturally infected field can be used but the most common alternative approach is the use of artificially infected fields through wilt-sick plots as the homogenization of the disease pressure across the field is crucial. Further, in a naturally infected field, the co-infection of other pathogens including nematodes is also a constraint that can lead to interference in the results (Personal information). On the other hand, the controlled environments where the optimum conditions can be managed for the disease development which in turn can facilitate the screening throughout the year, i.e. apart from crop season. One such method is the root dip technique where the roots of 7-10 days old seedlings are given a cut and later these are immersed in the inoculum suspension which permits the direct entry of the pathogen and thus the development of disease shall be faster leading to strong symptom development. Secondly, the phenotyping of the germplasm under hydroponics where the 7-10 days seedlings developed through hydroponic were exposed to the inoculum by allowing the inoculum to flow with the Hoagland solution for 4-5 days. This technique is similar to

Table 3 Wilt resistance gene in some grain legumes (Choudhary et al. 2013)

Fusarium race/variant	Number and nature of WR gene	Gene symbol	Remarks
Chickpea			
Race 0	Monogenic or digenic	*foc-0*$_1$/*Foc-0*$_1$	Marker-assisted characterization of Complete resistance
	Monogenic or Digenic	*foc-0*$_2$/*Foc-0*$_2$	-
	Polygenic	–	Act along with vertical resistance genes
Race 1	Trigenic	*H1/h1, H2/h2, H3/h3*	3 independent genes
	QTL	FW-Q-APR-6-1, FW-Q-APR-6-2	–
Race 1A	Trigenic	*h1* (syn *foc-1*), *h2 H3*	Recessive at first two loci and dominant at the third locus
Race 2	Monogenic	*foc-2*	Complete resistance
	Digenic	–	–
	Trigenic	*a, b, C*	Individually confers late wilting, first two genes impart complete resistance
	Polygenic	–	Influencing the major WR Genes
Races 3	Monogenic	*foc-3*/*Foc-3*	Complete resistance
Race 4	Monogenic recessive	*foc-4*	Complete resistance
	Digenic recessive	–	Complete resistance
Race 5	Monogenic	*foc-5*/*Foc-5*	Complete resistance
Variant not specified	Multiple genes	–	–
Variant not specified	Digenic interaction	–	Complementary genes
Variant not specified	Monogenic Recessive	*pwr1*	WR in ICP 8863
Variant not specified	Monogenic Recessive	–	WR in ICEAP 0040
Variant not specified	Digenic recessive Genes	–	WR in ICP 8863
Isolate 8801	Monogenic dominant	*FuR1*	Dominant gene
Variant not specified	Monogenic dominant	–	Dominant gene
Variant not specified	Digenic interaction	–	Resistance is inhibitory in NPP 725, and is complementary in NPP 726
Variants (V1, V2, V3, V4)	Double recessive	–	duplicate gene action

(continued)

Table 3 (continued)

Fusarium race/variant	Number and nature of WR gene	Gene symbol	Remarks
Lentil			
Strain not specified	Five genes	–	Independent genes
Strain not specified	Duplicate genes	–	Resistance in PL 234
Strain not specified	Two complementary genes	–	Resistance in JL 446 and PL 286
Strain not specified	Monogenic dominant gene	–	ICARDA experiments
Strain not specified	Monogenic dominant gene	*Fw*	Resistance in ILL 5588
Pea			
Pisi race 1	Monogenic	Fw	Complete resistance
Pisi race 2		Oligogenic/Poleygenic	
Fnw4.1, Fnw3.1, Fnw3.2		Major resistance QTL in LG4, Fnw4.1and two additional QTLs located in LG3	
Pisi race5	Monogenic	Fwf	Complete resistance

Fig. 2 Screening of chickpea germplasm in wilt sick plot Jhansi, India. The picture shows **a** Resistant lines **b** Highly susceptible checks **c** Late wilting check

the root dip technique and the symptoms develop strongly and faster thus permitting the screening of a large number of germplasm in a short period.

However, this inoculation process is a priori excluding the screening for resistance mechanisms that might be associated with the root penetration stage. Yet, there are clear indications of the existence of other resistance mechanisms acting at earlier stages. Focus on identifying variation for these mechanisms would add layers of resistance that will increase the efficacy and durability of major resistance genes (Sampaio et al. 2020). Several other screening methods wherein the germplasm can be phenotyped includes transmission electron microscopy and light, electron, fluorescence and laser confocal microscopy which allows an initial characterization of the resistance mechanisms among pea, lentil, and chickpea (Sampaio et al. 2020). Various strategies have been developed for the screening of wilt resistant genetic resources. Nene and Haware 1980 and Thaware et al. 2017 proposed and used a 0–5 scale for screening on a larger scale.

After screening and identification of the resistance source the introgression of the genomic regions responsible for conferring resistance into non-resistant genotypes is accomplished by crossing and selection. For instance, in chickpea, single crosses between Desi-type parents carrying *Fo* resistance, with Kabuli-type parents, characterized by their large seed size and seed quality, have been successfully adopted in *Fusarium* wilt resistance breeding programs (Gaur et al. 2007a). If accurate and precise data regarding the genetic basis of resistance is available usually an established methodology like backcross breeding is commonly used to introgress resistance into superior varieties. For example, when resistance is conferred by a single gene such as in chickpea against *Fo* f. sp. *ciceris* race 5, backcross breeding has been commonly used to introgress resistance into well-adapted varieties (Gaur et al. 2012).

7 Integrated Breeding Approaches

The exploitation of host plant resistance for the management of any disease remains a most effective and economical way to minimize yield losses likely to be caused by plant pathogens. The identification of stable donors possessing genes conferring resistance against fusarium wilt in several pulses including chickpea and lentil has paved the way for the development and release of highly resistant varieties of chickpea (H 82-2, DCP 92-3, JG 315, JG 16, JG 63, Pusa 547, Pusa 362, Vijay, KWR 108, GBM 2, etc.), lentil (DPL 62, IPL 316, JL 3, Pusa Vaibhav, etc.), pigeon pea (IPA 203, IPA 206, Narendra Arhar 1, Azad Arhar 1, BSMR 736, etc.), and pea (VL Matar 47) (Personal unpublished data). The large scale adoption of wilt resistant varieties ensured higher productivity in traditional areas where wilt was used to cause huge yield losses, and it is also evident from the enhanced productivity of these crops.

While conventional resistance breeding can be very successful it involves tedious processes for screening and repeated back-crossing. Moreover, fast-evolving pathogens like *Fusarium sp* have a dynamic relationship with the host and can overcome resistance hence resistance breeding is a continuous process requiring constant incorporation of genes from new sources. Also due to phenomena like linkage drag resistance may be evaded by fast-evolving pathogens (Veillet et al. 2020; Sperschneider et al. 2015) which warrants for pyramiding of genes conferring resistance against particular disease e.g. *Fusarium* wilt causing vascular wilt has 6-7 races in India, therefore pyramiding of genes to develop multiracial resistant chickpea varieties is inevitable.

Genome sequencing and genetic mapping can facilitate rapid identification of genes or Quantitative Trait Loci (QTLs) for their deployment in a systematic breeding program. The development of robust trait linked markers will certainly increase the efficiency of the selection of desirable segregants from large segregating populations. The use of molecular markers closely linked to genes or QTLs controlling *Fusarium* wilt resistance allows a faster and more precise breeding (Sampaio et al. 2020). Significant progress has been made for genomics-assisted breeding in lentil, chickpea, and pea including the development of genomic resources, high-density linkage maps, identification of candidate genes for functional genomics, development of draft genomes, and identification of Single nucleotide polymorphism (SNP) and Simple sequence repeats (SSR) markers linked tightly with traits of breeders' interest (Kumar et al. 2021; Pratap et al. 2017).

Marker-assisted backcrossing (MABC) is the simplest way to introgress genes/QTLs, particularly a finite number of QTL(s)/gene(s) experiencing strong and durable effects on the phenotype (Varshney et al. 2012; Xu et al. 2012). For instance, in chickpea, marker-assisted backcrossing (MABC) has allowed the targeted transfer of genomic regions conferring FW resistance (foc 4) from WR 315 to Annigeri 1 and JG 74, two elite yet FW-sensitive elite chickpea cultivars. The wilt resistant chickpea varieties viz., Super Annegeri 1 and Improved JG 74 were developed (Mannur et al. 2019) and later one more wilt resistant chickpea variety IPCMB 19-3 has been notified in 2021 for cultivation in central India. Genomics-assisted breeding approaches such as marker-assisted selection (MAS), haplotype-based breeding, allele modification through genome editing, and genomic selection (GS) in general are expected to be key components of designing future crops (Varshney et al. 2021; Jha et al. 2021). The genomic selection allows for simultaneous selection of multiple traits compared to traditional marker-assisted selection (Jha et al. 2021). The availability of several genome sequences of vascular pathogens has inspired novel research efforts to unravel the molecular basis of vascular wilt diseases. To design novel strategies to combat vascular wilt diseases, understanding the (molecular) biology of vascular pathogens and the molecular mechanisms underlying plant defence against these pathogens is crucial (Yadeta and Thomma 2013).

Cazzola et al. (2021) rightly pointed out that crop breeding is a time-consuming process and most of the traditional breeding programs take 10–15 years to release any improved cultivar. In view of a breeder to develop a model of the expected change in a trait in response to selection, reduced seed to seed duration (generation turnover duration) is the most powerful parameter for increasing genetic gain. In past, breeders use to take advantage of offseason generation advancement at an appropriate location to fix genes in a breeding program. Shuttle breeding, double haploids, and *in vitro* culture are some of the methodologies that have been developed so far; however, they have not been implemented efficiently in the breeding programs for pulses. In this context, speed breeding emerges as a technology that allows advancement by 4–5 generations per year under a controlled environment where immature seeds/embryos are used to develop plants and harvest seeds. This method has been found most useful for the development of mapping populations. It was recommended for the chickpea that the countries with environmental conditions similar to southern India, having short chickpea season (e.g., Myanmar), can try to take three generations per year (Gaur et al. 2007b). This method uses optimal light quality; light intensity, day length, and temperature control to accelerate photosynthesis and flowering, coupled with early seed harvest. Samineni et al. (2020) demonstrated that rapid generation advances (RGA) in chickpea can produce up to seven generations per year and enable speed breeding. Their results were having encouraging implications for breeding programs: rapid progression toward homozygosity, development of mapping populations, and reduction in time, space, and resources in cultivar development (speed breeding).

The transgenic technology also offers ample potential to develop resistant varieties having genes from other species or genera. Genetic engineering techniques permit the simultaneous use of several desirable genes in a single event, thus, allowing the introduction of novel genes/traits into elite cultivars. Earlier, Amian et al. (2011) stressed enhancing transgenic pea resistance against fungal diseases through the stacking of two antifungal genes (chitinase and glucanase) where stable inheritance of the antifungal genes in the transgenic plants was demonstrated.

8 Conclusion

Breeding for disease resistance will always be a priority from the breeder's point of view and therefore sourcing novel variations of disease resistance from unexploited landraces and wild relatives shall provide a way of broadening the genetic base. Knowledge about the pathogen has improved, but the challenges remain as the region-specific races need to be identified and exploited as there are probably differences in the reaction of different cultivars against different races of the pathogen infecting it. Thus, information on the distribution of races will be of great importance for breeding programs for the development of race-specific resistant genotypes. Further, there is also a need to explore a set of host differentials for correlating the pathogenicity. The robust phenotyping techniques for resistant donors for the pathogen are also required. Due to limited work carried out for host-pathogen interaction studies, the management of the disease management remains elusive and thus MAS and MABC offers a great opportunity for improved efficiency and effectiveness in the selection of plant genotypes with a desired combination of traits.

It is also important to explore non-transgenic approaches including RNAi technology and virus-induced gene silencing (VIGS) to understand the molecular mechanisms of host resistance in these pulse crops. Further, integrated disease management for wilt in these crops will remain a top priority area apart from the exploitation of host plant resistance to narrow down the yield losses due to *Fusarium* wilt in these pulses. An efficient combination of the frontier technologies like MAS, MABC, etc. needs to be integrated with conventional methods of the handling of segregating generation to enhance selection efficiency. Similarly, technologies such as transgenic development, gene silencing, or genome editing are going to play a major role in the creation of new variations. The integration of new approaches will certainly accelerate the development of resistant cultivars having targeted genes/QTLs in less time (Jha et al. 2021).

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Atmospheric Nitric Oxide (NO) Regulates Ozone (O_3)-induced Stress Signaling in Plants: Ally or Foe?

Soumya Mukherjee

Abstract

Atmospheric nitric oxide (NO) acts both beneficial and detrimental to plant growth. However, accuracy and precision of NO analysis in natural sites remain a major hurdle for conducting such investigations. Community assemblage, forest canopy and anthropogenic activities play a vital role in NO emission and its exchange in plants. Ecosystems in the humid tropics are characterized by higher biological activities thus leading to increased emission of atmospheric gases. Nitric oxide emission due to biological activity mostly involves its exhalation from the soil. NO liberated due to microbial activity thus depends upon the climate and ecosystem of a particular area. Apart from photolytic reduction of NO_2, there are other abiotic sources of NO accumulation like ammonia oxidation, fossil fuel burning and automobile emission. Urbanization effects on vegetation are usually manifested by a reduction in plant growth, chlorosis and altered metabolic activity of the plant. Among various gaseous components (natural and pollutants) present in air mixtures, nitrogen oxides (NO_x; NO_2, NO) are major photochemical pollutants increasing in the urban areas. However, beneficial effects of nitric oxide appear to be a specialised effect operative by the reduction in tropospheric ozone and upregulation of nitrogen metabolism. Atmospheric NO, ozone and CO_2 interaction require much attention to plant growth and stress management. Atmospheric pollutants are crucial in regulating gaseous diffusion through foliar parts of different plant systems. Recent developments have suggested that nitric oxide-mediated modulation of plant growth response operates through the regulation of tropospheric ozone levels. Current understandings thus provide substantial insights into the facet of plant-environment interaction with nitric oxide formation.

Keywords

Abiotic stress • Nitric oxide • Nitrogen oxides • Ozone • Reactive oxygen species

1 Introduction

Nitric oxide is a colourless, chemically active gaseous free radical prevalent in the atmosphere. Among various gaseous components (natural and pollutants) present in air mixtures, nitrogen oxides (NO_x; NO_2, NO) are major photochemical pollutants increasing in the urban areas (Peterson 1969; Lovett et al. 2000). Extensive industrialization in the urban areas of developing countries has led to an alarming increase in sulphur and nitrogen oxide levels in air ranging from 20 to 150 ppb (Fowler and Cape 1982). Diurnal fluctuations of air pollutants in urban and rural areas largely depend upon meteorological factors. According to Law and Mansfield (1982), the presence of NOx as an atmospheric component cannot be avoided in rural and urban areas. This pertains to the emission of NO_x mainly originating from the combustion of fossil fuels. Investigations across the past few decades have revealed both beneficial and detrimental effects of nitrogen oxides on plant growth and development (Freedman 1995; Gregg et al. 2003). Nitric oxide formation results from a reaction of nitrogen and oxygen catalyzed by the high heat of combustion. A lower amount of nitric oxide has also been reported to be present in unpolluted areas far away from the access of anthropological activities. The beneficial effects of nitric oxide as a gaseous pollutant is not only limited to its physiological response but also triggers alterations in the levels of O_3 and OH radicals in the atmosphere (Bakwin et al. 1990). Nevertheless, the beneficial effects of gaseous pollutants on urban plantations have been reconsidered through various investigations. In this context, it is important to understand the process of nitric oxide flux and its turnover between soil and atmosphere. Different content

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S. Mukherjee (✉)
Department of Botany, Jangipur College, University of Kalyani, Kalyani, 742213, West Bengal, India

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of atmospheric nitric oxide has been reported in forest and grassland ecosystems of tropical and temperate areas. Various terrestrial and extra-terrestrial sources of atmospheric NO influence plant growth in a concentration-dependent manner. The context of pollutant-NO affecting plant growth was initially investigated by Anderson and Mansfield (1979). The authors reported a concentration-dependent response of NO on the growth of tomato plants. Following such preliminary investigations, various reports have been documented on the potential role of atmospheric NO on plant growth. Air in polluted urban areas contains various poisonous emissions causing inhibitory effects to plant growth. However, irrespective of such deleterious factors elevated temperature and increased CO_2 percentages often contribute to enhanced plant growth in urban areas (Idso et al. 2001). Investigations have deciphered the multi-factorial effect of anthropogenic activities on atmospheric composition in relation to vegetation growth. Edaphic factors of nutrient status, precipitation levels, microbial activity and nitrogen turnover are not the sole factors affecting the rate of plant growth. Current understandings of the effect of atmospheric NO on plant growth shall provide interesting insights into the aspect of plant-environment interactions.

2 Sources of Atmospheric Nitric Oxide Generation

2.1 Abiogenic Sources of NO Emission

Various biotic and abiotic sources contribute to the accumulation of NOx levels in the atmosphere. An equilibrium exists between NO and NO_2 formation in form of a non-enzymatic reaction in the atmosphere. Nitric oxide formation in the atmospheric layers beyond the troposphere is mostly associated with the conjugation of charged nitrogen species to form their respective oxides (Fig. 1). Charged nitrogen species combine with oxygen to form NO in the thermosphere (Norton and Barth 1970). However, NO formed at the thermosphere is not penetrable into the lower layers of the stratosphere or mesosphere. Photochemical decomposition of nitrous oxide in the stratosphere leads to the liberation of NO. Free nitrogen and oxygen species produced as an act of ionization by cosmic rays also contribute to NO formation in the stratosphere (Warneck 1972; Nicolet and Petermans 1972). Extensive investigations have been reported for the understanding of NO accumulation in the troposphere. This amount of NO originating from the natural or anthropogenic activity is of active interest to biological interactions. Photochemical decomposition of NO_2 caused by solar radiation leads to NO formation in the troposphere (Hargreaves et al. 1992). NO being chemically active, a small proportion of it upon oxidation is immediately converted back to NO_2. In this context, it is worth mentioning that reaction equilibrium exists between ozone and NO levels present in the atmosphere. NO combines with O_3 to form NO_2 (Fig. 1). This reaction remains an important basis for variable O_3 levels affecting physiological responses in plants growing in rural and urban areas. This mechanism shall be elaborated in the following section of the chapter. Apart from photolytic reduction of NO_2, there are other abiotic sources of NO accumulation like ammonia oxidation, fossil fuel burning and automobile emission. Atmospheric lightening is an important source of NOx generation. Lightening has been reported to result in a high ratio of NO/NO_2 (Stark et al. 1996). However, the magnitude and percentage of NO accumulation from lightning flash need to be investigated. A higher amount of NOx and O_3 accumulation in the troposphere often results due to lightning in the humid climatic conditions.

2.2 Biogenic Sources of NO Emission

Nitric oxide emission due to biological activity mostly involves its exhalation from the soil. NO liberated due to microbial activity thus depends upon the climate and ecosystem of a particular area. Soils in both tropical and temperate areas have been reported to contribute up to 15% of NOx levels present in the atmosphere (Logan 1983). Among various soil systems, it has been observed that fertile and humid lands invariably liberate higher NO flux in the atmosphere in comparison with dry unfertile soils (Slemr and Seiler 1984; Williams et al. 1987; Johansson and Sanhuenza 1988). Bakwin et al. (1990) reported that photochemical activity leading to NOx formation in lower altitudes of the humid tropical area is important for NO generation. This has been attributed to increased solar UV flux and elevated atmospheric moisture in the tropics. Ecosystems in the humid tropics are characterized by higher biological activities thus leading to increased emission of atmospheric gases. Bakwin et al. (1990) suggested that tropical forests are a greater sink for soil-generated NO in wet weather conditions. The authors interestingly concluded that soil texture and moisture levels were important determinants of NO exchange capacity between the soil and atmosphere. Greater air-filled spaces of dry sandy/loamy soil allowed a higher flux of NO escaping in the atmosphere. Thus tropical forests were concluded to act differently in wet and dry seasons respectively. Furthermore, nitrate fertilization exhibited a concomitant rise in NO levels. Soil-based NO liberation is mostly associated with the biogenic activity of autotrophic or heterotrophic nitrifiers. Some other activities also include anaerobic denitrification and nitrate respiration by fermenters (Anderson and Levine 1987). The

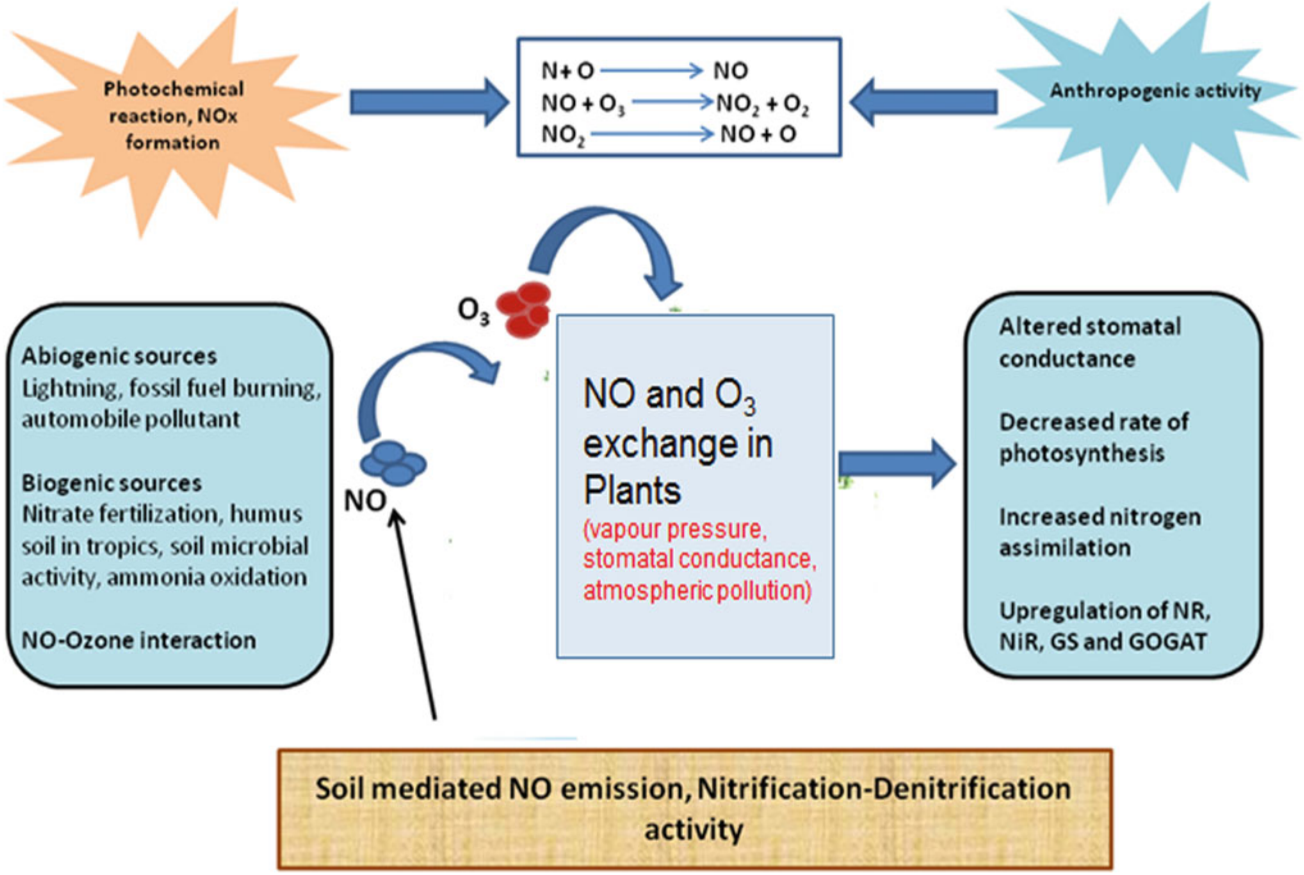

Fig. 1 Diagrammatic representation of nitric oxide-ozone interaction in the atmosphere-plant interface and its role in stress management in plants

authors reported that the proportion of NO liberation was higher for autotrophic nitrifiers present in aerobic soil. Nitric oxide thus produced results from oxidation of hydroxylamine or nitrite reduction. The aerobic process of NO biogenesis largely depends upon the levels of oxygen and moisture prevalent in the soil.

3 Nitric Oxide-Mediated Modulation of Plant Stress Response Operates Through Regulation of Tropospheric Ozone Levels

Ozone is a major secondary atmospheric pollutant known to affect plant growth and physiology. The concentration of ozone in the atmosphere is mostly seasonal and depends upon the intensity of sunlight and temperature (Lane 1983). The ozone layer prevalent in the stratosphere shields the entry of harmful mutagenic UV-B wavelengths from entering into the troposphere. However, apart from the beneficial effects, tropospheric ozone affects plant growth by acting as a pollutant. Ozone formation and breakdown is differentially regulated by the levels of nitrogen oxides present at the different layers of the atmosphere. Ozone freely diffuses across plant membranes and produces ROS in the apoplastic spaces. These results in oxidative damage to plants manifested by chlorosis, stomatal closure and stunted growth. The evolutionary relationships of NO and ozone have been interpreted to have been associated with the primitive atmosphere where ozone was a predominant molecule emitted as a result of photolysis of oxygen (Feelisch and Martin 1995). In this context, NO generation proved beneficial which detoxified the effect of ozone. Primitive cyanobacterial members respiring in such an atmosphere could involve NO generation as a defence mechanism. The authors also speculated that L-arginine mediated NO biosynthesis in mammalian cells resulted from the transformation of nitrification–denitrification reactions of prokaryotes. Nitric oxide combines with ozone in the troposphere to liberate nitrogen dioxide. Plants growing in different areas subjected to the variable composition of atmospheric gases reveal a difference in their growth and biomass accumulation (Gregg et al. 2003, 2006). Two similar investigations reported by Gregg et al. (2003, 2006) involved the effect of nitrogen oxide and ozone responsible for variable growth of cottonwood trees (*Populus deltoides*). Interestingly enough, the authors reported that reduced growth of *Populus* in the rural areas was attributed to detrimental effects of persistently higher ozone content. Correspondingly, urban areas experienced better tree growth facilitated by a reduction in ozone levels. Increased levels of NOx in the urban areas counter decreased the ozone levels. Monitoring of pollutant levels in rural and urban areas revealed more than a ten-fold increase in NOx levels in the rural atmosphere. This resulted in decreased ozone levels. The parameters implied for monitoring tree growth mostly included height and root-shoot biomass. Model-based predictions revealed that altered temperature and carbon/nitrogen turnover in rural areas were not the sole determinants of increased biomass accumulation of the cottonwood plants. Gregg et al. (2003) reported that implying similar conditions of soil, nutrient status and CO_2 levels in both rural and urban sites the investigations revealed doubling of biomass of urban grown plants. Thus, ozone accumulation in urban areas was subject to NOx mediated scavenging reaction. Therefore, higher levels of NOx resulted from photochemical reactions and automobile emissions in the urban site. *Populus deltoides* has been reported to exhibit uniform growth pattern and variable responses to external pollutants. Thus the plant response was successfully monitored as a phytometer (Wait et al. 1999). The effects of urban and rural atmospheric constituents on plant growth were found to be consistent across two consecutive growing seasons. Urban areas are reported to be characterized by low humidity and high CO_2 concentrations. This results in lower stomatal conductance of plants which partially lowers the deleterious effects of atmospheric pollutants (Jones 1996). NOx mediated ozone scavenging was found to be consistent in all urban sites monitored for plant growth. Earlier investigations on the effect of NOx on ozone levels revealed that nitric oxide levels act as indicators of ozone reduction in the urban polluted atmosphere (Milford et al. 1994). However, an increase in collective and total NOx levels may increase ozone levels as reported by Crutzen (1973). Thus these reports accentuate the fact that nitric oxide exerts partial effects on plant growth by reducing ozone levels in the urban atmosphere.

4 Nitrogen Oxides (NOx) Collectively Regulate Stomatal Conductance and Foliar Flux Rates of Nitric Oxide in Plants

Atmospheric pollutants are crucial in regulating gaseous diffusion through foliar parts of different plant systems. Atmospheric constituents in the phyllosphere regulate various parameters like mesophyll tissue diffusion pressure, stomatal conductance and water retention status of leaf cells. In this context, it is worth mentioning that nitrogen oxides (NOx) collectively affect the rate of NO diffusion across stomatal apertures. Teklemariam and Sparks (2006) reported the importance of leaf nitrogen content and ascorbic acid levels to act as major determinants of NO flux rate in foliar surfaces. Apart from considering stomatal conductance and partial pressure gradient of gases the authors also reported that internal factors are essential for diffusion of NO and NO_2 in foliar parts of different plant species. Since stomatal conductance is mostly a function of the osmotic state of guard cells it is worthwhile to consider the water potential measures during altered physiological conditions. The authors (Teklemariam and Sparks 2006) reported lower than expected values for NO flux rates in the leaves which could otherwise be higher due to conductance. Thus, leaf nitrogen content and ascorbic acid levels in mesophyll tissue were identified as major endogenous factors affecting NO and NO_2 flux. According to Mansfield et al. (1993) nitrogen oxides along with ozone and sulphur dioxide affect the water potential of stomatal cells. Thus, it is difficult to assess the sole effect of nitric oxide on stomatal conductance and its diffusion. The mixture of nitrogen oxide pollutants, carbon dioxide and sulphur dioxide are common urban pollutants. However, the saturation levels or external ambient levels of nitric oxide in the phyllosphere regulate NO flux in relation to internal NO generation. Interestingly, the compensation point of NO flux in scot pine was regulated both by UV-B irradiance and stomatal conductance (Raivonen et al. 2006). Endogenous levels of NO production are elicited in response to UV-B incidence which in turn regulates external NO diffusion. NO deposition and conductance in foliar regions are also subject to various factors like atmospheric moisture levels, canopy coverage and light intensity (Hanson and Lindberg 1991; Stocker et al. 1993). Forests in humid weather conditions have been reported to act as major sinks for NO liberated from soils. The ventilated NO levels over tropical forest canopies have thus been found to be lower (Jacob and Wofsy 1990). Investigations suggest that 20–50% of the total soil-emitted NO is absorbed by forests (Yienger and Levy 1995; Lerdau et al. 2000). The variable sensitivity of laboratory instruments implied for NOx turnover has raised questions regarding the correctness of the NO compensation point. Delaria et al. (2018) reported a comparison of NO and NO_2 exchange rates across the foliar surface of California oak (*Quercus agrifolia*). NO deposition velocities in the leaves were observed to be lower than that of NO_2. A higher rate of internal leaf resistance was attributed to slower NO diffusion. Interestingly NO compensation point was observed at a concentration range of 0.74–3.8 ppb. This suggests that endogenous NO production and ambient external NO levels result in a lower NO compensation point in forest areas. Breuninger et al. (2012) suggested that the rate of photochemical reaction in the atmosphere (formation of NOx) influences the compensation point of NO. According to Stella et al. (2013) the internal leaf resistance is important in the regulation of NO diffusion across mesophyll cells. Apoplastic pH, ascorbate levels and nitrate reductase (NR) activity have also been reported to be responsible for determining steady-state foliar exchange of nitrogen oxides (Eller and Sparks 2006). From an ecological perspective, it appears that the type of forest canopy determines the amount of ventilated NO released after its absorption by the forest sink. Sparks et al. (2003) anticipated that increased absorption of peroxyacetyl nitrate (PAN) by plants may reduce up to 3% of the total world's NOx emission. Urbanization has led to a significant increase in CO_2 concentrations in the atmosphere. This increased CO_2 levels in combination with water uptake in plants collectively regulate stomatal conductance. However, as present investigations report, NO flux and exchange in foliar parts largely depend upon the associated pollutant composition, internal resistance, endogenous NO levels and intensity of UV radiations. Although natural vegetations appear to act as a significant sink of NO, the intensity of NO diffusion is subject to both biotic and abiotic factors.

5 Evidences for Atmospheric Nitric Oxide-Induced Modulation of Plant Growth and Metabolism: Insights to Stress Management

Various investigations have revealed both detrimental and growth-promoting effects of atmospheric nitric oxide on plant systems. The effects have mostly been manifested through alterations in carbon and nitrogen metabolism. To assess the effect of NO on plant growth it has been applied separately or in a mixture with NO_2 to mimic the effects of nitrogen oxides acting as pollutants. Preliminary investigations by Anderson and Mansfield (1979) have revealed the effects of nitric oxide on the growth of tomato plants. A critical level of NO (40–80 pphm) was determined which on exceeding its limit showed detrimental effects to plant growth. The authors reported that NO was all the more beneficial in nitrogen-deficient soils being applied in the experimental setups. However, the growth-promoting effect was variable among different cultivars of tomato. The modern F1 hybrid (Sonato) exhibited growth-promoting effects in response to 40 pphm NO, thus suggesting its better growth in the presence of NOx pollutants. Extra-physiological concentrations of NO as high as 3500 ppb has been reported to be growth inhibitory to plants (Mansfield et al. 1982). NOx has been reported to persist as an atmospheric pollutant in urban air mostly in combination with SO_2. The effect of SO_2 appears to be deleterious as it operates through the inhibition of nitrite reductase enzyme activity. Down-regulation of NR activity results in the accumulation of nitrite toxicity in the cells. Thus, the detrimental effects of NO as a pollutant is expected to be higher when present in a mixture of pollutants. Caporn (1989) reported the detrimental effects of NOx on the photosynthesis rates of *Lactuca sativa* L. Application of NOx in presence of a high concentration of CO_2 led to a decrease in photosynthesis rate in per unit area of leaves. This was, however, not attributed to any change in stomatal conductance. Different inhibition rates were observed at high and low CO_2 concentrations applied to the plants. NOx has been reported to be a major automobile pollutant affecting the growth of plants (Bell et al. 2011). Interestingly CO_2 mediated photosynthetic inhibition has been reported to be recovered by nitric oxide (included as a part of NOx) in glasshouse lettuce (cvs Pascal and Talent). Supplementation of nitric oxide along with high CO_2 led to the elevation of enzyme activities namely RUBISCO (E.C. 4.1.1.39), 3PGA phosphokinase (E.C. 2.7.2.3) and NADP-G3P dehydrogenase (E.C. 1.2.1.13). Additionally, the activity of PEP carboxylase (E.C. 4.1.1.31) was increased at a higher rate. The activity of nitrite reductase (E.C. 1.7.7.1) was increased in both the cultivars in response to nitric oxide flux. These observations provide indications that atmospheric NO can circumvent the photosynthetic loss caused by high CO_2 concentrations in urban areas. Interesting insights into nitric oxide-induced regulation of nitrogen metabolism has been obtained by Wellburn et al. (1980). Different cultivars of tomato were observed to show differential responses to exogenous NO for both short and long term exposures at concentration ranges of 40–250 pphm. NO-sensitive cultivars exhibited an alteration in the enzyme activities associated with reductive amination pathways. A reduction in nitrate reductase activity was attributed to being a long term effect of NO exposure. However, in NO pollution resistant variety (sonata) the changes in the rate of N-metabolism were less prominent. Thus the fact that NO appears to act as a beneficial gaseous molecule is true at its lower concentration of 40 pphm. This low level NO facilitates the incorporation of nitrogen through the activity of GS-GOGAT pathway. However, higher concentrations of NO (>100 pphm) appear detrimental in terms of photosynthetic efficiency and crop yield. Nevertheless, the effectiveness or growth inhibitory role of NO exposure is largely regulated by the available CO_2 and SO_2 concentrations, stomatal conductance and internal cell resistance. Among various edaphic factors, water uptake and nitrogen availability are also some of the crucial factors affecting NO flux. In contrast to the effects in tomato plants, pepper plants exhibited less sensitivity to NO in terms of enzyme activity modulations (Murray and Wellburn 1985). Further investigations are necessary to decipher the metabolic changes associated with exogenous NO exposure. In this context critical analysis of cellular homoeostasis, free radical estimation and biomolecular-crosstalk analysis are required to be performed.

6 Nitric Oxide-Ozone Interaction in Plants: Recent Updates

Nitric oxide (NO) along with reactive oxygen species (ROS) is intimately associated with the regulation of several stress responses in plants. Not much information is available to elaborate NO-O_3 crosstalk in different plant systems. Ozone functions as an elicitor of ROS-induced stress which subsequently instigates signaling cascade accompanied by localized cell death. Ahlfors et al. (2009a) have demonstrated that O_3 application brings about a transient accumulation of NO in Arabidopsis leaves which coincided with the hypersensitive reaction in leaf tissues. Interestingly, the authors also reported that the application of NO or O_3 donors (alone or in combination) were effective in triggering some stress-related genes. NO has been observed to be a potential modulator of O_3-induced defence signaling where NO attenuated O_3-mediated SA biosynthetic genes and reduced SA accumulation in Arabidopsis (Ahlfors et al. 2009a). Thus, NO could have a possible beneficial role in O_3-induced stress responses. Since NO is an important regulator of ROS signaling, transient expression of NO-mediated secondary messengers are likely to modulate O_3-induced signaling pathways in plants. Although persuasive at present, extensive future investigations are required to summarize the integrative roles of NO and O_3 in plants. It is important to understand that both SA and ethylene are positive regulators of ROS-induced stress signaling in plants. In another previous report by Ahlfors et al. (2009b) NO was reported to modulate hypersensitive responses and gene expression in O_3-stressed Arabidopsis plants. It was also evident that O_3 stress resulted in transient NO accumulation in the vicinity of lesions formed on the leaf surface. Transcriptome analysis has affirmed that NO downregulated the O_3-induced expression of SA biosynthesis or SA signaling genes in Arabidopsis (Ahlfors et al. 2009b). NO-producing mutants revealed that endogenous NO generation was crucial for modulating O_3 responses in plant organs. Ethylene formation occurs as an early signaling event associated with O_3-stress in plant cells (Kangasjärvi et al. 2005). In this context, it is interesting to know that NO and ethylene act in combination in modulating O_3-induced genes, namely Alternative oxidase (Ederli et al. 2006).

Apart from the cytochrome chain, the plant mitochondrial electron transport chain also contains an alternative pathway which is comprised of a single homodimeric protein called the alternative oxidase (AOX). O_3 application has been observed to activate the AOX pathway in tobacco plants (*Nicotiana tabacum* L. cv BelW3) (Ederli et al. 2006). Furthermore, NO, ethylene, SA and jasmonic acid (JA) have been observed to be associated with the expression of the AOX1a gene during O_3 stress. Ozone application was primarily associated with hydrogen peroxide generation in the mitochondria which were further accompanied by rapid NO accumulation in the leaf tissues. The authors reported that NO-dependent regulation of AOX1a mRNA expression was orchestrated by JA and ET signaling routes. Although NO and ethylene exert regulatory roles in upregulating AOX1a expression under O_3 stress, according to the authors, the role of NO was crucial and indispensable for the regulation of alternate oxidase pathways (Fig. 2).

In the light of recent trends in investigations pertaining to NO in plant biology, it is important to focus on more work related to NO-O_3 interactions. Various anthropological activities have led to an alarming increase in atmospheric O_3 and NO production. Although NO has a beneficial role in plants, excess atmospheric NO is likely to interfere with the physiology and metabolism of plants. In an instance in 1996,

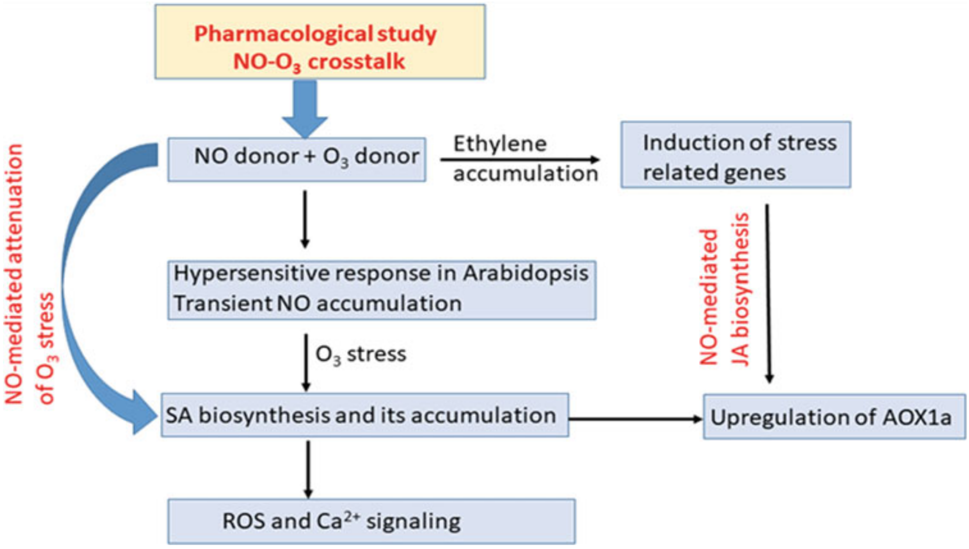

Fig. 2 The integrative roles of NO and O_3 in regulating stress signaling in plants. NO mitigates O_3 stress by promoting hypersensitive reaction, represses SA accumulation (Ahlfors et al. 2009b) and associates with ethylene and JA signaling. NO mediates the gene expression of alternate oxidase (*AOX*1a) during tolerance to O_3 stress (Ederli et al 2006)

working pharmacologists at the Free University of Berlin observed the regulatory effects of exogenous NO in experiments with guanylate cyclase (Friebe et al. 1996). The analysis of enzyme activity was undertaken in the vicinity of Berlin inner-city circular highway where they observed that atmospheric NO functioned as a positive regulator of guanylate cyclase enzyme. Thus, although plants undergo NO-mediated beneficial effects in evading O_3 stress, it is also important to understand that plants possess mechanisms to prevent NO interference from endogenous or atmospheric sources. Plant-derived non-symbiotic haemoglobins function in palliating hypoxia stress which is known to generate a considerable amount of NO (Dordas et al. 2003). These non-symbiotic haemoglobins from various plant systems like A. thaliana, barley and alfalfa have been reported to be involved in NADPH-dependent catabolism of NO to nitrate (Igamberdiev et al. 2004; Perazzolli et al. 2004; Seregelyes et al. 2004).

7 Future Perspectives

Community assemblage, forest canopy and anthropogenic activities play a vital role in NO emission and its exchange in plants. The fact that atmospheric nitric oxide acts both beneficial and detrimental to plants has been supported by various investigations. However, accuracy and precession of NO analysis in natural sites remain a major hurdle for these investigations. Furthermore, open-top chamber measurements of NO flux in the foliar surface are difficult in mimicking the natural conditions. The composition of atmospheric pollutants at any time is much transient and subject to essential factors like weather conditions, wind direction, seasonal fluctuation and extent of anthropogenic activities. Thus it is difficult to obtain a consistent physiological response to exogenous NO exposure in crop plants. Urbanization effects on vegetation are usually manifested by a reduction in plant growth, chlorosis and altered metabolic activity of the plant. However, the beneficial effects of nitric oxide appear to be a specialised effect operative by the reduction in tropospheric ozone and up-regulation of nitrogen metabolism. Increased urbanization has caused extensive atmospheric pollution in the troposphere. Thus serious concerns have developed to overcome the problems of global warming and crop productivity. In this context, it is necessary to develop simulation models and perform multi-factorial analysis for NO acting as a beneficial gaseous biomolecule on earth. Numerous reports have established the role of endogenous NO in plant signaling and biochemistry. However, atmospheric NO, ozone and CO_2 interaction require much attention concerning plant growth in the environment. Current understandings thus provide substantial insights into the facet of plant-environment interaction. There are requirements for extensive investigations for NO liberation and exchange across diverse ecological sites.

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Brassinosteroids: A Wonder Growth Regulator to Alleviate Abiotic Stresses in Plants

Somveer Jakhar, Kavita Rani, and Sombir Singh

Abstract

Abiotic stresses like rising or falling temperature, insufficient or abundant water, high salinity, heavy metals, and UV radiation are all detrimental to the plants' growth and development, affecting agriculture productivity and thus reducing sustainability around the world. These stresses are key limiting factors for crop productivity and sustainability around the world. As diverse abiotic stresses frequently occur concurrently in the field, it is becoming increasingly important to empower crops with multi-stress tolerance to alleviate the load of environmental changes and to meet the need for population expansion. There are several reports on the current state of different stresses that are limiting plant growth and yield. Moreover, there is an inadequacy of research on sustainable approaches for reducing the negative impacts of abiotic stress on plants. Brassinosteroids (BRs) are a new class of plant growth hormones that have a strong growth-promoting effect. BRs are thought to be pleiotropic growth regulators since they affect a variety of physiological processes in plants, including growth, seed germination, rhizogenesis, senescence and abiotic stress tolerance. In this chapter, we have aimed to provide an insight into BR-mediated plant responses under various abiotic stresses and mechanisms of BR-triggered abiotic stress tolerance.

Keywords

Antioxidants • Brassinosteroids • Cold stress • Drought • Heavy metals stress • Salinity • Signaling

Abbreviations

ABA	Abscisic acid
AP2	APETALA 2
APX	Ascorbate peroxidase
AsA	Ascorbic acid
BAK1	BRI1-ASSOCIATED RECEPTOR KINASE 1
BB6	BIOBRAS-6
BES1	BRI1-EMS suppressor 1
BIN2	Brassinosteroid insensitive 2
BSK1	BR-signaling kinase
BL	Brassinolide
BRI1	Brassinosteroids insensitive I
BRs	Brassinosteroids
BSK1	BR-signaling kinase 1
BSU1	BRI1 suppressor 1
BZR1	Brassinazole resistance 1
CAT	Catalase
CBF	C-repeat/dehydration-responsive element binding factor
COR	Cold responsive genes
CRT/DRE	C-repeat/dehydration-responsive genes
DHA	Dehydroascorbic acid
DREB	DRE binding factor
EBL	24-Epibrassinolide
EBR	24-Epibrassinolide
GA	Gibberellin
GR	Glutathione reductase
GSH	Glutathione
GSSG	Oxidized glutathione
HBL	28-Homobrassinolide
H_2O_2	Hydrogen peroxide
JA	Jasmonic acid
MAPK2	Mitogen-activated protein kinase

S. Jakhar (✉)
Plant Physiology and Biochemistry Laboratory, Department of Botany, Kurukshetra University, Kurukshetra, 136119, Haryana, India
e-mail: somveer.botany@kuk.ac.in

K. Rani
Plant Tissue Culture Laboratory, Department of Botany, Kurukshetra University, Kurukshetra, 136119, Haryana, India
e-mail: kavitadahiya05phd@kuk.ac.in

S. Singh
P.T.C.L.S. Govt. College Karnal, Karnal, 132001, Haryana, India

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MDA	Malondialdehyde
POD	Peroxide
PSII	Photosystem II
RBOH1	Respiratory burst oxidase homolog 1
ROS	Reactive oxygen species
SA	Salicylic acid
SOD	Superoxide dismutase
STP	Signal transduction pathway
TFs	Transcription factors

1 Introduction

Plants experience both biotic and abiotic stress throughout their life span which greatly decreases their productivity. A plant's reactions to such stresses are very complex which includes disruption in metabolism and many cellular, physiological and molecular adaptations. The detrimental impact of non-living forces on living organisms in a certain environment is known as abiotic stress. Drought, heavy metal toxicity, high and low temperature and salinity are some of the abiotic stresses that seriously decrease the crop yield globally (Aninbon et al. 2016). All these have the potential to threaten agriculture and disrupt ecosystem health, thereby causing significant losses in agricultural yield (Wania et al. 2016). Abiotic stresses are the most important yield-limiting factors (Zörb et al. 2019). Extreme temperatures, drought, flooding, saltiness and heavy metal stress all have an impact on plant development and production (Table 1). Around 90% of agricultural land is susceptible to one or maybe more than one of the aforementioned stresses (dos Reis et al. 2012), which may lead up to 70% of productivity loss in important food crops (Mantri et al. 2012). According to reports based on the combination of change in climate and crop production models, the yield of essential crops would continue to decline, thereby posing a severe threat to food safety (Tigchelaar et al. 2018). During the previous two decades (1990–2013), the amount of salt in irrigated areas has surged by 37% (Qadir et al. 2014). Drought stress has become more common and severe because of changes in rainfall patterns and a rise in evaporation and transpiration caused by global warming (Dai 2011). According to new meta-analysis research, the global mean temperature would rise by 2–4.9 °C by 2100 (Raftery et al. 2017). At the same time, increased heavy metal pollution in agricultural areas is reducing food yield while also posing severe health concerns to humans (Rehman et al. 2018).

Brassinosteroids (BRs) are steroidal hormones derived from plants that are low-molecular-weight compounds occurring universally in algae to angiosperms (Khripach et al. 1999; Takatsuto 1994). BRs play a crucial part in various physiological processes in particular cell elongation, cell division, germination, nutrition, photosynthesis, pollen germination, pollen tube formation, fertilization, fruit set, fruit quality, senescence and biotic and abiotic stresses (Bajguz and Hayat 2009; Albrecht et al. 2012; Fariduddin et al. 2013). BRs also have an important role in the differentiation of tracheary elements, stimulation of ATPases and hormonal signaling (Kroutil et al. 2010; Gruzska 2013). Besides this, BRs gained special attention because of their crucial role in the alleviation of many abiotic stresses (Vriet et al. 2013). BR-mediated stress response is a complex mechanism that involves enhancement in protein synthesis, defensive molecules and activation and deactivation of crucial enzymes (Bajguz and Hayat 2009). Earlier research indicated that BR controls different physiological, growth and developmental processes such as cell elongation, stomatal conductance, leaf expansion, development of the flower, male sterility and stress tolerance (Li et al. 2016a, b). BRs upregulate several cell division and differentiation-related genes (Bergonci et al. 2014). They have the potential to induce cell division and xylem differentiation (Nemhauser et al. 2004). They are also reported to regulate replication and transcription in plants (Khripach et al. 2003), activation of several enzymes (Hasan et al. 2008), and enhance fruit set (Fu et al. 2008). Besides that, BRs can resist osmotic stress (Vardhini and Rao 2003), low and high-temperature stress (Fariduddin et al. 2011), salinity stress (Hayat et al. 2007) and various heavy metals mediated stresses (Yusuf et al. 2011).

2 Brassinosteroids

Brassinosteroids (BRs) are a class of plant steroid hormones that were first isolated about 40 years ago from *Brassica napus* pollens (Grove et al. 1979). Nearly 70 related compounds have been reported that differ in structure and physiological activity (Li et al. 2016a, b), but the most bioactive of these are brassinolide, 24-epibrassinolide, and 28-homobrassinolide. BRs are analogous to animal steroid hormones, which promote processes from embryonic development to adult homeostasis (Bergonci et al. 2014), through a complex pathway of signal transduction. Previous studies confirmed that BR regulates different physiological and plant development processes, like leaf expansion, cell elongation, photomorphogenesis, flower development, stress tolerance, male sterility and stomatal stimulation (Tao et al. 2015; Li et al. 2016a, b). Like their animal counterparts, BRs stimulate thousands of genes linked to cell division and differentiation (Bergonci et al. 2014), which contributes to the regulation of all the growth processes (Abbas et al. 2013). Brassinosteroids not only influences plant developmental processes but (Liu et al. 2014; Wei et al. 2015a, b),

Table 1 Brassinosteroid mediated stress alleviation in different crop plants

Abiotic stress	Plant used	Dose	Impact of BRs	References
Heat stress	*Solanum lycopersicum*	0.2 µM EBR	• EBR treatment can promote photosynthesis by boosting the activities of key enzymes for antioxidant (SOD, CAT, GR and SOD) that reduces lipid peroxidation under stress	Ogweno et al. (2008)
	Solanum lycopersicum	0.2 µM EBR	• Upregulation of transcription level of defence-related genes such as APX5, GR1, Cu–Zn SOD, CAT1, NPR1, PR1, HSP90 and WRKY1 • BRs stimulate H_2O_2 accumulation in the apoplast (by activating/inducing *RBOH1*-NADPH oxidase) acts as a key signal to regulate BR-induced high-temperature stress tolerance	Zhou et al. (2014)
	Brassica napus	1 µM EBR	Enhances HSP synthesis during heat stress	Dhaubhadel et al. (2002)
Cold stress	*Solanum lycopersicum*	0.1 µM EBR	• The use of exogenous EBR improves cold tolerance by decreasing oxidative damage	Xia et al. (2018)
	Cucumis sativus	0.1 µM EBR	• Exogenous EBR application improves CO_2 assimilation and reduces the photoinhibition of PSII under cold stress mediated by the activation of enzymes involved in the AsA-GSH cycle and redox equilibrium	Jiang et al. (2013a, b)
	Vitis vinifera	0.1 mg/L EBR-ethanol solution	• EBR application modifies the AsA-GSH cycle component under cold stress temporarily, resulting in improved cold tolerance in seedlings of grapes	Chen et al. (2019)
	Grapevines	0.3 µM EBR	• Increases grapevine tolerance to cold stress by increasing antioxidative potential, which reduces membrane lipid peroxidation under stress circumstances	Xi et al. (2013)
	Brassica campestris	0.1 µM EBR	• EBR application under low temperature improves the chlorophyll biosynthesis at the transcriptional level and photosynthesis-related genes	Zhao et al. (2019)
	Capsicum annuum L	15 µM EBR	• 15 µM EBR was shown to be the most effective concentration for reducing chilling-induced damage in green bell pepper fruits	Wang et al. (2012)
	Mangifera indica	10 µM EBR	• EBR protects fruits against chilling-induced damage by enhancing the protein levels such as remorin, ABA stress ripening-like protein, and temperature-induced lipocalin and type II SK2 dehydrin	Li et al. (2012a)
Drought stress	*Solanum lycopersicum*	0.01 µM EBR	• EBR treatment improves drought tolerance, as seen by increased photosynthetic capacity, leaf hydration status, and antioxidant defence under stress circumstances	Yuan et al. (2012)
	Capsicum annuum	0.01 mg/L EBR	• Exogenous BR treatment to pepper leaves enhanced the light utilization efficiency and the dissipation of excitation energy in the PSII antennae under drought	Hu et al. (2013)
	Chorispora bungeana	0.1 µM EBR	• Exogenous BR application can enhance tolerance to drought caused by polyethylene glycol (PEG) treatment	Li et al. (2012b)
	Brassica napus	1 µM EBR	• EBR-induced increased transcript levels of BnDREB and BnCBF5 (two key drought-responsive genes) partly contribute to BR-induced enhanced tolerance to drought	Kagale et al. (2007)
	Brassica juncea	0.01 µM HBL	• Post-drought treatment with HBL at 30 days after sowing could remarkably improve both growth and photosynthesis after 60 days of sowing	Fariduddin et al. (2009a, b)
Salinity stress	*Cucumis sativus*	0.1 µM EBL	• EBR treatment increased activities of key antioxidant enzymes, decreased Na^+ and Cl^- ion concentrations, and improved K^+ and Ca^{2+} ion concentrations • BR enhanced tolerance to salinity stress by improving photosynthesis, nitrogen use efficiency and total polyamines	Yuan et al. (2012)
	Vigna radiate	0.01 µM HBL	• HBL can reduce the combined stress caused by salt and high temperatures	Hayat et al. (2010)

(continued)

Table 1 (continued)

Abiotic stress		Plant used	Dose	Impact of BRs	References
Heavy metal stress	Cd	*Solanum lycopersicum*	0.1 μM EBR	• Improves Cd stress tolerance by boosting photosynthesis, photosynthetic pigment content, photochemical efficiency of photosystems, activity antioxidative and detoxification-related enzymes at translational and transcriptional levels	Ahammed et al. (2013)
		Brassica juncea	0.01 μM EBR or HBL	• In Cd-contaminated soils, treatment of EBR or HBL can improve crop quality and quantity	Hayat et al. (2012)
		Solanum lycopersicum	EBR or HBL (0.01 μM)	• Can significantly boost photosynthetic rate in the leaves of tomatoes subjected to Cd stress up to 60 days	Hasan et al. (2011)
		Cicer arietinum	HBL 0.01 μM	• HBL treatment reduces Cd toxicity in *Cicer arietinum* by increasing the amounts of both enzymatic and non-enzymatic antioxidants	Hasan et al. (2008)
		Solanum lycopersicum	HBL 10 nM	• HBL treatment might ameliorate Cd-induced growth reduction, photosynthesis and PSII photochemistry problems	Singh and Prasad (2017)
	Cr	*Nicotiana tabacum*	EBR 0.1 μM	• EBR prevented chloroplast damage and aided in the development of grana and thylakoids	Bukhari et al. (2016)
	ZnO	*Solanum lycopersicum*	EBR 5 nM	• MS medium supplemented with EBR boosts the antioxidant enzymes activities and redox balance	Li et al. (2016b)

stimulation of cell division and elongation (Bergonci et al. 2014), and vascular differentiation and expression of several genes (Choudhary et al. 2012). BR improves plant tolerance to diverse forms of abiotic stress (Wei et al. 2015a, b).

2.1 History

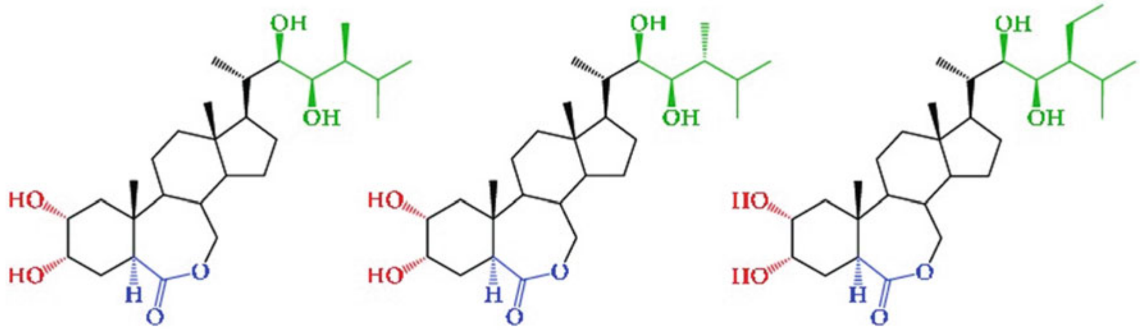
Mitchell and Whitehead published a paper in the Botanical Gazette in 1941 marked a beginning of a research programme that ultimately lead to the discovery of the most bioactive plant steroid hormones, i.e. brassinolide and other brassinosteroids. In that paper, they presented the previous pieces of evidence demonstrating that pollen extract often contains growth-promoting properties. After that Mitchell and his collaborators in the USDA, studied over thirty years on the organic pollen extracts from various plants to identify de novo plant hormones. *Brassica napus* pollen was used to extract the growth-promoting compound named “brassins”. In the second-internode bean bioassay (Mandava 1988), brassins impacted cell division and elongation and were shown to improve the yield. Focusing on such preliminary findings, the brassins were assigned hormonal status by Mitchell et al. (1970), “since these are unique plant-derived translocatable chemical compounds that have triggered observable development when administered to another plant in minute quantities”. A 227 kg of bee-collected *Brassica* pollens were collected by the coordinated efforts of many USDA laboratories and the chemical composition of the brassin was discovered in *B. napus* (Steffens 1991). Brassinolide is the net result of 4 mg pure material that was evaluated via single-crystal X-ray analysis (Grove et al. 1979).

2.2 Chemical Structure

Brassinolide is a 5α-cholestane polyhydroxylated derivative (Fig. 1). Plants, therefore, comprise a steroid that promotes growth with a structural affinity to animal steroid hormones derived from cholesterol. The BR family contains BL (brassinolide) and approximately sixty-eight other BRs including some conjugates (Bajguz 2011). These are dissimilar to brassinolides because of differences in A ring at C-2 and C-3; lactone, ketone and deoxo in C-6 in the B ring; the stereochemistry of the side chain hydroxy groups; the presence or lack of a methyl or ethyl group at C-24. In ring A or in the side chains the conjugates are glycosylated, myristoylated and laurylated hydroxyls. Most of the identified BRs are metabolic products or biosynthetic precursors of brassinolides (BL's), while in some plants castasterone is the direct precursor of BL biosynthesis.

2.3 Occurrence

BRs are distributed from lower to higher plants everywhere in the plant kingdom (Xia et al. 2011). BRs are found in many plant organs including seeds, anthers, leaves, pollen, roots, stems and flowers (Bajguz and Tretyn 2003). To date, over 70 BR analogues have been extracted from 66 plant



Brassinolide (BL) 24-epibrassinolide (EBL) 28-homobrassinolide (HBL)

Fig. 1 Structures of three natural Brassinolide

species including 56 angiosperms (44 dicots and 12 monocots), 6 gymnosperms, 1 pteridophyte, 1 bryophyte and 2 algae (Clouse and Sasse 1998). Castasterone, brassinolide and typhasterol are the most commonly distributed BRs. Bajguz and Tretyn (2003) reported that the composition of brassinosteroids varies in plants according to the species.

2.4 Mode of Action of Brassinosteroids

Over the last decade, the signal transduction route for BR was extensively explored (Fig. 2) and various investigations established a complex signal transduction pathway (STP) for BR required for the growth and development of plants. The signal transduction pathway (STP) demonstrates that BR is detected by the cell surface BRASSINOSTERIOD INSENSITIVE 1 (BRI1) receptor kinase, which activates the transcription factors BRASSINAZOLE RESISTANT 1 (BZR1) and BRI1-EMS SUPPRESSOR 1 (BES1) to generate stress tolerance. Exogenous BR binds to BRI1, causing it to associate with BRI1-ASSOCIATED RECEPTOR KINASE 1 (BAK1) and dissociate from BRI1 KINASE INHIBITOR 1 (BKI1, Fig. 2). BRI1 activation requires sequential transphosphorylation of BRI1 and BAK1 to phosphorylate BR-SIGNALING KINASE 1 (BSK1) and increase BRI1 SUPPRESSOR 1 (BSU1) activity. Furthermore, the activated BSU1 suppresses the BRASSINOSTEROID INSENSITIVE 2 (BIN2) by dephosphorylating the phospho-tyrosine residue of BIN2, leading to the accretion of unphosphorylated BZR1 and BZR2/BES1 transcription factors. Then, these two transcription factors, i.e. dephosphorylated BES1 and BZR1 move to the nucleus and help in regulating the BR-targeted genes to enhance tolerance of plants under stress by increasing the capacity of antioxidant enzymes (Takeuchi et al. 1996; Vardhini et al. 2015), regulating the accumulation of endogenous hormones (Wei et al. 2015a, b; Wu et al. 2017), and upregulating thousands of genes (Li et al. 2016a, b, Fig. 2).

3 Role of Brassinosteroids

3.1 Germination

The effect of brassinosteroids on seed germination in stress conditions and their vitality had been evaluated through germination test by various workers in *Brassica juncea, Triticum aestivum, Nicotiana tabacum*, *Lepidum sativus* (Steber and McCourt 2001; Leubner-Metzger 2001; Hayat et al. 2003; Sharma and Bhardwaj 2007). Shrivastva et al. (2011) examined different parameters of seed germination under the influence of BRs, such as germination speed coefficient, emergence index, germination rate index and relative seed germination in mung bean and found that BRs substantially promoted the seed germination by enhancing germination speed, germination rate index, emergence index, germination velocity coefficient and relative seed germination compared to control. Likewise, Ahammed et al. (2012) also found increased seed germination in 24-Epibrassinolide treated tomato plants. Brassinosteroids also facilitated seed germination by improving the tobacco seedling embryo's growth potential (Leubner-Metzger 2001). Brassinosteroids can also overcome abscisic acid-mediated germination inhibition in *Arabidopsis* plants (Steber and McCourt 2001). BRs are effective in mitigating cadmium toxicity and increasing seed germination of radish (Anuradha and Rao 2007). Under saline conditions, brassinolide seed priming resulted in considerable increases in germination parameters in *Vigna mungo* (Singh and Jakhar 2018), barley and common bean (Abd El-Fattah 2006). BRs greatly improved the growth of radish seedlings under water stress conditions (Mahesh et al. 2013). Treatments alone with Brassinosteroids also brought good improvement in the growth of seedlings and supplementing BRs to water-stressed plants not only protected the seedlings but also increased further growth (Mahesh et al. 2013).

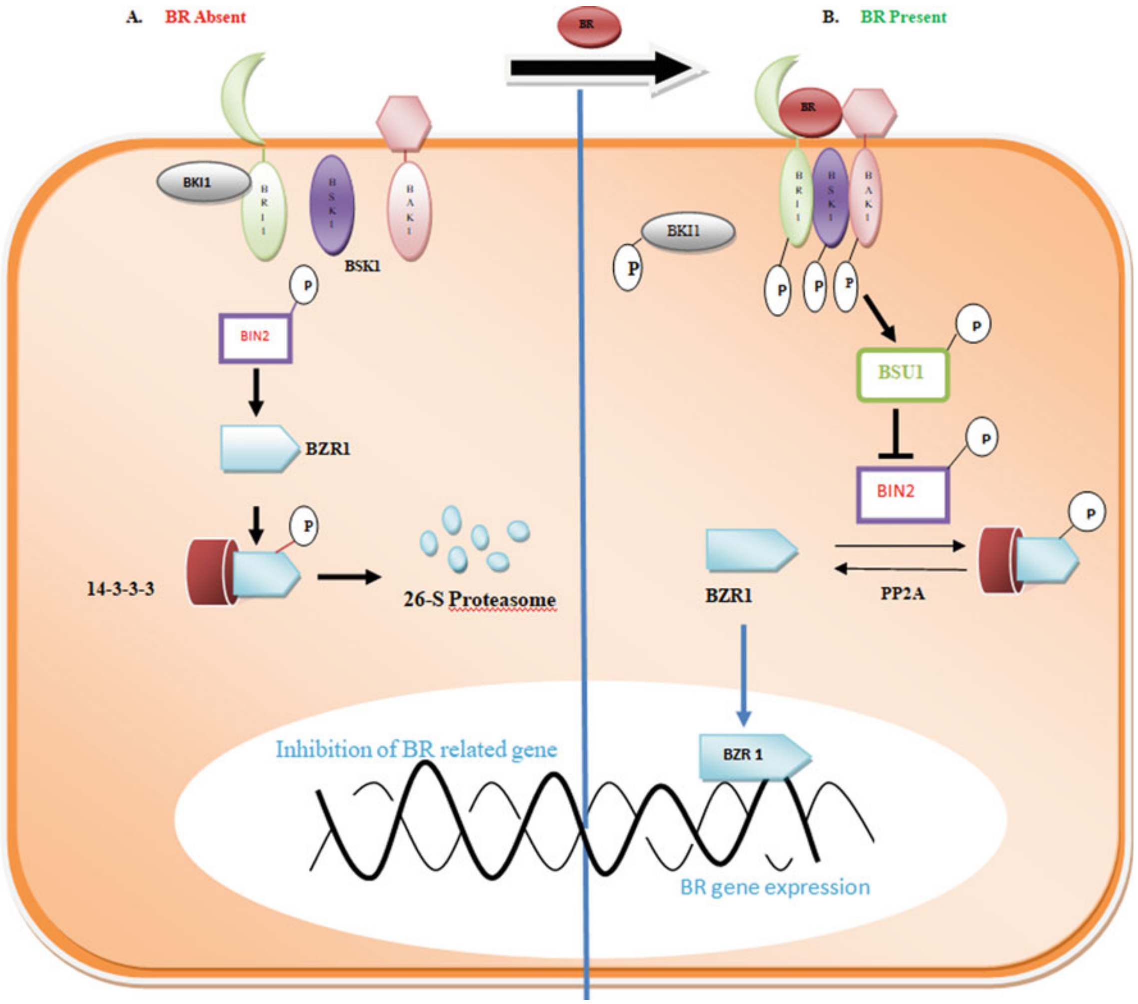


Fig. 2 Signal Transduction Pathway of BR. **a** Absent BRs, BRI1 (receptor of BR) is inhibited by its C-terminus and down regulator BKI1, which prevents it from interacting with other substrates (BSKs and BAKI). BSU1 is inactive, hence BIN2 functions like active kinase and phosphorylates BZR1/BES1, which is either maintained in the cytoplasm by 14-3-3-3 proteins or destroyed with 26S proteasome. **b** BRs present, BRs received by the extracellular domain of BRI1, inducing BKI1 dissociation from the cell membrane, the interaction between BAK1 and BRI1, and their transphosphorylation results in the formation of a BR receptor complex completely active in nature. Once the phosphorylation of BSKs occurs by BRI1 kinases, these bind to BSU1 resulting in enhancing BSU1's activity thereby causing dephosphorylation and inhibition of BIN2. When BSKs are phosphorylated by BRI1 kinases, they bind to BSU1, increasing BSU1 activity and inducing dephosphorylation and BIN2 inhibition. Therefore, dephosphorylated BES1/BZR1 stores in the nucleus and drafts proteins in BIN1 and Myb30 to form distinct transcriptional complexes that further binds to E-boxes of promoter regions of BR response genes and regulate their expression. The mechanism of bHLH regulation genes is still evolving

3.2 Growth

Clouse and Sasse (1998) reported that Brassinosteroids (BRs) are natural compounds that promote growth and have agricultural applications. Many types of brassinosteroids analogues have been created in an attempt to minimize the cost of BR production and boost BR stability, including the spirostane analogue of BR, BB6 and MH5 having Brassinosteroid like structural characteristics. Mazorra et al. (2004) reported that co-application of EBL and two other brassinosteroids analogues MH5 and BB6 reversed BR-inhibitor-induced dwarfism. The study confirmed that MH5 and BB6 are not only structural analogues to BR but also possess BR like growth-promoting activity (Mazorra et al. 2004). BRs enhanced the mitotic index in the root tip cells of *Allium cepa* (Howell et al. 2007), and aided in the proliferation of *Nicotiana tabacum* cells (Miyazawa et al. 2003). Chen et al. (2010) studied that BR biosynthesis mutant dwf7-1 *Arabidopsis* had slower rates of cell division. Initially, the increase in growth by BRs was considered as a result of cell elongation. Though, later, BR was also seen to play a significant role in cell division. At present, BRs are recognized to control numerous aspects of growth as well as development in addition to cell elongation and division, like plant reproduction, photomorphogenesis, xylem differentiation, and response to biotic and abiotic stresses (Nolan et al. 2019). According to Ali et al. (2019), BRs also influenced root elongation, cotyledon development, leaf development and plant biomass. Fathima et al. (2011) investigated the influence of BRs on different growth parameters and it was noticed that supplementation of BR (3%) showed the highest vegetative growth in *Vigna mungo* and *Gossypium hirsutum.* Jia et al. (2019) reported that in *Arabidopsis* under low Nitrogen conditions, BSK3 enhances Brassinosteroid sensitivity and signaling to amplify the extent of root elongation.

3.3 Reproduction

Pollens are the richest reservoir of natural BRs and cause elongation of the pollen tube (Hewitt et al. 1985). On the contrary, these genes are suppressed in BR mutants showing the abnormality in pollen and anther growth (Ye et al. 2010). Vogler et al. (2014) investigated that 24-EBL plays a significant role in the germination and development of *Arabidopsis* pollen. Further, expression analysis suggests that one of the BR biosynthesis enzyme promoters CYP90A1/CPD was greatly expressed in the reproductive tract which promotes germination and growth of pollens. Brassinosteroids also control ovule growth (Huang et al. 2013), pollen grain growth (Ye et al. 2010), embryo sac (Perez-España et al. 2011) and seed formation (Jiang et al. 2013a, b). BR deficient and insensitive mutants of *Arabidopsis* demonstrate postponed flowering, indicating a further function for BRs in controlling floral initiation (Azpiroz et al. 1998). Nole-Wilson et al. (2010) observed that BRs play a vital role in the development of gynoecium and ovules.

3.4 Senescence

In addition to decreased fertility, most BR mutants also exhibit increased longevity and delayed senescence. Application of BRs postponed senescence by significantly lowering the production of ethylene and the rate of respiration in *Ziziphus jujuba* fruits (Zhu et al. 2010). Hayat et al. (2012) confirmed that BR administered plants bear more fruit, as BRs delay the senescence cycle before and after pollination. Delayed senescence was also associated with accelerated photosynthesis (Yu et al. 2004) which in turn was attributed to faster translocation of photosynthates (Fuji and Saka 2001). The application of 28-HBL, kinetin and the interaction of both plant regulators has been confirmed to postpone senescence and abscission in the leaves of mung bean (Fariduddin et al. 2004). Additionally, Saglam-Çag (2007) stated that BR can induce or postpone senescence in a dose-dependent manner.

3.5 Photosynthesis

Photosynthesis is a vital event that converts light energy into an accessible chemical form of energy and takes place in all green plants (Pan et al. 2012). The application of 24-EBL enhances crop yield and photosynthetic capacity by regulating the sugar metabolism which reveals the regulatory function of BRs in photosynthesis (Jiang et al. 2012). Exogenous application of BRs improved photosynthetic efficiency by raising the level of CO_2 assimilation, RUBISCO activity and triggering the stomatal conductance (Gruszka 2013). Spraying of 28-HBL on the foliage of *Vigna radiata* influences photosynthesis in terms of improving net photosynthetic rate, carboxylation and leaf chlorophyll quality (Farriduddin et al. 2006). Application of 24-EBL has been reported to upregulate the expressions of rbcS, rbcL, other photosynthetic genes and the function of RUBISCO (Xia et al. 2009). Overall BRs stimulate photosynthesis by stimulating the genes of the Calvin cycle and by stimulating the different photosynthetic enzymes in cucumber plants (Xia et al. 2009). BRs are also known to protect the photosynthetic pigments by either enabling or inducing the chlorophyll biosynthesis enzymes, retaining the efficiency of PS II and improving the efficiency of photosynthetic carbon fixation (Siddiqui 2018). BRs are known to improve the efficiency of photosynthesis by increasing the level of CO_2 assimilation.

3.6 Yield

By upregulating the transcription of seed developmental pathways, BRs positively regulate the development of seed and seed weight (Jiang et al. 2013a, b). In addition, BR significantly influences the growth of ovules and the production of seeds (Huang et al. 2013). BRs are well documented for controlling the architecture and yield of rice grains (Zhang et al. 2018). Enhanced BR content can lead to more production in rice (Wu et al. 2008). Brassinosteroids also control rice seed size and weight in a positive way (Sahni et al. 2016). Tomato plants treated with BR displayed an improved fruit set (Hayat et al. 2012). Exogenous use of BRs was also known to increase groundnut growth and yield and this growth stimulation was correlated with enhanced nitrogen fixation (Vardhini and Rao 1998).

4 Role of Brassinosteroids in Abiotic Stresses

4.1 Salinity Stress

Salinity stress develops when the salts are elevated above the tolerance limits. Plant encounters three main challenges under salt stress, namely, osmotic stress, ion toxicity and oxidative damage which alter the normal cell structure by interfering with other cellular functions. The development of ROS under the severity of salt stress changes the antioxidant enzyme activity and results in oxidative damage (Smirnoff 1998). Membrane transporters such as carriers, channels, antiporters and symporters also exhibit modified behaviour to retain concentrations of ions. Salinity hampers the distribution of ions and the homeostasis of ions within the cell (Zhu 2003). Plants have inherent antioxidant machinery to maintain a dynamic balance of ROS to avoid oxidative damages caused by salt stress. Antioxidants and antioxidant enzymes are part of this system. SOD, CAT, and POD are the most common enzymatic ROS scavenging systems (Song et al. 2006).

Alteration of various components of the antioxidative protective mechanism through BRs in salinity-treated plants has been comprehensively documented (Abbas et al. 2013; Sharma et al. 2013; Fig. 3). Treatment with 28-HBL enhanced antioxidant enzyme activity in salinity exposed maize plants (Arora et al. 2008). Exogenous application of 24-EBL can help to alleviate the detrimental impact of salt stress in wheat cultivars grown under saline conditions by increasing the CAT and POD activity (Shahbaz and Ashraf 2007). Brassinolide treatment has been known to improve the activity of CAT, SOD and GR of saline-grown *Sorghum* plants, implying that they are capable of overcoming the negative effects of salinity stress (Vardhini 2011). Application of 24-EBL to salt-stressed seeds of *Cucumis sativus* cultivars stimulated the activity of numerous antioxidant enzymes like SOD, CAT, POD which ultimately enhanced the growth and photosynthetic efficiency (Fariduddin et al. 2013). Exogenous application of 24-EBL substantially decreased oxidative damage in salt-exposed *Oryza sativa* seedlings and increased seedling growth by enhancing APX activity (Ozdemir et al. 2004). Exogenously used 24-EBL to *Oryza sativa* grown under salt stress conditions showed an increase in protein levels, proline contents, the activity of antioxidant enzymes and eventually growth (Sharma et al. 2013). Salt stressed *Solanum melongena* seedlings showed decreased electrolyte leakage, superoxide production, MDA, H_2O_2 possibly due to increased activity of antioxidative enzymes and GSH and AsA when subjected with 24-EBL (Ding et al. 2012). Treatment of mungbean with 28-HBL neutralized the stress produced by salinity by promoting antioxidant enzyme activity and proline content, which in effect enhanced water potential and MSI (Hayat et al. 2010). In related research, Rady (2011) recorded that spraying 24-EBL to kidney beans subjected to salt stress enhanced the RWC and MSI, as a result of substantial elevations in antioxidant enzyme activity and proline content. Application of 24-EBL in salinity stressed *Pisum sativum,* greatly increased the activity of POD, SOD and CAT enzymes that supported plants to enhance photosynthetic efficiency, stomatal conductance, total chlorophyll content, seedling height (Shahid et al. 2011).

4.2 Heavy Metal Stress

The Industrial Revolution and anthropogenic activities resulted in increased leakage of hazardous metals into the environment and are non-degradable. Plants have the incredible capacity to absorb these heavy metals. Even though certain metals are required for the majority of redox reactions necessary for cellular activities but a high level of all metals, including those required for plant growth and metabolism, induce harmful consequences. Toxic metals by interacting with functional groups of molecules in cells, notably proteins and polynucleotides cause damage to plants (Chary et al. 2008). The consequences might include growth inhibition, decreased net photosynthetic rate, reduced photosynthetic pigment content, carbohydrates and the proline content, increased malondialdehyde content. Numerous plant hormones play an important function during oxidative stress. BRs, on the other hand, not only control numerous physiological and morphogenetic responses in plants but also aid in the reduction of biotic as well as abiotic stresses (Vardhini 2016, Fig. 3). 24-EBL and 28-HBL pre-soaked seeds of *Brassica juncea* ameliorate co-induced toxicity by increasing germination percentage, root and stem length (Sharma and Bhardwaj 2007, Fariduddin et al. 2009a, b). By maintaining the organization of grana and thylakoids in *Nicotiana tabacum* chloroplasts, EBR (24-epibrassinolide) prevents the effects of chromium induced damage (Ahammed et al. 2020). Owing to their capacity to sustain ion absorption into plant cells, BRs reduced metal uptake and also regulated ROS-induced lipid breakdown and improved antioxidative enzyme activity under metal stress (Cd, Al, Cu and Ni) (Fariduddin et al. 2014). 24-EBR reduced the zinc toxicity of soybean plants by improving the activity of APX, CAT and SOD enzymes (dos Santos et al. 2020) as mentioned in Table 1.

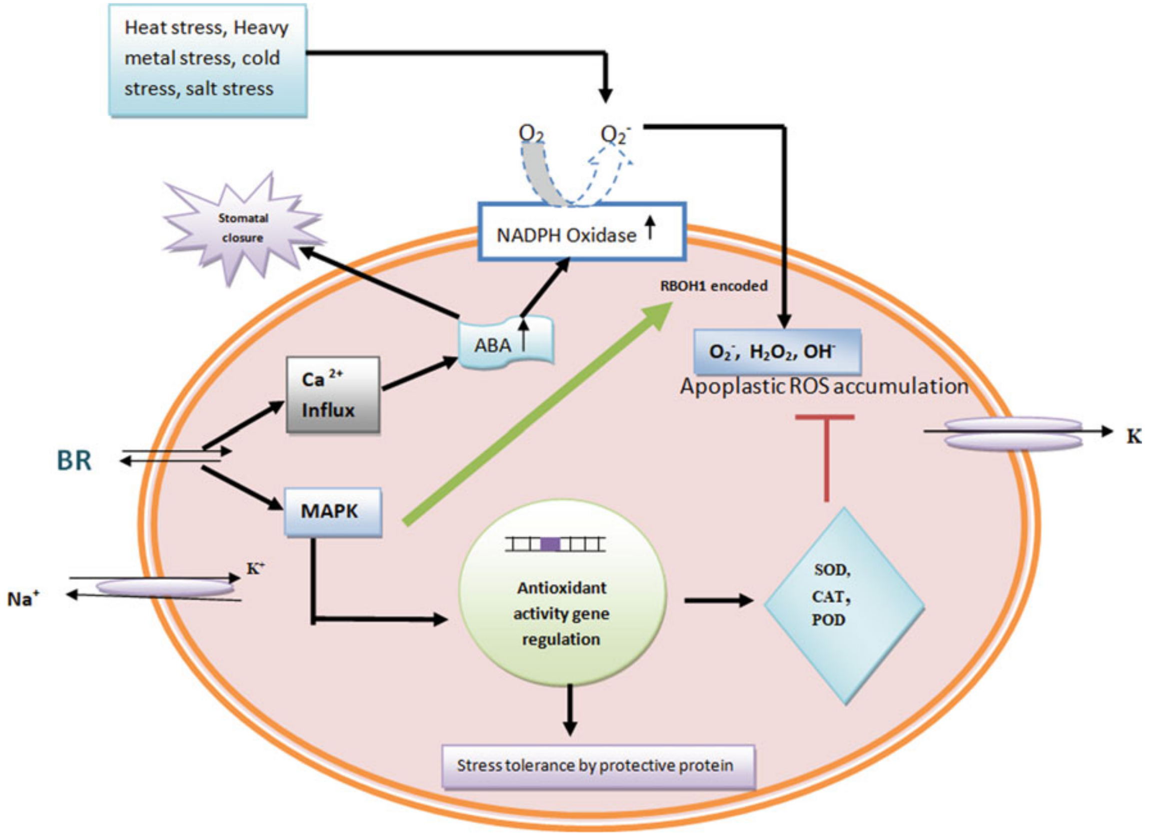


Fig. 3 Proposed mechanism of BR-induced regulation of abiotic stress response (Heat stress, Heavy metal stress, Cold stress, Salt stress) in plants. The process of BR-induced stress tolerance via the generation of ROS in the apoplast is depicted in this proposed working model. Exogenous BR application or endogenous BR modulation through BR biosynthetic gene stimulates the development of RBOH1-NADPH oxidase which ultimately produce ROS in the apoplast. These ROS signals mediated by BR disrupt the redox equilibrium, activating transcription factors (TFs) that govern transcription of BR-regulated genes and stress-responsive genes, enhancing tolerance to abiotic stimuli via protein accumulation. Notably, activation of the mitogen-activated protein kinase (MAPK) is required for BR-mediated stress tolerance, and RBOH1 MAPK, H_2O_2 work together in a positive feedback cycle to mediate BR-induced H_2O_2 build-up and subsequent signaling. Both stomatal opening and closure have been reported to be regulated by BR. Stomatal opening is induced by a low concentration of BR, which regulates H_2O_2-dependent redox poise, whereas stomatal closure is induced by a high concentration of EBR, which increases endogenous ABA levels

4.3 Drought Stress

The growth and development of plants essentially rely on water. Drought stress or water shortages are severe issues that restrict the production of various crops. They can impair plants' antioxidant systems, reduce chlorophyll content, reduce photosynthetic activity and compromise membrane integrity (Wei et al. 2015a, b). BR-treated radish seedlings when subjected to water stress showed elevation in the activity of antioxidative enzymes and reduction in the drought stress-mediated ill effects (Mahesh et al. 2013). BR improved chlorophyll accumulation, total protein levels, stomatal conductance and membrane stability in maize (Talaat and Shawky 2016) and tomato (Behnamnia 2015). The accumulation of ABA (Abscisic acid) is closely linked to drought resistance. Exogenous BR treatment has been shown in studies to increase ABA levels and reduce the negative effects of drought on plants (Wang et al. 2019). Studies show that BR treatments can help plants cope with the long-term effects of drought. For example, in a study, *Brassica juncea* plants exposed to a week of drought stress during their early growth stage demonstrate reduced growth and photosynthetic rate even after 60 days of sowing. However, a post-drought application of 0.01 µM HBL at 30 days after sowing significantly improved both growth and photosynthetic rate (Fariduddin et al. 2009a, b). These results show that BRs decrease the detrimental impacts of drought stress and increase plant production (Fig. 3).

4.4 Heat Stress

Plant growth hormones such as BR, ABA, JA, SA and GA) play a vital role in signal transduction pathways to boost the plant defence system (Acharya and Assmann 2009). Out of these phytohormones, BR regulates plant development and a wide range of physiological responses under abiotic stresses (such as high temperatures, Wu et al. 2017). By regulating physiological and antioxidant defence mechanisms, BR exhibited a compelling response towards high-temperature stress in *Ficus concinna* (Jin et al. 2015), *Brassica*, and *Arabidopsis* (Kagale et al. 2007). Reduced glutathione (GSH), GSH/GSSG, oxidized glutathione (GSSG), ascorbate (AsA), oxidized ascorbate (DHA) levels and key antioxidant enzyme activity (APX, GR, CAT, POD and SOD) increased significantly in *Ficus concinna* plants treated with BR and subjected to elevated temperature stress (Jin et al. 2015). It may be inferred that BR can reduce high-temperature stress via boosting antioxidant defences, both enzymatic and non-enzymatic, as well as the glyoxalase system (Fig. 3).

4.5 Low-Temperature Stress

Cold stress is severe abiotic stress that inhibits the growth and development of plants in many regions of the globe, causing significant physiological damage to plants (Hussain et al. 2018). Due to chilling stress plant development is slowed, photosynthetic processes are disrupted, chlorophyll levels are depleted, and flower buds are aborted, leading to suppressed production and economic losses. By modifying physiological, morphological and biochemical attributes of tomato extrinsic BR treatment was found to improve tolerance to chilling stress (Shu et al. 2016; Fig. 3). BR reduces the negative impacts caused by low temperature and cold stress via boosting chlorophyll content, photosynthesis rate, glucose metabolism, defence enzymes, gene expression, endogenous plant hormone concentrations and activation of signal transduction pathways (Eremina et al. 2016). Besides this, BRs are known to enhance salicylic acid (SA), jasmonic acid (JA) and ethylene biosynthetic pathways involving the role of BRs in alleviating low-temperature stress through a synergistic cross-talk with JA, SA and the ethylene signaling pathway (Wei et al. 2015a, b). Such findings indicate that BR protects plants from chilling stress by triggering cold stress response genes such as *C-REPEAT/DEHYDRATION-RESPONSIVE ELEMENT BINDING FACTOR* (*CBF*) transcriptional regulators that control cold responsive (*COR*) gene expression and C-REPEAT/DEHYDRATION-RESPONSIVE ELEMENT (CRT/DRE) is promoter of COR genes, which is bound by the CRT/DRE BINDING FACTOR (CBF/DREB) family of APETALA 2 (AP2) domain transcription factors (TFs), signal transduction pathways (BR and ethylene signaling pathway) and defence systems (Eremina et al. 2016; Shu et al. 2016).

5 Brassinosteroids in Agronomic Practices

The exploration of the potential of BRs for use in agricultural experiments started in the 1970s in the USA which showed positive effects (Mandava 1991). The introduction of BRs into modern agricultural practices and numerous field trials has revealed the fact that BRs can improve biomass and yield by improving the quantity and quality of different food crops. Studies performed in Japan and the USSR demonstrated the effectiveness of BRs as agricultural chemicals in the early 1980s (Takeuchi 1992). Implementation of BRs in agriculture was endorsed by Khripach et al. (2000), who reported that BRs play a crucial role in increasing the quality and quantity of crops and this hormone was also regarded as natural, non-toxic and environmentally friendly. Brassinosteroids have a critical function to play in enhancing crop yield and production. Brassinosteroids also increased the number of ears, weight and length of kernels per ear (Ali et al. 2008). Findings have shown that the foliar application of BL improves yields of wheat, mustard rice, maize and tobacco (Braun and Wild 1984). A piece of compelling evidence has emerged over the years about their ability to increase yield as well as improvement of crop quality (Prusakova et al. 1999). EBL—the active component of the plant growth promoter ‘Epin2’ has been officially documented in Russia and Belarus since 1992 and is prescribed for the treatment of agricultural plants, such as barley, cucumbers, potatoes, tomatoes and peppers (Moiseev 1998). While several brassinosteroids like 24-Epibrassinolides are commercially available and used in some countries but more detailed studies are needed on dose, method and period of application, plant or cultivar suitability and relation of brassinosteroids with other phytohormones, as many of the results were observed through experiments in greenhouses or small fields. Preliminary studies on easy metabolization, crop yield enhancement and anti-stress effects were seen in serradella and tomato at very low concentrations suggest brassinosteroids as ecologically safe growth promoters with promising use in horticulture and agriculture (Khripach et al. 2000).

6 Biosafety of Brassinosteroids

Brassinosteroids are naturally occurring non-toxic and environmentally friendly compounds so that the application of BRs at a large scale would not involve any ethical concerns. Therefore, in addition to its use in agriculture, it makes BRs an ideal candidate for use in therapeutics. Scientists researched biosafety before their commercial application in human welfare. Since BRs are the natural components of all plants, BRs are ingested extensively by mammals (Bhardwaj et al. 2012). The toxicological tests carried out in the Sanitary-Hygienic

Institute of Belarus for EBL have been used to confirm their biosafety. These studies showed that 0.2% EBL did not cause inflammation in mucous membranes when administered to rabbit eyes (Bhardwaj et al. 2012). Furthermore, the Ames test performed at Russia's Toxicological and Hygienic Regulation Scientific Research Centre gave negative results on mutagenic activity (Khripach et al. 2000). EBL showed non-toxicity and pronounced adaptogenic effects in repeated studies. The toxicity effect of HBL on Wistar rats was studied and reported that HBL is non-teratogenic at doses as high as up to 1g/kg body weight (Murkunde and Murthy 2010).

7 Conclusion

Abiotic stress is a major cause of productivity loss across the globe. Regarding this, plant growth regulators (PGRs) especially brassinosteroids have emerged as a wonderful sustainable option. Brassinosteroids are widely recognized for their important functions in promoting plant growth, development and metabolism, as well as their capability to alleviate abiotic stresses in plants. Considerable progress has been made in understanding the significance of BR signaling and communication, however, the interconnection of these signals leading to plant abiotic stress resistance needs further exploration. Observations on the effects of BRs at multiple stages, as well as the integration of these inputs, will most likely give a road map for tackling the challenge more holistically. Furthermore, the complexities of BR homeostasis, which is heavily reliant on its synthesis, degradation, and transport, must be investigated from the perspective of abiotic stresses. Understanding the interactions of different phytohormones with BRs is also very important. Inquiries into these interactions at the signaling level must be explored and understanding their regulation by abiotic stress will contribute to future information in this field. Furthermore, the advancement in genomics and proteomics resulting in the uncovering of crucial genes and proteins associated with stress responses in plants provide greater opportunities for investigating the significance of BR signaling in stress alleviation.

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Structural and Functional Role of Plant Dehydrins in Enhancing Stress Tolerance

Gurumayum Suraj Sharma

Abstract

Plants need to adapt to extremes of environmental conditions in which they thrive, which could otherwise, disrupt the physiological processes. These hostile environments include extremes of temperature, pH, dehydration and desiccation, high extracellular salt concentrations, etc. Plants are known to employ several mechanisms to counter these hostile conditions. One such mechanism of adaptation involves the intracellular accumulation of certain proteins; called dehydrins (DHNs). DHNs mainly constitute a family of proteins induced as a response to several abiotic stress conditions, including drought and desiccation, cold and freezing stress, along with several other associated stress, such as osmotic and oxidative stress. These proteins are ubiquitous in distribution and are found in a wide range of organisms, including yeast, cyanobacteria, algae and higher plants. Although they are known to play a crucial role in plant's adaptations and responses to hostile stress conditions, the precise mechanism of action for these proteins has not yet been fully established. Owing to their accumulation under several stress conditions, one basic function assigned to DHNs is the protection and maintenance of the cell's macromolecular structure and architecture. The proposed mode of action of these proteins accumulated under stress is that they stabilize membrane structure by directly interacting with cellular and organellar membranes, preserve the structural and functional property of cellular macromolecules (proteins, DNA, etc.) and provide protection against oxidative stress. The present chapter highlights the plant's response to abiotic stress with special reference to the structural compositions and the functional aspects of DHNs.

Keywords

α-helix • Dehydrins • Intrinsically disordered proteins • Late embryogenesis abundant proteins • Reactive oxygen species

Abbreviations

ABA	Abscisic acid
CD	Circular dichroism
DHNs	Dehydrins
IDP/IUP	Intrinsically disordered proteins/Intrinsically unstructured proteins
LDH	Lactate dehydrogenase
LEA	Late embryogenesis abundant
LEAPdb	LEA protein database
RAB	Responsive to ABA
ROS	Reactive oxygen species
SDS	Sodium dodecyl sulphate

1 Introduction

Plants need to adapt to extremes of environmental conditions that would ordinarily disrupt life-giving physiological and cellular processes. These hostile environments involve stresses, such as extremes of temperature, pH, cellular dehydration, desiccation, high extracellular salt, and even the presence of denaturing concentrations of cellular metabolites and free radicals inside the cells (Yancey 2003, 2004; Yancey et al. 1982). Plant's responses to such stresses are complex and vary significantly with several alterations at physiological and molecular levels. These include accumulation of protective solutes or osmolytes (sugars, amino acids, methylamines, etc.) that are thought to be compatible with macromolecular structure and function; or gross alterations in gene expression profiles and transcription factors, regulation of signal transductions, structural and metabolic

G. S. Sharma (✉)
Department of Botany, Bhaskaracharya College of Applied Sciences, University of Delhi, Delhi, 110075, India
e-mail: gurumayum.surajsharma@bcas.du.ac.in

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remodelling, that involve several plant hormones (Ingram and Bartels 1996). Amongst the different abiotic stress mentioned above, drought represents one of the most common hostile environment and pose a serious threat that adversely affects plant growth, health, yield and productivity (Riyazuddin et al. 2021). The extreme state of drought and desiccation may also lead to several related conditions, out of which, accumulation of reactive oxygen species (ROS) and oxidative stresses are some of the most common downstream phenomena. Such conditions may further lead to cellular membranes dysfunction, ionic imbalance, and oxidation of major biomacromolecules. Plants adapt to such environmental conditions through the accumulation of a number of different enzymatic and non-enzymatic antioxidants that help maintain cellular homeostasis (Halder et al. 2018) and minimize these negative harmful effects.

Additionally, plants also deploy another counter-measure to circumvent such abiotic stresses, which involve the expression of a class of proteins called Late Embryogenesis Abundant (LEA) proteins. LEA proteins comprise a group of diverse proteins induced in response to various environmental stresses (Battaglia et al. 2008; Bies-Etheve et al. 2008; Cuming 1999; Hundertmark and Hincha 2008; Tunnacliffe and Wise 2007). LEA proteins are non-catalytic in nature, which protect plant cells and tissues from damage by several abiotic stresses. Their accumulation is known to be one of the prominent components of plant adaptation to these extreme environmental conditions. This diverse collection of proteins may be classified into more than seven distinct groups with the classification depending on the nomenclature (Hundertmark and Hincha 2008) and based on their structural properties and conserved sequences (Battaglia et al. 2008). Amongst these LEA proteins, dehydrins (DHNs) are known to be accumulated to a relatively higher amount in different tissues, during drought, desiccations and associated stresses, and are grouped into type II LEA proteins (Liu et al. 2017a, b; Tommasini et al. 2008). DHNs are involved in protecting drought and desiccation via different mechanisms, through chelating ions, maintaining membranes stability and acting as molecular chaperones (Tunnacliffe and Wise 2007). Furthermore, DHNs can also function as ROS scavengers, thus helping in the maintenance of cellular membrane integrity, enzymes stabilization and cellular homeostasis. Some of the most common stress conditions encountered by plants, the physiological changes these stress may induce and counter mechanisms employed to overcome these hostile environments are highlighted in Fig. 1. The current chapter aims towards providing an overview of late embryogenesis abundant [LEA] proteins with special reference to DHNs and their exclusive role in maintaining cellular integrity and homeostasis under drought.

2 Late Embryogenesis Abundant [LEA] Proteins and Dehydrins (DHNs)

Late embryogenesis abundant (LEA) proteins, as the name suggests, were originally discovered to be accumulated during the late developmental stages of the embryo in seeds (Dure et al. 1981; Galau et al. 1986). The final stages of seed development and maturation are usually accompanied by a drastic reduction in water content within the seed. Several physiological and metabolic alterations can be observed during this process, which include a rapid increase in the abscisic acid (ABA) content, changes in gene expression and protein profiles (storage proteins and LEA proteins), etc. (Goldberg et al. 1989; Skriver and Mundy 1990). LEA proteins are commonly accumulated during this final developmental stage. Since seeds are known to possess an ability to withstand extreme desiccation at later stages, these groups of proteins have been attributed to confer desiccation tolerance in plants (Cuming 1999; Dure et al. 1981; Galau et al. 1986). Apart from seeds, several LEA proteins are also known to be accumulated in vegetative tissues that are exposed to dehydration, osmotic stress, low temperature and freezing (Bies-Etheve et al. 2008; Bray 1993; Dure et al. 1989; Hundertmark and Hincha 2008). A number of LEA proteins have been isolated from different plants, since the time of their discovery and description. Some LEA-like genes may be induced only by ABA or other environmental cues (Battaglia et al. 2008; Hand et al. 2011).

Based on the presence of specific domains, LEA proteins may be broadly categorized into seven distinct subgroups (Dure et al. 1989). With ever-increasing information and newly described members, variations in the expression profiles and their distributions, the classification of LEA has been subjected to various rearrangements with time (Battaglia and Covarrubias 2017; Battaglia et al. 2008; Bies-Etheve et al. 2008; Hundertmark and Hincha 2008; Tunnacliffe et al. 2005). Group I, Group II and Group III comprise the majority of LEA groups and contain the most members of the protein family. Additionally, a unique LEA protein database (LEAPdb) has also been made available, currently, that contains non-redundant and curated entries for several available LEA proteins (Hunault and Jaspard 2010). Amongst the LEA proteins, dehydrins (DHNs) comprise a distinct set of protein family which is grouped into the Group II LEA proteins. Most DHNs are shown to be commonly accumulated in dehydrating plant tissues, such as maturing seeds, or in different vegetative tissues that are subjected to environmental stress, most importantly drought and desiccation. Since the expressions of many DHNs are known to increase via the treatment of the phytohormone ABA, they are also being termed as RAB (Responsive to ABA) proteins. The induction of DHNs in plants is known to

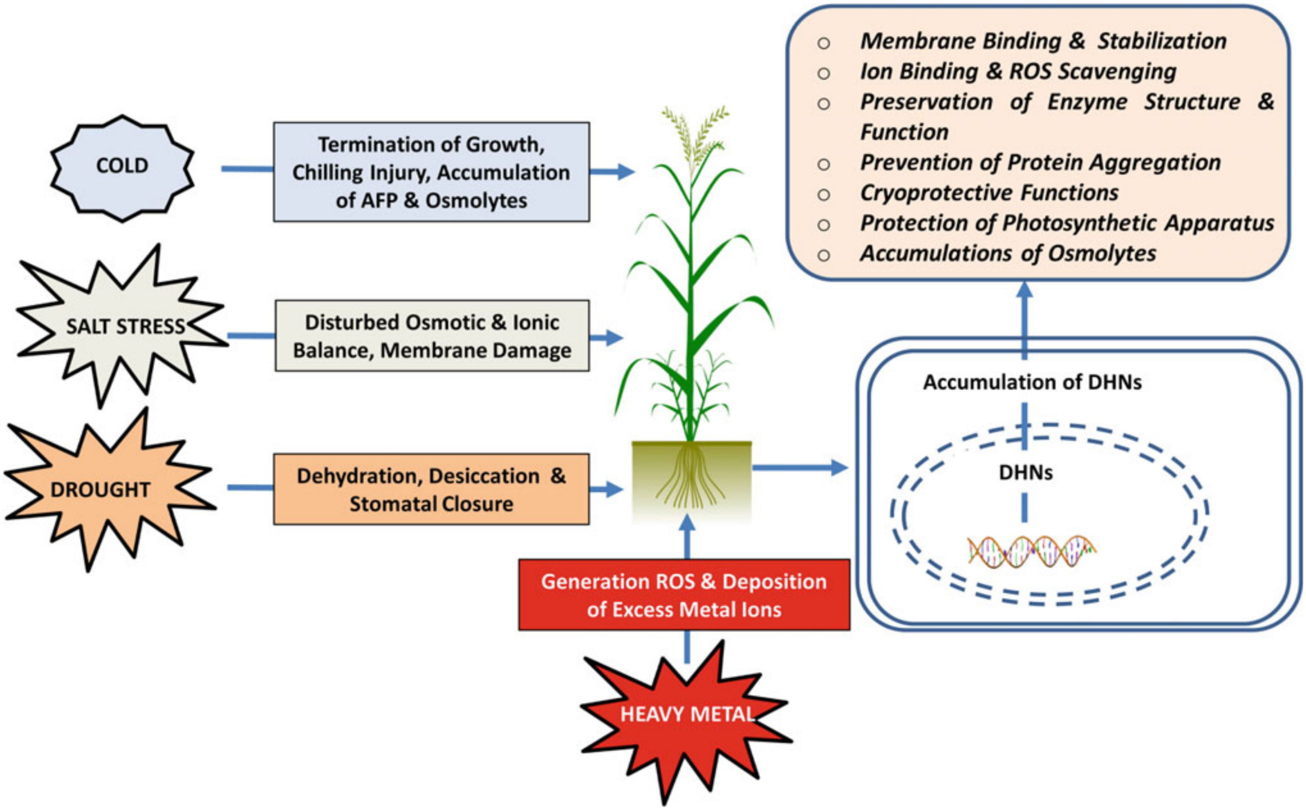

Fig. 1 A schematic representation of major stress encountered by plants and the counter mechanisms employed to overcome these hostile environments

provide tolerance to a plethora of environmental stresses conditions (Hara 2010) providing a clear indication that these proteins participate in establishing stress tolerance of plants. However, it remains unclear how these proteins confer such protection or how they actually function.

In addition to their production during later stages of embryogenesis and mature seeds and stress, DHNs are also known to accumulate in response to changes in photoperiod. Initially, the term "dehydrin" was introduced intending to mean "dehydration-induced proteins" (Close et al. 1989). The term, however, has become widely used to include proteins with specific sequence homology rather than expression characteristics.

3 Distribution

LEA proteins are known to be ubiquitous in nature, occurring amongst various plant species belonging to different groups, from lower plant, including mosses (e.g. *Tortula*, *Physcomitrella*) (Oliver and Solomon 2004), vascular seedless plants such as spike moss and ferns (Alpert 2005; Oliver et al. 2000; Reynolds and Bewley 1993) to gymnosperms and flowering plants (Bray 1993). Other photosynthetic organisms, such as algae and cyanobacteria have also been shown to accumulate these proteins at different conditions and phases (Honjoh et al. 1995). Additionally, they have now also been identified in some microorganisms (Garay-Arroyo et al. 2000; Stacy et al. 1999), fungi (Borovskii et al. 2000), protozoa, rotifers, nematodes (Browne et al. 2004; Solomon et al. 2000), insects and crustacean (Hand et al. 2007; Hoekstra et al. 2001; Tunnacliffe et al. 2005; Tunnacliffe and Wise 2007).

Group I LEA proteins have been reported to be present in the bacterium *Bacillus subtilis* (Stacy et al. 1999), in several soil bacterial species. The proteins have also been shown to be found in the crustacean, *Artemia franciscana*. Similarly, Group III LEA proteins are widely distributed in a number of prokaryotes, including *Deinococcus radiodurans* (Battista et al. 2001), *Haemophilus influenza* (Dure 2001), etc. In *Caenorhabditis elegans*, the expression of LEA is known to be directly correlated with the survival of the nematode under several environmental conditions, such as extreme dehydration and desiccation, heat stress and osmotic stress (Gal et al. 2004). Other anhydrobiotic organisms such as the nematodes *Steinernema feltiae* (Boswell et al. 2014; Solomon et al. 2000) and *Aphelencus avenae* (Browne et al. 2004), as well as the bdelloid rotifer *Philodina roseola*

(Lubzens et al. 2010), the chironomid *Polypedilum vanderplanki* (Wise and Tunnacliffe 2004) and the crustacean *A. franciscana* (Hand et al. 2007; Wang et al. 2007) also accumulate Group III LEA proteins in their extreme desiccated states. The correlation of LEA proteins in seed maturation stages, during water stress in vegetative plant organs, and in anhydrobiotic (desiccation-induced dormancy) animals suggests that LEA proteins represent a widespread adaptation to water deficit; however, their precise functions remain unclear.

4 Sequence and Structural Organization of DHNs

Originally identified as the D-11 family in cotton embryos, this group of LEA, i.e. DHNs, comprises one of the most studied and characterized groups of LEA proteins. DHNs show high variations in their molecular weight profiles, with the smallest dehydrin being 9.6 kDa (Labhilili et al. 1995) and the largest being 70 kDa (Kim et al. 2012). Additionally, these variations in the molecular weight profiles, a huge discrepancy exists regarding their molecular weights that reflect their anomalous behaviour when run on SDS PAGE, endowed due to their unordered structural features (Receveur-Bréchot et al. 2006).

Most DHNs may be characterized according to their common conserved structural motifs (Close 1996). One distinctive feature of DHNs is the K-segment, a highly conserved, Lys-rich 15-residue motif of the sequence “EKKGIMDKIKEKLPG” (Campbell and Close 1997). This sequence has been reported to be found ranging from one to eleven copies within a single polypeptide. The α-helix of DHNs may help maintain protein structural and functional integrity, and stabilize the cellular membranes under environmental stress conditions. The K_3S-type dehydrin CuCOR19, from *Citrus unshiu* is known to assume an α-helical structure in the presence of sodium dodecyl sulphate (SDS) (Hara et al. 2001). The K-segment of DHN1 (from maize) plays an essential role in binding anionic phospholipid vesicles, giving rise to α-helical conformation. Such interaction and a conformational switch of the K-segment accounts for the overall changes in DHNs upon binding to SDS or anionic phospholipid vesicles (Koag et al. 2009). The K-segment of DHN-5 (from wheat) is of prime importance in conferring protection and maintaining functional activities to LDH (lactate dehydrogenase) and β-glucosidase in vitro (Drira et al. 2013). Additionally, the lysine-rich segment of the disordered stress protein CDeT11-24 (from *Craterostigma plantagineum*) is crucial in its protective function and enzyme stabilization from hostile conditions caused by water stress (Petersen et al. 2012). Furthermore, the Lti30 (a cold-induced DHN) has been demonstrated to possess the ability to bind cellular membranes through its K-segments. Upon such binding, the segment tends to fold gradually into an α-helical structure on the cellular membrane. The K-segments of the DHN Lti30 trap the negatively charged lipid head electrostatically (Eriksson et al. 2016; Liu et al. 2017a, b), thus demonstrating its unique property in membrane stabilization and maintaining cellular integrity under stress.

An additional motif that is also found in this group of proteins is the Y-segment (due to the presence of a Tyr residue). This motif is shown to possess a conserved consensus sequence VTD [E/Q] YGNP (Battaglia et al. 2008), with Asp and Gly-Asn-Pro residues being highly conserved. This segment is usually found in one to thirty-five tandem copies in the N-terminus of the protein and possesses a similar amino acid sequence to the nucleotide-binding domain found in chaperones of several plants and bacteria. The Y-segment, representing a conserved segment [V/T]D [E/Q]YGNP, is usually found in various tandem copies in the N-terminus of DHNs (Campbell and Close 1997). The segment also possesses a sequence similarity to the nucleotide-binding site of plant and bacterial chaperones [(V/T) DEYGNP]. However, the Y-segment has no actual nucleotide-binding property on its own (Close 1996; Hughes et al. 2013; Liu et al. 2017a, b).

Another common motif in DHNs is the S-segment (named so as it consists of five to seven Ser residues in a row) and is often preceded by Ser-Asp. The S-segment is known to act as a site for protein phosphorylation (Campbell et al. 1998). The phosphorylation of the S-segment is considered a key event in promoting DHNs interaction with specific signal peptides, which is further followed by their translocation into the nucleus (Close 1996). Phosphorylation of the S-segment may be initiated by a protein kinase, which influences the location and the ability to bind metal ions (Alsheikh et al. 2003). The three amino acid residues EDD of the maize DHN Rab17 is known to serve as the CKII phosphorylation recognition site (Jensen et al. 1998; Liu et al. 2017a, b). Additionally, phosphorylation is also known to regulate the ion-binding properties of most DHNs (Heyen et al. 2002).

A much less conserved motif called the Φ-segment is found interspersed between K-segments, which are shown to be rich in polar amino acid residues (Close 1996; Dure et al. 1989). Contrary to the above-mentioned conserved motifs, neither the sequences of the Φ-segments nor their lengths appear to be conserved. Thus, the Φ-segments may be defined as all of the residues located between the three conserved segments, i.e. the Y-segments, the S-segments and the K-segments. Analyses of amino acid residues composition of the Φ-segments (i.e. all sequences without the Y-, S- or K-segments) reveals that the topmost common amino acids are Gly, Gln, and Thr, while Phe, Cys and Trp

Table 1 Classification of DHN proteins based on the presence of different segments in the polypeptide, their proposed function in stress tolerance and localization

DHN types	DHNs	Proposed function	Localization	Host plant	References
Kn	P80/DHN5	Increased tolerance to cold stress	Cytoplasmic	Barley	Bravo et al. (2003)
SKn	ERD10 ERD14	Membrane binding, Metal binding, ROS scavenging, Drought tolerance and Chaperone function	Nuclear and cytoplasmic	*Arabidopsis*	Kovacs et al. (2008), Maszkowska et al. (2019)
KnS	DHN13	Chaperone function, Antioxidant property	Nuclear	Maize	Liu et al. (2017a, b), Rorat et al. (2006)
YnKn	PCA 60	Increased tolerance to cold stress	Nuclear, plastid and cytoplasmic	Peach	Artlip et al. (1997), Wisniewski et al. (1999)
YnSKn	DHN-5	Drought tolerance	Nuclear and cytoplasmic	Wheat	Allagulova et al. (2020), Brini et al. (2007)

are present $\leq 1\%$ of the time (Graether and Boddington 2014).

The presence and arrangement of different motifs and the segments in a single polypeptide allow further classification of DHN proteins into five different subgroups (Campbell and Close 1997; Vaseva et al. 2014). DHNs that only contain the K-segment are classified under the K-subgroup, and those that include the S-segment followed by K-segment are in the SK-subgroup. In addition, there are the YSK-, YK- and KS-subgroups. Based on the presence of the conservative segments, DHNs may be subdivided into five distinct subclasses, namely YnSKn, Kn, SKn, YnKn and KnS [see Table 1] (Close 1997; Eriksson et al. 2011; Hanin et al. 2011; Hara 2010; Hundertmark and Hincha 2008). Depending on the types of environmental cues, all DHNs may show different responses to a number of abiotic factors (Allagulova et al. 2003; Rorat et al. 2006).

In aqueous solutions, DHN molecules are present in the conformation of a random coil, which lacks a finite three-dimensional structure. Thus, DHNs appear to be unstructured and share many typical characters with other types of intrinsically disordered/unstructured proteins (IDPs/IUPs) due to the low proportion of intramolecular H-bonds. These proteins are known to be extensively hydrophilic in nature due to the presence of a large amount of charged, polar amino acid residues with a low percentage of nonpolar and hydrophobic amino acids. The polypeptide usually consists of a high number of Ala, Gly and Ser residues with very minimal hydrophobic residues because of which these proteins lack a well-defined secondary structure in solution. As a result, the polypeptide thus tends to remain hydrated entirely and assume no hydrophobic core, explaining the structural disordered nature. Thus, this intrinsic property of the protein provides a wide array of functional adaptability under different stressful environments. Accordingly, they tend to change their conformational status according to the changes in their ambient microenvironment and water availability. The inter-conversion between the disordered states and ordered states could be the key to how DHNs perform their functions.

5 Protective Roles of DHNs in Plants Under Stress

5.1 Membrane Binding Properties of DHNs: Mechanism Towards Membrane Stabilization Under Stress

DHNs, like other IDPs, are characterized by their highly unordered structures in the aqueous environment. However, they are known to undergo significant change in conformation, with gain in structure, when bound to a particular ligand. One of the best pieces of evidence for the role of DHNs in stress protection came from studies with their binding with biological membranes. Conformational analyses of DHNs in association with different membrane systems in vitro revealed a switch from its unordered characteristics to an α-helical structure (Graether and Boddington 2014).

One of the first kinds of such reports came from studies in cowpea DHN (Ismail et al. 1999). The protein shows a negative peak around 200 nm in the far UV CD spectrum, which is a characteristic feature of random coils and IDPs. However, upon interaction with SDS micelles, a significant alteration in the spectrum was observed with a shift in the peak intensity, from 200 nm towards 220 nm region. Such conformational switch from random coil structure to an α-helix forms the basis of gain in protein function, a phenomenon termed as “moonlighting” (Tompa 2002). In the case of DHNs, alterations in protein solution properties and the environment (such as availability of water) could induce certain conformational and functional attributes of the protein molecules. The α-helical structure, thus formed, can interact with partly dehydrated surfaces of various other proteins and also with surfaces of biological membranes undergoing water stress. It is proposed that several K-segments within single a DHN molecule may assume a bundle-like structure when present in α-helical conformation. Such conformational transitions enhance the amphipathic nature in the protein–protein or protein–membrane interactions (Ingram and Bartels 1996). Interactions of DHNs with dehydrated protein surfaces may enhance the formation of more amphipathic alpha-helical structures. These mechanisms collectively could protect other protein molecules from further loss of water, thus protecting the hydration shell and resisting further alterations in the gross protein conformation. Such interactions between partly dehydrated surfaces of maize DHN1 molecules and other proteins and/or biological membranes could be the major driving force for the basis of protective functions of DHNs (Hanin et al. 2011; Koag et al. 2003). However, the binding propensities for DHNs tend to vary as per the variation in charge of the membrane partner. In most cases, DHNs were shown to have higher tendencies to bind negatively charged membrane, with a significant gain in its helical structure. In contrast, neutral membranes or membranes containing only zwitterionic lipids consisting of only PC or phosphatidylethanolamine (PE) were found to have lesser tendencies to bind DHNs. Additionally, there were no transitions from random coil to α-helical structure observed in case of PC liposome (Koag et al. 2003; Soulages et al. 2003).

In a recent study carried out on LEA11 and LEA25 from *Arabidopsis*, glycerol and trifluoroethanol were shown to induce an α-helical conformation in the proteins under in vitro conditions. This observed folding and compaction were further enhanced in the presence of membranes when added in the form of liposomes. Furthermore, stability assays of the liposomes also revealed a cryoprotective function of LEA11 and LEA25 proteins (Bremer et al. 2017). The study points towards a close association between the membrane association and stabilizing properties of these unordered proteins with several other factors, namely, drought, freezing, etc., that may lead to intracellular solute accumulation.

5.2 Ion Binding and Reactive Oxygen Species (ROS) Scavenging

Several DHNs, containing relatively high amounts of reactive amino acid residues towards their surface in their slightly folded conformations are known to possess reactive oxygen species (ROS) scavenging and metal ion-binding properties. Such functions are known to be mediated by direct interactions between amino acid residue and the prevalent ROS species, such as superoxide anion radical; singlet oxygen; hydroxyl radical and hydrogen peroxide, or a variety of metal ions. It is due to this property, DHNs can carry out the function as antioxidants, in ion sequestration, or even in metal ion transports. Studies involving transgenic tobacco had shown that overexpression of maize DHN (ZmDHN13) resulted in an enhanced tolerance of the plant to oxidative stress. It was reported that the conserved segments in ZmDHN13 exhibited a cooperative effect in response to environmental stresses in vivo (Liu et al. 2017a, b).

The ion-binding properties of most DHNs are well documented with a direct correlation with protein phosphorylation. An initial report of the calcium-binding of a phosphorylated DHN came from studies with DHN-like proteins, associated with vacuoles, wherein phosphorylation was found to regulate the binding (Heyen et al. 2002). Additionally phosphorylated DHN VCaB45 (from celery) was shown to possess an apparent calcium-binding property. However, dephosphorylated DHN was found to possess no such binding. The observation provided a clear indication of the role of such modification in activating the calcium-binding function (Hara 2010). The ion-binding properties seem to be confined to acidic DHNs, though not elucidated entirely. This came from the observation that the RAB18 (a neutral DHN) did not show any calcium-binding even when it was phosphorylated (Alsheikh et al. 2003, 2005).

Another common property endowed to DHNs is their metal ion bindings. Almost all DHNs (acidic, neutral and basic) are shown to possess this metal ion-binding function. The citrus DHN, CuCOR15 has been shown to bind a variety of metal ions, including Cu^{2+}; Co^{2+}; Ni^{2+}; Zn^{2+}; Fe^{2+}; Fe^{3+} (Hara et al. 2005). A positive effect of enhanced DHNs expression on plant heavy-metal tolerance has been demonstrated (Xu et al. 2008). Unlike calcium binding, which is regulated by phosphorylation at key residues, bivalent metal ion binding may proceed without any phosphorylation event. The observation thus provides a hint that metal ions could be a common target for several DHNs under different cellular environments. In fact, desiccation may lead to an enhanced leakage of metal ions from cellular organelles and membranes, thereby increasing their concentrations in the cytoplasm. It is believed that the metal-binding of DHNs may reduce various types of damage caused by free metals. A common notion is that His residues play a critical role in this metal binding property of DHNs and may be crucial in buffering the harmful effects of increased levels of metal ions within the cell. Additionally, such a mechanism may also be crucial as sensors of metal levels in the intracellular environments (Hara 2010; Kawachi et al. 2008; Persans et al. 2001).

5.3 Protective Function of DHNs Against Drought and Desiccation

Drought and desiccation represent one of the most common hostile conditions that may have a profound effect on plant health and growth at different stages and have drastic effects at anatomical and morphological levels, up to the molecular levels. Furthermore, drought and desiccation can also lead to a plethora of associated secondary stress conditions, such as oxidative and osmotic stress, which could directly affect the plant health and growth (Osakabe et al. 2014; Yu et al. 2018). A number of DHNs are directly related to providing tolerance against drought and desiccation.

Overexpression studies have shown that DHNs are associated with conferring protection against loss of water, ion leakage and oxidative stress in plant tissues (Brini et al. 2007; Guo et al. 2019; Halder et al. 2017; Verma et al. 2017). In *Arabidopsis*, overexpression of DHN5 (from wheat) was shown to enhance the drought tolerance when subjected to stress. Plants with transgenic DHN5 proteins were also shown to possess enhanced recovery and robust growth under desiccated conditions (Brini et al. 2007). Additionally, DHNs exhibit a protective role in the photosynthetic apparatus, by maintaining thylakoid and chloroplast membranes stability under drought (Hanin et al. 2011; Shakirova et al. 2016). DHNs overexpression has been shown to maintain fresh weight and brings about improved photosynthesis under drought stress. Such protective functions were attributed towards the reduction in the stomata density and opening, as well as enhancing the photosynthetic pigments and accumulation of compatible solutes contents within the cell (Xie et al. 2012; Yang et al. 2019). Moreover, overexpression of several other DHNs associated genes is also known to impart stress tolerance under drought (Liu et al. 2020).

Several in vitro and in vivo studies have indicated that DHNs possess potent chaperone function (Kovacs et al. 2008; Nguyen et al. 2020). For instance, the *Arabidopsis thaliana* ERD14 is known to counter the heat-induced functional activity loss and aggregation propensities of several client proteins. Studies carried out using lysozyme, luciferase, citrate synthase and alcohol dehydrogenase concluded that DHNs could be responsible for maintaining native state structural integrity thereby preserving their enzymatic activity (Kovacs et al. 2008; Murvai et al. 2021). Since cellular proteins are potentially exposed to an increased risk of aggregation and denaturation during drought and desiccation, induction of chaperoning activity of DHNs could be of an essential function in circumventing such risk. However, the chaperone activity of DHNs remains inconclusive, as they are not able to initiate reactivation of already denatured proteins. In fact, most DHNs (and other disordered proteins with large exposed side chains) possess certain unique properties that allow them to interact readily with water molecules. It is argued that DHNs can bind a large amount of water and at the same time retain their functional ability to interact with a large number of solute ions simultaneously. Such property enables DHNs to retain water and buffer to counteract the increase in ion concentration during an extreme state of drought and desiccation (Tompa et al. 2006). Such mechanism accounts for some of the most important roles they play under stress conditions, including chaperoning function and protection of macromolecular structures of proteins and enzymes. Another possible explanation is that DHNs prevent interactions between membrane bilayers and can chelate metal ions (whose concentrations are elevated under extreme loss of water). Nevertheless, DHNs remain to play a crucial role in rescuing molecular and cellular integrity under extreme states of drought and desiccation.

5.4 Cryoprotective Functions of DHNs

Low temperature is considered to be a major environmental stress and is known to promote the expression of several DHN proteins. This directly correlates to the cryoprotective properties of DHNs in general. Under the extreme low-temperature regime, DHNs are proposed to bind ice, thus conferring a cryoprotective property by behaving as antifreeze proteins (possess the ability to bind to and prevent the growth of ice crystals) (Wisniewski et al. 1999) which are known to be distributed in diverse organisms, including plants. Several DHNs have been demonstrated to keep enzymes functionally active even after freezing at very low temperatures (−20 °C) and subsequent thawing (Kazuoka and Oeda 1994). Such cryoprotective function was reported in *A. thaliana* COR15a protein for the first time (Lin and Thomashow 1992). The cryoprotective activity has been reported for several dehydrin proteins since then, including COR85 from spinach (Kazuoka and Oeda 1994), WCS120 from wheat (Houde et al. 1995), PCA60 from peach (Wisniewski et al. 1999), CuCOR19 from *Citrus unshiu* (Hara et al. 2001), DHN5 from barley (Bravo et al. 2003), etc. It is noteworthy to mention that the presence of K-segments in such DHNs is of prime importance for such cryoprotective function in DHNs (Reyes et al. 2008) since it plays a crucial role in regulating the overall structure of DHN proteins. This

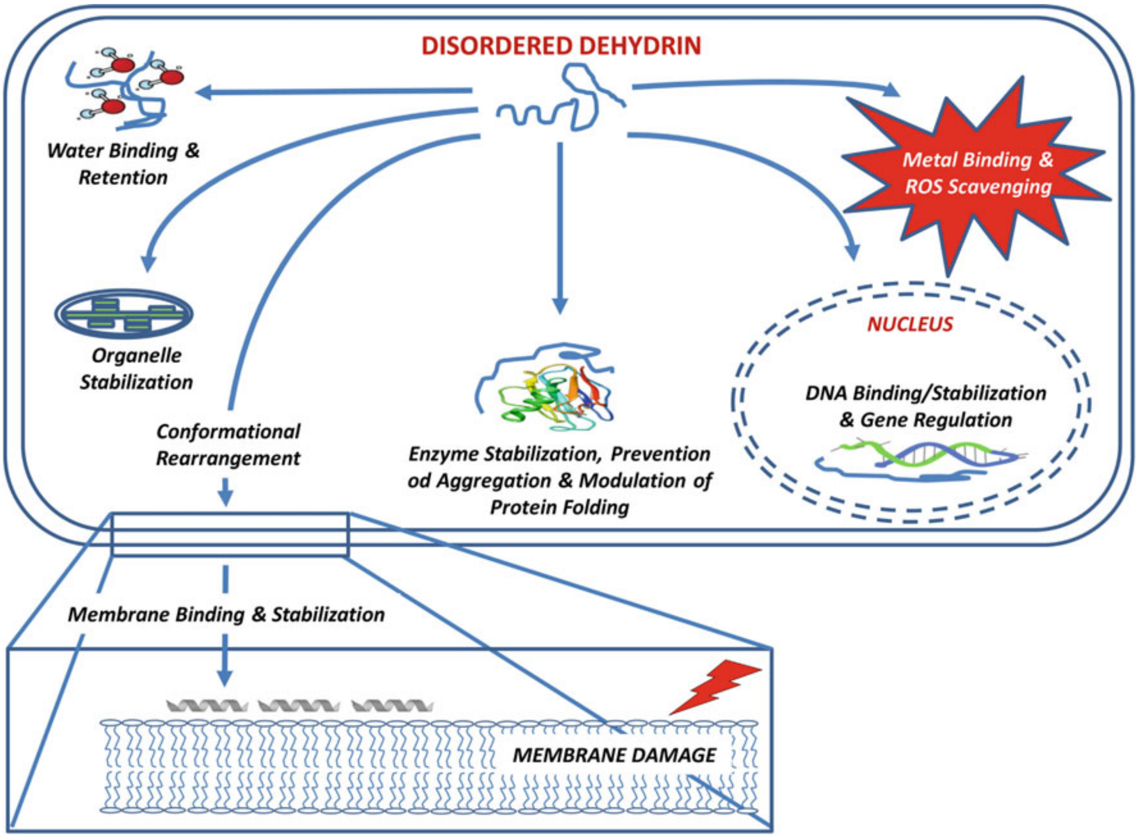

Fig. 2 A schematic representation of the proposed mechanism of DHNs in conferring tolerance to different environmental stress conditions

was further corroborated by the observation that such cryoprotective functions were lost upon the removal of the K-segments from the polypeptide sequence.

In essence, freezing and low-temperature stresses are known to induce an increased crowding in the intracellular milieu, which can be attributed to extracellular ice crystals formation, directly leading to dehydration. Under in vitro conditions, crowding induced by high glycerol concentrations has been shown to impart partial folding of COR15 proteins from *Arabidopsis* (Artus et al. 1996; Bremer et al. 2017; Steponkus et al. 1998; Thalhammer et al. 2014).

6 Conclusion and Future Perspectives

Several mechanisms of how DHNs confer protection against a wide range of stress have been put forth (Fig. 2). However, most of their functional characterization came from in vitro studies, which do not strictly replicate the in vivo physiological and macromolecular environments. Thus, a clear picture of how DHNs function in vivo remains to be elucidated. Nevertheless, most DHNs possess a very potent chaperoning function in preserving the macromolecular structure and activity of their client proteins and cellular membranes (Kovacs et al. 2008; Murvai et al. 2021; Nguyen et al. 2020), thus providing a clear indication of their protective role under stress. Additionally, since DHNs are usually unstructured in their native state, they may maintain their functional status without a significant conformational limitation when subjected to different solvent conditions and stressful environments. A better understanding of the functional aspects of each domain in the protein could yield insights into how these proteins behave in different environments (Hara 2010).

Of the several abiotic and biotic stress conditions, drought and desiccation form the major threats directly hampering crop productivity in arid and semi-arid zones, throughout the globe in recent years. Drought accounts for a major reason for crop failure and financial loss in the agricultural sector globally (Gupta et al. 2020; Riyazuddin et al. 2021). The current environmental crisis and climate change have led to a rapid depletion in freshwater supply and the shrinking size of cultivable land. In the face of such a situation, the future agricultural practice would depend heavily on stress-tolerant crops that can resist extremes of environmental conditions. The involvement of DHNs in providing tolerance to a wide spectrum of stress is well documented and established. The current genetic engineering approach in manipulating the expression profile of important crop plants would provide a promising outcome in developing new stress-tolerant crops in near future. Furthermore, future works focused on understanding the possible involvement of DHNs in the modulation of plant defence systems to pathogen attacks would be a promising avenue in stress physiological response in plants.

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Adaptation of Microalgae to Temperature and Light Stress

Sarita Kumari, Srota Satapathy, Mrittika Datta, and Savindra Kumar

Abstract

Microalgae, the photosynthetic autotrophs, are considered an important base of the food web. Furthermore, microalgae also have the potential to be a great candidate for sustainable sources of energy, soil conditioner, bioactive compounds and other economically important products as well as an alternative mode of agriculture. It is a well-known fact that the survival, growth and productivity of any organism including microalgae are strongly affected not only by their physiological and biochemical processes but also by biotic and abiotic factors in the environment. In the present scenario when global climate change which is one of the most important issues worldwide may also have a great impact on microalgal growth. Although there are many more but increased temperature and elevated light intensity (including ultraviolet radiations) are the two main repercussions of global climate change. Given that growth is balanced under a specific set of environmental conditions, therefore many microalgae can adapt to these two major stresses or extreme conditions. Interestingly by virtue of nature, we humans are blessed by such adaptation of microalgae which presents a source of a sustainable source of energy, valuable products and alternative modes of agriculture. In the present scenario where we are facing extreme climate changes, global warming and ozone depletion, understanding this adaptive behaviour of microalgae will be very useful so that we are future-ready to face such extreme stress conditions.

Keywords

Adaptation • Biofuel • Light-stress • Microalgae • Psycrophiles • Temperature-stress • Xanthophyll cycle

Abbreviations

ATP	Adenosine Triphosphate
Chl a	Chlorophyll A
Chl b	Chlorophyll B
Car	Carotenoid
DHA	Docosahexaenoic Acid
DNA	Deoxyribonucleic Acid
EPA	Eicosapentaenoic Acid
EPS	Extracellular Polymeric Substances
FA	Fatty Acids
HSP	Heat Shock Proteins
IBPs	Ice Binding Proteins
IPCC	Intergovernmental Panel on Climate Change
LHCx	Light harvesting complex protein
MAAs	Mycosporine-like Amino Acids
MUFA	Monounsaturated Fatty Acids
NPQ	Non-photochemical Quenching
PAR	Photosynthetically Active Radiation
PSI	Photosystem I
PSII	Photosystem II
PUFA	Polyunsaturated Fatty Acids
Q_{10}	Arrhenius Functions/ Temperature Coefficient
RNA	RiboNucleic Acid
ROS	Reactive Oxygen Species
RUBISCO	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RuDP carboxylase	Ribulose 1,5-Diphosphate Carboxylase
UV	Ultraviolet

S. Kumari
Department of Botany, Maitreyi College, University of Delhi, New Delhi, 110021, India

S. Satapathy · M. Datta · S. Kumar (✉)
Department of Botany, Zakir Husain Delhi College, University of Delhi, New Delhi, 110002, India
e-mail: savindra@zh.du.ac.in

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UVR	Ultraviolet Radiation
UV A	Ultraviolet A
UV B	Ultraviolet B

1 Introduction

> It is not the strongest of the species that survives, nor the most intelligent. It is the one that is most adaptable to change—Charles Darwin

Adaptation is the process by which all living forms attain the ability to sustain in the changing environment. Bacteria algae, fungi, protistans, and micro-invertebrates live in almost all of the habitats available on Earth, from the so-called 'normal ambient' environments to the harshest places. Microalgae, which originate dates back to 3.5 billion years, are one of the most fascinating life forms in this regard (Woese et al. 1990). Microalgae have an incredible ability to adapt to these abnormal ambients. Such environments are also known as 'stress' that pushes the entity to undergo physiological and chemical changes to thrive in the changing environment. Generally, the term "stresses" is used for microalgae when there is overproduction of secondary metabolites such as carotenoids and triacylglycerols (Borowitzka 2018). However, this term is also being used in another context by different authors in pieces of literature. Like mechanics, in biology, this term is also used in the sense of 'strain' but a wide range of other ill-defined meanings are also very common. All those definitions of stress are very subjective and depend in part on the discipline (medicine, psychology, ecology, physiology, etc.), the organism(s) and the type of stressor under consideration (i.e. physical, nutritional, biochemical) (Borowitzka 2018). We can define stress as the adverse conditions (physical or biological) that more or less prevent the particular species from obtaining its optimum growth in the desired time; in short, disturbs their normal physiological functioning (Munns and Tester 2008).

Although the word stress has negative connotations without any doubt it may not always be harmful. Therefore Lichtenthaler (1988) differentiated stress between 'eu-stress' and 'dis-stress', where eu-stress is activating, stimulating stress and a positive element for plant development, whereas dis-stress is a severe and a real stress that causes damage and thus harms the plant and its development (Borowitzka 2018). Similarly, Schulte (2014) classified environmental factors in two categories (1) stressful and (2) non-stressful. There is a very thin line between stressful and non-stressful factors for example microalgae are exposed to a constantly changing environment, and it appears that the microalgae acclimate to an 'average' state if these environmental changes are more or less regular. Such adjustment should be treated as 'regulation' and regulation cannot be considered a stress response (Minagawa 2011). The capability to adapt to a surrounding depends on two major factors, biotic and abiotic. These stresses can be classified broadly as biotic and abiotic stress which can be further classified in different subcategories (Fig. 8.1). Like in any other organism the term 'response against stress' is also widely used in the algal literature very often. Amongst all the different kinds of stress temperature and light play the most important role in the growth and survival of microalgae (Jabri et al. 2021). Therefore, an attempt has been made in this chapter to summarize the adaptation of microalgae during their encounter with these two stress or extreme conditions.

2 What are Microalgae?

Microalgae are a diverse group of prokaryotic and eukaryotic photosynthetic organisms which are being used as space food, single-cell proteins, biofertilizers, biofuel as well as important members of wastewater treatment plants. Microalgae can grow much faster than higher plants as well as have ability to convert solar energy into biomass and other bioactive molecules to produce different high-value products with commercial interest (Elisabeth et al. 2021). Therefore Chisti (2007) defined them as "sunlight-driven cell factories that convert carbon dioxide to potential biofuels, foods, feeds and high-value bioactive compounds

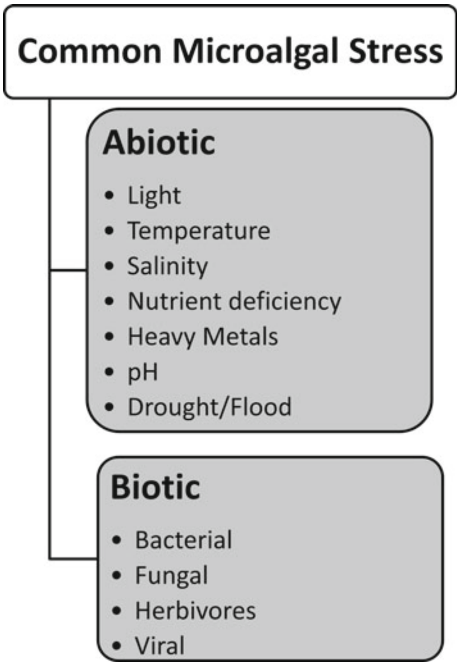

Fig. 8.1 Common abiotic and biotic stresses faced by microalgae

which are also useful in bioremediation applications, soil conditioning". At present when the entire world is facing climate change-related problems and simultaneously rapid urbanization happening around the world followed by the massive demand for clean energy resources, microalgae have proven that they can play a pivotal role in building a sustainable future for the people in future green cities (Chew et al. 2021). In this review, the term microalgae were used for all unicellular and simple multicellular photosynthetic prokaryotic or eukaryotic micro-organisms.

3 Responses of Microalgae in Stressed Environments

The equilibrium of the physiological processes and composition of an organism in balance with its environment is known as homeostasis. Stress is also known as the disruption of homeostasis due to a stressor and the stress response represents the changes in cell metabolism during acclimation and the restoration of homeostasis. It also affects an individual's performance and impairs its growth and reproduction. The industrialization of microalgae requires standardized quality parameters to obtain bioactive compounds with high added value at a commercial level. Many factors such as temperature, light or pH would make it more difficult to maintain the viability of the culture and protect the yield and condition of the target molecules in microalgae-based industries (Elisabeth et al. 2021). Whether or not a factor is considered stressful depends on the target organism, intensity, duration and the recurrence of that stress (Wahl et al. 2011). Streptophyte green algae which colonized land about 450–500 million years ago that gave origin to the terrestrial plants was also possible probably due to the emergence of the mechanism to tolerate drought stress. This transition could have been possible only after many physiological adaptations of those green algae linked to the ecological conditions characterizing modern terrestrial habitats (Pierangelini et al. 2017, 2019). There are many stages of stress response such as alarm, regulation, acclimation, adaptation and finally once homeostasis is restored the cell is no longer stressed (Borowitza 2018). As microalgae are a major primary producer of the food chain in both marine and terrestrial ecosystems, it is of great significance to understand the impact of such stress and extreme condition physiological and biochemical processes (Teoh et al. 2010). According to Peck et al. (2005), any organisms have a limited number of responses that ensure their survival in changing environments. These are (1) coping with the change using internal physiological flexibility and capacities, (2) evolving adaptations to the new conditions, or (3) migrating to areas consistent with survival. Recently Liu et al. (2021) summarized the microalgal strategies to adopt towards the light (light/dark, high-light, dark, chromatic and photosynthetic) or temperature (geothermal, snowball earth cold, or low temperature). Figure 8.2 depicts a simplified diagrammatic representation of such responses under a stress condition. In response to a stressor, the original homeostasis$_1$ of the cells is disrupted initiating an alarm signal leading to a 'response' which initiates 'acclimation' processes to restore homeostasis. Initially, there is a decline in metabolism. Once the cells have fully acclimated (i.e. homeostasis is restored), a new steady-state or homeostasis$_2$ is achieved (new steady-state may be higher than the original steady-state or it may also be lower. If the new conditions persist long adequately, the cells may also go for genetic changes to adapt to the new conditions. On the other hand, cell death may occur if the initial stressor is too disruptive (acute stress) and acclimation may not be possible. Similarly, if the acclimation response requires more resources than are available to allow full acclimation, cell death may occur (chronic stress) (Fig. 8.2) (Borowitzka 2018). Temperature and light are two important stressors and microalgal response to these two stressors depend on the magnitude and duration of stress condition. Any sort of variations in these environmental factors may change microalgal growth kinetics, macromolecular composition and physiological properties, including cell membrane permeability and fluidity (Jabri et al. 2021). For example, to maintain the photosynthetic efficiency under changing light conditions, microalgae used not only modified light-harvesting but also a different energy transfer process (Ueno et al. 2019). These two key factors not only determine the structure and function of algal communities or ecosystem functioning but also in enhancing lipid productivity and then biofuel or other valuable compounds production. Thus, in the coming sections of the review article, we will discuss microalgal responses to changing environments.

4 Microalgal Adaptations to Temperature

Temperature is not only one of the key abiotic environmental factor but also its ease of measurement make a vast body of knowledge exists concerning its effects on living organisms. According to Brock (1970), the average temperature of the earth is about 12 °C and the majority of living organisms are adapted to live in a moderate range of temperatures around this mean. However, it has been confirmed that the global temperature increased steadily over the last few decades and Intergovernmental Panel on Climate Change (IPCC) indicate that the average global surface temperature will likely rise a further 0.5 to 1.6 °C by 2030, and rising to 1.1 to 6.4 °C by 2100 (Teoh et al. 2010). This increase in global temperature is a critical issue and has a great impact on all living organisms, including algae (Barati

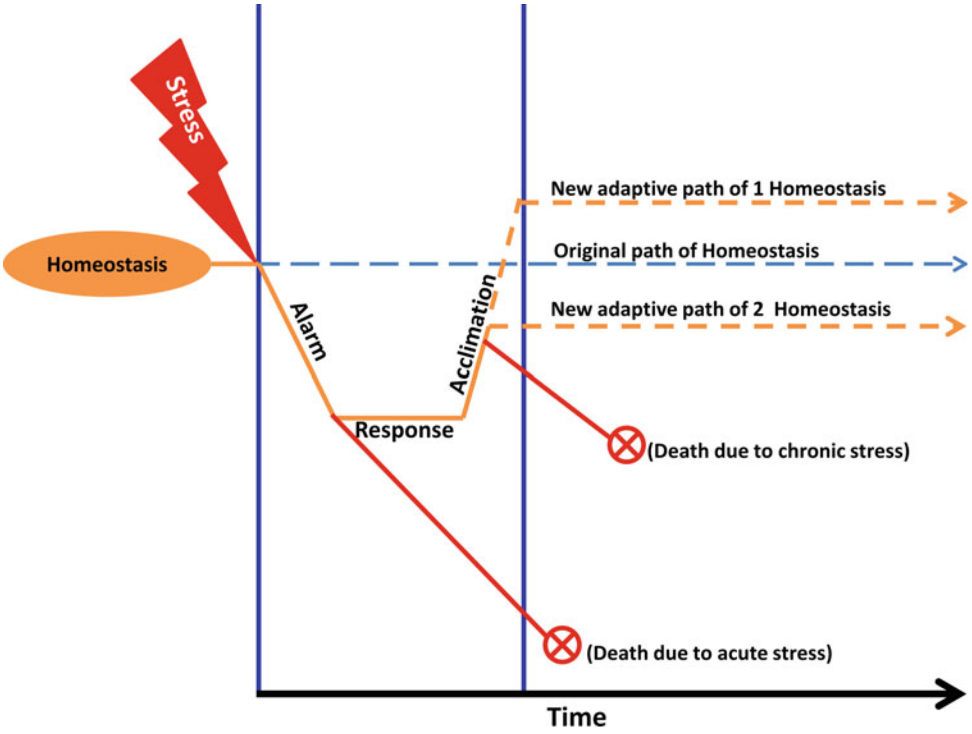

Fig. 8.2 Diagrammatic representation of the response to a stressor over time (Adopted from Borowitzka 2018)

et al. 2019). Microalgae are an ideal group in which to study the fundamental physiological responses in fluctuating or extreme temperatures. Many microalgae are not only adapted to survive at above or below the average temperature but also some microalgae live at a temperature that is extremely high or low by human standards such as *Chroococcidiopsis*, *Cyanidium*, *Galdieria*, *and Cyanidioschyzon*.

Extremely high or low-temperature environments usually have relatively simple species composition and short food chains. Our understanding of the biology of these high or low-temperature habitats is essential if we are to predict and control the consequences of thermal pollution by various industrial sources. Microalgal species have been reported from a wide range of temperatures, but no photosynthetic organisms have been reported that grow beyond 75 °C, possibly due to the instability of chlorophylls beyond this threshold (Varshney et al. 2015).

Many microalgal species are psychrophiles (cold-loving) such as *Chroococcidiopsis*, *Oscillatoria*, *Lyngbya*, *Microcoleus*, *Nostoc* and *Phormidium*. Some psychrophiles also grow on snow and ice such as *Chlamydomonas nivalis*, *Chloromonas*, *Mesotaenium*, *Chlorosarcina* and *Chlorella* (Hoham and Ling 2000; Leya 2013). Usually, these psychrophiles build up massive blooms resulting in a macroscopically visible pigmentation of the snow. One of such common green algae *Chlamydomonas nivalis* produce colourful spores and gives snow its characteristic bright red, pink, or yellow-green colour (Seckbach 2015). Psychrophilic microalgae of Arctic and Antarctic or other extreme cold environments may appear green (actively dividing sexual and asexual stages of the cell) or red (due to carotenoids, produced especially in resting stages). The catalytic efficiency of the enzymes from such psychrophilic microalgae like *Chlamydomonas*, *Chloromonas*, *Microglena*, *Chlorella* and *Scenedesmus* are adapted to cold temperatures. They are also adapted to tolerate the increased water viscosity, which roughly doubles in going from 37 to 0 °C (Varshney et al. 2015). Recently Zheng et al. (2020) compared many parameters like growth, photosynthetic activity, membrane lipid peroxidation, and antioxidant activity of psychrophilic microalgae *Chlamydomonas nivalis* with the model alga *C. reinhardtii*, under growing temperature and low temperatures. Their study reveals that photosynthetic activities *C. reinhardtii* was badly damaged by low temperature indicating a significant decrease in photosynthetic pigments (Chl a, Chl b, and Car) content and photosynthetic activity. Furthermore, this situation may also lead to photo-oxidative damage to the membrane system, proteins, lipids and DNA inside the cell. Contrary to this photosynthetic activities were maintained under these conditions in *C. nivalis* by reducing the light-harvesting ability of photosystem II and enhancing the cyclic electron transfer around photosystem I (Zheng et al. 2020). These two adaptations help this alga limit the damage to the photosystem from excess light energy and result in ATP production, supporting cellular growth and other physiological processes. In addition, reactive oxygen

Table 8.1 Adaptive strategies to cope with low temperatures and potential adaptation in *C. subellipsoidea* (Adapted from Blanc et al. 2012; Médigue et al. 2005)

Adaptive strategy	Specific genes potentially involved in the process
Increased fluidity of cellular membranes at low temperature	Lipid biosynthesis genes, including FA synthase type I, FA desaturases, lipases
Reduction of the freezing point of cytoplasm and stabilization of macromolecules	Production of antifreeze lipoproteins, exopolysaccharides and glycoproteins: lipid biosynthesis genes, including FA synthase type I and FA ligases; carbohydrate metabolism genes
Protection against reactive oxygen species	Dioxygen-dependant FA desaturases, DOPA-dioxygenase, loss of the gene encoding photosystem I subunit PsaN
Maintain catalytic efficiency at low temperatures	No apparent change in global amino acid composition relative to mesophilic plants and green algae

species levels were regulated by increased cyclic electron transfer rate, carotenoid content, and antioxidant enzyme activities to reduce photo-oxidative damage to the cell. Controlled transport of nutrients and metabolic waste products in and out of the cells is an integral part of cellular metabolism. Therefore, maintaining cell membranes fluidity under freezing temperatures is of utmost importance which is mainly done by increasing the unsaturated bonds (MUFA, PUFA) for looser packing of lipids and decreased temperature of solidification (Lyon and Mock 2014). Sun et al. (2018) also believed that lipid and carotenoid accumulation machinery can be triggered by the stress conditions to minimize the adverse effect of such stress conditions. A combined effect of high temperature and high light may help in more polar natural lipid accumulation in microalgae *Monoraphidium dybowskii* after conversion of carbohydrates and proteins (He et al. 2018). Some properties of ribulose-1,5-bisphosphate carboxylase/oxygenase (RUBISCO) was also adapted according to changing temperature. A comparative study of psychrophilic and mesophilic unicellular algae done by Devos et al. (2002) reveals that although psychrophilic "cold" RUBISCO enzymes were limited at low temperatures than that found with the enzyme of the mesophilic alga but it showed a greater thermosensitivity. This thermosensitivity may be a result of the substitution of a very highly conserved residue (cysteine247 → serine in the large subunit) from genes encoding small and large subunits of RUBISCO. On the other hand, high production of the RUBISCO can counterbalance its poor catalytic efficiency at low temperature is also a great example of adaptation at low temperature (Devos et al. 2002). Microalgae *Coccomyxa subellipsoidea* was the first polar eukaryote whose genome has been sequenced. Like psychrophilic prokaryotes, the genome of eukaryotic microalgae suggests similar adaptive routes such as cold-induced desaturation of fatty acids in membrane lipids, protective mechanisms against increased amounts of solubilized oxygen and reactive oxygen species (ROS), synthesis of antifreeze lipoproteins and glycoproteins, and global change in the amino acid composition of encoded proteins to decrease protein structural rigidity (Médigue et al. 2005). Some of the specific genes potentially involved in the adaptive process are enlisted in Table 8.1.

Despite all the above-mentioned adaptation in *Coccomyxa subellipsoidea,* the optimal growth temperature is close to 20 °C which indicate that this microalga is not fully specialized to grow in a permanent cold environment (Blanc et al. 2012). Suzuki et al. (2019) succeeded to optimize growth and PUFA production in bubble-tube and flat-plate photobioreactors when they cultivated a cold-loving polar microalga (*Koliella Antarctica*) at an enhanced 15 °C. Recently, Young and Schmidt (2020) summarized physiological adaptations of high-latitude marine microalgae to environmental changes. They explained during winter when light, temperatures and microalgal biomass are all low to survive microalgae remain in a resting state with limited metabolic activity (but maintain photosynthetic machinery and utilize storage compounds). In ice to compensate for reduced brine volume, production of extracellular polymeric substances (EPS) and ice-binding proteins (IBPs) restructure brine space, and along with compatible solutes, aid survival over winter. During early spring with increasing brine volume and lowering salinity, low light is sufficient to stimulate microalgal blooms in and under bottom ice and to begin release of compatible solutes. During late spring/summer when most of the ice has melted, high light boosts primary production in the marginal ice zone (dominated by larger centric diatoms and flagellates) and sympagic microalgal communities, such as *Melosira* sp. and pennate diatoms sink rapidly (Young and Schmidt 2020).

Any organism including microalgae required certain adaptation not only in low/extreme low temperature but also high/extreme high temperature for their growth, survival and productivity. In literature, the effect of high temperatures, above optimal temperatures, on growth is seldom reported and often described as more deleterious than the effect of low temperatures on growth (Ras et al. 2013). Three decades ago Raven and Geider (1988) explained the detailed effect of temperature on algal growth. Some of the thermophilic microalgae and their adaption were explained in detail four decades ago by Brock (1976, 1978) and Fogg (2001). Temperature coefficient or Q_{10} or Arrhenius functions is a factor by which a biological rate is increased by a 10 °C rise in the temperature. This Q_{10} or Arrhenius functions is being used to determine the relationship between temperature at a given biological rate such as algal growth and photosynthesis (Teoh et al. 2010). Recently Jabri et al. (2021) showed a high level of acclimation by microalgae *Nannochloropsis* to high temperature like in harsh desert conditions. Microalgae deployed different strategies to counteract the effect of above optimal temperatures such as energy re-balancing and cell shrinking (Ras et al. 2013). Cell shrinking adaptation or the plasticity of microalgae to unfavourably warm conditions can offer a long term solution for future outdoor cultures. Starting from the increase in the metabolic rate of organisms to displacement or even mortality of sensitive organisms are some of the common effects of enhanced temperature. Some of the common effects of changing temperature are (1) increase/decrease in total fatty acid/saturated/MUFA/PUFA content; (2) ratio of unsaturated and saturated fatty acid may also change with fluctuating temperature; (3) change in total carbohydrates/protein content. A strong reorganization of *Nannochloropsis* sp was observed during high light and temperature in relation to constant conditions, with a marked increase in cell volume and lipid content and a simultaneous reduction in protein (Jabri et al. 2021). Generally, common microalgal development parameters like photosynthesis, respiration and growth decline exceeded higher than optimal temperatures possibly due to the imbalance between energy demand and ATP production, inactivation or denaturation of proteins involved in photosynthesis (Ras et al. 2013). However, these responses of microalgae to temperature changes varied with species. Hanagata et al. (1992) reported that *Chlorella* was better able to tolerate very high temperatures than *Scenedesmus*, though both microalgae had similar growth rates at lower temperatures. Teoh et al. (2013) performed a very unique experiment where aimed to find out the response of the Antarctic, temperate, and tropical microalgae to temperature stress. In their experiment microalgal species of *Chlamydomonas*, *Chlorella* from all three Antarctic, temperate and tropical regions along with *Navicula* (from the Antarctic & temperate) and *Amphiprora* (from tropical) region grew over specific temperature ranges of 4 °C to 30 °C, 4 °C to 32 °C, and 13 °C to 38 °C, respectively. They reported *Chlorella* as the most tolerant alga whereas if further warming of Earth occurs, *Navicula* is likely to have the most deleterious consequences than the other two Antarctic microalgae. Some high altitude area creates a dynamic environment with a high level of temporal and spatial heterogeneity due to seasonal formation and melting of sea ice every year. Because of such high-level temperature adaptation (from polar, temperate to tropical). Lee et al. (2018) called *Chlorella* a "eurythermal algae". Barati et al. (2018, 2019) studied physiological and molecular responses of microalgae to elevated temperature and reported that proteins and enzymes of microalgae remain protected by molecular chaperones or degrade denatured proteins in processes involving ubiquitin. According to Barati et al. (2019) microalgae can show their adaptation towards to temperature stress in various ways such as (1) membrane homeostasis and lipid content; (2) protein homoeostasis; (3) carbohydrate homoeostasis; (4) compatible solutes; (5) oxylipins and polyamines; (6) antioxidant defence; (7) photosynthetic efficiency; (8) DNA damage and repair mechanisms and (9) programmed cell death (PCD). Microalgae of such regions are truly specialized for this environment. *Hormidiella parvula*, *Streptosarcina costaricana*, *Streptosarcina arenaria* and *Streptofilum capillatum* showed a temperature dependence of photosynthesis similar to respiration to cope with the high temperature (Pierangelini et al. 2019). Hu et al. (2021) used adaptive evolution technology to check the adaptive evolution of microalgae *Schizochytrium* sp. under high temperature for efficient production of docosahexaenoic acid. Under high temperature by using this technology Hu et al. (2021) were able to increase cell dry weight, lipid yield and DHA yield by 225%, 431% and 435% respectively. Furthermore, enhanced performance of the adaptive strain of *Schizochytrium* sp. might be related to the lower intracellular ROS, higher accumulation of pigments and less expression of HSP proteins. The above study shows that there is a great need to understand how these physiological responses of microalgae impact larger processes (ecosystem productivity, biogeochemical cycles) in these areas. It will help us for modelling high or low-latitude environments now and into the future.

5 Microalgal Adaptations to Light

Based on available data relating to microalgal adaptations to different photon flux densities shows a high-level adaptation of different microalgal groups towards light intensities. In general, dinoflagellates and blue-green algae are considered as best suited members for superior growth and photosynthesis under low light conditions. Although, diatoms also tend to be able to grow at very low light diatoms can also tolerate a relatively high light environment (Richardson et al. 1983). Many microalgae can survive in unfavourable environmental conditions that would shut down cellular processes in most organisms because of their adaptation to physiological mechanisms. Microalgae that grow on high latitudes are characterized not only by extremely low temperatures but also complete darkness in winter and continuous light and high UV in the summer (Lyon and Mock 2014). There are many reports on microalgae and their adaptation to varying light intensities. For example, five decades ago Jøsrgensen (1969) described *Chlorella* and the *Cyclotella* as two types of microalgal adaptation to different light intensities. *Chlorella* (green algae) type adapt by changing the pigment content and *Cyclotella* (diatoms) type by enhancing the light saturation in low light or vice-versa without changing the pigment content. The growth rate of microalgae also gets affected to adapt itself in low light stress. Ferro et al. (2018) reported negatively influenced growth rates, biomass concentration, carbohydrates and lipids content of *Chlorella*, *Scenedesmus* and *Desmodesmus* species under low light conditions. Molecular analysis of the light adaptation in the Yellow-green Xanthophycean alga *Pleurochloris meirinqensis* analysed by Biichel et al. (1988) revealed that chlorophyll a content and the dry weight on per cell basis is increased in low light with a reduced maximal photosynthetic capacity per chlorophyll. Whereas, in high light more photosystem I and cytochrome f in chlorophyll with twice diadinoxanthin and β-carotene were recorded than low light. The experiment done by Beardall and Morris (1976) with *Phaeodactylum tricomutum* at reduced light intensities reported (a) increased chlorophyll content; (b) decreased rate of light-saturated photosynthesis expressed on a chlorophyll, cell number or cell protein basis; and (c) decreased activity of RuDP carboxylase.

As discussed above continuous exposure to high light could limit the photosynthetic rate in microalgae by inducing photoinhibition. Therefore, it has been observed that microalgae usually adapt their pigment content according to the environment. Some microalgae like *Chlamydomonas raudensis* have very unique adaptations towards fluctuating light. *C. raudensis* has an extremely high PSII to PSI stoichiometry to maximize the harvesting of low light whereas in response to tenfold increased irradiance much faster growth rates were observed rather than exhibiting photoinhibition. On the other hand, some microalgae like *Chlorella* maintain an optimal photosynthetic activity under changing light conditions by balancing PSI and PSII light absorption (Morgan-Kiss et al. 2006, 2008). Non-photochemical quenching (NPQ) is a mechanism employed by many microalgae especially diatoms (including polar diatoms) to protect themselves from the adverse effects of high light intensity (Lacour et al. 2020). This mechanism dissipates excess energy by violaxanthin-zeaxanthin or diadinoxanthin-diatoxanthin or xanthophyll cycle (binding of xanthophylls pigment to the LHCx family of fucoxanthin chlorophyll proteins) to prevent photoinhibition and cellular damage (Lepetit et al. 2013; Robinson et al. 1997). All such studies prove that there is a clear link between the natural light environment of species/ecotypes and quenching efficiency amplitude (Lacour et al. 2020). Rmiki et al. (1996) explained the role of carotenoids in the photo adaptive response especially through the operation of xanthophyll cycles. Sometimes cold or dark treatment may help in reducing the effect of heat stress for instance cold or dark treatments (not both) to *Nannochloropsis oceanica* reported in overcoming heat stress. The impact of this treatment was also observed not only in larger chloroplast with more thylakoid membrane but also significantly induced EPA and carotenoids biosynthesis (Chua et al. 2020). Genome analysis comparison of polar diatom *Fragilariopsis cylindrus* with other temperate species also revealed a large expansion in the LHCx gene family in polar diatoms (Green et al. 2013). Similarly, microarray studies done by Park et al. (2010) with the polar diatom *Chaetoceros neogracile* also revealed significant elevations in LHCx proteins and antioxidant proteins but light harvesting proteins were significantly reduced at increased irradiance. By observing the delayed fluorescence spectra, light harvesting chlorophyll protein (LHCs) and photosystems (PSs) regulate their interactions in many green algae. Ueno et al. (2019) demonstrated that *Chlamydomonas reinhardtii* and *Chlorella variabilis* cells grown under different light qualities primarily modified the associations between LHCs and PSs (PSII and PSI). Much improved activity of an important antioxidant protein catalase was reported during high light exposure in sea-ice diatom *Entomoneis kufferathii* to protect cells from oxidative damage (Schriek 2000). Janknegt et al. (2008) studied oxidative stress responses in the marine Antarctic diatom *Chaetoceros brevis* during photoacclimation and reported elevated levels in superoxide dismutase activity, in addition to xanthophyll cycling, also to be important for dissipating ROS.

Like adaptation against high light, the survival of any photoautotrophic organism in the polar region during winters depends upon how much they are adapting themselves for low light. Seasonal and spatial distributions of microalgae also depend upon their dark adaptations. Some polar diatoms and green algae accumulate specific carbohydrate storage molecules such as glucan and are utilized during periods of darkness (Morgan-Kiss et al. 2006; van Oijen et al. 2004). In addition, many polar microalgae also uptake sugars, starches or other dissolved organic material for energetic breakdown while densely packed pigments and their binding proteins with better thylakoid fluidity facilitate efficient photosynthesis at dark or very low light (Lyon and Mock 2014). Furthermore, Neven et al. (2011) also reported plasticity in southern ocean phytoplankton to inorganic carbon uptake. Adaptation of cellular lipids is considered as one of the mechanisms of adaptation of microalgae to varying incident light intensity. Khotimchenko and Yakovleva (2005) reported an abundance of structural components of the cell membranes (such as sulfoquinovosyl diacylglycerol, phosphatidylglycerol and phosphatidyl choline} in *Tichocarpus crinitus* to low light, while 1.5 fold increase in the level of storage lipids, triacylglycerols at high light intensity. However, no significant differences in the fatty acid composition in *T. crinitus* remain unchanged while grown under different light conditions. The genome of a polar psychrotolerant green eukaryotic microalga *Coccomyxa subellipsoidea* reveals adaptation of microalgae in the form of enrichment in amino acid transporters and permeases to uptake organic nutrient sources (Blanc et al. 2012). Similarly, Parker et al. (2008) gave genomic insights into marine diatoms and their adaptability for recovering carbon and nitrogen depleted during photorespiration. Many genes of unknown function are generally considered as an adaptation of these psychrophilic microalgae. Perhaps, these strongly differentially-regulated gene codes those proteins which are required for unique signaling and transcription factor proteins which do not need to be expressed at the same concentrations as metabolic enzymes (Lyon and Mock 2014). A transcriptomic and metabolomic study done by Patelou et al. (2020) on *Nannochloropsis gaditana* revealed extensive metabolic adaptations triggered by different chromatic qualities of light. They observed (1) an overall induction in both transcripts and metabolites, involved mainly in amino acid metabolism, under red filtered light; (2) decreased carbohydrate concentration and elevated polyunsaturated fatty acids content under blue filtered light; (3) lowest responses in metabolite and gene transcript levels in green filtered light.

Photosynthetically active radiation or PAR (400–700 nm) produced very little or no growth inhibition in general. However, some microalgae can tolerate intense PAR or even the range of UV-A (315–400 nm) or UV-B radiation (280–315 nm) or both. Ultraviolet radiation also plays an important role in the adaptive strategy of microalgae in their high altitude habitats. Unusual changes in UV radiation can inhibit many biological processes in microalgae. There are many microalgal biomolecules such as nucleic acid (DNA/RNA) and proteins that can be damaged by directly absorbing the UV-B radiation or indirectly affected by various UV-induced photochemical reactions (Karsten and Holzinger 2014). To mitigate or prevent such biologically harmful UV effects many soil crust microalgae rely on several different strategies which can be broadly classified into three categories (1) avoidance (self-shading, cell aggregation); (2) protective mechanism (mucilage/cell wall, physiological acclimation, antioxidant potential, protective substances, *de novo* protein synthesis) and (3) repair of DNA. Some green algae like *Klebsormidium* make multi-layered mat-like structures or self-shading by surrounding cells or filamentous algae which act as an 'umbrella' (a protective mechanism) for individual filaments (Karsten et al. 2010). A similar thick mat-like protective layer was also reported for *Zygnema* as an umbrella protection from high UVR to PAR ratio by self-shading (Holzinger et al. 2009; Pichrtová et al. 2013). In addition, Holzinger and Lütz (2006) also reported the formation of various asexual spores and permanent stages like akinetes in *Zygnema* to cope with UV radiation. A unique chemically closely related, colourless, water-soluble, polar and zwitterionic amino acid derivatives or mycosporine-like amino acids (MAAs) act as nature's sunscreens in many algae by absorbing UV-A/B wavelengths radiations (Bandaranayake 1998). These photochemically stable amino acids can dissipate the absorbed UVR energy in the form of harmless heat without generating photochemical reactions (Karsten and Holzinger 2014). *Hormidiella parvula*, *Streptosarcina costaricana*, *Streptosarcina arenaria* and *Streptofilum capillatum* all four species accumulated different amounts of mycosporine-like amino acids (MAAs) to show protection against ultraviolet radiation (Pierangelini et al. 2019). Karsten et al. (2009) summarized knowledge of UVR effects on the ultrastructure of marine algal (mostly macro) cells of different systematic positions from polar to cold-temperate regions. Similarly, a detailed study on microalgae *Dunaliella salina* was done by Tian and Yu (2009) revealed that UV-B radiation can bring various kinds of ultrastructure changes such as swelled thylakoid, accumulated lipid globules, disintegrated cristae, reduced vacuoles and loose cisternae.

6 Role of Stress Adapted Microalgae in Biotechnology

Clean water, world food demand, air pollution and renewable energy resources have become critical issues worldwide in the twenty-first century. Scientists believe that microalgae will surely play an important role as a potential source of livestock feed, pharmaceuticals, and alternative fuels. Despite the large biodiversity of marine microalgae species and the almost unlimited availability of seawater, there are still some hurdles from realizing the undisputed potential provided by algae. Therefore, critical studies need to be conducted in regards to the algal species and the biomass production concerning algae technology (Chew et al. 2021). Like any other extremophiles, microalgae too adapted to extremes of environmental conditions which makes them the subject of some interest for biotechnology. Despite extensive worldwide research and development the commercial potential of microalgae on a large scale in a sustainable economic process is limited. One of the major constraints in achieving this goal is unfavourable outdoor conditions. However, two extremophiles *Dunaliella* and *Spirulina* already set the benchmark for commercial production of natural sources of β-carotene and as a food and feed additive respectively. Varshney et al. (2015) explored the potential of psychrophilic and thermophilic microalgae in biotechnology. Some of the common extremophilic

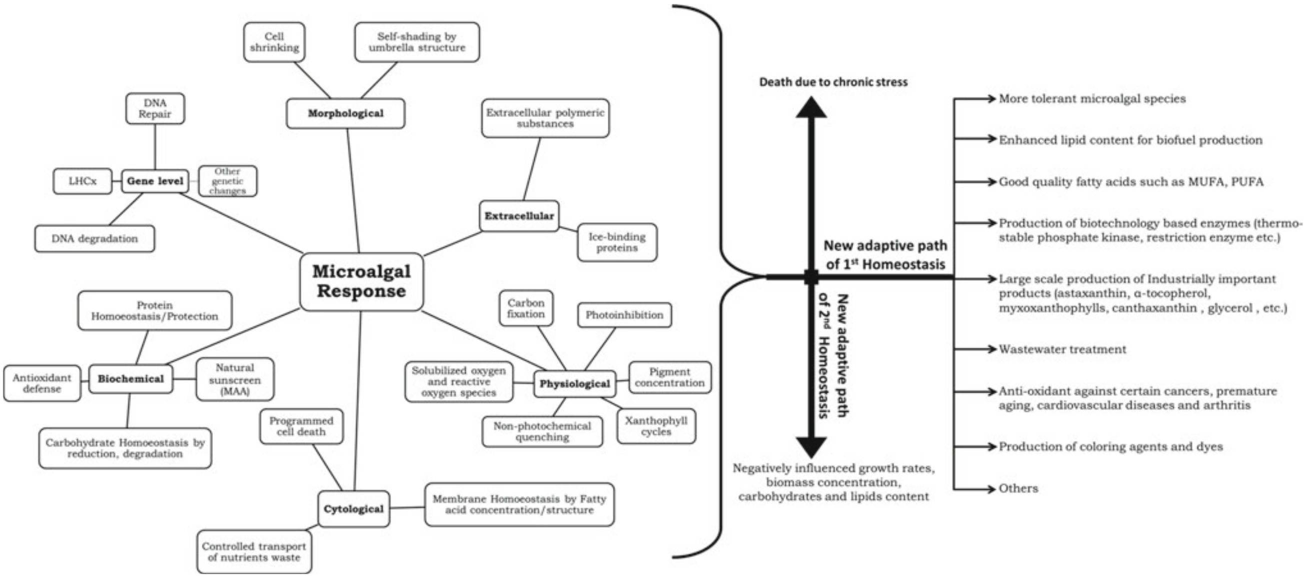

Fig. 8.3 Diagrammatic representation of the microalgal response to a stress condition and its possible three outcome

microalgal products are astaxanthin (*Chlamydomonas nivalis*); α-tocopherol (vitamin E) and xanthophyll cycle pigments (*Raphidonema* sp.); sucrose, glucose, glycerol (*Mesotaenium berggrenii* and *Chloromonas* sp.); myxoxanthophylls and canthaxanthin (*Nostoc commune*); thermostable restriction enzyme (*Phormidium* sp.); thermostable phosphate kinase (*Thermosynechococcus elongates*); lutein a xanthophyll (*Desmodesmus*); phycocyanin (*Galdieria sulphuraria*). In addition, *Galdieria sulphuraria* and *Chlorella sorokiniana* along with other microorganisms also commonly used in wastewater treatment (Varshney et al. 2015). Essential omega-3 fatty acids eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) are allegedly involved in the regulation of membrane fluidity and thylakoid membrane functioning of many polar and cold-temperate marine microalgal (Boelen et al. 2013). Therefore, such species are suitable candidates for commercial EPA and DHA production. Recently Cheregi et al. (2019) established the potential of local strains of microalgae in developing the biotechnological approach in Nordic countries.

Microalgae can also provide many other value-added products, and more recently, interest has focused on lipids and carotenoids (Sun et al. 2018). The lipid content of microalgae is usually in the range of 20–50% of dry weight and can be as high as 80% (Chisti 2007). Microalgal lipids can be used for the production of biodiesel (14–20 carbon fatty acids) or as health food supplements polyunsaturated fatty acids (PUFAs) (more than 20 carbon fatty acids) such as docosahexaenoic acid (DHA) and eicosapentaenoic acid (EPA). Recently Maneechote and Cheirsilp (2021) have proved the effectiveness of stepwise increasing of physicochemical factors to induce acclimation and adaptive evolution of microalgae. Many enzymes for biosynthesis and modification of membrane lipids, which are required by microalgae like *Coccomyxa subellipsoidea* for their adaptation in a cold environment, are of potential interest in developing technologies for converting lipids into diesel fuel or valuable fatty acids (Blanc et al. 2012). Microalgal carotenoids are not only responsible for light harvesting in photosynthetic metabolism but also have anti-oxidant properties in alleviating certain cancers, premature ageing, cardiovascular diseases, and arthritis (Chen et al. 2017; Vershinin 1999). Carotenoids are also used as colouring agents and dyes in various industries. Under stress conditions, microalgae can overproduce these lipids or carotenoids. Sun et al. (2018) summarized recent works on the manipulation of stress factors, including cultivation models and the development of novel stress-tolerant microalgae strains, which is mainly focused on overcoming the negative effects of stress-based strategies. Manipulation of stress factors can be done by multistage cultivation strategies to achieve maximum production of desired products. Therefore, there is a great potential of using light, temperature, salinity or other abiotic factors as environmental stress to improve biomass, lipid, astaxanthin, β-carotenoids, PUFAs or any other valuable content in microalgae. Therefore, Paliwal et al. (2017) used abiotic stresses as tools for metabolites in microalgae to influence PUFAs, phycobiliproteins and carotenoids. This review can be summarized in Fig. 8.3 that provides several examples of potential biotechnological applications of such special microalgae and the ranges of tolerated extremes.

7 Conclusion

Multiple factors affect the growth and occurrence of microalgae. Microalgae have potential as sustainable sources of energy, valuable products and alternative modes of agriculture. However, it is a challenge for mass outdoor cultivation due to their low survival under harsh conditions and competition from other undesired species. Therefore, extremophilic or stress-tolerant microalgae have a role to play by virtue of their ability to grow under stressed or extreme environments. This review proved that our understanding of morphological, physiological and molecular adaptations of microalgae has improved a lot in the last few decades which make them specialists of a particular niche. However, the authors still feel that it is only the beginning and extensive research needs to be done in terms of the physiology, molecular biology, metabolic engineering and outdoor cultivation trials before their true potential is realized.

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Halopriming: Sustainable Approach for Abiotic Stress Management in Crops

Tripti Gour, Ratan Lal, Monika Heikrujam, Anshul Gupta,
Vibhuti Singh, Akanksha Vashishtha, Lokesh Kumar Agarwal,
Rajesh Kumar, Siva P. K. Chetri, and Kuldeep Sharma

Abstract

Halopriming is a salt-based, pre-sowing approach that harmonies metabolic processes required for improving seed quality, enhanced emergence rate and healthy seedling vigour by controlling temperature and seed moisture content in the early stages of germination while preventing the seed from transitioning to complete germination. An aerated aqueous solution of different inorganic salts, viz., KNO_3, KH_2PO_4, KCl, NaCl, $CaCl_2$, $Ca(NO_3)_2$, $CaSO_4$, $CuSO_4$, $Mg(NO_3)_2$, $ZnSO_4$, etc. alone or in combination is applied to the seeds followed by redrying to their actual weight before sowing into seedbeds to achieve halopriming. Halopriming of seeds prevent seed degradation, breaks dormancy and induces systemic resistance to different abiotic stresses in the seedlings of various crops with amended physiological attributes, improved functional biochemistry and metabolic processes with subcellular changes despite some of its major limitations in terms of prolonged storage of imbibed (pre-soaked) seeds. On priming of the seeds, accumulation of osmolytes, and upregulation of antioxidant enzymes and signaling cascades are achieved in the seeds that persist even after germination in the seedlings as well. The technique has been proved beneficial for improved crop establishment and greater uniformity, increased plant performances with higher agricultural productivity and further for sustainable agricultural practices under the regime of abiotic environmental stresses to meet sustainable future food demand. The current study, therefore, is a compilation of literature to explore different dimensions of a simple, cost-effective, eco-friendly and potent halopriming technique, which could help to integrate seed germination, agricultural production and yield attributes in the pertaining changing climatic conditions.

Keywords

Abiotic stress tolerance • Antioxidants • Crop productivity • Germination • Halopriming • Osmolytes

Abbreviations

%	Percent
°C	Degree celsius
APX	Ascorbate peroxidase
AQP	Aquaporins
$Ca(NO_3)_2$	Calcium nitrate
Ca^{++}	Calcium ion
$CaCl_2$	Calcium chloride
$CaSO_4$	Calcium sulphate
CAT	Catalase
Cl^-	Chloride ion

T. Gour · Ratan Lal · K. Sharma (✉)
Department of Botany, Mohanlal Sukhadia University, Udaipur, Rajasthan, India
e-mail: kdsharmadu@gmail.com; drkdsharma@mlsu.ac.in

M. Heikrujam
Department of Botany, Maitreyi College, University of Delhi, Delhi, India

A. Gupta
Department of Agriculture, Rajasthan Govt, Jaipur, Rajasthan, India

V. Singh
Department of Botany, Swami Shraddhanand College, University of Delhi, Delhi, India

A. Vashishtha
Department of Botany, Department of Plant Protection, C. C. S. University, Meerut, India

L. K. Agarwal
Department of Chemistry, Mohanlal Sukhadia University, Udaipur, Rajasthan, India
e-mail: lokeshkumar@mlsu.ac.in

R. Kumar
Department of Botany, Hindu College, University of Delhi, Delhi, India

S. P. K. Chetri
Department of Botany, Dimoria College, Khetri, Kamrup Metro, Assam, India

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$CuSO_4$	Copper sulphate
GPOX	Guaiacol peroxidase
GR	Glutathione reductase
H_2O_2	Hydrogen peroxide
K^+	Potassium ion
KCl	Potassium chloride
KH_2PO_4	Potassium dihydrogen phosphate
KNO_3	Potassium nitrate
LEA	Late embryogenesis abundant
$Mg(NO_3)_2$	Magnesium nitrate
Na^+	Sodium ion
NaCl	Sodium chloride
POD	Peroxidase
ROS	Reactive oxygen species
SOD	Superoxide dismutase
$ZnSO_4$	Zinc nitrate

1 Introduction

As the World's population increases the global food security seems a great challenge ahead in order to sustain food production. In the era of rapid global climate changes, a wide range of environmental stresses severely affects the biochemical and physiological processes in plants which causes a reduction in agricultural production efficiency by 71% (Qin et al. 2010; Kaya et al. 2013; Petrov et al. 2015; Pirasteh-Anosheh and Hashemi 2020). The level of stress stimulation and the growth stage at which the plants are affected have a direct relationship with the impact of stress on plants. Among the various phases, seed germination and seedling establishment are essential aspects of a plant's life cycle in both natural and stressful environments (Kumar et al. 2016a). Since seed germination is highly sensitive to changing environmental conditions, therefore, treating seeds chemically or physically before sowing in the agriculture fields is a pre-sowing procedure, commonly known as seed priming has been seen as a viable biological approach that focuses on the management and production of crops to survive them under the stressful conditions (Ashraf et al. 2008). The method of seed priming requires pre-exposure to abiotic stress and treating seeds with some physical or chemical agents for a period of time to induce physiological conditions and bring metabolic changes in the seeds making them more likely to germinate further imparting stress tolerance in the seedlings in terms of increased seedling vitality, root length, photosynthetic efficiency and crop yield (Basra et al. 2005b; Bruggink et al. 1999; Hussain et al. 2016; Ibrahim 2016; Kaur et al. 2005; Karim et al. 2020; Kumar and Rajalekshmi 2021; Lal et al. 2018; Taylor and Harman 1990; Wojtyla et al. 2016).

There are various types of seed priming technology, viz., hydropriming, osmopriming, halopriming, biopriming, solid matrix priming, nutripriming, thermopriming and seed priming with plant growth regulators and other organic sources (Ashraf and Foolad 2005; Eskandari et al. 2013; Jisha et al. 2013; Maiti and Pramanik 2013; Nawaz et al. 2013; Paparella et al. 2015; Sher et al. 2019). Among the numerous seed priming techniques, halopriming is a simple and inexpensive agrotechnique that is simple, cost-effective and ideal for recommending to farmers for improved seedling emergence, germination consistency with greater uniformity, improved plant performance, high vitality, crop stand and higher yield in a variety of environmental circumstances (Ashraf and Rauf 2001; Basra et al. 2005a; Bose and Mishra 1999, Sadeghi and Robati 2015, Zhu and Wang 2008). Halopriming is a long-term biological strategy that involves soaking of seeds in the aerated solutions of inorganic salts viz. calcium chloride ($CaCl_2$), calcium sulphate ($CaSO_4$), copper sulphate ($CuSO_4$), monopotassium phosphate (KH_2PO_4), magnesium sulphate ($MgSO_4$), potassium chloride (KCl), potassium nitrate (KNO_3), sodium chloride (NaCl) and zinc sulphate ($ZnSO_4$) followed by drying and sowing into the agrifields (Table 1). Halopriming induces the pre-germination metabolic pathways by preventing radicle protrusion and decreased emergence time for enhanced nutrient uptake, optimization of germination consistency and germination rate with greater uniformity, improved plant performance, high vitality and crop yield in horticulture, floriculture and field crops even in adverse environmental conditions (Biju et al. 2017; Farooq et al. 2007, 2013; Guo et al. 2012; Iseri et al. 2014; Jisha and Puthur 2014; Nawaz et al. 2013; Patade et al. 2012; Pawar and Laware 2018; Sen and Puthur 2020; Srivastava et al. 2010).

Therefore, prospects, possibilities and mechanisms of halo-priming technology in the agroecosystems have been summarized in the present study.

2 Halopriming and Seed Germination

Seed priming improved the plant's biochemical profile by raising α-amylase function and soluble sugar content during seed germination even at low temperatures (Anaytullah and Bose 2007). Halopriming has been reported to enhance seed efficiency and seedling vitality of watermelon (Demir and Mavi 2004), rice (Farooq et al. 2006), maize (Kumari et al. 2017), and in several other crops. Seed priming with different inorganic salts such as NaCl, KCl and $CaCl_2$ has a beneficial impact on pepper germination under salinity stress by speeding up imbibition, allowing the seeds to faster metabolic function (Aloui et al. 2014). The salt-sensitive (PI94341) and salt-tolerant (Kharchia 65) genotypes of wheat (*Triticum aestivum* L.), primed with KCl and NaCl

Table 1 Differential responses of halopriming on seeds of different crops

Crop	Halopriming agents	Concentration	Duration	Germination/seedling growth %	Metabolomics	Enhance tolerance against stress	References
Vigna unguiculata	$CaCl_2$	1%	12 h	86.66	–		Karim et al. (2020)
Abelmoschus esculentus	$CaCl_2$ and KNO_3	1 and 2%	18 and 6 h	64	Antioxidants enzymes field emergence, lipid peroxidation, reserve mobilizing enzymes, viability, vigour index	Oxidative stress	Sharma et al. (2014)
Triticum sp.	$CaCl_2$, KCl and NaCl	100 mM	12 h		Antioxidant enzyme activities (CAT, POD, APX)	Salt stress	Islam et al. (2015)
Solanum lycopersicum	KNO_3	25 mM	24 h	81.33	α-Amylase activity	Salt stress	Nawaz et al. (2011)
Papaver rhoeas and *P. dubium*	KNO_3	0.5 gL^{-1}	24 h	50.1 and 49.61	–	Temperature, light regimes, pH, salt and osmotic stresses	Golmohammadzadeh et al. (2020)
Nigella sativa	KNO_3	−1 MPa	24 h	98	POX activity increased	Oxidative stress	Espanany et al. (2016)
Allium cepa	KNO_3	150 mM	6 days	42.5	Soluble sugars like raffinose, sucrose, glucose, and fructose contents were monitored, higher cytochrome c oxidase activity	–	Thakur et al. (2020)
Brassica rapa subsp. Pekinensis	KNO_3	200 mmol/L	8 h	34	Modulating POD, SOD, CAT, protein, sugar and proline content	Drought stress	Yan (2015)
Solanum lycopersicum	$Mg(NO_3)_2$	7.5 mM	24 h	98.7	Superoxide dismutase activity	Temperature stress	Nafees et al. (2019)
Triticum sp.	$Mg(NO_3)_2$	7.5 mM	10 h	94	Soluble and insoluble sugar contents and activity of α-amylase	Under heavy metal stress ($HgCl_2$)	Kumar et al. (2016a)
Cajanus cajan	NaCl	50 mM	2 h	–	beta-cyano-L-alanine, O-Acetylsalicylic	Salt stress	Biswas et al. (2018)
Nigella sativa	NaCl	1 and 2% (w/v)	24 h	88	–	Salinity stress	Gholami et al. (2015)
Vigna mungo	NaCl	50 mM	2 h	76	35 compounds altered significantly under salinity	Salt stress	Biswas and Saha (2020)
Abelmoschus esculentus	NaCl	3%	12 h	72.15	–	–	Tania et al. (2020)
Psophocarpus tetragonolobus	NaCl	125 mM	48 h	82.49	Enhance the germinability, antioxidant enzymes and biochemical activities	Oxidative stress	Kumar and Rajalekshmi (2021)
Vigna radiata	NaCl		6 h	–	–	NaCl and PEG stress	Jisha and Puthur (2014)
Oryza sativa	NaCl	75 mM	12 h	73	Generation of reactive oxygen species (ROS), accumulation of malondialdehyde, activities of enzymatic and content of non-enzymatic antioxidants and chlorophyll a fluorescence	Reduced the excess ROS generation and oxidative stress	Sen and Puthur (2020)
Nigella sativa	Urmia lake salt and Urea	5 M	16 h	74.6	Enhanced peroxidase and catalase activity	Osmotic stress	Ghiyasi et al. (2019)

increased germination percentage, triggered physiological attributes such as chlorophyll content and decreases mean germination time (Saddiq et al. 2019). Sesame seeds (*Sesamum indicum* L.) primed with $CaCl_2$ enhanced germination up to 88.75%, improved vigour and productivity (Tizazu et al. 2019). Halopriming with NaCl proved to be superior in maize and tomato for fast emergence, shoot and root length and other attributes such as photosynthetic pigments (Akter et al. 2018; González-Grande et al. 2020). NaCl priming enhanced breaking off hard seed coat which facilitates 20.56% seedling emergence in okra (Jonah et al. 2019). A better effect on crop productivity and a number of tillers per panicle was observed in different rice (*Oryza sativa* L.) varieties on priming with NaCl (Riadi et al. 2020).

Halopriming with NaCl and $CaCl_2$ improved germination and seedling growth parameters in maize (*Zea mays*) as compared to nonprimed seeds under salinity (Gebreegziabher and Qufa 2017). Sorghum seeds (*Sorghum bicolor* L.) treated with different inorganic salts such as NaCl, KCl and $CaCl_2$ provoked healthy germination and early seedling growth (Chen et al. 2021). Cowpea seeds (*Vigna unguiculata* (L.) Walp.) primed with $CaCl_2$ improve carbohydrate content, photosynthetic pigments and biomass production (Farooq et al. 2020). Priming of peanut seeds variety (Tainan 9) with $CaCl_2$ showed high germination, increase shoot length, root length and reduced mean germination time (Jeammuangpuk et al. 2020).

KNO_3 serves as a nutrient and initiator for pre-germination metabolic events such as increased water imbibition, cell division and elongation, essential germination and other growth activity in seedlings of rice (Dhillon et al. 2021). Priming of rice (*Oryza sativa* L.) cultivars KDML105 and RD15KDML105 with KNO_3 increased imbibition pattern, germination percentage and uniform germination of seedlings (Ruttanaruangboworn et al. 2017). Rice seedlings primed with 2.5 and 5% KNO_3 improved emergence percentage by 70 and 94% compared with control (54%) in dry conditions (Ali et al. 2021a). Priming of *Capsicum frutescens* with NaCl and KNO_3 enhances germination potential, final germination percentage, plant length and reduce mean germination time (Robledo 2020). *Citrullus lanatus* (Thunb.) (Watermelon) seeds and China aster seeds (*Callistephus chinensis* L.) primed with KNO_3 enhanced survival percentage of seeds, germination indices, plant height, shoot and root length, root dry matter and vigour index (Barbosa et al. 2016; Wani et al. 2020). Priming of cotton and soybean seeds with KNO_3 improved germination and seed vigour under salt stress conditions (Miladinov et al. 2015; Nazir et al. 2014). Priming with $ZnSO_4$ improved germination percentage, vigour, photosynthetic pigment and sugar content in *Momordica charantia* seeds (Bukhari et al. 2021). On-farm seed priming of maize and pea with $ZnSO_4$ enhanced the length and number of grains/pods and yield attributes in both crops (Sharma et al. 2021).

3 Halopriming and Abiotic Stress Tolerance

Environmental stresses, such as salinity, temperature extremes (heat and cold), drought, osmotic stress, nutrient deficiency and heavy metal toxicity cause adaptation issues to seedlings and challenge seedling emergence of plumules and radicles, and seedling growth and development leading to yield losses (Ghiyasi et al. 2019; Hasanuzzaman et al. 2012). Seed priming treatment mitigates the detrimental consequences of different abiotic stress (salinity, drought, heat, cold, heavy metals, etc.) responses via modifying the antioxidant metabolism and enhancing the accumulation of osmolytes (Basra et al. 2005a; Guan et al. 2009; Kausar and Ashraf 2003; Kumar et al. 2016a; Saha et al. 2010).

Halopriming with NaCl induces a physiological response in maize seeds that interact with plant stress memory causing the plants to respond swiftly and effectively to upcoming adverse environmental conditions (El-Sanatawy et al. 2021). The improved salt tolerance index (STI) based on growth parameters, such as shoot length, root length and relative water content in NaCl primed seeds were reported in sesame seeds and *Vigna mungo* L. (Biswas and Saha 2020; Mohammadi et al. 2013). NaCl pretreatments also efficiently reduced the harmful effects of salt stress facilitating effective germination due to increased K and Ca content and decreasing Na accumulation in stems and leaves of *Cucumis melo* (Sivritepe et al. 2005). Fenugreek seeds (*Trigonella foenum-greacum*) and tomato (*Solanum lycopersicum* cv.'Río Grande) primed with NaCl mitigated the deleterious effect of salt stress, significantly (González-Grande et al. 2020; Mohammadi et al. 2013). Sorghum seeds (*Sorghum bicolor* L.) treated with different concentrations of inorganic salts ameliorated the efficacy of saline stress (Chen et al. 2021). Besides, halopriming has also been reported to be beneficial for enhanced seed germination, seedling growth under drought and induced salt resistance in pepper (Amjad et al. 2007), *Triticum aestivum* L. (Afzal et al. 2008), sugarcane (Patade et al. 2012), *Vigna radiata* (L.) Wilczek varieties (Jisha and Puthur 2014) and *Cajanus cajan* L. (Biswas et al. 2018).

Seed priming with calcium salts has proved to be more efficient and cost-effective in enhancing plant stress resistance (Jafar et al. 2012; Tabassum et al. 2017), as the calcium serves as a secondary messenger in signal transduction (White and Broadley 2003) and promotes osmolyte and antioxidant production in stress conditions (Farooq et al. 2017). Halo-conditioning with $CaCl_2$ enhances crop establishment and confers cis-tolerance on salt-affected lands in wheat (Feghhenabi et al. 2020; Tamimi 2016; Yasmeen et al. 2013) and cowpea (*Vigna unguiculata* (L.) Walp.; Farooq et al. 2020). Seed priming with $CaCl_2$ increased seedling development, seedling establishment, plant length, grain number, grain weight, grain yield and tillers number under drought stress in wheat (Hussian et al. 2013). It was also elucidated when $CaCl_2$ primed seed supplemented by KCl stimulated salt tolerance in rice varieties that is revealed by increased germination performance, seedling emergence and dry weight under saline conditions (Afzal et al. 2012). The seeds of rice and maize primed with NaCl, KCl, $CaCl_2$ and KNO_3 solution enhance resistance against salt stress and exhibited improved growth (Gebreegziabher and Qufa 2017; Theerakulpisut et al. 2016). By priming with inorganic salts NaCl and KCl, salt-sensitive wheat (*Triticum aestivum* L.) genotype PI.94341 mitigated the negative effects of salinity stress through physiological seed enhancement (Saddiq et al. 2019). Halopriming with $CaCl_2$, KNO_3 and NaCl show a significant effect in alleviating salt-induced oxidative stress in rice (*Oryza sativa* L. cv.) (Riadi et al. 2020; Tahjib-Ul-Arif et al. 2019). In addition to this, the devastating effects of salinity stress on sunflower (Bajehbaj 2010; Kaya et al. 2006) and melon (Oliveira et al. 2019) seeds were reduced by treating them with KNO_3. *Nigella sativa* seeds primed with $ZnSO_4$ and KNO_3 increased germination percentage, germination rate and seedling growth under severe water stress (Fallah et al. 2018).

Among various abiotic stressors, Chilling (0–15 °C) is one of the most destructive abiotic stress which severely reduces crop yield (Thakur et al. 2010). Cold stress reduces membrane permeability and disturbs ion transport at the cellular level (Ahmad and Prasad 2011). Consequently, cold stress reduces seed emergence rates, causes seedling failure and accelerates the production of free radical ions (Yu and Rengel 1999). Under chilling stress, halo-priming facilitated the crop establishment and growth by enhancing germination rate and physiological parameters in Chickpea (*Cicer arietinum*) and hairy vetch (*Vicia villosa*) (Farooq et al. 2017; Yusefi-Tanha et al. 2019). Peanut seeds primed with $CaCl_2$ showed enhanced storability and faster germination under low-temperature conditions (Jeammuangpuk et al. 2020). Priming with KNO_3 followed by drying also allowed cotton seeds to be cold tolerant and produced vigorous seedlings (Cokkizgin and Bölek 2015). The priming of maize and eggplant seeds with $Ca(NO_3)_2$ promoted germination rate, radicle protrusion rate index and seedling dry mass under low and high-temperature conditions (Gouveia et al. 2017; Salles et al. 2019). Batista et al. (2016) observed that palisade grass (*Brachiaria brizantha* cv. MG-5) seeds primed with $Ca(NO_3)_2$ and KNO_3 improved physiological seed quality resulting in seeds with great stress tolerance under high temperature (Batista et al. 2016).

Heavy metals have been reported to reduce the germination parameters of a developing seedling. Halopriming with $Mg(NO_3)_2$ and $Ca(NO_3)_2$ reduced the severity of heavy metal ($HgCl_2$) stress in wheat var-HUW-468 during the germination process by increasing endosperm α-amylase activity and soluble sugar content resulting in enhanced germination percentage, seedling emergence and growth performance (Kumar et al. 2016a). Black cumin seeds haloprimed with KNO_3 also had the highest germination percentage (100%), plumule length, and dry weight mitigating cadmium toxicity (Espanany et al. 2016). Priming of garden cress (*Lepidium sativum*) with NaCl and KCl promotes seed germination, boosts seedling growth and develops seedling resistance under hazardous metals stress (Nouri and Haddioui 2021). Besides, different responses of conditioning of seeds, i.e. seed priming in several crops under the regime of different abiotic stresses have also been summarized in Table 1.

4 Halopriming and Anti-oxidative Responses

Seed priming allows morphological, physiological and biochemical changes leading to enhanced stress tolerance and amelioration of the adverse effects of abiotic stress in plants by up-regulating the activity of antioxidant enzymes (Ashraf et al. 2008; Basra et al. 2005b; Bussotti et al. 2014; Chiu et al. 1995; Chang and Sung 1998; Chandra Nayaka et al. 2010; Guan et al. 2009; Kausar and Ashraf 2003; Kumar et al. 2016a; Thakur et al. 2019).

Peroxidases probably played a vital role in reducing oxidative damage and hydrogen peroxide content. An enhanced guaiacol peroxidase content was found to play important role in haloprimed pea (*Pisum sativum* L.) under chilling effect (Yusefi-Tanha et al. 2019). Halopriming with 125 mM NaCl enhanced germination, antioxidant enzymes (CAT, APX, SOD and POD) and biochemical activities in winged bean [*Psophocarpus tetragonolobus* (L.) DC.; Kumar and Rajalekshmi (2021)]. NaCl priming of fenugreek seeds (*Trigonella foenum-graecum*) activated the antioxidant machinery that alleviated negative effects of salt stress and maintain ionic balance (Mahmoudi et al. 2020). Antioxidant enzyme activities (CAT, POD, APX) of wheat (*Triticum aestivum* L.) cultivars, Lu26s (salt-tolerant) and Lasani-06 (salt-sensitive) were found to be significantly increased after halopriming (Islam et al. 2015). Halopriming with KCl significantly increased the activity of antioxidants in chicory (Sadeghi and Robati 2015). Haloprimed Cowpea seeds (*Vigna unguiculata* (L.) Walp.) with $CaCl_2$ increases total antioxidants activity up to 22.2% under salt stress (Farooq et al. 2020).

Halopriming greatly increased SOD, CAT, APX and GPOX (guaiacol peroxidase) activities in primed seeds compared to non-primed seeds of different *Oryza sativa* varieties (Sen and Puthur 2021). KNO_3 substantially escalated CAT activity within the FARO44 rice seedlings that scavenged ROS indicated increased tolerance to drought (Ali et al. 2021a, b). Under salinity stress, rice seeds (*Oryza sativa* L. cv. BRRI dhan29) primed with KNO_3 mitigated the adverse effects of reactive oxygen species, i.e. H_2O_2 and O^- radical by up-regulating the activity of antioxidant enzymes such as APX at the seedling stage (Tahjib-Ul-Arif et al. 2019). Priming of Chinese cabbage (*Brassica rapa subsp. pekinensis*) with KNO_3 significantly enhanced POD, SOD and CAT activity under drought stress conditions (Yan 2015). Priming with KNO_3 showed increased POD activity in *Silybum marianum* L. and nitrate reductase activity in tomato under salinity stress (Lara et al. 2014; Zavariyan et al. 2015). KNO_3 primed sesame seeds (*Sesame indium* L.) increased the CAT and POD enzyme activities (Kumar et al. 2016b). $Ca(NO_3)_2$ treatment enhanced the activity of various antioxidant enzymes such as CAT, APX, SOD, GR and POD in germinating cucumber seeds (Fan et al. 2017). Halo primed tomato seeds with magnesium nitrate [$Mg(NO_3)_2$] significantly increased antioxidant enzyme activities such as SOD, POD, APX, and CAT at different temperature regimes (Nafees et al. 2019). Under water stress circumstances, seed priming of black cumin (*Nigella sativa* L.) with $ZnSO_4$ increased CAT activity in seedlings (Fallah et al. 2018). Priming with $ZnSO_4$ also increased POD activity significantly in fruits and leaves of *Momordica charantia* (Bukhari et al. 2021).

5 Halopriming and Production of Osmolytes

Halopriming stimulates seed metabolism by producing osmolytes and/or signalling agents, thus facilitating germination and improved growth and yield performances. Osmolytes are compatible solutes that accumulate within plant cells and act as osmoticum to hold water by lowering the osmotic potential, protecting macromolecules and cell membranes from oxidative stress and dehydration (Fahad et al. 2017; Tabassum et al. 2018; Verslues and Juenger 2011).

NaCl priming in tomato seeds resulted in the accumulation of osmoregulating defence molecules (anthocyanin and proline) and activation of the antioxidative enzyme mechanism (Sahin et al. 2011). Among the three varieties of *Vigna radiata*, haloprimed Pusa Ratna showed a 50% increase in proline content in normal conditions (Jisha and Puthur 2014). Priming of pepper (*Capsicum annuum* L.) seeds with $CaCl_2$ resulted in a significant increase in proline content under salinity stress to protect from oxidative stress (Aloui et al. 2014). Halopriming significantly increased leaf proline and phenolic contents under salt stress in both salt-sensitive Lasani-06 and resistant Lu26s wheat cultivars (Islam et al. 2015). Sesame (*Sesame indium* L.) and rice seeds primed with different concentrations of KNO_3 enhanced proline accumulation in seedlings to maintain osmoprotection (Kumar et al. 2016b; Tahjib-Ul-Arif et al. 2019).

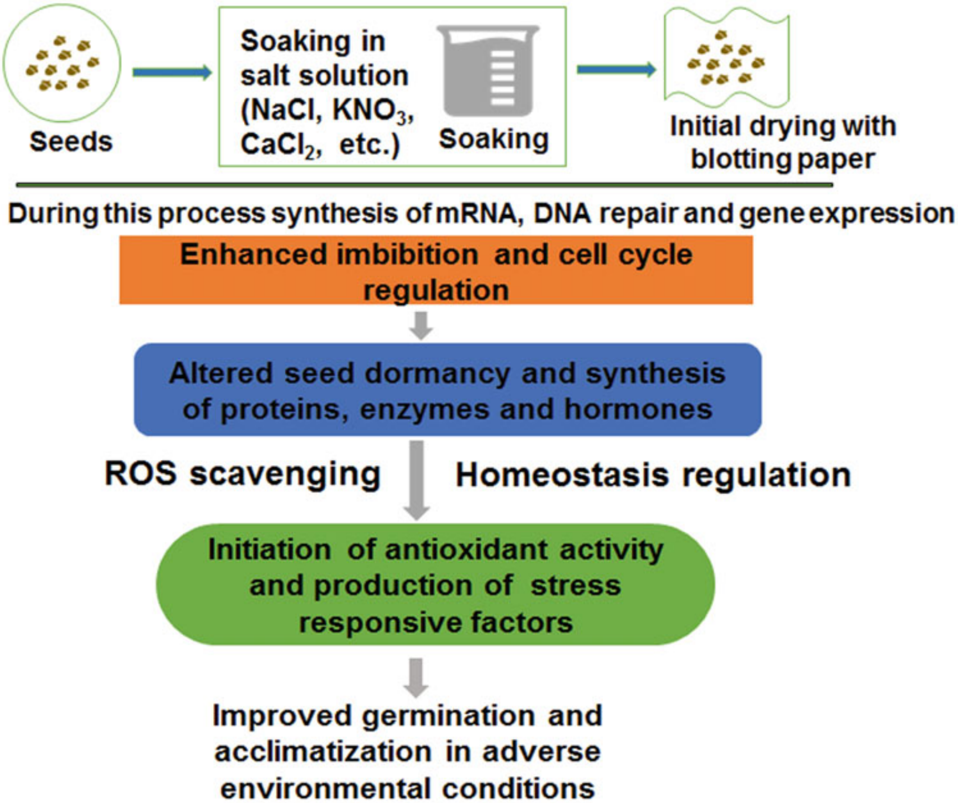
Tomato seeds primed with magnesium nitrate $(Mg(NO_3)_2$ enhanced production of osmolytes, proline and sugar that preserved plant cell structure and metabolism (Nafees et al. 2019). Halopriming treatment of soybean seeds with $ZnSO_4$ and $CaCl_2$ showed increased soluble sugar and proline content under soda saline-alkali stress (Dai et al. 2017). Priming of *Nigella sativa* and *Momordica charantia* seeds with $ZnSO_4$ significantly enhanced proline and phenolic compounds to ameliorate the stress effects (Bukhari et al. 2021; Fallah et al. 2018).

6 Mechanism of Halopriming

Halopriming is a pre-sowing method that includes exposing the seeds first to a salt solution for a certain period allowing them for partial hydration followed by washing with water and re-drying to original moisture content (Fig. 1). There are two important characteristics of priming such as desiccation tolerance and seed sustainability (Ellis and Hong 1994; Hay and Probert 1995; Gurusinghe and Bradford 2001). Priming enhances the sustainability of low vigour seeds (Varier et al. 2010). The time required for salt treatment is crop-specific and depends upon its variety or cultivar and the priming process activates pre-germinative metabolic activity to start the germination process without radicle emergence (Basra et al. 2003; Bradford 1986; Chen and Arora 2013; Dell'Aquila and Tritto 1991; Giri and Schillinger 2003; Ibrahim 2016; Paparella et al. 2015; Pill 2020). The metabolic activity includes water imbibition, activation of proteins, enzymes, hormones and signal transduction facilitating the breaking of seed dormancy (Ajouri et al. 2004). Under salty alkali stress, halopriming has been linked to a larger osmotic adjustment, more antioxidant defence system activities, more photosynthetic pigment levels, better membrane integrity and more added starch accumulation regulated by biochemical, physiological and molecular mechanisms related to development of embryo, protrusion of plumule and radicle and further with vigorous seedling growth and development (Bewley 1997; Bewley and Black 2013; Lutts et al. 2016; Rajjou et al. 2012).

The process of germination is divided into three stages, viz., imbibition phase (first phase), lag phase (second phase) and growth phase (third phase) (Bewley and Black 1994, 2013; Daszkowska-Golec 2011; Eskandari et al. 2013; Rosental et al. 2014). On priming of the seeds, rapid water absorption facilitates protein synthesis and respiratory activity via mRNA and DNA in the imbibition phase or first phase. Up-regulation of antioxidant enzymes and the accumulation of osmolytes and activation of ROS-mediated signalling pathways have also been documented during the first phase of imbibition (Paparella et al. 2015). The second phase is concerned with controlled water uptake and the start of various physiological processes associated with germination, such as the synthesis of proteins and the availability of soluble sugars (Varier et al. 2010). During the last phase, a marked increase in water intake takes place along with radicle protrusion developed from the seed coat (Bewley and Black 1994; Waqas et al. 2019). Further, the stress resistance of seedlings has been linked to the persistence of the antioxidant mechanism activated and metabolic changes that

Fig. 1 Mechanism of halo priming for enhanced stress tolerance in seeds



occurred during the hydration of seeds, even after germination, in the seedlings as well (Paparella et al. 2015). Re-drying is essential for seed storage (Di Girolamo and Barbanti 2012). It prevents quality loss that is caused by severe deterioration of seeds (Di Girolamo and Barbanti 2012; Halmer 2004; Maiti 2011; Parera and Cantliffe 1994; Varier et al. 2010). Priming can also be characterized as a form of preparative germination phase and the lag phase may be extended (Nonogaki et al. 2010). When a primed seed is in the growth phase, it can survive a restoration to its original moisture content without vigour loss thus primed seeds can be stored for a period till the time of sowing (Di Girolamo and Barbanti 2012; Ibrahim 2016; Rajjou et al. 2012; Taylor et al. 1998). However, the primed seeds have a drawback in utilizing the process for commercial purposes with shorter shelf life than seeds that haven't been primed, so seeds should be processed properly before planting (Ibrahim 2019). Seed priming enhances germination by regulating DNA repair mechanisms, decaying antioxidant scavenging enzymes like catalase, de novo nucleic acid, and protein synthesis, and production of sterols and fatty acids (Afzal et al. 2002; Chen and Arora 2011; Kubala et al. 2015; Paparella et al. 2015; Rajjou et al. 2012). Halopriming can affect seed osmotic balance by increasing K^+ and Ca^{2+} uptake while decreasing Na^+ and Cl^- absorption thus maintaining cell turgor by balancing membrane potential (Ibrahim 2016; Quintero et al. 2018). Priming triggers ROS scavenging mechanism by enhancing the activity of free radical scavenging enzymes such as catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR) and expression of other stress-responsive proteins that include aquaporins (AQP), dehydrins and late embryogenesis abundant (LEA) proteins (Anaytullah and Bose 2012; Bohnert and Shen 1998; Kumar and Rajalekshmi 2021; Lara et al. 2014; Mittal and Dubey 1995; Sadeghi and Robati 2015; Vander Willigen et al. 2006).

7 Factors Affecting Halopriming

The efficacy of seed priming has been strongly linked with various physical factors such as temperature, aeration, salt concentration, light, priming process, duration of treatment, dehydration after priming, oxygen availability, storage conditions, etc. and certain biological factors like species and its cultivar and variety, age of the seeds, seed vitality and quality (Corbineau and Come 2006; Farooq et al. 2012; Maiti and Pramanik 2013; Parera and Cantliffe 1994). Aeration is the most effective and critical factor that influences seed respiration, seed sustainability and seedling protrusion (Bujalski and Nienow 1991; Heydecker et al. 1973; Fig. 2).

Temperature is another critical factor affecting seed germination. For priming and germination, the optimal temperature varies from 15 to 30 °C (Wahid et al. 2008), however, haloprimed seeds can endure in low and high-temperature regimes. Magnesium nitrate ($Mg(NO_3)_2$ primed seeds at 40 °C showed the optimum germination ratio, fresh and dry weight of seedlings, shoot and root length, and overall seedling length up to 10 days (Nafees et al. 2019). Haloprimed seeds of a tomato hybrid variety (*Lycopersicon esculentum* Mill. NUN 5024) performed well at 40 °C and room temperature (35/28 °C, day/night), but poorly at 10 and 25 °C. Potassium primed seeds of *Papaver rhoeas* (55.01%) and *Papaver dubium* (49.61%) showed maximum germination rate on 25 and 20 °C temperatures, respectively, and the minimum germination (7.55%) was observed at 10 °C in either case (Golmohammadzadeh et al. 2020).

Duration of treatment solution also influenced the seed emergence, significantly (Wahid et al. 2008). By increasing the duration of $ZnSO_4$ treatment from 4 to 12 h, the greatest influence on yield attributes was recorded in 12-h duration in maize and pea crops (Sharma et al. 2021). *Papaver rhoeas* and *P. dubium* seeds primed for 24 h with 0.5 g/L KNO_3 solutions showed maximum seed germination and lowest germination when primed with 4_g/L g/L KNO_3 for 96 h (Golmohammadzadeh et al. 2020). Soaking of perennial rye seeds at 125 mM NaCl for 24 h enhanced germination percentage (Araghi Shahri et al. 2015). Soaking of three wheat varieties (Sherodi, Fajer, and Taram) for 12, 24, or 36 h in 0.5 or 1% calcium chloride ($CaCl_2$) solutions, 24 h exposure was found to be effective in terms of increased germination percentage in all three varieties in either case (Yari et al. 2012). Priming of China aster seeds (*Callistephus chinensis* (L.) with KNO_3 at 12 and 18 h, though priming duration for 12 h proved to be more favourable for seedling establishment in field conditions (Wani et al. 2020).

The concentration of priming agents is also a crucial factor for enhanced growth attributes in different crops. The optimum concentration of $CaCl_2$ for gerbera was 25 mM and for *Zinnia elegans*, it was 50 mM $CaCl_2$ (Ahmad et al. 2017). Maize seeds primed with 4000 ppm NaCl had a higher germination index and a shorter mean germination time than seeds primed with 8000 ppm NaCl (El-Sanatawy et al. 2021). Priming with 1.0% KNO_3 was more effective to enhance seed emergence and uniform germination of rice cultivars, but priming with 2.0% KNO_3 showed a lesser effect on seedlings (Ruttanaruangboworn et al. 2017). Halopriming with different concentrations of KNO_3 (10–

Fig. 2 Various factors prompting the plant responses during the process of halopriming

30 ppm) of *Capsicum frutescens* seeds, showed the highest influence on radicle and plumule length as well as fresh and dry biomass was observed at 25 ppm KNO_3 (Robledo 2020). Among the various concentrations of $ZnSO_4$, priming with 1% $ZnSO_4$ has been shown to be more efficient than priming with 2 and 3% $ZnSO_4$ in maize and pea crops (Sharma et al. 2021).

The type of halopriming agents and cultivar/variety of the seeds are also some other determinants for better growth and development. In various inorganic salts, priming with $CaCl_2$ proved to be stronger than other halopriming agents in mitigating salinity-induced suppression of germination in rice (*Oryza sativa* L. cv. BRRI dhan29) (Tahjib-Ul-Arif et al. 2019). Haloprimed seeds of two wheat (*Triticum aestivum* L.) cultivars, Inqlab-91 and SARC-1 with NaCl, $CaCl_2$ and $CaSO_4$ in saline environment showed cultivar dependent differential responses and $CaCl_2$ or $CaSO_4$ proved to be more effective than NaCl as a priming agent in mitigating the adverse effects of salinity on wheat growth (Afzal et al. 2008). Likewise, haloprimed seeds of two rice cultivars, Shaheen Basmati and Basmati 2000 with 2.2% $CaCl_2$ and KCl for 36 h showed optimum results with $CaCl_2$ in terms of increased germination potential, germination rate, seedling growth and salinity resistance in both cultivars (Afzal et al. 2012). Contrary to this, in the case of black seeds (*Nigella sativa*), of the various priming agents, viz., NaCl, $CaCl_2$, $KNO_{3,}$ $CuSO_4$ and $ZnSO_4$ tested NaCl proved to be the most efficient to combat salt stress in terms of higher germination efficacy and further growth and development (Gholami et al. 2015). The effects of the two halopriming agents, $CaCl_2$ and NaCl on maize physiology were distinct. $CaCl_2$ priming increased the germination process, while NaCl priming enhanced seed maturity and yield (Gebreegziabher and Qufa 2017). In the case of tomato seeds, KNO_3 was more successful than the other halopriming agents in increasing final germination, germination rate and seedling vigour (Farooq et al. 2005). Of the different inorganic salts such as NaCl and KCl, $CaCl_2$ proved to be the most efficient halopriming agent for improving *Sorghum* crop establishment (Chen et al. 2021). Halopriming of *Capsicum frutescens* with varying concentrations of two inorganic salts, i.e. NaCl and KNO_3, KNO_3 was found to be more effective than NaCl (Riadi et al. 2020). Pigeon pea seeds were primed with different salts, viz. $ZnSO_4$, $CaCl_2$ and KCl and $ZnSO_4$ showed maximum germination up to 92% (Vanitha and Kathiravan 2019).

8 Conclusion and Future Prospects

Since managing seeds is much easier for farmers in comparison to managing crops in the field, therefore, halo priming has been regarded as a viable remedy for germination issues and in the reduction of the risk of poor stand establishment when seeds are cultivated in adverse environments. The goal of the potent seed priming technique is to synchronize the emergence and protection of seeds against abiotic influences during the crucial seedling establishing phase, resulting in a uniform stand and increased production in the near future. Halopriming technique has proved promising in breaking seed dormancy, improving germination and yield potential of crops and rendering systemic resistance to abiotic stresses in a range of environmental conditions. As a result, halopriming would be a promising technique in the time ahead for sustainable food security and to sustain green agricultural practices with much fewer threats to the environment.

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Naturally Growing Native Plants of Wastelands: Their Stress Management Strategies and Prospects in Changing Climate

Nabanita Bhattacharyya

Abstract

Industrial and mining waste dumping is among the most concerning anthropogenic causes of the formation of stress-laden wastelands, which are characterized by loss of plant cover and subsequent land degradation. Under the pressure of changing climate, the revival of the degraded wastelands into productive lands becomes a sustainable option to meet the basic survival demands of the increasing human population. Restoration of vegetation cover is a widely accepted eco-friendly approach for remediation of degraded wastelands over physical or chemical strategies. However, the successful establishment of plants in wastelands is a difficult process due to the phytotoxic nature of the wasteland soils. Therefore, the use of naturally growing native plants, which thrive well in the adverse soil properties of degraded lands with little or no agronomical effort, is an effective option. Some of these plants might have phytoremediation potential, which is a sustainable technology for the remediation of contaminants including heavy metals from soil and water by using plants. Documentation of such stress-tolerant naturally growing plants of various wastelands and studying their mechanism of tolerance are among the major emerging areas of research in recent times. Such efforts may help in finding novel plant species that are more stress-tolerant with greater potential of creating vegetation cover on degraded wastelands. Therefore, for the benefit of interested researchers and policymakers, an attempt has been made to review and comprehensively document the discrete information, from available sources, on naturally growing native plants of various industrial and mining wastelands, their stress management strategies and phytoremediation prospects in changing climate.

Keywords

Dumpsites • Heavy metal • Native plants • Phytoremediation • Stress • Wastelands

Abbreviations

IPCS	International Programme on Chemical Safety
WHO	World Health Organization

1 Introduction

Wastelands are the landmasses that are degraded due to various natural or anthropogenic factors and are lying underutilized as non-productive land due to lack of appropriate water and soil management practices (Sarma 2006; Singh et al. 2003). Industrial and mining waste dumping are the two most concerning anthropogenic causes of wasteland formation post-industrialization era. Millions of hectares of land have been turned into wastelands in developed and developing countries due to gross mismanagement and unsustainable practices over the landmasses as a result of the indiscriminate scale of industrialization and mining activities (Zhu et al. 2018). Industrial and mining waste dumping areas are notorious sources of pollution and contamination that add various pollutants of organic and inorganic nature including toxic heavy metals to the environment. There is increasing evidence that heavy metal pollution of industrial and mined areas causes health damage to the local inhabitants (Lei et al. 2015; Shen et al. 2017; Xiao et al. 2017; Santucci et al. 2018). Therefore, rehabilitation of such wastelands should be a priority concern to be addressed for the respective governments, as public health and shortage of cultivable lands are among the burning problems of recent times. The most significant impact of dumping exercise is the loss of plant cover that leads to land degradation. Area of arable land is depleting fast with the increase in human

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N. Bhattacharyya (✉)
Department of Botany, Gauhati University, Guwahati, 781014, Assam, India
e-mail: nbh_17@gauhati.ac.in

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population due to increase in agriculture, industrialization and urbanization and hence, remediation of degraded wastelands is the much-talked need of the hour to meet the requirements of the increasing population (Bhattacharyya 2012).

The various abiotic stresses encountered by the plants in wastelands are water stress (flood and drought), temperature stress (high and low temperature), nutrient deficiency or overburden, heavy metal contamination, salt stress etc. (Das et al. 2021; Franzaring et al. 2018). The consequences of land degradation in wastelands are soil erosion, depletion of natural resources, lower productivity, groundwater depletion, shortage of drinking water, reduction in species diversity etc. Most of the potential productive lands have turned into wastelands due to gross mismanagement and unsustainable exploitation of its biosphere (Bhattacharyya 2012). Available physical or chemical strategies for remediation of degraded wastelands are temporary with multiple limitations, such as the threat of irreversible changes in soil properties, disturbance in native soil microflora, chances of secondary pollution as well as high cost of the processes (Jutsz and Gnida 2015). Therefore, sustainable biological methods like the restoration of vegetation cover on degraded sites are widely accepted as eco-friendly approaches (Wong 2003). Phytoremediation is a solar-driven, eco-friendly, sustainable and inexpensive technology with impressive public acceptance, where plants are used for the remediation of various contaminations including toxic heavy metals from soil and water (Marrugo-Negrete et al. 2016; Maharet al. 2016; Ali et al. 2013). Having great biomass with considerable metal tolerance capacity are among the important criteria to be the perfect plant species for phytoremediation (McGrath et al. 2002; McGrath and Zhao 2003). However, the successful establishment of plants in wastelands is a difficult process due to the stressful and phytotoxic nature of the wasteland soils (Bradshaw 1997). Moreover, restoration of natural dynamics of ecological succession in degraded soil of wastelands is required for systematic conversion into arable land and thoughtful and logical selection of plants is crucial for that purpose.

In this regard, the use of naturally growing native plants with inherent capabilities to adapt and withstand the adverse environment, soil properties and toxicity level of degraded lands can prove to be an effective option and information about such plant species from various wastelands may be beneficial in creating vegetation cover successfully in degraded sites (Yoon et al. 2006; Das et al. 2021). Several studies reveal the presence of numerous plant species growing naturally on industrial and mining wastelands, which can be prospected for their capabilities to clean up the environment by proper research-based approach and management. Therefore, realizing the discrete nature of such information, an attempt has been made to review and comprehensively document the available information on naturally growing native plants of various degraded wastelands including pulp and paper mill dumpsites, fly ash dumpsite of the thermal power plant as well as various metal mine tailing areas along with their stress management strategies and prospects in changing climate, for the better benefit of interested researchers, environmentalists and policymakers.

2 Pulp and Paper Mill Waste Dumpsite

Designated as one of the most notorious environment degraders, pulp and paper industries are the sources of a variety of wastes that are discharged into the environment in solid, liquid and gaseous forms (Buyukkamaci and Koken 2010). The most important solid wastes generated by a paper mill are the lime sludges, which are often disposed to nearby low-lying areas to form barren dumpsites without vegetation that are prone to be turned into degraded lands (Phukan and Bhattacharyya 2003). Analyses of various stress indices in established bio-monitor plants like *Ricinus communis* L. (Euphorbiaceae) as well as investigation of soil physico-chemical properties and nutrition status confirmed the stress burden and phytotoxicity of such degraded dumpsites (Das et al. 2021). However, despite of the unfavorable and harsh condition for vegetation growth, a few species of plants, with ethnomedicinal and economic importance, were reported to be grown naturally in paper mill dumpsite (Table 1), some of which had also been reported from mining and industrial dumpsites as tolerant natural vegetation (Das et al. 2021). These plants possibly have inherent capabilities to withstand stress and hence can be prospected to create vegetation cover by following proper management practices with minimal effort, in an attempt to recover paper mill dumpsites into arable lands in course of time.

3 Copper Mine Tailings

Finely ground wastes produced after copper are extracted from the ores and during the beneficiation process is called the copper tailings. High concentrations of toxic heavy metals like lead (Pb), zinc (Zn), arsenic (As) and cadmium (Cd) were found to be present in such copper mine tailings, from which several plant species were reported despite of metal overburdens (Table 2). It was suggested that the plants like *Imperata cylindrica, Cynodon dactylon* and *Paspalum distichum* that were dominant among all other species could have phytoremediation potentials for future revegetation programs in copper mine tailing sites (Chen et al. 2005; Zhan and Sun 2012).

Table 1 Native plants of paper mill dumpsite (Das et al. 2021)

Sl. no	Name of plant	Family	Type of stress tolerated
1	*Calotropis gigantea* (L.) Dryand.	Asclepiadaceae	Nutrient overburden, toxic trace elements, excess amount of calcium
2	*Chromolaena odorata* (L.) R. M. King & H Rob.	Asteraceae	
3	*Mikania scandens* (L.) Willd.	Asteraceae	
4	*Ricinus communis* L.	Euphorbiaceae	
5	*Rotheca serrata* (L.) Steane & Mabb.	Lamiaceae	
6	*Senna* sophera (L.) Roxb.	Fabaceae	
7	*Solanum myriacanthum* Dunal.	Solanaceae	

Table 2 Native plants of copper mine tailings (Chen et al. 2005; Llerena et al. 2021; Zhan and Sun 2012)

Sl no	Name of plant	Family	Type of stress tolerated
1	*Imperata cylindrica* var. major (Nees) C.E. Hubb	Poaceae	Heavy metals like Pb, Zn, As, Cd, Cu and Cr contamination
2	*Cynodon dactylon* (L.) Per.	Poaceae	
3	*Setaria viridis* (L.) Beauv.	Poaceae	
4	*Coreopsis drummondii* Torr. Et Gray	Asteraceae	
5	*Inula ensifolia* L.	Asteraceae	
6	*Erigeron acris* L.	Asteraceae	
7	*Kummerowia striata* (Thunb.) Schindl.	Leguminosae	
8	*Cyperus rotundus* L.	Cyperaceae	
9	*Pteris cretica* L.	Pteridaceae	
10	*Pteris vittata* L.	Pteridaceae	
11	*Miscanthus floridulus* (Labill.) Warb	Poaceae	
12	*Saussurea japoinca* (Thunb.) Dc.	Asteraceae	
13	*Paspalum distichum* L.	Poaceae	
14	*Phragmites communis* Trin.	Poaceae	
15	Miscanthus sinensis	Poaceae	
16	Zoysia sinica	Poaceae	
17	*Hippochaete debilis* (Roxb. ex Vaucher) Ching	Equisetaceae	

4 Antimony Mine Area

Antimony mine areas are contaminated with multiple heavy metals including a very high amount of antimony (Sb), As, Cd, as well as comparable concentrations of copper (Cu), Pb and Zn to the corresponding background values of study areas (Long et al. 2018). There were reports on several native plant species growing naturally in those areas (Table 3) and heavy metals were accumulated mainly on the aerial parts of those plants revealing their phytostabilization potential against multi-heavy metal pollution. Among all the colonized plants, *Bidens bipinnata* L. (Family: Asteraceae) was found to be the most suitable species in the antimony mine area considering the metal accumulation level and growing abundance of the plant.

Table 3 Native plants of antimony mine area (Long et al. 2018)

Sl no	Name of plant	Family	Type of stress tolerated
1	*Boehmeria nivea* (L.) Gaudich.	Urticaceae	Heavy metals like Sb, As, Pb, Cd, Cu and Zn contamination
2	*Symphyotrichum subulatum* (Michx.) G.L.Nesom	Asteraceae	
3	*Bidens bipinnata* L.	Asteraceae	
4	*Miscanthus sinensis* Andersson	Poaceae	
5	*Erigeron Canadensis* L.	Asteraceae	
6	*Artemisia umbrosa* (Besser) Turcz. ex Verl.	Asteraceae	

5 Gold Mine Area

Mercury (Hg) is used in the amalgamation process for the recovery of the gold during the Artisanal and small-scale gold mining (ASGM) process and therefore gold mines are considered as one of the major sources of Hg pollution in the environment (Marrugo et al. 2007). Improper handling of Hg has led to the contamination of different sections of the environment, threatening human health in surrounding areas (Olivero and Johnson 2002). There were reports on several native herbs and sub-shrubs that grow naturally on gold mine areas as promising plants for Hg remediation (Table 4) among which *Jatropha curcas* L., *Capsicum annuum* L., *Piper marginatum* Jacq. and *Stecherus bifidus* Willd. were found to be highly potential to be used in phytoremediation (Marrugo-Negrete et al. 2016).

6 Mercury Mining Area

Highly toxic inorganic and organic forms of Hg are accumulated and biomagnified at various trophic levels through food chains (Lindberg et al. 2007; Xia et al. 2010). Methylmercury (MMHg), an organic form of Hg, is the most toxic form of Hg (WHO and IPCS 1990) that poses a serious health risk to both humans and wildlife. One of the worst instances of Hg contamination in higher trophic levels is the Minamata disease that occurred in Japan after consumption of fish and other seafood contaminated with MMHg. The most prevalent anthropogenic sources of Hg are the mercury mining and retorting of cinnabar ores that release elemental Hg into the surrounding environment and generate numerous wastelands of Hg-rich mine tailings (Gray et al. 2004; Qiu et al. 2005, 2013). Therefore, there were attempts to identify native plant species from Hg mining areas that could effectively accumulate both organic and inorganic Hg as promising candidates for phytoremediation of Hg-contaminated soil. A total of 49 species under 29 families of plants (Table 5) were reported from heavily Hg-contaminated wastelands of the mercury mining area of cinnabar ore mine tailings (calcines) in the Wanshan region of southwestern China (Qian et al. 2018), out of which *Eremochloa ciliaris* (L.) Merr., *Buddleja lindleyana* Fortune, *Equisetum giganteum* L., *Artemisia herba-alba* Asso, *Plantago asiatica* L., and *Sonchus oleraceus* L. were proved to be the most Hg-tolerant species. Considering the accumulation of total Hg in aerial and underground parts, *E. ciliaris* and *A. hispidus* had been suggested as potential hyperaccumulators and candidates for phytostabilization respectively, in abandoned Hg mining sites.

7 Lead–Zinc (Pb/Zn) Mining Area

There were reports of erosion of unstable Pb/Zn mine tailings from the dumping sites and the spread of contaminants from mining wastes into the nearby farmlands and water bodies. Soils in these mining wastelands turn acidic and polluted with toxic heavy metals like Cd, Pb and Zn, which are serious health hazards. Several plant species, mostly herbaceous plants, were reported to be growing naturally on Pb/Zn mine tailings with heavy metal accumulation potential above the standard phytotoxic level in Thailand, China and Morocco (Hasnaoui et al. 2020; Rotkittikhun et al. 2007; Shu et al. 2002; Xiao et al. 2018; Zhu et al. 2018). In Pb/Zn mining areas, the contents of Cd, Pb and Zn in the most analyzed plants exceed the normal ranges and the phytotoxic level. Various plant species including *Crassocephalum crepidioides, Solanum nigrum*, *Bidens pilosa*, *Erigeron canadensis*, *Ageratum conyzoides*, *Crepidiastrum denticulatum* and *Echinochloa crus-galli* showed strong capability in accumulation and transport of Cd and they could be used as good candidates for Cd-phytoextraction (Table 6). Among all the species, *C. crepidioides* demonstrated the basic characteristics of a Cd-hyperaccumulator, as Cd concentration in the aerial part of this species exceeded the threshold of Cd-hyperaccumulator. The lower translocation ratios for Cd, Cu, Zn and Pb in *Pteris vittata* and *Carex chinensis* make them suitable for phytostabilization in the study area (Zhu et al. 2018).

Table 4 Native plants of gold mining area (Marrugo-Negrete et al. 2016)

Sl no	Name of plant	Family	Type of stress tolerated
1	*Tabebuia rosea* (Bertol.) Bertero ex A.DC.	Bignoniaceae	High level of Hg contamination
2	*Cecropia peltata* L.	Utricaceae	
3	*Cyperus ferax* Rich.	Cyperaceae	
4	*Cyperus luzulae* (L.) Retz.	Cyperaceae	
5	*Eleocharis interstincta* (Vahl) Roem. & Schult.	Cyperaceae	
6	*Cyperus blepharoleptos* Steud.	Cyperaceae	
7	*Jatropha curcas* L.	Euphorbiaceae	
8	*Phyllanthus niruri* L.	Phyllanthaceae	
9	*Ricinus communis* L.	Euphorbiaceae	
10	*Senna alata* (L.) Roxb.	Fabaceae	
11	*Stecherus bifidus* Willd.	Gleicheniaceae	
12	*Ceiba pentandra* (L.) Gaertn.	Malvaceae	
13	*Guazuma ulmifolia* Lam.	Malvaceae	
14	*Thalia geniculata* L.	Marantaceae	
15	*Calathea lutea* (Aubl.) E.Mey. ex Schult.	Marantaceae	
16	*Muntingia calabura* L.	Muntingiaceae	
17	*Psidium guajava* L.	Myrtaceae	
18	*Ludwigia octovalvis* (Jacq.) P.H.Raven	Onagraceae	
19	*Piper marginatum* Jacq.	Piperaceae	
20	*Pityrogramma calomelanos* (L.) Link	Pteridaceae	
21	*Capsicum annuum* L.	Solanaceae	

8 Coal Mine Dumpsites

Coal mine overburden dumps, produced during coal mining, create devastated landscapes with degraded soil that cannot support the natural growth of vegetation (Arshi 2017). Nevertheless, in a few elaborative studies, a total of 114 and 102 plant species were recorded from coal mine dumpsites of West Bengal (WB) and Jharkhand (JK), India, respectively (Table 7). Nine species from WB, namely, *Cassia fistula* L., *Emblica officinalis* Gaertn., *Dalbergia sissoo* Roxb., *Azadirachta indica* A.Juss., *Pongamia glabra* Vent., *Albizia lebbeck* (L.) Benth, *Holoptelea integrifolia* (Roxb.) Planch., *Acacia auriculiformis* Benth. and *Swietenia macrophylla* King were tested for their phytoremediation potential against various stresses including heavy metals Cd and Hg (Kar and Palit 2019). These plants could grow well with an increase in biomass and could change the soil conditions by reducing the heavy metal content of degraded wasteland into a favorable condition for plant growth. Studies suggest the potential of these nine plants for revegetation of wastelands. A total of ten species namely *Vachellia farnesiana* (L.) Wight & Arn., *Alternanthera sessilis* (L.) R.Br. ex DC., *Croton bonplandianus* Baill., *Chrysopogon lancearius* (Hook.f.) Haines, *Cynodon dactylon* (L.) Pers., *Lantana camara* L., *Launaea nudicaulis* (L.) Hook.f., *Phyllanthus niruri* L., *Saccharum spontaneum* L. and *Xanthium strumarium* L. were found to be growing naturally in the core mining area of coal mine in JK, which indicated their better adaptation to more adverse environmental conditions (Arshi 2017). However, more than a hundred other reported plants from coal mine areas are yet to be tested for their phytoremediation capabilities with potential research endeavors.

9 Dumpsite of Thermal Power Plants

With the increase in urbanization, coal-based thermal power plants have been increased in considerable numbers to meet the increased demand for energy. As a result, bulk generation of solid wastes in the form of fly ashes is creating havoc in the surrounding environment. Fly ashes are considered as serious pollutants of soil, air and water as they contain toxic metals like Cr, Cd, Zn, Pb and nickel (Ni) as well as create other stresses for vegetation growth like alkaline pH, less nitrogen and organic carbon in the dumping sites (Pandey et al. 2016). Therefore, management of fly ash dumpsite by removal or stabilization of heavy metals with eco-friendly approaches like phytoremediation practices has gained much

Table 5 Native plants of Hg mining area (Qian et al. 2018)

Sl no	Plant	Family	Type of stress tolerated
1	*Allium tuberosum* Rottler ex Spreng.	Amaryllidaceae	High level of Hg contamination
2	*Arthraxon hispidus* (Thunb.) Makino	Poaceae	
3	*Aster ageratoides* Turcz.	Asteraceae	
4	*Symphyotrichum subulatum* (Michx.) G.L.Nesom	Asteraceae	
5	*Brassica rapa* L.	Brassicaceae	
6	*Buddleja lindleyana* Fortune	Scrophulariaceae	
7	*Buddleja officinalis* Maxim.	Scrophulariaceae	
8	*Campylotropis trigonoclada* (Franch.) Schindl.	Fabaceae	
9	*Chamaecrista nomame* (Makino) H.Ohashi	Fabaceae	
10	*Oxybasis glauca* (L.) S.Fuentes, Uotila & Borsch	Amaranthaceae	
11	*Chromolaena odorata* (L.) R.M.King & H.Rob.	Asteraceae	
12	*Cibotium barometz* (L.) J.Sm.	Cyatheaceae	
13	*Cirsium japonicum* DC.	Asteraceae	
14	*Clerodendrum bungei* Steud.	Lamiaceae	
15	*Erigeron canadensis* L.	Asteraceae	
16	*Coriaria nepalensis* Wall.	Coriariaceae	
17	*Corydalis edulis* Maxim.	Papaveraceae	
18	*Thelypteris acuminata* (Houtt.) C.V.Morton	Aspleniaceae	
19	*Debregeasia orientalis* C.J.Chen	Urticaceae	
20	*Puhuaea sequax* (Wall.) H.Ohashi & K.Ohashi	Fabaceae	
21	*Equisetum giganteum* L.	Equisetaceae	
22	*Eremochloa ciliaris* (L.) Merr.	Poaceae	
23	*Euphorbia esula* L.	Euphorbiaceae	
24	*Reynoutria multiflora* (Thunb.) Moldenke	Polygonaceae	
25	*Gynura bicolor* (Roxb. ex Willd.) DC.	Asteraceae	
26	*Artemisia herba-alba* Asso	Asteraceae	
27	*Bidens bipinnata* L.	Asteraceae	
28	*Houttuynia cordata* Thunb.	Saururaceae	
29	*Imperata cylindrica* (L.) P.Beauv.	Poaceae	
30	*Crepidiastrum sonchifolium* (Bunge) Pak & Kawano	Asteraceae	
31	*Macleaya cordata* (Willd.) R.Br.	Papaveraceae	
32	*Mentha canadensis* L.	Lamiaceae	
33	*Neyraudia reynaudiana* (Kunth) Keng ex	Poaceae	
34	*Oenanthe javanica* (Blume) DC.	Apiaceae	
35	*Oenothera glazioviana* Micheli	Onagraceae	
36	*Sonchus brachyotus* DC.	Asteraceae	
37	*Plantago asiatica* L.	Plantaginaceae	
38	*Portulaca oleracea* L.	Portulacaceae	
39	*Lobelia nummularia* Lam.	Campanulaceae	
40	*Primula sikkimensis* Hook.	Primulaceae	
41	*Rumex acetosa* L.	Polygonaceae	
42	*Rumex japonicas* Houtt.	Polygonaceae	
43	*Sedum bulbiferum* Makino	Crassulaceae	
44	*Sedum emarginatum* Migo	Crassulaceae	
45	*Pseudogynoxys chenopodioides* (Kunth) Cabrera	Asteraceae	
46	*Sonchus oleraceus* L.	Asteraceae	
47	*Swertia bimaculata* (Siebold & Zucc.) Hook.f. & Thomson ex C.B.Clarke	Gentianaceae	
48	*Telosma cordata* (Burm.f.) Merr.	Apocynaceae	
49	*Xanthium strumarium* L.	Asteraceae	

Table 6 Native plants of lead–zinc mining area (Hasnaoui et al. 2020; Rotkittikhun et al. 2007; Shu et al. 2002; Xiao et al. 2018; Zhu et al. 2018)

Sl no	Plant	Family	Type of stress tolerated
1	*Thysanolaena latifolia* (Roxb. ex Hornem.) Honda	Poaceae	Heavy metals like Cd, Pb, Zn contamination
2	*Chenopodium album* L.	Amaranthaceae	
3	*Cirsium arvense* (L.) Scop.	Asteraceae	
4	*Setaria viridis* (L.) P.Beauv.	Poaceae	
5	*Silybum marianum* (L.) Gaertn.	Asteraceae	
6	*Tagetes erecta* L.	Asteraceae	
7	*Paspalum distichum* L.	Poaceae	
8	*Cynodon dactylon* (L.) Pers.	Poaceae	
9	*Erigeron canadensis* L.	Asteraceae	
10	*Artemisia lavandulaefolia* DC.	Asteraceae	
11	*Crassocephalum crepidioides* (Benth.) S.Moore	Asteraceae	
12	*Crepidiastrum denticulatum* (Houtt.) Pak & Kawano	Asteraceae	
13	*Pseudogynoxys chenopodioides* (Kunth) Cabrera	Asteraceae	
14	*Ageratum conyzoides* L.	Asteraceae	
15	*Taraxacum mongolicum* Hand.-Mazz.	Asteraceae	
16	*Bidens pilosa* L.	Asteraceae	
17	*Pteris vittata* L.	Pteridaceae	
	Pteridium revolutum (Blume) Nakai	Dennstaedtiaceae	
18	*Echinochloa crus-galli* (L.) P.Beauv.	Poaceae	
19	*Centella asiatica* (L.) Urb.	Apiaceae	
20	*Buddleja davidii* Franch.	Scrophulariaceae	
21	*Solanum nigrum* L.	Solanaceae	
22	*Carex chinensis* Retz.	Cyperaceae	
23	*Dysphania ambrosioides* (L.) Mosyakin & Clemants	Amaranthaceae	
24	*Reseda alba* L.	Resedaceae	
25	*Convolvulus althaeoides* L.	Convolvulaceae	
26	*Sulla spinosissima* (L.) B.H.Choi & H.Ohashi	Fabaceae	
27	*Phragmites australis* (Cav.) Trin. ex Steud.	Poaceae	
28	*Lotus corniculatus* L.	Fabaceae	
29	*Capsella bursa-pastoris* (L.) Medik.	Brassicaceae	
30	*Scolymus hispanicus* L.	Asteraceae	
31	*Rapistrum rugosum* (L.) All.	Brassicaceae	
32	*Cistus libanotis* L.	Cistaceae	
33	*Agathophora alopecuroides* (Delile) Fenzl ex Bunge	Amaranthaceae	
34	*Hirschfeldia incana* (L.) Lagr.-Foss.	Brassicaceae	
35	*Macrochloa tenacissima* (L.) Kunth	Poaceae	
36	*Artemisia herba-alba* Asso	Asteraceae	
37	*Capsella bursa-pastoris* (L.) Medik.	Brassicaceae	

Table 7 Native plants of coal mine dumpsite (Arshi 2017; Kar and Palit 2019)

Sl no	Plant	Family	Type of stress tolerated
1	*Andrographis echioides* Nees	Acanthaceae	Loose soil particles to support plant roots, challenges like soil erosion, dust, water pollution, heavy metal toxicity, deficiency in major nutrients and microbial activities in the soil system
2	*Andrographis paniculata* Nees	Acanthaceae	
3	*Hygrophila auriculata* (Schumach.) Heine	Acanthaceae	
4	*Rostellularia diffusa* (Willd.) Nees	Acanthaceae	
5	*Ruellia tuberosa* L.	Acanthaceae	
6	*Rungia pectinata* (L.) Nees	Acanthaceae	
7	*Agave sisalana* Perrine	Agavaceae	
8	*Trianthema portulacastrum* L.	Aizoaceae	
9	*Alangium lamarckii* Thwaites	Alangiaceae	
10	*Alternanthera paronychioides* A.St.-Hil.	Amaranthaceae	
11	*Alternanthera pungens* Kunth	Amaranthaceae	
12	*Alternanthera sessilis* (L.) R.Br. ex DC.	Amaranthaceae	
13	*Alternanthera tenella* Colla	Amaranthaceae	
14	*Amaranthus spinosus* L.	Amaranthaceae	
15	*Amaranthus viridis* L.	Amaranthaceae	
16	*Gomphrena celosioides* Mart.	Amaranthaceae	
17	*Ouret sanguinolenta* (L.) Kuntze	Amaranthaceae	
18	*Mangifera indica* L.	Anacardiaceae	
19	*Semecarpus anacardium* L.f.	Anacardiaceae	
20	*Annona reticulata* L.	Annonaceae	
21	*Annona squamosa* L.	Annonaceae	
22	*Alstonia scholaris* (L.) R.Br.	Apocynaceae	
23	*Catharanthus roseus* (L.) G. Don	Apocynaceae	
24	*Holarrhena pubescens* Wall. ex. G. Don	Apocynaceae	
25	*Thevetia neriifolia* Juss. ex Steud.	Apocynaceae	
26	*Borassus flabellifer* L.	Arecaceae	
27	*Phoenix sylvestris* (L.) Roxb.	Arecaceae	
28	*Calotropis gigantea* (L.) W.T. Aiton	Asclepiadaceae	
29	*Calotropis procera* W.T.Aiton	Asclepiadaceae	
30	*Hemidesmus indicus* (L.) R.Br. ex Schult.	Asclepiadaceae	
31	*Pergularia daemia* (Forssk.) Chiov.	Asclepiadaceae	
32	*Blumea axillaris* (Lam.) DC.	Asteraceae	
33	*Blumea lacera* (Burm.f.) DC.	Asteraceae	
34	*Cnicus wallichii* Hook.f.	Asteraceae	
35	*Eclipta alba* (L.) Hassk.	Asteraceae	
36	*Launaea nudicaulis* (L.) Hook. f.	Asteraceae	
37	*Mikania scandens* (L.) Willd.	Asteraceae	
38	*Spilanthes paniculata* Wall.	Asteraceae	
39	*Tridax procumbens* L.	Asteraceae	
40	*Vernonia cinerea* (L.) Less.	Asteraceae	
41	*Vicoa indica* (L.) DC.	Asteraceae	
42	*Xanthium strumarium* L.	Asteraceae	

(continued)

Table 7 (continued)

Sl no	Plant	Family	Type of stress tolerated
43	*Chromolaena odorata* (L.) R.M.King & H.Rob.	Asteraceae	
44	*Cleome gynandra* L.	Capparaceae	
45	*Cleome viscosa* L.	Capparaceae	
46	*Siphonodon celastrineus* Griff.	Celastraceae	
47	*Terminalia arjuna* (Roxb. ex DC.) Wight & Arn.	Combretaceae	
48	*Terminalia bellirica* (Gaertn.) Roxb.	Combretaceae	
49	*Terminalia elliptica* Willd.	Combretaceae	
50	*Commelina benghalensis* Forssk.	Commelinaceae	
51	*Evolvulus alsinoides* (L.) L.	Convolvulaceae	
52	*Ipomoea cairica* (L.) Sweet	Convolvulaceae	
53	*Ipomoea maxima* (L.f.) Sweet	Convolvulaceae	
54	*Ipomoea pes-tigridis* L.	Convolvulaceae	
55	*Ipomoea pinnata* Hochst. ex Choisy	Convolvulaceae	
56	*Hellenia speciosa* (J.Koenig) S.R.Dutta	*Costaceae* Nakai	
57	*Coccinia cordifolia* Cogn.	Cucurbitaceae	
58	*Trichosanthes cucumerina* L.	Cucurbitaceae	
59	*Cyperus rotundus* L.	Cyperaceae	
60	*Kyllinga monocephala* Muhl.	Cyperaceae	
61	*Schoenoplectiella articulata* (L.) Lye	Cyperaceae	
62	*Tacca leontopetaloides* (L.) Kuntze	Dioscoreaceae	
63	*Shorea robusta* C.F.Gaertn.	Dipterocarpaceae	
64	*Acalypha indica* L.	Euphorbiaceae	
65	*Croton bonplandianus* Baill.	Euphorbiaceae	
66	*Emblica officinalis* Gaertn.	Euphorbiaceae	
67	*Euphorbia antiquorum* L.	Euphorbiaceae	
68	*Euphorbia hirta* L.	Euphorbiaceae	
69	*Euphorbia prostrata* Aiton	Euphorbiaceae	
70	*Jatropha curcas* L.	Euphorbiaceae	
71	*Jatropha gossypiifolia* L.	Euphorbiaceae	
72	*Phyllanthus amarus* Schumach. & Thonn.	Euphorbiaceae	
73	*Tragia involucrata* L.	Euphorbiaceae	
74	*Acacia auriculiformis* A.Cunn. ex Benth.	Fabaceae	
75	*Acacia floribunda* (Vent.) Willd.	Fabaceae	
76	*Atylosia scarabaeoides* (L.) Benth.	Fabaceae	
77	*Bauhinia variegata* L.	Fabaceae	
78	*Butea monosperma* (Lam.) Kuntze	Fabaceae	
79	*Cajanus scarabaeoides* (L.) Thouars	Fabaceae	
80	*Cassia alata* L.	Fabaceae	
81	*Cassia fistula* L.	Fabaceae	
82	*Cassia obtusifolia* L.	Fabaceae	
83	*Cassia siamea* Lam.	Fabaceae	
84	*Cassia sophera* L.	Fabaceae	
85	*Cassia tora* L.	Fabaceae	
86	*Crotalaria juncea* L.	Fabaceae	
87	*Crotalaria linifolia* L.f.	Fabaceae	

(continued)

Table 7 (continued)

Sl no	Plant	Family	Type of stress tolerated
88	*Dalbergia sissoo* Roxb. ex DC.	Fabaceae	
89	*Desmodium gangeticum* (L.) DC.	Fabaceae	
90	*Entada gigas* (L.) Fawc. & Rendle	Fabaceae	
91	*Grona triflora* (L.) H.Ohashi & K.Ohashi	Fabaceae	
92	*Indigofera latifolia* Micheli	Fabaceae	
93	*Pithecellobium dulce* (Roxb.) Benth.	Fabaceae	
94	*Pongamia pinnata* (L.) Pierre	Fabaceae	
95	*Senna hirsuta* (L.) H.S.Irwin & Barneby	Fabaceae	
96	*Senna occidentalis* (L.) Link	Fabaceae	
97	*Tephrosia purpurea* (L.) Pers.	Fabaceae	
98	*Tephrosia villosa* (L.) Pers.	Fabaceae	
99	*Teramnus labialis* (L.f.) Spreng.	Fabaceae	
100	*Vachellia farnesiana* (L.) Wight & Arn.	Fabaceae	
101	*Vachellia nilotica* (L.) P.J.H. Hurter & Mabb.	Fabaceae	
102	*Flacourtia indica* (Burm.f.) Merr.	Flacourtiaceae	
103	*Clerodendrum viscosum* Vent.	Lamiaceae	
104	*Gmelina arborea* Roxb.	Lamiaceae	
105	*Hyptis suaveolens* (L.) Poit	Lamiaceae	
106	*Leonurus sibiricus* L.	Lamiaceae	
107	*Leucas aspera* (Willd.) Link	Lamiaceae	
108	*Leucas cephalotes* (Roth) Spreng.	Lamiaceae	
109	*Ocimum canescens* A.J.Paton	Lamiaceae	
110	*Tectona grandis* L.f.	Lamiaceae	
111	*Vitex negundo* L.	Lamiaceae	
112	*Abutilon indicum* (L.) Sweet	Malvaceae	
113	*Bombax ceiba* L.	Malvaceae	
114	*Sida acuta* Burm.f.	Malvaceae	
115	*Sida cordata* (Burm.f.) Borss. Waalk.	Malvaceae	
116	*Sida cordifolia* L.	Malvaceae	
117	*Sterculia urens* Roxb.	Malvaceae	
118	*Urena lobata* L.	Malvaceae	
119	*Azadirachta indica* A.Juss.	Meliaceae	
120	*Melia azedarach* L.	Meliaceae	
121	*Swietenia macrophylla* King	Meliaceae	
122	*Stephania japonica* (Thunb.) Miers	Menispermaceae	
123	*Albizia lebbeck* (L.) Benth.	Mimosaceae	
124	*Trigastrotheca pentaphylla* (L.) Thulin	Molluginaceae	
125	*Artocarpus heterophyllus* Lam.	Moraceae	
126	*Artocarpus lacucha* Buch.-Ham.	Moraceae	
127	*Ficus benghalensis* L.	Moraceae	
128	*Ficus cunea* Steud	Moraceae	
129	*Ficus racemosa* L.	Moraceae	
130	*Ficus religiosa* L.	Moraceae	
131	*Streblus asper* Lour.	Moraceae	
132	*Syzygium cumini* (L.) Skeels	Myrtaceae	
133	*Boerhavia diffusa* L.	Nyctaginaceae	

(continued)

Table 7 (continued)

Sl no	Plant	Family	Type of stress tolerated
134	*Mirabilis jalapa* L.	Nyctaginaceae	
135	*Argemone mexicana* L.	Papaveraceae	
136	*Pedalium murex* L.	Pedaliaceae	
137	*Phyllanthus urinaria* L.	Phyllanthaceae	
138	*Phyllanthus virgatus* G.Forst	Phyllanthaceae	
139	*Mecardonia procumbens* (Mill.) Small.	Plantaginaceae	
140	*Andropogon pumilus* Roxb.	Poaceae	
141	*Aristida adscensionis* L.	Poaceae	
142	*Chloris barbata* Sw.	Poaceae	
143	*Chrysopogon aciculatus* (Retz.) Trin.	Poaceae	
144	*Chrysopogon lancearius* (Hook. f.) Haines	Poaceae	
145	*Cynodon dactylon* (L.) Pers.	Poaceae	
146	*Eragrostis coarctata* Stapf	Poaceae	
147	*Eulaliopsis binata* (Retz.) C.E. Hubb.	Poaceae	
148	*Heteropogon contortus* Beauv. ex Roem. & Schult.	Poaceae	
149	*Oplismenus compositus* P. Beauv.	Poaceae	
150	*Panicum maximum* Jacq.	Poaceae	
151	*Poa annua* L.	Poaceae	
152	*Saccharum munja* Roxb.	Poaceae	
153	*Saccharum spontaneum* L.	Poaceae	
154	*Sporobolus indicus* (L.) R.Br.	Poaceae	
155	*Polygonum barbatum* L.	Polygonaceae	
156	*Ziziphus mauritiana* Lam.	Rhamnaceae	
157	*Ziziphus oenoplia* (L.) Mill.	Rhamnaceae	
158	*Dentella repens* J.R.Forst. & G. Forst.	Rubiaceae	
159	*Spermacoce hispida* L.	Rubiaceae	
160	*Scoparia dulcis* L.	Plantaginaceae	
161	*Aegle marmelos* (L.) Corrêa	Rutaceae	
162	*Atalantia monophylla* DC.	Rutaceae	
163	*Madhuca longifolia* (J.Koenig ex L.) J.F.Macbr.	Sapotaceae	
164	*Ailanthus excelsa* Roxb.	Simaroubaceae	
165	*Datura metel* L.	Solanaceae	
166	*Physalis minima* L.	Solanaceae	
167	*Solanum nigrum* L.	Solanaceae	
168	*Solanum sisymbriifolium* Lam	Solanaceae	
169	*Solanum surattense* Burm.f.	Solanaceae	
170	*Solanum virginianum* L.	Solanaceae	
171	*Triumfetta rhomboidea* Jacq.	Tiliaceae	
172	*Holoptelea integrifolia* (Roxb.) Planch.	Ulmaceae	
173	*Lantana camara* L.	Verbenaceae	
174	*Phyla nodiflora* (L.) Greene	Verbenaceae	
175	*Cayratia trifolia* (L.) Domin	Vitaceae	
176	*Tribulus terrestris* L.	Zygophyllaceae	

importance in recent times. Several plants have been reported (Table 8) to be growing naturally in fly ash dumpsites of thermal power plants of Bihar and Jharkhand, India, which are worth to be prospected for their phytoremediation potentials (Kumari et al. 2011, 2016; Pandey et al. 2016). *Ipomoea carnea* Jacq., *Lantana camara* L. and *Solanum virginianum* L. were the three most abundant species found in the fly ash dump sites of Patratu thermal power plant, Jharkhand, India (Pandey et al. 2016). *Pteris vittata* L., growing in fly ash dumpsites of a thermal power

Table 8 Native plants of fly ash dumpsite of thermal power plant (Kumari et al. 2011, 2016; Pandey et al. 2016)

Sl. no	Plant	Family	Type of stress tolerated
1	*Azolla pinnata* R.Br	Salviniaceae	Alkaline pH, less nitrogen and organic carbon; rich in heavy metals like Cr, Cd, Zn, Pb, Al, Si, As, Fe and Ni
2	*Ceratopteris thalictroides* (L.) Brongn	Pteridaceae	
3	*Hydrilla verticillata* (L.f.) Royle	Hydrocharitaceae	
4	*Marsilea minuta* L.	Marsileaceae	
5	*Typha latifolia* L.	Typhaceae	
6	*Achyranthes aspera* L.	Amaranthaceae	
7	*Argemone mexicana* L.	Papaveraceae	
8	*Amaranthus spinosus* L.	Amaranthaceae	
9	*Thelypteris prolifera* (Retz.) C.F.Reed	Aspleniaceae	
10	*Chenopodium album* L.	Amaranthaceae	
11	*Cannabis sativa* L.	Cannabaceae	
12	*Senna tora* (L.) Roxb	Fabaceae	
13	*Calotropis procera* (Aiton) W.T.Aiton	Apocynaceae	
14	*Croton bonplandianus* Baill	Euphorbiaceae	
15	*Cynodon dactylon* (L.) Pers	Poaceae	
16	*Datura metel* L.	Solanaceae	
17	*Diplazium esculentum* (Retz.) Sw	Aspleniaceae	
18	*Eclipta prostrata* (L.) L.	Asteraceae	
19	*Erigeron annuus* (L.) Desf	Asteraceae	
20	*Ipomoea carnea* Jacq	Convolvulaceae	
21	*Lantana camara* L.	Verbenaceae	
22	*Linum usitatissimum* L.	Linaceae	
23	*Momordica charantia* L.	Cucurbitaceae	
24	*Parthenium hysterophorus* L.	Asteraceae	
25	*Phyllanthus urinaria* L.	Phyllanthaceae	
26	*Plumbago zeylanica* L.	Plumbaginaceae	
27	*Persicaria hydropiper* (L.) Delarbre	Polygonaceae	
28	*Pteris vittata* L.	Pteridaceae	
29	*Tripidium bengalense* (Retz.) H. Scholz	Poaceae	
30	*Stellaria media* (L.) Vill	Caryophyllaceae	
31	*Solanum virginianum* L.	Solanaceae	

plant of Bihar, significantly accumulated toxic heavy metals like As, Cu and Cr in its above-ground parts, which revealed its potential as a suitable species for phytoremediation of metal contamination (Kumari et al. 2011). *Typha latifolia* L. and *Azolla pinnata* R.Br. were found to be the most efficient metal hyper-accumulator aquatic species and *Croton bonplandianus* Baill. was suggested to be the best metal accumulator terrestrial species for various heavy metals of thermal power plant dumpsites in Bihar (Kumari et al. 2016). As evidenced by better translocation of metals from below ground to above-ground parts *I. carnea* and *L. camara* were suggested to be promising species for phytoextraction. On the other hand, *S. virginianum* was considered as a better candidate for phytostabilization of metals in fly ash dumpsites, as metals were mostly found in the below-ground parts of the plant (Pandey et al. 2016).

10 Stress Management Strategies

In order to thrive in stress conditions, plants implement various mechanisms and adaptation strategies, such as enhancement of water-absorbing capacity by promoting root growth, increase in water-holding capacity through stomatal regulation, improvement in osmotic regulation by accumulation of osmoprotectants as well as reduction in oxidative damages by regulation of enzymatic and non-enzymatic antioxidant defense systems. In a broad sense, plants deploy two mechanisms as strategies for stress management, which include (i) mechanism of stress avoidance and (ii) mechanism of stress tolerance (Fig. 1).

10.1 Mechanism of Stress Avoidance

Stress avoidance strategy is one of the adaptive mechanisms acquired by plants to survive environmental stresses in course of evolution. Activation of avoidance mechanisms such as reduced physiological function like absorption and transport of water and minerals, reduced vegetative growth, early flowering, leaf shedding, accelerated senescence, as well as loss of biomass or yield, allow plants to escape the potentially detrimental effects of stressful conditions (Maggio et al. 2018). In most of the cases naturally occurring plant species of mine tailings have possibly developed the mechanism of avoidance to endure the stress of high levels of metal contaminations, as evidenced by relatively low metal concentrations found in the aerial parts in comparison to very high concentrations in underground parts (Chen et al. 2005). Plants in stress conditions can avoid stress by the synthesis of

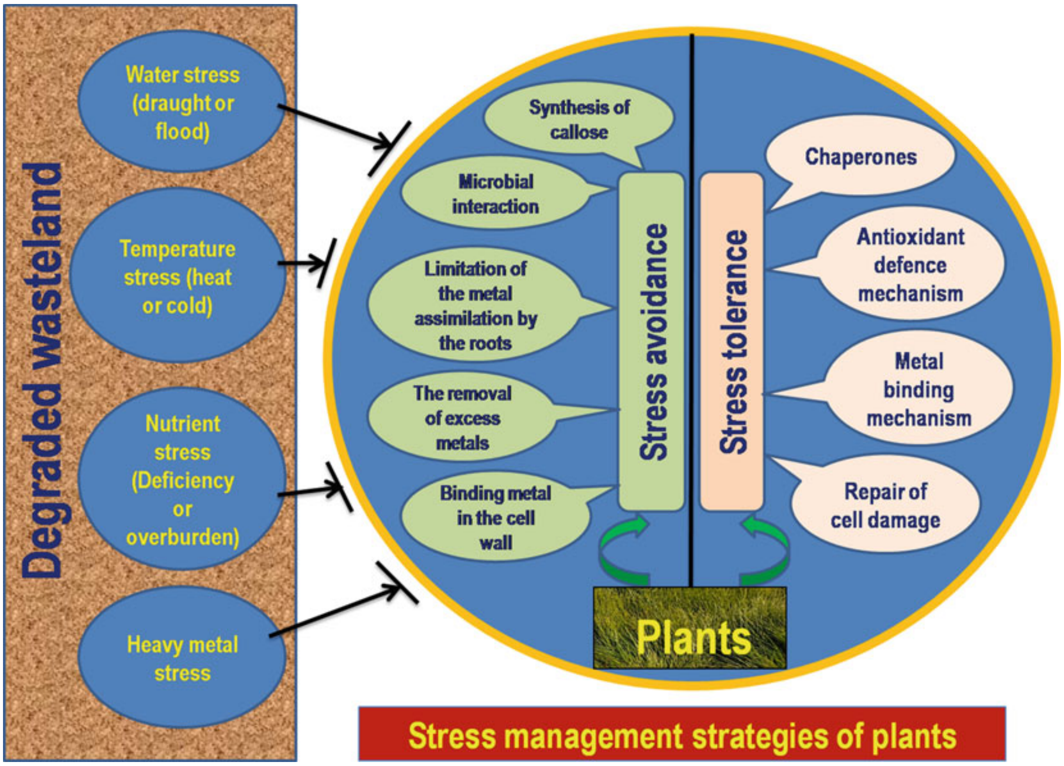

Fig. 1 Strategies for the management of stress in plants

callose, microbial interaction, limitation of the metal assimilation by the roots, the removal of excess metals as well as by binding metal in the cell wall (Jutsz and Gnida 2015).

10.1.1 Synthesis of Callose

Callose (β-1, 3 glucans) is a polysaccharide that is synthesized in a plant cell by the action of enzyme β-1, 3-glucan synthetase and is deposited on the outer side of the cell membrane. This polysaccharide reduces the diffusion of metal ions into the cell and thus serves as the earliest defense strategy in the presence of stress including heavy metal (Jutsz and Gnida 2015).

10.1.2 Microbial Interaction

Mycorrhizal Association

Mycorrhiza is the symbiotic relationship between non-pathogenic fungi and higher plant roots. Mycorrhizal fungi reduce the penetration of metals like Zn, Pb, Cu, Cd, Ni, Mn, Fe etc. into the plant cells by secreting metal chelating agents, such as organic acids, phenolic compounds, siderophores and phosphate ions forming insoluble metal salts. Metals are adsorbed on the surface of mycorrhizal fungal cells with the help of precipitated sulfides and hydrated iron oxides. Another strategy is the accumulation and immobilization of metal ions in the arbuscules, vesicles and hyphae of mycorrhizal fungi as well as metal detoxification by binding with metallothionein and vacuole polyphosphates within the fungal cells (Jutsz and Gnida 2015).

The Arbuscular mycorrhizal (AM) symbioses enhance the antioxidant defense system, improve water absorption, nutrient uptake, photosynthetic efficiency and maintain nutrient balance under stress conditions (Estrada et al. 2013; Santander et al. 2017, 2020). In several cases, metal (Zn, Cu etc.) contaminated wastelands are first colonized by non-mycorrhizal plant species followed by mycorrhizal species in course of ecological succession (Chen et al. 2005; Gucwa-Przepiora and Turnau 2001; Turnau 1998). Mycorrhizal colonization increases the tolerance capacity of plants to toxic heavy metal contamination making the mycorrhizal association a better application for remediation purposes than the application of either non-mycorrhizal plants or free-living micro-organisms alone (Haselwandter and Bowen 1996; Leyval et al. 1997). There is a need for more information on the role of the mycorrhizal association in the stabilization and remediation of contaminants for better planning and management of wastelands with the help of native tolerant plants.

Rhizospheric and Non-rhizospheric Microbial Interaction

Studies involving the PCR-DGGE approach to sequence nifH genes from environmental DNA extracted from tailing samples revealed the presence of considerable diversity of free-living nitrogen-fixing microbial communities in rhizosphere and non-rhizosphere of native plants growing on wastelands of copper mine tailings. Less than 90% sequence identity with bacteria in the available databases suggested the presence of novel nitrogen fixers in copper mine tailings that were possibly capable of modifying the degraded mining sites into a favorable site for plant growth (Zhan and Sun 2012).

Endophytic Microbiota

There are evidences that endophytic microbiota, that colonize a plant's internal tissues without causing any apparent harm to the host plant, confer resistance and tolerance to various abiotic stresses by increasing the levels of antioxidants or by the production of phytohormones, like indoleacetic acid (IAA) and cytokinin, that are responsible for plant growth as well as disease suppression in stress-laden ecosystems (Baltruschat et al. 2008; Brígido et al. 2019; Lata et al. 2018; Orozco-Mosqueda et al. 2018; Rajkumar et al. 2009; Rashid et al. 2012; Rho et al. 2018). Therefore, systematic study on the diversity of endophytic microbiota of native plants of wastelands can provide beneficial information on the possible mechanism of stress tolerance in these plants.

10.1.3 Limitation of the Metal Assimilation by the Roots

As another avoidance strategy in a stressed condition, especially in a heavy metal contaminated environment, roots exude some substances including organic acids, simple sugars, phenols, amino acids, polysaccharide gels etc. which bind metal ions and thus limit their assimilation by plants. Sometimes roots change the pH of the rhizosphere causing a reduction in metal availability. In some cases, roots produce an oxidizing zone around them resulting in the formation of oxidized forms of metals, which are less soluble and thus less available to plants (Meier et al. 2012; Miransari 2011).

10.1.4 Removal of Excess Metals

Plants can remove excess metals such as copper, nickel, zinc, iron and manganese by forming crystals with the involvement of salt glands present on leaf epidermis as well as through hydathodes and ectoderms. Another strategy is to avoid metal stress is by transporting them to the aging leaves and subsequent removal of the leaves. Sometimes heavy metals are accumulated and sequestrated in fibers and idioblasts to get rid of their harmful effects (Olko 2009).

10.1.5 Binding Metal in the Cell Wall

Immobilization of toxic metal ions in the cell wall is another stress avoidance mechanism. Dissociation of cell wall components like cellulose, hemicelluloses and pectins lead to the production of negatively charged groups that are eventually saturated with calcium. In the case of the heavy metal contaminated environment, calcium ions are competitively replaced by metal cations, and thereby heavy metals are immobilized in the cell wall. Sometimes, the cell wall becomes highly lignified or suberized in the presence of heavy metals, by the increase in transverse bonds among cell wall components like phenols, proteins and saccharides making the wall more compact, stiffer and hence less permeable to heavy metals (Miransari 2011).

10.2 Mechanism of Stress Tolerance

When contaminants or stress factors such as metal ions overcome the plant protective barriers and penetrate their cells by evading all the strategies of stress avoidance, plants deploy a second set of strategies for detoxifying the stress factors and tolerating stress effects. Rapid and effective detoxification of stressors including heavy metals is crucial for the survival of a particular plant species in a stressed condition. Plants install a bunch of mechanisms for stress tolerance, for instance, activation of molecular chaperons, antioxidant defense systems, metal binding with chelators like phytochelatins, metallothioneins, organic acids and amino acids and subsequent transportation and accumulation of metals in vacuoles as well as induction of quick cell repair system (Miransari 2011).

10.2.1 Chaperones

Chaperones are also referred to as heat shock proteins (HSPs), which are accumulated in cytoplasm and all cellular compartments of all kinds of living organisms to protect other proteins from being degraded and to re-establish cellular homeostasis under various stresses including temperature stress, water stress, salinity stress, osmotic and oxidative stress (Wang et al. 2004; Singh et al. 2019). Various stresses affect the proper folding of proteins and thus affect the protein functions. The molecular chaperones bind to the nascent polypeptide chain and stabilize unfolded and partially folded polypeptides by minimizing the protein aggregation and thus facilitate proper folding and errorless transportation of proteins to various subcellular locations (Roy et al. 2019). Some of the chaperones are assisted by certain co-chaperones, such as the HSP70-HSP90 organizing protein (HOP), during protein folding (Toribio et al. 2020). Elaborative investigation on cellular chaperones and co-chaperons in native plants of industrial and mining wastelands can unfold significant information about the stress tolerance mechanisms of plants for crop improvement programs.

10.2.2 Antioxidant Defense Mechanisms

Excessive exposure of plants to abiotic stresses, like salinity, drought, cold, heavy metals, UV irradiation etc., increases the production of reactive oxygen species (ROS), such as singlet oxygen, superoxide radical, hydroxyl radical and hydrogen peroxide in different cellular compartments including primarily the chloroplast, mitochondria and peroxisome as well as in some secondary sites like plasma membrane, endoplasmic reticulum, cell wall and the apoplast (Das and Roychoudhury 2014). Production of ROS by various cellular metabolic pathways results in lipid peroxidation and oxidative damage to pigments, carbohydrates, proteins and nucleic acids that eventually lead to plant cell death (Foyer 2018). The balance between ROS production and elimination is essential for normal cellular homeostasis and under environmental stress conditions, this delicate balance is disturbed (Miller et al. 2010). Plants modulate various stresses by changing the enzymatic and non-enzymatic antioxidant systems for scavenging ROS, which reduce oxidative damage and thereby enhance the plant tolerance to various stresses and sustain growth. Enzymatic ROS scavenging components involve the actions of superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), glutathione reductase (GR), mono dehydroascorbate reductase (MDHAR) and dehydroascorbate reductase (DHAR), whereas non-enzymatic antioxidants include mainly the osmolyte proline as well as other biomolecules like ascorbic acid (AA), reduced glutathione (GSH), α-tocopherol, carotenoids and flavonoids (Das and Roychoudhury 2014; Santander et al. 2020).

It was found that *Ricinus communis* plants that were naturally growing in a phytotoxic paper mill dumpsite showed a significantly higher level of proline and ascorbic acid than control, indicating induction of non-enzymatic antioxidant system as stress mitigation strategy (Das et al. 2021). In another study, a decrease in the lipid peroxidation as indicated by decreased malondialdehyde content with the increase in activities of antioxidant enzymes such as catalase and superoxide dismutase was observed in two native, metal hyperaccumulator plant species (*Baccharis salicina* and *Chenopodiastrum murale*) of a Cu mine wasteland (Llerena et al. 2021). Detailed investigation on antioxidant defense mechanisms of potential native plants of wastelands can be a game-changer in crop improvement challenges in coming ages of changing climate.

10.2.3 Metal-Binding Mechanism

Cells contain certain metal-binding molecules such as phytochelatins, different amino acids, glutathione, organic acids like malic acid, citric acid and oxalic acid. In the cytoplasm, metal ions are transported to the vacuole by attaching to the thiol groups of glutathione. Inside the vacuole, the complex undergoes decomposition and resulting metal ions subsequently bind to phosphates which are a more immobilized form of metals (Miransari 2011). Similarly, metals like iron and nickel can be transported to the vacuole and through the xylem vessels by associating with the carboxyl group (COOH) of organic acids like malic acid and citric acid. Amino acid histidine also forms complex with metals like nickel, zinc and copper in hyper-accumulator plants e.g. *Alyssum lesbiacum*, as evidenced by a manifold increase in histidine concentration in xylem after exposure to the metal. Similarly, another amino acid, nicotinamide, can chelate some metals including iron, copper and zinc (Singla-Pareek et al. 2006).

Some proteins known as metallothionein and phytochelatins are also involved in heavy metal tolerance and accumulation. Metallothioneins and phytochelatins help in the chelation of metal ions in the cytosol with subsequent compartmentalization of metals in the vacuoles. These proteins repair the stress-damaged proteins as well as remove and degrade proteins that fail to attain their native conformations (Hasan et al. 2017). Metallothioneins (MTs) are low molecular weight, cysteine-rich proteins that are involved in the detoxification of metals from the cytoplasm by binding metal ions like Cu, Cd and Zn ions with thiol groups. Correlation between MT RNA levels and differences in tolerance to heavy metals could be observed in *Arabidopsis* ecotypes that revealed their role in protection against abiotic stress (Murphy and Taiz 1995). Studies revealed that the native plants growing in copper (Cu) contaminated areas of a Cu mine in Arequipa, Peru, developed tolerance mechanisms, by enhanced MT production along with other stress-related physiological responses like changes in photosynthetic pigments, sugar contents, malondialdehyde contents and antioxidant enzyme activities (Llerena et al. 2021).

Phytochelatins (PCs) are small cysteine-rich peptides and products of the biosynthetic pathway, which are synthesized from reduced glutathione by enzyme phytochelatin synthetase in response to metal-induced stress. They can detoxify heavy metals, particularly cadmium by the mechanism of chelation and subsequent transportation from the cytoplasm to the vacuole. These peptides are important for maintaining metal homeostasis in cells as metals can be released from the immobilized complex whenever required for other uses, for instance, to produce metalloenzymes (Ahmad et al. 2019; Guo et al. 2008; Hasan et al. 2017; Liu et al. 2015; Pochodylo and Aristilde 2017).

During the process of ameliorating metal toxicity, besides the binding of metal ions by peptides like MTs and PCs, transportation of arrested metal ions from the cytosol to the vacuole for sequestration is equally crucial which involves the transporter proteins like ATP-dependent vacuolar pumps (V-ATPase and VPPase) and a bunch of other tonoplast transporters (Sharma et al. 2016). Isolation and characterization of MTs, PCs and transporter proteins in native plants of various wastelands can unravel the understanding of their stress management mechanisms in the stressed environment.

10.2.4 Repair of Cell Damage

Prompt and effective repair of stress-caused damages of cell components is an important strategy of plants for stress tolerance. Heat shock proteins (HSPs), which are expressed in plant cells exposed to stress conditions including high temperatures, heavy metal stress and others, help in the repair process (Singla-Pareek et al. 2006).

11 Climate Change, Land Degradation and the Prospect of Native Plants

Climate change affects adversely and intensifies severely the effects of abiotic stresses on crop production as plants experience multifactorial abiotic stresses including an elevated concentration of CO_2, temperature (low and high), waterlogging, drought, sunshine intensity as well as chemical factors like pH and heavy metals, in course of changing climate along with global warming and environmental pollution (Onyekachi et al. 2019; Pareek et al. 2020; Zandalinas et al. 2021). It has been predicted that in the coming years, climate change will bring about unavoidable ecological damages as well as widespread and severe crop yield losses which will threaten the food security of the growing global population (Ferguson 2019). Although most of the plants adapt to individual stress by various mechanisms, an increase in the number of different co-occurring multifactorial stress factors affect physiological processes of plants related to growth and survival, as well as the microbiome diversity that plants depend on. Therefore, it is important to the development of elite crop varieties with enhanced tolerance to multifactorial stress combinations that are conferred by changing climate, to meet the demands of a growing population. In this respect, biotechnological and breeding efforts to exploit the physiological and biochemical mechanisms of stress management are critical (Ferguson 2019). Advanced methods of biotechnology and genetic engineering tools can be used for developing stress-tolerant crops by introgression of the genes that are involved in stress management in naturally tolerant plants (Bhatnagar-Mathur et al. 2008; Ahanger et al. 2017). In this context, to ensure the viability of crop improvement efforts under the context of a dynamically changing environment, native plant species from stress-laden wastelands can be exploited on a priority basis to harness the stress-tolerant gene resources for better stress management.

Climate change and land degradation are two interdependent phenomena, cyclically affecting each other. Climate change is one of the major factors that lead to land degradation and affect subsequent sustainable development (Kumar and Das 2014). An increase in dry climates and decrease in polar climates result in shifts of climate zones, which have direct consequences on respective ecosystems and thereby on land fertility. Crop productivity, irrigation needs and management practices determine the land use pattern. Changes in land use and land cover due to loss of vegetation productivity are the two major impacts of global warming. On the other hand, land use changes alter the chemical composition, air quality, temperature, humidity and dynamics like the strength of winds of the atmosphere, which can amplify the consequences of climate change (Jia et al. 2019). Therefore, under the apparent pressure of changing climate and increasing human population, there remain no other options than reviving the degraded wastelands into productive lands to meet the subsequent increasing demands of basic survival needs like food, medicine and many other essential commodities. This is because the total arable land is not going to increase with the growing need for food grains for the expanding population which is projected to be doubled by 2050 (Bhattacharyya 2012). Therefore, emphasis has been put to remediate and utilize wastelands, which have the adequate potential to support the majority of the underprivileged population in solving basic problems like hunger and malnutrition in near future. By implementing scientific management techniques, wastelands can be transformed to produce fuel, fodder, forage, essential oil, medicine or vegetation cover to check further soil degradation. Hence, naturally growing native plants of wastelands can serve in two ways: (i) by providing genetic resources that are the molecular basis of the physiological and biochemical mechanism of stress management strategies for crop improvement programs to produce elite climate-resilient crops; and (ii) by remediating stress-laden wastelands into productive lands by creating vegetation cover with little effort.

12 Conclusion

Although wastelands like industrial and mining dumpsites are characterized by adverse physicochemical and biological properties of soil, still numerous plant species have been reported to thrive well in stressful conditions with little or no agronomical effort. Herbaceous and shrub species usually adapt faster to these conditions than other plant species because of their shorter life cycles, which allow them to produce various genotypes in a shorter time. Documentation of such stress-tolerant naturally growing native plants of various wastelands and studying their mechanisms of tolerance are two major emerging areas of research in recent times. Such efforts may help in finding novel plant species that are more stress-tolerant with greater potential of creating vegetation cover. However, more comprehensive investigations with modern multi-omics approaches are required to understand the underlying mechanisms of stress tolerance in those species, which will help improve the adaptation of economically important species of interest in stress-laden wastelands. Discovering important tolerance pathways, functions of antioxidant enzymes, osmolyte accumulation, membrane-bound transporters involved in efficient compartmentation of harmful ions and accumulation of toxic heavy metals as well as resistance mechanisms against pests and pathogens by the native plants of wastelands are some of the vital areas for future research-based study.

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Vulnerability and Resilience of Sorghum to Changing Climatic Conditions: Lessons from the Past and Hope for the Future

Rita Sharma and Mukul Joshi

Abstract

Climate change poses a serious threat to crop productivity. The rise in CO_2 levels, air temperature, soil salinity and variability in precipitation are the key factors that contribute to yield loss. Sorghum stands in the arid and semi-arid regions of the world that are particularly vulnerable to climate change. A comprehensive assessment of its vulnerability and resilience is required to adopt appropriate mitigation strategies. Here, we provide an overview of the projected and observed impact of the rise in temperature, CO_2, salinity, drought and flooding stress on plant physiology, growth and development, and overall productivity of sorghum. While an increase in CO_2 has been projected to enhance sorghum yields, a decrease in precipitation along with temperature rise would negatively impact sorghum productivity. Although sorghum is moderately tolerant to salinity and waterlogging, screening of germplasm for selection of improved varieties and development of tolerant cultivars is necessary for superior performance. The best agricultural practices, technological advances, and genetic enhancement desirable to mitigate the impact of climate change on sorghum productivity have been discussed.

Keywords

Climate change • Drought stress • Flooding • Genetic engineering • Heat stress • Sorghum

R. Sharma (✉) · M. Joshi
Department of Biological Sciences, Birla Institute of Technology and Science (BITS), Pilani, Rajasthan, India
e-mail: rita.sharma@pilani.bits-pilani.ac.in

M. Joshi
e-mail: mukul.joshi@pilani.bits-pilani.ac.in

Abbreviations

CERES	The Crop Environment Resource Synthesis
FACE	Free-Air Carbon dioxide Enrichment
IPCC	Intergovernmental Panel on Climate change
PEPCase	Phosphoenolpyruvate carboxylase

1 Introduction

With the continuous degradation of soil quality, rise in temperature and CO_2 levels, and increase in the frequency of extreme weather events, such as heatwaves, floods and dry spells, climate change poses a serious threat to food security, worldwide (Schmidhuber and Tubiello 2007; Muluneh 2021). The small-scale sustenance farms in rural areas of developing countries are more vulnerable to this challenge due to limited resources and adaptive capacity. Apparently, timely assessment of the level of sensitivity and vulnerability of the major crop plants to the changing climatic conditions is imperative to adopt appropriate adaptation strategies (Raza et al. 2019). Also, with the increase in population, decrease in resources, and changing nutritional requirements, taking cognizance of alternate crop plants with better resilience to adverse environmental conditions and higher nutritional value is necessary.

Sorghum, also known as camel of cereals, with its ability to grow on marginal lands is a spotlight candidate for crop diversification. It requires significantly less moisture for its growth compared to other staple crops with an estimated need of 332 kg water per kg of total dry matter, while wheat requires 514 kg, maize 368 kg and barley 434 kg of water per kg of the total accumulated dry matter (Rao et al. 2014). According to a recent study, adoption of alternate cereals with higher water use efficiency such as maize, finger millet, pearl millet and sorghum instead of rice can reduce the water

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requirement of India by 33% besides improved nutritional yields (Davis et al. 2018).

Sorghum is a multipurpose crop with all parts of the plant utilizable for food, feed, fuel or other value-added products (Mathur et al. 2017). With a high abundance of phenolic acids, tannins and flavonoids, sorghum is a rich source of antioxidants as well. Furthermore, it is a gluten-free alternative food grain with high nutrient, protein, and fibre content. While the grains are mostly consumed by humans or used as animal feed; the leafy biomass and crop residue, left after harvesting grains (stover), is used as quality fodder for livestock. Furthermore, the sugars accumulated in the sweet sorghum stalks and, lignocellulosic biomass are used for biofuel production (Mathur et al. 2017).

Sorghum is mainly cultivated in drier environments on shallow or deep clay soils with pH ranging from 5.5 to 8.5. It is a short-day plant with a growing season of about 115–140 days. Being a C4 crop, it has high photosynthetic efficiency. The optimum temperature for seed germination is 15 °C while optimal vegetative and reproductive growth has been reported in temperatures ranging between 27 and 30 °C (Assefa et al. 2010). Due to extensive fibrous root system, sorghum can draw moisture from deeper layers of soil and therefore, can grow in both irrigated and rainfed conditions though the yields are significantly affected under suboptimal conditions. With moderate tolerance to saline and alkaline soils, sorghum can also be grown on marginal lands with minimal input requirements (Huang 2018). Figure 1 illustrates some of the key characteristics of sorghum that make it a climate-ready crop for the future.

More than 40 million hectares of land are under sorghum cultivation worldwide while >4 million hectares are used for sorghum cultivation in India (World Agricultural Production Statistics by USDA, Aug 2021). The major producers of sorghum worldwide are the USA, Nigeria, India, Mexico, China, Sudan and Argentina. Mostly grown for animal feed in America, Europe and Australia, sorghum feeds almost half a billion people in over 90 countries of the developing world. While 90% production area of sorghum is in Africa and Asia, the highest production is reported from America (38.6%) followed closely by Africa (38.5%) with only 18.6% from Asia (Bhagavatula et al. 2013). The primary reason for this discrepancy in sorghum yields is the limited availability of resources and the rain-fed farming system practised in most of the Asian and African continents. The smallholder farmers with limited adaptive capacity and resources in these regions are, therefore, more vulnerable to stochastic variations in temperature and rainfall associated with the changing climatic conditions. Furthermore, since the impact of climate change would be spatially variable, the local impact might be more drastic than global predictions (Cooper et al. 2008; Srivastava et al. 2010; Raza et al. 2019). Therefore, understanding the resilience and vulnerability of the staple crops to climate change at the global, regional, national as well as local levels is crucial.

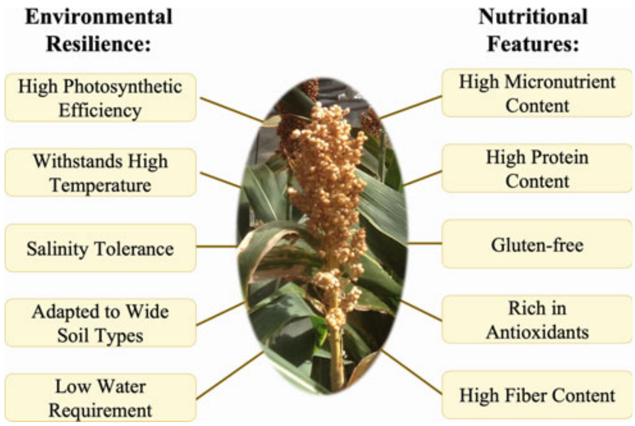

Fig. 1 Key sorghum traits that make it suitable for large scale plantation under changing climatic conditions

2 Impact of Climate Change on Sorghum Growth and Productivity

The key factors with a major impact on sorghum growth and productivity include a rise in CO_2 levels, air temperature, soil salinity and variability in rainfall/precipitation. Based on the geographical location and level of precipitation, some parts of the world have been predicted to experience prolonged dry spells leading to drought conditions while unexpected rains will lead to flooding. The impact of each of these factors on plant physiology, growth and development and, the overall yield has been illustrated in Fig. 2 and detailed in sections below.

2.1 Impact of Rising CO_2 Levels

The global CO_2 levels have been projected to reach between 421 and 936 ppm by the year 2100 (IPCC 2013). The increasing levels of atmospheric CO_2 will not only raise air temperature but will also affect precipitation patterns and water content in the soil. Generally, C3 plants are more vulnerable to elevated CO_2 than C4 plants because CO_2 levels in C4 plants are at near saturation, and photorespiration is suppressed within the bundle sheath cells of C4 plants (Wand et al. 1999). Some of the studies reported higher photosynthetic rates and water use efficiency in response to an increase in CO_2 levels in C4 plants particularly under water-limiting conditions (Hamim 2005; Lopes et al. 2011). Furthermore, analysis of sorghum leaves in response to elevated CO_2 levels (700 µl L^{-1}) revealed two folds decrease in cell wall thickness of bundle cells compared to

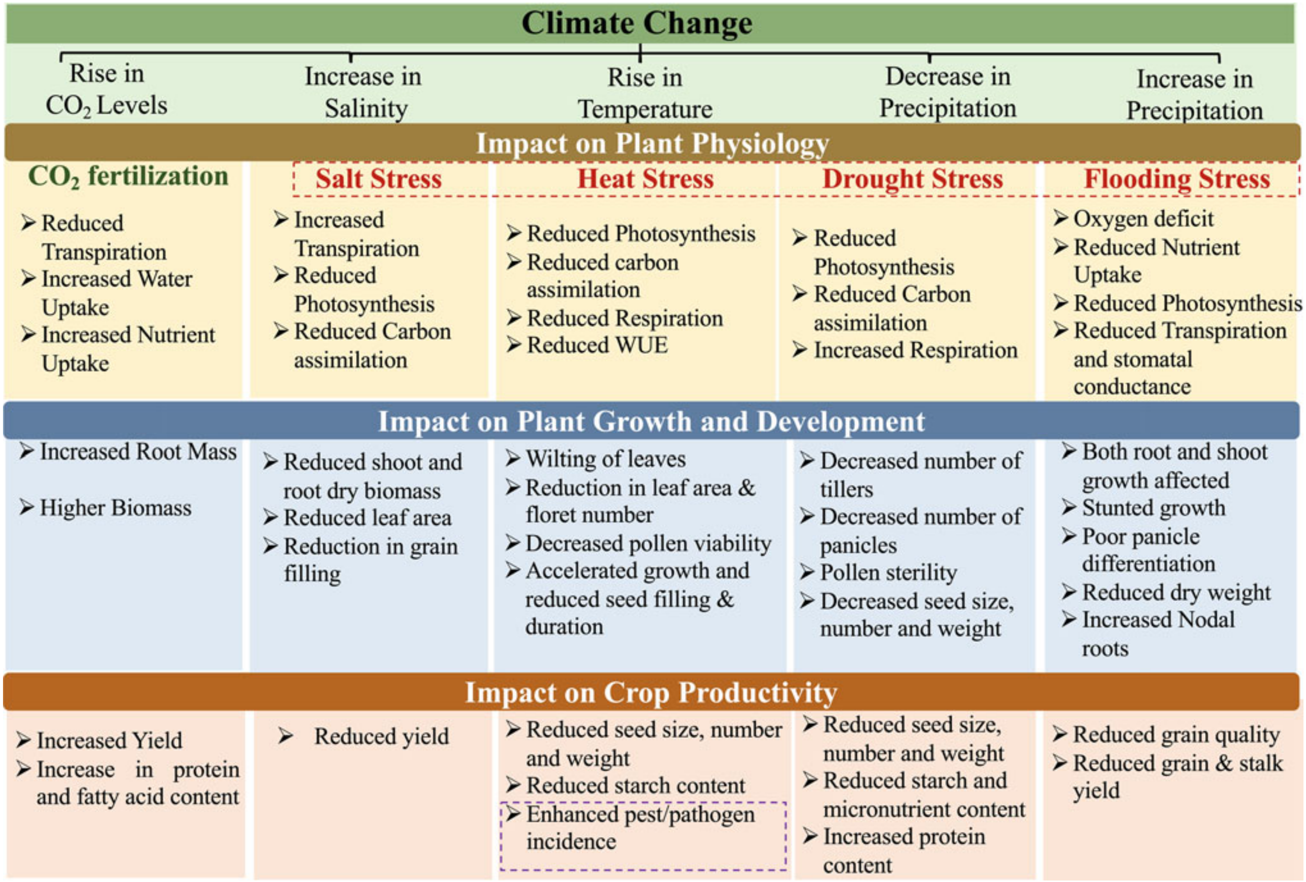

Fig. 2 Impact of climate change on sorghum growth, development and productivity. The upper panel shows the key stress conditions that are predicted to emerge due to climate change. The impact on plant physiology, growth and development and overall productivity of each stress condition has been illustrated. The dashed red line highlights the key abiotic stress conditions and the purple dashed line highlights biotic stress conditions that will augment in response to climate change

plants grown at ambient (350 µl L^{-1}) CO_2 levels thereby, affecting bundle sheath conductance though no change was observed in the quantum yield (Watling et al. 2000). The modification of the C4 phenotype in response to elevated CO_2 levels indicates the higher flexibility of C4 plants towards climate change.

Sorghum has also been reported to exhibit a significant reduction in transpiration rate in response to an increase in CO_2 levels under well-irrigated conditions resulting in increased water-use efficiency (Conley et al. 2001). Further, an increase in biomass production with continuous carbon gain and a significant rise in C:N ratio has been reported in sorghum in response to elevated CO_2 under drought conditions (Ottman et al. 2001; Torbert et al. 2004). As an increase in both root and shoot biomass enhances water absorption; this considerably benefits the crop under low water conditions (Chaudhuri et al. 1986; Ottman et al. 2001; Wall et al. 2001). However, CO_2 increase coupled with drought has been reported to induce reactive oxygen species, thereby, affecting the synthesis of carbohydrates, proteins, lipids and nucleic acids (Ahmad et al. 2018). Some studies reported reduced protein concentration and hence, nutritional quality with an increase in CO_2 due to reduced assimilation of nitrates (Taub et al. 2008). However, grain protein content has been reported to increase in response to elevated CO_2 under drought conditions (De Souza et al. 2015).

Overall, sorghum yields have been predicted to remain unaffected by elevated CO_2 levels under well-irrigated conditions (Ottman et al. 2001; Leakey 2009), while an increase in CO_2 under drought stress conditions has been projected to enhance grain yields and nutritional quality of sorghum (Samarakoon and Gifford 1996; Ghannoum et al. 2000; Ottman et al. 2001; von Caemmerer and Furbank 2003; Vu and Allen 2009). Further, the selection of appropriate genotypes and maintaining nitrogen levels can maximize the benefits of elevated CO_2 levels (Asadi and Eshghizadeh 2021).

2.2 Impact of Increase in Salinity

Salinity is one of the most important abiotic stresses that negatively impact plant growth and development, worldwide (Parida and Das 2005). The rising sea levels may result in more saline lands in Sub-Saharan Africa and South Asia where sorghum is a staple crop for millions. Sorghum is moderately salt-tolerant and is believed to tolerate up to 4.5 and 6.8 dSm^{-1} of electrical conductivity in response to water and soil stress, respectively (Ayers and Westcot 1985). However, further increase in salinity above this threshold has been reported to cause yield reductions of 16% per soil salinity unit (Francois et al. 1984; Tanji and Kielen 2002). Sorghum seedlings subjected to 8.0 dSm^{-1} for 40 days reduced dry weight by 51–76% in different genotypes (Niu et al. 2012).

Some of the adaptation strategies used by sorghum to combat salinity stress include (a) limiting bioaccumulation and transport of Na^+ from roots to upper parts of the plant, (b) compartmentalization of Na^+ and (c) selective absorption of K^+ and Ca^{2+} over Na^+ (de Lacerda et al. 2005; Yan et al. 2015; Shakeri et al. 2020). The sweet sorghum cultivars have been shown to maintain high sugar in stems under salt stress conditions by protecting photosystem assembly, enhancing photosynthetic efficiency and sucrose biosynthesis while simultaneously inhibiting sucrose degradation (Yang et al. 2020). Dehnavi et al. (2020) investigated salinity tolerance in ten sorghum genotypes at germination and seedling stages and concluded that seedling traits can be used to select salt-tolerant genotypes in sorghum.

2.3 Impact of Increase in Temperature

The global temperature has been projected to increase by 3.7–4.8 °C in the twenty-first century which will be perceived as heat stress by plants (IPCC 2014). An increase in temperature leads to deformation of chloroplasts and reduced activity of Rubisco and pigment concentration, thereby, reducing the rate of photosynthesis and carbon assimilation (Brooks and Farquhar 1985). With direct impact on gas exchange and rate of respiration and water use efficiency, the impact of heat stress is visible in the form of leaf wilting, reduction in leaf area, plant height, flower number, duration of growth, pollen viability and seed set thereby, reducing the overall biomass and grain yield of the plant (Schoper et al. 1986; Srivastava et al. 2010).

The Crop Environment Resource Synthesis (CERES)-Sorghum model has been used to simulate grain sorghum yield and water use efficiency with change in temperature and precipitations associated with elevated CO_2 levels using Free-Air Carbon dioxide Enrichment (FACE) analysis in western regions of the United States (Fu et al. 2016). Authors reported that the increased yields in grain sorghum in response to elevated CO_2 would likely be compensated by the decrease in yields with elevated temperature indicating that temperature rise is a major driver of global climate change. Further, narrowing of diurnal temperature amplitude which is calculated as the difference between maximum daytime and minimum night-time temperature, has also been predicted to impact sorghum growth observed in the form of narrowing of leaf area as well as reduced total sugars and biomass. The carbon trade-offs are also altered due to an increase in dark phase respiration with no change in photosynthesis (Sunoj et al. 2020).

Sorghum is a C4 plant with an optimum temperature for photosynthesis higher than C3 plants. The optimum temperature ranges from 21 to 35 °C for seed germination, 26–34 °C for vegetative growth and development and 25–28 °C for reproductive growth in sorghum (Maiti 1996). Maximum yields and dry matter have been reported at 27/22 °C (day/night temperatures) (Downes 1972). The reproductive stages including panicle initiation, flowering and grain filling are more sensitive to heat stress in sorghum compared to the vegetative stages as some of the most crucial developmental events including meiosis, anthesis, pollen germination and tube growth, fertilization and early embryo formation happen during these stages (Downes 1972; Craufurd et al. 1998; Hammer and Broad 2003; Prasad et al. 2006). Therefore, high temperature stress at these stages leads to a significant decrease in floret fertility, seed set and seed weight along with altered concentration and composition of carbohydrates and starch (Siddique et al. 1999; Jain et al. 2007; Djanaguiraman et al. 2014). Heat stress has also been reported to accelerate female development thereby, reducing the receptive duration for the pollen. Maximum decline in seed set was observed in grain sorghum when plants were exposed to heat stress at the flowering stage (Prasad et al. 2008).

The decline in yield in response to heat stress has been mainly attributed to faster growth, reduction of phenophase and duration of seed-filling (Chowdhury and Wardlaw 1978; Kiniry and Musser 1988; Attri and Rathore 2003; Fuhrer 2003). The duration of exposure to heat stress also determines the overall impact on plant growth and productivity in sorghum (Prasad et al. 2006, 2015).

Heat stress also adversely impacts grain quality traits in sorghum by affecting starch biosynthesis and accumulation, protein digestibility and amylose to amylopectin ratio (Hurkman et al. 2003; Li et al. 2013; Wu et al. 2016; Impa et al. 2019). The altered starch composition further negatively impacts saccharification efficiency, thereby reducing ethanol yields (Ananda et al. 2011). In addition, grain hardiness, micronutrient content, tannins and flavonoid are also adversely impacted (Taleon et al. 2012; Wu et al. 2016). Further, the management of insects and pests would be a major challenge due to their enhanced developmental rate and overwintering in response to the rise in temperature (Nguyen et al. 2013; Djanaguiraman et al. 2014; Prasad et al. 2015; Singh et al. 2015).

2.4 Impact of Drought

Drought is a major concern in developing countries where rain-fed agriculture is predominant and is the basis of livelihood and socio-economic system. The intensity and frequency of drought are expanding particularly in arid and semi-arid regions of the world which are major producers of sorghum. In India, sorghum is cultivated as both Kharif (rainy) and Rabi (post-rainy) crops and is also mostly rain-fed in the warm semi-arid regions. The daily water requirement of sorghum depends on the type of soil, crop transpiration, soil water evaporation, water stress and the growth stages, however, a short-season sorghum cultivar typically requires 450–700 mm of water irrigation during the growing season (Tolk and Howell 2001). On per daily basis, sorghum needs approximately 1–2.5 mm water at the early growth stage and 7–10 mm at the boot stage. However, the maximum daily requirement of water increases from the boot stage to anthesis which then gradually decreases during grain filling and maturation (Assefa et al. 2010). Under rainfed conditions, sorghum can extract about 90% of the total water from 0 to 1.65 m of soil depth while the rooting depth of sorghum can reach up to 2.5 m (Rachidi et al. 1993). The water level at soil depths of 1.0–1.8 m is important towards the end of the season (Moroke et al. 2005).

Drought stress due to reduced soil water content below the minimum requirement at either pre-or post-flowering stages results in significant yield loss in Sorghum (Kebede et al. 2001). Exposure to drought conditions at the vegetative and reproductive stage in sorghum has been reported to reduce more than 36–55% yield, respectively, indicating that the reproductive stage of sorghum is more sensitive to drought stress (Assefa et al. 2010). Water stress before anthesis affects tiller count, tillering number of panicles and number of seeds per panicle, whereas, post-anthesis water stress affects transpiration efficiency, CO_2 fixation and carbohydrate translocation ultimately leading to premature senescence (Xin et al. 2008).

Water scarcity at the pre-flowering stage also decreases the net rate of photosynthesis due to reduced photosystem II and phosphoenolpyruvate carboxylase (PEPCase) activities while stomatal closure further negatively impacts stomatal conductance and carbon assimilation (Jagtap et al. 1998). Studies have also reported a decrease in biomass content and plant height, increase in photorespiration and accumulation of reactive oxygen species in response to drought stress (Perry et al. 1983; Gano et al. 2021). Conversely, water deficit at the reproductive stage not only inhibits the gamete development but also affects fertilization and subsequent seed development. The decrease in the total number of panicles, number of seeds per panicle and individual grain size are also observed (Saini 1997; McWilliams 2003; Chadalavada et al. 2021). Although spikelet sterility, in response to drought stress, adversely impacts grain yield, the overall reduction in grain yield may be compensated by tillers that emerge at the later stage (Manjarrez-Sandoval et al. 1989). Overall, drought stress at the early booting stage affects both seed size and number, while water stress at later stages mainly influences seed size (Eck and Musick 1979). Depending on the severity, drought stress has also been shown to reduce the activity of various enzymes involved in starch biosynthesis and accumulation (Hurkman et al. 2003; Pang et al. 2018). Reduction in activities of several enzymes including starch synthase, starch branching as well as debranching enzymes has also been reported in response to drought stress (Yi et al. 2014). A recent study reported a change in quantity, crystal density and chemical composition of epicuticular wax in sorghum leaves in response to post-flowering drought stress (Sanjari et al. 2021).

Some studies have reported an increase in grain protein content coupled with a decrease in protein digestibility in response to drought stress (De Souza et al. 2015; Impa et al. 2019; Sarshad et al. 2021). In a few reports, increased kernel hardness and protein content were also observed compared to well-irrigated conditions (Wu et al. 2008; Njuguna et al. 2018). A recent study reported reduced grain hardness with a simultaneous decrease in weight and size under low soil moisture conditions in sorghum (Pang et al. 2018). Another study reported a reduction in individual grain size as well as diameter due to a decrease in duration of grain-filling but an increase in grain hardness in response to water stress (Impa et al. 2019). Since protein content was shown to be inversely proportional to starch content, increased protein content may lead to the formation of more starch–protein complexes thereby, decreasing the availability of starch for hydrolysis (Zhan et al. 2003; Wu et al. 2007). Ananda et al. (2011) reported increased ethanol yields from drought-stressed grain samples compared to controls, whereas contrary to this, Pang et al. (2018) observed a positive impact of irrigation capacity on bioethanol yields. The crude fibre content in drylands grown sorghum has also been reported to decline compared to irrigated lands (Wu et al. 2007). The same study reported no significant reduction in mineral content (ash) under drylands. On the contrary, Impa et al. (2019) showed reduced micronutrient concentration under moisture stress. An increase in tannin content in response to a decrease in soil moisture has also been reported (Njuguna et al. 2018). Overall, these studies suggest a negative impact of water stress on grain yields and quality in sorghum.

The stay-green trait is particularly important in sorghum to deal with drought stress. It confers the plant ability to delay the onset and slow down the rate of progression of leaf senescence by retaining chlorophyll during the post-flowering stage (Harris et al. 2007). As leaf senescence is negatively correlated with plant yield, delay in senescence mitigates reduced yield under water stress conditions. Stay green is also associated with reduced canopy size and coverage, tiller number and water usage during the vegetative stage thereby, increasing water availability during grain filling (Borrell et al. 2014). However, a more recent study indicated that canopy size before flowering has little effect on stay-green phenotype while post-flowering canopy exhibited a stronger association (Liedtke et al. 2020). Further studies linking stay-green QTL with associated genes and pathways are in progress and would be instrumental in understanding the molecular mechanism underlying stay-green-mediated drought tolerance (Kiranmayee et al. 2020).

2.5 Impact of Flooding Stress

With extreme changes in precipitation levels, waterlogging would be a major constraint to plant growth and productivity. Inhibition of aerobic respiration due to waterlogging leads to a significant decline in the rate of photosynthesis, stomatal conductance and transpiration thereby, restricting plant growth and development (Pardales et al. 1991; McDonald et al. 2002; Zhang et al. 2016). Rapid depletion of O_2 in wet soils also leads to denitrification further impacting the grain yield. Subsequently, the nutrient uptake decreases leading to stunted growth and reduced grain quality (Setter and Belford 1990; Promkhambut et al. 2011a; Zhang et al. 2016). A yield loss of 0.2 t h^{-1} per day is estimated in sorghum due to waterlogging. Though the severity of the adverse effects of waterlogging depends on the stage of development, the early growth stage is more susceptible compared to reproductive stages (Orchard and Jessop 1984; Pardales et al. 1991; Linkemer et al. 1998; McDonald et al. 2002). Flooding stress for 20 days at the early growth stage severely impaired both primary root and shoot growth in sorghum (Promkhambut et al. 2011a). Stunted root and shoot growths in turn adversely affect the stalk yield ultimately affecting seed set and grain yields (Promkhambut et al. 2011a).

However, the overall impact of waterlogging has been shown to vary in different genotypes with varying levels of resilience to flooding stress. Development of nodal roots and aerenchyma in nodal and lateral roots, allocation of more biomass to shoot and conservation of root surface are some of the acclimation strategies adopted by sorghum to flooding stress in tolerant genotypes (Promkhambut et al. 2010, 2011b).

3 Key Strategies to Mitigate the Impact of Climate Change on Sorghum Productivity

With the increase in area under cultivation of sorghum and changing climate scenario, it is imperative to devise appropriate strategies to ensure optimum yields and avoid unprecedented consequences in the future. These would involve adopting best agricultural practices, leveraging technological advances in the field and focused efforts for appropriate germplasm screening and crop improvement using both conventional breeding and biotechnological tools (Fig. 3).

3.1 Best Agricultural Practices/Crop Management Strategies

Based on the climate modelling and simulation studies for predicting climate change and its impact on sorghum productivity, several recommendations have been made over the past few years that can be adopted by farmers, policymakers and other stakeholders to ensure optimum productivity and a sustained marketplace for sorghum (Fig. 3).

Simulation of climate models in India predicted a decline in sorghum yields primarily due to a rise in temperature and shift in monsoon season (Srivastava et al. 2010; Sandeep et al. 2018; Saravanakumar and Balasubramanian 2018). However, by shifting sowing dates, use of long-duration varieties and supplemental irrigation, the adverse impacts of the shift in monsoon can be significantly reduced. Delayed sowing in some regions may also help in avoiding exposure to heat stress especially at the crucial stages of plant development. Sorghum yields in African countries such as Ghana are more sensitive to variability in precipitation in the growing season primarily because most of the agricultural area is rain-fed (Chemura et al. 2020). Implementation of irrigation techniques in such regions is recommended for sustained productivity. Another recent study in Sudanian regions of West Africa suggested that along with preponing the sowing date, deliberate choice of improved medium maturity varieties over local landraces can significantly reduce the negative impact of climate change on sorghum yields in these regions (Akinseye et al. 2020). It should also be noted that planting high-yielding varieties may not always be beneficial for overall productivity due to their higher vulnerability to environmental stresses.

Flood recession farming where crop plants are planted in flooded areas after the water recedes is also practised for sorghum. Seed priming, application of nitrogen fertilizers, planting on raised beds and improved drainage can help reduce the yield loss due to waterlogging in these areas

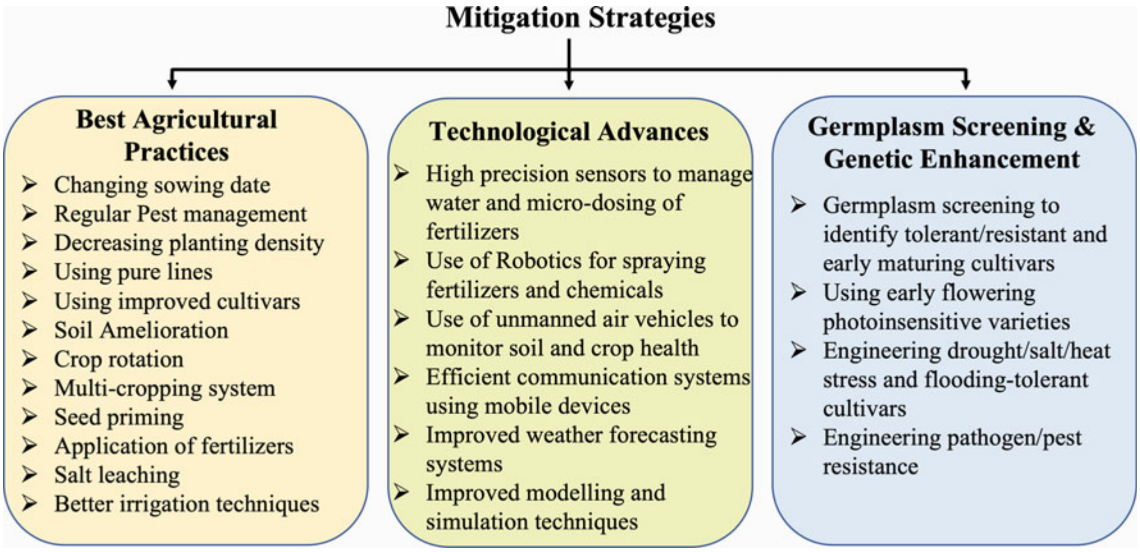

Fig. 3 Mitigation strategies to reduce the negative impact of climate change on sorghum productivity

while salt leaching and high irrigation volume can decrease the negative impact of salinity stress (Calone et al. 2020; Traore et al. 2020). Treatment of seeds with appropriate priming agents has recently been reported to alleviate the negative impact of salt stress on seed germination in sorghum (Chen et al. 2021). Likewise, decreasing planting density, judicious application of fertilizers, using pure lines, regular pest management, crop rotation, use of the multi-cropping system, establishment of wind protection belts and soil amelioration are some of the best agricultural practices that can be adopted to mitigate the impact of climate change (Sonobe et al. 2010; Raza et al. 2019; Fatima et al. 2020).

3.2 Technological Advances

Farmers with decades of experience in sorghum planting are not only aware of the shift in regional climatic patterns but have also been using their empirical knowledge to minimize the associated negative impact. Technological advances coupled with this knowledge have the potential to revolutionize the agricultural sector. The combination of artificial intelligence with big data analytics is already being used to facilitate precision agriculture where both input and output are carefully monitored to accurately manage the crops (Linaza et al. 2021). Smart sensing devices to monitor the status of nutrients and water in the soil as well as the status of crop health followed by automated weeding and delivery of the required nutrients, water and chemicals using drones and robotics will reduce the farm labour (Talaviya et al. 2020). Further, the relay of real-time data using mobile devices and implementation of control systems after taking inputs from the farmers would help in establishing an ideal agricultural ecosystem (Altieri and Nicholls 2017; Sung 2018).

More accurate weather forecasting systems, remote sensing and modelling strategies are also being used for predicting crop performance and to suggest corrective measures (Arora 2019). Performance of these models can be improved with the help of unmanned air vehicles, known as drones, to close the existing data gaps, minimize errors in data collection and apply deep learning models to identify unknown features that can directly or indirectly influence crop yield.

Further, the availability of financial assistance for the implementation of advanced technologies, technical training and clear communication between technology developers, farmers and other stakeholders is essential for successful implementation of these strategies at the ground level. Taking farmer perception and willingness to accept new technologies is also very important. A semi-structured questionnaire-based survey of farmer perception (352 Sorghum farmers with 25–28 years of experience) in Sudanian and Sahelian zones of Mali reported that the availability of drought-tolerant varieties with better water use efficiency has higher chances of adoption by experienced farmers (Traoré et al. 2021). Similar surveys to understand ground-level problems, perception of farmers and understanding of their needs is important to drive technological innovations with practical solutions.

3.3 Genetic Screening and Enhancement

The overall performance of sorghum cultivars in response to abiotic stresses varies with the genotypes, hence, screening and selection of appropriate cultivars as per local needs are required. Several studies focusing on changes in physiological parameters in response to abiotic stress treatments have identified key parameters for quick screening of germplasm for stress tolerance in sorghum (Krishnamurthy et al. 2007; Kausar et al. 2012; Almodares et al. 2014; Ding et al. 2018; Huang 2018; Mbinda and Kimtai 2019; Muller et al. 2020).

However, the low inheritability of yield traits and the impact of environmental factors can lead to confounding results. Therefore, testing of selected lines at the target location is crucial. Since some of the landraces exhibiting high tolerance to environmental stresses may not be suitable for cultivation, these germplasm resources can be leveraged for developing high yielding varieties with improved nutritional content and, biotic and abiotic stress tolerance using a combination of conventional plant breeding and modern biotechnological tools (Varshney et al. 2021). A recent study involving comparative analysis of salinity tolerance of 21 sorghum accessions overlaid on their phylogenetic placement suggested that salinity tolerance likely originated in combination with or because of drought tolerance during sorghum domestication (Henderson et al. 2020). However, salinity tolerance was lost in later lineages which were no longer exposed to salinity conditions. Based on their observations, the authors proposed that the landrace durra can serve as a valuable resource for genetic improvement of salinity tolerance in sorghum by using it as a parent line in breeding programmes or using functional genomic approaches (Henderson et al. 2020). The high-quality SNP and indel data for durra landraces concerning 43 other sorghum genotypes are already available and can be leveraged to dissect the molecular basis of salinity tolerance (Mace et al. 2013). Likewise, screening of 44 sorghum genotypes comprising improved cultivars, landraces and wild relatives, revealed Lodoka, a landrace, as the most drought-tolerant genotype further underscoring the importance of screening and deployment of germplasm for engineering stress tolerance in sorghum (Ochieng et al. 2021). Field trials of sorghum cultivars in Brazil identified key genotypes of sorghum with better grain stability under water stress conditions (Batista et al. 2019). International Crops Research Institute for the Semi-Arid Tropics, India has identified the sorghum germplasm for drought tolerance at different stages of development (Prasad et al. 2021). Further, the development of cost-effective and reproducible screening techniques would facilitate large-scale examination of sorghum germplasm in response to individual and combined stress treatments in the future.

Several drought-resistant cultivars with high photosynthetic efficiency such as stay-green phenotype that reduces water uptake and facilitates more efficient use of soil moisture during grain filling have been identified (Borrell et al. 2014). BTX642 cultivar, the source of stay-green trait, has been used to mitigate the impact of post-flowering drought in sorghum (Borrell and Hammer 2000; Jordan et al. 2010; Kassahun et al. 2010). In fact, the stay-green genotypes are also resistant to some of the stress conditions such as lodging and charcoal rot (Reddy et al. 2007). Similarly, BTX623 is a heat-tolerant cultivar and therefore, can be used for the introgression of heat-tolerant traits in cultivated varieties (Singh et al. 2015). Furthermore, genotypes exhibiting early morning flowering, photosensitive traits, higher seed filling rate and longer seed filling duration need to be identified to compensate for yield loss due to heat and drought stress.

Sorghum is susceptible to a wide range of pests such as shoot fly, stem borer, midge, head bug, aphids, armyworms and locusts therefore, pest management is also crucial for large scale cultivation of sorghum. Grain mould, rust, anthracnose, downy mildew, leaf blight and charcoal rot are the major diseases that can significantly impact sorghum productivity (Das 2019). With a rising temperature and more intensive rains; the severity of these diseases is projected to increase in the future requiring identification and engineering of disease-resistant lines (Reddy et al. 2011).

Investigation of the molecular mechanism of biotic and abiotic stress tolerance would facilitate the selection of appropriate candidates for plant engineering. Some of the studies aimed at elucidating transcriptomic dynamics in response to stress treatments revealed differential accumulation of heat shock transcription factors in response to heat stress in sorghum (Johnson et al. 2014; Nagaraju et al. 2019). Similarly, in addition to transcription factors, aquaporin genes that play important role in water transport have also been associated with waterlogging stress tolerance in sorghum (Ram and Sharma 2013; Kadam et al. 2017). Likewise, transcriptomic and proteomic studies in response to abiotic stress treatments unveiled key genetic components likely responsible for stress tolerance in sorghum (Ngara et al. 2012; Johnson et al. 2014; Zhang et al. 2019). Phylogenomic studies of key gene families further provide a clue to functional associations between candidate genes and stress pathways (Francis et al. 2016; Maheshwari et al. 2019; Baillo et al. 2020; Mathur et al. 2020; Nagaraju et al. 2020; Singh et al. 2020; Fan et al. 2021). Hybrid breeding in conjunction with recent biotechnological tools such as CRISPR/Cas technology can be adopted to characterize these candidate genes further (Reddy et al. 2011; Boyles et al. 2019). The candidate genes and QTLs characterized so far, for their role in drought and/or heat stress in sorghum have been recently reviewed (Prasad et al. 2021). These can be leveraged to design and develop abiotic stress-resilient sorghum genotypes.

A recent study reported changes in root-associated bacteria of sorghum in response to salinity stress indicating that sorghum plants might be manipulating the root bacterial communities to adapt to saline soils (Yukun et al. 2021). Analysis of phenotypic variability in conjunction with genetic variability using genome-wide association studies (GWAS) studies has the potential to identify nucleotide polymorphism associated with stress tolerance and environment-gene-stress tolerance associations in sorghum (Chen et al. 2017).

4 Conclusions and Future Prospects

Although sorghum is better equipped to deal with changing climate scenarios, its overall vulnerability varies based on the geographical location, exposure to climate change, choice of varieties and availability of resources. Climate modelling has the potential to predict the performance of crop plants under future environmental conditions. Several studies have been carried out at different scales that indicate sorghum stands in tropical countries are more vulnerable to climate change where about one-third of the resource-poor population is residing compared to temperate regions. Although the magnitude of severity is predicted to vary in different agroecology zones, all modelling and simulation-based studies predicted severe negative impact of climate change on sorghum yields by the end of the twenty-first century (Msongaleli et al. 2013; Gebrekiros et al. 2016; Eggen et al. 2019; Zewdu et al. 2020).

Analysis of climate change impact on biomass yield of sorghum in the United States revealed irrigation practices, vapour pressure deficit and technological advances as the most important predictors of sorghum productivity in the United States (Huntington et al. 2020). Whereas, rise in temperature and variability in precipitation seems to be the major factors affecting sorghum productivity in Asian and African countries (Akinseye et al. 2019).

The combination of different stresses can further confound the effect of climate change on plant yield. For example, high temperature exacerbates the impact of drought stress in sorghum (Ndlovu et al. 2021). Similarly, damage caused to roots that have already been exposed to flooding stress would make them more prone to root pathogens. Even the positive impact of CO_2 is also limited to water stress conditions (Grossi et al. 2015). The impact of fertilization on vulnerability to climate change also needs to be assessed to calculate trade-offs on overall productivity. For example, the application of nitrogen fertilizers would increase absolute yields of the crop but also enhance the sensitivity of crops to climate change leading to a net reduction in the relative yield of sorghum (Sultan et al. 2014). A recent study reported disruption in the symbiotic association of sorghum roots with arbuscular mycorrhizal fungi in response to drought adding another dimension to stress response dynamics in plants (Varoquaux et al. 2019). Therefore, no blanket approach can be applied to all the sorghum-growing regions to mitigate the impact of climate change. Specific strategies at different scales must be devised as per local geographical conditions and the composition of companion microbial communities.

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Recent Updates in Plant Disease Management

Sukhjeet Kaur and Rupeet Gill

Abstract

The ever-rising human population, declining arable land and concerns about food and nutritional security has become a major challenge for society, worldwide. In order to secure adequate food supplies, the last few decades were focused to enhance crop productivity by using significant resource inputs, intensive crop cultivation, monoculture of genetically superior plant varieties for higher yield and quality. These practices proved to be unsustainable in the long term due to over-exploitation of the available natural resources, irrigation water, cultivable soil and biodiversity. All this caused soil health depletion and made pest and disease management more difficult. Therefore, emphasis is now being given to the development of a sustainable plant disease management system, ensuring food security with minimum adverse effects on the ecosystem. Due to the awareness about human and environmental health concerns, rules and regulations about the use of chemical pesticide in agriculture has become more strict and led to the ban of several chemicals. Scientists are exploring safer strategies to manage pests and pathogens globally. The recent advances in molecular biology have strengthened plant pathology providing better opportunities for disease diagnosis and management. The application of genetic engineering, genome editing and recombinant DNA technology facilitated the scientists to improve biological control agents with enhanced activity against pathogens, genetic improvement of crop plants for pathogen resistance, silencing of pathogen genes vital for their growth, development and pathogenicity. This chapter includes a brief overview of the recent advancement in plant disease diagnosis and management.

Keywords

Biological control • Fungicides • Genome editing • Host resistance • Nanotechnology • Pathogen diagnosis • RNA interference

Abbreviations

ASM	Acibenzolar S methyl
BCA	Biological control agent
CRISPR	Clustered regularly interspaced short palindromic repeats
DIBA	Dot immuno-binding assay
DSBs	Double-stranded DNA breaks
dsRNA	Double-stranded RNA
ELISA	Enzyme-linked immuno-sorbent assay
EM	Electron microscopy
FRAC	Fungicide resistance action committee
FRET	Fluorescence resonance energy transfer
FSNPs	Fluorescent silica nanoparticles
ISEM	Immuno-sorbent electron microscopy
ISR	Induced systemic resistance
JA	Jasmonic acid
LAMP	Loop-mediated isothermal amplification
MIP	Molecular inversion probe
miRNAs	Micro RNAs
MNs	Meganucleases
NASBA	Nucleic acid sequence-based amplification
NGS	Next-generation sequencing
NHEJ	Nonhomologous ending-joining
Np	Nanoparticles
PBZ	Probenazole
PCR	Polymerase chain reaction

S. Kaur (✉) · R. Gill
Department of Vegetable Science, Punjab Agricultural University,
Ludhiana, 141004, India
e-mail: sk-randhawa@pau.edu

R. Gill
e-mail: rupeetgill@pau.edu

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PR	Pathogenesis-related
QDs	Quantum dots
qPCR	Quantitative PCR
RNAi	RNA interference
ROS	Reactive oxygen species
SA	Salicyclic acid
SAR	Systemic acquired resistance
SBI	Sterol biosynthesis inhibitors
SEM	Scanning electron microscope
siRNAs	Small interfering RNAs
SMS	Single-molecule sequencing
SNP	Single-nucleotide polymorphism
TALENs	Transcription activator-like effector nucleases
TGS	Third-generation sequencing
TIBA	Tissue immuno blot assay
ZFNs	Zinc finger nucleases

1 Introduction

Plant pathology is a dynamic field concerned with a detailed study of plant diseases caused by biotic and abiotic factors. Plant pathology science involves the study of mechanisms of inducing diseases in plants and efforts for their survival by overcoming diseases and achieving plants full genetic potential. It is worth studying all practical efforts needed to achieve the noble goal of providing safe and diverse food for our ever-increasing global population. On one side, societal demand for total, high-quality and diverse food are increasing due to the booming global population which is expected to reach 9 billion in 2050 (Godfray et al. 2010). On the other side, we have diminishing arable lands and depleting natural resources, reducing the potential for an increase in agricultural productivity (Ray et al. 2013). Furthermore, monocultures, intensification and other high resources (fertilizer, water and pesticides) input agriculture practices aimed at maximum yield as the sole target, thereby facilitating the evolution and epidemics of plant diseases globally (Zhan et al. 2015). In the coming future, what is required is that much greater emphasis must be given to sustainable plant disease management strategies that ensure food security and societal development but also pose less adverse impacts on environments and natural resources. To meet the challenge, the approach has to be multifaceted. Three components (society, economics and ecology) should be considered in future plant disease management strategies. Providing safe and adequate food for society is always the most important task of plant disease management.

Plant health management strategies preventing crop losses (yield and quality) enhance production and significantly contribute towards food security and safety. With an increasing world population and its food requirement, agricultural research in the twentieth century remained focused on increasing crop productivity (Strange and Scott 2005). Despite all the scientific and technological advancements and their contributions in controlling diseases which significantly reduced the occurrence and severity of epidemics to date, plant protection is still a big challenge for agricultural scientists, and it is more complex now than ever before (Sommerhalder et al. 2010). Furthermore, many plant disease management strategies together with many agronomic practices used in modern agriculture have also generated unintended problems including loss of biodiversity and other natural resources (Gonthier et al. 2014), environmental deterioration and accelerated evolution in pathogens (Zhan and McDonald 2013).

Ecological management of plant diseases is not a simple return to farming systems of ancient times. Rather, it aims to use the evolutionary principles and thinking to maximize the regulatory functions of nature to create suitable environments for healthy hosts ensuring high and stable yield through the efficient use of natural and societal resources including high disease resistance to create environments adverse for the infection, reproduction, transmission and evolution of pathogens (Lucas 2011). To achieve the goal of sustainable plant disease management, a multidisciplinary collaboration involving natural and biological sciences such as plant pathology, breeding, agronomy, soil science, environmental science, economics and social science is needed (Dun-chun et al. 2016).

Modern plant pathology has been greatly accelerated with the aid of molecular tools and advancements in plant disease control strategies. Since the last few decades, molecular plant pathology has been proved very helpful by introducing several new ways and providing better opportunities for disease diagnosis and control (Lévesque 2007). In this regard, biotechnology and genetic engineering played a key role. Molecular techniques such as DNA-based identification of plant pathogen(s), rapid sequencing, quantitative real-time PCR (qPCR), diagnostic assays, biomarkers and whole-genome sequencing greatly improved the way of pathogen(s) detection, disease diagnosis and management (Kumar et al. 2016). For an effective management strategy to be devised, the foremost requirement is timely detection and correct identification of the pathogen. This field has been revolutionized with modern-day technologies like polymerase chain reaction and its modifications, nano-diagnostics, on-field diagnostics and many more (Schena et al. 2013). As stated earlier, the management component needs to be in accordance with the society, economics and ecological balance. The recent trend in scientists working on the management aspect has been in synchronization with the above-said statement. The concept of integrated disease management itself is about the above-mentioned statement. More and more work on the use of biological control measures including bio-agents and bio-products, host plant resistance including various approaches of marker-assisted selection, sequencing, genome editing, transgenics, green chemistry fungicides, etc., (Gandhi and Rao 2019) is being done by plant pathologists all over the world. These strategies can be very precisely combined in many different ways and combinations to achieve the desired level of management, with minimum ill-effects to ecological balance and the economical level of farmers.

2 Pathogen Detection and Disease Management

As defined by Agrios (2005), 'Disease' can be defined as 'a physiological disorder or structural abnormality that is deleterious or harmful to the plant or its part or product that reduces its economic value'. In order to manage plant pathogens and restrict their movement as well as secondary spread in new geographical areas, early and timely detection is a prerequisite. Thus, plant disease diagnosis and detection of plant pathogens are critical and integral parts of successful disease management and serve as the first and crucial line of defence. Although, symptomatology remains the foremost criterion for the identification of disease, other high sensitivity methods like serological, biochemical and molecular assays are useful for the correct and concrete diagnosis of plant diseases (De Boer and Lopez 2012). The requirement and interest for quick, exact, delicate, standard, high throughput and simultaneous detection of pathogens have risen in recent times due to intensive cropping. Several other techniques have been in use in recent years for the detection and diagnosis of plant diseases.

2.1 Electron Microscopy (EM)

In this technique, the microscope uses a beam of electrons as the source of illumination. The specimen to be studied is mounted on a copper grid containing apertures covered with a thin film of plastic. Scanning electron microscope (SEM) produces high-quality three-dimensional images and has been potentially used for detection and identification of plant pathogenic fungi like *Colletotrichum lindemuthianum* in seeds of common bean (*Phaseolus vulgaris* L.) among many other pathogens (Alves and Pozza 2012). Cryo-SEM is mostly used when the imaging samples are having moisture. This technique delivers three-dimensional in situ visualization of fungal invasion within roots and is broadly applicable for the identification of necrotrophic plant pathogenic fungi. EM has become an essential tool for the detection and analysis of virus replication. It has enabled scientists to unravel the in-depth impact of viral infections on the host plants. EM combined with confocal laser scanning microscopy, facilitated the high-resolution imaging analysis of host cells and tissues (Richert-Pöggeler et al. 2019). However, it does have some constraints as it can be technically challenging, time-consuming and require expensive equipment including microscopes. Also, in the early stages of infection or resistant reaction, it may not always be clear where the pathogen is located. It can be challenging to find the pathogen along the surface of the organ (root, stem or leaf) as well as within the organ in a specific cell type or tissue. This can lead to additional frustration and expenses concerning both microscopy and a researcher's time.

2.2 Serological Techniques

Serological reactions that are in vitro antigen–antibody reactions provide methods for the diagnosis of disease and the identification and quantification of antigens and antibodies. These techniques include **(i)** ***Immuno-sorbent Electron Microscopy (ISEM)***—ISEM is a combination of the serological specificity and visualization of electron microscopy. It may serve as an ideal confirmatory test for very small samples if the EM facility and specific antisera are available (Narayanasamy 2011); **(ii)** ***Enzyme-Linked Immuno-sorbent Assay (ELISA)*** is a plate-based assay technique for detecting and quantifying soluble substances such as peptides, proteins, antibodies and hormones. The antigen (target molecule) is immobilized on a solid surface (microplate) and then complexed with an antibody that is linked to a reporter enzyme and detected by incubation with the appropriate substrate to produce a measurable product (Lopez et al. 2003). Depending upon the technique, the number of antibodies used and antigen being detected, Elisa may be DAS (double antibody sandwich) or DAC (direct antigen coating procedure) ELISA. Various types of ELISA have been widely used in the detection of plant viruses including potato viruses like PV-X, PV-Y; tomato viruses like tomato leaf curl virus and mosaic virus (Fegla et al. 2001) and cucumber viruses like cucumber mosaic virus (Abd El-aziz and Younes 2019), among many other viruses. Recently, there are several times in which ELISA has been employed for specific detection of plant pathogenic fungi, e.g., *Rhizoctonia solani*, *Pythium* spp. and *Sclerotinia* (Kamraj et al. 2012). **(iii)** ***Dot Immuno-binding Assay (DIBA)***—This technique follows the same principle as ELISA, except that a nylon or nitrocellulose membrane is used instead of a solid matrix-like polystyrene plate along with a precipitating chromogenic substrate. **(iv)** ***Tissue Immuno Blot Assay (TIBA)***—It is a variation in DIBA in which freshly cut samples of the leaf blade, stem, root or an insect is blotted on to the membrane, which is detected by labelled antibodies. A direct-TIBA procedure has been developed to detect *Fusarium* spp. in the transverse sections from stems and crown regions of cucumber and tomato plants.

2.3 Polymerase Chain Reaction-Based Diagnostics

PCR is a very popular and widely used technique in the detection of plant pathogens. This technique is comparatively inexpensive, highly sensitive and requires much less skill to perform. PCR carries out the amplification of a specific DNA sequence, generating multiple copies of the sequence in the repetitive cyclic process of DNA denaturation, primer annealing and elongation. Initially, ITS primers were mostly used in generic identification but with advancing science, more and more specific primers are being developed and used for the purpose. In addition to simple PCR, for accurate detection of plant pathogens different types of modified PCR are being used, viz., (i) ***Nested PCR***—It is a modification of standard PCR technique, as it uses two different sets of primers involved in two consecutive runs. The amplified product of the first round is used as a template for the second round. Generally, initial primer pair is used to generate a PCR product which may also have amplified some non-target sequences. Then a more specific second set of primers is used to amplify a particular area from the initially amplified sequence. This technique has been exploited in many pathogens targeting very specific regions for their correct detection and identification. Single-nucleotide polymorphism (SNPs) in FOW1 gene in *Fusarium oxysporium* fsp. *chrysanthemi* was exploited for its identification using the nested PCR technique (Li et al. 2010). (ii) ***Multiplex PCR***—This is a very useful technique to detect multiple pathogens/strains present in a single diseased sample as it allows simultaneous and yet sensitive detection of different target DNAs, reducing cost as well as time. This is very useful in plant pathology because most of the time, a single host is infected with various pathogens and this helps in reducing the initial number of tests required (James et al. 2006). This technique has been successfully used in the detection of various pathogens like simultaneous detection and differentiation of powdery mildew fungi, *Podosphaera xanthii* and *Golovinomyces cichoracearum* infection sunflower (Chen et al. 2008). (iii) ***Real-Time PCR***—This is also known as quantitative PCR or qPCR as it amplifies and quantifies a targeted DNA sequence. In this PCR technique, the progress of the reaction can be monitored by a detector or camera while the amplicons accumulate at each cycle. This eliminates the need for any post-PCR processing procedures like gel electrophoresis. The amplicons are detected using chemistries based on the fluorescence emission signal proportionally produced with each cycle. Majorly, four chemistries are used in real-time PCR: SYBR green, TaqMan probe, Molecular beacons and scorpion PCR method. This has been exploited in the detection and identification of various pathogens including *Rhizoctonia solani*, species of *Fusarium*, oomycete pathogens including *Phytophthora* and many more (Nezhad 2014).

2.4 Isothermal Nucleic Acid Amplification-Based Diagnostics

This technique facilitates the amplification of the target DNA sequence while incubating at a single temperature. This differs from a PCR reaction in terms of complexity, specificity and sensitivity as many enzymes and primers are involved. It includes several methods: **(i) *Nucleic acid sequence-based amplification* (NASBA)**—This technique is a very sensitive, transcription-mediated amplification system for in vitro replication of nucleic acids. This assay targets rRNA rather than mRNA, as the latter is highly unstable (Zhang 2013). NASBA follows a two-stage protocol: initial denaturation and primer annealing, then the cyclic phase for target amplification. It requires two primers and three enzymes: reverse transcriptase, RNase and DNA-dependent RNA polymerase. The first primer initiates reverse transcription after which RNase degrades the RNA–cDNA hybrid molecules. The second primer binds to this cDNA and initiates the synthesis of the complementary strand. After this, the RNA polymerase makes multiple RNA copies of the gene. This technology has been applied for the detection of several plant viruses such as *Potato virus Y*, bacteria like *Clavibacter michiganensis* and *R. solanacearum* (Szemes and Schoen 2003) and fungi such as *Candida* sp. and *Aspergillus* sp. (Zhao and Perlin 2013). **(ii) *Molecular Inversion Probe (MIP) Assay-Based Diagnostics***—This has been utilized for the detection of plant pathogens and can detect as little as 2.5 ng of pathogen DNA due to high specificity. MIPs are single-stranded DNA molecules that contain two regions complementary to the target DNA that flank the available SNP. A specific assay has been developed based on MIPs along with microarray having a detection limit of 5 pg of pathogen DNA for the detection of economically important plant pathogens including oomycetes (*Phytophthora* spp. and *Pythium* spp.), fungi (*Rhizoctonia* spp., *Fusarium* spp. and *Verticillium* spp.) and a nematode (*Meloidogyne* spp.) (Lau et al. 2014). **(iii) *Loop-Mediated Isothermal Amplification* (LAMP)**—LAMP is based on the principle of auto cycling strand displacement DNA synthesis performed by the Bst polymerase derived from Bacillus *stearothermophilus* (isolated from hot springs having temperature 70 °C, with polymerization and 5′–3′ exonuclease activity) for the detection of a specific DNA sequence (Chang et al. 2012). Amplification can be carried out in a simple and inexpensive device like a water bath at temperatures between 60 and 65 °C (Rigano et al. 2014). The technique makes use of four specially designed primers, a pair of outer and inner primers, which together recognize six distinct sites flanking the DNA sequence to be amplified. The final amplified product consists of a mixture of stem-loop DNA strands with various stem lengths and structures with multiple loops (De Boer and Lopez 2012).

2.5 Array-Based Diagnostics

Arrays both, microarrays and macroarrays, hold promise for quick and accurate detection and identification of plant pathogens due to multiplex capabilities of the system. Array refers to reverse dot blot assays in which assorted DNA probes are bound to a fixed matrix (e.g. nylon membrane or microscope slides for microarrays) in a highly regular pattern (De Boer and Lopez 2012). The macroarray technology is now commercially available in four European countries under the name DNA Multiscan for the test of plant pathogens (Tsui et al. 2011). A typical microarray slide can contain up to 30,000 spots (Webster et al. 2004). ssDNA probes are irreversibly fixed as an array of discrete spots to a surface of glass, membrane or polymer. Each probe is complementary to a specific DNA sequence (genes, ITS, ribosomal DNA) and hybridization with the labelled Paradigm Shift in complementary sequence provides a signal that can be detected and analysed.

2.6 Sequencing-Based Diagnostics

(i) *Next-Generation Sequencing (NGS)*—NGS techniques also referred to as second-generation sequencing (SGS) emerged in 2005 using commercial Solexa sequencing technology. In this technique, sequencing reaction is detected on amplified clonal DNA templates by emulsion or solid-phase PCR methods (Nezhad 2014). It involves isolation of total DNA or RNA from a diseased plant, elimination of host nucleic acid, enrichment of pathogen DNA and exploitation of different NGS technologies. A number of both known and unknown plant pathogenic fungi have been detected using NGS, e.g. *Phytophthora infestans* in sweet potato (Neves et al. 2013). **(ii) *Third-Generation Sequencing (TGS)*—**More recent single-molecule sequencing technologies are known as third-generation sequencing (TGS). TGS also referred to as single-molecule sequencing (SMS) uses single-DNA molecules for sequence reactions without the need for DNA template amplification. TGS has been used in plant genomics and pathogen detection.

2.7 Nano-Diagnostics

(i) Quantum Dots (QDs)—QDs are nanometer-scale semiconductor nanoparticles that fluoresce when stimulated by an excitation light source and are defined as particles with physical dimensions smaller than the exciton Bohr radius. QDs are ultrasensitive nanosensors based on fluorescence resonance energy transfer (FRET) that can detect a very low concentration of DNA and do not require separation of unhybridized DNA (Khiyami et al. 2014). QDs are linked to specific DNA probes to capture target DNA, which binds to a fluorophore-labelled reporter strand and thus forming FRET donor–acceptor assembly. Unbound DNA strands produce no fluorescence but the binding of even a small amount of target DNA (50 copies) may produce a very strong FRET signal. **(ii) Nanobiosensor**—In these, biological molecules (DNA, antibody and enzyme) are used as target-recognition groups which are coated on to the biosensor platform. Biosensors are integrated receptor–transducer devices. These molecules detect both the presence and concentration of target analytes. Then the information is passed on through the transducer for the analysis on a computer. These nanobiosensors can detect and quantify even very minute amounts of the pathogen in the titre. Fluorescent silica nanoparticles (FSNPs) combined with antibodies as a biomarker have been studied as the probe, which successfully detected plant pathogens such as *Xanthomonas axonopodis* pv. vesicatoria that cause bacterial spot diseases in Solanaceae plant (Perera et al. 2002). **(iii) Portable Devices and Kits**—On-site diagnosis of plant pathogens require portable devices and such a portable system in the form of PCR termed Palm PCR was developed by a Company in Korea in which DNA can be amplified in less than 25 **min**. The portable system presents a highly functional and user-friendly way to perform different types of PCR tests for both beginners and experienced researchers. **(iv) Lab on a Chip**—A Lab on a chip is a new microtechnique that possesses several advantages such as portability, low reagent consumption, short reaction times and on-site diagnosis. The first lab-on-a-chip system in the field of plant pathology was developed for rapid diagnosis of *Phytophthora* species (Julich et al. 2011). A portable real-time microchip PCR system was developed for the detection of *Fusarium oxysporum* f. sp. *lycopersici* (Fol) strains (Koo et al. 2013). **(v) *Phytophthora* Test Kits**—The Alert test kit for *Phytophthora* has been used to detect all common *Phytophthora* species. Pathogen detection can be accomplished when as little as 0.5% of a plant's roots are infected (http://danrcs.ucdavis.edu).

3 Biological Control and Plant Disease Management

Biological control of pathogens implies the utilization of microbial antagonists to suppress diseases and the microbial antagonist that conquers the pathogen is called the biological control agent (BCA) (Chaur 1998). The BCAs antagonistic to plant pathogens are generally fungal or bacterial strains isolated from the rhizosphere or phyllosphere of the plants. The knowledge of biological control dates back to the 1900s when suppression of plant pathogen activity by the accumulation of its metabolites was reported by Potter in 1908. Since then antagonistic behaviour of many microbial agents especially fungi and bacteria have been studied and exploited by many scientists against different plant pathogens (Sanford 1926).

Most of the microbial antagonists exhibit several direct or indirect mechanisms of action for disease control which includes; antibiosis (production of inhibitory metabolite or antibiotic by the antagonist), mycoparasitism (when antagonist derives some or all of its nutrients from the fungal host), induced resistance (induction of plant defence response against pathogens) and growth enhancement (where BCAs enhance plant growth and reduce the effects of the disease by releasing microbial hormones, viz., indoleacetic acid and gibberellic acid), secretion of extracellular hydrolytic enzymes, competition for nutrients and space and inactivation of pathogen phytotoxins (Deketelaere et al. 2017; O'Brien 2017). Even though the value of biological control agents in managing plant pathogens has been well known only very few have been successful in the field. Unfortunately, most of the biocontrol agents proved to be effective under some particular controlled environmental conditions such as in vitro laboratory assays, pot experiments or greenhouse studies as compared to large-scale field trials.

In recent years, with increased awareness about the harmful effects of chemical residues on human and environmental health, biological control of plant pathogens is being exploited for their better efficacy in the field. In order to make biological control a successful plant disease management strategy, scientists have exploited different ways to enhance their field efficacy and shelf life. For sustainable disease management, emphasis is now being given on the use of mixtures of bioagents, integration of bioagents with soil amendments like neem cake, farmyard manure etc. or with minimum use of chemicals (Vinale et al. 2009).

A number of studies revealed that mixed-use of more than one bioagent gave better disease management under different conditions in different crops like against late blight in potato (Slininger et al. 2007) and chilli (Muthukumar et al. 2011); against *Phytophthora capsici* in potato (Kim et al. 2008); *Botrytis cinerea* causing grey mould in tomato (Le Floch et al. 2009). This might be due to combinations of more than one mode of disease control as each bioagent has its different mode of action. However, in the case of mixed use of bioagents, one needs to consider both synergistic as well as antagonistic interactions between various bioagents. The control efficacy achieved against *F. oxysporum* f. sp. *melonis* causing Fusarium wilt in muskmelon was less when a mixture of two strains of *Pseudomonas putida* was used for seed treatment as compared when both the strains were used individually Bora et al. 2004. The antagonistic effect was also observed among three commercial biocontrol products (Sentinel, Serenade and Trianum) used against *Botrytis cinerea* in strawberries when applied together as a mixture (Xu et al. 2010). Kumar et al. (2020) found that combined application of neem cake + *Pseudomonas fluorescens* resulted in significantly higher yield and lowest *Meloidogyne incognita* in cluster bean.

The use of BCA in integration with fungicide or nematicide can enhance the efficacy of BCA and minimise the use of chemicals provided that fungicide or nematicide has no adverse effect on the BCA. The application of *Bacillus megaterium* along with a low dose of carbendazim fungicide enhanced the disease control against Fusarium crown and root rot on tomato and also performed better than the treatment with a tenfold higher dose of the fungicide (Omar et al. 2006). Similarly, combined application of rhizobacteria *Pseudomonas fluorescens* and a tenfold less dose of benomyl was better than treatment with either alone and gave disease control comparable to the full dose of the fungicide alone (Nobutaka et al. 2006). Gilardi et al. (2008), also reported that foliar application of *Bacillus subtilis* with fungicide, azoxystrobin resulted in the highest crop yield and disease control against powdery mildew on zucchini under greenhouse conditions. Similarly, enhancement in disease control using a BCA and fungicide mix was observed against powdery scab of potato (Nakayama and Sayama 2013); Combined application of *Pseudomonas fluorescens*, *Mesorhizobium cicero* and *Trichoderma harzianum* along with the fungicide Vitavax® resulted in minimum Fusarium wilt incidence in chickpea with maximum yield (Dubey et al. 2015). Moreover, in field experiments of rice, the combination of *T. harzianum*, *P. fluorescens* and carbendazim were most effective against *Magnaporthe oryzae* as compared to their application (Jambhulkar et al. 2018).

Further, the development of modern biotechnological techniques in recent years has enormously developed the biological control of plant diseases. The application of genetic engineering, genomics and recombinant DNA technology enabled the scientists to improve antagonistic microbial strains with enhanced biocontrol activity against pathogens (Droby 2006; O'Brien 2017). The pathogen inhibition potential of *Trichoderma virens* was greatly enhanced with the introduction of multiple lytic enzyme encoding genes into the *T. virens* genome (Djonovic et al. 2007). The resulting new *T. virens* strain produced a combination of glucanases and exhibited enhanced antagonistic activity against *Pythium ultimum*, *Rhizoctonia solani* and *Rhizopus oryzae.*

Despite the direct use of antagonistic organisms, antimicrobial metabolites (biochemical compounds, essential oils, chitin or chitosan, etc.) produced by microbes with phytopathogenic properties are being extensively exploited (Glare et al. 2012; Verma et al. 2020). The production of antimicrobial metabolites is considered the most potent mode of action of biological control microbes (Raaijmakers and Mazzola 2012; Verma et al. 2020). Antimicrobial metabolites with broad-spectrum activity have been reported to be produced by biocontrol bacteria belonging to the genus *Agrobacterium*, *Bacillus*, *Pantoea*, *Pseudomonas*, *Serratia*, *Stenotrophomonas*, *Streptomyces* and many others (Köhl et al. 2019; Keswani et al. 2020). Antimicrobial metabolites, especially lipopeptides (surfactin, fengycin and iturin), have been reported from *Bacillus* and antibiotic metabolites (DAPG, pyrrolnitrin and phenazine) have been investigated from *Pseudomonas* (Ongena and Jacques 2008; Raaijmakers and Mazzola 2012). DAPG, produced by different strains of fluorescent *Pseudomonas* spp., has shown broad-spectrum toxicity against plant-parasitic nematodes, fungi, protists, bacteria and peronosporomycetes (de Souza et al. 2003; Islam and Fukushi 2010). *Serratia* spp. are reported to produce various bacteriocins and antibiotics including prodigiosin, carbapenem, oocydin A, serratamolide, althiomycin, zeamine and serrawettin W1 and W2 which have antifungal, antibacterial and antiprotozoal activities (Williamson et al. 2008; Jafarzade et al. 2013). Several studies have assessed and proved the potential of *Trichoderma* secondary metabolites (SMs) in the biological control of phytopathogens (Hermosa et al. 2014; Keswani et al. 2014, 2020; Al-Ani 2019). Secondary metabolites known as Harzianolide isolated from *T. harzianum* strains exhibited antifungal properties against different plant pathogens and has also behaved as a plant growth promoter and systemic resistance inducer (Vinale et al. 2008). Many compounds such as 6-PAP, gliovirin, gliotoxin, viridian, etc., with antimicrobial potential have been investigated from *Trichoderma* and closely related genera such as *Clonostachys* (former *Gliocladium*) (Ghorbanpour et al. 2018). A broad-spectrum antimicrobial activity has been observed for diverse SMs during in vitro assays, in which pathogens of agricultural interest belonging to *Botrytis*, *Fusarium*, *Rhizoctonia*, *Phytophthora*, *Pythium*, *Penicillium*, *Sclerotinia*, *Stachybotrys*, *Colletotrichum*, *Penicillium*, *Aspergillus* or *Gaeumannomyces* genera among others were used as targets. The secondary metabolites of microbial origin being target specific, eco-friendly and biodegradable may serve as a potential alternative or supplement to the use of chemicals in plant protection (Prabavathy et al. 2008; Mathivanan et al. 2008; Jayaprakashvel and Mathivanan 2011).

4 Fungicides and Plant Disease Management

Worldwide plant pathogens caused an estimated 20% loss. The value of plant diseases loss was calculated to be about 2,000 billion dollars per year (Pimentel 2009). Fungicide is a compound that is toxic to fungi. They were developed after the great famines. Recently, it has become increasingly difficult for growers to control crop diseases. With more intensive cropping, new diseases have arisen which are devastating if not controlled. In addition, new races and more aggressive pathotypes of pathogens have arisen. Genetic resistance of crops towards diseases has been in many cases short-lived, and GMOs have only limited success for disease control and acceptability. All these changes require the rapid development of chemical control measures —new-generation fungicides. Today, a wide range of fungicides is available, and new products are being introduced to the market at regular intervals.

Despite the broad range of fungicides available on the market, innovative chemicals having novel and robust modes of action are needed. New chemistry fungicides discovered with available or new modes of actions are necessary for soilborne diseases, other fungal and bacterial and, possibly, viral diseases as these are a continuous challenge for crops. Resistance management and control of adapted plant pathogens are effectively performed by fungicides having novel modes of action, which are important because of their systemic and curative capability, and longevity (Leadbeater 2015). Among the 57 modes of action groups known thus far, the major market share, almost 70%, belongs to a few groups. Among them, some fungicides with a high to medium induced resistance risk have more share, as compared to low resistance risk fungicides (McDougall 2014). This shows that there is a great need for the continued availability of diverse and effective modes of action in the market for resistance management and effective plant disease control.

Valuable and innovative new fungicides can be discovered within the established mode of action groups or in areas with completely novel modes of action (more of a challenge since a good balance has to be found between high activity against the target plant disease and safety to humans and the environment). Fungicides having a novel mode of action (preferably with low resistance risk) are of course of special interest, since they play a key role in disease control in modern, adapted population of plant pathogens and also in resistance management strategies, but equally important are new fungicides with established modes of action with enhanced characteristics such as systematicity, curativity and longevity of disease control. Generally, a new crop protection product takes around 10 years and approximately 260 million USD to be developed (from discovery to first sales). This high cost of product development, which is driven by the extensive studies required on efficacy, safety to humans, safety to the environment, safety to other organisms, production optimization, etc., is, on the one hand, a burden to industry. On the other hand, this high investment and the science required to successfully bring a new product to market and maintain it is an assurance of the safety of the fungicides and other plant protection products on the market today to consumers. It has also resulted in new advances and innovation in fungicide invention which includes high activity against plant diseases at very low use rates (reducing the environmental burden), the development of more toxicologically benign chemistries and the achievement of crop protection via new technologies such as seed treatment, tree injection, etc. The process of identifying an active ingredient is only the start of the Research and Development process. For every active ingredient tested, only one in tens or hundreds of thousands makes it to the market. This is because there are a number of different obstacles that need to be overcome before a crop protection product is ready to go to market. Despite these high hurdles, it is clear that the industry has been very successful in discovering and bringing new fungicides to the market over the past 75 years. Key fungicide introductions till the mid-1900s included majorly Thiram, Zineb, Nabam, Captan, Blasticidin S, Maneb, Dodine, Dicloran, etc., among others. In the late-1900s, the market was then captured by fungicides like Mancozeb, Captafol, Chlorothalonil, Kasugamycin, Carboxin, Oxycarboxin, Benomyl, Tridemorph, Thiophanate, Thiophanate-Methyl, Carbendazim, Fosetyl-Al, Metalaxyl, Propamocarb, Etaconazole, Propiconazole among many others as around 50 new fungicides were introduced over these 30 years. In and around year 2000, fungicides which were introduced included Benalaxyl, Penconazole, Triflumizole, Diniconazole, Hexaconazole, Cyproconazole, Myclobutanil, Tebuconazole, Pyrifenox, Tetraconazole, Fenbuconazole, Dimethomorph, Fenpiclonil, Fludioxonil, Epoxiconazole, Bromuconazole, Pyrimethanil, Fluazinam, Azoxystrobin, Kresoxim-Methyl, Famoxadone, Mefenoxam, Quinoxyfen, Fenhexamid, Trifloxystrobin, Cyazofamid, Acibenzolar-S-Methyl and many others. After these, till now, around 35–40 fungicides have been introduced with many chemicals in the pipeline and are ready to be released in the market. These mainly included Picoxystrobin, Pyraclostrobin, Prothioconazole, Zoxamide, Ethaboxam, Benthiavalicarb, Mandipropamid, Boscalid Meptyldinocap, Ipconazole, Isotianil, Proquinazid, Ametoctradin, Valifenalate, Penthiopyrad, Bixafen, Fluxapyroxad, Benzovindiflupyr, Pyribencarb, Fenpyrazamine, Isofetamid, Oxathiapiprolin, etc. (Leadbeater 2015).

4.1 New-Generation Fungicides

Revolutions in Chemistry and Biochemistry leads to the development of novel and site-specific chemicals. New-generation fungicides have novel modes of action which had a significant impact on plant disease control. These are ecologically safer and are required in a lower dose. These are broad-spectrum fungicides and of site-specific action with low phytotoxicity and ecologically safer. The specific fungicides with systemic properties were regarded as true progress in crop protection. In new-generation fungicides, the majorly exploited mode of action and their respective group of fungicides are as follows: (a) Complex III inhibitors—these include Strobilurins and other complexes III inhibitors, (b) Succinate dehydrogenase (complex II) inhibitors—Anilides and Pyridinyl- Ethyl Benzamide, (c) NADH inhibitors (complex I)—Aminoalkyl pyrimidines (d) Uncouplers of Oxidative Phosphorylation—Dinitrophenol, Arylhydrazins, Diarylamines (e) Signal transduction inhibitors—Phenylpyrroles and Dicarboximides (f) Cell division inhibitors—Benzamides (g) Sterol Biosynthesis Inhibitors (SBI)—SBI class I, II, III (h) Nucleic acid inhibitors—Phenylamide (Leadbeater 2012). Their use has to be regulated as per FRAC guidelines to sustain their efficacy levels (Kuck et al. 2012).

4.2 Action of New-Generation Fungicides

4.2.1 Fungicides Acting on Oxidative Phosphorylation

These include complex—I, II and III inhibitors. The inhibitors can be divided into three classes: (a) Inhibitors of electron transport, (b) Inhibitors of phosphorylation, (c) Uncouplers. For example, Strobilurins, Boscalid, Penthiopyrad.

4.2.2 Uncouplers of Oxidative Phosphorylation

Uncouplers have effects on ATP synthase. Various chemicals cause uncoupling by increasing the permeability of the membrane to protons and other small ions (Kuck et al. 2012).

4.2.3 New Sterol Biosynthesis Inhibitors (SBI) Group Fungicides

SBI fungicides have been the most important group of specific fungicides worldwide. Fungi have specific sterols that differ from those in plants and animals. Fungal cell membranes are characterized by a common dominant sterol component, ergosterol (Anonymous 2010), e.g. Tetraconazole, Epoxiconazole, Triticonazole.

4.2.4 Fungicides Acting on Signal Transduction

Phenylpyrroles and phenoxyquinolines come under this group. They regulate the high osmolarity glycerol pathway. These are responsible for causing conidial and hyphal cells to swell and burst after the generation of high internal turgor pressure, e.g. Quinoxyfen.

4.2.5 Fungicides Acting on Mitosis and Cell Division

An anti-tubulin fungicide for the control of oomycete pathogens—zoxamide, was discovered and commercialized by Rohm and Haas Company in 2001. It is responsible for the inhibition of microtubule functions. The primary targets for zoxamide are a late blight on potatoes and downy mildew on vines and vegetables.

4.2.6 New-Generation Metalaxyl

Nucleic acid synthesis inhibitors—Metalaxyl-M (also known as Mefenoxam) was introduced by Syngenta in the market. Like metalaxyl, metalaxyl-M controls all pathogens of the Oomycetes. In all applications, the outstanding level of control by Metalaxyl-M is achieved at up to half the rate of its predecessor metalaxyl and its use is safe to the environment (Gandhi and Rao 2019).

4.3 General Mechanism of Induced Resistance

All plants possess an intrinsic capacity to defend themselves against attacks by pathogens. Induced resistance is typically a systemic response with long-lasting effects. Two major types of induced resistance have been identified: Systemic acquired resistance (SAR), which depends on salicylic acid (SA); and induced systemic resistance which requires jasmonic acid (JA) and ethylene, but not SA. SAR is most efficient against biotrophic and hemibiotrophic pathogens and leads to the expression of pathogenesis-related (PR) genes; in contrast, necrotrophic pathogens are generally controlled by induced systemic resistance (ISR).

Products (i) Probenazole (PBZ)—A new granular formulation of PBZ in combination with insecticides was launched. On treating rice with PBZ, the induction of PR genes (PBZ 1 and Os PR1a) has been reported, resulting in the induction of SA signaling pathway. (ii) Acibenzolar S methyl (ASM) is the most widely investigated molecule as a positive marker of SAR in various species of plants. ASM directly activates the PR-1 gene and improves callose deposition.

Fungicides, despite certain limitations, continue to play a crucial role in the management of plant diseases. In their history of more than a century, several fungicide classes have been introduced starting from multi-site inorganic salts to organic compounds with protectant action and then to single-site systemic fungicides with curative activity. However, site-specific fungicides are regularly confronted with the problem of resistance. New compounds with novel modes of action are introduced to manage resistance to the existing fungicides and to provide more effective options for the control of devastating diseases. Technological advances such as combinatorial chemistry, high-throughput screening and bio-rational screen designs have revolutionized the synthesis and development of new fungicide active ingredients (Thind 2012). However, stringent regulatory pressure has impacted the discovery of new active ingredients and this has led to the decline in the introduction rate of new fungicides. In future, natural compounds hold promise to serve as new fungicide leads in place of more toxic synthetic compounds.

5 Agronanotechnology and Disease Management

Nanotechnology is a technology involving everything of nanoscale, i.e. materials having 0.1–100 nm size, with many potential applications in daily life. Nanotechnology highlights the uses of submicron particles, molecules or individual atoms in biological, chemical and physical systems. Nanotechnology research involves the rediscovery of the biological effects of existing antimicrobial agents by controlling their size to modify their effect. Various inorganic and organic antimicrobial particles of nano-size were used to control bacterial, fungal and viral pathogens (Elshafie et al. 2019; Mohamed et al. 2021).

In recent years, products of nano-fertilizers or nano-pesticides containing nanomaterials have been developed into agricultural practices. Recently, biological materials such as microorganisms, plant extracts, marine organisms and micro-fluids have been used to synthesize nanoparticles (especially metallic ones) (Singh et al. 2018). Nanoparticles bioreduction using primary and secondary metabolites of plant extracts "green synthesis" are the most stable, economic and eco-friendly nanoparticles (Shabaaz Begum et al. 2020). These primary and secondary metabolites of plant extracts can not only promote plant growth, suppress fungal pathogens and efficiently reduce diseases of crops but can also synthesize eco-friendly nanoparticles via acting as an electron shuttle, besides assisting in the stabilization and reduction of metal ions (Banerjee et al. 2014).

The antimicrobial activity of nanoparticles may be related to several mechanisms. The nanoparticles can either directly interact with the microbial cells, e.g. interrupting transmembrane electron transfer, disrupting/penetrating the cell envelope or oxidizing cell components, or produce secondary products (e.g. reactive oxygen species (ROS) or dissolved heavy metal ions) that cause damage. Anti-microbial mechanisms of different nanoparticles:

- Titanium dioxide—Antibacterial activity significantly greater in light, photocatalytic ROS production and some additional mechanism may be involved.
- Zinc Oxide—Oxidative stress (ROS generation), interaction with proteins, DNA and lipids, membrane disorganization and release of Zn ions.
- Gold—Membrane potential modification and ATP level decrease and inhibition of tRNA binding to the ribosome.
- Silver—Induction of oxidative stress (ROS), the release of ions—death due to binding to the cell membrane, formation of “pits” on their surfaces, penetrate to cause DNA damage, protein inactivation, DNA condensation and loss of replication ability and disrupt the lipopolysaccharide or porins.
- MgO and CaO nanoparticles—Generation of superoxide, increase in pH by their hydration, damage cell membrane causing leakage of contents and death.
- Copper Nanoparticles—Ions cause toxicity either directly through the cellular membrane or intracellularly.

Some nanoparticles have been tested and reported by various workers for their anti-microbial activity, those are as under:

(i) Nanosilver: It is the most studied and utilized nanoparticle for Bio-system. It has long been known to have strong inhibitory and bactericidal effects as well as a broad spectrum of antimicrobial activities. Silver nanoparticles, which have a high surface area and a high fraction of surface atoms, have a high antimicrobial effect. Nanosilver colloid is a well dispersed and stabilized silver nano particle solution and is more adhesive on bacteria and fungus, hence are a better fungicide. Krishnaraj et al. (2012) used leaf extract of *Acalypha indica* for rapid synthesis of silver nanoparticles and reported their antifungal activity at a concentration of 15 *mg* against several phytopathogenic fungi such as *Rhizoctonia solani*, *Sclerotinia sclerotiorum*, *Alternaria alternata*, *Botrytis cinerea*, *Macrophomina phaseolina* and *Curvularia lunata*. Relatively few studies were conducted on silver nanoparticles used to control fungal diseases in plants in vivo. These studies demonstrated that silver nanoparticles significantly affect the colonial formation of spores of plant pathogenic fungi. Thus, the precautionary application of silver nanoparticles in agriculture may result in the superior efficiency of these nanoparticles due to their direct contact with the spores along with germ tubes of plant pathogenic fungi that suppress fungal viability.

(ii) Zinc Oxide Nanoparticles (ZnO NPs)—A study was conducted to synthesize inexpensive and eco-friendly zinc oxide nanoparticles by extract of *Parthenium hysterophorus* L. leaves and demonstrated that these nanoparticles could effectively reduce *Aspergillus flavus* and *Aspergillus niger* growth. Senthilkumar and Sivakumar (2014) used aqueous leaves extract of green tea (*Camellia sinensis*) to synthesize zinc oxide nanoparticles and confirmed their antifungal activity against *Aspergillus fumigatus*, *Aspergillus flavus* and *Aspergillus niger*. Lakshmeesha et al. (2019) reported biofabrication of ZnO NPs using buds extract of flowers and confirmed ability of these nanoparticles to control *Fusarium graminearum* via inhibiting its mycelial growth and mycotoxins production. In another study, zinc oxide nanoparticles biofabricated by Eucalyptus globules were proved to exhibit fungicidal effects on pathogenic fungi infecting apple orchards such as *Alternaria mali*, *Diplodia seriata*, etc. Consequently, these nanoparticles can control fungal diseases and protect fruit crops.

(iii) Gold Nanoparticles (Au NPs)—Green synthesis of antimicrobial Au NPs by diverse extracts of either fresh leaves or flowers of *Magnolia kobus* and *Diopyros kaki*, *Azadirachta indica*, *Mentha piperita*, *alfalfa*, *Helianthus annuus* (sunflower), *Moringa oleifera* and *Artemisia dracunculus* have been described. Additionally, the most frequently used reducing agents for Au NPs synthesis are sodium borohydride and sodium citrate. These Au NPs were also reported to exhibit efficient in vitro anti-fungal action that can be applied in the field of agriculture to control several phytopathogenic fungi. An example of this is Au NPs synthesized by aqueous extract of *Abelmoschus esculentus* seeds have demonstrated fungicidal effects on *Aspergillus niger*, *Aspergillus flavus* and *Puccinia graminis var. tritici* (Jayaseelan et al. 2012).

(iv) Copper Nanoparticles (Cu NPs)—Green synthesis of copper nanoparticles by leaf extract of *Magnolia*, *Euphorbia nivulia* stem latex, *Carica papaya* leaf extract and Aloe Vera leaf extract has been described. Shende et al. (2015) demonstrated the green synthesis of these nanoparticles using *Citrus medica* and confirmed their inhibitory effects on various *Fusarium* species. Therefore, after establishing the in vitro antifungal potentiality of copper nanoparticles against various phytopathogenic fungi, they can be applied in the management of plant fungal diseases (Banik and Perez-de-Luque 2017).

(v) Nanocarbon: Recently, scientists have reported that when they planted tomato seeds in soil that contained carbon nanotubes; these CNTs could not only penetrate the hard coat of germinating tomato seeds but also exerted a growth-enhancing effect. They envisaged that the enhanced growth was due to increased water uptake caused by penetration of CNT. This could be a boon for using CNT as a vehicle to deliver desired molecules into the seeds during germination that can protect them from diseases. Since it is growth-promoting, it will not have any toxic or inhibiting or adverse effect on the plant.

(vi) Nanosilica–Silver composite: Silicon (Si) is known to be absorbed into plants to increase disease resistance and stress resistance. Aqueous silicate solution, used to treat plants, is reported to exhibit excellent preventive effects on pathogenic microorganisms causing powdery mildew or downy mildew in plants. Moreover, it promotes the physiological activity and growth of plants and induces disease and stress resistance in plants. But, since silica has no direct disinfection effects on pathogenic microorganisms in plants, it does not exhibit any effect on established diseases. Silver in an ionic state exhibits high antimicrobial activity but ionic silver is unstable. A new composition of nano-sized silica silver for control of various plant diseases, which consisted of nanosilver combined with silica molecules and water-soluble polymer. It showed antifungal activity against *Pythium ultimum*, *Magnaporthe grisea*, *Colletotrichum gloeosporioides*, *Botrytis cinerea* and, *Rhizoctonia solani* with 100% growth inhibition at 10 ppm concentration (Elamawi et al. 2018). Whereas, *Bacillus subtilis*, *Azotobacter chrococuum*, *Rhizobium tropici*, *Pseudomonas syringae* and *Xanthomonas compestris* pv. *vesicatoria* showed 100% growth inhibition at 100 ppm.

(vii) Nanoalumino-Silicate: Leading chemical companies are now formulating efficient pesticides at the nano scale. One such effort is the use of alumino-silicate nanotubes with active ingredients (Youssef et al. 2019). The advantage is that alumino-silicate nanotubes sprayed on plant surfaces are easily picked up in insect hairs. Insects actively groom and consume pesticide-filled nanotubes. They are biologically more active and relatively more environmentally safe pesticides.

(viii) Mesoporous Silica Nanoparticles: Mesoporous Silica nanoparticles can deliver DNA and chemicals into plants thus, creating a powerful new tool for targeted delivery into plant cells. Lin's research group has developed porous, silica nanoparticles systems that are spherical and the particles have arrays of independent porous channels. The channels form a honeycomb-like structure that can be filled with chemicals or molecules. These nanoparticles have a unique "capping" strategy that seals the chemical inside. They have also demonstrated that the caps can be chemically activated to pop open and release the cargo inside the cells where it is delivered (El-Baky and Amara 2021). This unique feature provides total control for timing the delivery. Plant cells have a rigid cell wall. Hence to penetrate it, they had to modify the surface of the particle with a chemical coating. It has been successfully used to introduce DNA and chemicals into Arabidopsis, tobacco and corn plants. The other advantage is that with the mesoporous nanoparticles, one can deliver two biogenic species at the same time.

6 Host Resistance, Genome Editing and Disease Management

The ability of the host to limit or ward off pathogens is known as host resistance. It includes diverse mechanisms such as physical or structural barriers (cuticle, cell wall), antimicrobial compounds, enzyme inhibitors, post-infection defences like *cell wall* reinforcement (lignification, callose formation, suberin production), production of antimicrobial proteins, enzymes, etc., and hypersensitive response (Ahuja et al. 2012; Chisholm et al. 2006; Collinge 2009; Jones and Dangl 2006; Uma et al. 2011). The utilization of genetic resistance for crop protection is the most economical approach to limit yield losses caused by pathogens. Growing resistant varieties not only ensure protection against diseases but also conserve time, energy and money spent on other methods of control. Further, in the case of viral diseases, phytoplasma wilts and rusts, the use of resistant varieties (if available) can only be the practical measure to manage such diseases. Also, in the case of crops of low cash value, development of resistant varieties can be most acceptable and economical as compared to other measures of disease management and use of chemicals. Breeding for disease resistance is thus one of the major components of crop improvement programmes. It requires continuous updates regarding the pathogen adaptation to plant genotypes. The advancement in molecular biology continues to unveil the mechanisms which enable pathogens to parasitize host plants and how plants defend them against pathogen parasitism. The knowledge of molecular biology is being implemented and utilized for enhancing resistance against pathogens in crop species and accelerating resistance breeding in the field. The advancement in molecular biology has enabled scientists to identify and map and clone several resistance genes in different crops against different pathogens (McDowell and Woffenden 2003; Gururani et al. 2012). The identification and validation of molecular markers corresponding to different resistance genes in different crops, viz., wheat, rice, pulses and vegetables have empowered the breeders to utilize those genes and speed up the resistance breeding programmes (Goutam et al. 2015; Meziadi et al. 2016; Sahu et al. 2019; Yadav et al. 2017).

More recently, genome editing techniques have broadened the approaches to engineering host resistance. Genome editing technology is strengthening genetic improvement of plant disease resistance and accelerating the resistance breeding programmes by enabling accurate and targeted genome modifications.

Genome editing means making precise changes to the genomic DNA of a cell or organism. It involves the use of sequence-specific nucleases for recognizing specific DNA sequences and producing double-stranded DNA breaks (DSBs) at targeted sites. These DSBs are overhauled by; (i) the nonhomologous ending-joining (NHEJ) pathway and; (ii) the homologous recombination (HR) pathway (Voytas and Gao 2014). Generally, cells make use of the NHEJ pathway for repairing DSBs. But, NHEJ is error prone and usually results in insertion or deletion mutations. In the presence of a donor DNA template, DSBs are likely to be repaired by the HR pathway, which results in precise base changes or gene replacement. There are major four types of sequence-specific nucleases being used for genome editing; (i) Meganucleases (MNs); (ii) zinc finger nucleases (ZFNs); (iii) transcription activator-like effector nucleases (TALENs) and the clustered regularly interspaced short palindromic repeats (CRISPR)/associated protein (CRISPR/Cas9) system. Among these, CRISPR/Cas9 is being most exploited in comparison to other genome editing technologies as it is less expensive, requires less know-how for implementation and have a high success rate. CRISPR/Cas9 technology also makes it possible to target several genes simultaneously with a single molecular construct, e.g. simultaneous mutation of 14 different genes by a single construct has been demonstrated using CRISPR in *Arabidopsis* (Peterson et al. 2016) and cloning of four gRNAs has been reported in maize, by the ISU Maize CRISPR platform (Char et al. 2017).

CRISPR/Cas genome editing systems consist of a single guide RNA (sgRNA) and a Cas protein that exhibits nuclease activity. The CRISPR/Cas tools have been explored mainly against viral, fungal and bacterial disease resistance. CRISPR-edited plants for virus resistance have targeted ssDNA geminivirus genomes (Ali et al. 2015, 2016; Baltes et al. 2015) and achieved resistance to begomoviruses (Ali et al. 2015, 2016). Because of the innate ability of Cas13 to process pre-CRISPR RNA into functional CRISPR RNA, the multiplex targeting of several viral mRNAs could be markedly improved through this alternative system (Aman et al. 2018). For bacterial blight resistance in rice, CRISPR/Cas9-mediated mutagenesis of *OsSWEET13* was performed in rice for achieving resistance against γ-proteobacterium *Xanthomonas oryzae* pv. *oryzae* (Zhou et al. 2015). To achieve resistance against rice blast disease (causal agent; *Magnaporthe oryzae*), resistant phenotypes were produced through CRISPR/Cas9 by disrupting *OsERF922* and *OsSEC3A* genes in rice (Wang et al. 2016; Ma et al. 2018). Among others, TALEN-based genome editing was reported against the bacterial blight of rice caused due to *Xanthomonas oryzae* pv. *Oryzae* by insertion or deletion in rice (Li et al. 2012) and against Powdery mildew (casual organism: *Blumeria graminis* f. sp. *tritici*) in wheat (Wang et al. 2014). The replication of begomoviruses, Tomato yellow leaf curl China virus (TYLCCNV) and Tobacco curly shoot virus (TbCSV) was inhibited using artificial zinc finger nucleases which targets the conserved nucleotide motif of the virus (Chen et al. 2014).

7 RNA Interference and Plant Disease Management

RNA interference (RNAi) is a natural regulatory mechanism in eukaryotes that involves the use of small double-stranded RNA (dsRNA) molecules as triggers to direct homology-dependent control of gene activity. The small single-stranded RNAs (~21–24 nucleotides) can be classified into two types, i.e. small-interfering RNAs (siRNAs) and microRNAs (miRNAs). The miRNAs are encoded by the plant genome and generally play a role in the regulation of gene expression. While siRNAs can be of exogenous origin from viruses or artificial supply (Matranga and Zamore 2007). RNAi is a novel technology in the field of functional genomics with massive potential for managing plant diseases by the silencing of specific genes responsible for infection in the host plant, in a homology-dependent manner, before their translation. RNAi has been studied and used to knock down targeted genes and their expression in plants, microorganisms and lower animals. The technology has been successfully exploited to develop resistance against fungal, bacterial, viral pathogens, insects and nematodes (Niehl et al. 2018; Singh 2005).

Management of the fungal pathogens using RNAi is attributed to silencing of the target gene encoding particular functions related to the pathogen growth, development and pathogenicity. For example in *Fusarium graminearum* mycelium formation or growth was inhibited by silencing the 14α-demethylase and Chs3b (Cheng et al. 2015; Koch et al. 2013). In *Phytophthora infestans*, silencing of PiGPB1 resulted in impaired appressoria formation by the fungus (Jahan et al. 2015).

In the case of viral pathogens, replication of the viral nucleic acids is the main target of silencing. Silencing is achieved using antisense strategies or using the coat protein or by silencing pathogenicity-related genes directly. Similarly, in the case of bacterial pathogens, resistance or control is based on the silencing of genes responsible for pathogenicity or by silencing those genes that are negative regulators of the host defence, rendering the bacterial pathogen unable to establish the infection, e.g. in *Agrobacterium tumefaciens,* if the genes required for tumorogenesis (*gall*, *iaaH*, *iaaM* and *ipt* genes) are silenced, no tumours are produced and the disease is controlled (Escobar et al. 2001). *In Pseudomonas syringae* genes which are negative regulators of defence genes in the hosts were silenced to manage the pathogen (Katiyar-Aggarwal et al. 2006; Katiyar-Aggarwal and Jin 2007). In the case of plant-parasitic nematodes, silencing of genes essential for establishing a feeding site by the nematode in the host helps in reducing infection, i.e. silencing of 16D10 dsRNA responsible for *Meloidogyne* spp. host integration reduced the number of eggs laid by the nematode. However, despite various studies and developments, delivering RNAi gene silencing in the field, is not yet established or standardized on a large scale. Further, social ethics and apprehensions regarding the adoption of transgenic crops all over the world have restricted the technology to a few regions only.

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Heat Stress in Wheat: Impact and Management Strategies Towards Climate Resilience

Shubham Kumar Sinha and Koppolu Raja Rajesh Kumar

Abstract

Climate change adaptation and mitigation strategies for agriculture are crucial for future food security. In 2015, the United Nations (UN) adopted 17 Sustainable Development Goals (SDGs) for achieving a better sustainable future for all, intending to achieve them by 2030 using a holistic approach (https://sdgs.un.org/). Among these, SDG2 proposes achieving sustainable food security by integrating it with developing resilient agriculture practices (Target 2.4) to mitigate the impact of future climate change. Wheat is one of the cereal crops which provide the primary energy requirement of the human diet globally and is cultivated in over 215 Mha worldwide. Wheat is a cool-season annual; hence, it is sensitive to heat stress during all stages of its development, particularly during the reproductive stage. By the end of the twenty-first century, global mean temperatures are projected to be 1.8–4.0 °C warmer. With no mitigation strategies in place, yield losses are predicted for wheat in all major wheat-producing countries due to the impact of heat stress. Besides shortening the crop cycle, high temperature affects the morphological, physiological, and molecular responses in wheat's vegetative and reproductive phases. A better understanding of plant responses to heat stress has practical implications for developing novel methods for sustainable and climate-resilient wheat cultivation. This chapter will discuss the impact of heat stress on wheat phenology, development, physiology, metabolism, and gene expression and various management strategies to mitigate the impact of heat stress in wheat.

Keywords

Beneficial microbes • Biotechnology • Exogenous protectants • Genetic engineering • Stress tolerance

1 Introduction

Wheat (*Triticum aestivum* L.), along with maize and rice, are the major source of calories for humans and livestock globally (Lobell and Gourdji 2012). Wheat is cultivated globally in over 215 Mha, with a global yield exceeding 765 Mtonnes (FAOSTAT 2019). India is the second largest producer globally, producing more than 100 Mtonnes, and China, the leading producer of wheat worldwide, produces more than 130 Mtonnes (FAOSTAT 2019). Wheat is cultivated over different agro-climatic zones with an optimum growing temperature of about 25 °C, with minimum and maximum growth temperatures of 3–4 °C and 30–32 °C, respectively (Curtis 2002). FAO estimated that by 2050 world would need around 840 Mtonnes of wheat to meet the future demand of approximately 9 billion people. This increased demand has to be achieved with less available land and projected climate changes, such as high temperature and rainfall distribution (Sharma et al. 2015). Global mean temperatures have increased by 0.8 °C since the 1850s, and it is projected that by the end of the twenty-first century, the global mean temperature could be 1.8–4.0 °C warmer than at the end of the previous century (IPCC 2014). It is also very likely that more intense heat waves will occur more often and may last longer (IPCC 2014). With little or no mitigation efforts, the global mean temperature is more likely to exceed 4 °C above pre-industrial levels, which, combined with increased food demand, would pose a greater risk to global and regional food security by the end of this century (IPCC 2014). A global study on historical trends of climate change and wheat yield between 1980 and 2008 estimated that rather than precipitation, it was the warming

S. K. Sinha · K. R. R. Kumar (✉)
Department of Biotechnology, IGNTU, Amarkantak, Madhya Pradesh 484887, India
e-mail: krrkumar@igntu.ac.in

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trends that imparted a negative impact on wheat yields (Lobell et al. 2011).

Hence, heat stress caused due to high temperatures will be one of the critical limiting factors to future crop productivity worldwide. With no mitigation strategies in place, with every 1 °C global temperature increase, different simulation methods have estimated global wheat yield losses to be around 6% (Asseng et al. 2014; Liu et al. 2016, Zhao et al. 2017). Yield losses are projected for all top wheat-producing countries of the world. The estimated yield loss in the United States and France are similar to the global average. In contrast, India and Russia are more vulnerable to temperature increases, with yield losses estimated to be higher than the worldwide average (Zhao et al. 2017). Another important factor not receiving adequate attention is the impact of climate change on the increase in soil temperatures. Warmer soil temperature requires deeper sowing depth under rainfed conditions. Further, increased soil temperatures will lead to reduced coleoptile length, delayed emergence, and poor crop establishment, leading to subsequent yield losses in cereals (Rebetzke et al. 2016).

High temperatures cause heat stress which disturbs the cellular homeostasis and cause adverse effects on the growth and development of plants (Hall 2001; Mathur et al. 2014). These effects of heat stress depend on the magnitude, timing and duration of the stress, and the developmental stage of the plant exposed to heat stress (Balla et al. 2019). High temperature also increases soil temperature and may lead to reduced availability of soil moisture for plants (Rebetzke et al. 2016). Heat stress disturbs the plant water relations, alters metabolic activity, hormone level, and gene expression (Abdelrahman et al. 2019; Akter and Rafiqul Islam 2017; Sattar et al. 2020). Hence, understanding its impact and mitigation strategies for heat stress in wheat is necessary for sustainable climate-resilient wheat production.

2 Heat Stress and Plants

Heat stress can be defined as the rise in temperature for a sufficient time above a threshold level that can cause irreversible damage to plant function and development. Different crop species differ in their sensitivity to heat stress. Cool-season annuals such as barley, mustard, pea, and wheat are more sensitive to heat stress than warm-season annuals like finger millet, mung bean, sorghum, and tobacco (Hall 2001). The effect of heat stress in a plant is directly proportional to the duration of stress and the plant's growth stage exposed to heat. When exposed to heat stress, distinct parts of a plant may encounter different temperatures and respond differently. For example, reproductive tissues are more susceptible to heat than vegetative tissues (Balla et al. 2019; Jagadish et al. 2021). Poor germination, reduction in photosynthesis, leaf senescence, a decline in pollen viability, reduced production with smaller grain size are the major outcomes of heat stress in the plants (Ugarte et al. 2007). During vegetative growth, heat stress can damage the photosynthetic components and reduce the CO_2 fixing potential. Heat stress also affects electron transport, differentially affecting PSII and PSI (Ruelland and Zachowski 2010). Heat stress is reported to cause leaf wilting, leaf curling, leaf yellowing, and reduction in shoot growth, root growth, root number, root diameter, plant length, and biomass (Wassie et al. 2019). Plants at the reproductive stage are susceptible to heat stress due to damage to male and female reproductive tissues, with anthers (male reproductive tissue) being more sensitive to heat stress (Aiqing et al. 2018; Santiago et al. 2021). During the reproductive stage, heat can damage floral bud development, flowering, pollen development, pollen germination, and pollen tube growth (Ferguson et al. 2021). Substantial reduction in pollen viability, embryo abortion, and poor seed production are all outcomes of heat stress (Ozga et al. 2016). Rising temperatures alter carbon metabolism and disrupt reproductive growth, thereby reducing crop yield under heat stress (Abdelrahman et al. 2019; Bergkamp et al. 2018; Ferguson et al. 2021). Heat stress critically alters the plant membrane fluidity and permeability, causes disassembly of the cytoskeleton, changes in protein conformation, disabling enzyme activities, causing metabolic and redox imbalance (Ruelland and Zachowski 2010). Plants under heat stress undergo a remarkable reduction in their biomass, relative water content (RWC), chlorophyll content, and an increase in electrolyte leakage (EL) and malondialdehyde (MDA) content (Sattar et al. 2020; Wassie et al. 2019).

3 Impact of Heat Stress on Wheat

Being a cool-season plant, wheat is more sensitive to heat stress. The effects of heat stress are complex as it may alter the growth and physiology of the plants by influencing the availability of water and nutrients. Apart from shortening the crop cycle, high temperature affects the morphological, physiological, biochemical, and molecular responses in vegetative and reproductive phases (Farooq et al. 2011). Though every developmental stage is affected by heat stress, the pre-flowering and anthesis stages are most sensitive to heat stress (Bheemanahalli et al. 2019; Cossani and Reynolds 2012). Wheat is vulnerable to high temperature as it accelerates the leaf senescence (Balla et al. 2019; Wang et al. 2011), decreases the photosynthetic rate (Balla et al. 2019; Ristic et al. 2007), pollen viability and starch biosynthesis (Begcy et al. 2018), disturbs the chlorophyll content and rubisco activity (Degen et al. 2020; Demirevska-Kepova et al. 2005). Heat stress in wheat can also shorten the grain filling period (Dias et al. 2008, 2009) and drastically affect seed germination and seedling emergence (Tewolde et al. 2006). Early maturation, antioxidant production, disturbance in physiology and developmental stages, upregulation of heat tolerance genes, alteration in membrane lipid compositions are some of the heat-induced responses in wheat (Fig. 13.1).

3.1 Phenology

Plant phenology, in general, can be stated as a timing of the plant life cycle events such as flowering, leaf bursting, and fruiting. The phenological response of a plant is extremely sensitive to environmental drivers and thus greatly affected by climate change. (Chuine and Régnière 2017; Menzel et al. 2006). Therefore, phenological change is an indication of climate change, and it is an effective tool to assess regional and global climate change. Understanding phenological change in wheat is essential to develop measures for different climatic conditions and crop management. High temperature can reduce the life period of crop plants by disturbing their overall phenological duration. Phenological events in wheat such as the timing of shooting, heading, and harvest have undergone a significant advance over the past several decades as per the studies in Germany, the U.S. Great Plains, and China (Estrella et al. 2007; Hu et al. 2005; Ren et al. 2019; Tao et al. 2006). It was estimated that climate change would impact wheat by advancing heading dates by an average of 1 week by the middle of this century and 2–3 weeks by the end of this century (Gouache et al. 2012). High temperature in wheat can reduce the grain filling stage, reduce time duration between heading and maturity of wheat (Mohammadi et al. 2012), and reduce the period between successive phenological events (Zahedi and Jenner 2003). Further, it hastens the development stages to such an extent that necessary nutrient supply cannot be met (Blum et al. 2001; Laghari et al. 2012). Shortening of the overall growth period and vegetative growth period is the significant phenological impact of climate change on wheat that can lead to yield reduction (Ren et al. 2019). Phenological adjustment of various developmental phases has proven to be the convenient strategy for wheat to adapt under a heat stress environment (Gouache et al. 2012). To overcome the impact of high temperature, the crop calendar should be adjusted towards earlier heading dates on an average of over 5.6 days in the near future and close to 19 days in the far future (Gouache et al. 2012).

3.2 Development

Development in the plant life cycle includes a broad spectrum of processes, such as the formation of the zygote, embryo development, seed germination, and development of the mature vegetative plant, formation of flower, fruit, and seed set. High temperatures can restrict these developmental processes in plants. At every developmental stage, all

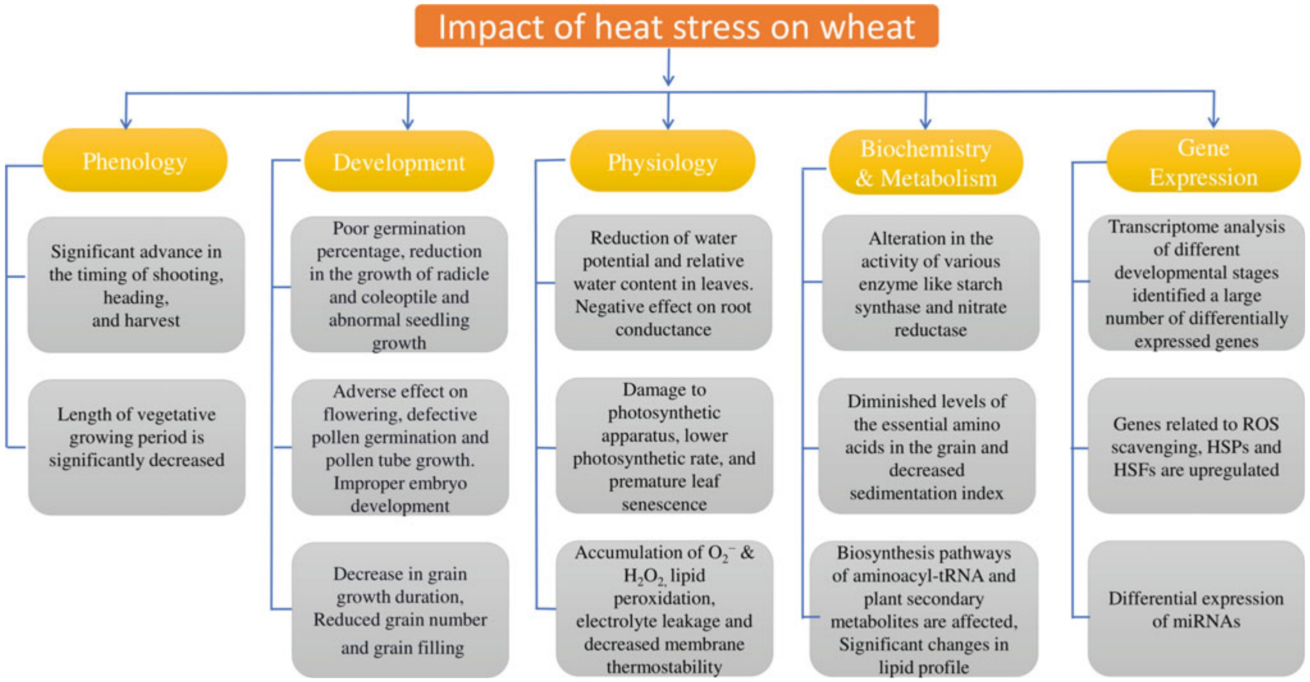

Fig. 13.1 Impact of heat stress on wheat

agronomic traits are badly affected under high temperatures. Good seed germination is one of the critical prerequisites to get a good and uniform crop. Under high temperatures, the first developmental stage to be distressed is seed germination. Significant effects on seed germination under heat stress are poor germination percentage, reduction in the growth of radicle and plumule, and abnormal seedling growth (Kumar et al. 2011; Piramila et al. 2012). The optimum temperature for seed germination in wheat is 20–25 °C. A linear decrease in coleoptile length in wheat genotypes were observed with an increase in temperature from 15 to 35 °C (Rebetzke et al. 2016). In warmer soils, decrease in coleoptile length may delay the emergence of shoot above the soil surface, resulting in the poor establishment of seedlings and subsequently affecting the yield (Rebetzke et al. 2016). The vegetative development has a threshold temperature of around 15–30 °C in wheat (Porter and Gawith 1999). Heat stress also impairs vegetative growth like shoot, root development, and leaf appearance.

At the reproductive stage, heat stress causes significant loss of yield in crops including wheat (Begcy et al. 2018). During the reproductive phase, wheat plants undergo many crucial development processes such as spikelet initiation, floral organs differentiation, male and female sporogenesis, pollination, and fertilization. Heat stress can impair any stage of these developmental processes, leading to a lower grain set (Rawson and Bagga 1979; Saini and Aspinall 1982; Aiqing et al. 2018). During the terminal spikelet stage, accelerated reproductive development was observed with an increase in temperature from 10 °C to 19 °C, whereas spikelet initiation was delayed and the number of spikelet primordia reduced with temperatures above 20 °C (Porter and Gawith 1999; Slafer and Rawson 1995). The optimum temperature was determined to be 10.6 °C for the terminal spikelet stage, 21 °C for anthesis, and 20.7 °C for grain filling (Porter and Gawith 1999). Compared with the post-flowering stage, pre-flowering stage and anthesis are much susceptible to high temperature (Ni et al. 2018; Yang et al. 2013). Heat stress can lead to no flowering or flowers may be unable to form fruit and seed. Saini and Aspinall (1982) reported that floret formation at high temperatures (above 30 °C) could lead to sterility. Five days before or after anthesis are particularly sensitive to heat stress, which reduces grain numbers (Wheeler et al. 1996). Short exposure to high temperature at flowering and pre-flowering stage led to reduced yield and grain number per spike, resulting from defective pollen germination and pollen tube growth (Yang et al. 2013). Pollen viability and tolerance to heat stress appears to be cultivar-specific, for example. It was observed that when moderate heat stress was applied during the pollen development stage, the viability of pollen was better in Australian cultivars compared to European cultivars (Begcy et al. 2018). High temperature induces pollen and anther sterility and shows an adverse effect on ovary development, resulting in improper embryo development, reduced grain number, and grain filling (Mondal et al. 2013). Temperature more than 31 and 35 °C limits the success of pollination and grain filling, respectively (Porter and Gawith 1999). The growth and development of a plant decline under heat stress due to source and sink limitations that restrict grain set and grain filling (Alghabari et al. 2021). Heat stress causes inhibition of photosynthesis, thereby limiting the available photosynthetic assimilates required for grain filling (Blum et al. 1994). Translocation of assimilates to the developing grain is hindered due to heat stress during the grain filling stage, thereby significantly reducing final kernel weight (Bergkamp et al. 2018). High temperatures between 30 and 38 °C during the reproductive phase decrease the average grain mass on the main stem by 20–44% among wheat genotypes (Tahir and Nakata 2005). Temperatures near 31 °C in the daytime and 20 °C in night-time can shrink grain size due to structural change in the endosperm and aleurone layer (Dias et al. 2008). The duration and rate of grain filling determine the final grain yield in wheat. Yin et al. (2009) reported that at a temperature of 25 °C and above, grain growth duration was reduced by several days with an increase in grain growth rate. Heat stress during flowering resulted in a reduced number of seeds and seed weight per spike. This effect is more prominent on primary spikes followed by the main spike suggesting pre-anthesis-associated events such as gametogenesis and gamete development to be more susceptible to heat stress (Bheemanahalli et al. 2019). Studies on the impact of heat stress on source–sink relationships in wheat under heat stress showed that there is no significant difference in the supply of assimilates between control and heat-stressed plants during flowering or grain filling time suggesting no source limitation (Abdelrahman et al. 2019). Grain weight is more affected by heat stress during the anthesis stage compared to the grain-filling stage (Alghabari et al. 2021).

3.3 Physiology

3.3.1 Water Relations and Photosynthesis

Water relations generally deals with how a plant manages the hydration of a cell. It is determined by characteristics such as leaf water potential, transpiration rate, and stomatal conductance. High temperature disturbs leaf stomatal conductance and leaf water relation. Heat stress may lead to dehydration inside plant tissue and further obstruct the development of a plant (Akter and Rafiqul Islam 2017). Heat stress often coexists with water shortage (Simões-Araújo et al. 2003). Global warming and subsequent temperature rise can become detrimental to plants due to the scarcity of water. In wheat, a rise in temperature results in the reduction of water potential and relative water content in leaves to a great extent (Farooq et al. 2009). Despite the sufficient quantity of water in the soil, the reduced leaf water content in wheat due to exposure to high temperature proves that heat stress has negative consequences on root conductance (Morales et al. 2003). Physiological response of flag leaf during terminal heat stress showed a reduction in the relative water content (RWC), turgor potential, and increase in the water potential of flag leaf (Sattar et al. 2020). Maximum water is lost in the daytime under heat stress due to the rapid rate of transpiration, which may disturb some of the physiological processes in the plant.

Wheat is a C3 crop, and it has a lower optimum temperature for photosynthesis than C4 plants. Photosynthesis is a heat susceptible physiological event that leads to poor growth in wheat (Feng et al. 2013). Damage to photosynthetic apparatus, lower photosynthetic rate, and premature leaf senescence are some of the adverse effects of heat stress in wheat (Ashraf and Harris 2013; Mathur et al. 2014). Protochlorophyllide (Pchlide) synthesis was inhibited by 70% under heat stress in wheat seedlings (Kumar Tewari and Charan Tripathy 1998). Accelerated flag-leaf senescence caused by heat stress could be attributed to lower levels of photosynthetic pigments and a decline in photosynthetic activity (Balla et al. 2019). Further, reduced photosynthetic activity results in a gradual reduction in net assimilation and stomatal conductance with an increased duration of heat stress (Balla et al. 2019). The decrease in photosynthetic assimilation was associated with a decrease in photochemical activities (Chovancek et al. 2019). Stroma and thylakoids are the two main sites in the chloroplast, which are highly sensitive towards high temperatures. Heat stress in wheat disrupts the thylakoid membrane and thus leads to reduced photosynthesis rate due to disturbance in membrane-associated electron carriers and enzymes (Ristic et al. 2008). High temperature of around 35–45 °C can lead to the destacking of thylakoids membrane in wheat (Mathur et al. 2010). Decreased photosynthetic rate and grain yield per plant and increased thylakoid membrane damage were observed due to heat stress during anthesis and grain filling (Djanaguiraman et al. 2020). PSII is relatively more sensitive to high-temperature stress than PSI and hence readily affected by heat stress (Marutani et al. 2012; Mathur et al. 2014). High temperature leads to disproportional flow of electrons to the acceptor site of PSII due to impairment of the oxygen-evolving complex I (De Ronde et al. 2004).

High temperature disturbs intercellular CO_2 concentration and deactivates the rubisco, thereby limiting CO_2 fixation (Mathur et al. 2014). The deactivation of rubisco occurs at high temperatures due to the production of inhibitory compounds exceeding the capacity of rubisco activase to remove them from the catalytic sites of Rubisco (Salvucci and Crafts-Brandner 2004). In wheat leaves, heat stress in the dark lead to a decrease in the abundance of rubisco subunit and rubisco activase. An irreversible decrease in photosynthetic pigments, soluble proteins, rubisco-binding protein, were also observed (Demirevska-Kepova et al. 2005). Heat stress in wheat accelerates the leaf senescence, reduces chlorophyll content, changes chlorophyll a/b ratio and damages chloroplast integrity (Al-Khatib and Paulsen 1984; Haque et al. 2014).

3.3.2 Redox Status

In plants, high temperature increases the level of reactive oxygen species (ROS) such as superoxide radical (O_2^-), hydrogen peroxide (H_2O_2), and hydroxyl radical (OH^-), causing oxidative stress and disturbing the redox homeostasis of the cell (Marutani et al. 2012; Suzuki et al. 2011). ROS are highly reactive and can potentially react and cause damage to intracellular components, including cell death at high concentrations. ROS is also generated in organelles like peroxisomes and mitochondria, along with the reaction centers of PSI and PSII of the chloroplast. ROS causes autocatalytic peroxidation of lipid molecules, which are the major component of cell and organelle membranes, thereby influencing membrane fluidity and stability (Hasanuzzaman et al. 2013; Narayanan et al. 2016). Heat stress leads to photoinhibition, and the generation of ROS during photoinhibition could cause chlorophyll degradation, damage to PSII components, and inactivation of enzymes involved in CO_2 assimilation thereby reducing the photosynthetic rate in plants experiencing heat stress (Djanaguiraman et al. 2018). Higher ROS generation could induce the processes of early senescence with a reduction in the photosynthetic capacity of the leaves in sensitive genotypes (Chovancek et al. 2019). Studies on short-term and long-term heat stress in wheat showed increased accumulation of superoxide radical (O_2^-) and hydrogen peroxide (H_2O_2) (Hasanuzzaman et al. 2013). With increasing temperature, a gradual increase in the accumulation of H_2O_2 was observed in wheat seedlings (Kumar 2012). Oxidative stress elevates membrane lipid peroxidation, promotes electrolyte leakage, and decreases membrane thermostability in wheat (Savicka and Škute, 2010). High temperature mediated membrane damage and reduction in antioxidant levels in wheat was observed in different stages of wheat growth, viz. seedling stage, anthesis stage, and grain filling stage (Djanaguiraman et al. 2018).

Management of oxidative stress has been correlated with tolerance to abiotic stress in many studies (Hasanuzzaman et al. 2012). Similarly, thermotolerance requires the deployment of mechanisms that can reduce oxidative damage under heat stress. Several studies on thermotolerant and susceptible genotypes have confirmed a positive correlation between heat stress tolerance and increased enzymatic or non-enzymatic ROS scavengers (De Pinto et al. 2015). Heat tolerance in different wheat genotypes is correlated with the capability of catalase (CAT) and ascorbate peroxidase (APX) to efficiently scavenge H_2O_2 (Dash and Mohanty 2002). A significant increase in CAT and SOD activity under heat stress was also observed in flag leaves during terminal heat stress (Sattar et al. 2020). Higher MDA content was observed in heat-sensitive genotypes of wheat. In contrast, higher antioxidant enzymes and lower MDA levels were observed in heat-tolerant genotypes, showing a negative correlation with membrane damage and heat susceptibility index (Hameed et al. 2011).

3.4 Biochemistry and Metabolism

The biochemistry and metabolism of a plant cell are affected by environmental stresses, influencing the metabolite content such as carbohydrates, protein, amino acids, production of several allergens, toxins, and various secondary metabolites. Starch is the most abundant carbohydrate in wheat, and it is made up of amylose and amylopectin. Starch synthases have a central role in the biosynthesis of starch. The effect of high temperature on starch accumulation in wheat grains is usually attributed to the direct effect of heat stress on the enzymes involved (Ferris 1998). Rijven (1986) reported that starch synthase from wheat was inactivated in vivo and in vitro at temperatures above 30 °C. A decline in starch biosynthesis and grain growth was also observed in wheat due to a heat stress-induced decrease in starch synthase activity (Prakash et al. 2003, 2004). There is a remarkable reduction in leaf total soluble sugar accumulation and plant biomass in wheat after imposing high-temperature stress at 35/27 °C of heat-primed seedlings (Wang et al. 2014). Decrease of sucrose content and increase of fructose and glucose content were observed in different winter wheat cultivars under heat stress (Mirosavljević et al. 2021). Under high temperatures, the activity of enzymes involved in nutrient metabolism like nitrate reductase is reduced in wheat (Klimenko et al. 2006).

Grain protein concentration increased when heat stress was imposed early during grain fill and the influence of heat stress on protein quality varied with different cultivars (Castro et al. 2007). Diminished levels of the essential amino acids in the grain and decreased sedimentation index following heat stress were also observed (Dias et al. 2008). Genotype dependent increase in proline content and increase in the activity of catalase, guaiacol peroxidase, and SOD were observed in wheat subjected to short-term heat stress (Gupta et al. 2013). An increase in proline content and total soluble sugars is also observed in wheat plants exposed to high temperatures during the grain-filling or anthesis stage (Alghabari et al. 2021). Relatively higher accumulation of proline was observed under heat stress in heat-tolerant genotypes compared to heat-susceptible genotypes (Ahmed and Hasan 2011; Katakpara et al. 2016). The biochemical response of flag leaf during terminal heat stress showed higher proline, soluble proteins, and soluble sugar levels was observed under heat stress compared to control (Sattar et al. 2020). Protein folding is adversely affected under heat stress, resulting in disruption of metabolism and molecular processes. Heat shock proteins (HSPs) are synthesized to mitigate this effect, which acts as a molecular chaperone and retain homeostasis in protein folding. Accumulation of HSPs was associated with thermal tolerance in wheat (Krishnan et al. 1989; Xiaozhi et al. 1995). Chloroplast protein synthesis elongation factor, EF-Tu and EF-1α, were accumulated under heat stress in wheat, and cultivars with greater accumulation of EF-Tu exhibited better tolerance to heat stress (Bukovnik et al. 2009; Ristic et al. 2008). Metabolites are the final products of cellular processes, and hence studying the metabolic profile of a plant can provide a snapshot of the biological state of that plant under a particular developmental stage or stress condition (Abdelrahman et al. 2019). Narayanan et al. (2016) observed significant changes in the lipid profiles in both heat-tolerant and susceptible wheat genotypes under high temperatures. Higher amounts of sterol glycoside [SG] and saturated species of acylated sterol glycoside [ASG], and lower amounts of ox-lipids were present in Ventnor (heat-tolerant genotype) compared to Karl 92 (heat-susceptible genotype). Heat stress also differentially influenced the molar percentage of unsaturated lipid species, monogalactosyldiacylglycerol (MGDG) and digalactosyl diacylglycerol (DGDG) in wheat (Djanaguiraman et al. 2020). Metabolomic analysis of wheat following post-anthesis heat stress showed a 1.5-fold or higher differential accumulation of 64 known metabolites. Further, aminoacyl-tRNA biosynthesis and plant secondary metabolite biosynthesis pathways are most affected (Thomason et al. 2018).

3.5 Gene Expression

Plant adaptive mechanisms against heat stress are under multigene control. Hence, in many plant species, molecular response under heat stress was explored to understand the mechanism of heat stress tolerance. Effect of heat stress on gene expression profile in different developmental stages of wheat (i.e. developing seed, 10-d-old seedlings and unfertilized flower) was reported (Chauhan et al. 2010). Heat stress significantly affects the gene expression in wheat seedlings, with several thousand genes being differentially regulated within 1 h of heat stress (Liu et al. 2015). Transcriptome analysis of wheat grain and flag leaf resulted in identifying 1705 differentially expressed genes (DEGs) under heat stress (Su et al. 2019). Large-scale analysis of gene expression in contrasting wheat genotypes for thermotolerance showed that a large number of genes are differentially expressed between thermotolerant and susceptible genotypes as well (Qin et al. 2008). Comparison of gene expression between heat-tolerant and susceptible cultivars of wheat showed that several heat-responsive candidate genes such as *Hsp90*, *Hsp-Sti*, hypothetical *Dnaj*, *ClpB1*, *PPIase*, *GAPDH*, *PSBR,* etc., were upregulated in heat-tolerant wheat cv. C306 compared to cv. HD2967 under heat stress during post-anthesis stage (Vishwakarma et al. 2018). High temperature was also shown to rapidly alter the rubisco activase (*Rca*) gene expression. Among the three isoforms of the Rubisco activase (*Rca*) in the wheat genome, heat-stable Rca1β transcript increased 40-fold within 4 h of heat stress, whereas control plants showed no expression of *Rca1β* (Degen et al. 2020).

Genes encoding Heat Shock Proteins (HSP), Heat Stress Transcription Factors (HSFs) are some of the early response genes induced during heat stress in wheat (Qin et al. 2008; Ohama et al. 2017). ROS scavenging and HSP related gene upregulation in high temperature was correlated with heat tolerance (Suzuki et al. 2014). Heat shock proteins (HSPs) act as molecular chaperones maintaining the homeostasis of protein folding. Higher HSP transcripts and protein levels were observed in some of the wheat genotypes with acquired thermotolerance (Vierling and Nguyen 1992; Skylas et al. 2002). Heat shock transcription factors (HSFs) are transcription factors that regulate the expression of HSPs and play an essential role in the thermotolerance of plants. Wheat *TaHsfA6f* was upregulated several-fold within 1 h of heat stress, suggesting it is an early heat response gene (Bi et al. 2020). *TaHsfA2–10* was induced highly under heat stress in the seedling stage (Guo et al. 2020). The role of miRNAs in heat stress was also studied in wheat with many heat stress-responsive miRNAs; their tissue-specific expression and their targets were identified in wheat (Kumar et al. 2014; Ni et al. 2018). For example, *TamiR159* was downregulated early under heat stress in wheat. Transgenic rice plants overexpressing *TamiR159* were more susceptible to heat stress, suggesting a role for *TamiR159* in the heat stress tolerance of wheat (Wang et al. 2012). Upregulation of various HSPs was observed in developing grains of different genotypes of wheat irrespective of their tolerance to heat stress (Rangan et al. 2020). Based on the comparative transcriptome profiling of the developing grain of three wheat genotypes under heat stress Rangan et al (2020) suggested that 6-phosphogluconate dehydrogenase (*pgd3*), S6 RPS6-2 ribosomal protein, peptidylprolyl isomerases, plasma membrane proton ATPase, heat shock cognate70, FtsH protease, and RuBisCO activase B might have a crucial role in heat stress tolerance. While comparing Australian and European cultivars, Begcy et al. (2018) observed that heat shock factor genes (HSFs) were expressed in substantial levels in heat-tolerant cultivars compared to susceptible ones and suggested that relatively stable expression of HSFs in Australian cultivars is associated with their high level of acquired heat stress tolerance. A recent genome-wide analysis of TaHSF genes in wheat showed that a significant number of TaHSFs are located on chromosome 3 (Duan et al. 2019). This is particularly interesting since chromosomes 3A and 3B are known to harbour quantitative trait loci for heat stress tolerance in wheat (Ni et al. 2018).

4 Management Strategies

Wheat is a staple food of many geographical areas, and heat stress has a drastic effect on wheat, making wheat production highly vulnerable to future climate change, as discussed above. The temperature increase due to climate change is expected to badly affect different stages of wheat production from sowing to harvesting and ultimately lead to an overall reduction in yield. Conventional breeding programs were primarily aimed at developing resistance to diseases, pests, and yield enhancement. Considering the impact of heat stress on wheat, it is necessary to focus the future breeding programs on developing varieties tolerant to heat stress. Management strategies involving agronomical practices and biotechnological approaches for sustainable wheat cultivation under heat stress are discussed below and presented in Fig. 13.2.

4.1 Agronomical Practices

By exploiting and adjusting some agronomical practices, wheat and many other crops can be cultivated at high temperatures. These practices include maintaining proper time and method of sowing, cultivar choice, using beneficial microbes and exogenous protectants and growth regulators.

4.1.1 Time of Sowing, Choice of Cultivar, Tillage, and Mulching Practices

A suitable sowing time and method is considered an excellent agronomical practice and non-monetary input for optimal plant growth and yield (Kajla et al. 2015). Modification in planting method and date of sowing with the appropriate wheat variety can ease the adverse effect of heat stress (Akter and Rafiqul Islam 2017). Proper planting time can avoid the warm and desiccating wind during the flowering and grain-filling period. For example, early planting appears to be a successful approach to avoid summer heat for spring wheat (Reilly et al. 2003). Nainwal and Singh (2000), in their experiment, reported a reduction in various growth parameters in late sown crops as it may be due to the reduction in the cellular activity like cell division and

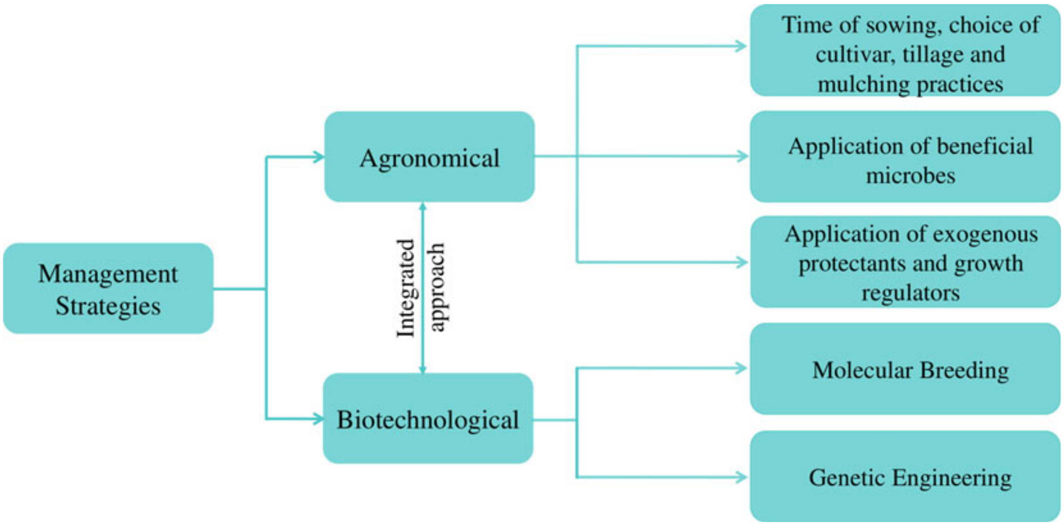

Fig. 13.2 Management strategies for improving wheat resilience to future climatic (high temperature) conditions

expansion. Selection and breeding of thermotolerant cultivars are necessary to overcome the negative effect of heat stress in wheat. Better grain yield was also observed in heat-tolerant wheat varieties than heat-susceptible varieties in wheat (Ali et al. 2019). Heat-tolerant wheat varieties generally exhibit lower membrane damage and are better able to cope with oxidative stress than heat-susceptible wheat genotypes (Khanna-Chopra and Chauhan 2015). Choosing an appropriate variety of wheat such as PBW-373, Kaushambi (HW 2045), Naina (K-9533), and Parbhani-51, which are heat-tolerant varieties, is very crucial to overcome the adverse effect of high temperature (Jena et al. 2017). Various cropping practices will help in adapting agriculture to climate change. Proper crop rotation and intercropping may reduce the harmful effects of climate change on agriculture without affecting the economic advantages. The planting method and tillage practice perform a crucial role in placing seeds in proper depth, ensuring the better emergence and growth of a crop. No-till and zero-tillage systems can conserve moisture, keep the soil temperature low during the day and hence protect the seedling against high temperature during its initial growth period (Jena et al. 2017). Zero-tillage practice for wheat in a rice–wheat system of Indo-Gangetic plain can save up to 20–25% of water in irrigation (Gupta et al. 2002). Zero-tillage advances planting time, thereby conserving soil moisture and also escaping terminal heat effect in wheat (Gupta et al. 2002).

Heat stress will have a direct impact on the availability of water in the soil. Mulching is considered to be important agronomic practice in conserving the soil moisture and helping in adjusting the soil temperature. Mulching has been proved to be beneficial for wheat by improving water use efficiency, growth, and yield under semi-arid conditions (Chakraborty et al. 2008). Early sowing with one additional dose of nitrogen and irrigation at the grain filling stage was found to most suitable adaptation option for reducing the impact of terminal heat stress in wheat in current and future heat stress scenarios (Dubey et al. 2020). Cultivating crops with a proper planting time, using appropriate variety, short life cycle, crop rotation, irrigation technique, weeding, mulching, etc., are some of the agronomical practices that help adapt wheat cultivation to climate change.

4.1.2 Application of Beneficial Microbes

The microbiome is the second genome of an organism with up to trillions of microbes, including bacteria, fungi, lichens, actinomycetes, etc., are residing in it and with it. The plant microbiome provides an essential ecosystem service as it enhances plant growth and alleviates abiotic stress such as high temperatures. Through a symbiotic association with plants, the plant microbiome help plants to cope up with adverse conditions such as high-temperature stress by enhancing the bioavailability of nutrient and water uptake, reducing oxidative stress, producing plant hormones, and regulating various signaling pathways (Arif et al. 2020). The application of such plant-associated microorganisms was shown to alleviate different abiotic stresses in diverse plant species (Lata et al. 2018). Under heat stress conditions, arbuscular mycorrhizal fungi (AMF) increased the number of grains per spike in wheat and altered nutrient allocation and tiller nutrient composition (Cabral et al. 2016).

Plant growth-promoting rhizobacteria (PGPR, Root microbiome) are considered compatible and favorable for wheat growth as it attributes protection against high temperature (Nain et al. 2009). PGPR nullify the effect of ROS produced due to heat stress by increasing the activity of catalase, peroxidase, and other antioxidant enzymes. Altering the microbiome by inoculating with a PGPR consortium can further enhance heat tolerance. For example, the treatment of wheat plants with *Bacillus amyloliquefaciens* and *Azospirillum brasilense* enhanced heat stress tolerance in wheat by reducing ROS levels (Abd El-Daim et al. 2014). PGPR priming with *Bacillus safensis* protected wheat seedlings from heat stress by maintaining cell viability and antioxidative response. This protection is associated with a reduced level of ROS, less membrane damage, enhanced chlorophyll content, increased expression of redox enzymes and osmolyte accumulation (Sarkar et al. 2021). A recent study by Shekhawat et al. (2021) showed that a root endophyte *Enterobacter* sp. SA187 induces thermotolerance in wheat. Under field conditions characterized by low rainfall and high temperatures, application of *Enterobacter* sp. SA187 resulted in increased plant height, seeds per spike, and seed weight. Further, a consistent increase in grain yield was also obtained (Shekhawat et al. 2021). An invasive weed associated bacteria was also shown to confer heat stress tolerance in wheat by enhancing the content of osmoprotectant and the activity of antioxidant enzymes CAT and APX. These examples signify that utilizing plant-associated microbes can be a potentially sustainable approach to wheat cultivation under heat stress.

4.1.3 Application of Exogenous Protectants and Growth Regulators

Another method to tackle the negative effect of high temperature is by supplying an adequate and balanced amount of nutrients and protectants, which can safeguard the plant by nullifying the adverse effect of heat stress (Waraich et al. 2012). Osmoprotectants (such as proline, trehalose, glycine betaine), phytohormones (like indole acetic acid, gibberellic acid, salicylic acid abscisic acid), signaling molecules, some trace elements, and essential nutrients are some of the protectants that can be applied exogenously to ameliorate thermotolerance in wheat (Upreti and Sharma 2016). Several studies on different plant species proved that exogenous application of osmolytes could protect plants against heat stress. Proline is an amino acid that acts as a membrane protectant and plays a crucial role in maintaining the protein structure and helping in scavenging ROS (Hameed et al. 2011). Further, under heat stress, proline decreases the hydrogen peroxide level, enhances the soluble sugar accumulation, and protects the tissue from heat. Exogenously applying trehalose can elevate the amount of endogenous trehalose, further enhancing the photosynthesis capacity in wheat under high temperatures (Luo et al. 2010). Similarly, another osmoprotectant glycine betaine (GB), also exhibited beneficial effects on plants under heat stress when applied exogenously (Yang et al. 2006). Applying glycine betaine through foliar feeding enhances the thermotolerance in wheat by raising the chlorophyll and GB content under heat stress with improved stomatal conductance (Wang et al. 2014). There are various phytohormones whose exogenous application can help in adapting to heat stress. Application of phytohormones like abscisic acid, indole acetic acid, and gibberellic acid improved the grain yield in wheat under high-temperature stress (Cai et al. 2014).

Kumar et al. (2014), reported that foliar spray of (100 mM) salicylic acid (SA) could ameliorate the heat tolerance in wheat by modulating the osmolyte accumulation, expression of stress-associated proteins, and total antioxidant capacity under heat stress. Applying (0.5 mM) SA also showed superior protection against heat stress by reducing ethylene formation through decreasing ACS (1-aminocyclopropane carboxylic acid synthase) activity. Further, a reduction in the loss of chlorophyll and rubisco activity was observed (Khan et al. 2013). The use of α-tocopherol and SA increased membrane stability in wheat, stabilized photosynthesis, and increased yield (Sandhu et al. 2018). Treatment of wheat plantlets with salicylic acid and hydrogen sulfide, independently or in combination, increased resistance to heat stress with increased accumulation of antioxidant enzymes and reduced lipid peroxidation (Karpets et al. 2020). Exogenous application of methyl jasmonate (MeJA) protected PSII, provided stability to photosynthetic apparatus and CO_2 assimilation under heat stress in wheat (Fatma et al. 2021). The study also showed that exogenous MeJA application enhanced the expression of *psbA* and *psbB* under normal and heat-stressed conditions, increased antioxidant activity, and decreased oxidative damage under heat stress (Fatma et al. 2021).

Nitric oxide (NO) acts as a signaling molecule and plays a crucial function in thermotolerance in the plant during heat stress. Applying NO exogenously can protect wheat seedlings from heat stress by upregulating antioxidant defence and glyoxalase system (Hasanuzzaman et al. 2012; Waraich et al. 2012). Under heat stress condition, NO_3^- delays abscisic acid synthesis and increase cytokinin activity, while K^+ application induces photosynthetic activity and boost grain yield (Singh et al. 2011). Exogenous application of inorganic nutrient elements such as selenium, calcium, magnesium, zinc, and nitrogen were also beneficial and protective against heat stress in wheat (Ali et al. 2019). Selenium is a trace element when applied exogenously, enhancing the antioxidant activity and chlorophyll content. It also helps improve the osmotic-adjustment capacity of wheat under heat stress (Iqbal et al. 2015). Applying potassium orthophosphate (KH_2PO_4) as a foliar spray after anthesis can increase thermotolerance, delay the heat stress-induced leaf senescence, and improve yield (Dias and Lidon 2010). Exogenous calcium promotes heat tolerance by inducing the activity of antioxidants like guaiacol peroxidase, SOD, and CAT in wheat. Calcium can guard chlorophyll against photo-destruction and maintain stomatal function, thereby decreasing the impact of heat stress through transpiration

(Dias et al. 2009). Recent studies showed that the application of polyamines (spermine and spermidine) could alleviate heat stress-induced injury during grain filling in wheat (Jing et al. 2020). Under high temperature, both spermine and spermidine application increased grain weight in heat-resistant and heat-susceptible wheat varieties with a significant increase in superoxide dismutase (SOD), peroxidase (POD), and catalase (CAT) activity during grain filling (Jing et al. 2020). Foliar application of potassium nitrate (KNO_3) during the booting and anthesis stage helped in mitigating the effect of terminal heat stress and improved the yield of late sown wheat under field conditions (Singh and Singh 2020). Exogenous application of natural growth promoting substances like moringa leaf extract and sorghum water extract was also shown to be useful in alleviating the impact of heat stress in wheat (Afzal et al. 2020).

4.2 Biotechnological Strategies

Previously, breeders main target was to establish high yielding variety and undoubtedly, they were successful only in improving yield under optimum conditions but not under stressful conditions. In recent decades, the advancement of molecular biology and a greater understanding of the mechanism of heat stress tolerance led to identifying several genes responsible for thermotolerance in wheat. Harnessing the available genetic resources using advanced breeding techniques and exploiting wild relatives to increase genetic diversity can help develop climate-resilient wheat.

4.2.1 Molecular Breeding

The availability of genetic diversity within species is a prerequisite for any breeding program. Conventional breeding may help improve temperature tolerance in crop plants and can mitigate the adverse effect of heat to a certain extent. Usually, conventional breeding is executed in the same climate region where the crop will be eventually be produced. Therefore, the selection of breeding lines in tropical regions occurs under tropical conditions (Driedonks et al. 2016). Using the ancestor *Triticum tauschii* as a donor parent, recurrent selection has been used to enhance grain size and grain filling rate in BC1F6 plants of *T. aestivum* under heat stress (Gororo et al. 2002).

However, crop improvement using conventional breeding is a time-consuming process with limitations such as selecting superior genotypes based on phenotypes. Heat tolerance in wheat is quantitative, regulated by multiple genes or quantitative trait loci (QTL) (Blum 1988). So, it is difficult to select a thermotolerant wheat variety through traditional breeding. In molecular or marker-assisted breeding, DNA markers that are tightly linked to phenotypic traits help in the selection. Another advantage of using molecular markers is that they are not affected by the environment as with morphological or biochemical markers and can be detected at any stage of the plant life cycle. Utilizing different traits as indicators, several QTL associated with heat tolerance were identified in wheat. QTL mapping associated with heat tolerance and using it in a marker-assisted selection can develop heat-tolerant wheat varieties. QTL for heat tolerance in wheat were reported using different traits like grain fill duration, canopy temperature depression, yield, senescence-related traits, heat susceptibility index, and thousand-grain weight (Paliwal et al. 2012). QTL trait associated with heat stress was reported on different chromosomes, for example, chromosome 1B, 1D, 2A, 2B, 2D, 3BS, 5A, 6A, 6B, 6D for grain filling duration (GFD) (Ogbonnaya et al. 2017; Shirdelmoghanloo et al. 2016), 1A, 2A, 3B, 4A, 5B for number of grains (Pinto et al. 2010), 1B, 1D, 2A, 2B, 3B, 4D, 5A, 5B, 5D, 6A, 6B, 6D, 7A, 7B, 7DS for days to maturity (Ogbonnaya et al. 2017) and 7BL for canopy temperature depression (Paliwal et al. 2012). Determining constitutive QTL for heat tolerance plays a crucial role in successful MAS breeding. Stable QTLs were identified in wheat, and QTL on chromosome 2B and 7B alone or together were suggested to be used in marker-assisted breeding to obtain enhanced heat stress tolerance in wheat (Paliwal et al. 2012). Near-isogenic lines (NILs) targeting major heat tolerance QTL on chromosome 7a were also developed (Lu et al. 2020). Understanding the molecular mechanism of heat tolerance and identifying the genes responsible can speed up the breeding for heat-tolerant varieties. MAS is considered one of the efficient methods for complex traits such as heat stress tolerance (Janni et al. 2020). With the availability of well-annotated genome sequences, marker-assisted recurrent selection (MARS) and genomic selection (GS) can aid in the development of new cultivars.

4.2.2 Genetic Engineering

Limitations of hybridization-based breeding programs such as linkage drag can be overcome by modern genetic engineering approaches. Genetic engineering can help develop heat-tolerant crops by incorporating the desired gene of interest into the crop genome without disturbing the total yield. However, the complexity of the genome, like large genome size, high ploidy number, repetitive DNA sequence, and low transformation efficiency of hexaploid wheat, make it challenging to alter genetically. There are innumerable examples of genetically engineered transgenic plants developed to overcome biotic and abiotic stresses. Genome sequence accessibility, along with modern genome editing techniques, provides opportunities for altering any desirable trait. Clustered regularly interspaced short palindromic repeats (CRISPR/Cas9), Zinc finger nuclease (ZFNs), and Transcription activator-like effector nuclease (TALENS) are examples of genome editing techniques that are precise and allow site-specific editing within the genome. Since the first knockout of Mildew Locus O (Mlo) using TALEN for generating stable genome-edited wheat plants, successful genome editing was achieved in wheat at several loci of interest (Smedley et al. 2021).

Several wheat genes were functionally characterized for their role in heat stress tolerance by homologous and heterologous expression studies (Ni et al. 2018). Overexpression of *TaHsfA6f* in wheat resulted in improved thermotolerance with upregulation of several HSP genes and other heat stress protection genes (Xue et al. 2014). A heat-induced ferritin gene (*TaFER-5B*), when cloned and overexpressed in wheat, transgenic plants exhibited enhanced thermotolerance. Further, *TaFER-5B* can complement the heat-sensitive ferritin mutant of Arabidopsis (Zang et al. 2017). High temperature-induced accumulation of EF-Tu was studied in various cultivars of wheat, and it was found that the greater accumulation of EF-Tu is associated with enhanced tolerance to heat stress (Ristic et al. 2008). When a maize plastidial protein synthesis elongation factor (EF-Tu), was overexpressed in wheat, transgenic plants displayed reduced thermal aggregation of leaf proteins, reduced heat injury to thylakoids, and enhanced rate of CO_2 fixation under heat stress (Fu et al. 2008). Transgenic wheat plants overexpressing rice soluble starch synthase genes exhibited longer photosynthetic duration and increased thousand kernel weight under heat stress (Tian et al. 2018). A wheat phosphoenolpyruvate carboxylase kinase-related kinase gene, *TaPEPKR2,* when overexpressed, provided enhanced tolerance to heat and drought stress in wheat and Arabidopsis (Zang et al. 2018). Overexpression of a transcription activator *TaHsfC2a-B* resulted in upregulation of heat protection genes with improved thermotolerance but not dehydration tolerance in transgenic wheat plants (Hu et al. 2017). In addition to the genes discussed above, other genes functionally characterized for their ability to confer heat stress tolerance in wheat are given in Table 13.1. Thus, with a better understanding of the molecular mechanism of heat stress tolerance in wheat and

Table 13.1 Genetic engineering for improved heat stress tolerance in wheat

Source of gene	Gene name	Trans-host	Studied by	Result	References
Zea mays	*EF-Tu* (*elongation factor*)	Wheat	Overexpression	Transgenic plants displayed reduced thermal aggregation of leaf proteins, reduced heat injury to thylakoids, and enhanced rate of CO_2 fixation under heat stress	Fu et al. (2008)
Atriplex hortensis	*BADH* (*Betaine aldehyde dehydrogenase*)	Wheat	Overexpression	Greater tolerance to high temperature through stabilization of lipid composition of the membrane. Glycine betaine over-accumulation led to increased photosynthesis under heat stress	Wang et al. (2010)
Triticum aestivum	*TaHsfA6f* (*heat shock factor*)	Wheat	Overexpression	Improved thermotolerance with upregulation of several HSP genes and other heat stress protection genes	Xue et al. (2015)
Zea mays	*PEPC* (*phosphoenolpyruvate carboxylase*)	Wheat	Overexpression	Increased photochemical efficiency and increased expression of photosynthetic genes. Transgenic wheat lines exhibited a lower rate of superoxide anion production, H_2O_2, and malondialdehyde content under high-temperature stress	Qi et al. (2016)
Vigna eylindrica	*VeFER (ferritin)*	Wheat	Overexpression	Reduced MDA content in transgenic plants after heat treatment. Improved thermal stability of cell membranes	Zhao et al. (2016)
Triticum aestivum	*TaFER-5B (ferritin)*	Wheat	Overexpression	Transgenic plants exhibited enhanced thermotolerance. *TaFER-5B* can complement the heat-sensitive ferritin mutant of Arabidopsis	Zang et al. (2017)
Oryza sativa	*SS I* (*soluble starch synthase I gene*)	Wheat	Overexpression	Increased thousand kernel weight under heat stress	Tian et al. (2018)
Triticum aestivum	*TaPEPKR2* (*phosphoenolpyruvate carboxylase kinase-related kinase*)	Wheat	Overexpression	Enhanced tolerance to heat and drought stress in wheat	Zang et al. (2018)
Triticum aestivum	TaHsfC2a-B (*heat shock factor*)	Wheat	Overexpression	Upregulation of heat protection genes with improved thermotolerance in transgenic wheat plants	Hu et al. (2017)

advancement in genome editing tools, genetic improvement of wheat against heat stress can be achieved speedily.

5 Conclusion

As a consequence of climate change, the global mean temperature is more likely to exceed 4 °C above pre-industrial levels, with more intense heat waves like to occur more often and may last longer. Heat stress is a major constraint for wheat production worldwide as it critically affects the development and reproductive period of the crop. Agronomical practices such as modification of crop calendars and the use of heat-tolerant cultivars can help mitigate the impact of heat stress in wheat. Though there is progress in the genetic improvement of heat stress tolerance in wheat using breeding and genetic engineering approaches, the complete molecular mechanism of heat stress tolerance in wheat is yet to emerge to exploit the full potential of modern genome editing techniques. The utilization of eco-friendly approaches like the application of biostimulants and beneficial microorganisms has proven to be a successful strategy in reducing the adverse effect of high temperature. However, more field studies are required to establish their use in the sustainable agriculture of wheat. An integrated approach of agronomic practices and biotechnological approaches can improve heat stress tolerance in wheat and make it more resilient to the impacts of future climate change.

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Potential of Microbes in Plant Stress Management

Plant–Microbe Interactions in Combating Abiotic Stresses

Namrata Konwar, Khomdram Niren Singh, and Diganta Narzary

Abstract

There is a significant decline in crop yield, quality of crops and soil fertility worldwide due to increased biotic and abiotic stresses that are either induced naturally or due to anthropogenic factors such as rapid urbanization and industrialization. Interaction of plants with several beneficiary microbes such as Plant Growth-Promoting Microbes (PGPM) comprising of actinomycetes, rhizospheric bacteria, and fungi help the plants to survive during abiotic stress conditions such as extreme temperatures (very low or very high temperature), flood or drought conditions, high salinity stress, heavy metal stress, nutrient deficiency and oxidative damages. Abiotic stresses harm plant growth, cellular morphology and physiology through obstruction in cellular pathways or gene regulation inside the cell. These microbes employ stress tolerance mechanisms in plants, such as the production of anti-oxidants, exopolysaccharides (EPS), phytohormones, osmolytes, formation of biofilms and siderophores, through various biosynthetic pathways. Here, in this chapter, we review recent findings in successful employment of microbial inoculation that induce abiotic stress tolerance in crop plants and study the role of bioactive metabolites liberated by microbes in association with plants which may help design strategies and tools for the development of improved and efficient microbial inoculant for optimizing plant growth in crop fields under adverse abiotic stressed conditions.

Keywords

Abiotic stress • Bioremediation • Mycoremediation • Plant growth-promoting microbe • Stress • Stress tolerant mechanism

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N. Konwar · K. N. Singh · D. Narzary (✉)
Microbiology & Molecular Systematics (MMS) Laboratory,
Department of Botany, Gauhati University, Guwahati, 781014,
Assam, India
e-mail: d_narzary@gauhati.ac.in

Abbreviations

ABA	Abscisic acid
ACC	1-Aminocyclopropane-1-carboxylate
APX	Ascorbate peroxidase
CAT	Catalase
CK	Cytokinin
DHAR	Dehydroascorbate reductase
EPS	Exopolysaccharides
GSH	Glutathione
GP	Guaiacol peroxidase
GPX	Glutathione peroxidase
GR	Glutathione reductase
HSP	Heat-shock proteins
IAA	Indole-3-acetic acid
JA	Jasmonic acid
MDA	Malondialdehyde
MDHAR	Monodehydroascorbate reductase
Pas	Polyamines
PGPB	Plant growth-promoting bacteria
PGPM	Plant growth-promoting microbes
PGPR	Plant growth-promoting rhizobacteria
POD	Peroxidase
ROS	Reactive oxygen species
MAP	Mitogen-activated proteins
SA	Salicylic acid
SOD	Superoxide dismutase

1 Introduction

There is a sharp decline in crop yield, quality of crops and soil fertility worldwide due to increased biotic and abiotic stresses. Biotic and abiotic stresses can be induced either naturally or by anthropogenic factors. Rapid urbanization and industrialization without sufficient regulations related to

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environmental health is a major cause of significant loss in crop yield, and this poses a potential threat to global food security (Egamberdieva et al. 2017a). Abiotic stress refers to the negative effects of non-living factors on living organisms in a given environment. The abiotic stress load can result from extreme temperatures (very low or very high temperature), flood or drought conditions, salinity, heavy metals, UV radiation, nutrient deficiency, or oxidative damage (Chaves et al. 2004). These stressful conditions adversely restrict plant growth and development (Fig. 1a) and show a negative effect on agricultural yield. High temperatures lead to an abrupt increase in the denaturation of cellular proteins in plants, which can lead to plant death, while low temperatures severely impair the metabolic processes within the plant cell by changing membrane properties and inhibiting various enzymatic reactions (Andreas et al. 2011).

Diverse spectra of epiphytic and endophytic microorganisms colonize the leaf zone (phyllosphere) or root zone (rhizosphere) of the host plants. They can either have a beneficial, neutral or adverse effect on the host plant (Bais et al. 2006). The rhizosphere consists of three different zones: endorhizosphere, rhizoplane and ectorhizosphere. The endorhizosphere comprises part of the cortex and endodermis in which microbes reside in the apoplastic regions, the medial zone which includes the root surface and mucilage is the rhizoplane, while the outermost zone which extends from the rhizoplane to the soil is the ectorhizosphere (Lynch 1990). The phyllosphere, on the other hand, refers to the entire above-ground part of the plants and can be divided into caulosphere (stems), phylloplane (leaves), anthosphere (flowers) and carposphere (fruits) (Cid et al. 2018).

In newly germinating seeds, the developing plant interacts with a variety of microbes by releasing certain bioactive organic compounds through the roots in the soil that aid the active development of microbial growth around the plant root. This phenomenon is known as the rhizospheric effect (Morgan et al. 2001). The rhizospheric microbes synthesize a variety of biologically active compounds like hormones, enzymes, and compatible solutes and also some anti-fungal or anti-bacterial metabolites that help increase disease resistance capacity in plants (Fig. 1b). These plant-microbial interactions play a vital role in plant growth, nutrient acquisition and development (Vorholt 2012; Sorty et al. 2016; Egamberdieva et al. 2017b). The species type and stage of development of plants also play a crucial role in determining the composition of the microbial communities in the rhizosphere (Broecking et al. 2008). The rhizospheric bacteria, also commonly known as plant growth-promoting rhizobacteria (PGPR), protect their host plant from various abiotic stresses, apart from various other beneficial effects such as providing nutrients, phytostimulation and biological control against pathogens (Kloepper et al. 1978). Under several stress conditions, PGPR promotes the growth and development of plants through various direct and indirect

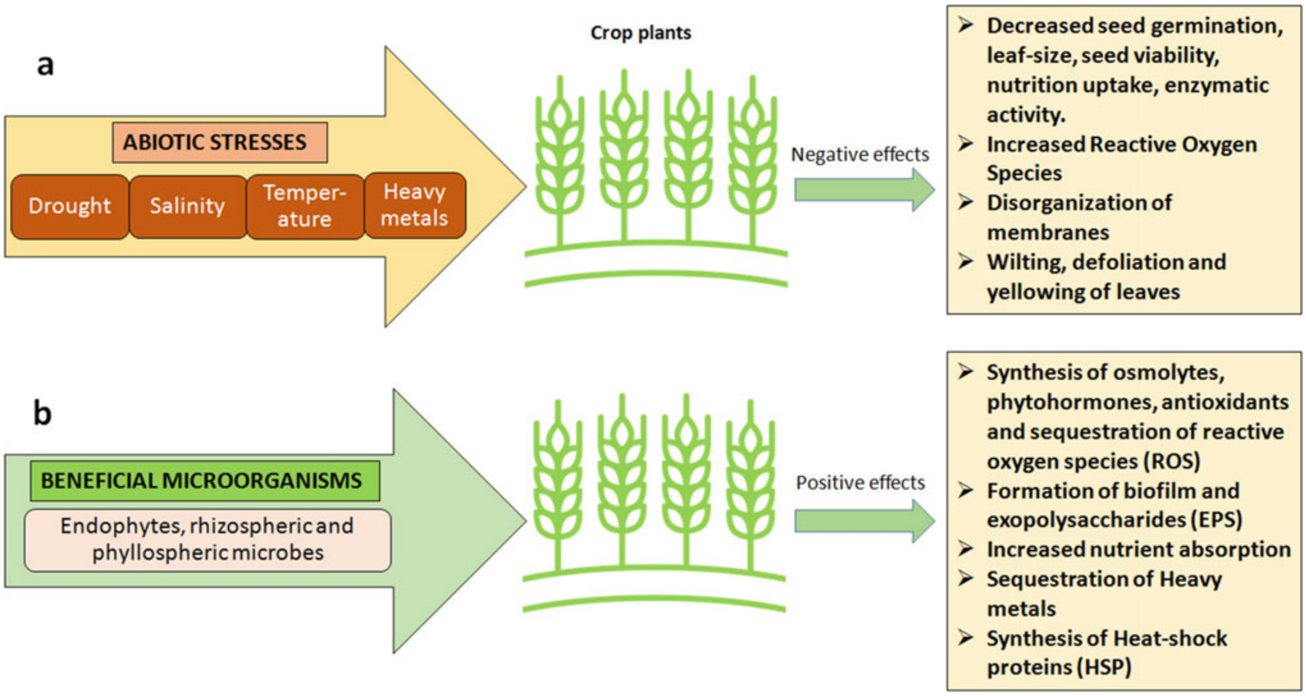

Fig. 1 Various effects of abiotic stress on crop plants. **a** Plants under abiotic stress. **b** Plants under the influence of microbes in abiotic stress

mechanisms that include: (1) production of phytohormones such as indole-3-acetic acid, cytokinins, abscisic acid and ethylene; (2) bacterial release of exopolysaccharides; (3) 1-Aminocyclopropane-1-carboxylic acid (ACC) deaminase; (4) induced systemic tolerance; (5) nitrogen fixation; (6) nutrient mobilization and (7) siderophore production (Farooq et al. 2009; Hayat et al. 2010; Porcel et al. 2014).

In the phyllosphere region, *Proteobacteria* together with *Bacteroides* and *Actinobacteria* are found to be dominant colonizers (Bodenhausen et al. 2013). Phyllospheric microbiota secretes various phyllosphere-specific metabolites that help to counter harsh climate by protecting against harmful UV rays, reactive oxygen species (ROS) and dehydration (Vorholt 2012). The phyllosphere microbiota penetrates the leaf cuticles through stomatal openings and wounds caused by lytic enzymes and osmotic pressure (Sivakumar et al. 2020). In this chapter, we will discuss the various abiotic stresses in plants such as drought stress, salinity stress, temperature stress and heavy metal stress in detail. We will also discuss the microbial interaction with plants and their possible role in abiotic stress mitigation.

2 Drought and Salinity Stress in Plants and Its Mitigation with the Help of Microbes

Drought stress in plants decreases seed germination capability, inhibits photosynthesis, creates membrane disintegration, and increases ROS such as hydroxyl radical ($OH\bullet$), singlet oxygen ($^1O_2$), hydrogen peroxide (H_2O_2), and superoxide anions ($O_2^{\cdot -}$) (Greenberg et al. 2008). They also trigger a decline in leaf water potential and stomatal opening, reduced leaf size, seed number, seed viability and suppresses root growth (Xu et al. 2016). Due to the lack of water in the soil, there is also an increased amount of electrically charged ions such as Na^+, Ca^{2+}, K^+, Cl^- and NO^{3-}, which may lead to ion toxicity and osmotic stress in plants (Daffonchio et al. 2014). Overall, drought stress harms agricultural productivity.

A low rate of stomatal conductance and transpiration occurs during salt stress which decreases the CO_2 concentration by disturbing the carbon metabolism within the plant cell (Geilfus et al. 2015). As a result of reduced intercellular CO_2 concentration inside the cell, oxidized $NADP^+$, which is the final electron (e^-) acceptor at Photosystem I during photosynthesis is depleted and the electrons are later transferred to O_2 for generating free radicals, like $O_2^{\cdot -}$ (Mehler 1951; Krieger-Liszkay 2005). It also triggers the synthesis of hydrogen peroxide (H_2O_2) in the peroxisome (Wingler et al. 2000) that further converts to ROS, like hydroxyl ($^{\cdot}OH$) radicals. Excessive accumulation of ROS compounds inside the plant cells seems to have harmful effects on the plant as they lead to metabolic disorders, oxidation of cellular proteins, destruction of nucleic acids, dis-organization of membranes, lipid peroxidation, and premature senescence (Moller et al. 2007). Synthesis of ROS mostly occurs in Photoelectron transport (PET) in the chloroplast, Respiratory electron (e^-) transport (RET) in mitochondria, peroxisomes, and NADPH oxidase in the plasma membrane by several enzymes like oxalate oxidase and amine oxidase (Hossain and Dietz 2016).

Antioxidant enzymes provide tolerance against salinity stress and lower oxidative stress by sequestering or scavenging the harmful ROS in the plant cells in several ways. Antioxidant enzymes use electron donors to dismutate $O_2^{\cdot -}$ into H_2O_2 and O_2, and ascorbic acid to convert H_2O_2 to H_2O and thiol-mediated pathways using nucleophiles such as GSH (Glutathione), thioredoxin (TRX) or glutaredoxins (GRX) for reducing H_2O_2 into H_2O (Hossain and Dietz 2016; Noctor et al. 2014).

Inadequate amount of rainfall, extensive irrigation and weathering of soil increases soil salinity. Salinity increases hyper-osmotic stress in plants which results in a water-deficit condition. However, some plants have in-built mechanisms to tolerate the deleterious effect of drought and salinity stress. Some drought-tolerant and salinity tolerant plants counteract the negative effects of salinity and drought by synthesizing and accumulating osmolytes such as proline or raffinose, which has the capability of stabilizing proteins and maintaining cell turgor pressure by osmotic adjustment and scavenging ROS generated due to stress responses. Some halophytes of Brassicaceae such as *Thellungiella halophila* combat salt stress by preventing the salts from entering the roots through membrane filtration, whereas *Lobularia maritima* accumulates and detoxifies salt by compartmentalization (Daffonchio et al. 2014). Other succulents in the *Aizoaceae, Cactaceae* and *Crassulaceae* families have permanently adaptive morphological features for combating drought and salinity stress, such as thick, fleshy swollen stems, reduced stomata, Crassulacean acid metabolism (CAM), waxy, hairy or spiny outer surface with reduced stomata (Daffonchio et al. 2014).

Most crops, however, do not have adaptive morphological or physiological properties sufficiently advanced to withstand adverse drought conditions. However, it is known that several root-associated microbes help plants to withstand drought and salinity stress by producing various plant growth regulators or plant hormones such as cytokinin (CK), gibberellin (GB), indole-3-acetic acid (IAA), salicylic acid (SA), abscisic acid (ABA) and jasmonic acid (JA), which improve plants' antioxidant potential, exopolysaccharide production and the accumulation of compatible osmolytes. This leads to an improvement in the photosynthetic capacity and membrane stability in plants, also promotes cell division and stomatal regulation, stimulates the growth of the root system, improves the root structure, improves the acquisition of water and nutrients and reduces damages within the plant cell caused by oxidative stress (Egamberdieva et al. 2017a). Thus, the application of such beneficial microbes having drought and salinity tolerance can impart drought and salinity stress resistance in plants and improve the quality of crops in agriculture.

2.1 Drought-Salinity Tolerant Bacteria and Their Mechanism of Tolerance

2.1.1 Production of Rhizoexudates and Exopolysaccharides (EPS) by Bacteria

Exopolysaccharides are high molecular weight carbohydrate molecules attached to the outer surface of many soil bacteria that have a slimy appearance. Drought tolerant bacteria produce EPS on their cell surface, which improve water retention in the rhizospheric region and protect the root surface from mechanical damage caused by the hardness of the soil under stress conditions (Kasim et al. 2016; Hasanuzzaman et al. 2019).

EPS production by PGPR strains during water-deficit conditions results in the development of an extensive root system, increased shoot growth and total dry weight in plants (Awad et al. 2012). EPS also binds excessive cations making it unavailable to plants under stress and offering resistance to salinity in plants (Vardharajula et al. 2011). It has been reported that application of EPS enriched *Azospirillum* strain AbV5, *Pseudomonas putida* strain GAP-P45, *Bacillus* sp., *Rhizobium leguminosarum* (LR-30), *Mesorhizobium ciceri* (CR-30 and CR39), *Phyllobacterium brassicacearum* strain STM196, *Trichoderma* sp., *Sinorhizobium* sp., *Funneliformis* sp., *Rhizophagus* sp., *Claroideoglomus* sp., *Kocuria* sp., *Glomus* sp., *Suillus* sp., *Paecilomyces* sp. in the field provides drought and salinity stress resistance in several plants (Duddridge et al. 1980; Vardharajula et al. 2011; Shukla et al. 2012; Bano et al. 2013; Bresson et al. 2013; Kasim et al. 2013; Armada et al. 2014; Hussain et al. 2014; Kang et al. 2014; Hashem et al. 2015; Sandhya and Ali 2015; Tiwari et al. 2015; Oliveira et al. 2017; Li et al. 2020; Pasbani et al. 2020).

Under water surplus conditions such as flooding, the plant roots become hypoxic or oxygen-limited. This leads to several harmful effects on plant growth and development such as reduced photosynthesis, excess production of free radicals, phytotoxin accumulation, and membrane dis-organization causing chlorosis, necrosis, and ultimately plant death (Najeeb et al. 2015; Voesenek et al. 2015). In low oxygen conditions, plants produce increased amounts of ACC synthase which ultimately converts to ethylene (Nascimento et al. 2012). Certain ACC deaminase-producing bacteria have been reported that can help terrestrial plants tolerate the adverse effects of waterlogging by lowering ethylene levels and promoting plant growth. For example, inoculation of *Pseudomonas* sp. UW4 in *Cucumis sativa* and *Brassica napus* has shown elevated shoot and root growth during water-logging stress conditions (Farwell et al. 2007; Ali and Kim 2018).

2.1.2 Phytohormone Production by PGPR Strains

Many PGPR strains such as *Azospirillum, Acetobacter, Alcaligenes, Bradyrhizobium, Enterobacter, Pseudomonas, Rhizobium* and *Xanthomonas* are known to produce plant growth regulators or plant hormones such as auxins, cytokinin, salicylic acid, jasmonic acid and gibberellic acid which promotes plant growth (Xiong et al. 2021). PGPR also helps alleviate the negative effects of drought and salinity stress by inducing vascular tissue differentiation, adventitious and lateral root proliferation, and improving root architecture under abiotic stresses (Patten and Glick 1996; Vessey 2003; Verbon and Liberman 2016). It has been reported that cucumber plants treated with the PGPR strains (*Burkholderia cepacia* SE4, *Promicromonospora* sp. SE188, and *Acinetobacter calcoaceticus* SE370), and soybean plants treated with *Pseudomonas putida* H-2-3 showed an increased amount of endogenous gibberellic acid production under drought and salinity stress when compared to the control one (Kang et al. 2014).

In normal conditions, the production of ethylene in plants helps in fruit ripening and also regulates growth and senescence, however during stress conditions it increases abruptly which has a deleterious effect on the germination of seeds and root proliferation (Iqbal et al. 2017). The increased amount of ethylene in plant tissues also result in stunted root and shoot growth in plants. Many rhizobacteria and a wide range of soil microbes have been shown to produce ACC deaminase that can hydrolyze ACC enzyme which is the precursor for ethylene production (C_2H_4) (Bal et al. 2013; Khan et al. 2021). Therefore, employing ACC deaminase-producing rhizobacteria in crop plants can help lessen excess ethylene production by hydrolysis of ACC enzyme thus protecting the plant from its negative effects like loss of chlorophyll, stem shortening, leaf abscission and seed dormancy (Khan et al. 2021). Treatment of *Pisum* sp. with potential ACC deaminase-producing bacterial strains (*Variovorax paradoxus* 5C-2 and *Pseudomonas* spp.), and pepper plant (*Piper nigrum*) inoculated with *Bacillus licheniformis* K11 showed reduced shoot ethylene production, improved nitrogen content in seed, improved nodulation, and improved water use efficiency under drought and salinity stress (Belimov et al. 2009; Lim and Kim 2013; Zahir et al. 2009). In another study, *Azospirillum brasilense* and *Phyllobacterium brassicacearum* strain STM 196 was found to alleviate ABA content in *Arabidopsis thaliana* which improved the biomass content and water utilization efficiency during drought and salinity stress (Bresson et al. 2013; Cohen et al. 2015).

2.1.3 Osmolyte Production by Bacteria

PGPRs associated with rhizospheric soil assist plants under salinity stress by enhancing osmolyte accumulation. Osmolytes are inert solute that accumulates inside the plant cell to maintain homeostasis within the cell when exposed to various abiotic stress due to heat, low temperature, osmotic shock, drought, heavy metals, salinity, etc. (Jogawat 2019). Osmolytes include various biochemical compounds such as sugars, polyamines, secondary metabolites, amino acids and polyols. During stress conditions, the biosynthesis of commonly occurring osmolytes that increases inside the plant is —mannitol, raffinose, stachyose, glycine betaine, trehalose and proline (Abdelaal et al. 2021). They protect the plant cells by neutralizing and detoxifying the accumulated inorganic salts and thus protect the cells from oxidative damages (Burg et al. 2008).

PGPR employs several mechanisms to combat osmotic stress during salinity stress conditions such as by endogenous accumulation of intracellular osmolytes in bacterial cells (Qurashi et al. 2011). Bacteria living in extreme halophilic environments induce the expression of proline biosynthesis genes *proH, proJ* and *proA* that help in survival in high saline conditions (Saum and Müller 2007). In genetically modified *Arabidopsis thaliana* with introgression of *proBA* genes from *Bacillus subtilis* enhanced the proline synthesis in the plant helping it to overcome the salt stress (Chen et al. 2007). Likewise, *Capsicum annum* inoculated with *Bacillus fortis* SSB21 increased the biosynthesis of proline and upregulation of stress-related genes *CAPIP2, CaKR1, CaOSM1* and *CAChi2* to overcome saline conditions (Yasin et al. 2018). Similarly, when *Oceanobacillus profundus* Pmt2 and *Staphylococcus saprophyticus* ST1 are inoculated to *Lens esculenta* var. Masoor 93 plants growing in salt stress conditions, there was an improvement in growth parameters and endogenous osmolytes accumulation in the plants (Qurashi et al. 2011). However, during exposure to high salt conditions, plants mostly prefer to uptake osmolytes liberated by salt-tolerant–PGPR, instead of synthesizing *de-novo* (Zhu et al. 2015; Fatima et al. 2019). Accumulation of osmolytes in cells under osmotic and water stresses makes the osmotic potential inside the cell negative that causes endosmosis of water which helps in maintaining the turgor pressure, ion homeostasis and integrity of cells (Sharma et al. 2019). It was observed that salt-tolerant PGPR strains like *Azospirillum* spp., *Bacillus* sp. through accumulation of proline, glycine betaine, and trehalose by several biosynthetic pathways supports the growth and development of rice and maize plants in both drought and salinity stress conditions (Rodríguez-Salazar et al. 2009; Vardharajula et al. 2011).

Co-inoculation of the PGPR strains, *Rhizobium* and *Pseudomonas* was found useful to overcome the baneful effects of drought and facilitate plant growth under saline conditions in *Zea mays* (Bano and Fatima 2009). Upon exposure to drought and salinity stress, microbial inoculation trigger the production of osmolytes and their accumulation in the plant cell which is regulated by various factors like nutrient availability in the rhizosphere, duration of osmotic stress, and several cell signaling processes such as ABA signaling, calcium signaling, ROS-MAP kinase, hydrogen sulphide (H_2S), nitric oxide (NO), polyamines (PAs), phytochromes, as well as downstream gene regulation factors, particularly some of the transcription factors (TFs) (DeFalco et al. 2010; Golldack et al. 2014; Jalmi and Sinha 2015; He et al. 2018; Cha-um et al. 2019). Plants inoculated with osmolyte producing PGPR have shown a significant increase in accumulation of proline content in shoot under induced drought and salinity stress and further aids in balancing cytosolic acidity, decrease in lipid peroxidation by sequestering ROS, and helps in stabilization of membrane proteins (Bharti et al. 2016; Oosten Van et al. 2017; Chandra et al. 2018a, b).

The enhanced production of free amino acids and soluble sugar content in maize plants under drought stress were reported when PGPR strains such as *Proteus penneri* Pp1, *Pseudomonas aeruginosa* Pa2, *Alcaligenes faecalis* AF3, *Azospirillum lipoferum* and *Bacillus* sp. were inoculated, thereby helping plants in the regulation of cellular physiology and restoring cell turgidity under drought and salt stress (Bano et al. 2013; Kaushal and Wani 2016). Bacterial strains such as *Bacillus megaterium, Enterobacter* sp. and *Bacillus thuringiensis* can increase the accumulation of shoot proline and the potassium ion (K^+) concentration, which decreases the stomatal conductivity and thus increases the resistance of plants to drought stress (Armanda et al. 2014). Rascovan et al. (2016) recovered a variety of microorganisms such as *Pseudomonas, Paraburkholderia* and *Pantoea* associated with wheat and soybean roots which have phosphorous solubilization, N_2 fixation, IAA and ACC deaminase production properties. Inoculation of *Arabidopsis* sp. with *Azospirilum brasilense* sp245, and *Brassica oxyrrhiza* with *Pseudomonas libanensis* TR1 and *Pseudomonas reactans* Ph3R3 showed increased proline levels and relative water content in leaves and decreased stomatal conductance and malondialdehyde in leaves (Cohen et al. 2015; Ma et al. 2016a, b).

2.1.4 Antioxidant Enzymes Production

Antioxidant enzymes produced by plants can also protect them from various stress-related damages. Plants inoculated with PGPR have been reported to survive abiotic stress conditions through antioxidant enzymes production (Radhakrishnan and Baek 2017). Enhancement of antioxidant production becomes significantly crucial under abiotic stress in plants as they provide the catalysis ability during ROS scavenging mechanism and aids in the detoxification mechanism in plant cells (Singh et al. 2016). There are several reports which state that PGPR-associated plants showed improved drought resistance by antioxidant enzyme production. Inoculation of PGPR strains such as *Bacillus cereus* Pb25 and *Azospirillum* sp. showed an increased promotion of plant growth and significantly decreased oxidative stress markers such as plant malondialdehyde (MDA), lipoxygenase and xanthine oxidase under salinity stress through the production of antioxidant enzymes such as superoxide dismutase (SOD), ascorbate peroxidase (APX), glutathione reductase (GR) and peroxidase (POD) (Vardharajula et al. 2011; Damodaran et al. 2014; Thiombiano et al. 2014; Ma et al. 2015; Islam et al. 2014; Li et al. 2020).

2.2 Drought-Salinity Tolerant Fungi and Their Mechanism of Tolerance

Fungal symbionts are generally seen associated with almost every plant where they express a wide range of relationships with their hosts including symbiotic, mutualistic, commensalism or parasitic behaviour. In the rhizosphere, plant root secretes several root exudates, chiefly strigolactones that attract many beneficiaries and mutualistic fungal interactions such as arbuscular mycorrhizal and endophytic fungal associations (Breuillin et al. 2010; Khan et al. 2021). It is seen that mutualistic fungi can increase plant growth, reproductive success and confer biotic and abiotic tolerance to their host plants.

2.2.1 Role of Mutualistic Fungi in Drought Stress

A mutualistic fungal association such as arbuscular mycorrhizal fungi (AMF) with plants are seen to increase water uptake, osmotic balance, photosynthetic rate, stimulate antioxidant properties, maintain ionic homeostasis to protect against oxidative damage, and trigger plant growth during salinity stress (Sheng et al. 2011; Auge et al. 2014; Hidri et al. 2016; Chen et al. 2017; Khalloufi et al. 2017). A meta-analysis experiment conducted by Dastogeer et al. (2020) shows that most of the photosynthetic parameters increased more in AMF-treated plants than in non-AMF-treated plants under salinity stress with improvements in water status in plant cells, enlarged leaf area, higher stomatal conductance which further helps in the assimilation of carbon dioxide (Wu et al. 2015; Chen et al. 2017). Mycorrhizal association in plants significantly reduces the degradation of photosystem II reaction core proteins (D1 and D2) under salinity stress and thus helps in the proper functioning of photosystem II (Porcel et al. 2016; Chen et al. 2017; Hu et al. 2017). AMF is also seen to increase the accumulation of inorganic ions like Potassium, Calcium and elevate biomass under salinity stress (Pan et al. 2020). It has been observed that AMF inoculation increased plant growth traits more efficiently in dicots than in monocots (Weishampel and Bedford 2006). A fungus *Piriformis indica* colonizes the roots of many plants and fosters growth and boosts seed and biomass production by improving the absorption of nitrates and phosphate and confers resistance to abiotic stress (Waller et al. 2005). *Neotyphodium* spp. are found to enhance drought tolerance to its host plants such as —*Festuca pratensis*, Perennial Ryegrass and *Festuca arizonica* (Barker et al. 1997; Morse et al. 2002). *Curvularia protuberata* offers heat-drought resistance to its host plants like *Dichanthelium lanuginosum, Leymus mollis, Oryza sativa, Lycopersicon esculentum, Triticum aestivum* and *Citrullus lanatus* (Rodriguez et al. 2008). In *Oryza sativa*, mycorrhizae compartmentalize the sodium ions (Na^+) in the vacuoles by upregulating *OsNHX3* (sodium/hydrogen exchanger), and it also enhances the removal of the cytosolic Na^+ to the apoplastic channel through the increased expression of *OsSOS1* and *OsHKT2* (Porcel et al. 2016).

The increased phosphorous (P) uptake in AMF-inoculated plants aids in maintaining membrane integrity by lessening ionic leakage, restricting toxic ions with vacuoles which consequently helps to combat with adverse effects of drought and salinity (Rinaldelli and Mancuso 1996; Evelin et al. 2012). It is seen that increased P absorption in AMF-colonized plants is due to the secretion of acid and alkaline phosphatase by fungal hyphae that release P in easily absorbable form by plants by encoding high-affinity phosphate transporter genes (*GvPT, GiPT,* and *GmosPT*), which can release P even at low concentrations (Nacoon et al. 2020).

2.2.2 Antioxidant Production by Fungi

During oxidative stress conditions, the levels of oxidative stress markers such as malondialdehyde (MDA), lipoxygenase and xanthine oxidase in plants are seen to rise (Asada and Takahashi 1987; Sharma et al. 2012; Ozgur et al. 2013; Bose et al. 2014; Kumar et al. 2017). However, it has been reported that AMF-colonized plants show a notable decrease in oxidative stress markers such as MDA levels, lower levels of electrical leakage and high levels of antioxidant enzymes (POD and SOD) production, which indicates less oxidative stress compared to non-AMF colonized plants (Dastogeer et al. 2020).

Endophytes, a group of microorganisms (often bacteria or fungi) that grow within the plant tissues, have a diverse range of relationships (obligate or facultative) with the host plant (Petrini 1991). They penetrate inside the host by producing cell wall degrading enzymes and colonize inside the roots, stems and flowers of the plant (De Vries et al. 2001; Lata et al. 2018). They confer abiotic stress tolerance by synthesizing anti-stress biochemicals to avoid or mitigate abiotic stresses (Schulz et al. 1999). Endophytic fungi like *Phoma glomerata* and *Penicillium* sp. are reported to significantly increase plant biomass, related growth parameters, assimilation of essential nutrients such as potassium, calcium, magnesium, and reduced the sodium toxicity in cucumber plants under NaCl and polyethylene glycol (PEG)-induced salinity and drought stresses (Waqas et al. 2012).

3 Role of Microbes in Combating Temperature Stress in Plants

Excessive heat stress and cold conditions—both act as significant abiotic stress in plant growth and productivity. The major effects of temperature stress are changes in plasma membrane components (extreme heat increases membrane-fluidity while extreme cold makes them more rigid), reduced water content (through excessive transpiration), impaired photosynthesis activity and enzyme functioning, cell division, and plant growth (Kumar et al. 2018). Plants employ various mechanisms to overcome heat stress which includes the production of phytohormones such as jasmonic acid, heat shock proteins, accumulation of enzymes and osmolytes. Heat-shock proteins (HSP20, HSP60, HSP70, HSP90, HSP100) and ROS scavenging enzymes (ascorbate peroxidase and catalase) are major functional proteins that enable the plant to tolerate heat stress (Kotak et al. 2007; Qu et al. 2013; Singh et al. 2016). But most crop plants are unable to tolerate extreme heat stress and cold shock. The use of microbes can help to reduce the adverse effects of heat and cold stress in plants.

Some microbes have intrinsic properties to tolerate heat and cold stress that can prove to be effective in protecting membrane proteins, and nucleic acid of the host plant to live under such extreme conditions. Based on growth, microbes are divided into two groups, psychrophilic and psychrotrophic microorganisms. The growth of psychrophilic microbe lies maximum at or below 15 °C, while psychotropic microbes grow at above 15 °C. The bacterial strains *Pseudomonas cedrina, Brevundimonas terrae, Arthrobacter nicotianae* that can adapt to low temperature showed plant growth-promoting abilities under cold stress (Yadav et al. 2014). In seeds of *Solanum lycopersicum*, endophytic bacteria *Pseudomonas vancouverensis* OB155-gfp and *Pseudomonas frederiksbergensis* OS261-gfp protect the plant cells against cold/chilling stress through upregulation of genes like *CBFs*, *COR15a*, *COR78*, *LeCBF1*, *LeCBF3* and *TomLOX* that reduce membrane damage and ROS level (Subramanian et al. 2015). Association of the fungus *Curvularia protuberata* and its mycovirus, *Curvularia thermal tolerance virus* (CThTV) with a grass species *Dichanthelium lanuginosum* enabled the plant to survive soil temperatures ranging between 38 and 65 °C in Yellowstone National Park (Redman et al. 2002). An endophytic fungus, *Burkholderia phytofirmans* PsJN that colonizes the roots of *Arabidopsis thaliana* induces the accumulation of pigments in the cold response pathway through downregulation of *rbcL* and *COR78* genes (Su et al. 2015). Thus, the application of these microbes in crop plants may be beneficial in upregulating plant growth and improving plant resistance capacity against extreme temperatures.

4 Microbe-Mediated Heavy Metal Stress Tolerance in Plants

Several anthropogenic activities such as mining, modern agricultural practices, fertilizer applications, smelting and sewage disposal, unplanned human habitations and rapid industrialization have prolonged detrimental effects on our environment (Aydinalp and Marinova 2009), and these lead to the heavy metal pollution in soil, water and air. Plants absorb these heavy metals, high concentrations of which often affect plant growth and survival; and may also have detrimental effects on human health as they ultimately enter into the food chain (Zhuang et al. 2014). Some of these metals viz. Zn, Cu, Mo, Co and Ni are essential micro-nutrients that are needed in trace amounts as they function as co-factors for various enzymatic reactions. But metals like Cd and Pb are present in pesticides having no distinctive advantageous role in plant growth and become toxic if their concentration exceeds over a certain limit (Gough et al. 1979; Adriano 1986; Gücel et al. 2009; Ashraf et al. 2010; Sharma and Ali 2011; Gill and Tuteja 2011; Ali et al. 2011, 2012, 2014, 2016, 2017).

Some metals (Fe, Ni, Mn, Cu, Sn, Co, As, Pb, Se, Cd, Hg, Cr, Al, Zn and Be) can cause morphological abnormalities and metabolic disorders that often lead to yield reduction in plants to a great extent when their concentration rises beyond supra-optimal values (Xiong et al. 2014; Amari et al. 2017). These abnormalities also trigger the accumulation of ROS, e.g. superoxide anion radical ($O_2^{\cdot -}$), H_2O_2 and hydroxyl radical (OH^-), resulting in disruption of the redox homeostasis of cells (Gill and Tuteja 2010; Pourrut et al. 2011; Ibrahim et al. 2015; Shahid et al. 2015).

Many plant-associated microbes have been shown to reduce metal accumulation in plant tissues and improve microbe-assisted metal tolerance against a metalliferous environment by reducing the bioavailability of metals in the soil through various mechanisms (Table 1) (Tiwari and Lata 2018). Plant-associated microbes, namely, bacteria and fungi, are known to exhibit plant-growth-promoting traits under heavy metal stress in plants via several direct and indirect mechanisms such as the formation of biofilms, siderophores, exopolysaccharides and phytohormone production (Tiwari et al. 2012, 2015). Some microbes can alter the bioavailability of metals from the soil by chelation, acidification and precipitation. Heavy metal tolerant (HMT) microorganisms release several organic acids like gluconic acid, oxalic acid, malic acid, which lower the pH of the soil and aids in the sequestration of metal ions (Ullah et al. 2015; Mishra et al. 2017).

HMT microorganisms perform various mechanisms to avoid heavy metal stress including (a) translocation of metals across the cytoplasmic membrane, (b) bio-absorption and bioaccumulation of metals to the cell walls, (c) metal entrapment in the extracellular capsules, (d) heavy metals precipitation and (e) metal detoxification via oxidation–reduction mechanisms (Zubair et al. 2016). The use of such HMT microbes alone or in a consortium can serve as an effective microbial remediation in plants growing in polluted areas (Mishra et al. 2017).

4.1 Bacteria-Mediated HM Stress Tolerance in Plants

Some plant growth-promoting microbes (PGPM) also assist plants to tolerate and/or accumulate heavy metals directly or indirectly. The major processes that are involved in the direct uptake process by plants under the influence of PGPM consist of solubilization, bioavailability and accumulation of heavy metals (Vymazal and Brezinová 2016). Siderophore formation is an important mechanism through which plant-associated microbes aid in the removal of heavy metals from metal-contaminated soil. Siderophore is an organic compound with a low molecular weight that chelates heavy metals and increases their availability in the rhizosphere. Siderophore primarily chelates with ferric iron (Fe^{3+}), but also has a high affinity with other metals and form complexes and undergo exocytosis and thus help in Fe absorption (Saha et al. 2016; Złoch et al. 2016). It has been found that rhizospheric bacteria are more potent in the production of siderophore than endophytic bacteria (Ma et al. 2016a, b; Złoch et al. 2016). PGPM also secrete low molecular weight organic acids such as gluconic, oxalic and citric acids which are effective in mobilization of heavy metals and play an effective role in phytoremediation (Janoušková et al. 2006; Ullah et al. 2015). Mobility of heavy metals such as As, Cr, Hg and Se is highly influenced by oxidation or reduction reaction as some metals are more soluble in their lower oxidation state than the higher oxidation state (Bolan et al. 2014).

Bio-methylation of heavy metals such as Pb, Hg, Se, As and Sn is another method for mobilization of heavy metals which involves the transfer of methyl group through bacterial activity (Bolan et al. 2014). Some bacteria and fungi synthesize a group of metal-binding cysteine-rich peptides (enzymes), i.e. phytochelatins (PCs) in response to heavy metal stress which confers abiotic stress tolerance to their host plants growing in a metalliferous environment (Gadd 2010, 2014). Sulphate-reducing bacteria reduce the bioavailability of sulphate-containing heavy metals in plants by converting toxic metals into insoluble forms of metal sulphides (Khan et al. 2021).

Heavy-metal-tolerant PGPR including *Bacillus, Pseudomonas, Streptomyces* and *Methylobacterium* have shown the potential to improve the growth and production of crops by reducing the detrimental effects of heavy metals during heavy metal stress (Table 1) (Sessitsch et al. 2013). Bacterial species like *Bacillus cereus, Bradyrhizobium* sp. 750, *Curtobacterium* sp. NM1R1, *Ochrobactrum cytisi*, *Pseudomonas azotoformans* strain ASS1, *P. moraviensis* and *P. putida* reduces detrimental effects during heavy metal stress caused by Cu, Cd, Pb, Ni, Zn, Hg and As in many plant species (Dary et al. 2010; Pandey et al. 2013; Kamran et al. 2015; Hassan et al. 2017; Román-Ponce et al. 2017). *Pseudomonas* and *Gigaspora* aid in the tolerance of heavy metals directly through upregulation of plant ethylene levels by increasing ACC enzyme levels (Friesen et al. 2011).

The use of microbes with some additives in the plants grown in heavy metal polluted soil is more beneficial than without additives (Mishra et al. 2017), for example, the addition of thiosulfate with metal-tolerant microbes elevates the mobilization and uptake of As and Hg in *Brassica juncea* and *Lupinus albus,* stimulating bioavailability and phytoextraction and can be used in the biocontrol and bioremediation process simultaneously in polluted soils (Franchi et al. 2017; Tiwari and Lata 2018).

Like rhizospheric bacteria, some of the endophytic bacteria also have metal resistance properties and promote plant growth under metal stress by directly providing mineral nutrient and plant growth regulator enzymes (Table 1) (Sziderics et al. 2007; Kafle et al. 2018). Some of the endophytic microbes can synthesize nitrogenase enzymes under the metals stress and poor nitrogen conditions by providing abundant nitrogen to the associated plants. In *Populus trichocarpa* and *Salix sitchensis*, four bacterial endophytic genera *Burkholderia, Rahnella, Sphingomonas,* and *Acinetobacter* were isolated and found to have the ability to synthesize nitrogenase enzyme to fix atmospheric nitrogen (N_2) which promotes plant growth during heavy metal stress (Kafle et al. 2018). Alleviation of certain stress hormones also confers heavy metal tolerance in plants such as increase in the levels of ACC deaminase by bacteria *Pseudomonas* and *Gigaspora* promote heavy metal tolerance directly through the regulation of plant ethylene levels (Friesen et al. 2011; Ghosh et al. 2019).

In recent times, the use of genetically transformed PGPR has been suggested for the elimination of toxic metals as

Table 1 Different abiotic stress, microbes used, and the induced stress tolerance mechanisms developed in plants due to microbial interaction

Abiotic stress in plants	Microbes used	Microbially induced tolerance mechanism in plants	References
Drought and salinity stress in maize (*Zea mays*)	*Glomus versiforme, Azospirillum lipoferum, Bacillus* sp., *Kocuria rhizophila, Bacillus* sp. and *Enterobacter* sp.	Increased accumulation of proline, sugars, free amino acids and decrease electrolyte leakage and facilitate water uptake. It also reduces the activity of antioxidants enzyme (catalase, glutathione peroxidase) and regulates plant hormones (IAA, salicylic acid, and ABA levels)	Vardharajula et al. (2011), Bano et al. (2013), Ma et al. (2015), Begum et al. (2019), Li et al. (2020)
Drought and salinity stress in rice (*Oryza sativa*)	*Azospirillum* sp., *Trichoderma harzianum*	Increased photosynthetic activity and promote root growth independent of water status and delay drought response	Ruíz-Sánchez et al. (2011), Shukla et al. (2012)
Drought and Salinity stress in *Pinus halepensis*	*Pseudomas fluorescens*	Increased photosynthetic activity	Rincón et al. (2008)
Drought stress in Soybean (*Glycine max*)	*Pseudomonas putida* H-2-3	Regulate plant hormone levels and antioxidants by declining superoxide dismutase, flavonoids, and radical scavenging activity	Kang et al. (2014)
Drought and salinity stress in Wheat (*Triticum aestivum*)	*Rhizophagus intraradices, Funneliformis mosseae, F. geosporum, Bacillus amyloliquefaciens* 5113, *Azospirillum brasilense* NO40, *Rhizobium leguminosarum* (LR-30), *R. phaseoli* (MR-2) and *Mesorhizobium ciceri* (CR-30 and CR39)	Increased pigment production; production of catalase, exopolysaccharide, and IAA; and improved homeostasis, growth, and drought tolerance index	Kasim et al. (2013), Hussain et al. (2014), Mathur et al. (2018)
Drought stress in *Lavandula dentate*	*Bacillus thuringiensis*	Improved physiological and metabolic activities and reduced ROS elements	Armada et al. (2014)
Drought stress in *Cicer arietinum* L	*Pseudomonas putida* MTCC5279, *Bacillus subtilis, Bacillus thuringiensis, Bacillus megaterium*	Osmolyte accumulation and scavenge of ROS and enhanced transcription of stress-responsive gene expression	Tiwari et al. (2015), Khan et al. (2019)
Drought stress in Lettuce (*Lactuca sativa*)	*Azospirillum* sp.	Promote growth, biomass, pigments, chlorophyll, chroma and antioxidant capacity	Fasciglione et al. (2015)
Drought stress in *Arabidopsis*	*Azospirilum Brasilense* Sp 245, *Phyllobacterium brassicacearum* strain STM196	Decreased Malonialdehyde and increased proline, water levels, and water use efficiency	Bresson et al. (2013), Cohen et al. (2015)
Drought stress in *Brassica oxyrrhina*	*Pseudomonas libanensis* TR1, *Pseudomonas reactans* Ph3R3	Increased plant growth, leaf relative water and pigment content	Ma et al. (2016a, b)
Drought stress in *Medicago truncatula*	*Sinorhizobium medicae*	Improved root architecture and acquisition of nutrients	Staudinger et al. (2016)
Drought stress in *Pinus sylvestris*	*Suilus* sp.	Facilitate nutrients and water through vascular tissues	Duddridge et al. (1980)
Salinity stress in *Panicum turgidum*	*Funneliformis mosseae, Rhizophagus intraradices, Claroideoglomus etunicatum*	Enhanced chlorophyll content, nutrient uptake, and antioxidant enzymes like SOD, POD, CAT and GR	Hashem et al. (2015)
Salinity stress in *Pisum Sativum* L	*Rhizoglomus intraradices, Funneliformis mosseae, Rhizoglomus fasciculatum* and *Gigaspora* sp.	Accumulation of compatible solutes; decrease cellular-membrane leakage of electrolyte	Parihar et al. (2020)
High-temperature stress in *Triticum aestivum*	*Pseudomonas brassicacearum, Bacillus thuringiensis, Bacillus subtilis, Bacillus velezensis* 5113	Secretion of Heat-shock proteins, increase the production of compatible solutes and phytohormones	Ashraf et al. (2019a, b), Abd El-Daim et al. (2019)
High-temperature stress in Tomato (*Lycopersicon esculentum*)	*Bacillus cereus*	Enhanced biofilm formation, reducing ABA levels, and increased HSP levels	Khan et al. (2019)

(continued)

Table 1 (continued)

Abiotic stress in plants	Microbes used	Microbially induced tolerance mechanism in plants	References
Low-temperature stress in *Cucumis sativus* L. cv. *Zhongnong No.* 26	*Rhizophagus irregularis*	Improved phosphorus (P) uptake, induced of Pi transporter gene	Ma et al. (2015)
Low-temperature stress in *Solanum melongena L*	*Funneliformis mosseae, Claroideoglomus etunicatum*, *Rhizophagus irregularis*, and *Diversispora versiformis*	Improved photochemical reactions, antioxidant defence systems, and reduced membrane damages	Pasbani et al. (2020)
Low-temperature stress in *Solanum lycopersicum* L. cv. *Zongza* 9	*Funneliformis mosseae*	Reduced levels of MDA, H_2O_2 and $O^{-\ 2}$, induced activities of antioxidant enzymes APX, MDHAR, GR, and DHAR, expression levels	Liu et al. (2015)
Nutrient deficiency in *Nicotiana tabacum* L. cv. *Petit Havanna*	*Rhizophagus intraradices*	Promote phosphorous (P) absorption	Del-Saz et al. (2017)
Nutrient deficiency in *Sorghum bicolor* L	*Glomus intraradices*, *Glomus mosseae*, *Glomus aggregatum*, *Glomus etunicatum*	Promotion of Iron (Fe) absorption, increase in siderophore, upregulation of SbDMAS2 (deoxymugineic acid synthase 2), SbNAS2 (nicotianamine synthase 2), and SbYS1 (Fe-phytosiderophore transporter yellow stripe), increased S-containing antioxidant metabolites (Methionine, Cysteine, and GSH) and enzymes (CAT, SOD and GR)	Prity et al. (2020)
Nutrient deficiency in *Poncirus trifoliata*	*Glomus versiforme*	Promote growth, iron (Fe) absorption, and increase in Phenylalanine ammonia-lyase activity (PAL) enzyme activity	Li et al. (2015)
Heavy metal stress in *Helianthus annuus* L	*Funneliformis mosseae*, *Rhizophagus intraradices*, *Claroideoglomus etunicatum*	Provide tolerance against heavy metals such as Cd, Increase in shoot/root biomass, accumulation of pigments, antioxidant enzymes such as SOD, POD, CAT, GPX and GR	Abd Allah et al. (2015)
Heavy metal stress in *Robinia pseudoacacia* L	*Funneliformis mosseae*, *Rhizophagus intraradices*	Increased metal tolerance against Lead (Pb), Higher gas exchange capacity, enhanced superoxide dismutase (SOD), ascorbate peroxidases (APX) and glutathione peroxidase (GPX)	Yang et al. (2014)
Heavy metal stress in *Triticum aestivum*	*Bacillus cereus*, *Pseudomonas moraviensis*, *Enterobacter ludwigii*, *Klebsiella pneumonia*	Increased metal tolerance against Hg, Cu, Cr, Co, Cd, Ni, Mn and Pb	Hassan et al. (2017); Gontia-Mishra et al. (2016)
Heavy metal stress in *Brassica nigra*	*Microbacterium* sp. CE3R2, *Curtobacterium* sp. NM1R1, *Kocuria* sp. CRB15	Increased metal tolerance against Zn, Pb, Cu and As	Román-Ponce et al. (2017), Hansda and Kumar (2017)
Heavy metal stress in *Brassica napus*	*Bacteroidetes bacterium*, *Pseudomonas fluorescens*	Increased metal tolerance against Cd, Cu, Pb and Zn	Dabrowska et al. (2017)
Heavy metal stress in *Oryza sativa*	*Klebsiella pneumoniae*	Increased metal tolerance against Cd	Pramanik et al. (2017)
Heavy metal stress in *Panicum virgatum*	*Azospirillum* sp.	Increased metal tolerance against Pb and Cd	Arora et al. (2016)
Heavy metal stress in *Zea mays*	*Enterobacter* sp., *Leifsonia* sp.	Increased metal tolerance against Cd	Ahmad et al. (2015)

they serve as a novel phytobacterial strategy to mitigate heavy metal stress (Ullah et al. 2015). Since genetically transformed bacteria possess one or more encoding genes for remediation of heavy metals, therefore they can perform better as metal chelators, metal homeostasis, transporters, metal uptake regulators and can produce more efficient biodegradative enzymes (Singh et al. 2011; Tiwari and Lata 2018). In PGPR strains like *Pseudomonas putida, Mesorhizobium huakuii, Enterobacter cloacae*, and *Ralstonia eutropha*, the genes coding for phytochelatin synthase, metallothionein, ACC deaminase have been modified for enhanced bio-remedial activity against most of the heavy metals such as—Cd, Cu, Zn, As, Hg and Ag. Thus, these strains can be employed to confer metallic stress in economically beneficial plants to improve yield and crop health (Valls et al. 2000; Nie et al. 2002; Sriprang et al. 2002, 2003; Wu et al. 2006; Ike et al. 2007, 2008; Yong et al. 2014; Ullah et al. 2015).

4.2 Fungi-Mediated HM Stress Tolerance in Plants

Fungal cell walls possess efficient metal-binding properties because of the presence of negative charge in various functional groups, e.g. carboxylic, amine, sulfhydryl or phosphate, in different wall components (Tobin 2001; Ong et al. 2017). AMF are also one of the most prominent soil microorganisms that are involved in reducing metal toxicity to their host plant (Leyval et al. 1997; Meharg and Cairney 2003).

Several mechanisms have been hypothesized for the transport of toxic metal ion and their allocation in plant roots in the presence of AMF that includes (a) deposition of heavy metals and bound to the cell wall in the vacuoles of AMF, (b) metal sequestration by siderophores in the soil or into root apoplast, (c) metals bound to metallothioneins or phytochelatins inside the plant or fungal cells, (d) metal transporters at the tonoplast of both plants and fungi catalyze the transport of metals from cytoplasm, (e) oxalate crystal production for immobilization and detoxification of toxic metals (Jan and Parray 2016). Numerous filamentous fungi belonging to the genera *Trichoderma, Penicillium, Aspergillus,* and *Mucor* possess the ability to tolerate heavy metal stress (Ezzouhri et al. 2009; Tripathi et al. 2013, 2017; Oladipo et al. 2018). A dark septate endophytic (*DSE*) fungi, *Exophiala pisciphila* isolated from *Zea mays* was shown to elevate antioxidant enzyme activity under prolonged Cd stress (Wang et al. 2016).

It has been reported that the fungus, *Laccaria bicolor* encodes some putative heavy metal transporter genes for Zn, Cu and Mn ions (Martin et al. 2008). Two genes, i.e. *HcZnT1* and *OmZnT1* encode for zinc membrane transporters have been reported in ectomycorrhizal fungi such as *Hebeloma cylindrosporum* and *Oidiodendron maius,* respectively (Khouja et al. 2013; Blaudez and Chalot 2011). Six genes encoding putative metal tolerance proteins are found in the genome sequencing of ectomycorrhizal association in *Populus trichocarpa* (Tuskan et al. 2006; Migeon et al. 2010); of them, PtMTP1 protein act as a Zn transporter that facilitates Zn transfer into the vacuole (Blaudez et al. 2003), whereas PtMTP11.1 and PtMTP11.2 proteins are involved in Mn exocytosis (Peiter et al. 2007; Migeon et al. 2010). The fungus *Paxillus involutus* can aid in Cd detoxification by binding Cd to the cell wall and accumulation of Cd in the vacuole (Blaudez et al. 2000). Thus, such plant-associated HMT fungal species can be potent microbial remediation agents that can be employed in agricultural fields for quality improvement and survival of crops in contaminated lands.

5 Conclusion

To meet the global food requirements and feed the world population, there is a need to increase crop productivity and quality, plant immunity to suppress unwanted parasitic and pathogenic attacks, and at the same time to enhance agricultural sustainability. The declining of global food production is directly linked to industrialization, environmental pollution and decline in the forest area. In addition to biotic stress, various abiotic stress such as heavy metal stress, drought stress, salinity stress and temperature stress is also responsible for a reduction in plants' growth and yield. Symbiotically associated microbes have been known to use several strategies to overcome these abiotic stress in their host plants like—detoxification of heavy metal stresses through binding of metals to the cell wall in the vacuoles for exocytosis, metal sequestration, transportation of heavy metals through metal transporters; reduction of drought and salinity stress by releasing hormones and osmolytes that increase water uptake, osmotic balance, and maintain ionic homeostasis in a plant cell; overcoming of temperature stress by releasing several heat-shock proteins, ROS scavenging proteins, and enzymes, antioxidants, etc.; overcoming of the nutritional deficiency by increasing bioavailability of nitrogen, phosphorous and other essential macro- and micro-nutrients through various enzymatic reactions.

Thus, the use of beneficial microbes such as AMF, PGPB, PGPR or endophytes in the crop fields has enormous potentiality in promoting plant growth and nutrient absorption in stressful environments. The use of microbial inoculums should be encouraged as it also acts as environmentally friendly active alternatives to chemical fertilizers or pesticides. Efforts should be made for the enhancement of shelf-life and a viable load of microbial inoculation at the time of application, as well as developing faith in farmers for consistent utilization of such environmentally friendly inoculants in their crop fields.

At present, there is a need for advanced tools and techniques and extensive research on plant–microbe interactions to understand more about microbes' molecular, cellular, and physiological responses during stress, its effect on the plants and environment, and their efficiency rates when exploited commercially in agro-ecosystems. Genetically edited or engineered microbes will undoubtedly have greater potential in enriching plant growth or reducing soil toxicity as compared to non-genetically modified microbes, but they should be allowed for commercialization only after completely analyzing their impact on the ecosystem. Microorganisms being highly useful, their further exploitation in optimizing plant growth in adverse abiotic stressed conditions is expected in agriculture.

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Cadmium Stress Management in Plants: Prospects of Plant Growth-Promoting Rhizobacteria

Prasanta Kumar Ghosh and Sukanta Majumdar

Abstract

Cadmium (Cd) pollution in agricultural soils has become a great concern for global food security and the environment. Cd is a nonessential heavy metal and a group-I carcinogen. Excessive uses of phosphate fertilizers, dispersal of municipal waste, sewage sludge disposal and atmospheric deposition have polluted agricultural soils with cadmium. Accumulation of Cd in crops may cause severe damages to plant growth and agricultural productivity. Human beings get exposed to cadmium toxicity through the food chain. In recent times, plant growth-promoting rhizobacteria (PGPR)-mediated Cd detoxification in plants emerged as an excellent alternative to physicochemical approaches as it is economical and environmentally sustainable. Generally, PGPR enhances plant growth by nitrogen fixation, producing phytohormones, ACC deaminase (ACCD), siderophores, and solubilizing inorganic or organic phosphates. PGPR enhance Cd bioremediation through different mechanisms, such as biosorption, complexation, chelation, sequestration and biotransformation. The application of Cd resistant PGPR to alleviate Cd stress in plants has an exciting prospect, and early findings look promising for boosting food security, especially in contaminated soil, for the increasing global population.

Keywords

ACC deaminase • Bioremediation • Cadmium • Detoxification • Immobilization • Plant growth promoting rhizobacteria (PGPR) • Siderophore

Abbreviations

ABC	ATP-binding cassette
ACC	1-Aminocyclopropane-1-carboxylic acid
ACCD	1-Aminocyclopropane-1-carboxylic acid
APX	Ascorbate peroxidase
ASA	Ascorbic acid
CAT	Catalase
CAX	Cation/proton exchangers
CDF	Cation Diffusion Facilitator
CBA	Capsule Biogenesis/Assembly
Cd	Cadmium
Czc	Cobalt/zinc/cadmium
DHAR	Dehydroascorbate reductase
EPS	Exopolysaccharide
GPX	Glutathione peroxidise
GR	Glutathione reductase
GSH	Glutathione (reduced)
H_2O_2	Hydrogen peroxide
IAA	Indole Acetic Acid
IARC	International Agency for Research on Cancer
IRT	Iron-Regulated Transporter
LCT	Lysosomal Cystine Transporter
MDHAR	Monodehydroascorbate reductase
MT	Metallothionein
NRAMP	Natural Resistance-Associated Macrophage Protein
PC	Phytochelatin
PEPCase	Phosphoenolpyruvate carboxylase
PGPR	Plant Growth Promoting Rhizobacteria
POX	Peroxidase
Q_A	A bound primary plastoquinone
Q_B	A secondary plastoquinone

P. K. Ghosh
S.B.S. Government College, Hili, Dakshin Dinajpur, 733126,
West Bengal, India

P. K. Ghosh · S. Majumdar (✉)
Microbiology and Microbial Biotechnology Laboratory,
Department of Botany, University of Gour Banga, Malda, 732103,
West Bengal, India

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RuBisCo	Ribulose-1, 5-bisphosphate carboxylase
ROS	Reactive Oxygen Species
SAM	*S*-Adenosyl-1-methionine
SOD	Superoxide dismutase
TF	Transfer Factor
WHO	World Health Organization
ZIP	ZRT-IRT-like Proteins

1 Introduction

Agricultural soil health deteriorated considerably in the last few decades due to heavy metal contamination in soil. In general, heavy metals are found in the earth's crust; however, heavy metal contamination is mainly the consequence of increased industrial activities, combustion of coal and petroleum products, mining, smelting, use of agrochemicals (e.g. fertilizers) and disputed agricultural practices, such as the release of industrial effluents, municipal wastes and sewage sludge in agricultural soils. Atmospheric deposition, geogenic activities such as weathering, leaching and volcanism have also contributed to heavy metal pollution to a great extent (Kubier et al. 2019; Singh et al. 2021). Heavy metals are non-biodegradable; most show toxicity even at a low concentration and accumulate in the soil. Consequently, they adversely impact the functions of all the living entities present there and eventually invade the food chain via edible crops and pose a major threat to human well-being and food safety (Kumar 2012; Sharma and Archana 2016).

Heavy metals may be classified as a group of metals that have a high atomic weight and high density (>5 g cm^{-3}) (Nies 1999). They may be essential in trace amounts (e.g. Mn, Cu, Fe and Zn) or nonessential with no known physiological role (e.g. Cd, Hg, As and Pb) (Shanmugaraj et al. 2019). Cadmium (Cd) is highly mobile in soils and is the most toxic nonessential metal with a long biologic half-life. Cadmium is a trace element in the earth's crust (0.2 mg/kg) and generally occurs as oxides, sulfides, and carbonates in zinc, lead, and copper ores. In the past, cadmium was used mainly in metal electroplating, pigments and stabilizers for plastics. In recent decades, the use of cadmium has been growing up for its application in cadmium-nickel batteries, the modern electronics and communication industry, and the power industry. Cadmium is also released into the environment, naturally through volcanic activity and weathering, but mostly it is released into the environment through municipal waste incineration, fossil fuel combustion and smelting. Use of phosphate fertilizers and pesticides, irrigation with municipal waste, and sewage sludge are mainly liable for agricultural soil contamination with cadmium (Fig. 1). Cadmium content in agricultural soils ranges between 0.01 and 1 mg kg^{-1}, averaging 0.36 mg kg^{-1} worldwide (WHO 2000; Kubier et al. 2019). The World Health Organization (WHO) has recommended a guideline value of 3 µg/L for cadmium in drinking water (WHO 2010).

Chronic Cd exposure causes kidney damage, respiratory disorders, cardiovascular disorder, hypertension, cerebral infarction, disorders in glucose, calcium and vitamin-D metabolism, bone lesions, osteoporosis, and diabetes in humans. Cadmium also has embryotoxic, teratogenic and carcinogenic effects. It has been reported in several studies that the lung, kidney, breast and prostate are the primary target organs for Cd carcinogenicity. The first documented chronic cadmium poisoning incidence was the Itai-Itai disease that occurred in Japan in the 1950s. Cadmium is toxic to living beings even at a low level, and has been classified as a Group-I carcinogen to humans by International Agency for Research on Cancer (IARC) in 1993 (WHO 2000; Hu et al. 2016; Khan et al. 2017b). Cadmium entry into the human body takes place mainly through the dietary intake (e.g. cereals, vegetables) and bio-accumulates in different organs as it is non-degradable, persistent, and has a biological half-life of 10–35 years. In comparison to other cereals, the accumulation of cadmium in rice is much higher and, therefore, increases the health risk in manifold of the rice-consuming population of the world (Hu et al. 2016; Kubier et al. 2019).

Besides animal toxicity, cadmium exhibits phytotoxicity even at a low concentration. Cadmium is easily absorbed by roots of crop plants, especially rice and other cereals and leafy vegetables, during cultivation in Cd-polluted soil and can be translocated to the aerial parts. Cadmium accumulation in plant parts severely damages crop productivity (Bolan et al. 2014). Cadmium toxicity triggers diverse morphological, physio-biochemical, and molecular disturbances in plants, such as stunting overall plant growth, wilting, senescence, reduced photosynthesis, reduced pigment synthesis, leaf chlorosis, inhibition of seed germination, interference in nutrient uptake and disruption in the electron transport chain. Cadmium stimulated oxidative stress may also injure plasma membranes and a variety of different biological molecules, such as nucleic acids and proteins, by generating an excessive amount of reactive oxygen species (ROS) (Gallego et al. 2012; Roy et al. 2016; Moradi et al. 2019; El Rasafi et al. 2020).

Many traditional methods, such as soil dressing, soil removal, chemical washing, soil liming, electrochemical treatment, reverse osmosis, biochar amendment, bio-slurries and other agronomic approaches, are used for cadmium-contaminated soil remediation. These conventional physicochemical Cd remediation methods are usually expensive, require high maintenance and skilled labour, and typically cause harm to the soil in the long run by the

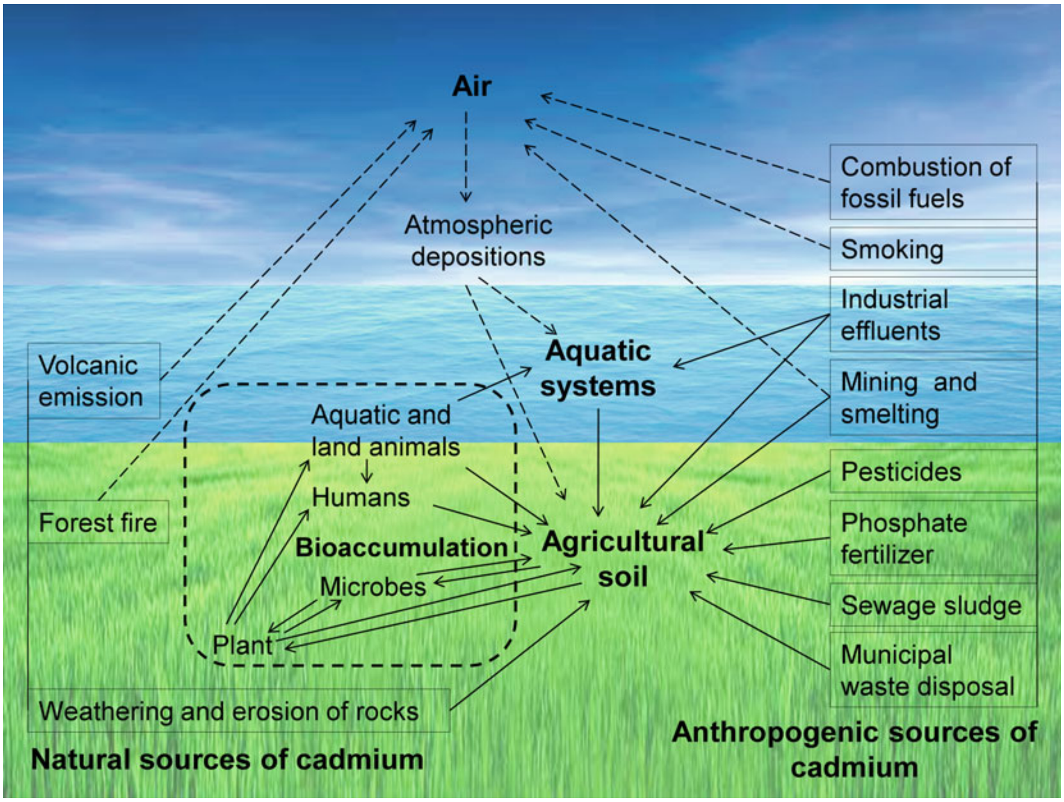

Fig. 1 Sources of cadmium in agricultural soil

resultant secondary toxic products (Volesky 2001; Vinod and Sashidhar 2011; Singh and Gadi 2012). Phytoremediation through hyperaccumulator plants is a possible alternative technique for the bioremediation of contaminated sites. However, they have little practical value in the heavy metal toxicity alleviation from the soil due to their slow growth rate and small biomass (Blaylock et al. 1997; Kayser et al. 2000).

Bioremediation involving microorganisms has attracted increasing interest in recent years (Dixit et al. 2015). The free-living rhizospheric bacteria that assist in plant growth and development are generally regarded as plant growth-promoting rhizobacteria (PGPR). The approach of using PGPR to alleviate heavy metal stress, including cadmium, is environment-friendly and inexpensive. PGPR also promote plant growth by producing growth promoters (Kloepper et al. 1980; Pramanik et al. 2017; Abbas et al. 2018). Microbial remediation of heavy metal toxicity involves bioadsorption, bioaccumulation, complexation, precipitation and biotransformation. PGPR like *Bacillus subtilis*, *Burkholderia gladioli*, *Citrobacter* spp., *Enterobacter aerogenes* and *Pseudomonas* spp., have been found effective in mitigating Cd toxicity in plants (Kumar 2012; Pramanik et al. 2018; Khanna et al. 2019a; Halim et al. 2020). In this chapter, we summarized Cd uptake, its toxicity and plant response to cadmium stress. Furthermore, we have discussed Cd tolerance strategies found in PGPR and the different PGPR mechanisms involved in Cd detoxification in plants.

2 Cadmium Uptake and Transport in Plants

Cadmium is readily taken into the inside of plant root and then translocated to the aerial plant parts. The uptake of Cd in the higher plants is regulated by diverse aspects of soil and plant characteristics, such as soil type, soil pH, presence of organic matter, Cd availability, plant species, and their genotypes, plant age and growth stage, presence of organic matter, mineral elements, and nutrients. The adsorption and complexation of Cd with soil minerals regulate its mobilization and bioavailability in soil. An increase in soil pH and organic matter stimulates Cd immobilization in soil mainly through precipitation and chelation. Cd ions could be absorbed by root cell transmembrane carriers, meant for uptake of essential micronutrients, such as Ca^{2+}, Fe^{2+}, Mg^{2+}, Cu^{2+} and Zn^{2+} (Dalcorso et al. 2008; El Rasafi et al. 2020; Halim et al. 2020). The presence of Zn in ample amount in soil decreases Cd uptake by plants as both of them use the same route to gain entry into the root cell. It is worth noting that modulation of soil conditions through soil management approaches can significantly change the bioavailability of Cd (Hu et al. 2016). The quotient of Cd concentration in the plant to that in the soil defines the Cd transfer factor (TF), which ranges between 0.01 and 0.3 (Smolders 2001). Plant root cell walls can transport cadmium to the xylem through passive transport (diffusion) (Redjala et al. 2011). Cd can be transported symplastically in root cortical cells through membrane transporters, such as zinc transporter [ZIP], iron transporter [IRT]) and metals pumping ATPase (Gallego et al. 2012; Wu et al. 2015; Yamaguchi et al. 2011; Sebastian and Prasad 2018). Also, natural resistance-associated macrophage protein (NRAMP) family, cation/proton exchangers (CAX), P-type ATPase, lysosomal cystine transporter (LCT) family and ATP-binding cassette (ABC) transporters distribute Cd in different plants parts (Gallego et al. 2012; Song et al. 2017; El Rasafi et al. 2020). Cd ions are chelated to organic molecules and distributed to different parts of the plant body through xylem and phloem translocation after xylem loading via apoplast or symplast route (Dalcorso et al. 2008).

3 Phytotoxicity of Cadmium

Due to the toxic effects of Cd, plants and other living beings have no use for it. However, a few diatoms present in seawater utilize Cd in the enzyme Cd-carbonic anhydrase (Lane and Morel 2000). In plants, the bioaccumulation of Cd causes severe toxicity symptoms, such as reduced photosynthesis, chlorosis, wilting, altered enzyme activities, altered membrane functioning, stunted growth and development, and finally, plant death. However, the severity of Cd toxicity depends on plant species and their genotypes (Shanmugaraj et al. 2019). Cd binding with sulfhydryl groups in proteins, due to its high affinity for it, interferes with protein configuration, inhibits enzymatic activities and their regulation (Hall and Brown 2002). Also, Cd^{2+} ions can displace chemically identical cations, such as Cu^{2+}, Ca^{2+}, Zn^{2+} and Fe^{2+}, from catalytic sites of enzymes. The released free ions increase the oxidative stress and could cause damage by the Fenton reaction triggered by free Fe/Cu ions (Roy et al. 2016).

3.1 Effect on Plant Root

Roots accumulate more Cd, like other heavy metals, than above-ground parts and show initial symptoms of Cd toxicity (Singh and Shah 2015). Cd interferes with the micronutrient (Ca, Mg, Zn, K, P and Fe) uptake by the roots and thus, disturbs the plant-water balance. Cd^{+2} ions mainly bind with the negatively charged components of the cell walls of the root. Exposure to Cd inhibits root growth and lateral root formation but stimulates root hair formation (Benavides et al. 2005; Daud et al. 2009). Cd could disrupt the growth and elongation of the root in a dose-dependent manner, as seen in soybean (Sahile et al. 2021). The reduction of root length, decline in root surface area and swelling of root diameter affect the nutrient uptake capacity of roots. Cd forms a callus-like structure in the root through enlargement of parenchyma cells and unorganized cell differentiation (Halim et al. 2020). Cd stress changes the appearance of the root system, and the roots become rigid, necrotic, decomposing, twisted, and mucilaginous. Browning of the root is commonly associated with cd stress (Rascio and Navari-Izzo 2011; Abbas et al. 2017). In tomato plants, roots become thick and sturdy under Cd stress (Chaffei et al. 2004). Cd stress injures the DNA and the nucleoli in the root-cap and root tip cells (Seth et al. 2008). Also, prolonged exposure to Cd could increase the nucleus number in the differentiated root cells and disrupt the mitotic index, induce chromosomal anomaly, irregular mitotic behaviour, and affect micronucleus formation when exposed to Cd (Fusconi et al. 2006; Shanmugaraj et al. 2019).

3.2 Effect on Photosynthetic Apparatus

When a plant counters Cd contamination in its vicinity, it affects photosynthetic growth parameters, such as total chlorophyll and carotenoid contents, photochemical efficacy, and intensity of photosynthesis. Cd exposure causes leaf roll, damages chlorophyll content in old leaves and inhibits biosynthesis of chlorophyll in newer ones to cause leaf chlorosis (He et al. 2008; Xue et al. 2013). In several economically important crops, such as *Pisum sativum*, *Zea mays*, Hordeum vulgare, *Brassica juncea*, *Triticum* and *Oryza sativa*, inhibition of photosynthesis due to a short and long period of Cd exposure was well documented (Ci et al. 2010; Popova et al. 2012; Irfan et al. 2014; Pramanik et al. 2018; Almuwayhi 2021). Cd toxicity also triggers stomatal closing and, subsequently, a reduction in photosynthetic activity in higher plants. Cd strongly binds with several proteins involved in photosystems I (PSI) and II (PSII). Cd toxicity also injures the light-harvesting complex (Küpper et al. 2007; Haider et al. 2021). Ribulose-1, 5-bisphosphate carboxylase (RuBisCo), and phosphoenolpyruvate carboxylase (PEPCase) are essential enzymes for CO_2 fixation during photosynthesis. Cd replaces cofactor Mg^{+2}, needed for the carboxylation step of Calvin cycle, of enzyme RuBisCo and inhibits its activity. It also decreases the activity of PEPCase (Siedlecka et al. 1998; Tran and Popova 2013). Cd toxicity also reduces the e^- flow from Q_A to Q_B by altering the Q_B binding site. Cd ions can bind competitively at Ca-binding sites and replace Ca^{+2} ions in Ca/Mn clusters of the water-splitting complex of PSII (Sigfridsson et al. 2004; Faller et al. 2005). Cd exposure induces striking changes in chloroplast number and ultrastructure, resulting in distortion of shape and size of thylakoids (Najeeb et al. 2011). Cd stress also deforms thylakoid discs and grana, decreases stored starch, and plastoglobuli deposit, as reported in *Picris divarticata*, *Hordeum vulgare*, Oryza *sativa* L.) and *Brassica* (Ying et al. 2010; Wang et al. 2011; Elhiti et al. 2012; Parmar et al. 2013).

3.3 Effect on Plant Growth and Biomass

Cadmium toxicity negatively affects general growth, induces growth deformities in many species of plants (Haider et al. 2021). A substantial decrease in the leaf growth and development was reported in *Capsicum annuum* L. and *Brassica oleracea* L. under Cd exposure (León et al. 2002; Jinadasa et al. 2016). Also, Cd toxicity decreased shoot and root growth of *Solanum tuberosum* L. at 60 mg/kg of Cd in pot trials, shoot dry matter of cucumber at 0.05 mM of Cd concentration, and the development of root, stem, and leaves of pepper at 2 mM and 10 mM of Cd, respectively, in the hydroponic system (Xin et al. 2014; Hassan et al. 2016). The long-term effect of Cd stress exhibits a rapid and significant decline in crop yields, especially in cereal production, due to disruption of nutrient uptake and photosynthesis in plants (Rizwan et al. 2016). Plant growth inhibition under Cd stress is well reported in many species, such as rice (*Oryza sativa)*, rape plant (*Brassica napus* L.), mungbean (*Vigna mungo*), chickpea (*Cicer arietinum* L.), tomato (*Lycopersicon esculentum* L.), sorghum (*Sorghum bicolour)*, lentil (*Lens culinaris* L.), durum wheat (*Triticum turgidum*) and soybean ((*Glycine max* L.) (Rizwan et al. 2012; Mondal et al. 2013; Roy et al. 2016; Dutta et al. 2018; Pramanik et al. 2018; Pal and Sengupta 2019; Zhao et al. 2019; Zhi et al. 2020; Bansal et al. 2021).

3.4 Effect on Seed Germination

Cadmium toxicity to plants diminishes water content in seedlings and delays the breaking of seed dormancy, and ultimately, the seed fails to germinate. The failure of seed germination severely hampers crop productivity. The inhibitory effect of reduced water content for embryos resulting from Cd stress was reported in seedling and seed germination of *Arabidopsis* sp., and cowpea (*Vigna unguiculata* L.) (Li et al. 2005; Vijayaragavan et al. 2011). Water deficiency, endospermic starch immobilization, and a decrease in sugar transport to the embryo resulted in the failure of seed germination (Kuriakose and Prasad 2008). Under Cd exposure, low activity of hydrolyzing enzymes, such as α-amylase, has resulted in slow transport of stored foods (Kalai et al. 2016; Haider et al. 2021). Under Cd stress, seeds were failed to germinate in sunflower (*Helianthus Annuus*) by >50% after being treated with 40 and 50 mg kg^{-1} Cd, wheat by 31% at 0.03–4.8 mM of Cd, soybean by 8.0% at 5 mg/L, lettuce by 19% at 5 mg/L, sugarbeet by 18% at 5 mg/L and rice by 100% at 1.0 mM of Cd (Ahsan et al. 2007; Jadia and Fulekar 2008; Li et al. 2013; de Souza Guilherme et al. 2015). However, a little increase in germination at low Cd concentration was reported due to the limiting effect of metal on free oxygen radicals and nitric oxide, which regulate oxidative stress (Shanying et al. 2017). Moreover, Cd has a strong affinity for the Ca-calmodulin binding sites. The binding of Cd to calmodulin greatly affects metabolic activity and seed germination (Huybrechts et al. 2019).

3.5 Oxidative Stress

Cadmium toxicity in plants is mainly caused due to reactive oxygen species (ROS) generation and change in the antioxidant system, which increases oxidative stress. However, Cd is redox-inactive and cannot transfer single electrons to generate reactive oxygen species (ROS). Cd toxicity may generate ROS indirectly through the alternation of the electron transfer chain by disrupting chloroplasts and also by damaging antioxidant defence (Gallego et al. 2012). ROS examples include superoxide (O_2^{-}), hydrogen peroxide (H_2O_2), and hydroxyl radicals (OH^{-}). In plants, Cd-induced oxidative damage results in lipid and protein peroxidation, and consequently, disrupts lipid-rich plasma membrane, as well as DNA (Younis et al. 2016; Shanmugaraj et al. 2019). Plants have evolved an advanced antioxidant system to manage oxidative stress that primarily involves enzymatic, such as glutathione reductase (GR), peroxidase (POX), superoxide dismutase (SOD), glutathione peroxidase (GPX), ascorbate peroxidase (APX), catalase (CAT), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR) and non-enzymatic antioxidants, such as α-tocopherols, non-protein amino acids, alkaloids, phenolic compounds, carotenoids, ascorbic acid (ASA) and reduced glutathione (GSH). Cd stress alters the activity of antioxidative enzymes and non-enzymatic antioxidants (El Rasafi et al. 2020). Under the exposure to Cd, the activity of GR and APX increases in wheat. GR activity also increases in rapeseed (*Brassica juncea* L.), cotton, and mungbean (*Vigna mungo* L.) (Gill and Tuteja 2010; Tran and Popova 2013). However, the scavenging activities of POX in rapeseed, SOD, and CAT in sunflower, common bean, and pea, decrease under Cd stress (Sandalio et al. 2001; Markovska et al. 2009; Haider et al. 2021).

4 Cadmium Detoxification Mechanisms in Plant

To manage Cd toxicity, plants can employ either or both tolerance and avoidance approaches. To avoid Cd toxicity, plants minimize the uptake of Cd through the roots by immobilization. In the tolerance approach, plants store and accumulate Cd in vacuoles, bind it to cell walls, phytochelatins (PCs), peptides, amino acids and proteins. Stress signaling pathways and signaling molecules, such as jasmonic acid, salicylic acid, ethylene and nitric oxide, take part in key pathways to reduce toxic effects of Cd in plants (Tran and Popova 2013; Haider et al. 2021). Plants have several strategies to minimize Cd stress, such as immobilization, dissemination, expulsion, chelation, vacuolar sequestration and compartmentalization, synthesis of stress-signaling molecules and proteins. Plants can immobilize Cd in the rhizosphere by secreting root exudates which contain several low- and high molecular weight organic compounds, including proteins, polysaccharides and phenolic compounds. In the root cell wall, pectins, having egg-box structures, and hemicelluloses are the primary site for cd binding and retention. The plasma membrane can exclude Cd ions from entering the cytosol and help in efflux from the cell. Under Cd stress, plants activate the synthesis of phytochelatin, small metal-binding peptides linked to sulfur metabolism. Phytochelatins with thiolic (–SH) groups of Cys chelates Cd to form complex structures, and as a result, prevent dissemination of free Cd^{+2} ions inside the cytosol. Synthesis of metallothioneins also helps in the chelation of Cd in the cytosol. Plant vacuoles play a very significant role in Cd detoxification by sequestrating it with the help of different ions and metabolites inside the vacuoles. Vacuolar sequestration checks the distribution of free Cd ions inside the cell. Vacuoles have ATPases, NRAMP family transporters, Ca^{2+} ion transporters, and ATP-binding cassette (ABC) type C transporters in their wall, which controls Cd detoxification in the cell vacuole. In *Arabidopsis*, heavy metal ATPase3 (HMA3) in roots regulates Cd concentration in leaves by accumulating Cd in the roots (Di Toppi and Gabbrielli 1999; Halim et al. 2020). Plant antioxidant defence mechanisms can also minimize oxidative damages caused by Cd toxicity (Wang et al. 2008).

5 Mechanisms of Cadmium Tolerance in Plant Growth-Promoting Rhizobacteria

Plant-associated non-symbiotic rhizospheric bacterial strains that assist in plant growth, directly or indirectly, are regarded as Plant growth promoting rhizobacteria (PGPR) (Glick 1995). PGPR plays a significant part in increasing agricultural yield through plant–microbe interaction even in contaminated soil. They are also utilized for the remediation of heavy metals, including Cd, polluted sites. Cd-tolerant PGPR, which helps in phytoextraction to remove Cd from the soil, improve Cd mobilization and bioavailability, increase root surface area for Cd uptake, and elevate translocation of Cd from root to aerial parts to boost Cd accumulation in plants. However, many PGPR strains help in plant growth promotion without raising Cd levels in edible crops that grow in contaminated soils. Several mechanisms have evolved in Cd-tolerant PGPR to cope with the heavy metal toxicity, and as a result, reduce Cd stress in plants. These include efflux, extracellular complexation, biosorption, precipitation, biotransformation and sequestration (Sharma and Archana 2016).

After entry into the cell, Cd must be rapidly and effectively removed from the cell or transformed into a non-or-less toxic form. The energy-dependent cadA efflux transporter protein, encoded by *cadA* gene of plasmid pI258 in *Staphlococcus aureus*, is involved in the removal of cadmium from the cell (Ganesan 2008). The gene *CadB* located on the same plasmid also confers Cd resistance by changing the binding site (Wheaton et al. 2015). The Cad system was also reported in *Ralstonia* sp. CH34. The *cadA* gene codes for cadmium resistance. The *cadB* gene expression is possible only when there is no *cadA* gene. *Alcaligenes eutrophus* confers Cd resistance due to the presence of the Czc system which effluxes cadmium and other heavy metals (zinc and cobalt) (Nies 2003; Hynninen 2010). The efflux system for Cd resistance, consisting of *czcB* and *smtAB* gene, is also present in the *E. coli* P4 strain (Khan et al. 2015). P-type ATPases, cation diffusion facilitator (CDF) family, CBA (Capsule biogenesis/assembly) family, and chemiosmotic family of transporters help in the efflux of Cd ions and Cd resistance (Nies 2003).

Biosorption plays a significant role in minimizing Cd toxicity to the bacterial cell under Cd exposure. The biosorption of Cd ions depends on metal adsorption, complexation, and bioaccumulation and makes it non-available to other organisms (Coelho et al. 2015). Metallothioneins in bacteria are cysteine-rich low molecular weight cytoplasmic proteins that help in positively charged metal (Cd) binding (Naik and Dubey 2017). Many bacteria with negatively charged cell walls or envelop can bind with dissolved Cd^{+2} cations. Bacterial exopolysaccharides (EPSs) with their anionic groups play a significant part in absorbing Cd ions from their vicinity. Metal biotransformations through oxido-reduction reactions, methylation and demethylation confer resistance against heavy metals in bacteria (Silver and Phung 2005).

6 Cadmium Resistant PGPR in Cadmium Detoxification in Plants

Cd bioavailability in the rhizospheric region has been the major reason for Cd toxicity in plants. The use of PGPR strains for plant growth and minimization of Cd uptake in edible crops provides an efficient, ecologically sustainable alternative strategy for bioremediation and maintaining food safety. However, in non-hyperaccumulator plants, Cd-tolerant PGPR could lower the uptake and distribution of Cd into the above-ground plant parts; whereas in hyperaccumulator plants, it may facilitate the Cd uptake and bioaccumulation in the plant. Cd resistant PGPR, such as *Bacillus* sp., *Pseudomonas* spp., *Burkholderia* sp., *Ochrobactrum*, *Chryseobacterium* sp., *Enterobacter* sp., *Serratia* sp., *Klebsiella* sp., reduce a significant amount of the Cd content in edible crops (Table 1). PGPR can alleviate cadmium toxicity through several mechanisms, ensuing plant growth. PGPR characters, such as the production of plant growth regulators including IAA, 1-aminocyclopropane-1-carboxylate deaminase (ACCD) production, siderophore production, organic acid secretion, and phosphate solubilization (Fig. 2), help in plant growth enhancement and minimization of Cd toxicity in Cd-polluted soil (Table 2) (Pramanik et al. 2018).

6.1 Cadmium Immobilization in Soil

PGPR-induced Cd stabilization in soil has great importance for diminishing Cd bioaccumulation in crops and simultaneously enhancing agricultural productivity and crop quality. PGPR can reduce the mobilization and phytoavailability of Cd by acting directly as biosorbents or as bioaccumulators (Voleskya and Holant 1995). Due to the high area-to-volume ratio of the bacterial cell and many metal attachment sites, PGP bacteria can act as excellent biosorbents (Gadd 1990). Cd binding extracellular polymers, such as exopolysaccharides and proteins, are produced by PGPR strains and could bind a substantial quantity of harmful heavy metals including Cd to immobilize them by precipitating as insoluble sulfides and oxides. Cd ions bind to the polyphosphate bodies, phytochelatins (PCs), metallothioneins (MTs) and other proteins to form various types of metal complexes, as reported in *Pseudomonas putida.* Chelator-Cd complexes are then transported to the vacuole for sequestration (Rayner and Sadler 1989; Dong et al. 2007). The release of organic molecules and slimes outside the bacterial cell wall increase Cd biosorption and sequestration in the root (Madhaiyan et al. 2007).

6.2 Cadmium Precipitation

PGP bacteria have anions, such as sulfides and phosphates on their cell walls. Cd^{2+} ions could bind with these negatively charged surfaces. The binding and subsequent precipitation of Cd^{2+} reduces its phytoavailability (Lamelas et al. 2006). For example, sulfate-reducing bacteria carried out sulfate reduction in presence of organic substances or H_2, and as a by-product, precipitate less soluble Cd sulfides (CdS) (Violante et al. 2010; Menon and Voordouw 2018). Also, PGPR under Cd and other heavy metals exposure produce H_2S that reacts with free Cd^{+2} extracellularly to precipitate, as CdS.

6.3 Plant Growth-Promoting Activities to Counter Cadmium Toxicity

6.3.1 Nitrogen Fixation

Nitrogen (N) is by far the most vital micronutrient for plant growth enhancement and agricultural productivity. It also enhances Cd tolerance in plants, with the production of nitrogen metabolites, such as GSH and phytochelatins, which play a significant part in defence against Cd toxicity. The presence of nitrogen in agricultural soil increases RuBisCo activity and photosynthetic yield, along with Cd tolerance (Jalloh et al. 2009). PGPR can fix free atmospheric nitrogen, act as a biofertilizer and remove N limitation in soil for plants. It was reported in a study that N_2-fixing Cd-tolerant *Klebsiella mobilis* promotes grain production in barley and reduces Cd concentration under Cd stress (Pishchik et al. 2002).

6.3.2 Phosphorus Solubilization

Phosphorus (P) also plays a significant function in overall plant growth and crop productivity. Complexation and biosorption of Cd with the phosphate groups present in the cell wall play significant roles in regulating Cd uptake and distribution in plant parts. P amendment in Cd-polluted soil enhances the quantity of chlorophyll and, as a result, improves photosynthetic yield in *Zea mays* (Jiang et al. 2007). (Many bacteria are capable of organic and inorganic phosphate complexes solubilization in soils, resulting in enhancement of P bioavailability. Application of phosphate solubilizers in Cd-polluted soils stimulates Cd immobilization as a result of the precipitation of Cd-phosphate complexes (Park et al. 2010). Similarly, many zinc solubilizing PGPR increases Zn phytoavailability (Saravanan et al. 2011). It is believed that Zn solubilization in the soil is an efficient strategy to promote crop productivity by limiting Cd bioavailability to plants and diminishing Cd uptake through roots.

Table 1 Cadmium resistant PGPR-plant interaction in alleviating cadmium stress in plants

PGPR strains	Plant	Cd concentration	Effects and mechanisms	References
Pseudomonas sp. K32	*Oryza sativa*	Exhibit resistance to 4000 µg/ml of Cd	Improve rice seedling growth through IAA production, nitrogen-fixation and phosphate solubilization under Cd stress; Cd bioaccumulation by the strain reduces Cd uptake by plant	Pramanik et al. (2021)
Bacillus licheniformis	*Spinacia oleracea* L	25, 75 and 125 ppm of Cadmium chloride (CdCl$_{2)}$	With the exogeneous application of melatonin, enhance antioxidant enzymes (SOD, POX, CAT) activity, inhibits lipid peroxidation and chlorophyll damage	Asif et al. (2020)
P. fluorescens 21, *P. putida* 23	*Hordeum vulgare* L	10 mg Cd kg^{-1} soil	Increase root growth, decrease Cd content in roots and improve mineral nutrition of the plant; Cd immobilization in soil organic matter due to Cd sequestration by bacterial siderophores	Shabayev et al. (2020)
Enterobacter sp. EG16, *Enterobacter ludwigii* DJ3	*Lycopersicon esculentum* L	50 and 100 mg kg^{-1} of CdCl$_2$ concentration	Improve shoot and root dry weight, decrease Cd transport to aerial parts; Cd immobilization due to bacterial adsorption, bioaccumulation and chelation, resulting in a decrease in Cd bioavailability in soil	Li et al. (2020)
Serratia sp. CP-13	*Linum usitatissimum* L	5–10 mg Cd kg^{-1}	Increase plant biomass, antioxidation, photosynthetic pigments, minerals uptake, decrease lipid peroxidation through IAA production, ACC deaminase activity and phosphate solubilization	Shahid et al. (2019)
Bacillus cereus M4	*Oryza sativa* L	Cd exposure of 1.0 mg/kg soil	Reduce Cd uptake and bioaccumulation in rice, reduce oxidative stress by producing Glutathione, enhance IAA production	Wang et al. (2019)
Pseudomonas aeruginosa, *Burkholderia gladioli*	*Lycopersicon esculentum* L	Cd stress of 0.4 mM	Enhances photosynthetic pigment content, fresh weight, root and shoot length through the production of phytohormone, mineral uptake, N$_2$ fixation; Production of Cd chelating thiol compounds reduces Cd bioavailability in soil and bioaccumulation in seedling	Khanna et al. (2019a)
Klebsiella michiganensis	*Oryza sativa* L	Cd concentrationof 200 µg/ml	Promotes plant growth through IAA production, ACC deaminase activity and phosphate solubilization reduces Cd bioavailability due to Cd sequestration	Mitra et al. (2019)
Paenibacillus sp. ISTP10	*Gossypium hirsutum* L	60 mg of Cd kg^{-1} of dry soil	Increase chlorophyll content, plant fresh and dry weight, shoot and root length through N$_2$ fixation, phosphorous solubilization, production of IAA, EPS, ammonia, HCN, and siderophores	Kumari and Thakur (2018)
Enterobacter Aerogenes MCC 3092	*Oryza sativa* L	Show resistance to 4000 mg ml^{-1} Cd	Enhance chlorophyll pigments, increase shoot and root length through IAA production, N$_2$ fixation, phosphate solubilization, and ACC deaminase activity	Pramanik et al. (2018)
Serratia marcescens RSC-14	*Solanum nigrum*	Cd resistance up to 4 mM (minimum inhibitory concentration)	Enhance plant growth, root elongation through bacterial cell wall binding, Cd efflux, production of (IAA), antioxidant enzymes, non-enzyme antioxidants, acetoin, butanediol, and phosphate solubilization, three CzcD proteins provide Cd tolerance and transportation	Khan et al. (2017a)

6.3.3 Secretion of Organic Acid

Excretion of organic acids, such as gluconic acid, succinic acid, salicylic acid, oxalic acid and citric acid by PGPR, are well reported. These organic acids help in Cd detoxification in plants by chelating with free Cd^{+2} ions. The release of organic acids by PGPR is a well-known mechanism that affects the mobility of Cd ions in rhizospheric soil by altering soil pH, organic matter contents and ionic strength (Halim et al. 2020). For instance, gluconic acid production by glucose dehydrogenase enzyme was studied in many PGPR. It was reported that gluconic acid produced by *Enterobacter asburiae* enhances growth in *Vigna radiata* under Cd exposure. Organic acids also upregulate antioxidant defence systems, such as SOD and POX under Cd stress (Goldstein 1995; Kavita et al. 2008), and help in phosphate solubilization in soil.

6.3.4 Siderophore Production

Siderophores play an important role in improving the iron status of the plant. It also binds with heavy metals to restrict metal mobility and increase accumulation (Rajkumar et al. 2010). These are low molecular weight compounds released by rhizospheric bacteria that bind to iron (Fe^{+3}) ions with great affinity. Siderophores, with their iron-binding ability, improve iron bioavailability which would result in plant growth. Also, the increase in iron level, in return, would affect the uptake of Cd, thus imparting Cd resistance. In *Pseudomonas* sp., synthesis of green pigmented siderophore, i.e. pyoverdine, has been reported under Cd stress (Dao et al. 1999). It enhances plant growth and reduces Cd intake in *Vigna mungo* (Tripathi et al. 2005). Siderophore producing *P. aeruginosa* also enhances iron intake in *Brassica* sp. under Cd stress (Sinha and Mukherjee 2008).

6.3.5 ACC Deaminase Production

Ethylene, a stress-signaling molecule, is produced from L-methionine through the intermediate products, *S*-adenosyl-1-methionine (SAM) and 1-aminocyclopropane-1-carboxylic acid (ACC). Ethylene triggers the production of SOD, APX and ROS, which ultimately results in senescence in plants. ACC deaminase (ACCD) cleaves the immediate ethylene precursor, ACC, to produce α-ketoglutarate and ammonia, and resultantly, reduce ethylene formation. The production of ACCD plays a significant role in Cd resistance mechanisms in plants (Glick 2005; Saleem et al. 2007). ACCD activity stimulates seed germination, root formation in tomato and plant growth in mustard and rape plants under Cd stress (Grichko et al. 2000; Belimov et al. 2001).

6.3.6 IAA Production

PGP traits, such as root hair formation and root elongation, shoot elongation, are immensely controlled by the productions of phytohormones, e.g. IAA, gibberellins and cytokinins. IAA production is regarded as one of the widely accepted plant growth-promoting traits for PGPR. IAA produced by PGPR strains enhances root elongation in *Brassica napus* (Sheng and Xia 2006). Plant growth promotion and alleviation of Cd toxicity by IAA producing *Enterobacter aerogenes* MCC 3092 and *Pseudomonas* sp. SNA5 in rice and wheat, respectively, was reported when exposed to Cd (Verma et al. 2015; Pramanik et al. 2018).

7 Conclusions and Future Prospects

PGPR has been enhancing crop productivity and crop quality in stressed soil through different plant growth-promoting mechanisms. With the recent interesting progress, bioremediation of cadmium stress in plants through PGPR has emerged as a promising technique. However, the use of PGPR on a commercial scale will require much deliberation regarding the preservation of the quality and efficacy of the PGPR product and delivery mechanisms. Future studies will also look into the bacterial genes responsible for PGP traits. It might help in developing and designing bacteria with many PGP traits. The use of genetically engineered PGPR will be more effective in reducing Cd toxicity and plant growth promotion with their multifunctional PGP traits (Glick 2012). Rapid improvement and application of modern tools and nanotechnology open the door for the production of PGPR-mediated bionanohybrids, nano-fertilizers and biosensors. These bionanohybrids will play a vital role in Cd immobilization and maintaining macro and micronutrient balance in the rhizospheric soil. Future improvement and advancement of PGPR-based new technology in Cd detoxification in soil and plants will guide and bring in agricultural prosperity in the coming decades.

In recent decades, rapid accretion in anthropogenic activities led to cadmium contamination in the environment. The increase of cadmium pollution in the agricultural soil has led many scientists to focus on developing rapid, low-cost and efficient Cd detoxification technologies for

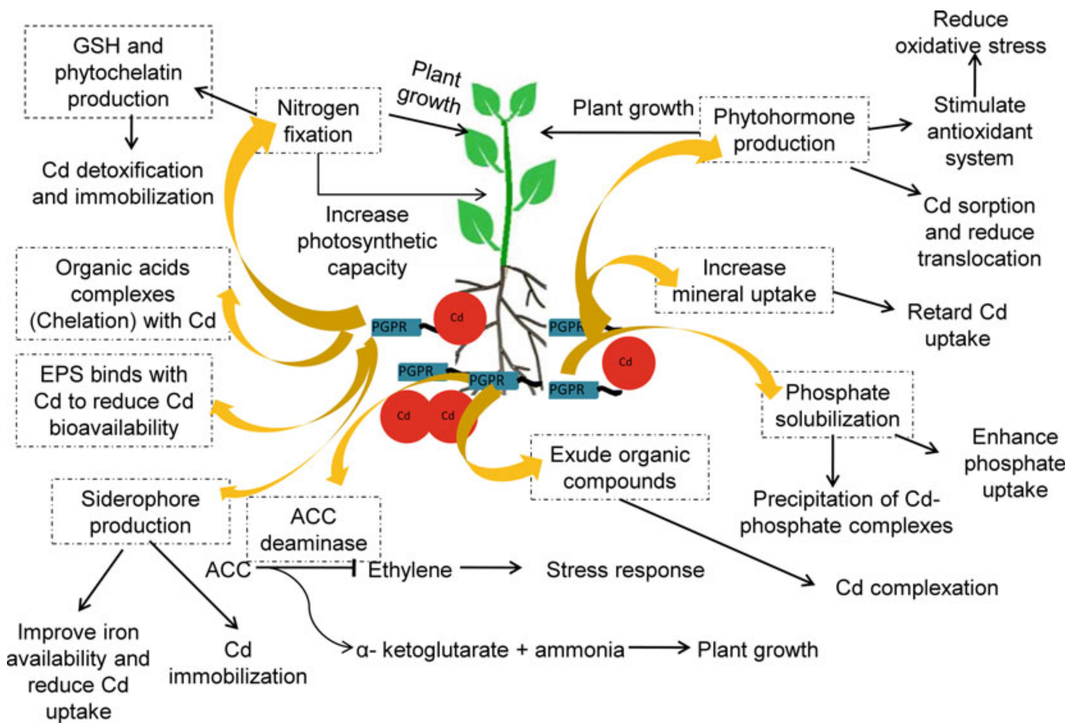

Fig. 2 Mechanisms of PGPR in alleviating cadmium stress in plant

Table 2 Mechanisms of PGPR for cadmium detoxification in plants

Plant growth-promoting traits	Mechanisms of plant growth	Cd detoxification mechanisms	Examples of PGPR strains	References
ACC deaminase (ACCD) production	Alteration of ethylene, which enhances senescence, synthesis by producing α-ketoglutarate and ammonia; NH_4^+ act as N-source	Indirectly decreases Cd-stimulated ROS generation and decreases oxidative damage	*Pseudomonas* sp., *Pseudomonas fluorescens*, *Enterobacter aerogenes* MCC 3092, *Azoarcus* sp. CIB, *Klebsiella michiganensis*	Govindasamy et al. (2015), Pramanik et al. (2018), Mitra et al. (2018b), Fernández-Llamosas et al. (2020), Halim et al. (2020)
IAA production	Act as a plant growth regulator, enhance root hair development and root elongation	Stimulates Cd biosorption and translocation; decrease oxidative damage	*Azospirillum* spp., *Bacillus subtilis*, *Enterobacter* sp. *strain* EG16, *Pseudomonas putida*, *Lysinibacillus varians strain* KUBM17, *Klebsiella michiganensis*, *Bacillus cereus* strain *ALT1*	Bhattacharyya and Jha (2012), Chmielowska-Bąk et al. (2014), Chen et al. (2016), Mitra et al. (2018b), Sahile et al. (2021)
P solubilization	Enhance phosphate bioavailability by converting insoluble phosphorus to a soluble form	Precipitation of cadmium-phosphate compounds	*Burkholderia* sp., *Azotobacter* sp., *Bradyrhizobium* sp., *Klebsiella michiganensis*, *Leifsonia* sp., *Enterobacter* sp., *Enterobacter ludwigii* GAK2	Bhattacharyya and Jha (2012), Guo and Chi (2014), Ahmad et al (2016), Mitra et al. (2018b), Adhikari et al. (2020)
Zn solubilization	Increase Zn bioavailability	Reduce Cd uptake	*Pseudomonas aeruginosa*, *Serratia liquefaciens*, *Pseudomonas moraviensis*, *Enterobacter hormaechei*, *Pseudomonas frederiksbergensis*	Saravanan et al. (2011), Kumar et al. (2019), Fahsi et al. (2021)

(continued)

Table 2 (continued)

Plant growth-promoting traits	Mechanisms of plant growth	Cd detoxification mechanisms	Examples of PGPR strains	References
Siderophore production	Improve iron availability; promote the formation of complexes with Fe_3^+	Lowers Cd availability to plants and its uptake, repress ZIP transporters	*Pseudomonas putida*, *Lysinibacillus varians strain* KUBM17	Rascio and Navari-Izzo, (2011), Pal and Sengupta (2019)
Nitrogen fixation	Improve N_2 content in soil and their bioavailability; increase photosynthetic yield	Production of reduced glutathione (GSH) and phytochelatin (PC) (redox agents)	*Bradyrhizobium* sp., *Enterobacter* sp., *Klebsiella michiganensis*, *Pseudomonas putida strain* KUBM18, *Lysinibacillus varians strain* KUBM17	Guo and Chi (2014), Mitra et al. (2018a, b), Pal and Sengupta (2019)
Organic acid secretion	Solubilization of organic and inorganic phosphates, Zn and other essential nutrients	Cd chelation and precipitation	*Enterobacter asburiae*, *Burkholderia gladioli*, *Pseudomonas aeruginosa*, *Bacillus cereus*	Majewska and Kurek (2011), Kavita et al. (2008), Khanna et al. (2019b), Sahile et al. (2021)

plants. Further research on how plant growth-promoting rhizobacteria interact with Cd ions and plants in response to cadmium stress would allow us to comprehend the knowledge of the phytoavailability of cadmium in rhizospheric soil effectively. The knowledge about these processes provides insight into the strategies employed by bacteria for Cd detoxification in plants. It would also aid in the prediction of the plant response in a stressed environment. This chapter summarizes the current understanding of natural and anthropogenic sources of cadmium contamination, the intricate interaction between rhizospheric growth-promoting bacteria, soil and plant under Cd stress. Here, PGPR acts as a mediator that regulates bioavailable Cd level and their detoxification in plant cells in a sustainable manner. The knowledge about these processes offers valuable insights into the strategies for developing PGPR-based bioremediation technologies to mitigate the growing risk of Cd toxicity for worldwide agricultural yield and productivity.

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Harnessing the Power of Microbes to Overcome Heavy Metal Stress in Crop Plants

Khomdram Niren Singh and Diganta Narzary

Abstract

The declining of crop productions due to various biotic and abiotic factors is evident these days. Among the various factors, heavy metal stress is one of the major abiotic factors which is responsible for lower crop productivity that needs to be addressed and resolved. There are a few ways to overcome heavy metal stress in crop plants, which require appropriate selection for effective results. Many strains of microbes (bacteria, fungi, algae) have intrinsic properties to either absorb, uptake, or change the chemical properties of metals available to the plants. There are several reports that claim the effective use of microbes in mitigation/bioremediation of heavy metal contamination in soil and water. Being microbial treatment of the heavy metal contaminated soil is one of the best options available in terms of their cost-effectiveness and environmental friendliness in overcoming metal stress in crop plants. Therefore, in this chapter, we have highlighted and discussed the various sources of heavy metal contamination in crop fields, their toxic effects on crop plants, the various mechanism adopted by plants to resist the toxic effects of heavy metals, and the microbial potential in bioremediation of heavy metals that include the heavy metal resistance and uptake mechanism in microbes, their effective use in bioremediation, and finally, we have discussed the application of advanced technologies such as genetic engineering and omics technology in the field of microbiology for their potential use in the bioremediation of heavy metals.

Keywords

Algae • Bacteria • Crop plant • Fungi • Metal stress • Soil bioremediation

Abbreviations

ABC	ATP-Binding Cassette
ACC	1-Aminocyclopropane-1-Carboxylate
AMF	Arbuscular Mycorrhizal Fungi
ASA	Ascorbate
ATM	ABC Transporters of the Mitochondria
CAX	Calcium Cation Antiporter
CDF	Cation Diffusion Facilitator
COPT	Copper Transporter
CRISPR	Clustered Regularly Interspaced Short Palindromic Repeats
GEMs	Genetically Engineered Microorganisms
GMMs	Genetically Modified Microorganisms
GRFC	Global Report on Food Crises
GSH	Glutathione
HM	Heavy Metal
IRT	Iron-regulated Transporter
MT	Metallothionein
PCS	Phytochelatin Synthase
PCs	Phytochelatins
PGPR	Plant Growth Promoting Rhizobacteria
ROS	Reactive Oxygen Species
SOD	Superoxide Dismutase
V-ATPase	Vacuolar Proton-ATPase
V-PPase	Vacuolar Proton-Pyrophosphatase
ZRT	Zinc-regulated Transporter

K. N. Singh · D. Narzary (✉)
Microbiology and Molecular Systematics (MMS) Laboratory, Department of Botany, Gauhati University, Guwahati, Assam 781014, India
e-mail: d_narzary@gauhati.ac.in

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1 Introduction

The growing world population and food crisis cannot be ignored, and an estimated 155 million people worldwide have suffered acute food insecurity according to GRFC reports in 2021 (Global Report on Food Crises 2021). Therefore, to meet the world's food needs, it has become a very important and challenging task for mankind to increase the global food production capacity by all possible means. As we know, the quality of the soil is the key factor in food production. The deterioration of soil quality due to increasing human interference, industrialization, and other anthropogenic activities is the main reason for the reduced food production capacity, however, soil quality can be improved by using appropriate soil treatment methods. The contamination of heavy metal(s)/metalloid(s) in soil is one of the important factors that often creates tremendous plant stress resulting in decreased plant growth and food production.

The stress experienced in a plant when exposed to different external factors such as physiological, biological, or chemical that affect plant growth, reproduction, and productivity is known as plant stress. As mentioned earlier, heavy metal(s)/metalloid(s) is one of the major abiotic factors responsible for stress in crop plants, but some of them (e.g., Fe, Cu, Mn, Mo, Zn, Ni, Co) are required as micronutrients for enzyme stabilization and metabolic reactions in plants (Bruins et al. 2000; Alloway 2013), whereas many of them are non-essential heavy metals (e.g., As, Al, Be, Cd, Cr, Hg, and Pb), i.e., not required in plant metabolism. Both essential and non-essential heavy metals are highly toxic to plants if present at high concentrations in the soil, which often leads to a drastic effect on the plant growth and metabolism (Tiwari and Lata 2018). In China alone, over 20 million hectares of agricultural land are contaminated with heavy metals (He et al. 2020). The order of metal toxicity reported in plants is Cd > Co > Hg > Mn > Pb > Cr (Chibuike and Obiora 2014), whereas the order of metal inducing mutagenic effects in plants is: Hg, Cd > Zn, Pb, Cu, Ni, Co, Al, Cr > Mn (Küpper and Andresen 2016). Heavy metal toxicity varies with the plant species, specific metal, concentration, chemical form, and soil composition (Nagajyoti et al. 2010). Heavy metal pollution in the soil not only affects plant growth and metabolism, but it can also enter into the food chain system that ultimately reaches the human body and causes the body to suffer serious illness, disorders, disabilities, and cancer (Iyengar and Nair 2000; Türkdoğan et al. 2003; Briffa et al. 2020).

Microbes are small living organisms that generally have short generation times and small genome sizes, which allows them to adapt quickly to a changing environment (Bleuven and Landry 2016). Their habitats on earth are so vast that they have been reported from all the spheres of the earth. The utilization of microbes and microbial products is a decade-old practice and is well associated with the growth and development of humankind. Microbes have been utilized for the large-scale production of a wide variety of biochemicals and metabolites such as amino acids, vitamins, alcohols, drugs, antioxidants, immuno-suppressants, enzymes, and enzyme inhibitors (Demain and Sanchez 2009; Demain 2014; Gupta et al. 2014). There are also several reports on microbes being used for cleaning heavy metal contaminated environments such as sewage and soil (Congeevaram et al. 2007; Chaturvedi 2011; Bhattacharya and Gupta 2013; Marzan et al. 2017). The ability of microbes to remove heavy metals can be harnessed for effective use in the fields to remove or reduce the toxicity of heavy metals and their stress on plants.

This chapter discusses microbes and their potential use as bioremediation tools to overcome heavy metal stress experienced in crop plants. The first section of the chapter provides an overview of heavy metal pollution in arable land and its influence on plant growth. The second section provides the heavy metal signaling and tolerance in crop plants. The third section deals with the heavy metal resistance in microbes and their potential for the bioremediation of heavy metals to improve crops. The final section provides the recent advancement in omics technology for heavy metal bioremediation.

2 Heavy Metal Contamination in Croplands and Their Influences on Plant Growth

Heavy metals are those having an atomic number above 20 and an atomic density above 5 g/cm (Duffus 2002). Their toxicity in plants is determined by their bioavailability in the soil (Hossain et al. 2012) and the degree of resistance that a plant develops against them (Hossain et al. 2012). Their toxic effect on plants mainly involves disruption of important enzyme function and ion regulation, which inhibits DNA and protein formation (Hossain et al. 2012). The various effects of heavy metals on plants are listed in Table 1.

2.1 Sources of Heavy Metal Pollution in Soil

Heavy metals occur naturally in trace amounts (<1000 mg/kg) in the soil and are generally non-toxic to the living plants and animals at such low concentrations (Wuana and Okieimen 2011). The man-made disturbance in the geochemical cycle of metals can, however, lead to an accumulation of heavy metals in a concentration that is far above the defined background of heavy metals in the soil

Table 1 Toxic effects of heavy metal exposure on plants

Heavy metals	Toxic effects on plants	References
Aluminium (Al)	It mainly affects the root system and causes reduced plant growth. In the root system, it causes stunted and brittle roots, poor development of root hair, swollen, and damaged root apices. Al interferes with the replication of DNA and cell divisions in the root system, also reduces root respiration, and interferes with the enzymes governing polysaccharide deposition in the cell wall	Panda et al. (2009), Bojórquez-Quintal et al. (2017)
Arsenic (As)	Inhibits root extension and proliferation, severely inhibits plant growth, compromises reproductive ability. At high concentrations, As interferes with critical metabolic and physiological processes and may lead to the death of the plant	Finnegan and Chen (2012), Kalita et al. (2018)
Cadmium (Cd)	Causes chlorosis and shunted plant growth. Inhibition of plant growth and necrosis occurs at a higher level. Cd also decreases seed germination	Haider et al. (2021)
Chromium (Cr)	Alter germination process, also negatively affects the growth of root, stem, and leaves. High Cr concentration causes degradation of photosynthetic pigments which leads to deficiency in light-harvesting capacity	Shanker et al. (2005), Srivastava et al. (2021)
Cobalt (Co)	It mainly affects on growth and metabolism of plants. It causes leaf fall, discoloured veins, greening inhibition, reduced shoot size. A high concentration of Co also leads to the production of ROS, OH^- radicals, H_2O_2 radicals in plants and also alter antioxidant enzyme activities, which may lead to the dysfunction of plants	Palit et al. (1994), Mahey et al. (2020)
Copper (Cu)	It mainly damages plant roots in the form of root cuticle disruption, reduction of root hair proliferation, and deformation of the root structure	Sheldon and Menzies (2005)
Iron (Fe)	It causes discolouration of leaves and stunted root systems in plants. It leads to reduced chlorophyll content in plants and therefore limited photosynthetic activities. Higher Fe concentration leads to the production of ROS which causes damages to DNA, proteins, carbohydrates, and lipids which further leads to cellular death	Li et al. (2016a), Zahra et al. (2021)
Lead (Pb)	Inhibits plant growth, germination of seed, development of seed, elongation of a root, transpiration, chlorophyll production, and reduction of protein content	Pourrut et al. (2011)
Mercury (Hg)	Inhibits plant growth, effects on nodulation and N_2 fixation of legumes, decreases photosynthetic activity, water uptake, and antioxidant enzymes	Mondal et al. (2015)
Manganese (Mn)	It causes interveinal chlorosis, the appearance of pale mottled leaves, and the development of grey speck in leaves in severe conditions. It also causes necrotic spots on older leaves	Alejandro et al. (2020)
Molybdenum (Mo)	Molybdenum toxicity is extremely rare in plants. Mild effects include turning leaves yellow and reducing seedling growth	Bittner (2014)
Nickel (Ni)	The negative effects/toxic effects of Ni include reduced seed germination, reduced root and shoot growth, and reduced biomass accumulation. Higher Ni concentration also induces chlorosis, necrosis, and wilting	Bhalerao et al. (2015), Hassan et al. (2019)
Zinc (Zn)	It causes curling of young leaves; shoot stunting, leaf tips death, and chlorosis. A high concentration of Zn in the soil leads to reduced growth, reduced photosynthetic rate, imbalanced nutrition, and enhanced production of ROS	Rout and Das (2003), Kaur and Garg (2021)

(D'Amore et al. 2005; Zhang and Wang 2020). Heavy metal pollution in the soil is mainly associated with anthropogenic activities such as mining, industry, use of fertilizers and pesticides in farmland, and other vehicular sources (Wuana and Okieimen 2011; Zhang et al. 2020b) which are described below.

2.1.1 Fertilizers and Pesticides

To counteract the nutrient deficiency in the soil, fertilizers are often added to the arable land regularly. However, it has been found that commercially available fertilizers often contain traces of impurities such as As, Cr, Cd, and Pb which after several years of use in the soil can increase the heavy metal load in many folds (Atafar et al. 2010; Nacke et al. 2013). The use of phosphate fertilizers also adversely increases the heavy metal concentration of Cd, Cu, Pb, and Zn in the soil (Thomas and Ogundayomi 2012).

2.1.2 Industrial and Municipal Wastewater

Irrigation of soils with municipal and industrial wastewater is widely practised in urban areas around the world. The municipal and industrial wastewater is mostly contaminated with various heavy metals (As, Cd, Cr, Cu, Fe, Hg, Ni, Pb, Tl, and Zn) (Al Enezi et al. 2004; Barakat 2011; Kinuthia et al. 2020), and therefore, irrigation with such wastewater act as a source of soil pollution. The vegetables grown on soils that were irrigated with wastewater from industrial and municipal wastewater showed a high concentration of heavy metal accumulations (Jan et al. 2010a, b; Khan et al. 2013).

2.1.3 Mining Industries

The mining of minerals, metals, and coal through surface or opencast mining contributes to severe soil pollution. Heavy metals are naturally occurring substances in many parent rock materials and soils of various types (Ali et al. 2019; Singh and Narzary 2021). The excavation of such heavy metal-laden overburdened materials during the mining process exposes the heavy metals and acts as a major source of pollution for the natural environment. The seepage water that carries heavy metals from the mining area (mineral dump or overburden dump) through drainage systems found its way to the arable soil either directly or indirectly via the water. The reports on heavy metal contamination of soils in the vicinity of the mining areas have already been documented in many studies (Jung and Thornton 1996; Zeng et al. 2018; Nguyen et al. 2020).

2.1.4 Atmospheric Deposition

The accumulation of heavy metals from polluted air is also a major source of soil pollution. Emissions from vehicles to the air lead to the release of toxic heavy metals such as Cu, Pb, and Zn into the air (Popescu 2011) and act as a source of soil pollution near roadsides and urban areas. Metals such as As, Cd, and Pb are highly volatile and at high temperatures volatilize into the air, which later on oxidizes and condenses, and becomes a source of soil pollution (Smith 1995; Artiola et al. 2019). Atmospheric deposition contributes to the major heavy metal contamination in agricultural land in England and Wales where 85% of the Hg, 78% of the Pb, 60% of the Ni, 56% of the As, and 53% of the Cd accounts for annual deposition (Nicholson et al. 2003). In one of the studies, deposition of 20–85% of Cu and Cd in the shoot of *Brassica chinensis* L. from atmospheric source via soil has also been documented (Liu et al. 2019).

2.2 Bioavailability of Heavy Metals

When it comes to the question of the toxicity of a heavy metal, it is not the total heavy metal content that is responsible for the toxicity, but only a fraction that is available for absorption/entry to the plants and organisms that causes toxicity (Peijnenburg et al. 2007; Scheckel et al. 2009). According to Kim et al. (2015), the bioavailability of heavy metals in soil concerning plant uptake comprises three steps of a complex and dynamic process, as given below.

(a) Environmental availability
The total available heavy metals in the soil include both the potential fraction that can be dissolved in pore water and the actual fraction.

(b) Environmental bioavailability
The fraction of dissolved heavy metals in the pore water available for plant/microorganisms to be taken up.

(c) Toxicological bioavailability
The amount/fraction of heavy metals in soil which can induce plant physiologically for its bioaccumulation or other effects based on translocation, detoxification, and metabolism.

The bioavailability of heavy metals depends on the type of soil and the fraction of heavy metals that can be dissolved in the pore water (Antoniadis et al. 2017). The heavy metal when dissolved often reaches a dynamic equilibrium that is strongly influenced by the pH, moisture, organic carbon, clay, sulfide, carbonate, and metal oxide contents of the soil (Okoro and Fatoki 2012; Kim et al. 2015; O'Connor et al. 2019). Bioavailability also varies for different heavy metals. For example, although Pb is found 100 times higher than Hg and 40 times higher than Cd due to its high natural background in soil (Mulligan et al. 2001; O'Connor et al. 2019), the bioavailability of Pb in the soil is comparatively lower than that of Hg and Cd since Pb forms insoluble compounds such as pyromorphite and is also strongly adsorbed on other soil minerals such as manganese oxide (Hettiarachchi and Pierzynski 2004). On the other hand, the bioavailability of

Cd in the soil is very high, as it is mainly available in an exchangeable form and its adsorption potential on soil minerals is rather low (Shahid et al. 2017).

2.3 Influence of Toxic Heavy Metals on Plants

When expose to high heavy metal concentrations, plants experience a major growth effect caused due to the accumulation of heavy metals into the cell, where there is a subsequent inhibition of photosynthesis and growth, altered water and nutrient balance, chlorosis, and senescence, which ultimately leads to plant death (Singh et al. 2016). Heavy metals when taken up by plants, cause the formation of free radicals such as reactive oxygen species (ROS) in the plant cells, followed by uncontrolled oxidation chain reactions and eventual damage of biomolecules such as DNA, RNA, proteins, and lipids (Phaniendra et al. 2015). Most plant species are susceptible to high concentrations of heavy metals in the soil, but the metallophytes that can grow in the presence of high metal concentrations are the exceptions. For example, *Brassica napus* and *B. juncea* can tolerate high metal concentrations as well as accumulate heavy metals in their cells (Mourato et al. 2015). The influence of high concentrations of heavy metals in plants has been reported in many studies (Table 1). Li et al. (2007) reported inhibition of seed germination and seedling growth in wheat after exposure to a high As concentration. It has also been reported that As reduces the length of plumule and radicles in sunflowers (Imran et al. 2013), reduces photosynthesis and enzyme activity, changes the nutrient balance and protein metabolism, and damages the chloroplast membrane in plants (Li et al. 2006; Singh et al. 2009; Ahsan et al. 2010; Arikan et al. 2022). Singh et al. (2007) reported a decrease in germination percentage and reduced length of plumule and radicle when exposed to a high concentration of Cu. Tamás et al. (2009) found overexpression of the dehydration-stress-related gene in barley as an early sign of exposure to Cd and Hg which is similar to the early sign of drought stress. The formation of stress signaling molecules, oxidative stress, and depletion of glutathione has also been reported in plant roots when exposed to heavy metals (Hernández et al. (2012).

3 Molecular Mechanism of Heavy Metal (HM) Toxicity and Tolerance in Plants

3.1 Molecular Mechanism of HM Toxicity in Plants

The molecular mechanism of HM toxicity can be grouped into three categories based on their different physical and chemical properties:

(a) Redox-active groups, which include HMs such as Co, Cr, Cu, and Fe that are involved in redox reactions and the production of reactive oxygen species (ROS) directly through auto-oxidation and Fenton reaction (Dietz et al. 1999; Schützendübel and Polle 2002)

(b) Redox-inactive groups, comprising HMs such as Al, Cd, Hg, Ni, Zn, etc. that causes oxidative stress in plants indirectly by blocking essential functional groups in biomolecules that disrupt the antioxidant defence systems, interrupt the electron transport chain, and induce lipid peroxidation (Hossain et al. 2012)

(c) Displacement of essential metal ions from biomolecules, which leads to the inhibition or loss of enzyme functions, e.g., displacement of Mg^{2+} by other divalent cations such as Co^{2+}, Ni^{2+}, and Zn^{2+} in ribulose 1,5-bisphosphate carboxylase/oxygenase that ultimately leads to the loss of cellular function (Schützendübel and Polle 2002).

3.2 Molecular Mechanism of HM Tolerance in Plants

Many plant species have evolved to tolerate heavy metals by employing various mechanisms made up of several inter-related physiological and molecular mechanisms. It has been reported that plants use two mechanisms to cope up with the elevated HM concentrations:

(a) constitutive mechanisms, which are constitutively present in most of the phenotypes and

(b) adaptive mechanisms, which are only present in HM-tolerant phenotypes (Meharg 1994).

Some of the adaptive mechanisms adopted by HM tolerant plants are membrane exclusion, immobilization, uptake, transport restriction, chelation, and sequestration of HMs, antioxidant and glyoxalase upregulation, stress protein induction, and biosynthesis of prolines and polyamines, and other signaling molecules such as nitric oxide and salicylic acid (Hossain et al. 2012; Shrivastava et al. 2019). Some of the mechanisms that plants adopt to tolerate heavy metals are described below in detail.

3.2.1 Exclusion of HMs as a First Defense Mechanism in Plants

Once the bioavailable HMs are present in the soil, they enter the plants via the roots and later translocate into the shoots. The mode of HM transfer in plant cells can be either extracellular where HM ions enter the plant cells through apoplast, or intracellular where HM ions are transferred from one cell to another through symplast. HMs usually enter the plant cell by ATP-dependent pathway through specific or unspecific ion carriers and channels. Therefore, plants protect themselves as the first line of defence against the toxic effects of HMs by checking/avoiding the entry of excess heavy metals into the body, which occurs either through precipitation of the HMs or through the formation of metal complex in the root zone (Hossain et al. 2012). Precipitation of HMs occurs when plants increase their rhizospheric pH by excreting phosphate ions. In addition to phosphate, root exudation of malate, citrate, and oxalate in crop plants (maize, sorghum, and tomato) has been reported in response to heavy metal stress, stabilizing the HMs in the root environment (Pellet et al. 1995; Pinto et al. 2008; Zhu et al. 2011; Ghori et al. 2019). Iron plaque formation in the root zone of *Oryzae sativa* due to the release of oxygen and oxidizing agents in the root surface has also been reported (Chen et al. 1980; Liu et al. 2008; Li et al. 2019). All of these can act as an important mechanism for preventing HMs from entering plants by reducing the HMs available for uptake.

3.2.2 Compartmentation/sequestration of HMs Inside the Plant Cell Vacuoles

When HMs enter the plant cell, as one way of defence mechanism plants sequestered HMs inside the vacuolar compartments either by direct transport or vesicular cycling. In hyperaccumulator plants, HMs are stored/compartmentalized in leaf cell vacuoles after the efficient transport of HMs from the root to the shoot. However, in non-hyperaccumulator plants, HMs are mostly stored in root vacuoles. The vacuolar compartmentalization of HMs depends on two proton pumps viz., vacuolar proton-ATPase (V-ATPase) and vacuolar proton-pyrophosphatase (V-PPase) (Sharma et al. 2016). The combined proton motive force of V-ATPase and V-PPase at tonoplast creates a proton gradient and membrane potential for the transport of compounds including heavy metals in the vacuoles (Krebs et al. 2010). Therefore, vacuoles act as suitable stores for excess heavy metals in plants. Several heavy metal transporter proteins so far characterized are ATP-binding cassette (ABC) transporter, ABC transporters of the mitochondria (ATM), Calcium cation antiporter (CAX), cation diffusion facilitator (CDF) protein family, copper transporter (COPT) protein family, iron-regulated transporter (IRT) like protein family, zinc-regulated transporter (ZRT) like protein family, and so on (Lee et al. 2005; Chiang et al. 2006; Krämer et al. 2007; Dubey 2010). Compartmentalization of HMs in the vacuole is demonstrated in barley where Zn and Cd were sequestered in vacuoles with increased exposure to Zn and Cd (Brune et al. 1994, Thomas and Reid 2021).

3.2.3 Complexation of HMs by Metallothionein and Phytochelatins

Metallothionein (MT) is a low molecular weight, a cysteine-rich metal-binding protein found in Golgi membranes. MT is expressed by the MT gene when the plant is exposed to heavy metal stress conditions at various stages of growth (Cobbett and Goldsbrough 2002). They play an important role in metal detoxification and metal homeostasis in plants (Macovei et al. 2010), in addition, they play a role in redox maintenance (Macovei et al. 2010), ROS scavenging activities (Wong et al. 2004), repairing plasma membrane (Mishra and Dubey 2006), and also maintaining the growth and repair of damaged DNA (Grennan 2011).

Phytochelatins (PCs) are low molecular weight thiol rich peptides that are synthesized from glutathione (GSH) by the enzyme phytochelatin synthase (PCS) (Emamverdian et al. 2015). They have a strong affinity for HMs and are induced by HMs such as, As, Cd, Cu, Hg, Pb, Zn, Sr, St, Au, Sb, and Se in corn and wheat (Yu et al. 2019). PCs are synthesized in the cytoplasm, where they form stable metal-phytochelatin complexes and are then are transported to vacuoles as their final destination (Chaffai and Koyama 2011; Javed et al. 2019).

3.2.4 Mechanisms of Hyperaccumulation

Some plant species are defined as hyperaccumulators. They can survive in a high concentration of heavy metals due to their hyperaccumulation capacity. Hyperaccumulators have a very high HM uptake capacity at the root membrane level and a very high HM translocation capacity from root to shoot through the xylem. It has been reported that the expression of the HM transporter gene in the plasma membrane of roots of the hyperaccumulating plant *Thlaspi caerulescens* is very high (Pence et al. 2000; Lombi et al. 2001; Sytar et al. 2021). Thus, hyperaccumulator plants, like *T. caerulescens* under HM stress enhance HM translocation from root to shoot and enhance the accumulation of HMs in the leaf or their above-ground tissues, and less accumulation of HMs in the root vacuoles (Lasat et al. 2000; Sytar et al. 2021).

3.2.5 Antioxidant Defence System in Plants

Antioxidants are compounds that are responsible for protecting cells from damage caused by reactive oxygen species (ROS). The antioxidant defence system comprises non-enzymatic components as well as enzymatic components. Non-enzymatic antioxidant components are composed mainly of ascorbate (ASA) and glutathione (GSH), including alkaloids, carotenoids, flavonoids, and tocopherol (Pandey 2018). On the other hand, the enzymatic antioxidant components consist of superoxide dismutase, catalase, glutathione peroxidase, glutathione *S*-transferase, phospholipid-hydroperoxide glutathione peroxidase, ascorbate peroxidase, guaiacol peroxidase, monodehydroascorbate reductase, and glutathione reductase (Pandey 2018).

ASA and GSH are strong antioxidants as they can donate an electron to most of the enzymatic and non-enzymatic reactions (Blokhina et al. 2003). ASA has direct scavenging activity of $^1O_2$, O_2^- and OH radicals and also H_2O_2 reducing activity (Foyer and Noctor 2011). On the other hand, the enzymatic action of superoxide dismutase (SOD) can directly convert O_2^- to reduced H_2O_2 (another ROS) (Kordrostami et al. 2019), which in turn is detoxified by another set of the enzymatic antioxidant system, e.g., ascorbate peroxidase, catalase, peroxidase, glutathione peroxidase (Pandey 2018).

3.2.6 Heat Shock Proteins

Heat Shock Proteins (HSPs) are stress proteins that are expressed when cells experience temperature stress as well as heavy metal stress. They are known as molecular chaperones and play an important role in cellular functions such as the folding and unfolding of proteins, as well as assembly, aggregation, and disaggregation of proteins (Sottile and Nadin 2018). However, under certain stress conditions such as heavy metal stress and temperature stress, HSPs play an important role in protecting and repairing proteins and also maintaining cellular homeostasis (Rhee et al. 2009).

4 Microbial Bioremediation of Heavy Metals in Reducing Metal Stress in Crop Plants

In some plants despite showing some tolerance to heavy metals, heavy metal stress drastically reduces the plants' growth and production (Tiwari and Lata 2018). Microbes are one of the useful natural machinery systems which can be utilized for the bioremediation of heavy metal-contaminated crop fields. This will greatly reduce the stress due to heavy metals in crop plants. Microbial bioremediation is the employment of microbes such as bacteria, fungi, and algae or their products to remove the contaminants (e.g., heavy metals) or to convert them to their non-toxic form in the environment (Tekere 2019). Microbial bioremediation is mainly carried out by two mechanisms, one is biosorption and the other is bioaccumulation (Fernández et al. 2018). Biosorption occurs on the cell surface while bioaccumulation takes place within the cell (Timková et al. 2018). The biosorption generally adsorbs the positively charged heavy metals non selectively to the cell surface and is fast, and therefore the uptake capacity of heavy metal is higher in biosorption than in bioaccumulation where heavy metals are transported from extracellular to the intracellular space via energy-dependent mechanism (Timková et al. 2018). However, biosorption is disadvantageous than bioaccumulation, since the heavy metal bound to the surface during the biosorption process is reversible under certain physico-chemical changes in the environment, which is not in the case with bioaccumulation (Malik 2004).

Not all microbes have the ability to perform HM bioremediation. The bioremediation efficiency of microbes may also vary from strain to strain and from metal to metal. Besides, some microbes are highly tolerant to a wide range of HMs and others to only a few heavy metals. Therefore, considering all these factors in mind, adequate scientific investigation is required to identify the correct microbial species and combinations of microbes for a given contaminated site. Considering that, the use of microbial consortium is more advantageous than using a single strain of microorganism for heavy metal bioremediation (Kang et al. 2016), a well-designed microbial consortium is always a better option.

4.1 Heavy Metal Uptake and Detoxification Mechanism in Microbes

Many strains of microbes are resistant to HMs, which can be inherited or acquired during exposure to elevated HM conditions. The resistant microbes have several protective mechanisms against the toxic effects of HMs, from the restriction of HMs entry into the cell through various binding/biosorption mechanisms on the cell surface to the detoxification or compartmentalization of HMs within the cell or their exclusion from the cell after they get entry into the cell (Fig. 1). The various mechanisms that microorganisms use to cope with the elevated heavy metal concentration in the soil can involve one or more of the following mechanisms:

(a) HMs biosorption at the cell surface such as adsorption, precipitation, complexation, or ion exchange
(b) Extracellular sequestration which is metal-metabolite complexation in the periplasmic space
(c) Intracellular sequestration which is complexation or chelation of metal ions by various compounds, enzymes, and regulatory molecules inside the intracellular space
(d) The metal transformation which involves methylation, oxidation, reduction, and dealkylation of metal or organo-metal compounds and
(e) Exclusion of metal ions/metal complex out of the cell which is either through volatilization of volatilizable metal compounds or through efflux mechanism (Javanbakht et al. 2014; Diep et al. 2018; Rehan and Alsohim 2019).

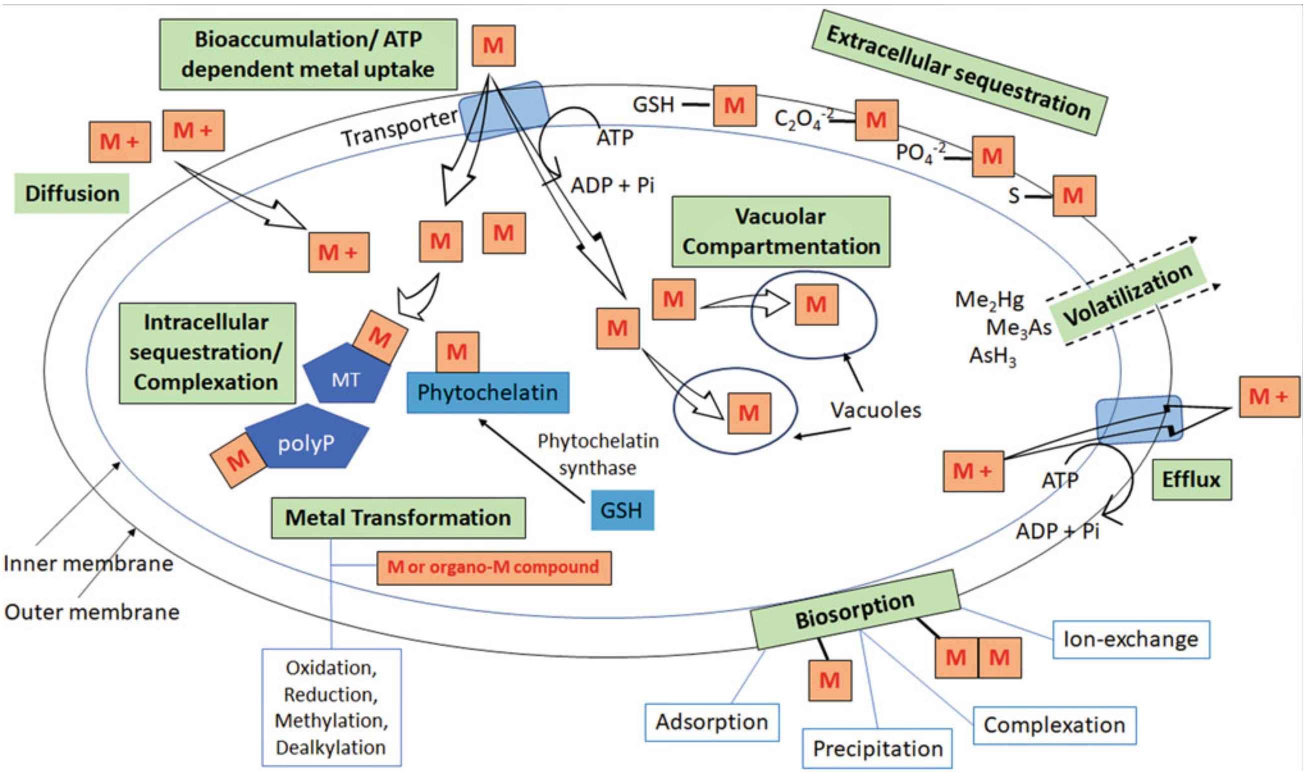

Fig. 1 Mechanisms involved in the microorganisms mediated alleviation of heavy metal stress

HMs can enter the microbial cell either via a diffusion mechanism which is an energy-independent mechanism or via bioaccumulation through various membrane protein complexes or membrane transport protein, which is an energy-dependent mechanism (Diep et al. 2018).

4.1.1 Biosorption

Biosorption occurs at the cell surface of the cell wall or cell membrane, they are non-specific, non-metabolic, and do not discriminate between live and dead cells (Fomina and Gadd 2014). The presence of anionic moieties in the microbial cell surface such as carboxyl, carbonyl, hydroxyl, sulfhydryl, and phosphoryl groups provides the binding sites for heavy metals in the cell wall, where they immobilize the metal ions for uptake (Volesky 2003; Michalak et al. 2013; Fomina and Gadd 2014). In the below subsections, various mechanisms by which HMs are biosorbed in the cell wall are given below.

Adsorption

Adsorption of heavy metals on the cell surface may occur either due to van der wall force or due to electrostatic interaction which is rapid, and reversible (Javanbakht et al. 2014). The heavy metal absorption mechanism of Cd, Cu, Co, Zn, and U on the dead biomass of fungi and algae is mainly due to the electrostatic interactions between the cell wall and the metal ions (Igiri et al. 2018).

Complexation

The metal removal by complex formation on the cell wall is also one of the important biosorption mechanisms adopted by microorganisms. Certain groups such as amino, carboxyl, thiol, hydroxyl, phosphate, etc., present in the cell wall are involved in the complexation of heavy metals in the cell wall (Sag and Kutsal 2001). A complex compound formed can be positive, negative, or neutral charge and usually consists of one or more central atoms surrounded by many other atoms or groups of atoms. The complex compound when its central atom is bound or attached with other ligands through two or more coordinating atoms is termed as chelate (Naja et al. 2010). In some cases, microbes produce organic acids such as citric acid, malic acid, lactic acid, fumaric acid, etc. on their cell surface which chelates the metals to form organo-metal molecules (Javanbakht et al. 2014). It has been reported that the sole removal mechanism of Cu^{+2} from aqueous solution is by complexation with anionic ligand (CO_3^{-2}, OH^- and SO_4^{-2}) present in the microbial cell surface (Sarioglu et al. 2009), and also the main mechanism for absorption of heavy metals (Ca, Cd, Cu, Hg, Mg, and Zn) in *Pseudomonas syringae* is through complexation (Javanbakht et al. 2014).

Ion Exchange

Ion exchange is another important defence mechanism adopted by microorganisms, where heavy metals are absorbed through ion exchange between metal ions and the microbial cell wall preventing entry of toxic metals into their intracellular space. The microbial cell wall contains polysaccharides as one of the major components where the exchange of metal ions takes place with the ions already present in the polysaccharide (Javanbakht et al. 2014). Extracellular polymeric substance (EPS) is also secreted in some cases of bacteria which facilitates absorption of metal ions by ion exchange (Mwandira et al. 2020). Some examples of absorption due to ion exchange are biosorption of Pb (II) and Cd (II) in biomass of fungus *Lactarius scrobiculatus* (Anayurt et al. 2009), and fungus *Amanita rubescens* (Sari and Tuzen 2009), biosorption of Pb^{+2} in marine alga *Gelidium amansii* (El-Naggar et al. 2018), and biosorption of Pb (II) and Zn (II) in EPS of *Oceanobacillus profundus* (Mwandira et al. 2020).

Precipitation

Precipitation of metals may occur either on the cell surface or in the solution when microbial cells secrete hydrogen sulfide (H_2S) or inorganic phosphate outside the cell. Microbial precipitation of heavy metals occurs either as a result of metabolic processes or dissimilatory reduction of metals (Valls and de Lorenzo 2002). Precipitation of metals by microbial metabolism generated alkalinity has been demonstrated in a study by Remoudaki et al. (2003). In another study, precipitation of HMs to insoluble metal sulfides by H_2S production by yeast cells has been demonstrated (Minney and Quirk 1985).

4.1.2 Bioaccumulation

Bioaccumulation involves extracellular as well as intracellular processes that depend on many physical, chemical, or biological mechanisms (Fomina and Gadd 2014). The bioaccumulation process starts when the microbial cells uptake HMs inside the intracellular space through a metabolically active process, followed by HMs sequestration by proteins and peptide ligands present there in the cytoplasm (Mishra and Malik 2013). The fate of metals inside the intracellular space may be different where they may be transformed into different compounds via oxidation, reduction, methylation, and alkylation, or compartmentalized inside the vacuoles in the case of fungi, or they may be excreted out (Mahmoud 2021).

4.1.3 Diffusion

HM ions can also be transported to intracellular space via energy independent diffusion mechanism which usually functions for the transportation of other metabolically important ions such as sodium, potassium, and magnesium. Diffusion is the passive form of transportation mechanism which does not require ATP during the process and the metal ions pass through the permeable membrane across a concentration gradient mimicking other metabolically important ions. The membrane permeability greatly accounts for the uptake of metal ions in this process (Mane et al. 2011), which is affected by temperature. Increasing temperature increases the membrane permeability and the rate of diffusion of metal ions in microbial cells (Ayangbenro and Babalola 2017).

4.1.4 Extracellular Sequestration

Microbes produce several metabolites such as phosphate, glutathione, oxalate, sulfur, etc., in their cell membrane which can bind metals, forming metal-metabolite complexes accumulating in the periplasmic space and thus, preventing the passage through the membrane. Copper-resistant bacteria, when exposed to copper, induce proteins such as CopA and CopB, both periplasmic proteins, and CopC, an outer membrane protein that binds the copper ions preventing copper toxicity (Andrei et al. 2020). Metal precipitation using microbes (bioprecipitation) used for the bioremediation of heavy metals in effluents and other aqueous solutions is also an example of an extracellular sequestration mechanism. Bioprecipitation occurs via the excretion of certain metabolites by the microbial cells such as carbonate, sulfide, phosphate, and hydroxide, out of which sulfide precipitation produces the most stable precipitation product (Kumari et al. 2016). Metal immobilization via carbonate precipitation has also been reported (Kumari et al. 2016). *Geobacter* spp. (Iron-reducing bacterium) and *Desulfuromonas* spp. (sulfur-reducing bacterium) can reduce the toxic form of metals to their non-toxic forms. *G. metallireducens* have been reported to reduce toxic Mn (VI) to less toxic Mn (II), and toxic U (VI) to less toxic U (IV) (Gavrilescu 2004). Similarly, *G. sulfurreducens* and *G. metallireducens* have been reported to reduce toxic Cr (VI) to less toxic Cr (III) (Gavrilescu 2004).

4.1.5 Intracellular Sequestration

Intracellular sequestration can be defined as the complexation of metal ions inside the cell cytoplasm by various compounds, enzymes, and regulatory molecules such as metallothionein (MT), glutathione (GSH), and polyphosphate present inside the intracellular space. The mechanism is triggered as a protective mechanism to protect the essential cellular components when more and more metal ions enter the intracellular space either through diffusion or via active transport (Raja Sathendra et al. 2018). In yeasts, metal accumulation is mainly due to ATP-dependent bioaccumulation and intracellular sequestration rather than ATP-independent biosorption (Gadd 1994). However, the percentage of the metal absorbed via extracellular or intracellular pathway may vary from microbe to microbe and from strain to strain (Sedlakova-Kadukova et al. 2019). Intracellular sequestration of metals such as Cd, Cu, and Zn have been reported in *Pseudomonas putida* and Cd in *Rhizobium leguminosarum* (Igiri et al. 2018).

4.1.6 Methylation of Metals

Methylation of metals inside the microbial cell cytoplasm occurs as a part of the detoxification mechanism or as a part of cellular metabolism in forming intermediates. One or more methyl groups may be added to the metals and may play a significant role in metal bioremediation. Methylation of metals increases the permeability of metals across the cell membrane and in some instances volatilization of volatilizable methylated-metal compounds, which helps regulate metal homeostasis in the cell cytoplasm. Methylation of metals such as As, Bi, Cd, Ge, Hg, Pb, Sb, Se, Sn, Te, and Tl has been reported in microbes (Thayer 2002). Methylation of Hg (II) to form gaseous methyl mercury has also been reported in bacteria viz. *Bacillus* spp., *Escherichia* spp., *Clostridium* spp., and *Pseudomonas* spp. (Ma et al. 2019; Priyadarshanee et al. 2022). Methylation of other metals such as Arsenic to gaseous arsines, Selenium to volatile dimethyl selenide, and lead to dimethyl lead has also been reported (Ramasamy et al. 2007).

4.1.7 Reduction of Metals

Microbes use metals as electron donors by reducing them. This changes the oxidation state of metals from one oxidation state to another and reduces their toxicity. The reduction of heavy metals from their toxic form to non-toxic form by the enzyme activities of microbes has been reported in many studies. Reduction of Cr(VI) to Cr(III), Hg(II) to Hg(0), and Se(V) to Se(0) are a few examples of reduction of heavy metals from toxic form to their non-toxic form due to the microbial enzyme action (Mishra et al. 2012; Tan et al. 2016; Liu and Wiatrowski 2017).

4.1.8 Vacuolar Compartmentation of Heavy Metals

The vacuoles present in fungus plays an important role in fungal metabolism and has a wide variety of functions like degradation of macromolecules, storage of small molecules and biosynthetic precursors (amino acids and polyphosphates), regulation of cytosolic ions, pH, and amino acid concentration in the intracellular space (Klionsky et al. 1990; Yang et al. 2017; Ying and Feng 2018; Nguyen et al. 2019; Demes et al. 2020). Vacuoles also have an important function in the maintenance and regulation of metal ion concentration in the cytosol, by storing extra metal ions inside the vacuolar compartment. Thus, vacuoles play an important role in regulating the essential metabolic functions as well as detoxifying the potentially toxic metals in fungi (Priyadarshini et al. 2021).

4.2 Bioremediation Approaches

Bioremediation of contaminated sites can be achieved by either addition of microbes having heavy metal bioremediation capacity or stimulating the growth of native microbes already present in the heavy metal polluted sites. These have been described below.

4.2.1 Bioaugmentation

Bioaugmentation is the introduction of microbes directly into the contaminated sites for bioremediation. The microbes used for the bioaugmentation may be of natural origin or genetically engineered, and the application may involve either a single strain or multiple strains. However, the bioaugmentation method employing a consortium of multiple microbial strains is considered to be more effective than using a single microbial strain type (Emenike et al. 2018). Since the bioaugmentation process involves the direct application of microbes to the contaminated area, both biotic and abiotic factors influence the microbial growth as well as the bioremediation processes.

4.2.2 Biostimulation

Biostimulation is another approach that can be used for the bioremediation of heavy metals in a contaminated environment. It involves stimulating the already present microbial community in the contaminated site to flourish and resist more heavy metals by providing them with suitable growth conditions (Adams et al. 2015). The nutrients such as carbon, nitrogen, phosphorus, and oxygen can be added to enhance the growth of the native microbiota, which helps enhance the bioremediation process (Bundy et al. 2002; Al-Sulaimani et al. 2010).

4.3 Bacterial Bioremediation and Reduction of Heavy Metal Stress in Plants

Bioremediation of heavy metal contaminated sites using bacteria have been studied widely. Bacteria can help the plants in two ways, one by reducing the metal stress experienced in plants by directly removing or decreasing the toxic metals bioavailable to the crop plants, and other by providing nutrients and chemicals, which promotes and induce plants for their growth, proliferation, and metal tolerance under the heavy metal stress condition. A class of bacteria called plant growth-promoting rhizobacteria

(PGPR) have been shown to induce various tolerant mechanisms in plants against heavy metal stress conditions besides improving plant growth (Swamy et al. 2019; He et al. 2020). Many other bacteria have also been reported to show bioremediation capacity to different heavy metals in a wide range of heavy metal contaminated sites (Table 2). Due to their high efficiency in metal removal, eco-friendly and low cost, the use of bacteria for bioremediation of heavy metals is suggested by many scientists for reducing heavy metal stress in plants. Emenike et al. (2017) conducted bioremediation of heavy metal contaminated soil using a consortium of bacteria containing *Bacillus* sp., *Lysinibacillus* sp., and *Rhodococcus* sp. and reported a reduction of 72% Al, 41% Cd, 88% Cu, 65% Mn, and 71% Pb. Fauziah et al. (2017) also reported individual bioremediation potential of bacteria such as *Bacillus thuringiensis, Lysinibacillus sphaericus,* and *Rhodococcus wratislaviensis* to Al, Cd, Cr, Fe, Ni, Pb, and Zn from heavy metal contaminated soil. It has been suggested that immobilization of bacteria in sodium alginate beads, chitosan beads, or other materials, before use in the field is a very critical factor for achieving successful bioremediation as it protects the bacterial cell against the direct effect of extrinsic factors and ensures viability over a long period in the application site (Zommere and Nikolajeva 2017). The other advantage of immobilization is the prevention of inhibition between the interacting bacteria when applied in the form of a consortium, which otherwise negatively affects the bioremediation efficiency (Zommere and Nikolajeva 2017).

4.3.1 PGPR in Reducing Heavy Metal Stress in Plants

The use of plant growth-promoting rhizobacteria (PGPR) for heavy metal bioremediation is also widely studied. PGPR improves plant growth by producing volatile organic compounds which control plant pathogens, increasing nutrient uptake in plants, and reducing the toxic effects of heavy metals by producing siderophores, amino acids, proteins, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase (Swamy et al. 2019; He et al. 2020). In one of the studies, the reduction in heavy metal contents and improvement in crop production was reported as a result of the application of heavy metal tolerant PGPR such as *Bacillus, Methylobacterium, Pseudomonas,* and *Streptomyces* in the cropland (Sessitsch et al. 2013). Several other studies also reported the reduction in the bioavailability of heavy metals and improvement of crop production with the application of PGPR in soil (Solano et al. 2008; Ma et al. 2011; Prasad et al. 2019; Bano and Javed 2021). In another study, Pandey et al. (2013) demonstrated the growth improvement in rice cultivar with the application of two metal resistant PGPR isolates, *Ochrobactrum* sp. (resistant to Cd) and *Bacillus* spp. (resistant to Pb and As). Therefore, the use of PGPR is one great option for reducing heavy metal stress in crop plants and promoting their growth and production.

4.4 Fungal Bioremediation and Reduction of Heavy Metal Stress in Plants

Fungi are one of the key organisms for breaking down many natural and xenobiotic materials. They are also considered to be one of the important groups of organisms that play important role in the global geochemical cycle. The use of fungi for bioremediation of contaminants is known as mycoremediation (Rhodes 2014). Like PGPR, a group of plant root-associated fungi called arbuscular mycorrhizal fungi (AMF) are very promising as they can improve plant growth under the metal stress by providing nutrients, improving water absorption, and controlling stomata conductivity, and they can also reduce the bioavailability of the heavy metal concentration in the soil by various mechanisms such as immobilization inside their cell, precipitation and chelation in their cell surface, and compartmentalization in their vacuoles (Dhalaria et al. 2020). The use of fungi as a bioremediator has also certain advantages as they can colonize diverse niches and habitats and leave no harmful products on the treatment sites. Since many of them are also isolated from various heavy metal contaminated sites, their use as a bioremediator is more logical and efficient, as their chance of survival in a metal-contaminated environment is always high. So far there have been many reports on the use of fungi as bioremediation agents for the bioremediation of various heavy metals (Table 2). *Saccharomyces cerevisiae* was found to bind up to 65–79% of Pb and Cd from contaminated soils (Damodaran et al. 2011). In another study, *Aspergillus* sp. was found to remove 65% of Cr contaminant from tannery effluents (Srivastava and Thakur 2006a). The removal of various other heavy metals such as Cd, Zn, Fe, Ni, Pb, Ag, Th, Ra, and U using various common filamentous fungi from the contaminated wastewater was also documented (Bishnoi and Garima 2005). Therefore, fungi can be an effective agent for the bioremediation of cropland contaminated with heavy metals. However, the efficiency of mycoremediation will also depend on multiple factors such as selection of fungal strain, use of different combinations of fungi, abiotic factors such as pH, temperature, moisture content, etc.

4.4.1 Arbuscular Mycorrhizal Fungi in Reducing Heavy Metal Stress in Plants

Arbuscular mycorrhizal fungi (AMF) are reported as one of the most potent fungi for bioremediation of cropland as they can uptake HMs from the rhizospheric zone and store them in their vesicles which is analogous to vacuoles of other fungi, thus preventing the plants against HM stress (Dhalaria

Table 2 List of microorganisms used for heavy metal bioremediation

Heavy metal	Microorganisms	References
Bacteria		
Arsenic (As)	*Stenotrophomonas* sp.	Bahar et al. (2012)
	Sporosarcina ginsengisoli	Achal et al. (2012), Coelho et al. (2015)
	Desulfovibrio desulfuricans	Kim (2015)
Cadmium (Cd)	*Bacillus laterosporus*	Zouboulis et al. (2004)
	Bacillus licheniformis	
	Pseudomonas veronii	Vullo et al. (2008)
	Desulfovibrio desulfuricans	Joo et al. (2015)
	Kocuria rhizophila	Haq et al. (2015)
	Rhodobacter sphaeroides	Peng et al. (2018)
	Microbacterium oxydans	Dabir et al. (2019)
	Rhodococcus sp.	Dabir et al. (2019)
Chromium (Cr)	*Bacillus laterosporus*	Zouboulis et al. (2004)
	Bacillus licheniformis	
	Pseudomonas aeruginosa	Kang et al. (2005)
	Bacillus subtilis	Mangaiyarkarasi et al. (2011)
	Staphylococcus sp.	Kumar et al. (2011)
	Streptomyces sp.	
	Bacillus cereus	Kanmani et al. (2011), Dong et al. (2013), Coelho et al. (2015)
	Pseudomonas putida	Balamurugan et al. (2014)
	Kocuria rhizophila	Haq et al. (2015)
	Desulfovibrio desulfuricans	Joo et al. (2015)
	Enterobacter cloacae	Rahman et al. (2015)
	Cellulosimicrobium sp.	Bharagava and Mishra (2018)
Cobalt (Co)	*Pseudomonas aeruginosa*	Kang et al. (2005)
	Serratia marcescens	Marrero et al. (2009)
Copper (Cu)	*Methylobacterium organophilum*	Kim et al. (1996)
	Pseudomonas jessenii	Rajkumar and Freitas (2008)
	Pseudomonas sp.	
	Pseudomonas veronii	Vullo et al. (2008)
	Micrococcus luteus	Puyen et al. (2012)
	Kocuria flava	Coelho et al. (2015)
Lead (Pb)	*Methylobacterium organophilum*	Kim et al. (1996)
	Bacillus firmus	Salehizadeh and Shojaosadati (2003)
	Bacillus iodinium	De et al. (2008)
	Staphylococcus sp.	Kumar et al. (2011)
	Streptomyces sp.	
	Micrococcus luteus	Puyen et al. (2012)
	Enterobacter cloacae	Kang et al. (2015)
	Rhodobacter sphaeroides	Li et al. (2016b)
	Pseudomonas sp.	Kalita and Joshi (2017)
	Gemella sp.	Marzan et al. (2017)
	Micrococcus sp.	Marzan et al. (2017)
	Pararhodobacter sp.	Mwandira et al. (2017)
	Microbacterium oxydans	Dabir et al. (2019)
	Rhodococcus sp.	Dabir et al. (2019)

(continued)

Table 2 (continued)

Heavy metal	Microorganisms	References
Mercury (Hg)	*Bacillus cereus*	Sinha et al. (2012)
	Vibrio fluvialis	Saranya et al. (2017)
Nickel (Ni)	*Pseudomonas aeruginosa*	Kang et al. (2005)
	Pseudomonas jessenii	Rajkumar and Freitas (2008)
	Pseudomonas sp.	
	Desulfovibrio desulfuricans	Joo et al. (2015)
Zinc (Zn)	*Pseudomonas jessenii*	Rajkumar and Freitas (2008)
	Pseudomonas sp.	
	Pseudomonas veronii	Vullo et al. (2008)
	Desulfovibrio desulfuricans	Kim (2015)
	Rhodobacter sphaeroides	Peng et al. (2018)
Fungi		
Arsenic (As)	*Rhizophagus intraradices*	Spagnoletti and Lavado (2015)
	Aspergillus niger	Acosta-Rodríguez et al. (2018)
	Aspergillus sp.	Segura et al. (2018)
	Penicillium sp.	
	Talaromyces sp.	Nam et al. (2019)
Cadmium (Cd)	*Trichoderma viride*	Joshi et al. (2011)
	Pleurotus platypus	Vimala and Das (2011)
	Saccharomyces cerevisiae	Farhan and Khadom (2015)
	Trichoderma brevicompactum	Zhang et al. (2020a)
	Rhizophagus irregularis	Wang et al. (2020)
Chromium (Cr)	*Aspergillus niger*	Srivastava and Thakur (2006b)
	Aspergillus sp.	Congeevaram et al. (2007)
	Aspergillus sp.	Fukuda et al. (2008)
	Penicillium sp.	Fukuda et al. (2008)
	Aspergillus versicolor	Taştan et al. (2010)
	Gloeophyllum sepiarium	Achal et al. (2011)
	Trichoderma longibrachiatum	Joshi et al. (2011)
	Rhizopus oryzae	Sukumar (2011)
	Rhizophagus irregularis	Kullu et al. (2020)
	Trichoderma brevicompactum	Zhang et al. (2020a)
Cobalt (Co)	*Aspergillus niger*	Acosta-Rodríguez et al. (2018), Cárdenas González et al. (2019)
	Paecilomyces sp.	Cárdenas González et al. (2019)
	Penicillium sp.	
Copper (Cu)	*Phanerochaete chrysosporium*	Iqbal and Edyvean (2004)
	Aspergillus niger	Dursun (2006)
	Aspergillus versicolor	Taştan et al. (2010), Coelho et al. (2015)
	Aspergillus flavus	Gazem and Nazareth (2012)
	Rhizopus oryzae	Fu et al. (2014)
	Trichoderma brevicompactum	Zhang et al. (2020)

(continued)

Table 2 (continued)

Heavy metal	Microorganisms	References
Lead (Pb)	*Phanerochaete chrysosporium*	Iqbal and Edyvean (2004)
	Botrytis cinereal	Akar et al. (2005)
	Aspergillus niger	Dursun (2006)
	Aspergillus terreus	Joshi et al. (2011)
	Aspergillus flavus	Gazem and Nazareth (2012)
	Saccharomyces cerevisiae	Farhan and Khadom (2015)
	Aspergillus fumigatus	Gill et al. (2021)
Mercury (Hg)	*Aspergillus niger*	Acosta-Rodríguez et al. (2018), Khan et al. (2019)
	Aspergillus flavus	Khan et al. (2019)
	Aspergillus fumigatus	
	Aspergillus terreus	
Nickel (Ni)	*Aspergillus* sp.	Congeevaram et al. (2007)
	Aspergillus versicolor	Taştan et al. (2010), Coelho et al. (2015)
	Aspergillus niger	Joshi et al. (2011)
Silver (Ag)	*Pleurotus platypus*	Das et al. (2010)
	Aspergillus alliaceus	Cecchi et al. (2017)
	Clonostachys rosea	
	Trichoderma harzianum	
Zinc (Zn)	*Phanerochaete chrysosporium*	Iqbal and Edyvean (2004)
	Aspergillus niger	Acosta-Rodríguez et al. (2018)
	Trichoderma brevicompactum	Zhang et al. (2020a)
Algae		
Arsenic (As)	*Annochloropsis* sp.	Upadhyay et al. (2016)
	Botryococcus braunii	Podder and Majumder (2016)
	Chlorella vulgaris	Upadhyay et al. (2016)
	Anabaena sp.	Ranjan et al. (2018)
Cadmium (Cd)	*Arthrospira indica*	Kiran et al. (2012)
	Hydrodictyon reticulatum	Ammari et al. (2016)
	Cladophora rupestris	Zhang et al. (2019)
	Microcystis aeruginosa	Deng et al. (2020)
Chromium (Cr)	*Cladophora glomerata*	Al-Homaidan et al. (2018)
	Enteromorpha intestinalis	
	Microspora amoena	
	Chlorella sp.	Losada et al. (2018)
	Scenedesmus sp.	Losada et al. (2018)
Cobalt (Co)	*Scenedesmus bernardii*	Fawzy et al. (2020)
	Synechocystis pevalekii	
	Chlorella vulgaris	Kim et al. (2020)
	Haematococcus sp.	
	Vacuoliviride crystalliferum	Kim et al. (2020)

(continued)

Table 2 (continued)

Heavy metal	Microorganisms	References
Copper (Cu)	*Chlamydomonas reinhardtii*	Flouty and Estephane (2012)
	Chlorella vulgaris	Suresh Kumar et al. (2015)
	Fucus vesiculosus	El-Naggar et al. (2021)
Lead (Pb)	*Spirulina* sp.	Chen and Pan (2005)
	Chlamydomonas reinhardtii	Bayramoğlu et al. (2006)
Mercury (Hg)	*Chlamydomonas reinhardtii*	Bayramoğlu et al. (2006)
	Chlorella vulgaris	Suresh Kumar et al. (2015)
Nickel (Ni)	*Planothidium lanceolatum*	Doshi et al. (2008), Sbihi et al. (2012)
	Spirulina sp.	
Zinc (Zn)	*Planothidium lanceolatum*	Doshi et al. (2008), Sbihi et al. (2012)
	Spirulina sp.	
	Microcystis aeruginosa	Deng et al. (2020)

et al. 2020). They also secrete glomalin, a glycoprotein that binds heavy metals by forming glycoprotein–metal complexes which help reduce the toxic metals available for uptake by the plants (Dhalaria et al. 2020). One example of AMF which can accumulate heavy metals is *Glomus intraradices,* which can accumulate large amounts of HMs like Zn, Cu, and Cd in their subcellular structures (cell wall, cytoplasm, and vacuoles) (González-Guerrero et al. 2008). AMF such as *Rhizophagus intraradices* has been shown to reduce As stress in soybean plants by decreasing the exposure to As toxicity which leads to the decrease As accumulation (Spagnoletti and Lavado 2015). In another study, Gunathilakae et al. (2018) showed the increased remediation of Cd from contaminated water with the co-inoculation of AMF and water hyacinth *Eichhornia crassipes* (Mart.) Solms.

4.5 Algae in Reducing Heavy Metal Stress in Plants

Microalgae are the major group of microorganisms that are photosynthetic and found mostly in aquatic environments. Due to their high efficiency in HM bioremediation, sometimes microalgae are termed as a wonder organism (Sreekumar et al. 2020). The bioremediation using algae is termed phycoremediation. Microalgae work by either bio-assimilation or biosorption mechanism to reduce the heavy metals available to the plants (Sreekumar et al. 2020). To date, algae have been found efficient for the bioremediation of several toxic HMs viz. Cd, Cr, Co, Cu, Fe, Hg, Ni, Pb, and Zn. Immobilized *Chlamydomonas reinhardtii* in alginate beads has been reported for potential bioremediation of Hg^{2+} and Pb^{2+} (Bayramoğlu et al. 2006). Similarly, *Spirulina* spp. and *P. lanceolatum* have been reported as potential bioremediator of Ni^{2+} and Zn^{2+} (Doshi et al. 2008; Sbihi et al. 2012). Living or non-living and free or immobilized forms of *C. vulgaris* have been used many times for the bioremediation of Cu^{2+} and Hg^{2+} from contaminated sites (Suresh Kumar et al. 2015). Mostly used algal taxa for heavy metal bioremediation belongs to *Anabaena, Lyngbya, Microcystis, Oscillatoria, Spirulina, Synechocystis, Microcystis,* etc. (Bhattacharya et al. 2015).

4.6 Genetically Engineered Microorganisms for Heavy Metal Bioremediation

Any microorganisms whose genetic make-up has been altered or modified using recombinant DNA technology are termed genetically engineered microorganisms (GEM) or genetically modified microorganisms (GMM). In GEM, a foreign gene of novel quality from other organisms is inserted into their genome through recombinant DNA technology. Therefore, GEM can inherit multiple functions from different organisms, making them more efficient in any purpose than their natural counterparts. Bioremediation of heavy metals using GEM has been reported in several studies (Gupta and Singh 2017; Diep et al. 2018). Despite having greater efficiency in heavy metal bioremediation, GEMs are restricted only to the laboratory scale and not in the field conditions due to the high risk associated with the uncontrolled release of them into the environment and probable horizontal gene transfer. Most of the genetic modifications carried out in microbes for heavy metal bioremediation involve the insertion of metal uptake genes such as *mer*A for mercury removal and *Ars*M for arsenic removal into the competent cells (Ojuederie and Babalola 2017). Other modifications involve cloning and expression of *phytochelatin (PC) synthase* gene, *manganese transporter* gene (*mnt*A), and *metallothionein* (*MT*) gene for uptake and accumulation of cadmium (Kim et al. 2005; Gupta and Singh 2017). Genetically engineered *Pseudomonas putida* strain KT2442::mer73 containing mer TPAB operon has been reported for efficient removal of mercury ion in a three-phased fluidized bed (TPFB) bioreactor (Deckwer et al. 2004). In another study, *E. Coli* was genetically engineered by incorporating heavy metal capturing gene (encoding SynHMB protein) and a synthetic type VI secretory system (T6SS) cluster of *Pseudomonas putida* for the effective removal of Cd^{2+} and Pb^{2+} (Zhu et al. 2020).

Recently, genome editing technology based on cas9 protein called Clustered Regularly Interspaced Short Palindromic Repeats (CRISPER)-Cas9 technology has been developed which has a wide scope of application (Kanchiswamy et al. 2016). CRISPER-Cas9 technology however has not been utilized yet for editing genes in the microbial system for heavy metal bioremediation purposes, but there are some reports on the use of this technology for the reduction of heavy metals in plants (DalCorso et al. 2019). The CRISPER-Cas9 system has very high specificity in gene sequence editing, therefore this technology can be a boost for the bioremediation of heavy metals using microbes in the future (Jaiswal and Shukla 2020). This technology can be implemented for the improvement of heavy metal bioremediation potential in microbes which can be achieved either by editing a gene of interest or modulating the gene expression for the synthesis of metal ligands or other metal biosorption/bioaccumulation pathways.

5 Omics Technology in Heavy Metal Bioremediation

Omics technologies which include genomics, transcriptomics, proteomics, metabolomics, metagenomics, metatranscriptomics, and metaproteomics are the advanced molecular tools that are useful for studying the structural and functional properties of a single organism or a group of organisms (microbiome). Genomics, transcriptomics, proteomics, and metabolomics are termed traditional omics technology which is a lengthy process and requires the isolation of individual microbes from the environment. On the other hand, metagenomics, metatranscriptomics, and metaproteomics are regarded as advanced omics tools or post-genomics tools since the structure and functions of microbes at the community level can be studied at one go in a very rapid way.

Genomic analysis is necessary for the prediction and/or identification of gene(s) associated with the HM resistance or accumulation of an organism. Ayangbenro and Babalola (2020) analysed the genome of bacteria *Bacillus cereus* NWUAB01 and reported putative genes for the resistance and uptake of heavy metals such as As, Cd, Cr, Pb, and Zn. Thus genome study helps in the proper understanding of the mechanism of resistance and transport of heavy metals which is important to design and improve a microorganism for efficient bioremediation purposes. The genomic analysis provides the total gene contents of an organism, but it does not provide which genes are expressed and which are not. The transcriptomic study, therefore, is another branch of omics which provides the expression profiles of an organism. Transcriptomics is the study of the total mRNA of an individual organism and it helps in finding genes in microorganism which is expressed when they are exposed to various physiological conditions. Therefore, using transcriptomic tools, one can find out the genes exactly responsible for heavy metal bioremediation. Accordingly, Lu et al. (2017) reported the upregulation of six new heavy metal resistance genes viz. *CueO* (a multicopper oxidase gene), *Omp* (an outer membrane protein), *YedYZ* (a sulfite oxidoreductase gene), and three other hypothetical protein genes in bacterium *Sinorhizobium meliloti* CCNWSX0020 through transcriptomic analysis. Proteomic analysis, on the other hand, provides the phenotypes of the microorganisms that are not possible in genomic analysis. The proteomic analysis allows us to identify the key proteins involved and their changes in the structure and function in a given environmental condition (Singh et al. 2020). It also allows us to study the upregulation and downregulation of various protein sets on exposure to a particular heavy metal or other types of pollutants (Hivrale et al. 2015). In bioremediation studies, the proteomics approach is very useful in analysing the physiological changes occurring inside microbes as well as observing the regulation of related genes. Proteomics also helps in identifying unknown genes and proteins in microbes that are involved in specific heavy metal bioremediation. For example, Chuanboon et al. (2019) discovered a new cadmium binding protein DUF326-like domain in *Enterobacter cloacae* which are involved in the tolerance and accumulation of Cd.

In any natural ecosystem, microbes live in a community and they show a complex network of interactions. The community structure of an ecosystem may change with the changing environmental conditions. As some groups of microbes are more favourable to a particular environment than the other, microbial succession is a phenomenon in such changing environment. The successional change of microbial structure and metabolism at the community level can be studied through various meta-omics technologies such as metagenomics, metatranscriptomics, and metaproteomics. Metagenomics is the study of environmental genomics or community genomics by directly taking environmental DNA from an environmental sample representing the microbiome (Riesenfeld et al. 2004). Thus, they provide the overall genome content and the structural or taxonomic composition of an environmental microbiome. Metatranscriptomics, on the other hand, is the study of expression profiles of microbial community genes by taking the total mRNA directly from the environment (Aguiar-Pulido et al. 2016) and they provide the total functional profile of an environment. Metaproteomics also called community proteomics or environmental proteomics is the quantitative and qualitative study of all the proteins collected from an environment (Bharagava et al. 2019). However, the use of single meta-omics technology has certain limitations such as metagenomics alone cannot identify the expression of genes, metatranscriptomics which employs mRNA are highly unstable, and metaproteomics alone cannot give complete bioremediation pictures and therefore the use of multi-meta-omics or microbiome technologies is suggested as a preferred approach for better understanding the molecular mechanisms involved in bioremediation (Malik et al. 2021). Noble genes responsible for the biodegradation of aromatic compounds have been identified in a study conducted by Yadav et al. (2015) using comparative metagenomics and real-time qPCR. However, this kind of work employing omics technology for heavy metal bioremediation is very rare to find and can be employed as an effective tool in the future.

6 Prospects of Microorganisms in Heavy Metal Stress Management

Microbes have been studied for bioremediation of a wide range of heavy metals and isolated from a wide range of contaminated sites. We also know their effectiveness in the bioremediation of heavy metals and underlying heavy metal absorption and detoxification mechanism, but despite this, their application in the field is still rare and mostly limited to the laboratory condition or pilot scale. For a successful usage of microbes in the field, it becomes very important to study rigorously and systematically the various microbial strains keeping in mind the specific type of HMs contamination to be treated. Since, microbes may be tolerant to only some groups of heavy metals and may be sensitive to other metals, prior screening of microbial strains to different heavy metals at different concentrations is very important to identify the potential multi-metallotolerant strains. Microbiome study of rhizospheric soils taken from the croplands treated with potent microorganisms can help in a proper understanding of the mechanisms that the microbes detoxify or accumulate the HMs while in association with the crop plants.

7 Conclusion

Heavy metal pollution in cropland in both urban and rural areas due to natural and anthropogenic activities is of great concern because of its accountable impact on global crop production. There are many approaches for remediation of heavy metal polluted soils, but bioremediation using microbes (bacteria, fungi, and algae) are eco-friendly, less expensive, and leaves no toxic chemicals upon application. Therefore, microbial bioremediation is regarded as the gold option for cleaning heavy metal pollution in cropland. Free-living metallotolerant microbes with heavy metal accumulating capacity could be used to remove the HM contaminants from the croplands. Alternatively, the use of metal accumulating or detoxifying PGPR or AMF can be applied together with the crop plants to overcome the HM stresses in the crop fields. Some improved genetically engineered microorganisms (GEMs) have already been developed for HM bioremediation, but their application in the field is not widely accepted due to various ethical concerns, including the possibility of horizontal transfer of an artificial or modified gene from the GEM to other naturally occurring microbes. However, in recent years, the development of eco-friendly hyperaccumulator microbes through gene-editing technology is very much possible which can be used for either bioremediation or reduction of HM stress in croplands.

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Halotolerant Plant Growth Promoting Rhizobacteria: A Futuristic Direction to Salt Stress Tolerance

Kavya Bakka, P. V. Gopika, Haresh Sreelakshmi,
and Dinakar Challabathula

Abstract

Salinity is one of the most devastating abiotic stresses known to affect all the major processes such as germination, photosynthesis, water relations, nutrient uptake, reproduction, etc., affecting the growth and yield of the majority of the plants. High salinity-induced decrease in water potential causing osmotic stress and accumulation of salt-induced oxidative damage are major causes for the limitation in plant growth, productivity and cell death in the majority of plants. Employment of Plant Growth Promoting Bacteria (PGPB) is a well-studied alternative for the protection of plants from salinity stress-induced detrimental effects. Since rhizospheric bacterial communities have a direct influence on the physiology and development of plants, identification and characterization of plant beneficial microbes are important. Halotolerant Plant Growth Promoting Rhizobacteria (PGPR) are beneficial microbes that colonize internal and external parts of the plant roots and play a pivotal role in improving plant growth and alleviating the adverse effects of salinity stress. They influence the physiology and development of plants by producing various plant growth-promoting traits that have a direct effect on the growth and stress tolerance of plants. Efforts are taken to identify and characterize the PGPR from different rhizosphere zones and prepare the consortia for agricultural applications thereby reducing the usage of synthetic fertilizers and agrochemicals. In the current chapter, we describe the general effects of salinity stress in plants, highlighting the importance of employment of PGPR either in isolation or consortia for the preparation of bioformulations for agricultural applications and improvement of salinity tolerance.

Keywords

Exopolysaccharides • Osmolytes • Phytohormones • Plant growth promoting rhizobacteria • Salinity stress

Abbreviations

ABA	Abscisic acid
ACC	1-Aminocyclopropane-1-carboxylic acid
IAA	Indole-3-acetic acid
PGPB	Plant growth promoting bacteria
PGPR	Plant growth promoting rhizobacteria
ROS	Reactive oxygen species

1 Introduction

An increase in soil salinity is one of the adverse abiotic stress conditions that occur through natural and anthropogenic reasons. Accumulation of water-soluble salts in the soil is the main cause of soil salinization, having a strong impact on agricultural productivity and environmental health (Rahman et al. 2021). Soil salinity changes the fertile land to unproductive land, ultimately resulting in loss of crop productivity and economical loss. The high salt accumulation in the soils can be due to low precipitation, weathering of native rocks, geological deposits, ground water with high salt, poor agricultural practices, evapotranspiration and lack of rainfall to flush the salts (Parihar et al. 2015; Hanin et al. 2016). The soils having an electrical conductivity of the saturation soil extract of more than 4 deciSiemens/meter (dS/m^{-1}) at 25 °C are considered saline soils. However, the limit can be lowered to 2 dS m^{-1} for the fruits and ornamental plants which can be seriously affected by the salinity range of 2–4 dS m^{-1}. Compared to normal soil, saline soils show an excessive

K. Bakka · P. V. Gopika · H. Sreelakshmi
Department of Microbiology, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu 610005, India
e-mail: kavyabakka@cutn.ac.in

D. Challabathula (✉)
Department of Life Sciences, School of Life Sciences, Central University of Tamil Nadu, Thiruvarur, Tamil Nadu 610005, India
e-mail: dinakarc@cutn.ac.in

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amount of ionic salts, higher electrical conductivity and lower water potential. Although sodium and chloride are the dominant ions present in saline soils, chlorides and sulphates of sodium, calcium and magnesium are also commonly present. The irrigation water contains calcium, magnesium and sodium and upon water evaporation, calcium and magnesium often precipitate into carbonates leaving sodium in the soil. Accumulation of sodium and chloride in the soil restricts the nutrient-ion activities and generates external osmotic potential restricting the influx of water into the roots thereby resulting in water deficit in plants (Acosta-Matos et al. 2017). Salinity stress is known to adversely affect crop productivity by reducing the net cultivable area, especially in arid and semiarid areas all over the world (Singh and Roychoudhury 2021). High salinity is known to cause ion toxicity, oxidative stress and alteration of metabolism leading to reduced growth, development and crop productivity (Parihar et al. 2015). The situation warrants the development of sustainable methods to increase the productivity of saline soils without causing any damage to the environment (Guzmán et al. 2021). Although breeding for salt-tolerant plants and the development of transgenic plants with salt tolerance capacity can be the solution, the approaches are cumbersome and time-consuming. Under these circumstances, microbes with the potential for plant growth promotion seem to be a viable option. Soil being a reservoir for diverse microorganisms such as bacteria, fungi and archaea is known to host microbes that have the inherent capacity to tolerate high concentrations of salt in soil and possess plant growth-promoting traits. These salt-tolerant microbes particularly bacteria are important for promoting the growth and improving crop productivity in arid and semiarid regions (Egamberdieva et al. 2019). Additionally, several of the bacteria colonize the plant roots and are involved in imparting beneficial effects to the plants. These bacteria are termed Plant Growth Promoting Rhizobacteria (PGPR).

Extensive studies have been performed on the bacteria belonging to the genera, *Acetobacter, Achromobacter, Acinetobacter, Alcaligenes, Arthrobacter, Azoarcus, Azotobacter, Bacillus, Burkholderia, Enterobacter, Exiguobacterium Gluconacetobacter, Methylobacterium, Microbacterium, Ochromobacter Paenibacillus, Pantoae, Pseudomonas, Rhodococcus, Staphylococcus, Serratia, Stenotrophomonas* and *Streptococcus* for their plant growth-promoting traits (Babalola 2010; Dodd and Perez-Alfocea 2012; Chauhan et al. 2015; Egamberdieva et al. 2019). Additionally, since many species of the phytomicrobiome are non-culturable, metagenomics approaches were utilized to decipher the variation in the composition of the microbiome genotype wise (Hirsch and Mauchline 2012; Wintermans et al. 2016). Researchers have used either a single bacterium or a consortium of bacteria under controlled laboratory conditions, greenhouse and field conditions for analysing plant growth promotion in plants (Chauhan et al. 2015). The PGPR strains have also been utilized for commercial agriculture. The ability of the plant growth promoting bacteria to colonize the plant roots and their efficient release of stimulants are critical determinants for evaluating the suitability of utilizing the plant growth promoting bacteria as inoculants for crop improvement and increased productivity under salinity stress conditions. Additionally, research also indicated that the plants efficiently control the composition of the rhizomicrobiome by producing root exudates of varying compositions (Chaparro et al. 2012; Trabelsi and Mhamdi 2013; Zhang et al. 2017). The root exudates as a source of reduced carbon serve as signals to attract specific microbes, favouring their growth, modulate the expression of several genes and induce the cell to cell signaling by quorum sensing (Meneses et al. 2011; Alquéres et al. 2013; Beauregard et al. 2013; Massalha et al. 2017; Smith et al. 2017). In the current chapter, the general effects of salinity stress in plants are briefly outlined with a major focus on highlighting the importance of employment of halotolerant PGPR either in isolation or consortia for agricultural applications and improvement of salinity tolerance.

2 Salt Stress in Glycophytes

Based on the plant's ability to grow and survive under saline environments, they are classified as glycophytes (salt-sensitive) and halophytes (salt-tolerant). Among the angiosperms, while a majority of the crop species are glycophytes whose growth is compromised under saline stress conditions, halophytic plants survive, reproduce and complete their life cycle under high saline soils since they are endowed with varied mechanisms to tolerate salinity (Flowers et al. 1977; Mishra and Tanna 2017; Chen et al. 2018). Salt stress in glycophytic plants affects morphological, physiological and biochemical functions seriously affecting their growth and development at every stage of their life cycle. Salinity stress seriously affects germination, photosynthesis, water relations, nutrient balance, growth and development of crops leading to increased oxidative damage and a drastic reduction in yield (Parihar et al. 2015). Salinity stress in glycophytic plants seriously affects photosynthesis, increases the production of reactive oxygen species thereby causing damage to DNA, membrane lipids and proteins triggering cell death. The decrease in photosynthesis during salinity stress is mainly due to a decrease in chlorophyll content, reduced photosystem II efficiency and electron transport rate (Acosta-Matos et al. 2017).

High salinity in the soil is known to inhibit plant growth either by reducing its ability to take up water, causing water deficit or dehydration in cells or causing excess accumulation of ions resulting in ionic stress (Tester and Davenport 2003; Munns and Tester 2008). The net movement of the water is zero when the salt concentration in the soil is equal to that of the plant, however, the higher salt concentration in the soil leads to movement of water from the plant to the soil causing physiological drought and cellular dehydration (Munns and Tester 2008). While physiological drought imposed by high salinity does not lead to a build-up of either Na^+ or Cl^- ions, whereas the physiological and metabolic processes that are affected are similar to drought stress-affected plants. Contrary to this, ionic stress induced by excess accumulation of Na^+ or Cl^- ions during salinity stress causes oxidative stress leading to damage and cell death. While Na^+ is a non-essential element in the majority of the plants, its intracellular accumulation during salinity stress interferes with K^+ uptake leading to stomatal regulation disturbance causing water loss through transpiration. Compared to Na^+ ions, Cl^- ions are essential for the regulation of turgor pressure, pH and enzyme activities in the plant cell cytoplasm. Accumulation of Cl^- ions cause disturbance in the production of chlorophyll and cause chlorine toxicity symptoms (Tavakkoli et al. 2011; Parihar et al. 2015). Salinity stress-induced excess accumulation of Na^+ in plants causes ionic stress leading to disturbances in K^+ ion efflux thereby causing an imbalance in cellular homeostasis and oxidative stress (Tester and Davenport 2003; Munns and Tester 2008). High salinity-induced accumulation of Na^+ or Cl^- leads to a decrease in uptake of essential nutrients such as phosphorus (P), potassium (K^+), nitrogen (N) and calcium (Ca^{+2}) (Zhu 2001). While maintenance of high tissue and cytosolic K^+/Na^+ ratios are required for salt tolerance, salinity stress-induced Na^+ accumulation in the cytoplasm leads to K^+ ion efflux from both leaf and root cells leading to activation of K^+ outward rectifier channels (GORK, guard cell outward rectifying K^+ channel) for exclusion of K^+ ions (Wang et al. 2009; Demidchik et al. 2014; Shabala and Pottinson 2014). The ability of the plants to retain intracellular K^+ ions is a very important feature for salt stress tolerance since K^+ is an essential nutrient important for many enzymatic reactions and participates in a plethora of plant physiological functions (Ahmad and Maathius 2014; Assaha et al. 2017).

Since the accumulation of high levels of Na^+ ions is detrimental for plants, regulating Na^+ transport in leaves of glycophytic plants is very crucial for salt tolerance. Plant roots exposed to salt in the soil activate several signaling cascades restricting Na^+ influx into the roots and reducing its translocation. While halophytes compartmentalize the Na^+ ions effectively into the vacuoles, the majority of the glycophytic plants succumb to death due to overaccumulation of Na^+ ions in the cytoplasm (Bartels and Dinakar 2013). The reduced influx and increased efflux along with sequestration of Na^+ ions into the vacuole are the major determinants of plants aiding in acclimation or tolerance to salinity stress. Salinity stress-induced accumulation of compatible osmolytes and increased antioxidants to scavenge the reactive oxygen species leading to a decrease in oxidative stress are considered important strategies to combat salinity stress by plants (Bartels and Dinakar 2013; Flowers et al. 2015; Acosta-Motos et al. 2017; Liang et al. 2018). The uptake of Na^+ from the soil by the roots is reported to occur through high-affinity K^+ transporters (HKTs), K^+ channels, *Arabidopsis* K^+ transporter (AKT1), high-affinity K^+ uptake transporter (AKT1), cyclic nucleotide-gated channels (CNGCs) and glutamate receptors (GLRs) (Tester and Davenport 2003; Hanin et al. 2016; Assaha et al. 2017). Additionally, SOS1, a plasma membrane-localized Na^+/H^+ antiporter is known to transport Na^+ from root to shoot in both glycophytes and halophytes under salinity stress conditions (Munns and Tester 2008; Shabala 2013; Foster and Miklavcic 2019; Gupta et al. 2021). High salt in the soil favours the absorption of Na^+ by the roots which moves through the xylem with the aid of transporters and reaches the shoot and the leaf blades (Munns and Tester 2008). Hence, downregulation of the genes coding for Na^+ influx transporters may be are required to limit the Na^+ uptake by the roots in glycophytic plants. Although glycophytic plants can withstand mild salinity stress by operating various stress tolerance mechanisms, increased salinity accelerates oxidative damage resulting in cell death.

3 Mitigation of Salinity Stress by Halotolerant Plant Growth Promoting Rhizobacteria

Salt tolerance mechanisms in plants are intricate and complex requiring the operation of multiple metabolic pathways and activation of a network of genes. Although salt tolerance in crops can be attained by conventional breeding approaches and genetic engineering, long-duration along with high costs for generating breeding varieties and public acceptance of the genetically modified crops are major concerns (Egamberdieva et al. 2019; Bakka and Challabathula 2020). Under these circumstances, the usage of beneficial microorganisms for stress amelioration is gaining importance for salinity stress management in plants. PGPR are rhizospheric or endophytic bacteria capable of colonizing either in the interior or exterior parts of plant roots imparting plant beneficial effects and mitigation of salt stress. Although PGPR constitutes only around 2–5% of the rhizospheric bacteria, reports suggest that they can be effectively used under nutrient deficiency conditions as a replacement for chemical fertilizers aiding in the improvement of soil fertility (Grover et al. 2021). In recent years, usage of halophilic/halotolerant PGPR has gained importance, since they are environment friendly and their inoculation to glycophytic crops species has shown remarkable improvement in stress tolerance and increased productivity (Egamberdieva et al. 2019). Halotolerant PGPR has the inherent ability to tolerate high amounts of salts and is found in areas such as coastal dunes, saline deserts, hypersaline lakes, salt marshes, and inland salt seas. Although they are usually isolated from the high saline environment, they do not require high salt for their growth (Bremer and Kramer 2019). One of the adaptative strategies employed by halotolerant bacteria to survive in high salt conditions is the maintenance of lower intracellular levels of ions along with the accumulation of compatible solutes to balance the osmotic level inside the cytoplasm than the outer medium (Bremer and Kramer 2019). Along with this, the halotolerant PGPR have evolved several mechanisms to protect the cellular integrity thereby coping with salinity stress conditions. Accumulation of compatible solutes, activation of different salt efflux systems, reduced generation of ROS, limitation in oxidative damage is some of the mechanisms they operate to withstand high salinity stress (Egamberdieva et al. 2019). The halotolerant PGPR employs diverse mechanisms such as the production of phytohormones, possessing ACC deaminase activity, production of exopolysaccharides, and osmolytes which are directly or indirectly involved in the amelioration of salt stress in crop plants (Egamberdieva et al. 2016; Mishra et al. 2021). Additionally, activation of plant defence responses and antioxidant enzymes is observed in PGPR inoculated plants during salinity stress conditions to protect plant cells from oxidative stress. The list of plant growth promoting bacteria and their beneficial effects on plants in modulating the expression of plant genes and their involvement in salinity tolerance is shown recently by Mishra et al. (2021). The changes that are observed in the aerial and underground plant organs upon inoculation with PGPR under salinity stress conditions is shown in Fig. 1.

4 Attributes of Halotolerant Plant Growth Promoting Rhizobacteria

4.1 Production of Phytohormones

4.1.1 Indole-3-Acetic Acid

Halotolerant PGPR is known to produce a variety of phytohormones such as auxins, gibberellins, cytokinins and abscisic acid for plant growth, development and increased salt stress tolerance (Dodd et al. 2010; Dodd and Perez-Alfocea 2012). Among the auxins, indole-3-acetic acid (IAA) produced by the bacteria stimulates root growth and cell division not only under normal conditions but also under salt stress conditions. Halotolerant PGPR such as *Azotobacter, Arthrobacter, Azospirillum, Pseudomonas, Stenotrophomonas* and *Rahnella* are known to produce IAA under salt stress conditions (Piccoli et al. 2011; Egamberdieva et al. 2018). During tryptophan-dependent IAA synthesis, the PGPR utilizes the tryptophan released from the root exudates and converts them into IAA (Backer et al. 2018a, b). The IAA produced by the PGPR acts like a signaling molecule to trigger auxin signaling in plant roots along with causing induction in the expression of phytohormone related genes, defence genes and antioxidant genes resulting in increased auxin signaling, production of longer roots, increased root biomass and enhancement in plant growth and development (Hong et al. 1991; Spaepen et al. 2014; Ruzzi and Aroca 2015; Lorente et al. 2016). Although L-tryptophan has been identified as the main precursor for IAA biosynthesis, tryptophan independent mechanisms of IAA biosynthesis also exist possibly by using other small molecules produced from the root exudates (Myo et al. 2019). Identification and characterization of intermediates of IAA biosynthesis from bacteria and plants revealed the existence of significant similarity in the biosynthesis of IAA by tryptophan-dependent pathways in PGPR and plants (Spaepen et al. 2007; Spaepen and Vanderleyden 2011). Protection from salt stress-induced yield loss has been reported in different crops species such as tomato, cotton, and wheat by the inoculation of IAA producing PGPR such as *Psuedomonas putida*, *Streptomyces* sp., *Leclercia adecarboxylata* MO1 and *Azospirillum* sp. (Egamberdieva et al. 2008, 2019; Yao et al. 2010; Piccoli et al. 2011; Sadeghi et al. 2012; Kang et al. 2019).

4.1.2 Gibberellins

Gibberellins are a group of hormones that are known to stimulate seed germination with multiple growth attributing functions in plants. Gibberellins regulate reproductive organ formation and development, cell division and elongation, promote ripening of fruits, stimulate hypocotyl extension and stem growth (Plackett and Wilson 2016; Urbanova and Leubner-Metzger 2016). Many gibberellin producing bacteria such as *Acinetobacter calcoaceticus, Bacillus pumilus*, *Bacillus licheniformis*, Azospirillum sp., etc., have been isolated and their ability to induce endogenous gibberellin biosynthesis thereby promoting plant growth was reported (Bottini et al. 2004; Kang et al. 2009). Although a significant increase in the production of gibberellins was observed in the shoots of tomato, cucumber, radish and red pepper plants inoculated with PGPR strains *Bacillus cereus* MJ-1, *Leifsonia soli* SE134 and *Promicromonospora* sp. SE188, the mechanism of bacterial mediated synthesis of gibberellins in plants and their role in conferring salt tolerance to inoculated plants is not clearly understood (Joo et al. 2005; Kang et al. 2012, 2014).

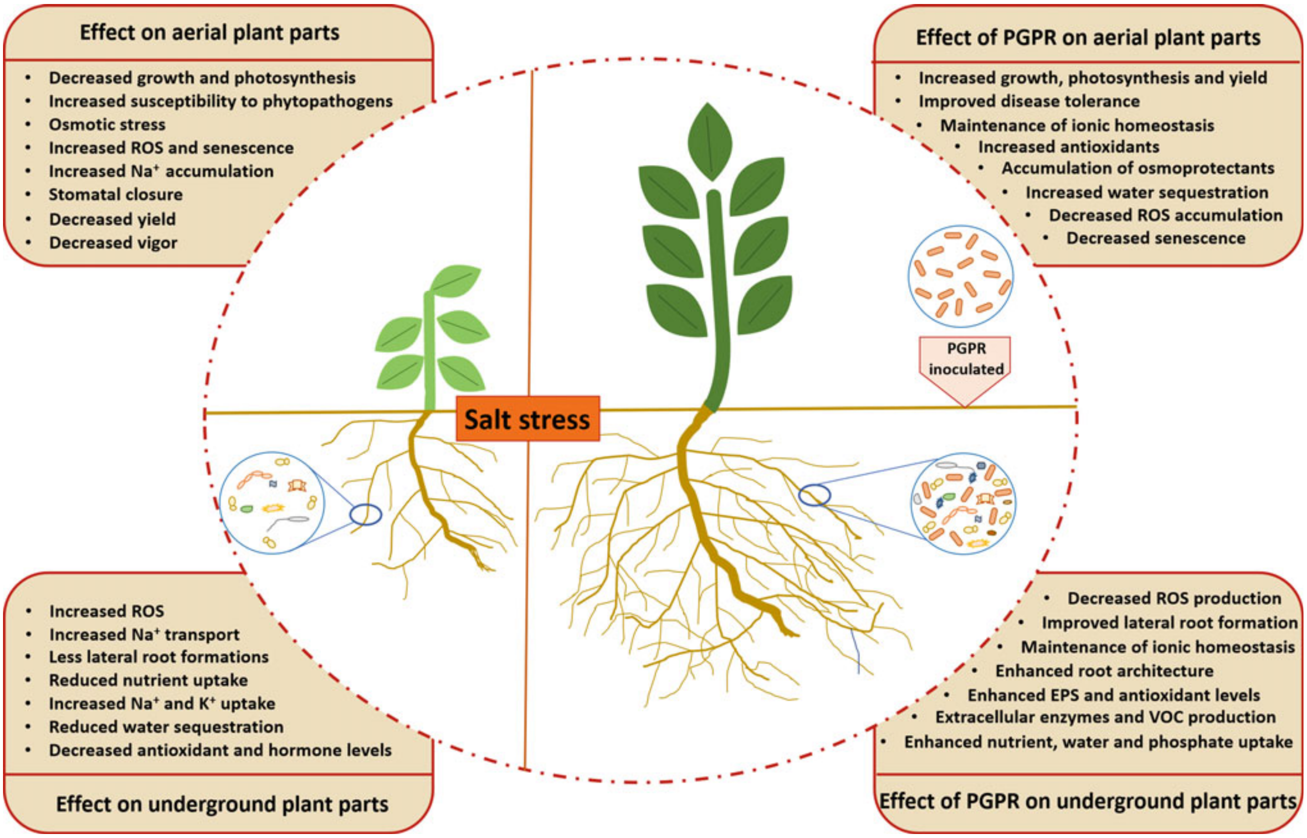

Fig. 1 Schematic representation of the effect of PGPR inoculation in aerial and underground plant organs of glycophytic plants under salinity stress conditions. The changes that are observed in PGPR inoculated and uninoculated glycophytic plants during salinity stress are shown

4.1.3 Cytokinins

Cytokinins which are involved in cell proliferation and differentiation in plants are known to be produced by PGPRs. Compared to auxins, although the role and functions of bacterially synthesized cytokinins were not studied in detail, reports suggested that PGPR effectively produce cytokinins which may be are important for plant growth and development under normal and stress conditions. The PGPR—*Pseudomonas entomophila*, *Pseudomonas stutzeri*, *Pseudomonas putida*, *Pseudomonas syringae* and *Pseudomonas monteilli* isolated from the rhizosphere of *Pennisetum glaucum*, *Helianthus annus* and *Zea mays* plants produced cytokinins not only under normal conditions but also under osmotic stress conditions (Sandhya et al. 2010b). Increased cytokinin levels in the shoot and root tissues of *Platycladus orientalis* and *Arabidopsis thaliana* plants upon inoculation with cytokinin producing PGPR strains *Bacillus subtilis* and *Bacillus megaterium* were observed suggesting the importance of bacterially synthesized cytokinin for inducing cytokinin synthesis along with plant growth promotion (Ortíz-Castro et al. 2008; Liu et al. 2013). Several halotolerant bacteria such as *Arthrobacter* sp., *Bacillus* sp., *Halomonas* sp., *Azospirillum* sp. and *Pseudomonas* sp. are known to produce cytokinins and promote cell division leading to growth in plants (Egamberdieva et al. 2019). Furthermore, organic volatiles emitted by PGPR *Bacillus subtilis* SYST2 led to increased cytokinin content and increased expression of cytokinin biosynthesis genes in tomato plants indicating the involvement of PGPR for increased synthesis of cytokinins in plants (Tahir et al. 2017). Although PGPR are known to synthesize cytokinins directly, they are also known to employ different mechanisms to induce cytokinin levels in plants to promote plant growth, however, the detailed underlying mechanisms of PGPR induced cytokinin mediated stress tolerance in plants is not clearly understood.

4.1.4 Abscisic Acid

Abscisic acid (ABA) is a stress hormone specifically synthesized in plants that are exposed to abiotic stress conditions such as salt, drought, cold, etc. It is the central regulator of abiotic stress tolerance mechanisms and is known to activate stress tolerance genes coordinating an array of functions for the growth and development of plants. Several of the halotolerant PGPR such as *Proteus mirabilis, Bacillus megaterium*, *Bacillus licheniformis*, *Pseudomonas fluorescens*, *Achromobacter xylosoxidans, Azospirillum* *brasilense* and *Azospirillum lipoferum,* are known to synthesize ABA (Karadeniz et al. 2006; Forchetti et al. 2007; Cohen et al. 2009; Salomon et al. 2014). Inoculation of these bacteria in the majority of the instances showed increased ABA levels in plants correlating with stress tolerance (Salomon et al. 2014; Cohen et al. 2015). Although the role of PGPR synthesized ABA in plants and its influence on the growth and development of plants under salt stress conditions is not clearly understood, modulation in ABA synthesis and ABA-dependent signaling pathways in plants upon PGPR inoculation contribute to the stress tolerance and enhanced plant growth under salt stress conditions is shown in few studies (Yao et al. 2010; Bharti et al. 2016; Barnawal et al. 2017). Inoculation of halotolerant PGPR *Dietzia natronolimnaea* STR1 to wheat plants showed upregulation of ABA-responsive genes and induced salinity tolerance suggesting the bacterial mediated modulation of ABA responses in plants (Bharti et al. 2016). Additionally, the expression of salt overly sensitive (SOS) pathway genes and ion transporter genes were also modulated in inoculated plants indicating the upregulation of salt tolerance mechanisms and enhanced protection against salt stress (Bharti et al. 2016).

4.1.5 ACC Deaminase Activity

The presence of ACC deaminase activity is one of the key characteristics that is observed in halotolerant PGPR for decreasing endogenous ethylene levels in plant cells thereby improving their plant growth. Stress induces the expression of 1-aminocyclopropane-1-carboxylic acid synthase (ACC synthase) genes which upon translation catalyzes the conversion of S-adenosylmethionine to ACC leading to ethylene accumulation in plants. Although ethylene as a plant hormone is implicated in the regulation of various plant physiological processes, stress-induced ethylene production and accumulation promotes senescence and is detrimental for plant growth and development wherein it serves as an indicator for plants' sensitivity towards stress (Glick 2014; Müller and Munné-Bosch 2015). Abiotic and biotic stresses cause a substantial increase in ethylene levels causing adverse effects on the growth of the plants (Dubois et al. 2018). Halotolerant PGPR with ACC deaminase activity hydrolyzes ACC to ammonia and α-ketobutyrate, significantly decreasing the ethylene levels in the plants (Gamalero and Glick 2015; Singh et al. 2015a, b; Gupta and Pandey 2019). The produced ammonia and α-ketobutyrate are utilized by the bacteria as nitrogen and carbon sources (Glick 2014). Inoculation of ACC deaminase producing bacteria *Stenotrophomonas maltophilia* SBP9 to wheat plants stimulated the plant growth under salinity stress conditions and augmented the resistance against abiotic and biotic stresses (Singh and Jha 2017). In another study, the improvement in growth along with other physiological properties was observed in plants inoculated with ACC deaminase enzyme-producing PGPR *Pseudomonas fluorescens* and *P. migulae* strains under salt stress (Egamberdieva et al. 2011; Ali et al. 2014). ACC deaminase producing PGPR such as *Variovorax paradoxus* 5C-2, *Bacillus amyloliquefaciens* SQR9, Arthrobacter sp., *Brevibacterium* sp., *Gracilibacillus* sp., *Virgibacillus* sp., *Salinicoccus* sp., *Pseudomonas* sp., *Pseudomonas fluorescens*, *Exiguobacterium* sp., *Alcaligenes* sp., *Bacillus* sp. and *Ochrobactrum* sp. induced salt tolerance and stimulated the growth in tomato, rice, maize and pea plants under salt stress conditions suggesting the efficacy of PGPR with ACC deaminase activity for the amelioration of salt stress responses and phytoremediation in crop plants (Bal et al. 2013; Ali et al. 2014; Wang et al. 2016; Habib et al. 2016; Aslam and Ali 2018; Kang et al. 2019).

4.2 Exopolysaccharides

While exopolysaccharide production is considered as one of the characteristic features of rhizobacteria, the amount of production and its composition varies in different halotolerant PGPR inhabiting different ecological niches. Exopolysaccharide production by the bacteria is considered as a protection mechanism employed to survive under environmental stress conditions such as salinity, temperature, heavy metals or pollution (Morcillo and Manzanera 2021). Many halotolerant PGPR secrete exopolysaccharides that form biofilms promoting cell to cell aggregation facilitating the rhizobacterial anchorage and adhesion to root surfaces. Exopolysaccharides are formed with either homo or heteropolysaccharides binding to the surface of the cell and play an important role in nutrient acquisition, formation of hydrophilic biofilms, water transport to the roots and regulation of soil aggregation favouring the growth of plants under salt stress conditions (Dar et al. 2021; Morcillo and Manzanera 2021). The exopolysaccharides produced by the halotolerant PGPR form rhizo-sheaths, a physical barrier around the host plant roots complexing with the Na^+ ions decreasing their availability to the inoculated roots thereby decreasing Na^+ toxicity under salt stress conditions. Exopolysaccharides of halotolerant PGPR such as *Pseudomonas* sp. AK1, *Bradyrhizobium japonicum* and *Bacillus subtilis* have the potential to bind to Na^+ ions limiting their uptake by the roots of soybean thereby maintaining normal growth under salinity stress conditions by maintaining K^+/Na^+ balance (Han and Lee 2005; Kasotia et al. 2016). Inoculation of exopolysaccharide producing PGPR *Bacillus subtilis* to *Arabidopsis thaliana* significantly decreased the influx of Na^+ ions to the roots by downregulating the expression of HKT1/K^+ transporter (Zhang et al. 2008). *Helianthus annus* plants inoculated with exopolysaccharide producing *Pseudomonas aeruginosa* showed enhanced salt stress tolerance along with increased growth, development and yield (Tewari and Arora 2014). In another study, increased plant growth and improved soil stability are observed in Chickpea plants inoculated with the exopolysaccharide producing halotolerant PGPR *Halomonas variabilis* (HT1) and *P. rifietoensis* (RT4) suggesting the importance of PGPR secreted exopolysaccharides for plant salinity tolerance (Qurashi and Sabri 2012; Dar et al. 2021).

4.3 Osmoprotectants

Halotolerant PGPR exposed to salt stress conditions accumulate osmoprotectants such as proline, trehalose, polyamines and glycine betaine in their cytosol to maintain osmotic balance inside the cell. While secretion of root exudates attracts the halotolerant PGPR to colonize the root surface and other internal tissues, the osmolytes secreted by halotolerant PGPR are absorbed by the plant roots thereby helping in the osmotic adjustment of plants during salinity stress (Chandran et al. 2021). Although salinity-induced accumulation of osmolytes is also observed in plants, the bacterial osmolytes mimic the plant metabolites during the plant–microbe interaction and the response in bacteria is quicker (Ilangumaran and Smith 2017). Salt stress-induced accumulation of osmolytes such as proline, glycine betaine, polyamines, quaternary ammonium compounds and other amino acids are reported in many plant species inoculated with halotolerant PGPR (Sandhya et al. 2010a; Wang et al. 2016). The accumulation of these metabolites in the cytoplasm of the plant cell renders osmotic adjustment and protects the macromolecules such as proteins, nucleic acids and lipids from oxidative damage during salinity stress conditions (Parihar et al. 2015; Acosta-Motos et al. 2017). Inoculation of PGPR such as *Burkholderia*, *Arthrobacter*, *Bacillus*, *Rhizobium* and *Pseudomonas* are reported to increase the proline content in plants during salinity stress (Bano and Fathima 2009; Choudhary 2012). Increased proline accumulation along with reduced ROS generation, reduced lipid peroxidation and upregulation of stress-responsive genes is observed in *Capsicum* plants inoculated with PGPR *Bacillus fortis* SSB21 (Yasin et al. 2018). While exogenous application of glycine betaine in salt-stressed soybean plants improved salt tolerance along with increased antioxidant enzyme activities and decreased intracellular Na^+ levels, inoculation of halotolerant PGPR *Bacillus* HL3RS14 and *Bacillus subtilis* BERA71 increased the accumulation of glycine betaine in plants and protected the plants from salinity stress-induced oxidative damage (Malekzadeh 2015; Hashem et al. 2016a, b; Mukhtar et al. 2020). Maize plants inoculated with *Azospirillum brasilense* harbouring a yeast trehalose biosynthesis gene showed higher trehalose levels along with an increase in leaf and root biomass (Rodríguez-Salazar et al. 2009). These kinds of studies signify the importance of osmolytes for increased stress tolerance.

4.4 Antioxidant Enzymes

The Reactive Oxygen Species (ROS) are continuously produced in different organelles as metabolic by-products during normal conditions in plant cells. Under salt stress conditions, the production of ROS such as hydrogen peroxide, hydroxyl ion, superoxide ions and singlet ions is aggravated posing a threat of oxidative damage (Sharma et al. 2012). Increased ROS causes oxidative stress leading to damage to nucleic acids, proteins and lipids finally resulting in cell death (Apel and Hirt 2004; Gill and Tuteja 2010; Hasanuzzaman et al. 2020). Management of ROS in plant cells although is efficiently done by antioxidant systems comprising of enzymatic (superoxide dismutase, catalase, peroxidase, glutathione reductase, etc.) and non-enzymatic components (ascorbate, glutathione, carotenoids, flavonoids, etc.) to protect the cells from oxidative damage, salinity stress-induced aggravation in ROS causes inactivation of antioxidant systems leading to cell damage (Miller et al. 2010). Inoculation of halotolerant PGPR to plants is reported to increase the potential of plants to produce more antioxidant enzymes during salinity stress conditions. Higher amounts of antioxidant enzymes such as superoxide dismutase, catalase, peroxidase and glutathione reductase were reported in plants inoculated with halotolerant PGPR (Islam et al. 2016; Ha-Tran et al. 2021). Soybean plants inoculated with PGPR *Bacillus firmus* SW5 showed increased expression of genes encoding antioxidant enzymes suggesting better protection from salinity stress-mediated injury (El-Esawi et al. 2018). The *Abelmoschus esculentus* plants inoculated with *Bacillus megaterium* UPMR2 and *Enterobacter* sp. UPMR18 showed improvement in germination rate and increased growth correlating with decreased ROS levels and increased superoxide dismutase, catalase and ascorbate peroxidase activities (Habib et al. 2016).

4.5 Siderophores

The halotolerant PGPR possess specialized strategies to overcome iron (Fe) limitation by using chelators called siderophores which can extract Fe from Fe^{3+} complexes in soil aiding in the supply of usable iron to the plants (Ferreira et al. 2019). Since Fe is an essential micronutrient important for photosynthesis, respiration and chlorophyll biosynthesis in plants and salinity stress is known to reduce the availability of Fe due to lower release of iron-chelating compounds, the halotolerant PGPR chelates the Fe and provides the nutrient to the plants for their survival under stress conditions (Abbas et al. 2015; Chakraborty et al. 2016; Ferchichi et al. 2016). The secretion of siderophores by halotolerant PGPR is considered as an alternative strategy for Fe uptake by plants facilitating improved nutrition along with inhibition of phytopathogens under salt stress conditions. While the bacterial genera *Bacillus*, *Burkholderi*a, *Enterobacter* and *Grimontella* are known to produce high siderophores, improvement of salinity tolerance in plants such as alfalfa, corn, wheat and mungbean has been observed upon inoculation with siderophore producing halotolerant PGPR (Ramadoss et al. 2013; Singh et al. 2015a, b; Souza and Ambrosini 2015; Zhu et al. 2020).

4.6 Other *M*echanisms

Phosphate solubilization is another important plant growth promoting trait possessed by halotolerant PGPR. Since the majority of the phosphorous in the native soils will be in an insoluble form, strategies for increasing the bioavailability of phosphorous in the usable form for plants are required. Phosphorus in plants is a macronutrient that plays a vital role in the growth and development of plants for improving photosynthesis, root growth, cell division, flower and seed formation, resistance to plant diseases, etc. Being the second most important macronutrient, it is also an essential component of nucleic acids, enzymes, nucleotides and phospholipids (Souza and Ambrosini 2015). Often the phosphorous fertilizers are sprayed onto the crops to protect them from deficiency symptoms, however, continuous usage negatively affects the soil pH, soil structure and microbiome. Utilization of plant growth promoting bacteria with phosphate solubilization potential is an alternative way for supplementing phosphorous to the plants thereby improving crop productivity. The halotolerant PGPR are known to solubilize inorganic soil phosphates, through the production of organic acids particularly gluconic and carboxylic acids, and hydroxyl ions (Rodríguez et al. 2006; Sharma et al. 2013; Anand et al. 2016). The bacteria belonging to the genera *Bacillus, Rhodococcus, Arthrobacter, Serratia, Chryseobacterium, Gordonia, Phyllobacterium* and *Delftia* are known to produce acids such as citric acid, gluconic acid, lactic acid, succinic acid and propionic acids to solubilize inorganic phosphates and supply phosphorous to the plants (Chen et al. 2006). Roots and rhizospheric soil are reservoirs for phosphate solubilizing bacteria. The rhizosphere of the rice plants dominated by the genera *Burkholderia, Cedecea, Cronobacter, Enterobacter, Pantoea* and Pseudomonas showed phosphate solubilization potential leading to improved plant growth (Costa et al. 2013; Granada et al. 2013; Souza et al. 2013, 2014). The halotolerant PGPR are also known to release a wide variety of secondary metabolites and volatile organic compounds for improvement of plant growth and salt stress tolerance. The PGPR are reported to produce polyamines that induce polyamine biosynthesis in host plants resulting in increased photosynthesis, growth and biomass under stress conditions and producing HCN as biocontrol for controlling the pathogenic microbes in the rhizosphere (Kumar et al. 2015; Backer et al. 2018a, b). The volatile organic compounds released by the PGPR *Bacillus subtilis* promoted the biosynthesis of choline and glycine betaine in host plants along with inhibition of Na^+ ion transport to root cells resulting in improved salt stress tolerance (Zhang et al. 2008; Timmusk et al. 2014; Backer et al. 2018a, b; Lopes et al. 2021).

5 Methods of Inoculation of Halotolerant PGPR to Plants

Although a majority of the halotolerant PGPR show high potential for plant growth promotion and salinity stress amelioration under laboratory conditions, the favourable responses are often not observed under field conditions mainly due to the inoculation methods used and due to variations in soil and fluctuations in external environmental factors such as light and temperature (Lopes et al. 2021). Although carbon, nitrogen, organic matter content, water availability and pH are the main factors determining the growth of the microorganisms, the soil type, the geographical location and seasonality also play a crucial role in the establishment and survival of halotolerant PGPR on the rhizospheric zone (Bossio et al. 1998; Drenovsky et al. 2004; Garcia-Pausas and Paterson 2011; Kristin and Miranda 2013). Alterations in the soil conditions are known to modify the microbiome diversity. While low soil moisture content is detrimental to the growth of bacteria, high soil moisture content generally observed during flooding reduces oxygen availability resulting in the decrease of microbial biodiversity (Gouda et al. 2018). Increasing the efficacy of the bacteria to colonize the soil, root or seed is an effective way to establish PGPR-plant connection to observe a bacterial mediated increase in the growth of plants under salinity stress conditions. The compatibility of the bacterial strain to the roots of the host plants along with the stability of the bacteria in the soil is critical for establishing effective colonization thereby having a consistent growth performance of the plants (Egamberdieva et al. 2018; Lopes et al. 2021). While microbial inoculants are mainly inoculated onto seeds, soil, roots and leaves, improvement of the plant—PGPR interaction and evaluating the responses of PGPR to changing environmental conditions are important to have efficient bacterial inoculation to see the desired plant growth promoting effect (Callaghan 2016) (Fig. 2b).

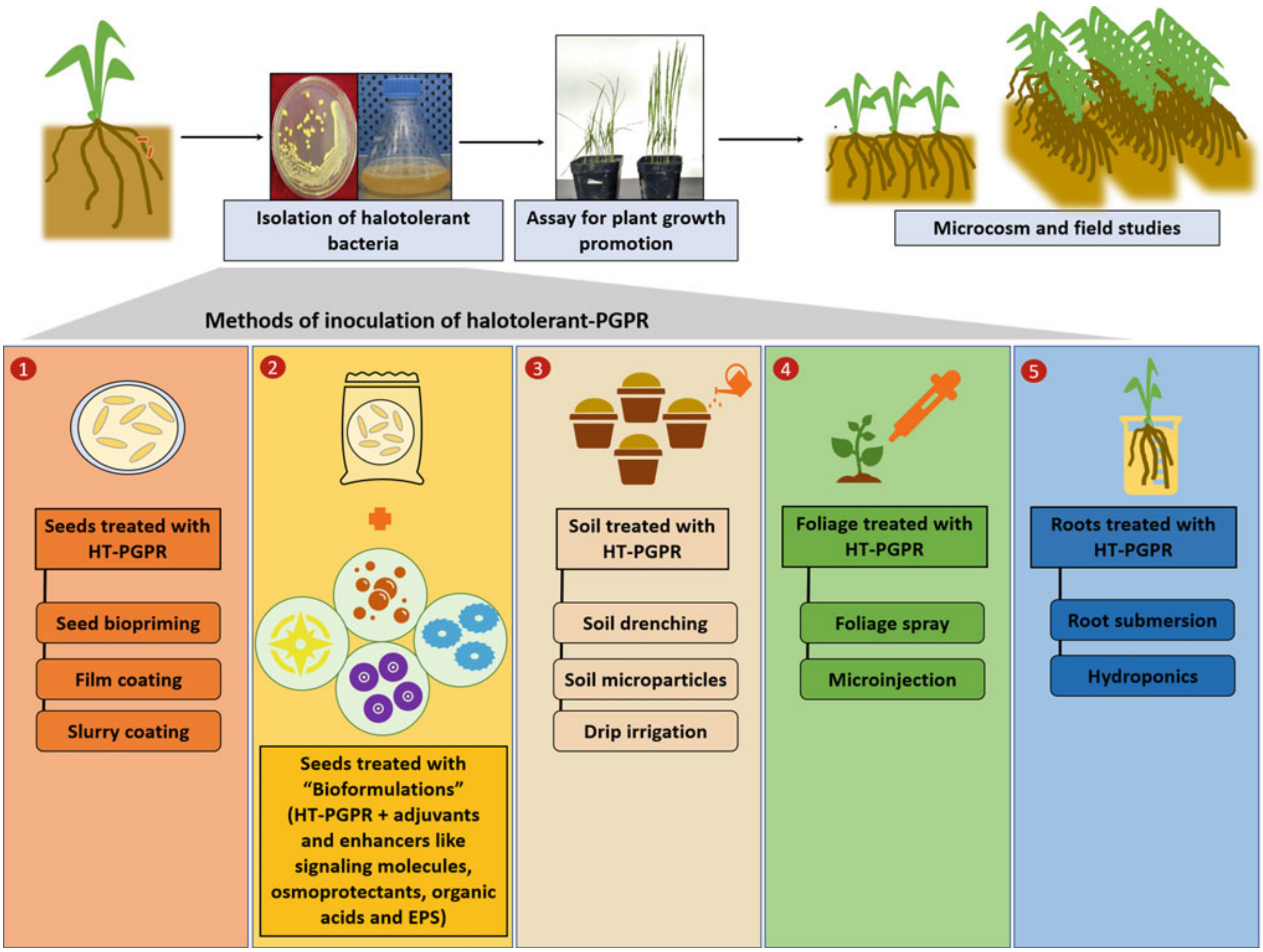

Fig. 2 Diagrammatic representation of different methods of halotolerant PGPR inoculation in plants. **a** Depiction of different steps such as isolation of halotolerant bacteria from rhizosphere combined with lab and field studies for analysing plant growth promotion. **b** Different methods of inoculation of halotolerant PGPR to seeds, leaves and roots of glycophytic plants

Since salinity stress induces serious changes in the composition of the rhizospheric environment, different methods such as inoculation of the halotolerant PGPR to seeds, soil amendments by directly adding the inoculum onto soil and dipping of the roots in the PGPR suspension before transplanting are employed to ensure efficient inoculation of the bacteria to the plants thereby increasing the efficiency of bacteria for survival and colonization (Mahmood et al. 2016). Since the method of PGPR inoculation determines the survival efficacy of the bacteria, several methods such as seed priming with PGPR, seed priming with bioformulations, soil drenching, foliar application and root dipping were developed to increase the colonization efficiency of the PGPR to the plant tissues (Fig. 2b). Several modifications of every method have also been evaluated and standardized. Different methods employed for the efficient inoculation of halotolerant PGPR are shown in Fig. 2.

Inoculation of the halotolerant PGPR to seeds is an efficient method since it delivers the microorganisms to soil and ensures efficient root colonization (Philippot et al. 2013). Different methods of seed inoculation such as (i) Seed biopriming, involving immersion of the seeds in the PGPR microbial suspension for a definite period followed by drying, initiates the physiological processes inside the cell thereby ensuring colonization of PGPR (Taylor and Harman 1990) (ii) Film coating, involving the coating of the PGPR inoculum in a film as a thin layer on the seed surface complexing with methylcellulose, paraffin oils and polysaccharide materials is used to increase the adherence capacity of the PGPR to roots (iii) Slurry coating, involving inoculation of PGPR to the surface of the seeds by using carriers such as peat (Fig. 2b1). However, the survival of the inoculum in the seed is stronger and efficient in the bioprimed seeds, than film coating and slurry coating inoculums

(Callaghan 2016). Biopriming of the seeds of maize with different strains of Azotobacter and Azospirillum showed a significant increase in growth, development and yield (Sharifi 2011). Inoculation of *Rhizobia* and *Bacillus* species to the seeds of *Oryza sativa* and *Cicer arietinum* L. plants resulted in increased biomass production (Ullah et al. 2017; Khan et al. 2019).

Decoding the signaling components and the metabolites involved in plant-PGPR interaction during salt stress conditions is important to modify the Phyto microbiome for increasing the colonization potential of the bacteria. The bioformulations with the signaling molecules like AHL (N-acyl homoserine lactone) which is a known elicitor of plant–microbe interactions evokes biochemical and molecular changes to avert salinity-induced injuries in plants (Zhou et al. 2017). The external application of osmoprotectants like glycine betaine and proline along with halotolerant PGPR to the seeds helps in the initial acclimatization of the bacterial inoculants to the salinity stress (Arif and Ghoul 2018). Exopolysaccharides and organic acids are used as adjuvants for maintenance of osmotic equilibrium, water activity, cell protection and better mineral solubilization, respectively (Sunita et al. 2020, Fig. 2b).

Soil inoculation is done by either drenching the soil in PGPR solution or by incorporating PGPR into soil mixed with a substrate in the form of microcapsules. This method provides an advantage over other methods by increasing the PGPR density over indigenous soil microbiota. Soil inoculations with microcapsules lead to a gradual release of inoculum offering a higher probability for root colonization and viability (Hernandez-Montiel et al. 2017, Fig. 2b3). Foliar PGPR inoculation usually involves spraying of PGPR solution on foliar regions of the plant and the interaction between plant leaf surface and microorganism leads to improved growth and yield in plants (Efthimiadou et al. 2020). Foliar microinjection of PGPR is also practised, however, the foliar spray is found to be a superior method (Basha et al. 2006, Fig. 2b4). Root inoculation involves a submersion of seedling roots for a definite period in PGPR solution, thereby improving root colonization of bacteria. In rice plants, the root inoculation was found to be more effective than the seed inoculation method resulting in increased panicle length and plant height (Ullah et al. 2017, Fig. 2b5). In soybean, tomato and cucumber plants, hydroponics has been used to provide the roots with a continuous source of PGPR inoculum wherein inoculated plants showed a remarkable increase in yields respectively (Gagnè et al. 1993; Gül et al. 2013; Yasmin et al. 2020). Inoculation of *Burkholderia phytofirmans* PsJN to the roots of *Vitis vinifera* increased the plant's tolerance to low-temperature stress, modified the carbohydrate levels in leaves and increased plants growth (Fernandez et al. 2012).

6 Usage of Halotolerant PGPR as an Alternative to Chemical Fertilizers

Increased population growth demanding for higher agricultural productivity, nutrient deficiency in soils and abiotic stress factors causing a serious decline in crop productivity are the major factors that created a demand for chemical fertilizers in agriculture applications worldwide (Scagliola et al. 2021). Excessive usage and application of chemical fertilizers in agricultural fields were found to be a serious threat to soil quality causing pollution to the environment and having significant detrimental effects on human health (Zhang et al. 2018; Scagliola et al. 2021). Additionally, the depletion of nutrients and soil biodiversity that occurs due to the application of chemical fertilizers on agricultural soils has created an urgent need to recycle the available organic resources and alternative sources such as beneficial rhizospheric microbes for improving plant growth under stress conditions and restoring the soil fertility. Soil is heterogenous with innumerable microorganisms such as bacteria and fungi interacting with others and each other through symbiosis, antagonism, mutualism, parasitism and saprophytism. The halotolerant PGPR are considered as suitable candidates either in isolation or in consortia to improve the plant growth directly by producing plant growth promoting traits, by enhancing the nutrient bioavailability to the roots and indirectly helping the host plants by restricting the growth of phytopathogenic organisms near to rhizosphere and activating systemic resistance against plant pathogens (Marastoni et al. 2019; Kolega et al. 2020). The halotolerant PGPR is known to colonize in the rhizosphere or the interior of the plant and act like biofertilizers aiding in increasing the availability of nutrients and production of siderophores for iron uptake. Research has convincingly demonstrated that inoculating plants with halotolerant PGPR or treating plants with the signaling compounds released by the PGPR stimulates plant growth even under high salinity stress conditions (Backer et al. 2018a, b).

Halotolerant PGPR is equipped with a plethora of mechanisms to cope up with salinity stress in the soil and provide benefit to host plants. These halotolerant PGPR can be applied to the agricultural fields as bioinoculants or multifunctional PGPR-based formulations to improve crop productivity not only under optimal conditions but also under salinity stress conditions. Application of halotolerant PGPR like *Bacillus subtilis*, *Bacillus amyloliquefaciens* NBRISN13, *Enterobacter* sp., *Lysinibacillus* sp., *Pseudomonas strain* 002 and *S. sciuri* SAT-17 to rice, wheat and maize plants promoted plant growth, decreased intracellular ROS levels by increasing the antioxidant enzyme activities, increased osmolyte accumulation and modulated the expression of salt stress-responsive genes during salinity stress (Upadhyay and Singh 2015; Singh and Jha 2016; Nautiyal et al. 2013; Zerrouk et al. 2016; Rima et al. 2018; Sarkar et al. 2018; Damodaran et al. 2019). Further, *Azospirillum, Bacillus, Burkholderia, Enterobacter, Flavobacterium, Pseudomonas, Rhizobium, Frankia, Klebsiella, Clostridium, Serratia* and *Streptomyces* are known to increase agricultural productivity under salinity stress conditions (Abhilash et al. 2016; Oosten et al. 2017; Gouda et al. 2018). Research findings highlight the importance of phytohormones, phosphate solubilization potential, siderophore production, ACC deaminase activity, production of osmoprotectants and modulation in antioxidant defences as key elements for ameliorating the salinity stress responses in halotolerant PGPR inoculated crop species (Egamberdieva et al. 2019; Kumar Arora et al. 2020; Shilev 2020). Usage of halotolerant PGPR as a whole or preparation of bioinoculants or bioformulations not only improves the crop growth and productivity but also helps the plants survive under high salinity conditions. Hence, the halotolerant PGPR can be considered as an alternative to chemical fertilizers due to various growth promoting attributes under salinity stress conditions and environment-friendly nature.

7 Commercialization

The interaction of the PGPR with plant roots and its effect on the plant growth promotion is a complex process involving several steps such as root exudation followed by attachment, colonization by the PGPR, the release of phytohormones, release of volatile organic compounds by the PGPR and finally influencing the growth of the plant. Any microbe if identified as a potential PGPR through isolation and characterization should colonize and show the plant growth promoting traits. Although many of the halotolerant PGPR have been isolated from different rhizospheric zones and characterized for their plant growth promoting traits, many of the bacteria fail to colonize the root system under field conditions and hence they cannot be exploited for commercial purposes. However, they may be important for plant growth promotion and restoration of soil fertility by employing unexplored and uncharacterized mechanisms. Single PGPR, consortia of PGPR or the signal molecules can be exploited for commercialization and can be used for enhancing agricultural productivity. The process involves PGPR isolation, screening, laboratory pot tests, field trials, development of formulation, formulation testing, product registration and availability in the market (Backer et al. 2018a, b, Fig. 2a).

Halotolerant PGPR can be isolated from the rhizospheric zones of the salt-tolerant plants and their characterization is done based on biochemical and molecular characteristics (Bakka and Challabathula 2020; Taj and Challabathula 2021). Further, they are screened for the presence of plant growth promoting traits and growth inhibition of plant pathogens. While the biochemical characterization is done based on Bergey's manual of determinative bacteriology, DNA and RNA-based homology testings are mostly used for molecular characterization. The cultivable bacteria with high plant growth promoting activity are selected and are tested under laboratory and field conditions for preparing the consortia (Backer et al. 2018a, b). For the isolation of potential signal compounds also referred to as biostimulants, the entire PGPR culture supernatant tested positive for plant growth promotion will be fractionated by HPLC and the individual active compounds are isolated, purified and subjected to mass spectrometry for identification. Formulations are done with either consortium comprising of multiple PGPR isolates or by using a single PGPR isolate (Backer et al. 2018a, b; Scagliola et al. 2021). To minimize the loss of bioactivity of the PGPR in formulations and for even distribution, stickers/binders such as corn flour, carboxymethyl cellulose; surfactants such as Tween 80; desiccants such as silica gel and anhydrous sodium sulphate; dispersants like microcrystalline cellulose; thickeners like xanthan gum; stabilizers such as lactose and sodium benzoate; and UV protectants are added (Schisler et al. 2004; Callaghan 2016; Backer et al. 2018a, b; Egamberdieva et al. 2019). Although recent studies indicated biochar as the promising carrier material for PGPR inoculations mainly due to its porosity and nutrient content and its feasibility to be applied as seed coatings replacing peat-based inoculants (Backer et al. 2018a, b), due to variations in biological, physical and chemical properties of the produced biochar, it can harm soil fertility and growth of microbes and plants (Nguyen et al. 2017; Wang et al. 2017). The formulations can be liquid-based, talc-based, saw-dust-based, fly ash-based, encapsulation-based and peat-based with specific advantages and disadvantages upon inoculation onto different plant species (Gopalakrishan et al. 2016). Liquid-based formulations can be sprayed onto the seeds before sowing or seeds can be drenched in the inoculum. Isolation of halotolerant PGPR that can sustain plant growth under salinity stress conditions in laboratory and field conditions is cumbersome. Further, isolating the halotolerant PGPR with high efficacy, multiple benefits, long shelf life and high root colonization rate is achievable. However, preparation of the formulations that can be applied on the field with a high success rate combined with commercialization requires a strong research link between the public and private funded universities, research organizations with private industries to observe augmentation in the production of crops under salinity conditions.

8 Conclusion

High salinity poses a serious threat to agricultural systems worldwide and inoculation of halotolerant PGPR has shown increased salinity stress tolerance along with growth promotion in not only model plants but also in many agriculturally important crop species. Compared to the usage of fertilizers and pesticides for plant growth promotion and removal of pests which were reported to have negative effects on the soil and environment, inoculation of halotolerant PGPR as bioinoculants is an environment friendly approach. Additionally, the halotolerant PGPR were reported to replenish the fertility of the soil and protect the plants from pathogens. Over the past few years, many halotolerant PGPR with plant beneficial effects have been isolated from different rhizospheric zones and were efficiently characterized. However, the significant effects were always observed under laboratory conditions and their suitability to be used as bioinoculants under field conditions is questionable. At this juncture, steps are necessary for the isolated and well-characterized halotolerant PGPR to be used as products for commercial agriculture particularly for mitigating the salinity stress in plants. Since stressor-specific and non-specific responses are observed in plants exposed to abiotic stress conditions, the bioformulations with a single bacterium, consortia of bacteria or the signal molecules should be custom-made for their usage for saline soils to observe the improvement of salt tolerance in plants. Isolation of new halotolerant bacterial strains with potent plant growth promoting traits, improvements in inoculation technologies for increasing the efficiency of inoculum along with the survival of the bacteria and preparation of novel bioformulations are key to combat the challenges of crop growth and productivity in saline soils.

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Outside the Cell Surface: Encoding the Role of Exopolysaccharide Producing Rhizobacteria to Boost the Drought Tolerance in Plants

Mamun Mandal, Soumya Chatterjee, and Sukanta Majumdar

Abstract

Broad ranges of microbes are present in the soil; some of them can produce exceptionally hydrated polymers (such as exopolysaccharides) outside the cell wall which have a tremendous role in adverse conditions. Exopolysaccharides (EPS) play a crucial role in microbes as helpful substances in several physiological parameters and provide a safe environment against stress conditions. EPS producing rhizobacteria show an enormous effect on plant growth promotion under drought conditions by increasing water holding capacity. The environment exclusively benefits from EPS because these rhizobacteria beneficially change the soil physicochemical properties that also aggregate soil particles around the root zone. Rhizobacterial EPS can balance soil moisture and entrap a sufficient amount of nutrients for plant growth and development even in sandy soil. EPS producing PGPR survival and existence increases by biofilm architecture because EPS effectively participates in biofilm formation, microbial aggregation, and communication with other microbes. In addition, EPS helps in nodule formation, siderophore production, and protection from desiccation, surface attachment, bioremediation, plant–microbe interaction, and other plant-promoting attributes in water limiting conditions. This chapter highlights EPS-producing bacteria and their impact on plant growth under drought stress.

Keywords

Drought stress • Exoploysaccharides • Plant growth promoting rhizobacteria • Mitigation

Abbreviations

CPS	Capsular polysaccharides
EPS	Exopolysaccharides
PGPR	Plant growth promoting bacteria
LPS	Lipopolysaccharides
Pap	*Pseudomonas* Acidic polysaccharide
RAS	Root adhering soil
RIDER	Rhizobacterial-induced drought endurance and resilience
RS	Rhizosheath
WHC	Water holding capacity

1 Introduction

Crop plants continuously face various types of biotic and abiotic stresses during their life cycle that decrease their growth and development. Abiotic stress factors include heat, chilling, drought, salinity, and nutrient deficiency (Pouri et al. 2019). Among them, drought stress may range from short and moderate to extremely intense and prolonged-time duration can limit crop growth and yields. Drought condition is expected to create serious plant growth and development difficulties to higher than 50% of the arable fields by 2050 (Kasim et al. 2013; Vurukonda et al. 2016). Drylands such as arid, semi-arid, and dry sub-humid lands take up around 40% of the terrestrial ecosystem. This percentage gradually increases because the amount of annual rainfall is continuously decreasing due to environmental pollution, climate changes, and decreased biodiversity (Millennium Ecosystem Assessment 2005). Water scarcity conditions predominating in drylands hinder crop plants production as the limited availability of water changes biochemical, morphological, and physiological processes (Debaeke and Aboudrare 2004). As a result, cellular dehydration increases, which excites osmotic stress, therefore impeding cell enlargement (Bartels

M. Mandal · S. Chatterjee · S. Majumdar (✉)
Microbiology and Microbial Biotechnology Laboratory,
Department of Botany, University of Gour Banga, Malda, West
Bengal 732103, India

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and Sunkar 2005). Drought stress causes loss of turgor pressure by reducing water potential, stomatal closure, nutrient deficiency, oxidative stress, and cell membrane integrity disruption by denaturation of protein. Stomatal closure in response to water deficiency generates deterioration in photosynthesis rate (Alcázaret al. 2011; Yang et al. 2010). In the current situation, drought stress is among the most devastating abiotic stresses that adversely affect global food security.

For higher crop production, chemical fertilizers are used worldwide, but these are used in an enormous amount that negatively alters the environmental condition along with water quality also declines. The chemical fertilizers application in excessive amounts can further be dangerous to regular consumers. Consequently, it is compulsory to utilize natural and eco-friendly substitutes, which can help in healthy crop production and reduce environmental contamination (Arora et al. 2018). In this aspect, the use of biostimulants/biofertilizers can be a more suitable alternative for healthy crop production in a nonhazardous way (Rajput et al. 2019). Organic cultivation is developing as a better substitute for increasing crop yield even under biotic and abiotic stress conditions (Verma et al. 2019). In organic cultivation, several types of biofertilizers such as farmyard manure, vermicompost, and microbes-based bio inoculant are practised to get sustainable agricultural targets and mitigation of water and soil contamination.

Under drought conditions, the application of plant growth promoting bacteria (PGPR) in a plant can be beneficial not only to amplify productivity but also to help in the mitigation of soil contamination (Nazari and Smith 2020). PGPR alleviates the impression of water deficiency on plants through the rhizobacterial-induced drought endurance and resilience (RIDER) process, which involves morphological, cellular, and genetic changes (Kaushal and Wani 2016). A variety of RIDER mechanisms include (1) changes in root morphology; (2) modification of phytohormonal activity levels like indole-3-acetic acid (IAA), abscisic acid (ABA), cytokinins (CK), gibberellic acid (GA) Khalid et al. 2006); (3) 1-aminocyclopropane-1-carboxylate (ACC) deaminase to decrease the amount of ethylene production; (4) antioxidant defence enzymes and non-enzymatic components; (5) enhancing the siderophore and biofilm production; and (6) bacterial exopolysaccharides (EPS) (Oleńska et al. 2020). PGPR also accumulates several osmolytes (such as glycine betaine, proline and trehalose) and some compatible organic solutes (like polyamines, sugars, and amino acids), which are associated with metabolic adjustment. The production of volatile organic compounds, dehydrins, and heat-shock proteins also play a pivotal role in imparting drought stress tolerance (Vurukonda et al. 2016). This chapter mainly focused on the role of EPS and EPS producing PGPR in drought conditions. The term exopolysaccharides were suggested by Sutherland (Sutherland 1972), which is the essential component for biofilm production. EPS producing rhizobacteria have great strategies to rescue the plant from water desiccation in soil. Polysaccharides have a hygroscopic character and therefore, can hold a higher amount of water in the micro-environment colony in contrast to bulk soil in drought conditions (Roberson and Firestone 1992). Polysaccharides producing rhizobacteria can control higher soil moisture and promote plant growth also in granular soils. They also release a higher amount of soluble carbohydrates in the plant rhizospheric zone, so the plant survival rate increases. Besides this EPS produced by rhizospheric bacteria, through the adjoining mineral contents, can make rhizosheath encompassing the roots of the plant. This helps to defend the plant from aridness for a higher period which can further lead to rising in the establishment of micro and macro-aggregates as an additional effect (Khan et al. 2017). So, if the density of EPS producing bacterial community is increased in the plant rhizospheric zone, it might be beneficial for the plants under a drought stress environment.

2 Classification, Chemical Nature, and Structure of Bacterial EPS

Bacteria generate several types of biopolymers with diverse chemical compositions by using simple to complicated substrates. Several of these biopolymers provide a similar function, while many others are particular for specific taxa and contribute to individual biological activity (Anderson et al. 1990). Based on cellular location two types of biopolymers are found in bacterial species, viz. (a) intracellular and (b) extracellular. Intracellular biopolymers are very rare, and their use is also restricted. On the other hand, extracellular biopolymers are very common in bacterial taxa. The extracellular biopolymers are collectively known as the extracellular polymeric substance which is divided into four main classes, viz. polyamides, inorganic polyanhydrides, polyesters, and polysaccharides (Rehm 2010; Ruas-Madiedo et al. 2002). In the extracellular polymeric substance, polysaccharide components are most abundant (Dogsa et al. 2005). Three major types of polysaccharides are found, such as capsular polysaccharides (CPS), EPS, and lipopolysaccharides (LPS). Cohesive layers of surface-associated CPS are covalently bound generally, anatomically located at the outside of the bacteria cells (Whitfield et al. 2020). CPS covers the bacterial cells and protects them from bacteriophage attack, phagocytosis, osmotic stress, and desiccation. EPS excreted as slime layers are not tightly attached to the bacterial cells which can be separated easily (Angelin and Kavitha 2020). Nevertheless, the difference between loosely bound and unbounded extracellular polymeric substances is related or dependent on the functional and structural relationship of the cell. Bacterial EPS is synthesized and released into the exterior environment or maybe sometimes synthesized extracellularly with the help of cell wall attached enzymes (Nwodo et al. 2012). The diversity of bacterial EPS is categorized by chemical structure, charge, molecular weight, linkage bonds, functionality, and presence of substitution and repeated side-chains (Castro-Bravo et al. 2018). According to the chemical composition, EPS can be divided into two groups based on monosaccharides composition: (i) homopolysaccharides (HoPs) and (ii) heteropolysaccharides (HePs) (Osemwegie et al. 2020). HoPs have one type of monosaccharide whereas HePs are contained of repeating units, have varied in size from disaccharides to heptasaccharides (MohdNadzir et al. 2021).

Based on the bond linkages and monomeric units, HoPs can be divided into four categories thus; glucans (α-D-glucans and β-D-glucans), fructans, sialic acids, and polygalactans (Sutherland 1990). On the other hand, the categorization of HePs is a complex process because it can be classified in many ways. Generally, it is observed that HePs are classed into these groups based on the repeating units of D-galactose, D-glucose, L-rhamnose, and derivatives (Bajpai et al. 2016) (Fig. 18.1). In addition to sugar, other types of substituents such as organic acids, amino acids, inorganic acids, amino sugars, uronic acids are also found in HePs (Table 18.1).

Acetan, alginates, heparin, xanthan, gellan are some examples of HePS (Sanalibaba and Çakmak 2016). The information regarding the monomers and the chemical bonds of some EPS has been represented in Table 18.2.

EPS are biosynthesized generally in the late logarithmic or logarithmic phase, sometimes also produced in the stationary phase. Although, the maximum amounts synthesize only during the logarithmic phase than the stationary phase. The production of EPS quality and quantity varies with bacterial strains type. Although, physicochemical factors such as temperature, incubation time, pH, medium composition (carbon/nitrogen ratios and cation sources), and salinity also plays a vital role in EPS yield (Angelin and Kavitha 2020; Moghannem et al. 2017).

3 Genetics of EPS Production

The diverse groups of EPS-producing bacterial communities are found in different niches. So, these bacterial communities contain a diverse set of gene/gene clusters. These are involved in the EPS formation, which effectively participates in plant growth promotion and maintains lifestyle in adverse conditions. Although the molecular mechanisms and inducers of EPS biosynthesis are not well known in rhizobacteria to date, many bacterial species are known to contain specific gene/gene clusters (Lu et al. 2018). For example, Blanco-Romero et al (2020) found a novel gene cluster *pap* (*Pseudomonas* acidic polysaccharide; size 2 *kb*) in the well-known PGPR strain, *Pseudomonas fluorescens*

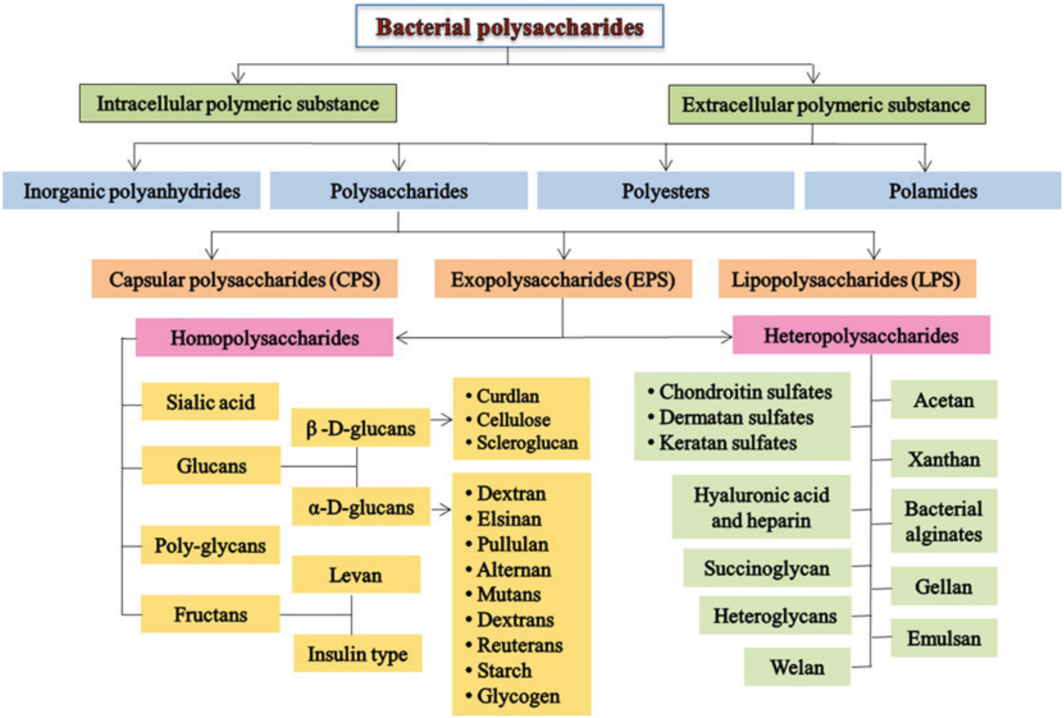

Fig. 18.1 Classification of bacterial EPS production

Table 18.1 List of the common substituent of bacterial EPS

	Substituent	Linkage	Charge	Examples of bacteria	References
Non-carbohydrate	Organic acids				
	Acetate	Ester	None	*K. oxytoca*	Moghannem et al. (2017)
	Succinate	Ester	Negative	*Rhizobium* spp., *Sinorhizobium meliloti*, *Agrobacterium* spp.	Sutherland (2001), Mishra and Jha (2013)
	Propionate	Ester	None	*Escherichia coli*	Li et al. (2021)
	Hydroxybutanoate	Ester	None	*Rhizobium leguminosarum*, *R. trifolii*	Sutherland (2001), Mishra and Jha (2013)
	Glycerate	Ester	Negative	*Sphingomonas elodea*, *Pseudomonas elodea*	Sutherland (2001), Mishra and Jha (2013)
	Pyruvate	Ketal	Negative	*Klebsiella* spp.	Sutherland (1972)
	Amino acids				
	L-glutamate	–	Negative	*Klebsiella aerogenes*	Sutherland (2001)
	Serine	–	None	*E. coli*	Li et al. (2021)
	Inorganic acids				
	Sulphate	–	Negative	*Haloferaxmediterranea*, Cyanobacteria, *Phormidium* sp.	Sutherland (2001), Mishra and Jha (2013)
Carbohydrate	Pentose sugars				
	D-arabinose	–	None	*Azospirillum brasilense*	Mora et al. (2008)
	D-xylose	–	None	*K. oxytoca*	Moghannem et al. (2017)
	Hexose sugars				
	D-glucose	–	None	*Pseudomonas* spp., *Bacillus* spp.	Ali et al. (2020)
	D-galactose	–	None	*K. oxytoca*	Moghannem et al. (2017)
	D-mannose	–	None	*Pseudomonas* spp.	Ali et al. (2020)
	L-rhamnose	–	None	*Sphingomonas* spp.	Roca et al. (2015)
	L-fucose	–	None	*K. oxytoca*	Moghannem et al. (2017)
	Amino sugars				
	D-glucosamine	–	Positive	*Pseudomonas* spp.	Ali et al. (2020)
	D-galactosamine	–	None	*Methanobacterium formicicum*	Sutherland (2001), Mishra and Jha (2013)
	N-acetyl-D-glucosamine	–	None	*Streptococcus* sp.	Roca et al. (2015)
	N-acetyl-D-galactosamine	–	None	*Vibrio neocaledonicus*	Sutherland (2001), Mishra and Jha (2013)
	Uronic acids				
	D-glucuronic acids	–	Negative	*Klebsiella oxytoca*	Moghannem et al. (2017)
	L-iduronic acids	–	Negative	*Butyrivibrio fibrisolvens*	Roca et al. (2015)
	D-galacturonic acids	–	Negative	*Klebsiella oxytoca*	Moghannem et al. (2017)
	D-mannuronic acid	–	Negative	*K. oxytoca*	Moghannem et al. (2017)

F113. Another study demonstrated that, *Anabaena* sp. PCC 7120 contains EPS producing *exoD* domain. In *Anabaena* sp. PCC 7120, EPS production was enhanced in lower sulfate concentrations with the increases of alr2882 (gene ID) expression (Kharwar et al. 2021). The genome of *Paenibacillus polymyxa* WLY78, an N_2-fixing bacteria, contains two putative gene clusters, such as the *pep-1* clusters (13 *kb*) and *pep-2* clusters (20 *kb*), where the only *pep-2* clusters are involved in EPS and biofilm formation (He et al. 2021). For the alginate biosynthesis, the *alg* gene is responsible but some *alg* genomic region functions are not the same in all rhizospheric PGPR (Fig. 18.2). Like, in the case of *P. fluorescens* F113 (Blanco-Romero et al. 2020), the *alg44* gene (2 *kb*) is performed in C-di-GMP binding but in the case of *Pseudomonas chlororaphis* PcPCL1606 (Heredia-Ponce et al. 2020a) and *Pseudomonas syringae* pv. *syringae* UMAF0158 (Heredia-Ponce et al. 2020b) this gene performs as a hemolysin-D. The same type of distinguishable putative functions is also found in the case of *psl* gene clusters (Fig. 18.2). Many others EPS responsive gene/gene clusters found in PGPR and are summarized in Fig. 18.3 with their putative functions, and their different type of functional activity in plant growth promotion under water limiting conditions are discussed in Table 18.3.

4 Role of EPS on the Plant Under Drought Stress Condition

Rhizobacteria can produce a higher quantity of EPS in presence of drought conditions compared to non-stressed conditions. Production of EPS also enhanced with the increase of drought intensity. EPS are mainly essential elements of the extracellular matrix which always serves 40–95% of the bacterial mass. The major roles presented by bacterial EPS are (a) soil aggregation, (b) surface attachment, (d) biofilm formation, (f) microbial aggregation, (e) plant–microbe interaction, and (g) bioremediation, and many others (Fig. 18.4). Due to plant–microbe interaction plant roots through EPS also forms rhizosheath (RS), which increases adherence of root-soil. This RS provides the active site for bacteria-soil interaction and helps in micro aggregates. Hence, EPS can change root morphology by forming RS and also increase the root hair numbers in adverse conditions (Karthik and Arulselvi 2016). Bacterial EPS might reserve carbon, for the complete degradation required a broad range of different enzymes because EPS are generally complex types. EPS formed an extensive network with other bacterial EPS (Costa et al. 2018). In addition, many studies revealed that rhizobacterial EPS can entrap the nutrients like minerals, soluble/insoluble metals, and ions on their EPS matrix with soil particles (Flemming et al. 2016). In most cases, bacterial EPS are negatively charged in presence of carboxyl and hydroxyl functional groups (Ding et al. 2018) that influence the metal biosorption. Many other binding sites and their diverse chemical natures (pH, ionic strength, surface properties, metal content, molecular weight, and branching) are responsible for nutrient entrapment (Costa et al. 2018). These properties have increased the bioavailability of nutrients for plants in the rhizosphere under water deficiency conditions. Some EPS producing bacterial species and their functional role in adverse conditions are listed in Table 18.4. The different mechanisms of EPS-producing bacteria in plant growth promotion under stress conditions are briefly described below.

4.1 Soil Physicochemical Properties and Aggregation of Soil

Physicochemical properties of the soil are the main criteria in the agricultural field. Because it affects several biological processes that negatively impress on the productivity of the crop. But the different types of biotic and abiotic stress change the biochemical and physicochemical characters of soil and cause it incompatible for maximum yield of the crop, also reducing the rhizospheric bacterial activity (Millennium Ecosystem Assessment 2005). By changing the physicochemical properties of infertile soil, improving the soil fertility rate for sustainable agriculture (Naseem et al. 2018). The interactions amid the plant roots, soil, water, and bacteria in the rhizosphere cause alterations in structural and physicochemical properties of the rhizospheric soil. EPS producing PGPR plays a significant function in soil texture and health maintenance. In soil organic matter, EPS are the very important active constituents that have a slimy texture and ionic charges. So, bacterial EPS acts like glue substances and gets attached to ions and clay. As a result, they can hold solid particles together and form various types of soil aggregates, such as micro aggregates and macroaggregates of <250 µm and >250 µm in diameter respectively.Rhizobiaceae, Hyphomicrobiaceae, and Comamonadaceae family bacteria significantly produce EPS and LPS which can help in soil aggregation and reclamation during soil formation (Vuko et al. 2020). Rhizobacteria establish an association with plants and then plant roots produce exudates or organic carbon, which stimulates the microbial community growth. Then the rhizospheric bacteria release mucilaginous EPS

Table 18.2 Chemical configuration of Homo and Hetero-exopolysaccharide

	EPS	Molecular weight (Da)	Monomers	Linkage	References
Homopolysaccharides	Dextran	10^6–10^9	Glucose	α-1,6 glycosidic bonds; in some cases 1,2-, 1,3 or 1,4 bonds are also present	Díaz-Montes (2021)
	Mutan	5.654×10^3	Glucose	α-1,3-D-glucan	Koo et al. (2010)
	Alternan	10^6–10^7	Glucose	α-1,3 and α-1,6 glycosidic bonds	Gupta and Diwan (2016)
	Reuteran	–	Glucose	α-1,4 glycosidic bonds	Gupta and Diwan (2016)
	Curdlan	5×10^4–2×10^6	Glucose	β-1,3-D-glucan and α-1,3-β-D-glucans	Gupta and Diwan (2016)
	Levan	5.044×10^2	Fructose	β-2,6 glycosidic bonds	Monsan et al. (2001)
	Inulin-type	$(4.62$–$6.2) \times 10^3$	Fructose	β-2,1 glycosidic bonds	Angelin and Kavitha (2020)
	Cellulose	$\sim 10^6$	Glucose	β-1,4	Angelin and Kavitha (2020)
	Scleroglucan	7.145×10^2	Glucose	β-1,3 and β-1,6	Osemwegie et al. (2020)
	Pullulan	$(3.62$–$4.8) \times 10^5$	Maltriose	α-1,4 and 1,6	Osemwegie et al. (2020)
	Poly-galactans	1.8016×10^2	Galactose	Pentameric repeating unit of galactose	Angelin and Kavitha (2020)
Heteropolysaccharides	Alginate	$(0.3$–$1.3) \times 10^6$	α-L-guluronosyl and β-D-mannurosyl	1,4 bonds	Marshall et al. (2019)
	Xanthan	$(2.0$–$50) \times 10^6$	Glucose, mannose, glucuronic acid, acetyl and pyruvil residues	β-1,4; β-1,2 and β-1,3	Angelin and Kavitha 2020
	Hyaluronan	7.766×10^2	*N*-acetyl-glucosamine and Glucuronic acid	Alternate β-1,4 and β -1,3 bonds	Freitas et al. (2011)
	Gellan	15–4×10^5	Rhamnose, glucose and glucuronic acid	1,3-β-D-glucose, 1,4-β-D-glucuronic acid, 1,4-β-D-glucose, and 1,4-α-L-rhamnose	Angelin and Kavitha (2020)
	Succinoglycan	5×10^3–1×10^6	Glucose and galactose	β-1,3 and 1,6	Medeot et al. (2016)
	Welan	$\sim 1.0 \times 10^6$	Glucose, glucuronic acid, and rhamnose	α-1,3 and α-1,6	Coleman et al. (2008)

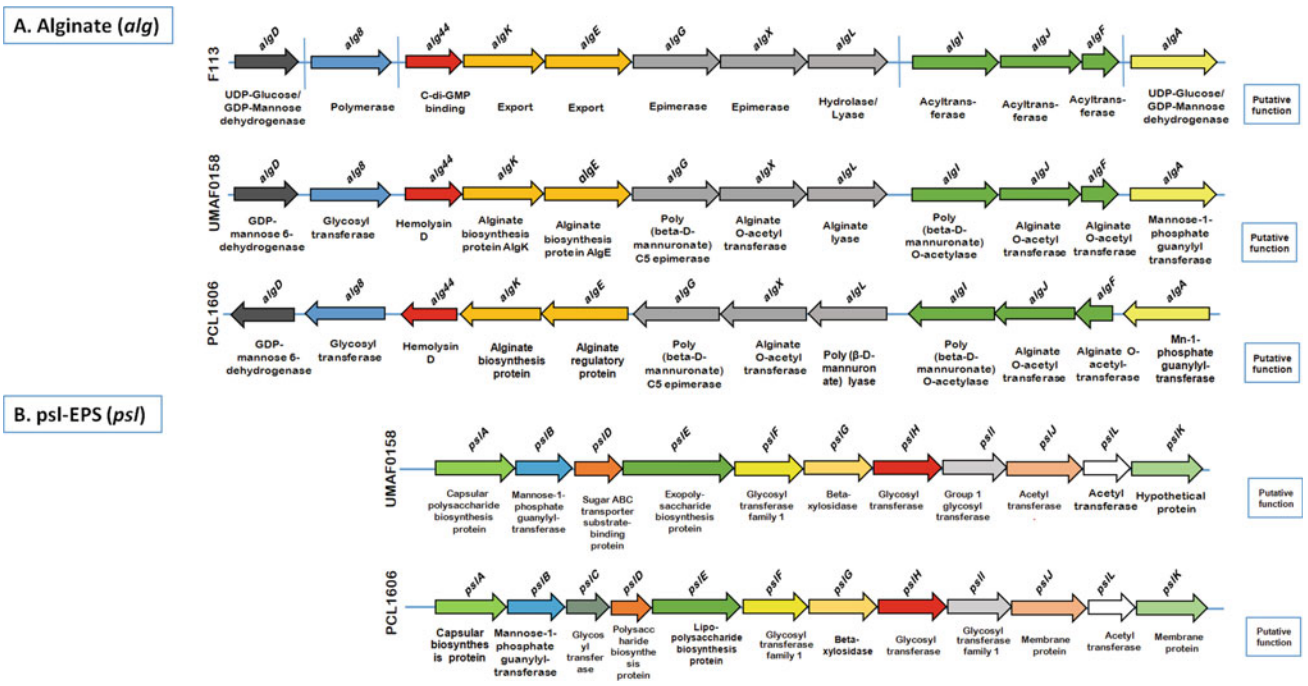

Fig. 18.2 A comparative diagram of PGPR gene clusters: **A.** Compare the *alg* gene clusters functions between *Pseudomonas fluorescens* F113 (Blanco-Romero et al. 2020), *P. chlororaphis* PcPCL1606 (Heredia-Ponce et al. 2020a) and *P. syringae* pv. *syringae* UMAF0158 (Heredia-Ponce et al. 2020b); **B.** compare the *psl* gene clusters functions between *P. chlororaphis* PcPCL1606 and *P. syringae* pv. *syringae* UMAF0158

that promotes aggregation of soil and enhances the quantity of root adhering soil (RAS). Increasing the RAS aggregation amount forms a protective environmental condition where plant nutrients and water uptake improve. So, the bioavailability of nutrients (N, Fe, P, and K) enhances, thus promoting plant growth in adverse conditions (Rashid et al. 2016). Plants treated with EPS producing *Planomicrobium chinense* and *Bacillus cereus* show resistance to drought stress, which was seen due to improving the soil texture by EPS (Khan and Bano 2019). Under drought stress, rhizobacterial strains like *B. licheniformis, B. amyloliquefaciens, B. subtilis, B. thuringiensis,* and *Paenibacillus favisporus* increase the RAS/RT (root tissue) ratio by EPS-production (Vardharajula et al. 2011). *P. fluorescens* produced alginate by alginate synthesizing genes like *algB*, *alg44* and *algD* which can hold a higher amount of water by soil colonization in dehydrating conditions (Marshall et al. 2019).

4.2 Water Holding Capacity

EPS have intense water holding capacity (WHC). Xanthan can hold 15 times more water than its weight. But on the other hand, dextran had a lesser WHC for structural differences (Costa et al. 2018). Bacterial EPS are hydrated biomolecules with 97% (more or less) water holding capacity in the polymeric matrix. The availability of water also improved the soil structure, physicochemical and biochemical properties. Water potential in rhizospheric soil is the pivotal parameter that defines the bioavailability of oxygen, water, nutrients to microorganisms and plants (Naseem and Bano 2014). EPS can protect soil texture, microorganisms, and plants in water scarcity conditions and also provide hydrating conditions. Rhizobacterial EPS can form the bridge between soil particles and clay that increases water holding capacity in the plant root zone. In addition to these functions, microorganisms still maintain nutrient diffusion and physiological function even in dry conditions. EPS producing soil bacteria *Pseudomonas* sp. can hold water greater than many times of it's weight. When applied in sandy soil the it increase moisture content by holding more water in comparision to uninoculated soil (Roberson and Firestone 1992). The EPS producing Cyanobacteria such as *Phormidium* 94a (Vicente-García et al. 2004) and *Nostoc calcicola* (Bhatnagar et al. 2014), isolated from arid regions showed the water retention capacity and express a strategy of nutrient entrapment and endurance.

4.3 Significance of EPS in Symbiosis

In the establishment of a symbiotic relationship between plants and nitrogen-fixing bacteria, polysaccharides play a

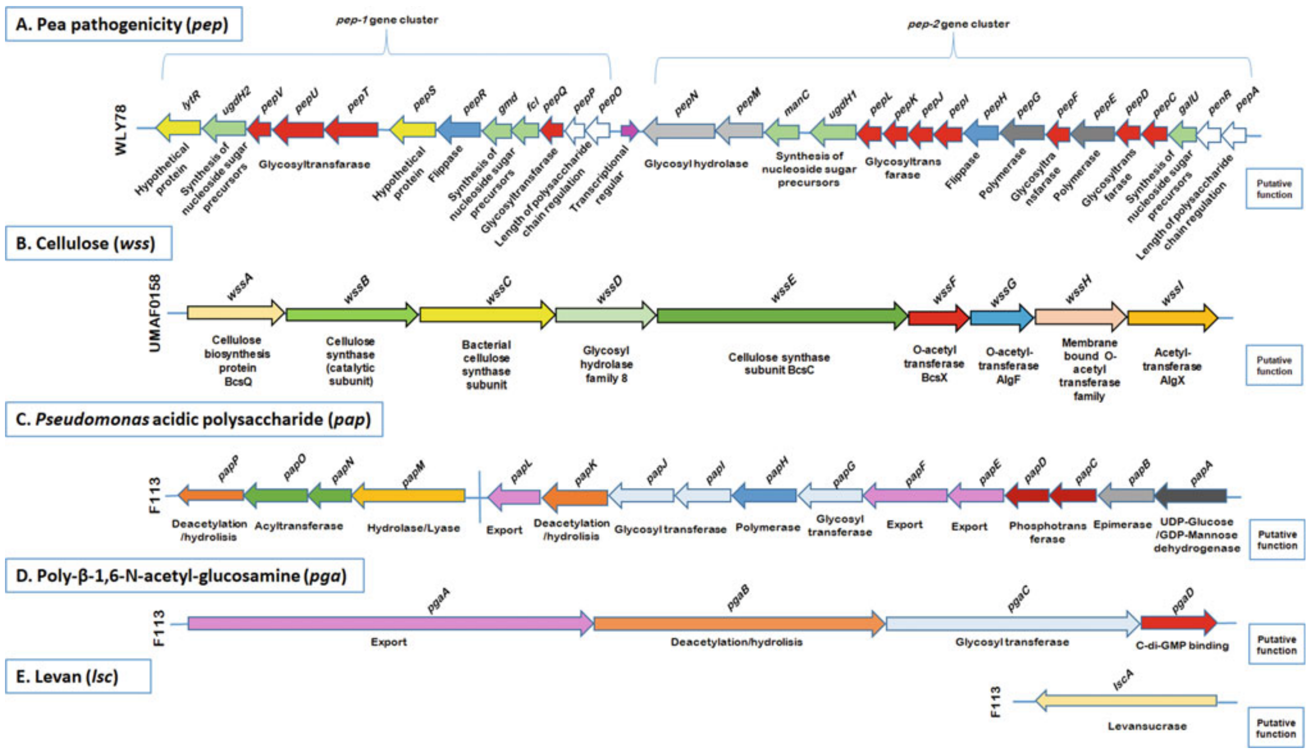

Fig. 18.3 Different type genes/gene clusters and their putative functions: **A.** *pep* gene clusters of *Paenibacillus polymyxa* WLY78 (He et al. 2021); **B.** *wss* gene of *Pseudomonas syringae* pv. *syringae* UMAF0158 (Heredia-Ponce et al. 2020b); **C.** *pap* gene, **D.** *pga* gene and **E.** *lsc* gene of *Pseudomonas fluorescens* F113 (Blanco-Romero et al. 2020)

significant role in plants, such as *Leucaena* sp., *Trifolium* sp., *Medicago* sp., and *Pisum* sp. (Sharma et al. 2020). EPS contributes intrinsic roles in establishing the first connection between bacteria and the surface of the plant. Extracellular polymeric substances are the fundamental molecules in many legume plants for nodulation at the rhizospheric zone, which are also considered as signaling molecules (Nod factors) necessary for identifying specific host plants (Ghosh and Maiti 2016). Nod factors modulate the cytokinin biosynthesis and improve nutrition and nodule formation in soybean plants under water deficiency conditions (Prudent et al. 2016). Although the exact molecular mechanisms are not still determined completely. As an example, to penetrate alfalfa nodules including establishing the successful symbiotic relation, *Sinorhizobium meliloti* has to synthesize succinoglycan. On the other hand, mutants cannot produce succinoglycan, synthesize excessive or transformed EPS, which decreases the ability of infectious activity and symbiosis process (Cheng and Walker 1998). *Rhizobium sullae* produces fucose-rich EPS which can help in nodule formation in *Hedysarum coronarium* L. plant. This strain also produces Kdo-rich CPS, LPS, and cyclic β-(1,2)-glucans (Gharzouli et al. 2013). The *Rhizobium*-legume symbiosis requires specific chemical signaling between the symbiotic partners. In addition to the flavonoids and Nod factors that initiate the symbiotic program, like EPS, LPS, CPS, and cyclic β-(1,2)-glucans play essential roles in the formation of the infection thread and are successful in symbiosis by nodule development in nutrient deficiency or stressful conditions. Nevertheless, the precise functions of these complex carbohydrates are still being investigated. *Hydrogenophaga* sp. (SL48) and *Rhizobium* sp. (SL42) were co-inoculated with *Bradyrhizobium japonicum* (532C) in soybean plant; shoot dry weight, root dry weight, flowering significantly increased via nodule formation under stress conditions (Ilangumaran et al. 2021). *Lotus japonicus* produces EPR3 receptor that binds with only bacteria which synthesize specific type EPS (*Mesorhizobium loti* strain R7A) and permits infection thread formation (Kawaharada et al. 2015).

4.4 Microbial Aggregation

The phenomenon of bacterial aggregation is of great interest for agriculture application because it promotes bacterial survival, dispersal, and facilitates adhering to the plant root surfaces. The bacterial cell surface components act a key role in bacterial cell aggregation (Bogino et al. 2013). EPS participates in aggregation and surface colonization of plant-associated bacteria (Burdman et al. 2000). *A.*

Table 18.3 Genes of exopolysaccharides and their functions in plant growth

Bacteria	Gene clusters or genes of EPS producing	Role in plant growth promotion	References
A. brasilense	rmlD (dTDP 4-rhamnose reductase), phbC (poly-beta-hydroxyburyrate synthase), exoC (phosphomannomutase), and exoB (UDP-glucose 4′-epimerase)	Aggregate the bacterial cell in rhizospheric zone	Bahat-Samet et al. (2004)
Paenibacilluspolymyxa WLY78	*pep-2* gene cluster of *P. polymyxa* WLY78 genome	Formed biofilm which helped in nitrogenase synthesis and activity by providing microaerobic environment	He et al. (2021)
Pseudomonas putida	*algD* (promoter of alginate biosynthesis)	Formed biofilm and microcolony by alginate production in water limiting conditions	Li et al. (2010)
*P. fluorescens*Pf0-1	*algB*, *alg44* and *algD* (producing some important product in alginate synthesis)	Soil colonization and water holding capacity	Marshall et al. (2019)
P. chlororaphis PcPCL1606; *P. syringae* pv. *syringae* UMAF0158	*Psl* (polysaccharide synthesis loci) gene cluster	Display plant colonization and antagonistic activity by the biofilm formation	Heredia-Ponce et al. (2020a, b)
P. fluorescens SBW25	*wss* operon (cellulose)	Helps in plant–microbe interactions and improved the nutrient supplement	Gal et al. (2003)
P. fluorescens F113	*pga* (poly-β-1,6-N-acetyl-glucosamine), *pap* (*Pseudomonas* acidic polysaccharide), *alg* (*alginate*), *lsc* (*levan*)	Formation of biofilm in rhizosphere, host-bacteria interaction and colonization	Blanco-Romero et al. (2020)

brasilense, a wild-type strain promotes plant growth by producing monomeric-based EPS. In a fructose-supplemented medium, *A. brasilense* (Sp7) produced glucose, and arabinose-rich EPS during the stationary and death phase of growth (Mora et al. 2008) which helped in bacterial cell aggregation. The *exoC* (phosphomannomutase), *exoB* (UDP-glucose 4-epimerase), and *phbC* (poly-b-hydroxybutyrate synthase) mutant strains produced arabinose-rich EPS and showed potential capacity in the bacterial aggregation process. But while the mutant not produce LPS (dTDP 4-rhamnose reductase; rmlD) and glucose-rich EPS, they failed to successfully aggregate the cell (Bahat-Samet et al. 2004). Thus, the bacterial cell aggregate mechanism could establish a protected plant growth that gives survival efficacy in a harsh environment.

4.5 Biofilm Formation

Biofilms are protected against hostile conditions, by their secretion of EPS, which is suspected to defend these cells, from heavy metals too. Drought tolerant *B.*

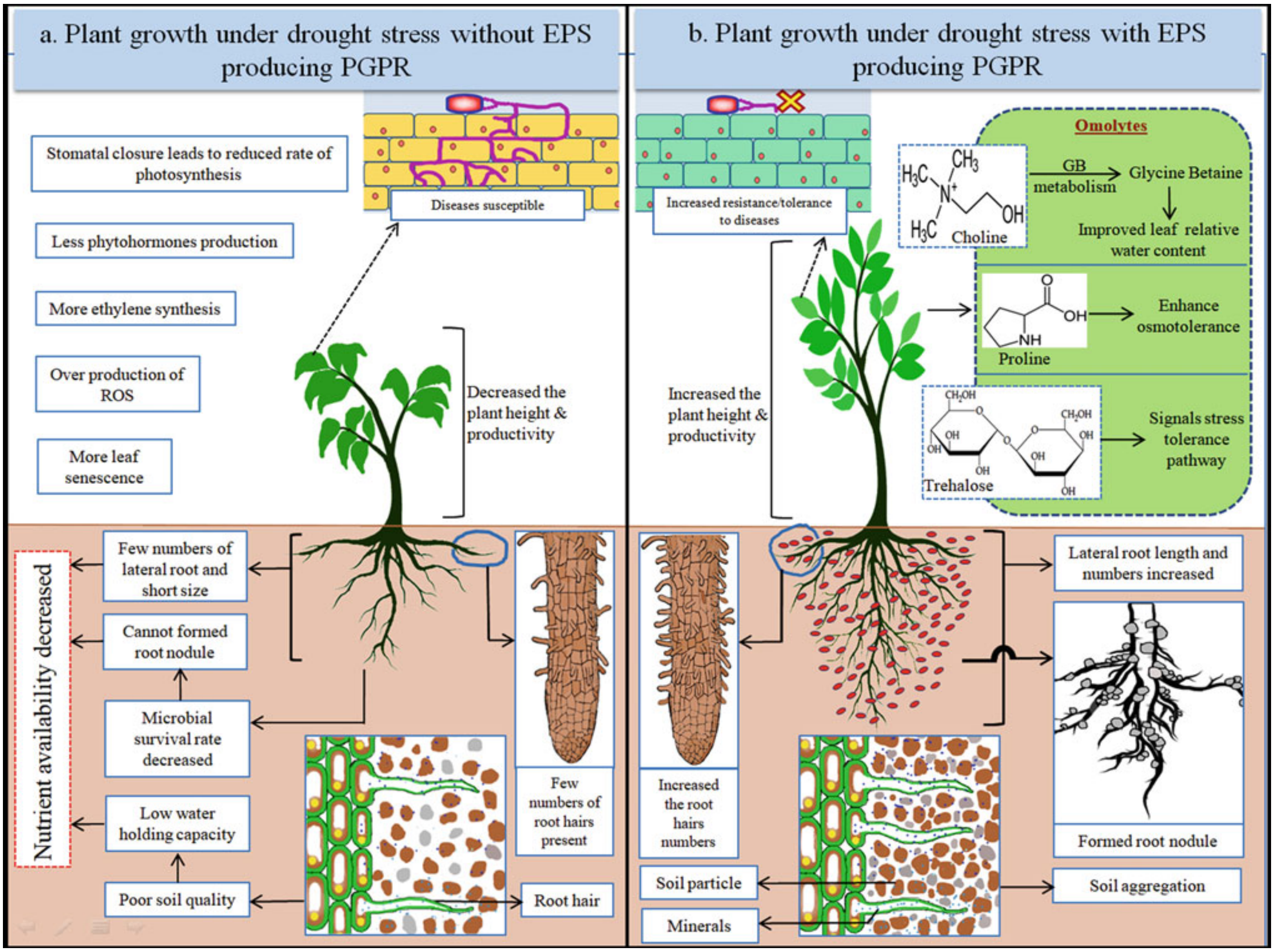

Fig. 18.4 A comparative diagram of plant growth under drought conditions: **a.** effect of drought stress in plants; **b.** representation showed different functions of EPS producing PGPR under drought conditions

amyloliquefaciens-54 synthesized biofilms which can positively induce tomato plant's growth by increasing expression levels of stress-responsive genes, such as *tdi65*, *lea*, and *ltpg2* (Wang et al. 2019). It also observed that the extracellular matrix encapsulates, the differentiated cell population of a microbial community in biofilms. In microbial communities, biofilms differentiated cell populations are encapsulated by bacteria-made extracellular matrices. Bacterial species residing in the most natural, clinical, and industrial setup are valuable for forming biofilms. Apart from that, bacteria like the Rhizobacterium living at the root of plants, are known to form micro-colonies or biofilm-like structures (Nayak et al. 2020). Biofilms also stimulate root exudates and therefore enhance soil accumulation, increase microbial biomass and improve water potential to plants. Consequently, viscous extracellular matrix production at the rhizosphere possesses a powerful selectivity edge, especially when they are under stress. Mechanical stability of the biofilm is also due to the matrix, which interacts with various low molecular weight solutes and macromolecules that is responsible for the formation of many microenvironments in the biofilm (Khan et al. 2020). *P. chlororaphis* (Heredia-Ponce et al. 2020a) and *P. syringae* (Heredia-Ponce et al. 2020b) secret some EPS in their extracellular matrix that contributes to an effective role in formation of biofilm. *P. syringae* synthesizes some psl (polysaccharide synthesis loci)-like polysaccharides and alginate in extracellular matrix components which are strongly involved in biofilm formation and niche competition. Interestingly, Heredia-Ponce et al. (2020b) evaluated the presence *psl*-like gene cluster in all strains of the *P. chlororaphis* phylogroup which indicates that this EPS could be related to the biofilm architecture in this species. *P. putida* mt2 created a hydrated micro-environment by producing alginate, cellulose and a

Table 18.4 EPS producing PGPR and their functional role

Examples of PGPR (source)	Quantity of EPS production	Secreted product	Functional Role	References
Pseudomonas putida (Rhizospheric soil)	63.30 µg/ml (NS)	Glucose, mannose, and rhamnose	Increased the plant biomass, survival rate, and root adhering soil/root tissue ratio of sunflower seedlings under drought stress conditions	Sandhya et al. (2009)
Pseudomonas aeruginosa and *Bacillus coagulans* (Collected from culture collection)	–	–	Increased the different parameters of plant growth under water stress conditions	Yadav et al. (2018)
Planomicrobium chinense and *Bacillus cereus*	–	Sugar, Protein, Uronic acid	Improved plant growth and drought tolerance under rainfed conditions	Khan and Bano (2019)
Pseudomonas fluorescens (Soil)	11.63 mg/mg protein (NS)	Sucrose	Improved the plant growth in adverse environments feature by water deficiency conditions	Niu et al. (2018)
Enterobacter hormaechei (Soil)	5.44 mg/mg protein (NS)			
Pseudomonas migulae (Soil)	3.33 mg/mg protein (NS)			
Bacillus amyloliquefaciens (Rhizospheric soil)	4.88 mg mg^{-1} (NS); 32.4 mg mg^{-1} (DS)	Glucose, mannose, xylose, and raffinose	Improved relative water content, root adhering soil/root tissue ratio, leaf water potential, plant biomass, aggregate stability and reduced leaf water loss, the activity of antioxidant enzymes in drought conditions	Vardharajula et al. (2011)
Paenibacillus favisporus (Rhizospheric soil)	2.46 mg mg^{-1} (NS); 18.9 mg mg^{-1} (DS)	Glucose and raffinose		
Bacillus licheniformis (Rhizospheric soil)	2.98 mg mg^{-1} (NS) 19.8 mg mg^{-1} (DS)	Glucose and mannose		
Bacillus thuringiensis (Rhizospheric soil)	2.39 mg mg^{-1} (NS); 18.2 mg mg^{-1} (DS)			
Bacillus subtilis (Rhizospheric soil)	2.69 mg mg^{-1} (NS); 22.3 mg mg^{-1} (DS)			
Bacillus thuringiensis, *Bacillus subtilis*, and *Bacillus megaterium* (Rhizospheric soil of chickpea)	–	Sugar, protein, uronic acid	By changing physiology and biochemical properties in the plant, increased growth and drought tolerance potentiality	Khan et al. (2019)
Azospirillum brasilense and *Bacillus subtilis* (Soil)	–	Protein, sugar, and uronic acid	Promote plant growth under drought stress	Ilyas et al. (2020)
Proteus penneri, *Pseudomonas aeruginosa*, and *Alcaligenesfaecalis* (Soil)	–	Sugar, Protein, Uronic acid	Plant growth significantly increases in drought conditions	Naseem and Bano (2014)
Fluorescent *Pseudomonas* strain Psd (Soil)	–	Alginate	Possesses PGP properties, high Zn^{2+} biosorption ability, and also showed biocontrol potentiality	Upadhyay et al. (2017)

NS—Non-stressed; DS—Drought-stressed

novel putida exopolysaccharide A (pea) that can help in the formation of biofilm architecture which protects from desiccation stress and increase survival efficiency (Chang et al. 2007; Nielsen et al. 2011). Not only *P. putida* but also *P. aeruginosa* PAO1 and *P. syringae* pv. *syringae* B728a produces alginate and shows stress tolerance activity under water-limiting conditions by producing EPS-rich biofilm (Chang et al. 2007). By the expression of *algD* promoter, *P. putida* produced alginate within the biofilm under water-limiting conditions which have also a relationship with microcolony formation. The *alg8* gene is the second gene in the *algD* operon which has an important role in alginate gene expression during biofilm formation; many others single transduction networks regulate and modulate the *algD* operon activity at transcriptional levels (Chang et al. 2007; Li et al. 2010).

4.6 Improved Plant–microbe Interactions

Plant-associated rhizobacteria can interact with the aerial parts, rhizospheric zone, or even the vascular system of the plant host using a great diversity of EPS. Beneficial bacteria produce EPS in the rhizospheric zone, which can improve the plant–microbe interaction. Among all the EPS, cellulose, alginate, and Psl (contains D-glucose D-mannose, and L-rhamnose) are mainly studied in rhizobacteria that have an important role in plant–microbe association (Blanco-Romero et al. 2020). As an example, *P. chlororaphis* PcPCL1606 (Heredia-Ponce et al. 2020a) and *P. syringae* pv. *syringae* UMAF0158 (Heredia-Ponce et al. 2020b) synthesize Psl EPS in presence of a *psl*-like gene cluster which shows significant roles in colonizing the soil and roots of plants; some other pseudomonads by using these mechanisms also help in the surface colonization and participate against some stressors. Though bacterial cellulose is synthesized by several biosynthesis and regulation mechanisms which have been shown a common role of this constituent is to help the establishment of effective role in plant-microbes interactions (Heredia-Ponce et al. 2020a). *P. aeruginosa* produced alginate and Psl have a beneficial effect on plant-microbes interactions and microcolony formation (Heredia-Ponce et al. 2021; Zhao et al. 2014). *P. fluorescens* SBW25 is a potential rhizobacterium that helps in plant nutrition and health by producing a cellulosic type of EPS which requires the colonization of plant root surfaces and promotes plant growth (Gal et al. 2003). During plant-bacteria interactions, the bacterial cellulose of SBW25 strain contributes to the beneficial ecological performance in the sugar beet phyllosphere and rhizosphere. Recently one study revealed that *P. fluorescens* F113 strain produced biofilm around plant rhizospheric zone by some extracellular matrix (ECM) (Blanco-Romero et al. 2020). This ECM is mainly composed of lipids, proteins, DNA, and EPS including alginate, levan, poly-*N*-acetyl-glucosamine (PNAG), and *Pseudomonas* acidic polysaccharide (Pap) which have a crucial role in host plant-bacteria interaction and rhizosphere colonization for plant growth promotion (Blanco-Romero et al. 2020). The polysaccharide of pea produced by *P. putida* mt2 in water-limiting conditions is typically involved in the production of galactose, glucose, and mannose-rich polymer that has an important contribution to rhizosphere colonization and cell–cell interactions which is necessary for pellicle formation (Nielsen et al. 2011).

4.7 ACC-Deaminase and Antioxidant Activity

In plants, drought stress causes biochemical and physiological disorders such as hormonal concentration imbalance including stimulated ethylene production. Ethylene is one type of growth hormone that is required for plants at a lower concentration; it decreases the root growth in presence of a higher concentration which also leads to retard the plants' growth and development (Wang et al. 2019). Under stress conditions, ethylene is synthesized from ACC, thus any disturbance on ACC synthesis can decrease ethylene production (Gupta and Pandey 2019). Previously reported that during the improvement of plant growth under drought conditions *B. velezensis* D3 (Nadeem et al. 2020) and *Pseudomonas* sp. (Ali et al. 2014) performed better when it pause both EPS-producing and ACC-deaminase activity than the other strains which pause only one of the above activities.

At the cellular level, huge damages occur due to oxidative stress under water limiting conditions; from this injury, imbalance status occurs between the reactive oxygen species production and their detoxifying enzymes. Plants produce some antioxidants enzymes like catalase, superoxide dismutase, peroxidase, glutathione peroxidase, ascorbate peroxidase, glutathione reductase, and transferase that detoxify the reactive free radicals. Therefore, by boosting the production of antioxidants PGPR can facilitate in imparting drought tolerance in plants (Ilyas 2020). For example, *Pseudomonas oryzihabitans, Pantoea brenneri, Acinetobacter calcoaceticus, Pseudomonas putida, Chryseobacterium* sp. isolated from halophytes and drought-tolerant plants contain one or more numbers of antioxidant mechanisms involving genes (such as *cat*, *pox*, *sod*, *gpx*, *gr*, and *gst*) that control the plants from great damages (Leontidou et al. 2020).

4.8 Antagonistic Activity

Rhizobacteria protect the plant by the inhibition of various soil-borne plant pathogens by producing EPS. *B. subtilis* requires an extracellular matrix for antagonistic activity, which is also involved in biofilm formation and promotes bacterial cell colonization on the plant root surface. This extracellular matrix is encoded by *tapA-sipW-tasA* and *epsA-O* operons (Chen et al. 2013). Extracted EPS from the *P. aeruginosa* PF23 showed highly antagonistic activity against *Macrophomina phaseolina* (80–90%) under stress conditions and promoted plant growth in a greenhouse (Tewari and Arora 2014). Alginate is produced in extreme amounts by some strains of *P. syringae* after the exposure of copper that is generally applied for the reduction of disease incidence which is caused by some plant pathogens (Kidambi et al. 1995). *P. chlororaphis* PCL1606 strain produced alginates, psl-like polysaccharides and other extra polymeric substances (Fap-like fibre) which helped in biofilm formation and niche competition. Psl-like EPS performs a significant role in surface adhering and contributes to biocontrol activity against the *Rosellinia necatrix* which is responsible for the formation of white root rot disease in avocado plants (Heredia-Ponce et al. 2020a). Generally, biocontrol agents (viz *P. chlororaphis*, *P. putida*, etc.) can synthesize EPS-rich biofilms, and several pieces of evidence suggest that biofilm formation capability should deliberate in assessing their effective crucial role (Pandin et al. 2017). *P. putida* A1, rhizobacteria act as effective biocontrol agent against some plant pathogenic soil born bacterial disease (including *Ralstonia solanacearum*, *Xanthomonas* pv. *oryzae*, *X. citri* subsp. *citri* and *X. oryzae* pv. *oryzicola*) by forming biofilms (Sun et al. 2017) as well as promotes the tomato plant growth by the colonization on the root surface area and found to microbial aggregation around wound sites. *P. simiae* PICF7 is a rhizospheric bacteria, involved in biofilm formation that can effectively suppress Verticillium wilt disease in olive plants, caused by the plant pathogenic soil-borne fungus *Verticillium dahlia* (Montes-Osuna et al. 2021).

4.9 Accumulation of Osmolytes and Sugars

At the cellular level, osmotic adjustment is a fundamental adaptation mechanism that maintains the cells' turgor pressure at high levels and also protects cellular organelles, different enzymes, proteins, and membranes from oxidative damage in stress conditions. Under drought conditions, plants accumulate several compatible organic solute/osmolytes such as proline, glycine, sugars (glucose, sucrose, and raffinose, etc.), some proteins (dehydrins), betaine, quaternary ammonium compounds, polyhydric alcohols, and polyamines (Vurukonda et al. 2016). EPS producing PGPR like *P. aeruginosa* (Pa2), *Proteus penneri* (Pp1), and *Alcaligenes faecalis* (AF3) showed that the accumulation of soluble sugar and proline induced tolerance of plants in drought stress, proline also behaves as an antioxidant defence mechanism and signaling molecule (Naseem and Bano 2014). Inoculation of *Bacillus subtilis* and *A. brasilense* strains in wheat plants improved the proline and sugar content in plants that can help to maintain the water status of the cell and other metabolisms which protect from dehydration (Ilyas et al. 2020). Compatible solutes/osmolytes accumulation in plant vacuoles mainly proline and sugars insist in the enzyme inactivation, decreases the osmotic potential and maintains membrane integrity under water scarcity conditions. Leontidou et al. (2020) detected different osmoprotectant genes like betaine-aldehyde dehydrogenase, choline dehydrogenase, and proline dehydrogenase in drought tolerant PGPR genomes thus, *P. oryzihabitans*, *Pantoea brenneri*, *Acinetobacter calcoaceticus*, *P. putida* which are involved in drought stress responses.

5 Conclusion and Future Perspectives

The application of PGPR in the agricultural field is an important practice in the present time. In agronomy, among other obstacles, drought stress became a very relentless threat now-a-days as the growth of different plants and their productivity is very badly abated by this. The uses of EPS-producing bacteria related to plant growth are playing a major role to increase future food security globally. Under drought conditions, the application of EPS and PGPR not only helps the plant but also the property of soil and the morphology of root changes. On the physiological and molecular level, the combination of PGPR and EPS generally triggered the osmotic response and induced a few novel genes which help the plant to survive and grow under heavy drought stress. Through plant breeding and genetic engineering, drought stress-tolerant plant production became easy, but it is very time-consuming and cost-effective. Inoculation of EPS producing PGPR strains in the agricultural field to overcome the drought stress is getting interest as it is very environment friendly and less cost-effective.

A few rhizobacterial EPS has been reported till now. But there are a lot of rhizobacterial EPS that show high water contain capacity (welan, dextran), which help to overcome the drought stress, which has not been well studied so far. So, research is needed to know more about the diversity of rhizobacterial EPS. In future, research is necessary to gather more knowledge regarding the identification of the particular microbes, application of delivery methods, and more information about the stress mitigation mechanisms. Overall the future should be focused on: (1) To expand knowledge insight in the biosynthetic path of EPS synthesis in Rhizobacteria; (2) To know more about in drought stress conditions how the EPS producing bacteria sense the signal it needs to produce more EPS or active via plant root-specific pattern-recognition; (3) To decode the activation pathway/mechanisms behind the advantageous properties of rhizobacterial EPS in plants. Such knowledge will enhance the understanding of the complicated process of interaction between eukaryotes and prokaryotes.

Conflict of Interest The authors declare that they have no conflict of interest.

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Potential of Plant Growth Promoting Rhizobacteria for Enhancement of Plant Growth and Its Role in Improving Soil Health Under Abiotic Stress

Shyama Prasad Saha and Deepika Mazumdar

Abstract

With the increase of population worldwide, we have been introduced to a significant challenge in the recent decade which is to feed the population that is growing at an alarming rate. There are several factors responsible which affect the mass production of crops/feed such as the limitation of agricultural land, environmental damage, and especially the number of biotic and abiotic stresses such as drought, salinity, and heavy metal. To overcome those stress barriers several scientific approaches such as the use of chemical fertilizers, pesticides, and herbicides, are adopted, which have their drawbacks in the environmental perspective. Therefore, in the context of sustainable agriculture, the use of plant growth promoting rhizobacteria (PGPR) is a good alternative approach which not only enhances plant growth under controlled environment but also helps plants to alleviate several biotic and abiotic stresses. PGPR produce various phytohormones, exopolysaccharides, organic acids, and small bioactive molecules which play an important role in the overall improvement in the plants' health not only in the fertile environment but also under stress conditions. Hence, this chapter mainly focuses on the mode of action of various PGPR and highlights their role in stress conditions to improve plant growth.

Keywords

Drought • Exopolysaccharides • Heavy metal stress • PGPR • Phytohormones • Salinity

S. P. Saha (✉)
Department of Microbiology, University of North Bengal, Siliguri, West Bengal 734013, India
e-mail: shyamaprasad@nbu.ac.in

D. Mazumdar
Department of Microbiology, North Bengal St. Xaviers College, Jalpaiguri, West Bengal 735134, India

1 Introduction

Since the beginning of agricultural practices, one of the important challenges we face today is how to enhance agricultural productivity to feed the growing population. According to the Global Agricultural Productivity (GAP) Index 2018, the current growth rate of crop productivity is not enough to meet the food demand of an ever-increasing world population that is estimated to be 10 billion people in 2050 (GAP Report 2018). In agroecosystems enhancing crop productivity is very difficult and very much influenced by environmental conditions, management techniques, and farming systems (Egamberdieva et al. 2019). A number of abiotic factors which are imposing challenges in agro-systems are salinity, drought, temperature, chemical pesticides and fertilizer application, soil pH, and contamination of heavy metal hampering crop production (Egamberdieva et al. 2019). Although various abiotic stress management strategies are adopted to overcome all these stress challenges, those strategies are very costly and hence not being able to adopt by the farmers. Thus, an alternative method is always required to achieve the aim of high crop production under stressed conditions. PGPR is one such strategy that is useful in the proper growth of crops in stressed conditions. There are a number of microorganisms reported which can promote the growth and yield of a plant in drought, saline, acidic/alkaline, and other abiotic conditions. *Arthrobacter, Pseudomonas, and Enterobacter* are reported to alleviate crop production (Niu et al. 2018). The volume of the soil which directly surrounds the root system is known as rhizosphere and harbours a huge variety of microorganisms (Dessaux et al. 2009). These microbes may have neutral, positive, or negative effects on the plant. The group of rhizospheric bacteria competent in colonizing the root environment is known as rhizobacteria (Kloepper et al. 1991). There is a mutualistic association between PGPR and plants.

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The structural design of the root plays a vital role in plant growth and development. It helps in the uptake of water, nutrients, and minerals, and provides the plant with a strong anchorage in the soil. The main and secondary branching of the root depends on the continuous incorporation of internal and environmental factors (Asari et al. 2017). On the one hand, the plant synthesizes and secretes a wide range of compounds like sugars, amino acids, proteins, organic acids, various enzymes, etc. through the root exudates which provide nutrition to the rhizobacteria, and on the other hand these bacteria promote the growth of the plants (Asari et al. 2017). Microorganisms usually found in the rhizosphere are termed rhizobacteria. But several microbes that reside on the surface of the root are termed as rhizoplane microbes and some microbes that live inside the root system are known as endophytic microbes (Barea et al. 2005). PGPR includes the species of A*grobacterium, Azotobacter, Azospirillum, Bacillus, Burkholderia, Chromobacterium, Erwinia, Flavobacterium, Micrococcus, Pseudomonas, Serratia*, etc. (Bhattacharyya and Jha 2012). Rhizobacteria may be free-living or in a symbiotic relationship with plants. Groups of PGPR like *Allorhizobium, Azorhizobium, Bradyrhizobium, Mesorhizobium,* and *Rhizobium* belonging to the family Rhizobiaceae grow in a symbiotic relationship with plants (Niu et al. 2018). PGPR have various characteristics that can either directly or indirectly promote the growth of plant under biotic or abiotic stress conditions (Casson et al. 2009). There are numerous reports on the mechanisms used by PGPR. Some mechanisms which directly facilitate plant growth are nitrogen fixation, phytohormone production, organic and inorganic phosphate solubilization, and iron entrapment by bacterial siderophores (Glick et al. 1999). In stress conditions, PGPR leads to the synthesis of enzymes like 1-aminocyclopropane-1-carboxylate (ACC) deaminase which is related to stress signaling (Glick et al. 1999). According to the report of Arshad et al. (2007), there are many PGPR that alleviate drought stress effects in plants by reducing plant ethylene levels that are usually increased by unfavourable conditions. In this respect, those rhizobacteria which are drought tolerant can be more beneficial than others to grow in a new drought environment in sufficient numbers to deliver beneficial effects on plants (Arshad et al. 2007).

2 Insight into the Attributes of PGPR

Numerous research works have been reported on the beneficial effect of PGPR on plant growth and yield (Cardinale et al. 2015; Sang-Mo et al. 2014). These mechanisms employed by the PGPR directly or indirectly help in the stimulation of plant growth, development, and yield. Direct mechanisms involve facilitation in the uptake of nutrients, nitrogen fixation, solubilization of complex nutrients, production of components under stressed conditions, production of phytohormones, etc. (Casson et al. 2009). They also indirectly promote plant growth by producing siderophores, antibiotics, hydrolytic enzymes, hydrogen cyanide (HCN), etc. Hence, the PGPR constitute the leading driving force in restoring soil health (Babalola and Glick 2012; Ahemad and Kibret 2014).

2.1 Direct Mechanisms

2.1.1 Nitrogen Fixation

Nitrogen (N) is one of the important macroelements required for the growth, development, and productivity of plants. Plants take up nitrogen from the soil in the form of ammonium ions (NH_4^+), nitrites (NO_2^-), and nitrates (NO_3^-). PGPR can convert atmospheric nitrogen into ammonia by the process of nitrogen fixation. N_2-fixing microorganisms are of symbiotic and non-symbiotic nature. Symbiotic N_2-fixers form symbiotic association with leguminous (e.g., *Rhizobium* species) and non-leguminous (e.g., *Frankia*) plants (Ahemad and Khan 2012; Zahran 2001). The non-symbiotic N_2-fixing bacteria include cyanobacteria, *Azotobacter, Azospirillum, Gluconacetobacter diazotrophicus* (Bhattacharyya and Jha 2012); but they can add only a small amount of the fixed N_2 compared to the total N requirement of the plant (Glick 2012). Symbiotic N_2-fixing rhizobia under the family Rhizobiaceae lead to the formation of the nodules wherein the rhizobia reside as intracellular symbionts. Diazotrophic microbes (free-living N_2 fixers) are capable of establishing a non-obligate interaction with the host plants (Glick et al. 1999). N_2-fixing microorganisms carry out nitrogen fixation with the help of a complex enzyme system known as nitrogenase which is a two-component metalloenzyme consisting of dinitrogenase reductase (iron protein) and dinitrogenase (Glick 2012).

2.1.2 Solubilization of Organic and Inorganic Phosphorous

The next important plant growth-limiting nutrient after N is phosphorus (P). Despite soil being a large reservoir of organic and inorganic P, the amount available to plants is generally very limited. Phosphorous available in the soil is present in insoluble form and so is not readily available to plants. Monobasic (H_2PO_4) and dibasic (HPO_4^{2-}) ions are the forms of P absorbed by plants (Bhattacharyya and Jha 2012). The chemical P fertilizers added in the agricultural fields are not completely taken up by the plants. The excess portion is rapidly converted into insoluble complexes in the soil which leads to a change in the pH of the soil (Zaidi et al. 2009). Application of microorganisms with phosphate solubilizing activity is widely known as phosphate solubilizing microorganisms (PSM), which may improve the soil health, and hence can be an alternative to chemical P-fertilizers (Khan et al. 2006). Some of the bacterial genera like *Azotobacter, Bacillus, Enterobacter, Erwinia, Microbacterium, Pseudomonas, Serratia,* etc. are reported to be the most significant PSB (Bhattacharyya and Jha 2012). The mechanism of action of PSM is the secretion of low-molecular weight organic acids which carry out the solubilization of insoluble P (Zaidi et al. 2009). The presence and performances of PSM are strictly affected by environmental factors especially under stress conditions (Ahemad and Khan 2010, 2012).

2.1.3 Solubilization of Potassium

Potassium (K) is another very important element required for the growth, metabolism, and development of plants. K can enhance plant resistance to diseases, pests, and abiotic stresses and activates different enzymes and proteins responsible for various plant processes such as starch synthesis, nitrate reduction, energy metabolism, and photosynthesis (Gallegos-Cedillo et al. 2016; Hussain et al. 2016). K is present as mineral forms in the soil and most of them are unavailable to plant (Sparks and Huang 1985). PGPR could solubilize the insoluble K to soluble forms by various mechanisms. During the solubilization process of K, the major mechanisms involved are the production of the organic acids, inorganic acids, and protons (acidolysis mechanism) (Sheng et al. 2008; Maurya et al. 2014; Meena et al. 2014). In the acidolysis process, H^+ are released which can help to dissolve the mineral K resulting in the release of readily available soluble K. There are numerous reports in which several organic acids such as citric, fumaric, gluconic, glycolic, lactic, malic, malonic, oxalic, propionic, succinic, and tartaric acids are mentioned to be produced and secreted by K solubilizing bacteria, which are effective in releasing K from insoluble mineral to soluble K (Krishnamurthy 1989; Hu et al. 2006; Sheng and He 2006; Liu et al. 2012; Prajapati et al. 2012, 2013; Saiyad et al. 2015).

2.1.4 Phytohormones Production

Plant hormones also known as phytohormones are the signal low molecular weight produced within the plants that occur in extremely low concentrations. The term phytohormone was coined by Went and Thimann in 1937 (Went and Thimann 1937). Phytohormones play a significant role in plant metabolism and development. These are the endogenous secondary metabolites that effectively activate plant defence response against both biotic and abiotic stresses. Furthermore, these molecules act as regulators of the growth, development, and physiological processes of the plants. PGPR produce several phytohormones such as auxins, cytokinins, ethylene, gibberellin, and abscisic acid. There are reports of PGPR producing phytohormones that promote the health of the plants. Generally, IAA is responsible for plant cell division and differentiation. It stimulates seed germination rate and also enhances the rate of development of xylem and root. According to a report by Patten and Glick (1996), 80% of microorganisms isolated from the rhizosphere of various crops can synthesize auxins. IAA produced by PGPR promotes the plant root surface area and length helping in greater access to soil nutrients. PGPR produce auxins to affect host physiological processes for their benefit (Shih-Yung 2010). In 2012, Glick has reported that rhizobacterial IAA loosens plant cell walls and helps in enhancing the amount of root exudation providing nutrients for growth and colonization of rhizobacteria. Hence, PGPR IAA is recognized as an important effector molecule in plant–microbe interactions (Spaepen and Vanderleyden 2011). For the synthesis of IAA, tryptophan is an important amino acid that is the main precursor (Zaidi et al. 2009). Anthranilate, a precursor for tryptophan, represses IAA synthesis. By this mechanism, tryptophan finely regulates the IAA biosynthesis with a negative feedback regulation on the enzyme anthranilate synthase and thus suppressing anthranilate formation which ultimately results in an indirect induction of IAA synthesis (Spaepen et al. 2007). There are other important phytohormones that impart the positive effects of rhizobacteria in plants. These include abscisic acid (ABA), cytokinins (CKs), ethylene, and gibberellins (GAs). In addition to these classical phytohormones, there are some other molecules including salicylic acid, jasmonic acid, nitric oxide, strigolactones, and brassinosteroids, which have been known to function as plant growth regulators. Many of the proteins such as some transcription factors and protein kinases involved in phytohormone signaling have been studied. The phytohormone signaling system influence osmotic balance and salt tolerance mechanisms and regulate acclimatization of a plant to salinity (Lyu et al. 2019).

2.1.5 Production of 1-Aminocyclopropane-1-Carboxylate (ACC) Deaminase

Ethylene also known as a stress hormone gets increased under stress conditions like drought, salinity, extreme soil pH, heavy metal contamination, and pathogenicity. This affects the overall performance of the plants in a negative way. The high level of ethylene in plants signifies defoliation and ageing which can reduce crop productivity (Saleem et al. 2007; Bhattacharyya and Jha 2012). PGPR also have a special attribute, i.e., production of ACC deaminase which plays a vital role in stressed conditions. Plants treated with PGPR producing the ACC deaminase prove increased growth and development. ACC deaminase induces salt tolerance and reduces drought stress in plants by reducing the level of ethylene (Nadeem et al. 2007; Zahir et al. 2008). Various bacterial genera have been reported which can produce ACC deaminase. These are *Acinetobacter, Alcaligenes, Azospirillum, Bacillus, Burkholderia, Enterobacter, Pseudomonas, Serratia*, etc. (Shaharoona et al. 2007; Nadeem et al. 2007; Zahir et al. 2008; Kang et al. 2010). ACC is an important precursor for ethylene production. The mechanism of action of ACC deaminase produced by PGPR is to break down ACC into 2-oxobutanoate and NH_3 (Arshad et al. 2007). ACC deaminase producers also tend to reduce the effects of phytopathogens like viruses, bacteria, and fungi. Not only that, but these bacteria also relieve the stress from high temperature, high light intensity, heavy metals contamination, polyaromatic hydrocarbons, radiation, insect attack, and water-logging condition (Glick 2012; Lugtenberg and Kamilova 2009). The direct effects of ACC deaminase producing PGPR on the inoculated seeds or roots are root elongation, root nodulation, shoot growth, mineral uptake, etc. in many crop plants (Shaharoona et al. 2007; Nadeem et al. 2007; Glick 2012).

2.2 Indirect Mechanisms

The main indirect mechanisms of PGPR are related to their biocontrol activity which involves competition for nutrients, production of antifungal metabolites, niche exclusion, and siderophores production and induced systemic resistance (Lugtenberg and Kamilova 2009). Various antifungal metabolites like, HCN, 2, 4-diacetylphloroglucinol, pyoluteorin, pyrrolnitrin, phenazines, tensin, and viscosinamide are produced by many rhizobacteria (Bhattacharyya and Jha 2012). Interaction of some PGPR with the plant roots promotes plant resistance against some phytopathogenic microbes like bacteria, fungi, and viruses. Such phenomenon of acquired resistance in the plant is called induced systemic resistance (ISR) (Lugtenberg and Kamilova 2009). ISR involves ethylene and jasmonic acid signaling pathways within the plants that can stimulate the plant defence responses against a large group of phytopathogens (Glick 2012).

2.2.1 Siderophore Production

Iron is an important micronutrient for almost all forms of life. Siderophore production is a very important attribute of PGPR. Siderophore not only sequester iron but also other heavy metals. Thus, soil contaminated with heavy metals can be improved by the application of potent PGPR. In soil, iron occurs mainly in the form of Fe^{3+}, which is likely to form insoluble hydroxides and oxy-hydroxides. These insoluble forms of iron make it unavailable to both plants and microorganisms (Rajkumar et al. 2010). Siderophores are low molecular weight water-soluble iron-chelating ligands produced by rhizobacteria which are having a high affinity for iron produced under low iron stress (Verbon et al. 2017; Kumar et al. 2016). On the one hand, it is acting as a solubilizing agent for insoluble iron complexes and helps in iron nutrition, and on the other hand, it inhibits phytopathogen. Siderophore producing PGPR compete for iron with the pathogens and thus create iron deficiency leading to the death of pathogens (Khurana and Sharma 2000; Sharma and Kaur 2010; Schiessl et al. 2017; Shaikh et al. 2016). Siderophores are not only forming a stable complex with Fe but also form complexes with other heavy metals like Al, Cd, Cu, Ga, In, Pb, and Zn (Kiss and Farkas 1998; Neubauer et al. 2000). Chelation and release of iron, uptake of siderophore-Fe complexes directly, or by a ligand exchange reaction are different mechanisms by which plants acquire and assimilate iron from bacterial siderophores (Schmidt 1999). There are several studies on plant growth promotion via siderophore-mediated Fe-uptake, obtained by inoculations of plants with siderophore-producing rhizobacteria (Rajkumar et al. 2010). For example, under iron-limited conditions, a siderophore-mediated iron transport system is reported in oat plants and siderophores-producing rhizobacteria which delivers iron to the plant (Crowley and Kraemer 2007).

2.2.2 Production of Hydrogen Cyanide (HCN)

Cyanide is considered one of the typical attributes of rhizobacteria as it is a phytotoxic agent capable of inhibiting the main enzymes involved in vital plant metabolic processes (Bakker and Schippers 1987). However, its application as a biocontrol agent is increasing (Rajkumar et al. 2010). HCN is produced during the initial stationary growth phase of bacteria. It is not playing any role in growth, storage of energy, or primary metabolism, but it generally plays a significant ecological role as a selective advantage is bestowed on the HCN producing strains (Vining 1990).

2.2.3 Production of Protective Enzymes

A number of compounds are produced by PGPR which controls phytopathogenic agents and indirectly promotes plant growth (Meena et al. 2014). Enzymes like chitinase, β-1, 3-glucanase, and ACC deaminase are generally involved in the degradation of cell walls of phytopathogens neutralizing them (Goswami et al. 2014). Mostly fungal cell walls are composed of β-1, 4-N-acetyl-glucosamine and chitin, and hence their growth is inhibited by β-1, 3-glucanase and chitinase-producing bacteria. In a report by Ramadan et al. (2016), fusarium wilt causative organisms like *Fusarium oxysporum* and *Fusarium udum* can be inhibited by *Sinorhizobium fredii* KCC5 and *Pseudomonas fluorescens* LPK2. Also in another report by Islam et al. (2016) *Rhizoctonia solani* and *Phytophthora capsici*, the most devastating crop pathogens in the world can be inhibited by the application of PGPR.

2.2.4 Production of Volatile Organic Compounds (VOCs)

PGPR produce several volatile organic compounds (VOCs) which are low molecular weight (MW) compounds. These include aldehydes, alcohol, acids, hydrocarbons, ketones, and terpenes (Bhattacharyya and Lee 2017). Some examples of VOCs like indole, 2,3-butanediol, cyclohexane, benzene, benzene (1-methylnonadecyl), 2-(benzyloxy) ethanamine, 3-hydroxy-2-butanone (acetoin), methyl, decane, 1-chlorooctadecane, 1-(N-phenylcarbamyl)- 2- morpholino cyclohexene, dodecane, 11-decyldocosane, tetradecane, 2,6,10-trimethyl dotriacontane can promote the growth of plants (Ryu et al. 2003; Minerdi et al. 2011; Kanchiswamy et al. 2015). In the absence of pathogens, they can also promote plant growth and confer resistance against abiotic stresses (Bhattacharyya et al. 2015). According to Zou et al. (2010), VOCs like 2-pentylfuran show an increase of fresh weight of *Arabidopsis thaliana*, with an optimum dose of 10 *g*. Several bacterial species from diverse genera producing VOCs include *Arthrobacter, Bacillus, Serratia, and Pseudomonas* which enhance plant growth. Acetoin and 2, 3-Butanediol produced by *Bacillus* sp. are most effective for inhibiting the growth of fungal pathogens and promoting the growth of the plants (Santoro et al. 2016). It has been reported by Sharifi and Ryu (2016), that VOCs produced by PGPR are an important factor for excelling plant-induced systemic resistance (ISR).

3 Role of PGPR in Various Stressed/challenging Conditions

3.1 Drought

Drought is one of the major challenges faced by the farmers. It is responsible for the reduction in crop productivity in arid and semi-arid regions leading to a shortage of food. A change in the patterns of global air temperature and precipitation lead to longer drought periods. Scientists all over the world are trying to find out strategies to combat this challenge. Some of the strategies are the development of drought-resistant crops, traditional breeding, use of low water irrigation systems, or water-saving irrigation. Although these strategies are useful, their use is highly labour intensive, costly, and highly technical. Therefore, an alternative method is highly required to achieve the aim of high crop production under dry conditions. PGPR is useful in the proper growth of crops in stressed conditions. There are a number of microorganisms reported which can promote the growth and yield of a plant under drought conditions. *Arthrobacter, Pseudomonas, and Enterobacter* are reported to alleviate crop production (Niu et al. 2018).

To increase the osmotic potential under the condition of low water availability, the plant synthesizes certain osmolytes which help them to adapt to the drought condition (Farooq et al. 2009). PGPR also synthesize and extracellularly secrete several osmolytes that help to increase the plant drought tolerance potential. Yuwono et al. (2005) reported that IAA produced by plant growth promoting rhizobacteria is one of the crucial factors that help plants to combat drought stress. Affecting the ethylene pathway in plant root rhizosphere, ACC deaminase producing PGPR also help the plant to alleviate drought stress. Due to the ACC deaminase activity, ethylene production is significantly reduced which in turn lowers the damage caused by low water scarcity (Mayak et al. 2004). Mayak et al. (2004), also noticed that ACC deaminase producer *Achromobacter piechaudii* help the tomato and pepper plant to adapt to drought stress and their biomass get enhanced as compared to the control plant. Inoculation of Maize plant with *Azospirillum brasilense* has been found to have higher water content as compared to control plant. Plant proline content both in root and shoot were found to be significantly higher when plants were treated with low water activity tolerant bacteria (Casanovas et al. 2002). By accumulating chemicals related to plant growth promotion, PGPR under drought stress can improve the availability of micronutrients in plants (Creus et al. 2004). In this same study, it has also been reported that the content of Mg, K, and Ca in wheat grains were increased upon inoculation of PGPR. PGPR produce exopolysaccharides (EPS) which are complex carbohydrates released in the environment and are found to have an important role in protecting plants under desiccation (Pal and Sharma 1999). The important phenolic compound salicylic acid (SA) produced by PGPR which has an important role in plant cell signaling was also found to protect plants under desiccation. SA induces the production of various genes in plants such as antioxidants, chaperons, and heat shock proteins (hsp) which has a direct role in protecting plants under temperature increased due to the water scarcity in the environment (Jumali et al. 2011) (Table 1).

3.2 Heavy Metal Contamination

Cu^{2+}, Fe^{2+}, Zn^{2+}, and P have very limited mobility in soil. Plant root exudates contain organic acids and enzyme phosphatase that help to mobilize insoluble phosphorus. On the other hand, carbon present in the plant root exudates supports the growth of microorganisms present in the rhizosphere, and hence indirectly help to solubilize phosphorous by the microorganisms. It had been observed that plants treated with IAA (a hormone that is produced by PGPR) induced approximately 52% increased liberation of

Table 1 Effect of PGPRs on crop plant under stress condition

PGPRs	Stress condition	Effect	Plants	References
Achromobacter piechaudii	Drought	Produced glucosyl glycerol (GG) which help to adapt to water deficit condition	*Solanum lycopersicum*	Alavi et al. (2013)
Arthrobacter sp. and *B. subtilis*	Salinity	Increased dry weight of the plant	*Triticum aestivum*	Upadhyay et al. (2012)
Bacillus cereus	Salinity	Plant growth enhancement	*Oryza sativa*, *Vigna mungo*, *Cicer arietinum*	Chakraborty et al. (2011)
Bacillus lentimorbus	Antioxidant	Increased production of antioxidant in plant and enhance plant root growth	*Lactuca sativa*, *Spinacea oleracea*, *Daucus carota*	Nautiyal et al. (2008)
Brachybacterium sp.	Heavy metal	Increased the K^+ content in plant	*Arachis hypogaea*	Shukla et al. (2012)
Burkholderia sp.	Drought	Increased the plant chlorophyll and water content	*Cucumis sativus*	Kang et al. (2014)
Burkholderia phytofirmans PsJN	Low temperature	Higher plant biomass, root growth and adaptation to low temperature	*Vitis vinifera*	Ait et al. (2006)
Curtobacterium sp.	Drought	Production of osmoregulant proline	*Hordeum vulgare*	Cardinale et al. (2015)
Geobacillus sp.	Drought	Enhance photosynthesis and proline production	*Zea mays*	Abdelkader and Esawy (2011)
Haererohalobacter sp.	Heavy metal	Increased K^+ level	*Arachis hypogaea*	Shukla et al. (2012)
Oceanobacillus sp.	Drought	Increased exopolysaccharide production in root exudates	*Lens esculentus*	Qurashi and Sabri (2011)
P. putida H-2,3	Drought	Regulation of stress hormones, antioxidants. Also, secrete gibberellic acid (GA) which promote plant growth	*Glycine max*	Sang-Mo et al. (2014)
Pantoea sp.	Salinity	Salt tolerance through ACC deaminase activity	*Vigna radiata*	Panwar et al. (2016)
Pseudomonas putida	Heat	Plant growth enhancement by synthesis of high-molecular weight protein and cellular metabolites	Wheat	Ali et al. (2011)
Serratia sp.	Salinity, Drought	Production of exopolysaccharides in root exudates	*Triticum aestivum*	Singh and Jha (2016), Nadeem et al. (2013)
Variovorax sp.	Salinity	Increased salinity stress through the production of ACC deaminase	*Pisum sativum*	Wang et al. (2016)

carbohydrates in plant root exudates as compared to the plant group treated with soluble phosphorus (Wittenmayer and Merbach 2005). Micro- and macronutrient uptake by maize plants was found to be increased when the plant was treated with PGPR such as *Bacillus polymyxa* BcP26 and *Pseudomonas alcaligenes* PsA15, *Mycobacterium phlei* MbP18. This stimulation of nutrient uptake and absorption of nitrogen, phosphorus, and potassium was found to be observed in calciols than fertile soil (Egamberdiyeva 2007). Plant root colonizing microorganisms also secrete metal-chelating compounds such as siderophores which influence plants by the uptake of various metal ions through its chelating mechanism (Egamberdiyeva and Kucharova 2009; Dimkpa et al. 2009). Acidification of the soil change the redox potential of the soil and thus change the microenvironment. Microorganisms can use this mechanism to increase the bioavailability of nutrients in the soil (Gadd 2004). Volatilization by methylation, autotrophic leaching, and heterotrophic leaching are the mechanisms of metal mobilization in bacteria, whereas the reduction of heavy metal can be done by sorption to cellular materials followed by intracellular quenching and precipitation as insoluble organic and inorganic molecules (Gadd 2004). *Klebsiella mobilis* CIAM 880 was found to enhance the growth of barley plants in comparison to control plants under cadmium contaminated soil. Potters et al. (2007) reported that the ability of a plant to face several challenging conditions like heavy metal toxicity and nutrient deficiency is actually due to the effect of phytohormones produced by PGPR.

3.3 Salinity

Soil salinity is another serious issue for global food security. It is estimated at present that about 62 million hectares or 20% of the world's agricultural land are affected by salinity. Excess amount of soluble salt deposited in cultivable land directly affects crop yields. The physiological and metabolic processes of plants are highly affected due to the uptake of a high amount of salt which even impacts their survival. The various conventional methods of getting rid of salinity in soil involving leaching, flushing, scraping, or adding of gypsum, $CaCl_2$, etc. are not producing good results and also adversely affect the agroecosystems. For a long time, breeding salt-tolerant plants and developing salt-resistant crop varieties are some methods that are not able to solve the problem. Hence the search for a sustainable method that can increase the crop productivity of saline soil without affecting the environment is necessary (Kumar et al. 2019).

Microbes tolerant to salt are also able to thrive under high ionic and osmotic stress. A diverse group of microorganisms have been isolated from extreme saline, alkaline soils and found to have plant growth promoting activity. Numerous abiotic and biotic stresses that plants generally encounter were being neutralized by these bacteria. Recent literature suggested that PGPR can be used to enhance the productivity of plants facing salt stress and restore the agroecosystem. According to Sultana et al. (2020), two locally isolated PGPR strains identified as *Bacillus tequilensis and Bacillus aryabhattai* show salt tolerance and plant growth promoting characteristics under saline conditions. Inoculation upon plants revealed that these strains were capable of increasing the rate of transpiration, photosynthesis, and stomatal conductance of three varieties of rice, consequently leading to higher crop productivity. Given this promising potential, the *Bacillus tequilensis* and *Bacillus aryabhattai* strains would be a potent candidate for biofertilizer practices for reclamation of salinity in saline-affected coastal areas.

4 Conclusion

Sustainable agriculture suggests not only the condition where crop production will be carried out in adequate quantity without hampering human health and the environment but also where both the crop producers and consumers were benefitted. But the major constraints are the different kinds of biotic and abiotic stresses in the environment. PGPR can play an important role to mitigate these stress conditions and improve plant health. With its diverse mechanisms of action such as triggering N_2 fixation, phosphate solubilization, zinc solubilization, phytohormone production, siderophore production, and acting as a biocontrol agent PGPR help in the enhancement of crop yield, control environmental pollution, and reduce the use of chemical fertilizer which further helps in sustainable agriculture. Soil agriculture health can be restored by the use of the consortia of PGPR microbes under challenging stress conditions.

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Soil Application of Plant Growth Promoting Fungi for Sustainable Agriculture in the New Decade

Parimal Mandal and Zerald Tiru

Abstract

The plant rhizosphere is a micro-ecosystem at the vicinity of the plant root system comprising hot spot zone of the microbial community (like fungi, bacteria, virus, insect, etc.) interacting with each other by several mechanisms influenced by root exudates. The fungal community, which are non-pathogenic and promote the growth of plants are called plant growth promoting fungi (PGPF), is a major focusing area for sustainable agriculture. It was experienced that the non-judicious application of numerous chemical fertilizers and fungicides is liable to enhance environmental pollution, deteriorate soil health, and increase human health hazards in course of biological magnification due to the non-degradable nature of these chemicals. Presently, plant growth promoting fungi (PGPF) are getting much more attention for sustainable agriculture as it is supposed to be economically more viable due to its effectiveness and harmlessness to the environment. Different mechanisms are involved for plant growth promotion such as the production of plant growth substances (e.g., indole acetic acid, soluble phosphate, etc.), antagonistic activity against the pathogen (through antibiosis, competition, and mycoparasitism), and induction of systemic resistance (ISR) in a plant through the expression of defense-related enzymes (such as peroxidase, polyphenol oxidase, and chalcone synthase) and defense chemicals (such as phytoalexin and anti-microbial phenolic compounds) for conferring structural and chemical barrier against a pathogen. PGPF is also known to increase the health of soil with the addition of humus by decomposing plant debris in the rhizosphere.

Keywords

Environmental pollution • Induced systemic resistance • Mycoparasitism • Plant growth promoting fungi • Polyphenol oxidase • Rhizosphere

Abbreviations

AFP	Antifungal protein
BOFs	Bio-organic fertilizers
ET	Ethylene
GA	Gibberellic acid
HCN	Hydrogen cyanide
HSPs	Heat shock proteins
IAA	Indole Acetic Acid
ISR	Induced systemic resistance
JA	Jasmonic acid
PAL	Phenylalanine ammonia lyase
PGPF	Plant growth promoting fungi
POX	Peroxidise
P	Phosphorus
PPO	Polyphenol oxidase
PR proteins	Pathogenesis-related proteins
ROS	Reactive oxygen species
SA	Salicylic acid
SAR	Systemic acquired resistance
VOCs	Volatile Organic compounds

1 Introduction

The worldwide human population is predicted to reach approximately 9.7 billion by the year 2050 from the current population of 7.9 billion in 2021 (Hashem et al. 2021). This explosion of human population has created a huge problem of food security all over the world; and hence, it is now a global challenge to increase food production by above 70% of the current levels to feed the ever-increasing population

P. Mandal (✉)
Mycology and Plant Pathology Laboratory, Department of Botany, Raiganj University, Raiganj, West Bengal 733134, India

Z. Tiru
Department of Botany, Raiganj University, Raiganj, West Bengal, India

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(Murali et al. 2021). Further, various problems such as diseases, pests, droughts, indiscriminate use of hazardous chemical pesticides, pollution, and global warming due to conventional agricultural practices have vastly affected the quantity and quality of food production (Saba et al. 2012). In order to supply food to the ever-increasing population and ensure food security, pre- and post-harvest diseases must be controlled very cautiously. Apart from diseases, many of the other problems faced, are associated with traditional cultivation practices of crops, and pollution of soil occurs as a result of excessive and uncontrolled use of inorganic fertilizers (Babu et al. 2015).

The present objective is to develop new approaches for the management of diseases caused by various agents, including pests, bacteria, fungi, nematodes, etc. Adopting the use of some of the beneficial soil microbiome including fungi can greatly improve soil health, control diseases by antagonistic mechanisms and induced systemic resistance (ISR), promote plant growth, and create a better option than the use of inorganic chemical fertilizers (Bhardwaj et al. 2014). Recently, rhizosphere-dwelling plant growth promoting fungi (PGPF) has been validated as one of the effective biocontrol agents for eco-friendly management strategies of plant diseases, and they may also serve as an alternative strategy to boost the growth of plant and trigger defense mechanisms in plants. Hence, The application of PGPF reduces the use of inorganic chemical fertilizers and also helps the plants to mitigate various biotic and abiotic stresses through various mechanisms.

Many PGPF species like *Trichoderma*, *Talaromyces*, *Fusarium*, *Phytophthora*, *Penicillium*, *Rhizoctonia*, *Gliocladium*, and *Phoma* have been reported by various investigators for their significant contribution in plant growth promotion, enhancement of innate immunity, and production of other important secondary metabolites in plants (Hyakumachi 1994; Hyakumachi and Kubota 2004; Murali et al. 2021; Naziya et al. 2020). All the beneficial attributes (Fig. 1) of PGPF are associated with their root colonizing efficacy, ability to produce growth hormones, mineralization, nutrient uptake, disease control by antagonistic mechanisms, and defense strategies against pathogen which includes induction of systemic resistance (ISR) and systemic acquired resistance (SAR) through the production of defense enzymes, defense chemicals, and pathogenesis-related proteins (PR-proteins) in plants (Islam et al. 2014; Nogueira-Lopez et al. 2020). These potential PGPF would play a significant role in agriculture for sustainable productivity, management of soil health, and restoration of the environment as a cost-effective input for coming decades which could be a great relief in future for food security.

Fig. 1 Diversified function of plant growth promoting fungi

2 Rhizosphere

In the natural environment, plants share a micro-ecosystem at the vicinity of the plant root system comprising hot spot zone of the microbial community (like fungi, bacteria, viruses, and insects) interacting with each other by several mechanisms influenced by root exudates. Some of these plant-microbial interactions protect plants against pathogenic microorganisms and provide nutrients to plants (Igiehon and Babalola 2018). The plant rhizosphere harbours both beneficial and pathogenic microorganisms comprising up to 10^{11} microbes per gram of soil and above 3000 prokaryotic species in general; and therefore, it represents a composite ecosystem on earth (Hossain et al. 2017a, b; Mendes et al. 2013). Microorganisms involved in rhizospheric soil include bacteria, fungi, nematodes, viruses, arthropods, oomycetes, protozoa, algae, and archaea (Akinola and Babalola 2021). Among the microbial community inhabiting the rhizospheric zone, bacteria and fungi are the most common microorganisms which have been studied extensively for their beneficial impact on plant life through their mutual biological activities. This rhizospheric zone offers great opportunities for plant–microbial interactions, and therefore significantly affects plant growth, disease resistance, and nutrient recycling (Akinola and Babalola 2021).

Plant roots are extremely significant for mineral nutrient uptake and productivity, and therefore there is an extreme need to explore plant–microbial interactions at the rhizosphere. Plants establish a positive interaction with a diverse group of microorganisms through their roots and a large fraction of these vastly complex microbial groups have not been characterized (Igiehon and Babalola 2018). The intimate association between plants and root colonizing microbial community is brought about by root exudates reflecting the microbial community structure and function for qualitative productivity (Gahan and Schmalenberger 2014; Hossain et al. 2017a, b). Root exudates supply major requirements like primary metabolites including carbohydrates, amino acids, and organic acids; and secondary metabolites such as flavonoids, glucosinolates, and auxins to the microbial community for their proliferation; and hence establish a mutual relationship with plants (Badri and Vivanco 2009; Vives-Peris et al. 2020). It is assumed that some chemical signals produced and secreted by the root may be deployed to improve beneficial microbial colonization of the root for sustainable agriculture in the near future (Igiehon and Babalola 2018). Therefore, understanding the microbial interactions in the rhizosphere is crucial towards organic farming methods that are less dependent on the use of conventional inorganic chemical fertilizers which imparts negative impacts on surroundings (Rascovan et al. 2016).

3 Plant Growth Promoting Fungi (PGPF)

The soil-dwelling fungal community which are non-pathogenic and promote the growth of plants are called plant growth promoting fungi (PGPF). PGPF are a heterogeneous group of non-pathogenic saprophytic fungi that establish a close association with plants and increase the improvement of plant growth and health through several activities (Naziya et al. 2020). Further, fungi under PGPF may differ distinctly from each other with respect to their taxonomy, habitats, physiology, and even to their interactions with plants. A fungus that promotes the growth of a plant may or may not have a similar effect upon the growth of another plant, and also act differently under different environmental conditions (Hossain et al. 2017a, b). Not all fungi that promote plant growth are considered as PGPF, for example, mycorrhizal fungi, which are known to boost the growth of the plants, are not considered as PGPF. An important feature that gives PGPF a different identity is that the PGPF are non-symbiotic saprotrophic fungi that live freely on a zone of soil at the vicinity of the root or the interior of the root itself, whereas mycorrhizal fungi behave as obligate biotrophs and develop an intimate association with the roots of most host plants (Hossain et al. 2017a, b; Mehrotra 2005). Therefore, the term PGPF is not absolute, rather it is an operational term (Bent 2006). Root colonization ability is considered as one of the most important characteristics of PGPF which helps to promote plant growth (Islam et al. 2014). Fungi of the genera such as *Aspergillus*, *Fusarium*, *Penicillium*, *Piriformospora*, *Phoma,* and *Trichoderma* are the strains mostly used in research as PGPF (Hossain et al. 2017a, b; Javaid et al. 2020; Masunaka et al. 2009). The non-pathogenic fungi such as *Pythium oligandrum* and *Phytophthora cryptogea* colonizing the root ecosystems are also considered as PGPF (Attitalla et al. 2001; Benhamou et al. 2012; Bent 2006). The role of PGPF is crucial in rhizosphere and is known to play a very significant role in plant growth and development, and soil health. As both pathogenic and non-pathogenic fungal communities inhabit the rhizosphere, it is exceedingly urgent to know their mode of interactions and consequences. With respect to plant pathogens, fungi are one of the most noxious soil-borne pathogenic microorganisms that cause serious root disease in plants and pose a serious threat to soil micro-ecological balance, plant health, and agricultural productivity (Doehlemann et al. 2017). The fate of a successful infection, i.e., whether it immediately becomes symptomatic or remains asymptomatic, may depend upon the tissue in which the infection begins (Sukno et al. 2008). The growth or activity of soil-borne pathogenic fungi can be inhibited by PGPF present in the rhizosphere (Raaijmakers et al. 2009). The activity and effects of PGPF like *Trichoderma*, *Gliocladium*, *Penicillium,* and non-pathogenic *F. oxysporum* on plant growth, productivity, nutrient availability, disease suppression, and soil health are well documented.

3.1 Plant Growth Promotional Activities of PGPF

Plant growth promoting fungi (PGPF) are universally known for their eco-friendly role in the overall growth of the plant and subsequent improvement of yield and quality of the plant. Their role in seed germination, seedling vigour, shoot growth, root growth, photosynthetic efficiency, flowering and yield are the most commonly realized attributes (Hossain and Sultana 2020). However, the plant growth promotional activities of PGPF are attributed to the production of plant growth hormone and mineralization and as such many more (Fig. 2).

3.1.1 Production of Plant Growth Hormone

Plant growth hormones also called phytohormones help to regulate the growth of the plants through various developmental processes. Plant growth promoting fungi (PGPF) can exogenously produce phytohormones such as auxins (IAA), gibberellins, and cytokinin. IAA and gibberellins are responsible for inducing important physiological responses at different stages of plant development (Islam et al. 2014). The IAA is one of the highly important phytohormones which is widely distributed and is essential for the development of plants. Exogenous applications of IAA stimulate root formation and root hair development. Thereby enhancing nutrient absorption by the plants which consecutively increases plant biomass (Fu et al. 2015). PGPFs like

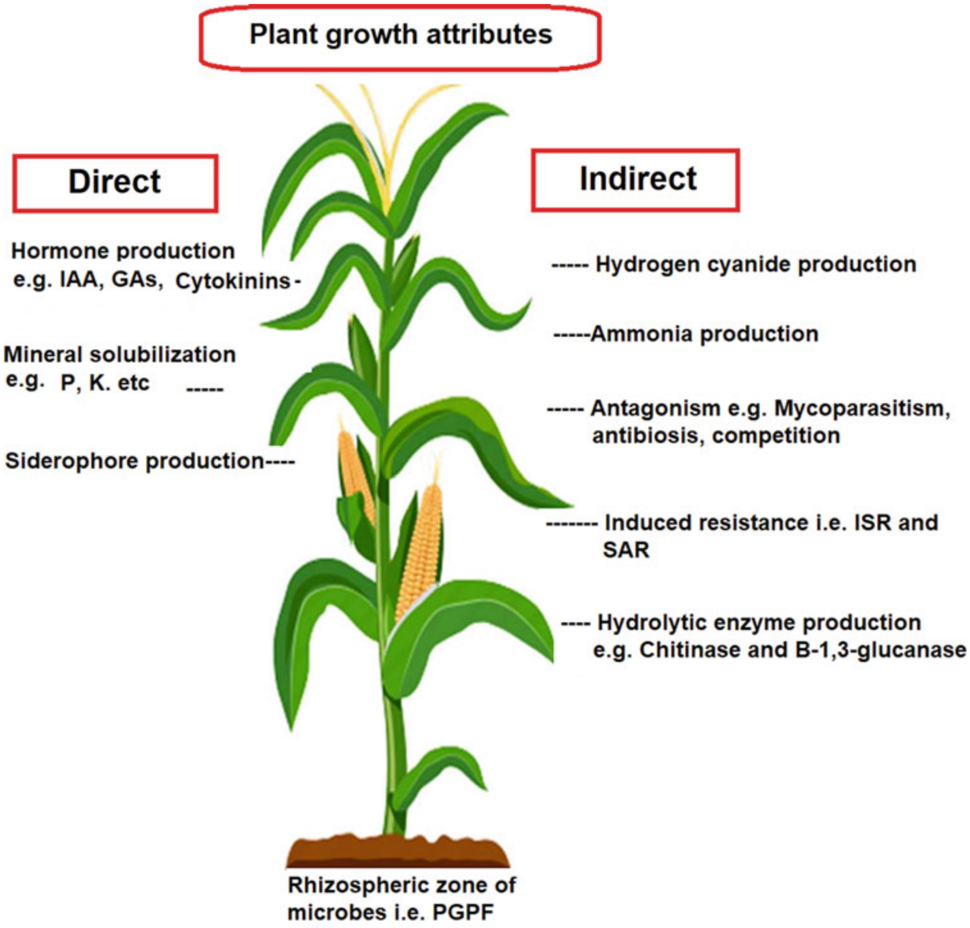

Fig. 2 PGPF in contributing overall growth of the plant through direct and indirect mechanisms

Trichoderma, *Penicillium*, *Aspergillus*, *Fusarium*, *Talaromyces,* and *Mortierella* are reported for IAA production in host plants like chickpea, rice, and wheat, which facilitates increased growth and yield (Abri et al. 2015; Kumar et al. 2017; Murali et al. 2021). Apart from IAA, GA is another important phytohormone produced by fungi such as *Fusarium*, *Aspergillus,* and *Penicillium*, and is reported to deal with abiotic stress along with plant growth and developmental activities (Syamsia et al. 2021). The GA produced by the fungi *Cladosporium* species in wheat and cucumber plants was known to enhance plant growth (Hamayun et al. 2010). It has also been reported that endophytic fungi such as *Penicillium citrinum* and *Aspergillus fumigatus* potentially promote plant growth by secreting gibberellins (GAs) in the rhizosphere (Ahmad et al. 2010). Another important plant growth regulator, cytokinin has been reported to be produced by PGPF which can also trigger plant growth promotional activities (Hossain and Sultana 2020). The most important phytohormone, cytokinin (predominantly zeatin), elicited by *Piriformospora* spp., *Phoma* spp., and *Trichoderma* spp. caused growth promotion in melon and *Arabidopsis* (Martínez-Medina et al. 2014; Speakman and Kruger 1984). *Piriformospora indica* produces low amounts of auxins, but relatively high levels of cytokinins and stimulate plant growth promotion in *Arabidopsis* (Vadassery et al. 2008).

3.1.2 Mineralization

Minerals deficiency is one of the major problems in agriculture. Deficiency occurs when their availability in the soil becomes lower than the requirement. Deficiency may occur due to the absence of minerals in the soil or lack of mobility or poor solubility of the minerals (Rengel and Marschner 2005). The unavailability of minerals is an important factor in reducing the yield and quality of the crop. The availability of minerals in the rhizosphere is controlled by combined effects of soil properties, plant characteristics, and the interaction of roots with associated microorganisms (Jones et al. 2004; Rengel and Marschner 2005). The mutual interaction of rhizospheric fungi may compensate for the deficiency of minerals by simply making them available to plant and enhancing their uptake. Phosphorus is the second most important plant mineral nutrient after nitrogen and exists in different organic and inorganic form (Alam et al. 2002). Deficiency of phosphorus (P) in the soil is one of the most important chemical factors limiting plant growth and hence phosphate-containing fertilizers are widely used to achieve optimum yields. Soluble forms of P fertilizer are easily precipitated as insoluble forms, and therefore excessive and repeated application of P fertilizer to soil is required which could be harmful to the soil ecosystem and also appears to be a quite expensive affair. PGPF in the rhizosphere greatly increase the availability of P to plants through the solubilization of phosphate. Many investigators have reported that active conversion of insoluble phosphate to soluble primary and secondary orthophosphate ions by phosphate solubilizing fungi (PSF) may be a viable alternative to P fertilizers (Alam et al. 2002; Chabot et al. 1996; Pal 1998). Many PGPF can solubilize the unavailable P and release it through their metabolic activities by secreting organic acids which directly dissolve the rock phosphate or chelate calcium ions (Mwajita et al. 2013). The mineralization and solubilization of complex organic phosphorous into their simple forms are known to be catalyzed by PGPF-produced enzymes such as phytase and phosphatases; and inorganic acids (HCl, nitric acid, sulphuric acids) and organic acids like α-ketobutyric acid, malic acid, glyoxylic acid, succinic acid, oxalic acid, fumaric acid, gluconic acid, tartaric acid, citric acid, 2-ketogluconic acids (Altomare et al. 1999; Gyaneshwar et al. 2002; Murali et al. 2021). Rhizospheric fungi like *Penicillium, Aspergillus, Trichoderma, Phoma, Rhizoctonia, Rhizopus,* and *Alternaria* have been documented for their efficiency in solubilizing the insoluble phosphate (Alori et al. 2017; Dotaniya and Meena 2015).

Among the PGPF, different *Trichoderma strains* have been exploited to enhance mineralization and mineral absorption of Fe, N, P, and K, and increase the accessibility of ammonium, nitrogen, zinc, copper, iron, and manganese (Molla et al. 2012). Many PGPF compete for nutrients by decreasing Fe availability for the pathogens, and thereby limiting their growth by producing siderophores. Iron (siderophore-Fe complexes) released by PGPF is also taken up instantly by plants through ligand exchange reactions (Altomare et al. 1999; Berg 2009). A hydroponic culture experiment has shown the significant increase in iron status of cucumber and maize in the presence of ferrated siderophore mixture (1 μM) obtained from a culture of *Penicillium chrysogenum* (Hordt et al. 2000). The ammonia and HCN produced by various *Trichoderma* isolates have also been reported to contribute to plant growth promotion activity (Naziya et al. 2020).

3.2 Abiotic Stress Management

Crop plants are often subjected to different kinds of abiotic stress which include heavy metal stress, water stress, temperature stress, and salinity stress. These stresses are major limiting factors for plant growth. They have the great potentiality for substantial damage to crop plants and consequently reduce the yield and productivity of the crops all over the world. The incidence of abiotic factors affecting plants is still on the rise. Plant root colonizing microbes are capable of influencing plant physiological processes, including tolerance to abiotic and biotic stresses through different mechanisms like induction of osmoprotectants and heat shock proteins (HSPs) in plant cells (Zaidi et al. 2014). Plant growth promoting fungi (PGPF) are known for alleviating different abiotic stresses. *Penicillium* species isolated from the rhizospheric soil of peanut was found to improve the salinity tolerance ability in sesame plants along with defense activity against pathogen and plant growth promotion (Radhakrishnan et al. 2014). *Trichoderma harzianum* enhances root growth and helps in water absorption and nutrient uptake under osmotic stress. The role of a different strain of *Trichoderma* for attenuating the oxidative, salinity, drought, and osmotic stress in the plant has been well documented (Zaidi et al. 2014). The PGPF such as *Microsphaeropsis*, *Mucor*, *Steganosporium*, *Phoma*, *Aspergillus*, *Alternaria,* and *Peyronellaea* have been reported to protect *Arabidopsis* plants from heavy metal accumulation (Murali et al. 2021). A common mechanism to improve the level of tolerance under abiotic stress employed by the fungi could be the amelioration of destruction triggered by ROS under stressful conditions. It has been reported that *Trichoderma* helps the plants to raise the activities of antioxidant enzymes and consequently protects the plants against ROS formation and membrane damage in plants under stress (Guler et al. 2016).

3.3 Management of Disease

Plant disease caused by different pathogens is one of the major detrimental factors for food production all over the world (Shimizu et al. 2013). Plant disease management through chemical fungicides does not hold good for today and in near future. It is dangerous not only for plants but may also pose a serious threat to soil microbial community and surroundings. Therefore, finding a sustainable solution to manage the problem is quite a big challenge. However, the use of microorganisms to induce resistance in plants against pathogens is gaining appreciation from all over the world for its consistency and sustainability (Bejarano and Puopolo 2020). PGPF may adopt different strategies to protect the plant from invading pathogens by inducing defense resistance in plants apart from their usual role in plant growth promotion. Application of PGPF in the plant is one of the eco-friendly disease management strategies that cause a long-lasting induction of plant innate immunity. The ability of PGPF to colonize the plant root, help the plant to take up nutrients and trigger plant growth is considered to be the first and foremost mechanism towards sustainable disease management (Hossain et al. 2017a, b; Murali et al. 2013). Apart from this, PGPF directly or indirectly participate in disease management in a plant (Hossain and Sultana 2020; Jogaiah et al. 2013; Muslim et al. 2019; Tiru et al. 2020; Yedidia et al. 1999). The major disease management strategies adopted by PGPF can be summarized as follows:

3.3.1 Antagonism

Plants often get attacked by diverse groups of the pathogen which causes serious diseases and consequently reduce productivity and yield. The disease-causing pathogens can be controlled by PGPF which has been referred as bio-control mechanism. The bio-control mechanism can be achieved through the antagonistic efficacy of microorganisms. PGPF restrict the pathogen and reduce the damage by several mechanisms which include ***antibiosis*** via inhibition of pathogen by antibiotics and surface-active compounds called biosurfactants; ***competition*** for colonization sites, nutrients, and minerals; ***parasitism*** by the production of extracellular cell wall-degrading enzymes such as chitinase and β-1,3-glucanase (Berg et al. 2005). Different PGPF, namely, *Trichoderma*, *Gliocladium virens*, *Phoma* sp., *Fusarium equiseti,* and *Penicillium simplicissimum* have been reported to be antagonistic against *Rhizoctonia solani*, *Pythium aphanidermatum*, *Pythium irregulare*, *Sclerotium rolfsii*, *Fusarium oxysporum*, *Pseudomonas syringae,* and *Colletotrichum orbiculare* (Lewis et al. 1998; Murali et al. 2021; Sreenivasaprasad and Manibhushanrao 1990). Patale and Mukadam (2011) have successfully tested the antagonistic activity of *Trichoderma viride* and *Trichoderma harzianum* against seven pathogenic fungi, namely, *Aspergillus niger*, *A. flavus*, *Phytophthora* sp., *Fusarium oxysporum*, *Rhizoctonia solani*, *Penicillium notatum*, and *Alternaria solani*. Gliovirin, an antibiotic produced by *Gliocladium virens,* was shown to inhibit the growth of *Pythium ultimum* (Howell and Stipanovic 1983). *Aspergillus giganteus* also has been reported to produce an antifungal protein (AFP) which shows antifungal property against *Botrytis cinerea* in Geranium plants (Moreno et al. 2003). The non-pathogenic *Fusarium oxysporum* isolated from soil microflora has been reported to inhibit pathogenic *Fusarium* via competition for carbon source and nutrients at the site of infection (Kaur et al. 2011). However, antagonistic property of PGPF cannot be considered alone as a factor for the management of disease caused by pathogen attack; other attributes like plant growth promotion, disease suppression via antibiotic production, mycoparasitism, competition for nutrient, and colonization of spaces also contribute to disease management (Akinola and Babalola 2021).

3.3.2 Induction of Disease Resistance

Induction of disease resistance is the mechanism of resistance that develops in plants upon the pathogen attack. The most studied forms of induced resistance are systemic acquired resistance (SAR) triggered by necrotizing pathogens, and ISR triggered by root-colonizing microbes, like *Trichoderma* spp. (Romera et al. 2019; Walters et al. 2005). SAR is characterized by increased levels of endogenous salicylic acid (SA) with the expression of pathogenesis-related proteins (PR-proteins), while ISR is characterized by jasmonic acid (JA) and ethylene (ET)-mediated pathway and production of defense enzymes and defense chemicals for structural barrier (Van Loon 2000). The most prominent species of *Trichoderma*, *Penicillium*, *Fusarium*, and *Phoma* have profound ability to stimulate immune response upon pathogen attack and are one of the safest modes for triggering ISR (Jogaiah et al. 2013). In this connection, the application of *Trichoderma harzianum* and *Penicillium chrysogenum* has been known to stimulate ISR against downy mildews of sunflower and pearl millet (Murali et al. 2013; Nagaraju et al. 2012). Plant growth promoting fungi (PGPF) such as *Phoma* sp., *Cladosporium* sp. and *Ampelomyces* sp. also triggered ISR in *Arabidopsis* plants against *Pseudomonas syringae* pv. tomato through the production of volatile organic compounds (VOCs) (Naznin et al. 2014). *Trichoderma* spp. has been reported to trigger ISR in some agriculturally important crops such as rice, wheat, bean, maize, cucumber, lettuce, cotton, tobacco, and tomato and *Rhododendron* against fungi and bacteria, and even virus (Hossain et al. 2017a, b). Induction of resistance is associated with the production of various types of defense enzymes such as phenylalanine ammonia-lyase (PAL), polyphenol oxidase (PPO), chitinase, peroxidase (POX), and β-1,3 glucanase. (Jogaiah et al. 2013; Prasannath 2017; Wu et al. 2019). The PGPF-induced systemic resistance was found to be associated with a high increase in plant defense-related enzymes such as POX, PPO, and PAL in cucumber cultivars (Hassan et al. 2014). It was investigated that *Trichoderma viride*—a biocontrol agent—elicited the production of POX, PPO, and PAL enzymes to mitigate the *Fusarium* and *Alternaria* induced stress in *Vigna mungo* (Surekha et al. 2014). The antioxidant enzymes like superoxide dismutase (SOD), CAT, and POX played important roles in reducing damage caused by pathogen, with delay in symptom development in pear calli (Zhao et al. 2012). Biochemical analysis revealed that inoculation of cucumber plants with *Trichoderma harzianum* increased peroxidase and chitinase activities as a part of defense response (Yedidia et al. 1999). Enhanced activity of PAL and POX enzymes was reported when cucumber, chilli, pearl millet, and *Salvia* seedlings were subject to challenge inoculation with PGPF (Hassan et al. 2014; Murali and Amruthesh 2015; Zhou et al. 2018). Plant growth promoting Fungus (PGPF) *Penicillium oxalicum* isolated from rhizospheric soil of pearl millet showed a significant increase of chitinase activity (Murali and Amruthesh 2015). *Trichoderma* *atroviride* TRS25 enhanced the PPO and PAL enzyme activity when the cucumber plant was challengingly inoculated with *Rhizoctonia solani* (Nawrocka et al. 2018). Defense enzymes such as PPO and PAL are associated with the synthesis of cell wall components, thickening, lignification, and callose deposition following the biosynthetic processes triggered by PGPF (Abhayashree et al. 2017). Expression of POX and PAL plays a key role in the biosynthesis of phenolic compounds, and lignin which not only restrict the extent of pathogen attack but contribute significantly to enhancing the mechanical strength of the host cell wall (Bruce and West 1989; Karthikeyan et al. 2006). PGPF-treated chilli seedlings enhanced the activity of PAL and POX upon challenge inoculation with the accumulation of lignin and callose deposition (Naziya et al. 2020). The PGPF-*Penicillium simplicissimum* GP17-2 treated cucumber plant showed an increase in lignin formation apart from other defense-related enzymes like chitinase, peroxidise, and β-1,3 glucanase (Shimizu et al. 2013). The soil-borne fungi *Trichoderma harzianum* induced a significant change in root architecture of *Arabidopsis thaliana* through callose deposition (Alonso-Ramírez et al. 2015). *Trichoderma* spp. are highly studied worldwide for their role in controlling the plant pathogen through the production of cell wall degrading enzymes such as cellulases, chitinases, and glucanases (Nogueira-Lopez et al. 2020). With enhanced activities of glucanases and chitinases, *Trichoderma* sp. was reported to induce the resistance in chickpea against dry root rot and wilt diseases (Dubey et al. 2011; Lavanya et al. 2017). *Trichoderma hamatum* T382 involved in inducing systemic resistance against *Botrytis cinerea* in *Arabidopsis thaliana* stimulating the defense enzymes such as glucanases, chitinases, and other pathogenesis-related proteins of the SA and Et-pathways (Lavanya et al. 2017; Mathys et al. 2012). The soil application of *Pseudomonas fluorescens*, *Trichoderma viride,* and *T. harzianum* in combination with chitin induced the phenolics and defense enzymes such as POX, PAL, chitinase, and β-1,3-glucanase in the *Ganoderma lucidum* infected palms seedlings (Karthikeyan et al. 2006).

4 Bioformulations

Biocontrol agents (bio-agent) comprising fungi have become attractive in terms of sustainable management of diseases and improved quality of crop productivity (Hussain et al. 2020). The antagonistic property of PGPF can be successfully exploited through proper identification of efficient bio-control agents, their multiplication, and formulation for delivery. A large number of bio-based products are being produced and sold worldwide in the form of granules, wettable powders, dusts, and aqueous or oil-based liquid products using different carriers to control fungal pathogens (Ardakani et al. 2009; Nega 2014). Apart from these, various agricultural wastes have also been recognized as potent organic carriers for many bio-control agents. Different organic and inorganic carrier materials have been studied for the effective delivery of bio-control inoculants (Hossain and Sultana 2020). Several microbial antagonists have been successfully patented and evaluated for their commercial usage to control the pathogen, and these agents are frequently recommended worldwide for plants disease management (El Ghaouth et al. 2002; O'Brien 2017). However, the ideal conditions required for the development of high-efficiency formulations of biofertilizer include the selection of potent strains, shelf life, storage, application technology, quality control, biosafety, registration, and marketing strategies (Keswani et al. 2016). *Trichoderma*-based formulation was developed using the scrapping method with the biomass of fungi having high colony-forming units and long shelf life (Singh and Nautiyal 2012). The application of *Trichoderma*-based bio-fertilizer (composted of cattle manure + inoculum) not only produced the antifungal compound which may suppress the pathogen but potentially improved grassland biomass (Zhang et al. 2018). A *Trichoderma*-based spray-dried flowable powder formulation was developed using a CO_2 generating dispersant system, based on polyacrylic acid, citric acid, sodium bicarbonate, and polyvinyl alcohol as adhesives and lecithin as wetting agent (Oancea et al. 2016). Bio-organic fertilizers (BOFs) enriched with *Trichoderma* and animal manure have been found not only to cause plant growth promotion but also found to have the controlling effect against *Fusarium* wilt in cucumber plants (Chen et al. 2011; Zhang et al. 2013, 2016). The foliar sprays of the liquid formulation of *Penicillium oxalicum* (6×10^6 CFU ml^{-1}) with sodium alginate (0.5%) and Tween 80 (0.01%) substantially improved the yield and acted as biofungicide for controlling mango malformation (Haggag and El Soud 2013). The greenhouse experiment of *Trichoderma* and *Talaromyces*-based bioformulations with talc and rice bran showed their effectiveness in controlling sugar beet damping-off disease (Kakvan et al. 2013). Bioformulation with use of antagonistic fungi such as *Trichoderma* and *Talaromyces* along with organic and inorganic carriers such as rice bran and talc has performed well for controlling garlic white rot disease in greenhouse conditions (Mahdizadehnaraghi et al. 2015).

5 Conclusion and Future Prospects

Understanding the beneficial aspects of PGPF, and thereby subsequent application of the same is extremely important for developing new strategies for the management of crop disease and better yield of a crop. Though the use of PGPFs is already successful in many countries, some countries are still lagging behind this and continue to use chemical fungicides for disease management. Therefore, it is very important to address the issues related to the successful use of PGPF. It has been noticed that the practical use of PGPF is often hindered by inconsistency in their performance and may be due to variations in genotype, environment, and other factors. In order to popularize the widespread use of PGPF, the development of some innovative and effective techniques for their mass culture, formulation, and application of these fungi are urgently needed to be addressed. Above all, it is also very important to convince the different stakeholders including the farmers. The recent development in molecular tools and techniques can give more insight and elaborate on the mechanisms and outcome of plant–microbial interaction. The PGPF can be made more effective and promising in every aspect through the application of innovative knowledge of biotechnology like the development of genetically modified strains with improved features and expression of PGPF genes in target plants to confer beneficial properties. Further, the active and justified participation of private industry in product research and development could be more effective and may help to overcome the problems and issues.

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Deep Insights into the Role of Endophytic Fungi in Abiotic Stress Tolerance in Plants

Prabha Toppo and Piyush Mathur

Abstract

Fungal endophytes live inside the plants and play a significant role in their fitness and survival under extreme conditions of stress. Due to climatic uncertainties and variability, it has been observed that a number of abiotic stresses hamper plant growth considerably and have become a major concern for scientists all around the world. Abiotic stresses like salinity, drought, temperature as well as heavy metal toxicity are frequently encountered and affect plant health and agricultural crop productivity. Numerous studies have shown the immense potential of endophytic fungi in the modulation of plant responses towards various stresses. Endophytic fungi stimulate plant growth, lower oxidative stress, increase nutrient uptake, and alter levels of various phytohormones in plants grown in stressed conditions. All such changes escalate plant adaptive response and enhance their tolerance capability to withstand stress. Endophytic are also known to augment the accumulation of various osmoprotectants that enable the plant to maintain osmotic balance under various stresses and sustain better growth. Additionally, a number of reports have suggested that these endophytic fungi affect the host plant system at cellular and molecular levels. Endophytic fungi regulate the molecular expression of several genes, transcription factors, and proteins in response to stress. Concomitantly, under stress conditions, endophytic fungi encourage the synthesis of various secondary metabolites that play a crucial role in enhancing plant resistance against abiotic stress. Therefore, endophytic fungi are now considered to act as a dominant player in the development of biostimulants or biofertilizers for sustaining agricultural productivity. The present chapter will delineate the role of endophytic fungal symbioses in abiotic stress tolerance in plants and their associated mechanisms. Moreover, the chapter also entails an account of novel strategies for the application of endophytic fungal inoculants in agricultural fields.

Keywords

Abiotic stress • Beneficial microorganisms • Phytohormones • Photosynthesis • ROS • Stress signaling

Abbreviations

ABA	Abscisic acid
AAO	Ascorbic acid oxidase
ASA	Ascorbic acid
APX	Ascorbate peroxidase
CAT	Catalase
Cd	Cadmium
CKs	Cytokinins
CDKs	Calcium dependent kinases
DSE	Dark septate endophyte
Et	Ethylene
GA	Gibberellic acid
GR	Glutathione reductase
GST	Glutathione-S-transferase
HSPs	Heat shock proteins
H_2O_2	Hydrogen peroxide
JA	Jasmonic acid
IAA	Indole acetic acid
JA	Jasmonic acid
MAPK	Mitogen activated protein kinases
PCs	Phytochelatins
POD	Peroxidase
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicylic acid
SOD	Superoxide dismutase

P. Toppo · P. Mathur (✉)
Microbiology Laboratory, Department of Botany, University of North Bengal, Rajarammohunpur, Darjeeling, West Bengal 734013, India
e-mail: piyushmathur316@nbu.ac.in

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1 Introduction

Endophytes are well known for their mutualistic association with plants as they impart several beneficial effects without causing any deterrent harm (Saikkonen et al. 1998; Khare et al. 2018). A large number of fungal endophytes are associated with different plant parts, and this association between fungal partner (holobiont) and host plant is observed to be highly specific in terms of micro-niches (Dudeja and Giri 2014; Gouda et al. 2016; Stępniewska and Kuźniar 2013). Several researchers have isolated these endophytic fungi from conventional culture-dependent approaches but a huge diversity of these endophytic fungi have still not been explored as most of the endophytes are not culturable (Zheng et al. 2021). To overcome this problem, modern-day approaches have helped widely in this respect; techniques like metagenomics assisted easy isolation and identification of these endophytic fungi directly from soil and plant samples saving time and resources (Adeleke and Babalola 2021; Kohout et al. 2012; Li et al. 2010).

Fungal endophytes have been very well associated with almost every group of plant kingdom, i.e., starting from algae, lichens, bryophytes to lower cryptograms, i.e., pteridophytes, gymnosperms and to the most advanced angiosperms growing in wild and under cultivation (Verma et al. 2017). Interestingly, fungal endophytes have also been isolated from plant parts growing in extreme conditions and this enormous diversity of these fungal endophytes in different conditions may be correlated with their huge beneficial role in the ecosystem and its processes (Sangamesh et al. 2018).

Plants are now facing many stresses in the present scenario due to which huge losses in crop productivity and food security have been observed (Raza et al. 2019). Extensive use of chemical fertilizers or pesticides has also affected soil quality as well as the nutrient content of food crops (Prashar and Shah 2016). The utilization of endophytic fungi is a most sustainable approach with a multifarious positive role that benefits both crops and their surrounding environment. In the last few years, there is an upsurge in the number of studies regarding the isolation and identification of endophytic fungi and their prospective role in agriculture as biostimulants or biofertilizers (Al-Ani et al. 2021; De Silva et al. 2019; Lugtenberg et al. 2016). These endophytic fungi have proved to be valuable for augmenting crop growth and productivity and enhancing the stress tolerance ability of plants against various abiotic and biotic stresses (Lu et al. 2021). As evident from the number of previous studies, endophytic fungi sustain the growth of crop plants in the presence of various abiotic stresses such as salinity, temperature, drought, heavy metals (HMs), and ultraviolet radiation (UV) (Bouzouina et al. 2021; Guler et al. 2016; Hussain et al. 2021; El-Sayed et al. 2019).

Endophytic fungi are known to secrete various growth-promoting substances like phytohormones indole acetic acid (IAA), cytokinins (CKs), and gibberellins (GAs) that helped to substantiate plant growth (Badawy et al. 2021; Hamayun et al. 2017). Concomitantly, many studies have shown that these endophytic fungi release various secondary metabolites responsible for increasing the defence of plants such as phenols, flavonoids, and lignins (Yan et al. 2021). Endophytes also enable the nutrient and water uptake ability of plants from the soil by bringing about changes in root architecture (Verma et al. 2021b). Endophytic fungi also maintain the ionic balance and redox homeostasis of plants and regulate the levels of various osmoprotectants such as proline and glycine betaine under salinity and drought stress (Gupta et al. 2021; Kour et al. 2020). Endophytic fungi are known to protect the plants from oxidative stress under various stresses by enhancing the production of various antioxidative enzymes such as catalase (CAT), peroxidase (POX), and superoxide dismutase (SOD) (Fecht-Christoffers et al. 2006; Guler et al. 2016). A meta-analysis study on endophyte and growth promotion under stress has been observed by the work of Rho et al. (2018). The study showed 96 endophytic fungal strains stimulated growth in 42 plant species under drought, salinity, and nitrogen deficiency.

Endophytic fungi also modulate the functioning of various genes, transcription factors at the cellular and molecular levels. Studies have reported that endophytic fungi enhance the expression of various stress-responsive genes and proteins such as COR, DREB, heat shock proteins (HSPs), and phytochelatins (PCs), and alleviate the plant from various stresses (Bilal et al. 2020; Ogbe et al. 2020). Interestingly, these genes are regulated under the effect of several transcription factors such as WRKY, MAPK, and calcium-dependent kinases (CDKs) that affect stress signaling pathways (Khare et al. 2018).

The present chapter will entail the role of endophytic fungi in abiotic stress alleviation. The chapter will also highlight the stress alleviation mechanisms and associated changes in gene expression in plants.

2 Endophyte-Mediated Phytohormones Production Under Non-stressed and Stressed Conditions

Phytohormones like IAA, GAs, CKs, ABA, Et are well pronounced for their role in various physiological and biochemical processes in plants such as cell division, growth, senescence, and germination. At the same time, these phytohormones assist plants in facing different types of abiotic stresses such as drought, salinity, temperature, HMs, and

UV. A number of the previous article have shown the efficient production of these phytohormones by endophytic fungi in the different host plants. These endophytic fungi stimulate enhanced production of phytohormones well under normal and in stressed conditions and stimulate growth promotion in host plants (Egamberdieva et al. 2017; Yan et al. 2019). Khan et al. (2013) reviewed the GA_3 production by endophytic fungi and revealed the substantial role of endophytic fungi in abiotic stress tolerance of crop plants. Recently, Wu et al. (2020) demonstrated the changes in the gene expression pattern of different phytohormones like IAA, GA, ABA, SA, JA in response to endophyte inoculation. The study showed that *an Anteaglonium* (T010) a DSE affects the expression of genes involved in phytohormones in *Vaccinium corymbosum* L. plants; there was an increase in transcript expression of genes for IAA and SA biosynthesis while a decrease was observed for GA, ABA, and JA as evident from transcriptomics data (Wu et al. 2020). Similarly, the production of IAA by endophyte was shown by the work of Khan et al. (2015b) where endophytes (*Fusarium tricinctum* RSF-4L and *Alternaria alternata* RSF-6L) have been shown to induce production of IAA under in vitro studies. Priyadharsini and Muthukumar (2017) showed growth-promoting attributes by a DSE *Curvularia geniculata* as well as IAA production under in vitro conditions. Bilal et al. (2018) revealed growth-promoting attributes of two endophytic fungi *Aspergillus fumigatus* TS1 and *Fusarium proliferatum* BRL1 as well as phytohormones production mainly GA and IAA under in vitro conditions.

Phytohormone modulation by endophytic fungi has been observed in many previous studies under stressed conditions. Waqas et al. (2012) showed altered levels of different phytohormones in salt and drought-stressed rice plants inoculated with two endophytes *Phoma glomerata* LWL2 and *Penicillium* sp. LWL3. There was increased accumulation of GA and IAA that led to growth promotion while decreased levels of two stress-responsive hormones ABA and JA that led to mitigating effects from salt and drought stress. Jan et al. (2019) reported that endophytic fungi, *Yarrowia lipolytica* FH1, isolated from the spines of *Euphorbia milli* produced different metabolites in maize that reduced the negative effects of salt stress. Endophytic fungus inoculated plants were able to accumulate higher IAA and low levels of ABA hormones that played an important role in controlling the root growth, reducing ROS production, abscission, and promoting overall growth of maize plants (Fecht-Christoffers et al. 2006). A study by Waqas et al. (2015) showed the inoculation of endophyte *Paecilomyces formosus* LWL1 to heat-stressed rice plants led to decreased production of ABA and JA production and further promoted growth. Recently, Hamayun et al. (2021) demonstrated that inoculation of an endophyte *Gliocladium cibotii* to heat-stressed soybean and sunflower plants led to decreased concentration of ABA. Stress amelioration effects of endophytic fungi were seen in the work of Ripa et al. (2019), where endophytic fungi isolated from wheat plants showed IAA producing properties as well as growth-promoting traits. Additionally, the study also showed that these different fungal endophytes were capable of multiple stress tolerance like drought, salinity, and HMs. Alleviating effects of endophytes were also seen from the work carried out by Hamayun et al. (2017) in salt-stressed soybean plants. There was increased production of GA_3 while decreased production of ABA and JA in response to inoculation of *Porostereum spadiceum* AGH786 in the presence of salt stress. A study by Khan et al. (2012) demonstrated a remarkable increase in GA_3 levels and IAA levels in salt-stressed cucumber plants due to inoculation with *Paecilomyces formosus* LHL10 and exhibited growth-promoting effects in the presence of salt stress. Ameliorating effects of endophytic fungi from HMs stress via increased production of phytohormones IAA have been observed in a study by Ikram et al. (2018) that demonstrated increased production of IAA by *Penicillium roqueforti* in wheat plants grown under HMs stressed soil. Wheat plants inoculated with *P. roqueforti* in the presence of different HMs showed better growth and phytostabilization due to the secretion of IAA. Similarly, an endophyte *Paecilomyces formosus* LHL10 alleviated soybean plants from Ni stress via modulation of different hormones as evident from gene expression data (Bilal et al. 2017). There was increased transcription expression of genes involved in the synthesis of IAA and GA while decreased transcript expression of genes involved in ABA and JA (Bilal et al. 2017). In another study, fungal endophyte *Penicillium janthinellum* LK5 (PjLK5) led to increased expression of SA in Al-stressed tomato plants and assisted in growth promotion under Al stress (Khan et al. 2015a).

3 Endophytes-Mediated Secondary Metabolites Production Under Stressed Conditions

It has been observed that fungal endophytes prevent the plant from oxidative stress under different stresses through the production of various secondary metabolites like phenolics, alkaloids, etc., and osmoprotectants like proline and glycine betaine that helps to maintain ROS balance in plants (Ogbe et al. 2020). Endophytic fungi secrete a large number of secondary metabolites that play a crucial role in abiotic stress management as evident from the work of Qin et al. (2019). The study showed an increase in concentration of *N*-(4-hydroxystyryl) formamide (NFA), an analogue of coumarin with inoculation of an endophyte *Aspergillus fumigatus* SG-17 to drought-stressed rice plants (Qin et al. 2019). In a different study, inoculation with endophytic fungi

Gliocladium cibotii led to the enhanced concentration of phenolics under heat stress in soybean and sunflower plants. Plants inoculated with *G. cibotii* showed improved growth and lower oxidative stress under heat stress conditions (Hamayun et al. 2021). A study revealed that *Penicillium resedanum* LK6, an endophytic fungus isolated from leaves of *Solanum nigrum*, alleviated capsicum plants from heat stress, and inoculated plants showed higher biomass as well as increased accumulation of proline and flavonoids (daidzin, daidzein, and m-glycitin) (Khan et al. 2013). Similarly, an increase in total flavonoid content was observed in soybean plants grown under HMs stress inoculated with *Aspergillus welwitschiae* (Hussain et al. 2021). Interestingly, endophytic fungi are considered a great reservoir of secondary compounds that have wide applications not only in agriculture but also in pharmaceuticals as well as in biotechnology (Torres-Mendoza et al. 2020).

4 Endophytic Fungi and Abiotic Stress Alleviation in Plants

4.1 Salinity

Salinity is the major limiting factor and a great threat to agricultural food production mostly for semi-arid or arid regions (Munns and Tester 2008; Tufail et al. 2021). Most of the agricultural land worldwide have been severely affected and some reports suggest that around 50% of arable lands will be under serious salinity risk by 2050 (Ciftci et al. 2010; Chandrasekaran et al. 2014; Gupta and Huang 2014; Rubin et al. 2017). Soil exposure with Na^+ ions obstructs the plants' regular physiological functions as well as the yield of crops production (Gupta et al. 2021). Simultaneously, soil salinity can disrupt the ion distribution and metabolism in the cell (Raghuwanshi and Prasad 2018). In terms of soil salinity stress the plants are subjected to ion toxicity, osmotic stress, nutritional (N, K, P, Ca, Fe, Zn) deficiencies, and oxidative stress which inhibits water uptakes (Bano and Fatima 2009; Talaat and Shawky 2013).

Different types of salt-tolerant fungi have been explored to improve crop growth under salinity stress. Bouzouina et al. (2021) reported that in wheat plant the application of endophytic fungi (*Chaetomium coarctatum* and *Alternaria chlamydospore*) enhanced the plant growth rate, relative water content (RWC), the balance of ions (Na^+ and K^+), along with sugar and proline levels under salt stress (Fig. 1). Another study reported that dark septate endophytic fungi (DSE) *Sordariomycetes* sp1-B'2 and *Melanconiella elegans*-21W2 improved the growth of cowpea plants under saline conditions (Farias et al. 2020). In another study, *Aspergillus ochraceus* has been reported for the enhancement of 15–30% of seawater stress tolerance in barley as plants inoculated with *A. ochraceus* showed enhanced growth traits, higher IAA accumulation, increased concentration of antioxidant compounds, and increased content of leaf pigments, sugars, and protein (Badawy et al. 2021). Abdelaziz et al. (2019) reported the growth-promoting activity of *Piriformospora indica* in *Arabidopsis thaliana* under salt stress. These fungi help the plants to manage salts by improving the higher expression of ion channels like *HKT1*, *KAT1*, and *KAT2* that lower the ions (Na^+/K^+) ratio. Lanza et al. (2019) also reported that root endophytic fungi *Serendipita indica* (formerly *Piriformospora indica*) co-cultivation in *Arabidopsis* plants under saline conditions improves plant growth by maintaining Na^+ concentration. Moreover, two fungal endophytes *Penicillium brevicompactum* and *P. chrysogenum* isolated from roots of two Antarctic plants, *Colobanthus quitensis* and *Deschampsia antarctica*, express *NHX1* gene (Molina-Montenegro et al. 2020). The up-regulation of vacuolar *NHX1* Na^+/H^+ antiporters helps to store Na^+ in vacuoles and regulates the Na^+/K^+ ions concentration resulting in tolerance towards salt stress in tomato and lettuce (Molina-Montenegro et al. 2020) (Fig. 1). Table 1 enlists the various studies that reported positive effects of endophytic fungi in the amelioration of salinity stress in different plants.

4.2 Drought

Drought is a recurring, more extreme, and unpredictable rapidly changing climatic condition that affects crop production throughout the world especially in dry and semi-arid areas (Attafi et al. 2021; Kogan et al. 2019). Drought stress strongly influences plant growth and yield (Bartlett et al. 2019; Park et al. 2021; Sperry et al. 2002; Tardieu et al. 2017; Ullah et al. 2021). Plants respond to drought stress by modulation of their physiological and biochemical mechanisms (Basu et al. 2016; Zandalinas et al. 2018).

Symbiotic association of endophytic fungi such as *Penicillium minioluteum* with *Chenopodium quinoa* enhances the performance of the crop under severe drought. Endophyte-inoculated plants showed a 40% improvement in root growth (González-Teuber et al. 2018). Different studies have shown that endophytic fungi inoculation improves plant resistance through improved root architecture (González-Teuber et al. 2017), prevents membrane damage to cells (Xu et al. 2017), elevates antioxidant enzyme activities (Guler et al. 2016), increases chlorophyll content (Idhan et al. 2018), and enriches osmoregulatory network (Tyagi et al. 2017) (Fig. 1). Endophytic fungi protect the drought-stressed plant from ultrastructural damage (including mitochondria), alter root morphology, and influence the balance of endogenous hormones (IAA, ABA) (Liu and Wei 2019). Guler et al. (2016) studied the effect of *Trichoderma*

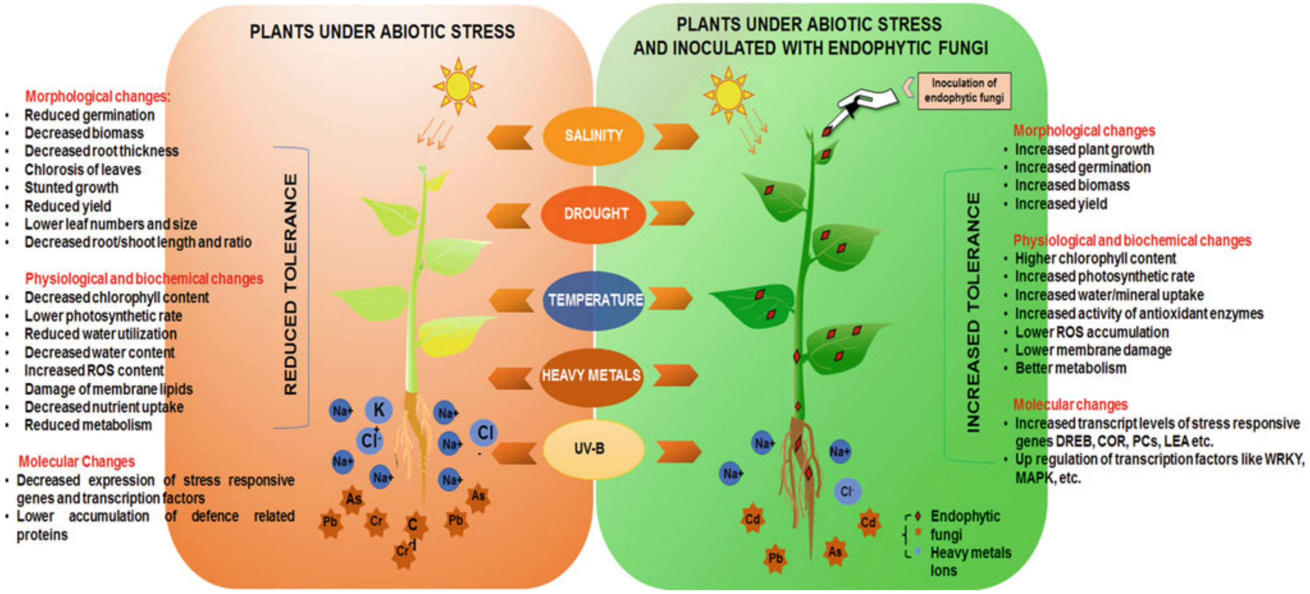

Fig. 1 Endophytic fungi mediated abiotic stress amelioration mechanisms in plants

atroviride ID20G application to drought-stressed maize seedlings and demonstrated that enhancement of fresh and dry weight of roots increased chlorophyll and carotenoid contents and prevented membrane damage. In a different study, endophytic fungi *Trichoderma atroviride* ID20G isolated from roots of tea plant helped in reducing the toxic effects of drought stress. Endophyte-inoculated plants under drought stress showed a lower rate of lipid peroxidation, increased hydrogen peroxide (H_2O_2) level, and elevated antioxidant enzyme activity (e.g., SOD, CAT) (Guler et al. 2016). Li et al. (2019), investigated the roles of DSE *Paraphoma* sp., *Embellisia chlamydospora*, and *Cladosporium oxysporum* isolated from *Hedysarum scoparium* growing in extreme drought conditions. When these isolates were inoculated in *H. scoparium*, inoculated plants showed increased root biomass and length. DSE such as *Acrocalymma vagum*, *Paraboeremia putaminum*, and *Fusarium acuminatum* which colonize the Licorice (*Glycyrrhiza uralensis*) plants help their host to survive drought through increased biomass production, glycyrrhizin content, and nutrient absorption (He et al. 2019). A study showed positive effects of five endophytic fungi in amelioration of drought stress in barley plants (*Hordeum murinum* subsp. *murinum*); inoculated plants showed a high number of tillers, increased grain yield, and higher shoot biomass (Murphy et al. 2015). Various studies that demonstrated the beneficial effects of endophytic fungi in tolerance of drought stress in different plants have been depicted in Table 2.

4.3 Temperature

The temperature of the Earth's surface has significantly increased from 0.3 to 5 °C in the last few years which is above-normal temperature (Rennenberg et al. 2006; Khan et al. 2013). Due to increased temperature, crop plants are now facing huge losses in their yield and productivity, and at the same time, it affects plants' physiological, biochemical, and molecular responses. There are several reports that state that under temperature stress in plants there is a decrease in the fluidity of plasma membrane, changes in metabolite and osmolyte concentrations, modification in essential amino acids composition, alteration in protein structures, etc. (Djanaguiraman et al. 2018; Muhlemann et al. 2018; Wahid et al. 2007; Takahashi and Shinozaki 2019; Zinn et al. 2010).

Fungal endophytes play a crucial role in the alleviation of temperature stress in crop plants as evident from the number of previous studies. It has been observed these endophytic fungi are associated with plants growing in extreme conditions and sustain the growth of these plants. Some thermotolerant endophytic fungi have been reported by Sangamesh et al. (2018) from plants growing in the Thar Desert, Rajasthan. Some of the dominant endophytic fungi that were isolated were ACJ-2, ACJ-5 (*Aspergillus flavus*), SAP-3 (*Aspergillus* sp.), SAP-6, LAS-4 (*Aspergillus* sp.), and LAS-6 (*Chaetomium* sp.). Studies have demonstrated that the application of endophytic fungi, *Gliocladium cibotii*, which was isolated from *Verbena officinalis* improved plant

Table 1 A list of recent studies depicting the effect of endophytic fungi in the alleviation of salinity stress in different host plants

Endophytic fungi	Host plant	Effects on host plant	References
Epichloë sp.	*Hordeum vulgare*	• Increased biomass • Higher N, P, and K^+ contents • Lower Na^+ • Lower ratios of C:N, C:P, Na^+:K^+ and higher ratio of N:P	Song et al. (2015)
Trichoderma harzianum	*Brassica juncea*	• Improved uptake of essential elements • Modulation of osmolytes and antioxidants • Restricted Na^+ uptake	Ahmad et al. (2015)
Piriformospora indica (PiHOG1)	*Oryza sativa*	• Increased biomass • Increased shoot and root lengths • Enhanced photosynthetic rate, pigment, and proline contents • Delayed phosphorylation	Jogawat et al. (2016)
Trichoderma longibrachiatum	*Triticum aestivum*	• Increased water content in leaves and roots • Higher chlorophyll content and shoot proline content	Zhang et al. (2016)
Trichoderma sp.	*Oryza sativa*	• Increased chlorophyll content, decreased MDA and H_2O_2 contents, increased proline and phenolics concentration	Rawat et al. (2016)
Piriformospora indica (DSM11827)	*Medicago truncatula*	• Increased antioxidant enzymes activities • Increased hyphae density in roots • Reduced malondialdehyde (MDA) activity, Na^+ content, and relative electrolyte conductivity (REC)	Li et al. (2017)
Porostereum spadiceum AGH786	*Glycine max*	• High GAs • Low ABA • Enhanced endogenous level of two isoflavones including daidzin and genistein	Hamayun et al. (2017)
Piriformospora indica	*Arabidopsis thaliana*	• Lower Na^+/K^+ ratio • Increased KAT1 and KAT2 expression	Abdelaziz et al. (2017)
Piriformospora indica	*Zea mays*	• Decreased levels of Na^+ and K^+ in roots	Yun et al. (2018)
Sordariomycetes sp1-B'2 *Melanconiella elegans*-21W2	*Vigna unguiculata*	• Increased leaf concentration of K • Decreased leaf concentration of Ca, Na, and Cl	Farias et al. (2020)
Chaetomium coarctatum and *Alternaria chlamydospora*	*Triticum durum*	• Higher proline content	Bouzouina et al. (2021)
Serendipita indica	*Hordeum vulgare*	• Enhanced plant growth • Up-regulation of several proteins involved in photosynthesis and carbohydrate metabolism	Sepehri et al. (2021)
Epichloë bromicola	*Hordeum brevisubulatum*	• Higher conducting tissues • Increased thickness of leaf veins, epidermis in different organs	Chen et al. (2021)

growth and increased ROS degrading enzymes (like ascorbic acid oxidase, CAT, glutathione reductase (GR), POD, and SOD) content in *Glycine max* and *Helianthus annuus* exposed to heat stress (Hamayun et al. 2021) (Fig. 1). Likewise, the study conducted by Ismail et al. (2021) showed that the endophytic fungi, *Aspergillus foetidus* (AdR-13), isolated from *Adiantum capillus-veneris*, increased chlorophyll content, height, and biomass of *G. max* and *H. annuus*. A thermophilic endophytic fungus *Thermomyces* sp. isolated from the roots of desert-adapted

Table 2 A list of recent studies depicting the effect of endophytic fungi in the alleviation of drought stress in different host plants

Endophytic fungi	Host plant	Effects on host plant	References
Cladosporium sp.	*Nicotiana benthamiana*	• Increased root dry mass and relative water content • Differential accumulation of metabolic compounds like cytosine, diethylene glycol, etc.	Dastogeer et al. (2017)
Penicillium minioluteum	*Chenopodium quinoa*	• Improved plant growth and root formation	González-Teuber et al. (2018)
Nectria haematococca	*Solanum lycopersicum*	• Higher proline accumulation • Enhanced growth of the host plant	Valli and Muthukumar (2018)
12 endophytic fungi	*Oryza sativa*	• Regulated contents of NADPH oxidases, antioxidants, and heat shock proteins	Qin et al. (2019)
Neocamarosporium chichastianum *N. goegapense* *Periconia macrospinosa*	*Cucumis sativus* *Solanum lycopersicum*	• Increased proline and antioxidants levels	Moghaddam et al. (2021)
Acrocalymma vagum	*Ormosia hosiei*	• Increased leaf length and width • Increased leaf area, leaf dry weight, and leaf thickness • Higher photosynthetic pigments and increased net photosynthetic rate	Liu and Wei (2021)

plant *Cullen plicata* ameliorated cucumber plants from heat stress. Inoculated cucumber plants showed better adaptation, higher photosynthetic rate as well as higher water content, and increased root length (Ali et al. 2018).

Cold stress, like high temperature, is another big challenge for the plants which affects plant growth and productivity. Cold stress is mainly due to lower temperature and has a significant impact on the physio-hormonal characteristics of crops and lower crop yields. Low-temperature stress severely impacts the vegetative state such as the seedling stage generally in the areal parts of the plants especially the shoots (stems and leaves) as compared to roots (Andrews 1987; Yadav 2010a) and reproductive phases of the plant life cycle such as abscission of flowers, sterility of both male and female organs, and ultimately decreased yields due to failed fruit production (Foolad and Lin 2000; Nishiyama 1995; Thakur et al. 2010). A study on barley seed grown under low-temperature stress exhibited significantly better survival rates in presence of root endophytic fungi *Chaetomium globosum*, *Epicoccum nigrum*, and *Piriformospora indica*. Results showed that seed inoculated with endophyte *P. indica* have higher nutrient input, early flowering, and higher grain dry weight (Murphy et al. 2014). Additionally, a study carried out by Rosa et al. (2010) revealed that fungal endophytes associated with the leaves of *Colobanthus quitensis* such as *Aspergillus* sp., *Cadophora* sp., *Davidiella* sp., *Entrophospora* sp., *Fusarium* sp., *Geomyces* sp., *Gyoerffyella* sp., *Microdochium* sp., *Mycocentrospora* sp., *and Phaeosphaeria* sp. provided resistance to the host plants against freezing temperatures as well as high rates of UV radiation via increased production of melanin. Fungal melanin is an amorphous polymer and has the properties to transduce electromagnetic radiation into metabolic energy that may be helpful for survival at extremely low temperature areas such as the north and south pole of the Earth that are exposed to high UV radiation (Cordero and Casadevall 2017; Dadachova et al. 2007; Robinson 2001). Besides this, another work reported that the application of a combination of calcium nitrate with endophytic fungi *Epichloë* sp. imparts better survivability of *Festuca sinensis* plant at lower temperatures (Zhou et al. 2021). Inoculated plants showed higher total chlorophyll content, increased soluble sugar, and higher root metabolic pathways that increase the plant survival rate at cold temperatures (Zhou et al. 2021). Some of the studies that showed the affirmative response of endophytic fungi in alleviation of temperature stress in different plants have been revealed in Table 3.

4.4 Heavy Metal/Metalloids Tolerance

Endophytic fungi have been shown to play an incredible role in increasing tolerance of plants towards heavy metal and metalloid stress. Many endophytic fungi (like *Aspergillus niger* DR02, *Trichoderma atroviride* DR17 and DR19, *Alternaria* sp. DR45, *Annulohypoxylon stigyum* DR47, and

Table 3 A list of recent studies depicting the effect of endophytic fungi in the alleviation of temperature stress in different host plants

Endophytic fungi	Host plant	Effect on host plant	References
507 endophytic fungal Dominating fungi were *Aspergillus flavus* (ACJ-2, ACJ-5), *Aspergillus* sp., (SAP-3, SAP-6, LAS-4) *Chaetomium* sp. (LAS-6)	*Oryza sativa*	• Higher shoot and root growth	Sangamesh et al. (2018)
Aspergillus japonicas (EuR-26)	*Helianthus annuus* *Glycine max* *Oryza sativa*	• Improved plant biomass • Higher content of phenolics, flavonoids, soluble sugars, proteins, and lipids • Increased ABA levels • Increased activity of catalase and ascorbic acid oxidase	Hamayun et al. (2018)
Thermomyces sp.	*Cucumis sativus*	• Enhanced photosynthesis and water use efficiency • Increased antioxidant enzyme activities and metabolite pool	Ali et al. (2018)
Thermomyces lanuginosus	*Cullen plicata*	• Enhanced growth-promoting activity	Ali et al. (2019)
Aspergillus niger (SonchL-7)	*Helianthus annuus* *Glycine max* *Oryza sativa*	• Increased plant height and biomass • Higher chlorophyll contents • Lowered lipid peroxidation and reactive oxygen species (ROS) • Enhanced proline and phenolics concentration	Ismail et al. (2020)
Paecilomyces formosus LHL10 *Penicillium funiculosum* LHL06	*Glycine max*	• Increased plant growth • Higher photosynthetic activity • Decreased lipid peroxidation • Enhanced micronutrient uptake	Bilal et al. (2020)

Talaromyces wortmannii DR49) are the producers of various enzymes such as polysaccharide degradation enzymes mainly xylanases, cellulases, lipases, amylases, and proteases that help in the degradation of hydrocarbons and are found to be heavy metal resistant (Corrêa et al. 2014; Robl et al. 2013). A study showed that *Aspergillus welwitschiae*, endophytic fungi, efficiently alleviate metal stress from soybean plant and inoculated plants demonstrated higher root and shoot length, increased fresh/dry mass, higher antioxidative enzymes activity such as CAT, ascorbic acid oxidase (AAO), and POD (Hussain et al. 2021) (Fig. 1).

Shadmani et al. (2021) isolated DSE fungi and non-DSE fungi from the roots of *Hordeum vulgare* and evaluated their tolerance in Cd-contaminated soil. It was found that *Alternaria* sp. (TBR5) and *Bipolaris zeicola* (Tw26) showed the highest tolerance to Cd on 0.9 mg kg^{-1} and inoculated barley plants showed enhanced growth and development, higher chlorophyll content, increased fresh and dry weight as well as higher root weight. Similarly, Yu et al. (2021) found that working on DSE fungi *Exophiala pisciphila*, under Zn, Cd, and Pb stressors, on pre-treatment of *E. pisciphila* with 200 μM exogenous melatonin, dramatically boosted the activity of SOD. After exposure to HMs, the melatonin concentration becomes higher within two days and *E. pisciphila* tryptophan decarboxylase (*EpTDC1*) and serotonin N-acetyltransferase (*EpSNAT1*) were transcriptionally up-regulated. Further, these genes overexpressed in *Arabidopsis thaliana* enhanced its heavy metal-induced stress tolerance.

Endophytes-mediated bioremediation is one of the most promising tools for in-situ bioremediation methods for contaminants soil (Dixit et al. 2015; Xiao et al. 2010). Higher concentrations of heavy metals can cause trouble to plants by producing excessive reactive oxygen species

(ROS) by preventing the antioxidant system, disrupting the electron transport chain, and disturbing the metabolism of essential elements (Edwards et al. 2000; Lushchak 2011; Opdenakker et al. 2012; Verma et al. 2021a; Yadav 2010b; Yin et al. 2015; Yu et al. 2021). The generation of ROS creates a significant imbalance, which causes dramatic physiological problems for the plant, which we refer to as "oxidative stress" (Morina et al. 2010; Kováčik et al. 2010). Various metals like Cu, Fe, Pb, Cd, Cr, As, Hg, Cr, and Zn, have the capacity to induce the formation of ROS (Duquesnoy et al. 2010; Vanhoudt et al. 2010; Márquez-García et al. 2011; Körpe and Aras 2011).

A study showed elevation of some compounds by endophytic fungi *Daldinia eschscholtzii* such as napthoflavone, syringaldehyde, 3,4,5-trimethoxy benzoic acid, 2-furoic acid, and gossypetin 3′ O glycoside that prevent ROS-mediated oxidative damage to the *Abutilon indicum* plant (Musthafa et al. 2021). Endophytic fungi JP4 (50 µM) alleviate Cd stress in seeds of *Oryza sativa* cv. Liaoxing No.1 w grown in a pot by enhancing pigment content and photosynthetic rate, and also increases antioxidative enzymes such as SOD, CAT, POD, and GR as well as ascorbic acid (ASA) and glutathione (GSH) content (Ma et al. 2019). Exogenous application of a dominant root-associated DSE fungus *Exophiala pisciphila* H93 ameliorated the effect of Cd stress in maize and improved growth via production of antioxidant systems, as well as converted toxic forms into inactive Cd (Wang et al. 2016). Endophytic-mediated mitigation of HMs stress in different host plants can be visualized in Table 4.

4.5 Ultraviolet B (UV-B) Radiation

UV-B is electromagnetic radiation that ranges from 280 to 315 nm and it becomes a shorter wavelength with high energy (Kim et al. 2015). Due to the high energy of UV-B radiation, it causes biological damages to several plants and that becomes a point of concern (Sharma et al. 2017). The increased intensity of UV-B light due to depletion of the stratospheric ozone layers can have a disproportionately damaging effect on plant cells as well as change their physiological, biochemical, and molecular profile (Bornman et al. 2015, 2019). Plants are highly sensitive to excessive UV-B radiation and are unable to avoid the radiation that causes direct or indirect effects towards basic plant metabolic processes such as growth, photosynthesis, respiration, and reproduction (Suchar and Robberecht 2016; Zlatev et al. 2012; Mpoloka 2008). To date, only a handful of information is available regarding endophytic fungi and the amelioration of UV radiation stress on plants (Ramos et al. 2018). One of the studies by Ramos et al. (2018) reported the effect of UV-B on Antarctic pearlwort (*Colobanthus quitensis*) plant inhabited with fungal endophytes, namely, *Penicillium* sp., *Alternaria* sp., and *Geomyces* sp. It was observed that the plants were severely affected by photochemical efficiency, cell damage, and reproductive biomass at different levels or duration of UV-B. However, due to the presence of fungal endophytes, plants survived well under extreme conditions of UV and showed higher biomass, high numbers of flowers, lower oxidative stress as shown by decreased lipid peroxidation. In addition, there were changes in some phytohormone content like salicylic acid, jasmonate, IAA, and ABA in the shoots of plants.

There are reports that stated the ability of endophytic fungi in protection of plants from UV radiation by enhancing the production of different secondary metabolites involved in the plants defence system. For instance, in a study reported by El-Sayed et al. (2019) two endophytic fungi *Aspergillus fumigatus* TXD105 and *Alternaria tenuissima* TER995 associated with *Taxodium distichum* and *Terminalia arjuna* plants significantly enhanced the production of paclitaxel by 16.25 and 19.86% on exposure to UV and gamma irradiation, respectively. Simultaneously, another study by Lu et al. (2021) reported that endophytic fungus *Phomopsis* sp. XP-8 isolated from the bark of *Eucommia ulmoides* when co-cultured with UV radiation for certain periods (20 min) enhances production of oligomeric proanthocyanidins (100 µm) that has the potential to improve plant health. The study also showed that endophytic fungi have potentially increased the production of other secondary metabolites such as resveratrol up to 240.57 µg/l. Resveratrol has a stilbenoid, a kind of natural phenolic compound that participates in many signaling pathways (Ahmadi and Ebrahimzadeh 2020). Furthermore, high intensities of solar UV-B radiation on *Colobanthus quitensis* (Antarctic pearlwort) plant in presence of fungal endophytes have shown that flavonoids (a phenolic metabolite) play a critical role to protect plants under excessive light (Ramos et al. 2018).

5 Endophyte-Mediated Modulation at the Molecular and Cellular Level Under Different Abiotic Stress

All the abiotic stresses such as high temperature, drought, salinity as well as heavy metal toxicity largely impact the plants and are a serious threat to agronomic important crops and ultimately damages the environments (Abo Nouh et al. 2021; Singh and Kalamdhad 2011; Saxena et al. 2016). In the presence of different stresses, plants often face oxidative burst and cellular damage (Abo Nouh et al. 2021). To cope up with stresses plants regulate their biochemical and physiological profile as seen in the above sections of the chapter. Additionally, plants fine-tune gene regulatory networks and showed variation in transcript levels of different

Table 4 A list of recent studies depicting the effect of endophytic fungi in the alleviation of heavy metal (HMs) stress in different host plants

Heavy metal	Endophytic fungi	Host plant	Effects on host plant	References
Cd	*Paraphaeosphaeria* sp. SR46	*Zea mays*	• Increased plant growth • Increased Cd cycling and restoration	An et al. (2015)
Cu, Zn, Pb	*Phialocephala fortinii* *Rhizodermea veluwensis* *Rhizoscyphus* sp.	*Clethra barbinervis*	• Enhanced growth enhancement • Increased nutrient uptake • Decreased HMs concentration	Yamaji et al. (2016)
Pb, Cu	*Serendipita indica*	*Ocimum basilicum*	• Increased shoot and root dry weight	Sabra et al. (2018)
Cd, As, Pb	*Acrocalymma vagu* (NYN8C05 and NYN8G01)	*Nicotiana tabacum*	• Increased leaf size • Reduced toxicity of HMs	Jin et al. (2018)
Hg^{2+}	*Aspergillus* sp. A31 *Curvularia geniculata* P1 *Lindgomycetaceae* P87 *Westerdykella* sp. P71	*Aeschynomene fluminensis* *Zea mays*	• Increased host biomass	Pietro-Souza et al. (2020)
Cr, As	*Aspergillus welwitschiae*	*Glycine max*	• Enhanced growth • Higher root, shoot length, and fresh/dry • Increased enzymatic antioxidants like CAT, AAO, POD	Hussain et al. (2021)
Ni, Cd, Cu, Pb, Cr, Al	*Paecilomyces formosus* LHL10 *Penicillium funiculosum* LHL06	*Glycine max*	• Enhanced plant growth promotion • Increased levels of carbohydrates, minerals, amino acids, and antioxidants	Bilal et al. (2021)
Cd, Zn, Pb	*Exophiala pisciphila*	*Arabidopsis thaliana*	• Increased activity of antioxidant enzyme SOD • Reduced HMs accumulation	Yu et al. (2021)
Cd, Cr	*Aspergillus flavus* (Ch-01)	*Solanum lycopersicum*	• Increased plant growth-promoting activity • Increased transcript expression of SlGSH1 and SlPCS1 genes	Aziz et al. (2021)
Cd	*Piriformospora indica*	*Nicotiana tabacum*	• Increased expressions of genes of POD, glutathione synthase (GS) • Upregulation of photosynthesis-related proteins	Su et al. (2021)

stress-responsive genes, transcription factors as well other signaling components (Fig. 1).

Various research approaches have given an idea about a complete understanding of how plants respond to salinity stress at combined levels of molecular, physiological, and biochemical processes. Alternative splicing (AS) is a significant gene expression modulator that has the potential to increase proteome diversity while at the same time regulates mRNA levels (Duque 2011). Similarly, Sampangi-Ramaiah et al. (2019) reported that endophyte-induced alteration in the frequency of alternative splicing events in plants is subjected to salinity stress. Alternative splicing of transcripts events per gene decreased from 2.28 to 2.11 upon colonization of an endophytic fungus, *Fusarium* sp. in IR-64 rice plants, under 150 mM saline stress. On the other hand, drought stress affects plant health by decreasing photosynthetic rate, modulating cellular redox potential, brings about hormonal imbalance, induces oxidative damage by increasing ROS which ultimately results in cellular membrane damage (Cohen et al. 2015). Qin et al. (2019) isolated 12 strains of endophytic fungi (*Aspergillus fumigatus* SG-17, *A. oryzae* HY-1, *A. tubingensis* MG-23, *A. flavus* MY-15, *Fusarium concentricum* HG-2, *Alternaria alternata* MY-22, *A. tenuissima* SG-5, *Chaetomium globosum* QY-1, *Fomitopsis palustris* SG-16, *Penicillium oxalicum* SG-4, SY-15, *Pestalotiopsis microspore* SG-6) from *Myricaria laxiflora* and evaluated their drought stress effects in rice cv. Nipponbare by applying crude extracts of endophytic fungi. Predominant *Aspergillus fumigatus* SG-17 functioned most effectively and exhibited relatively higher antioxidant capacity. Follow-up MS and NMR analysis showed the compound (Z)-N-(4 hydroxyethyl) formamide (NFA) which is responsible for antioxidant activity an analogue of coumarin and regulating reactive oxygen species (ROS) compounds such as NADPH oxidases, antioxidants, and heat shock proteins.

An experiment revealed that inoculation with *Piriformospora indica* on two tomato cultivars superluna and caspian grown under drought stress ameliorates the negative effect of drought. The study revealed that increased expression of *LEA14*, *TAS14*, *GAI*, and *P5CS* under drought stress assisted the plant in overcoming drought (Azizi et al. 2021). Similarly, temperature stress can cause changes in gene expression, differential expression of proteins, altered concentration of bioactive metabolites, hormonal signaling alterations, antioxidant enzyme activity, etc. (Raza et al. 2021).

Ghorbanpour et al. (2018) postulated that inoculation of *Trichoderma harzianum* AK20G strain (endophytic fungi) to cold stressed tomato (*Solanum lycopersicum* L. cv. CaljN3) elevated the expression level of *NAC1* dehydrin *TAS14* and *P5CS* in comparison to non-inoculated. Results showed that *T. harzianum* was found to effectively mitigate the negative effects of cold stress, resulting in increased photosynthetic and growth rates. *T. harzianum* was also found to minimize lipid peroxidation and electrolyte leakage while enhancing leaf water content and proline accumulation. Another study by Bodjrenou et al. (2021) demonstrated endophytic fungi (*Serendipita indica*) that helped the *Musa acuminata* cv. Tianbao plant to tolerate high-temperature stress. The study revealed that *S. indica* inoculated leaf of banana plant sustains the growth and enhances tolerance of plants by regulating microRNAs (miRNAs). A set of 278 differentially abundant miRNAs in response to heat stress regulates the genes involved in heat shock protein, peroxidase, transcription factor, phenylalanine, sucrose synthase, protein kinase, and 7-hydroxymethyl chlorophyll. Further, gene ontology (GO) and Kyoto encyclopedia of genes and genomes (KEGG) pathway enrichment analyses uncover the differentially expressed (DE) miRNAs that were significantly associated with nutrient sources uptake, secondary metabolism, growth regulators, auxin-responsive factor, signal transduction pathways.

Increased heavy metal accumulation and its toxicity have severely affected both plants as well as animals. In plants, a symbiotic association of endophytic fungi and their host plant has been shown to develop tolerance against metal toxicity via the expression of regulatory genes. For example, inoculation of endophytic fungi *Aspergillus flavus* (Ch-01) to tomato plants grown under heavy metal (Cd, Cr) improved its growth via up-regulation of *SlGSH1* and *SlPCS1* genes that in turn enhanced physicochemical traits under HMs stress (Aziz et al. 2021). A study reported by Bilal et al. (2020) a synergistic association of endophytic fungi (*Paecilomyces formosus* LHL10 and *Penicillium funiculosum* LHL06) enhances *Glycine max* resistance to combined abiotic stresses like metal toxicity, drought, and extreme temperature. Endophytic fungi reduce the metal toxicity by down-regulating heavy metal ATPase genes such as *GmHMA13*, *GmHMA14*, and *GmHMA18* expression and a few genes like *GmDREB2*, *GmDREB1B*, *GmERD1*, *GmRD20*, heat shock protein 90 (include *GmHsp90A2* and *GmHsp90A1*) expression lowered endogenous ABA and JA.

6 Conclusion

Available literature suggested that there are about 300,000 plants species in the world that harbour one or more endophytic fungi. Each endophytic fungi have its functions that helped plants to improve growth and development, and adaptability to environmental stresses (biotic or abiotic). Endophytic fungi quickly respond in the stimulation of immune defence through modulation of phytohormone signaling, production of novel secondary metabolites through responses in different stresses (high temperature, drought, heavy metal, salinity, etc.), and preparing for plant defence response pathways. However, further molecular experimental research is needed to confirm these mechanisms that increase host lifetime health fitness and crop productivity. The development of metagenomic analysis techniques over the last decade has revealed new aspects of endophytic fungal diversity, such as the identification of new unculturable/culturable species with lesser time and the establishment of endophytic fungal diversity, which reveal physiological and ecological functions of the complex host plant and their interactions. Future studies and evaluating the potential of advanced agronomical strategies to preserve the natural variety of plant endophytic fungi should become a key component of developing sustainable agroeconomic ways. Additionally, these endophytic fungi are a large reservoir of different metabolites, which are known for the production of commercially important enzymes that makes powerful resources to use in pharmaceutical and different industrial purposes. At the same time, these endophytes are used as environmentally beneficial bioremediation agents to remove heavy metals and other harmful contaminants from water and soil.

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Post-Green Revolution Degradation of Agricultural Land in India: Role of Mycorrhizae in the Sustainability of Agriculture and Ecosystems

Prashanta Kumar Mitra and Vivekananda Mandal

Abstract

The Green Revolution in India was initiated in the 1960s by introducing high-yielding varieties of rice and wheat to increase food production; this led to the loss of specific indigenous crops from cultivation and caused the extinction. India lost more than 1 lakh indigenous rice varieties after the 1970s, which took several thousand years to evolve. There is a clear indication of increasing consumption of chemical fertilizer in Indian agriculture over the past decades; urea showed the highest consumption in agriculture. A significant fraction of the heavily used pesticides and commercial fertilizers accumulates in the soil and severely affects soil properties and micro-flora, leading to soil degradation. Mycorrhiza-assisted remediation (MAR) is an aspect of bioremediation that can be used to treat both organic and inorganic pollutants. It has received much attention in recent years because it enhances the establishment/re-establishment of vegetation on the remediated soil and can equally be achieved at a reasonable cost, which will help to resist abiotic stress, disease, pathogen attack; and increase nutrient availability and growth of plants leading to greater yield. Five plant genes, namely CASTOR, POLLUX, NUP85, NUP133, and CYCLOPS, were identified, which were required to develop the mycorrhizal symbiosis in the plant root. Using mycorrhiza-assisted remediation (MAR) to re-establish a sustainable agricultural ecosystem and increase plants' nutrient uptake capacity, stress resistance, and disease resistance could be a sustainable approach for satisfying food demand without damaging the ecosystem.

Keywords

Bioremediation • Crop yield • Mycorrhiza • Post-Green Revolution • Research trend • Sustainable agriculture

1 Introduction

The key term "agriculture" originates from Latin *agricultura*, from *ager*, *agr-* "field" + "*cultura*" growing, cultivation. The cultivation of certain wild plants (agriculture) has narrowly been conceptualized to feed the human population, feed domesticated animals, and meet the significant economic demand of society and global transformation (https://www.sciencedaily.com/terms/agriculture.htm). Based on the ecosystems and environmental factors, certain crops have been cultivated in certain geographical provinces, for example, rice, millets, and soybean production in Asia, wheat farming in Europe, etc. (Leff et al. 2004). However, this trend leads to the disruption of terrestrial habitats in specific ways. Over time, the anthropogenic interferences for clearing vegetation or treating the soil caused various localized changes. The demand for such domestication and massive cultivation of crops has revolutionized global agriculture and economics to meet the demand of ever-expanding human civilization, commonly termed the **Green revolution**.

1.1 Post-Green Revolution Agricultural Practices and Soil Degradation

The Green Revolution in India was initiated in the 1960s with the introduction of high-yielding varieties of rice and wheat for increasing food production (Eliazer et al. 2019). Green Revolution has doubled the production of wheat and rice due to major government initiatives, but the post-Green Revolution scenario is that we lost many indigenous

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P. K. Mitra
Department of Botany, University of Kalyani, Nadia, WB, India

V. Mandal (✉)
Plant and Microbial Physiology and Biochemistry Laboratory,
Department of Botany, University of Gour Banga, Malda, 732103,
WB, India
e-mail: vivek.bot@ugb.ac.in

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varieties of rice and millets due to constant reduction in cultivation and declined production (Eliazer et al. 2019). Globally, India possesses the second-largest agricultural land with 20 agro-climatic zones and about 157.35 million hectares of land under cultivation (Anonymous 2017). During the Green Revolution era, major crops cultivated were rice, millets, sorghum, wheat, maize, and barley (Anonymous 1963; Hall 1964 (Fig. 1).

Rice and millets were produced more than wheat, barley, and maize combined. The crops that once were major staples became fodder crops in the past few decades after the Green Revolution. Meanwhile, India lost more than 1 lakh indigenous rice varieties after the 1970s, which had taken several thousand years to evolve, and traditional rice varieties have decreased to 6000 (Anonymous 2012; Nelson et al., 2019). This loss of species was mainly due to the focus on subsidized high-yielding hybrid crops production and the emphasis on monoculture by the government (Eliazer et al. 2019). Green Revolution influenced the increase in consumption of chemical fertilizer in Indian agriculture and also forced research toward chemical fertilizers over the past decades, and urea found the highest increasing trend of agricultural use, and Potash found with the lowest (Fig. 2). In a comparison of research interest between the application of pesticides, fungicides, and mycorrhizae for increasing/retaining crop yield, pesticide was found to be the most widespread research interest in various disciplines from different institutes in India during the Green Revolution and post-Green Revolution era (Fig. 3a), and mycorrhiza was found the least preferred topic among Indian researchers (Fig. 3b).

Urea was the highest preferred chemical fertilizer in agricultural practices during the last few decades; it may be hypothesized that reducing soil quality also increased nitrogen demand in agricultural fields and hence nitrogen-based chemical fertilizers (Fig. 4a). Green Revolution strongly influenced research interest in academia about agricultural practices and crops; there is concrete

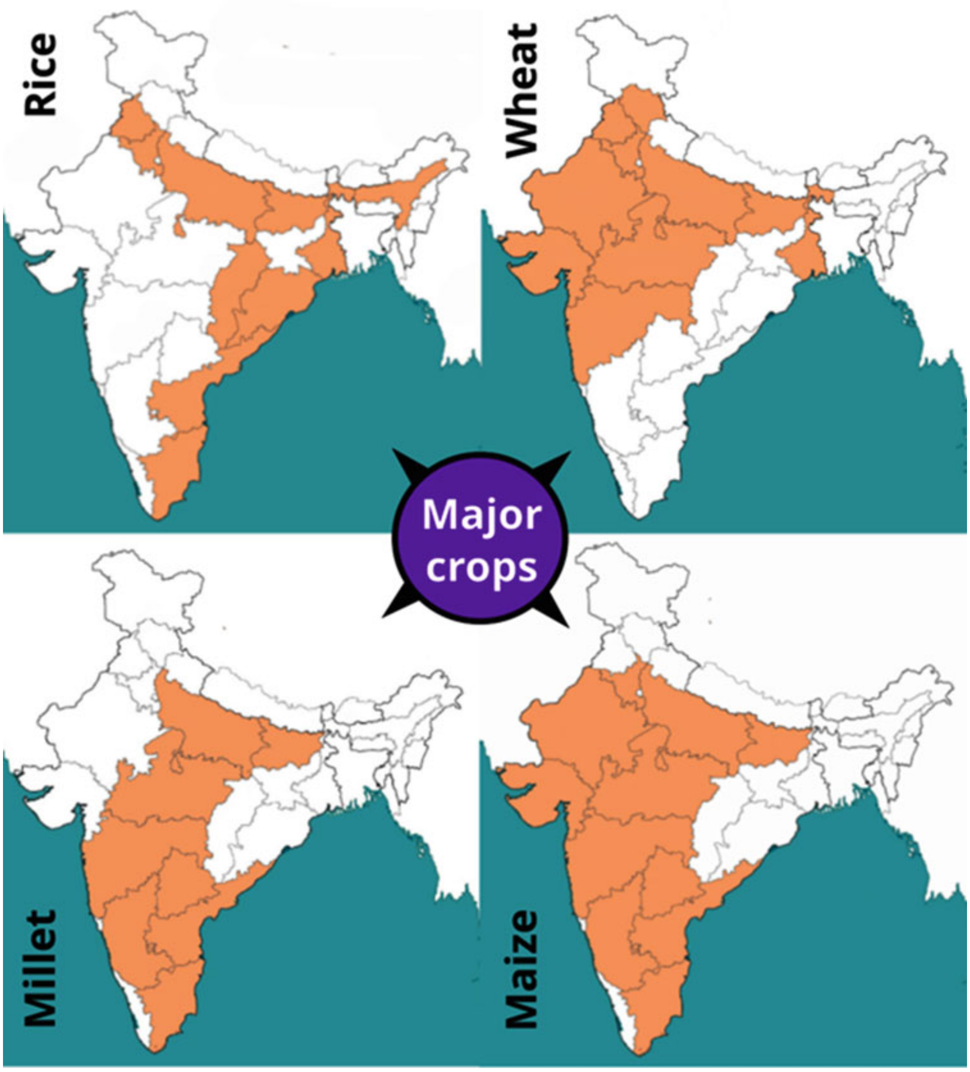

Fig. 1 Indian scenario of major crops like rice, wheat, millet, and maize cultivating areas for the last few decades

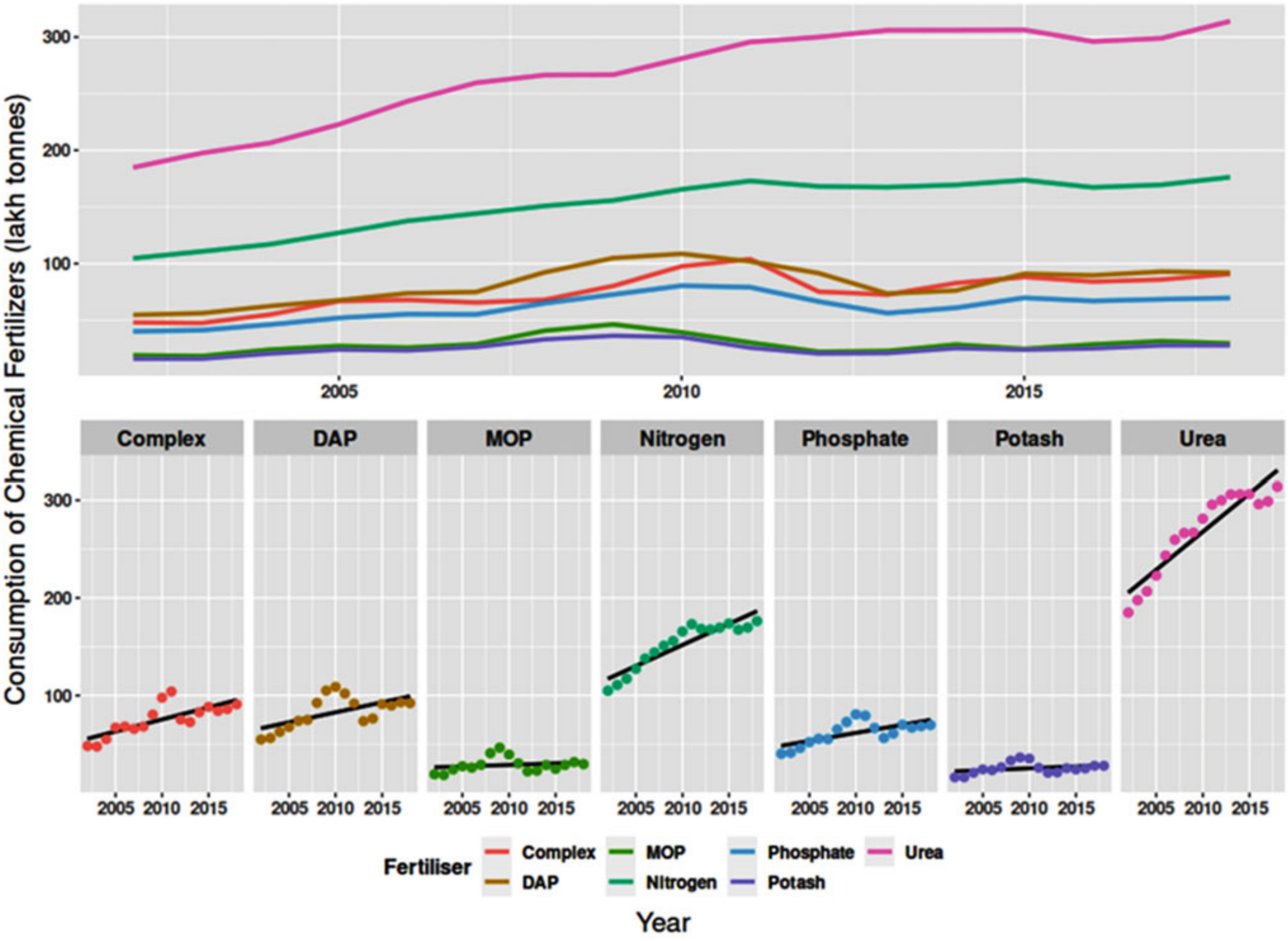

Fig. 2 Comparison of chemical fertilizer consumption between the years 2002 and 2018 in India (Anonymous 2019, 2020, 2021)

evidence of a research gap that could have had precious objectives for sustainable agriculture research (Fig. 4b1, b2).

The Food and Agricultural Organization (FAO) of the United Nations predicted that world food production requires to be increased by 70% to cope with the growing demand (Gill and Garg 2014). Increasing food production at a global scale depends on developing more infrastructure for production, which creates more burden on the ecosystem, thus increasing food production faced with ever-growing challenges (Gill and Garg 2014). Urbanization, industrialization, and increased food demand enforced more chemical agents, which accumulated over the years as pollutants in the environment, and soil pollution is a global problem directly concerned with agriculture (Raffa and Chiampo 2021). Therefore increasing world population has put tremendous pressure on the existing agricultural system, and since the 1940s, soil amendments are being used in higher quantities than in the past (Gill and Garg 2014). After 1945, the agrochemical field grew rapidly and introduced various insecticides, fungicides, herbicides, and other chemicals to control pests and ensure yields (Raffa and Chiampo 2021). Over the past era, newly developed pesticides targeted a broad spectrum of pests, and frequent use of these chemicals have posed a significant challenge to the targeted pests causing them to disperse and/or adapt to new environments. The adaptation of the pest to the new environment ultimately resulted in an increased pest resurgence and the appearance of pesticide-resistant pests (Gill and Garg 2014). A significant fraction of the used pesticides and commercial fertilizers accumulates in the soil; repeated use significantly affect soil properties, soil micro-flora diversity, biochemical reactions, and enzymatic activity (Gill and Garg 2014). Vital biochemical reactions such as nitrogen fixation, nitrification, ammonification, etc., when influenced by the accumulated pesticides and chemical fertilizers, augment synergistic and additive interactions between pesticides, microorganisms, and soil properties, ultimately governing soil degradation (Gill and Garg 2014). Chemical fertilizers, pesticides, have also been reported to influence the mineralization of soil organic matter, ultimately degrading soil quality and reducing crop productivity (Gill and Garg 2014).

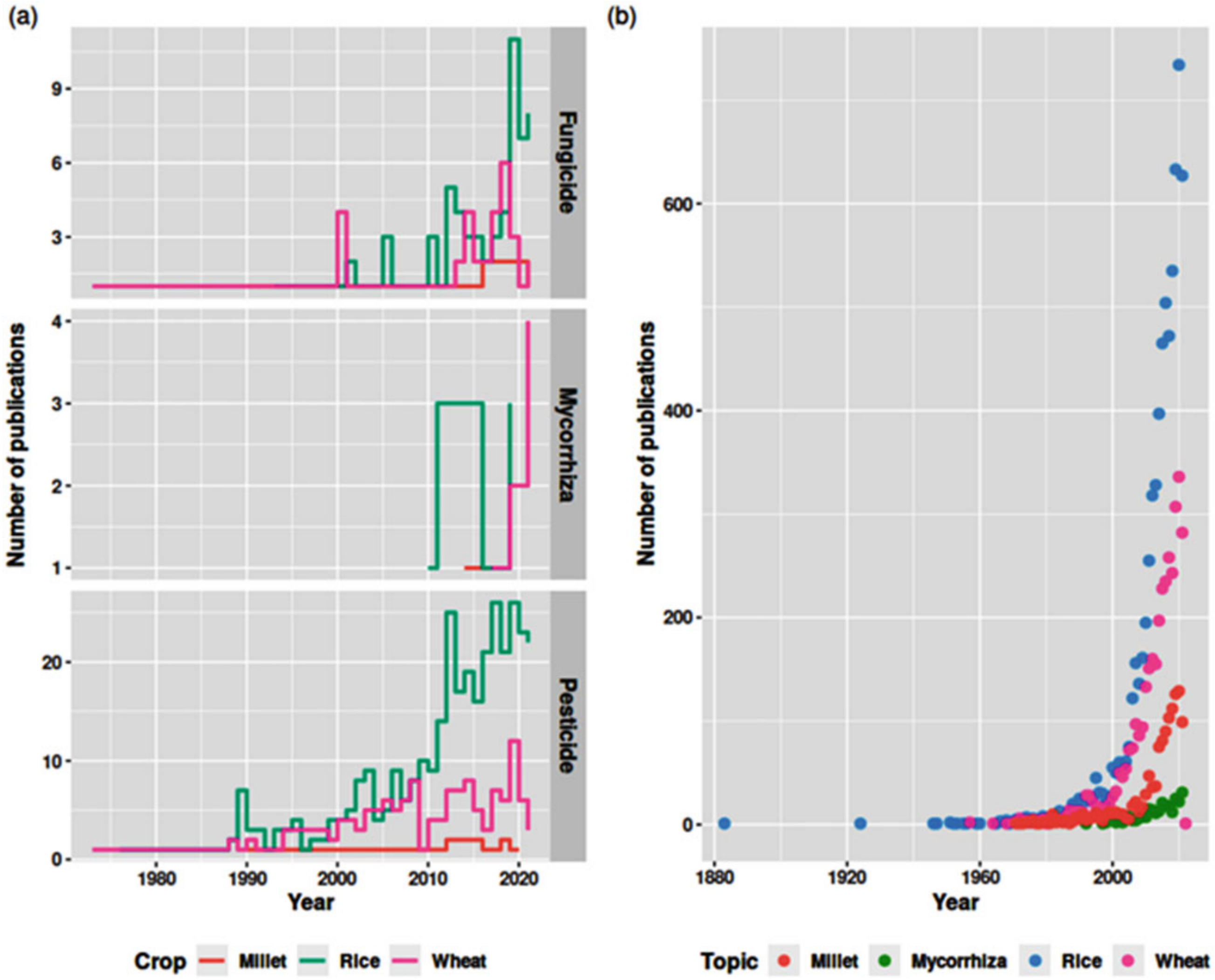

Fig. 3 Comparison of the number of published literature enlisted in PubMed

1.2 Soil Remediation

A variety of soil remediation approaches have been developed in past decades to reclaim contaminated soil which mainly took mechanical or physio-chemical techniques into focus, such as soil incineration, excavation and landfill, soil washing, solidification, and electric field application. Cost efficiency and results determine the success of large-scale commercial processes, and our current methods are unable to attain that balance; reports indicated high cost and inefficiency as the major limitations of these physicochemical approaches, and additive to that these methods are prone to cause irreversible changes to the physicochemical and biological properties of soils leading to the deterioration of the soil ecosystem and introducing secondary pollutions (Yan et al. 2020; Wan et al. 2020). Therefore, cost-effective, efficient, and environment-friendly remediation technologies are crucial to reclaim contaminated soil (Yan et al. 2020; Wan et al. 2020). A summarized flowchart representing soil remediation approaches are given below (Fig. 5).

2 Why Are Mycorrhizae Essential in Sustainable Agriculture?

2.1 Soil Remediation by Mycorrhizae

Mycorrhiza-assisted remediation (MAR) is a low cost, efficient, and sustainable bioremediation approach applicable for both organic and inorganic pollutants (Fig. 6). In recent years, it is slowly gaining attention for effectively enhancing the establishment/re-establishment of vegetation on the remediated soil at a reasonable low cost even though it is a time-consuming process.

Using arbuscular mycorrhizal fungi (AMF) infested hyper-accumulator plants were found as a promising strategy

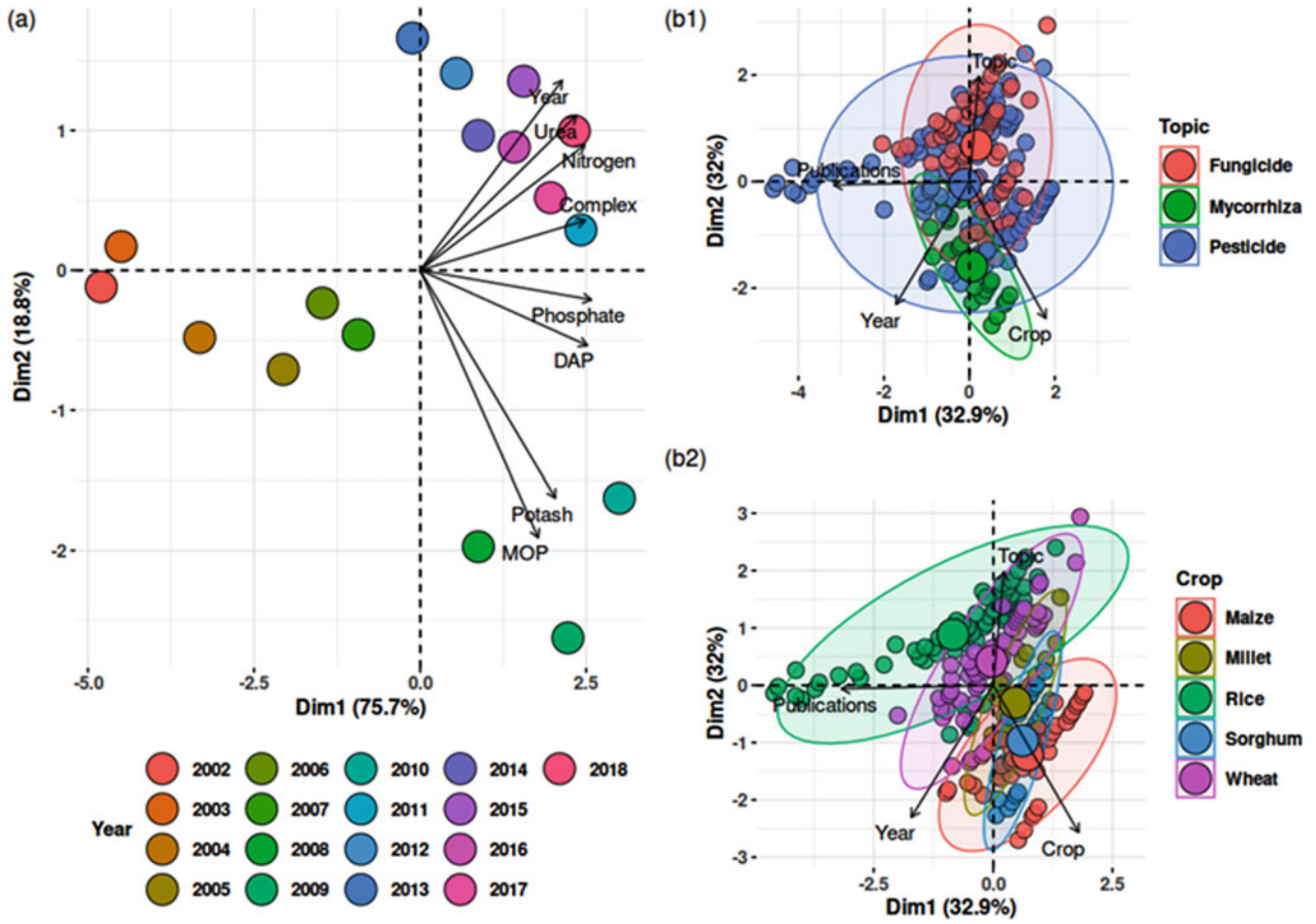

Fig. 4 Principal component analysis showing the correlation between parameters, created with literature search results from PubMed

to increase phytoremediation efficiency (Chibuike 2013). AMF is one of the most critical soil microorganisms that form a symbiotic association with most terrestrial plants, which helps the host plants to uptake and transport phosphorus (P) along with water and other relatively immobile soil nutrients, and promotes plant growth stress tolerance (Yang et al. 2016).

In most environmental conditions, arbuscular mycorrhizal (AM) fungi help to improve plant growth directly by providing access to more nutrients, especially Phosphorus, to the plants. The AM symbiosis improves **disease resistance** in host plants and also suppresses the growth of non-mycorrhizal weeds. In addition, AM fungi help exude photosynthetically derived carbon into the mycorrhizosphere, stabilizing soil aggregates and promoting other soil organisms' growth. A glycoprotein named Glomalin, produced by AM fungi, acts as a protective coating on fungal hyphae which helps to retain water and nutrients from being lost before it reaches the host plant and protects the hyphae from microbial attack. Glomalin also stabilizes soil aggregates by forming a polymer-like lattice on the aggregate surface. AM fungi engineer well-structured soil with the distribution of water-stable aggregates and pore spaces that resist wind and water erosion, improve air and water infiltration, and help plant and microbial growth (Siddiqui and Futai 2008).

The mutualistic relationships between AMF and most of the terrestrial plant species help to adapt different biotic and abiotic conditions, along with the promotion of plant growth, disease resistance, and stress resistance, and hence utilization of this naturally selected relationship for developing an eco-friendly, efficient biological alternative to chemical fertilizers and pesticides for higher productivity in agriculture, horticulture, and forestry is recommended (Shuab et al. 2017).

2.2 AM Fungi a Crucial Global Player in Sustainable Agriculture

The AMF placed under the phylum Glomeromycota are considered to be a less diverse ancient group of root symbionts that originated alongside the first land plants. The AM fungi engage in symbiosis with about 80% of land plants,

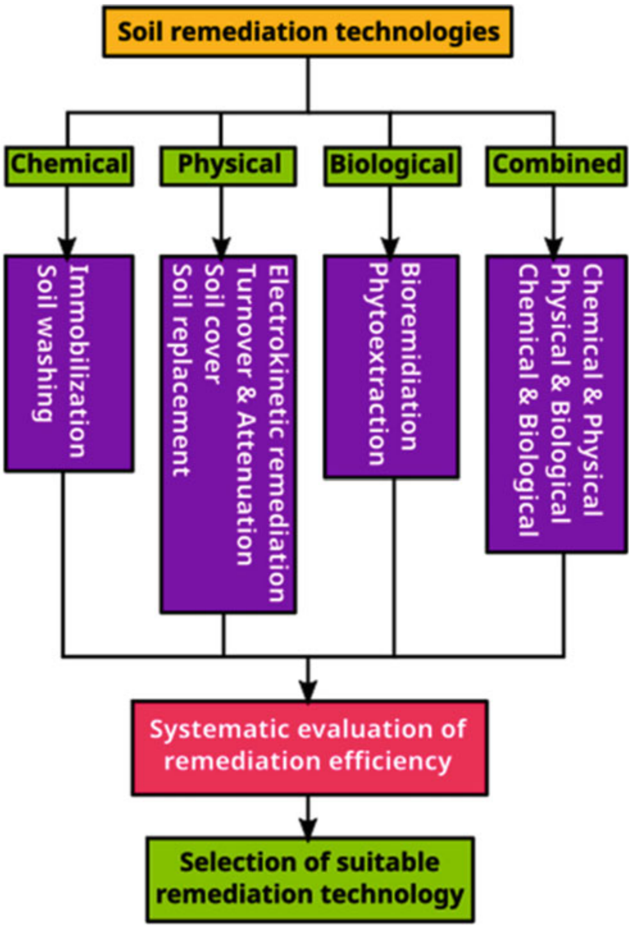

Fig. 5 Flow chart showing summarized general technologies for soil remediation approaches (Redrawn after Wan et al. 2020)

and the group contains about 250 morphologically defined and 350 to 1000 molecularly defined AM fungi. In this relationship, the fungus receives plant-synthesized carbon while exchanging to the plant an increased nutrient, but while considering a wider scale, the symbiosis influences plant–plant interactions and the structure of plant communities affecting agricultural production. To avoid errors, the identification of AM fungal taxa is principally dependent on DNA-based methods and are classified into approximately species-level taxonomic units using clustering algorithms (Davison et al. 2015). Most of the classification approaches generate operational taxonomic units (OTUs) that are either which cannot be readily compared or very difficult to compare between different studies or study areas; hence many geographic regions, biomes, and ecosystems remained entirely unstudied (Davison et al. 2015). Davison et al. (2015) tried to compare the global distribution of AM fungi and their community composition, a summarized figure is given in Fig. 7.

3 AM Fungi in Stress Resistance, Disease Resistance, and Crop Production

3.1 Stress Resistance

Abiotic stresses, such as drought, salinity, extreme temperatures, and exposure to pollutants, result in soil deterioration resulting in reduced crop yield worldwide, and AM fungi helps to increase tolerance to abiotic and biotic stresses (Lenoir et al. 2016). AM fungi promote **salinity tolerance** by enhancing nutrient acquisition, producing plant growth hormones, improving rhizospheric and soil conditions, changing gene expressions, altering biochemical (accumulation of antioxidants, proline, betaine, etc.) and influencing physiology (photosynthetic activity, relative permeability, water relation, nodulation and nitrogen fixation, etc.) (Adamec and Andrejiová 2018). AM symbiosis increases the **resistance of plants to drought** by improving soil structure and stability, which helps increase the water retention of soil (Adamec and Andrejiová 2018). AMF symbiosis protects plants from several **heavy metals** in the soil. Recent studies with electron-dispersive X-ray spectrometry (EDXA) showed that Zn, Cu, and Cd are accumulated in the cell wall, but cytoplasm was essentially found free of these elements, while other studies showed that Glomalin was produced by AM fungi in large quantities and got released into the soil keeping a significant amount of metal immobilized, thus helping host plants from heavy metal stress (Adamec and Andrejiová 2018). AM fungi result in a well-established temperature-related stress defence by alleviating oxidative stress and protecting the photosynthetic apparatus in mycorrhizal host plants, increasing host plants' tolerance (Adamec and Andrejiová 2018).

3.2 Disease Resistance

Mycorrhizal roots are often found with intense fungal colonization, both intercellularly and intracellularly, releasing many molecular signals like chitin oligomers. Plants can recognize these signals, which trigger defence responses in host plants. Pathogens are also well equipped and usually produce inhibitors against plant defence known as effectors. Recent studies found numerous effectors and are predicted to occur in the AMF genomes; assumptions are made that lowering the host defence mechanisms to allow AM fungal infection and colonization of the roots could be the best possible reason for AMF producing those effectors. However, the general defence of mycorrhizal plants remains active to cope with rhizospheric pathogens. Mycorrhizal plants exhibit increased disease resistance, and experiments

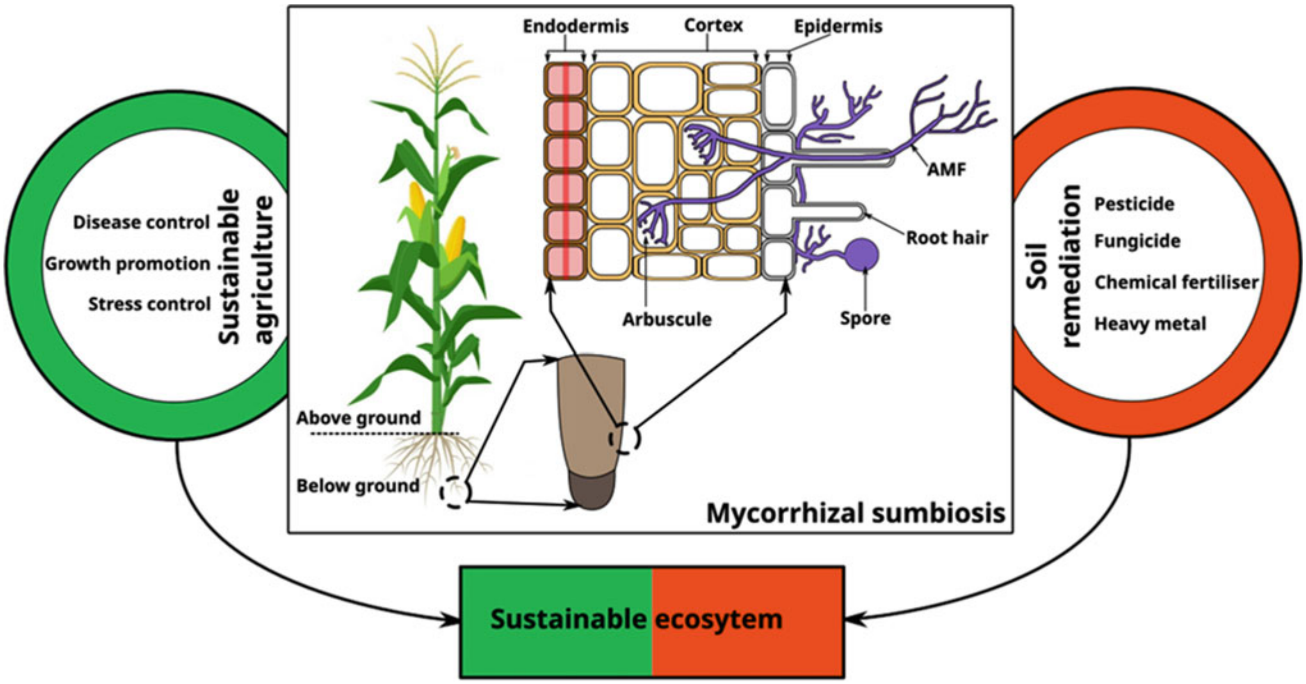

Fig. 6 Mycorrhizal impacts on sustainable agriculture (Redrawn after Chen et al. 2021)

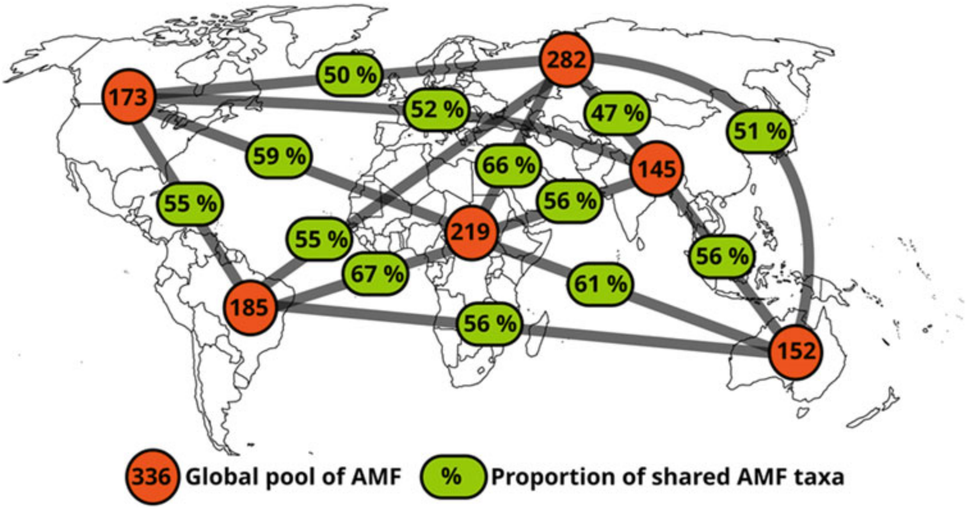

Fig. 7 Comparison of global distribution and similarity of AMF taxa (Redrawn from Davison et al. 2015)

with **split root systems** revealed that the entire host plant gains protection against pathogens; this phenomenon is termed systemic acquired resistance (SAR). Mycorrhizal plants can be primed to react faster and more robust to pathogen attacks by triggering a phenomenon known as induced systemic resistance (ISR) (Chen et al. 2018).

3.3 Crop Production

For enhancing crop production across the globe, chemical fertilizers and pesticides had been used heavily, which led to the degradation of soil health and its biodiversity at all levels sustainable agricultural practices are very less popular that resulted in demolishing agricultural ecosystems throughout the globe, which makes it the uttermost necessity to replace conventional agricultural approaches with cost-effective eco-friendly and sustainable implementation. The strategy of manipulating soil microbial communities and their interactions within the agri-ecosystems and their rhizosphere seems promising. AM enormously enhance transport of inorganic nutrients, micronutrients, the absorption rate of fertilizers; produce a glycoprotein named Glomalin (which helps improve the soil structure); increase water availability to their host plant; resist abiotic stress, disease, pathogen attack; and thus directly or indirectly promote plant growth and produce a greater yield (Sharma et al. 2017).

4 Molecular Insights of Host-Mycorrhizae Association

Successful formation of mycorrhizae with AM fungi relies on the appropriate expression of host genes and their physiological responses. Complex molecular interaction between the host plant and the AM fungus is required for successful root colonization. The plant root exudes Strigolactones (SLs) and stimulates AM fungal spores for germination. SLs originate from the carotenoid biosynthetic pathway. Carotenoid-cleavage-dioxygenase 7 and 8 (CCD7 and CCD8) play significant roles in SL biosynthesis; also, it was reported that plant hormone abscisic acid derived from the carotenoid biosynthetic pathway is involved in regulating SLs production. In turn, the fungal hyphae produce "Myc factors," a class of diffusible molecules that are identified and perceived by plant roots. After perceiving the Myc factor, the host triggers a rapid elevation in the intracellular calcium ion modifying the cellular architecture and transcriptional programming in the root. AM fungi also secrete lipochitooligosaccharides that stimulate the formation of mycorrhizae. The genes encoding germin-like, nodulin 26-like, and other proteins are activated at the appressorium stage and have a crucial role in mycorrhizal colonization. The gene ENOD11 encodes proline-rich protein that helps in activating epidermal cells before and during the formation of pre-penetration apparatus formation (PPA), and at the late stage of mycorrhizal development. Mutants of *Lotus japonicus* were used to identify five genes, namely CASTOR, POLLUX, NUP85, NUP133, and CYCLOPS that are required to develop the mycorrhizal symbiosis (Mohanta and Bae 2015).

5 Conclusion: Need of the Hour

India has been climbing the ladder of higher economic growth during the last two decades, but the growth also inflates the food price because of the very sluggish and uneven agricultural growth. The increase in per capita income increased the food demand significantly, but agricultural production would not cope with the growing demand (Sasmal 2015).

India's economy is growing at 9% and has acquired the third largest place in Asia, behind China and Japan. Green Revolution was armed with high-yielding seeds, canal irrigation, and chemical fertilizers during the mid-1960s and was hailed as the foolproof solution to world hunger. A large country like India requires more than 210 million tons of grain, with a constantly increasing demand to feed its people. India thus desperately needs agricultural diversification and innovative approaches for improving yield (Agoramoorthy 2008). To achieve the goal of producing more than 210 tonnes of grain, we should take some serious steps toward mycorrhiza-assisted remediation (MAR) approaches and re-establishment of the sustainable agricultural ecosystem at a low cost. The AM symbiosis would be a low cost, efficient, sustainable approach having tremendous potential for agricultural production, conservation, and restoration of ecosystems.

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Strategies and Technological Advances for Crop Improvement

Integrated OMICS Approaches to Ameliorate the Abiotic Stress in *Brassica Napus*

Tripti Sharma and Astha Gupta

Abstract

Brassica napus L. commonly known as rapeseed or canola is a member of the family Brassicaceae and developed through hybridization of *Brassica rapa* (turnip) and *B. oleracea* (cabbage). It is an allotetraploid ($2n = 4x = 38$, AACC) that has arisen from diploid genomes of *B. oleracea* ($n = 9$, CC) and *B. rapa* ($n = 10$, AA). The crop is economically important for its edible root, greens, oil yield, biodiesel fuel and food for livestock. Also, it is a rich source of essential fatty acids like linoleic acid (17.11–20.92%), oleic acid (56.80–64.92%) and palmitic acid (4.18–5.01%). Rapid changes in environmental conditions result in abiotic stress for plants, however, they are also prone to attack by pests and pathogens causing biotic stress. Under both the stress conditions, overall production and yield of a crop are compromised. Several pathways regulate the expression of genes involved in the stress response that includes the perception of external stress by plant receptors which elicit production of Reactive Oxygen Species (ROS), secondary messengers (Ca^{2+}/Calmodulin), accumulation of stress-responsive phytohormones and cascade of stress-responsive pathways. There exists an interplay between various physiological and biochemical pathways to produce a stress response. Furthermore, 'OMICS' refers to the integration of genomics, transcriptomics, proteomics, metabolomics and phenomics together with genome editing approaches like CRISPR/Cas9. With the development of OMICS strategies, it has been possible to gain insights into the underlying mechanisms of stress response to decipher the candidate genes, regulatory components like transcription factors, proteins and other metabolites involved. Further, multiple OMICS approaches, i.e. 'Panomics' will unravel new avenues for the production of varieties with improved stress tolerance without compromising with yield and other essential attributes.

Keywords

Abiotic stress • *Brassica napus* • OMICS • Proteomics • Transcriptomics

Abbreviations

ABA	Abscisic Acid
AT	Associative transcriptomics
An	Net photosynthetic rate
CBFs	C-repeat-binding factors
Ci	Internal carbon dioxide concentration
Cys	Cysteine
DEGs	Differentially Expressed genes
DEMs	Differentially Expressed Metabolites
DEPs	Differentially Expressed proteins
DFR	Dihydroflavonol 4reductase
DSI	Drought stress index
E	Transpiration rate or evapotranspiration
FW	Fresh weight
GA	Gibberellin
GEMs	Gene Expression Markers
GP	Germination percentage
GO	Gene Ontology
Gsw	Stomatal conductance to water vapor
iTRAQ	Isobaric tags for relative and absolute quantification-based quantitative proteomic analysis
LG	Linkage Group
LT	Low temperature
MAB	Marker Assisted Breeding
MAS	Marker Assisted Selection
MS	Mass spectrometry
NaCl	Sodium chloride
PAGE	Polyacrylamide gel electrophoresis

T. Sharma · A. Gupta (✉)
School of Agricultural Sciences, Sharda University, Knowledge Park III, Greater Noida, Uttar Pradesh 201310, India
e-mail: astha.gupta@sharda.ac.in

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PRK	Phosphoribulokinase
QTL	Quantitative Trait Locus
RL	Root length
SL	Shoot length
R/S	root to shoot length ratio
PV	Phenotypic Variation
WT	Waterlogging tolerance
SNPs	Single Nucleotide Polymorphisms
RIL	Reciprocal Inbred Line
ROS	Reactive oxygen species
SSR	Simple Sequence Repeates
IP	Intron polymorphic
SAT	Serine Acetyltransferase
SEM	Scanning Electron Microscopy
SPAD	Soil Plant Analysis Development
TRI	Triosephosphate isomerase
Trx	Thioredoxins
WGS	Whole genome sequencing
WTC	Waterlogging tolerance coefficient

1 Introduction

Erratic changes in the climatic conditions globally project stress to the normal growth and development of a plant. These stress conditions are commonly grouped under abiotic stresses, which include heat, drought, cold, waterlogging, salinity and deficiency of nutrients, and biotic stresses that include attack by herbivores and other pathogens. However, approximately 40% of the total world land area is affected by water deficit or drought stress (Gad et al. 2021). This severely affects seed germination, plant development, growth and yield at a significant level. Drought is expected to be a major abiotic stress in future that may affect crop productivity. This has urged scientists to develop varieties capable of adapting to changing environmental conditions without affecting the crop yield. Oilseed crops are most desirable and important for oil production and also have an industrial application that includes sunflower, safflower, soybean, groundnut and Brassica. Therefore, there is a need to focus on these economically significant crops to understand and explore the genes/loci, process and biological pathways under abiotic stress conditions for further improvement.

Several species of genus Brassica belongs to the family *Brassicaceae* that includes *Brassica rapa, B. oleracea, B. carinata, B.juncea* and *B. napus* L. Rapeseed ($2n = 4x = 38$) is an economically important crop that adds to commercial value by producing high-grade vegetable oil, biodiesel fuel and contributing to food for animals. Edible oil obtained from *B. napus* is nearly 12% of the total market worldwide (Paterson et al. 2001). Nearly 50% of the vegetable oil supply in China is met by rapeseed (Ding et al. 2020). Meal cake obtained as a by-product forms a protein-rich food for livestock (Wanasundara et al. 2016). Its agronomic importance is of particular interest for researchers to enhance its yield by genetic improvement.

Drought affects the plant productivity and yield through alterations of physiological mechanisms and metabolic pathways (Zhu et al. 2016). Therefore, making drought-tolerant high yielding varieties have become a major goal for researchers. Likewise, waterlogging is also known to affect rapeseed at the seedling establishment stage as well as at maturity. Significant reduction in yield, i.e. 1.1–34.9%, 6.5–55.5% and 8.7–93.2% has been observed at the seedling stage, seedling establishment stage and at maturity, respectively (Zou et al. 2014). A large number of studies have been carried out to study the physiological effects of waterlogging stress in rapeseed that includes reduced stomatal conductance, photosynthetic rate, etc. (Zhou et al. 1997; Ku et al. 2009). Molecular studies have been carried out to study transcriptional level response to waterlogging (Lee et al. 2014; Zou et al. 2013, 2015). However, there are few studies on genetic mechanisms of waterlogging tolerance (WT).

Soil salinity hinders the growth, development and yield of the plants due to the presence of high concentrations of salts in soil that shows deleterious effects on metabolism, physiology and disturb cellular homeostasis. As a result, Reactive Oxygen Species (ROS) accumulation occurs and oxidative stress is imposed on a plant (Triantaphylides and Havaux 2009). According to reports, 7% of the total land area across the world and more than 20% of the arable land is saline (Flowers et al. 1997; Munns and Tester 2008; Parida et al. 2004). Roots are the primary organs to sense salt concentration in soil and to elicit a response to maintain functionality and relay the signal to shoot for modification in shoot function (Zhao et al. 2013). Hence, understanding the responsive mechanisms to salinity in roots is essential to improve salt tolerance in plants.

Since different abiotic stress conditions pose threats and limitations to the productivity of crop species including *Brassica* (Raza et al. 2021) therefore, developing tolerant varieties has become a major concern to maintain production levels. Researchers have employed various approaches for understanding the underlying molecular mechanisms responsible for tolerance to various stress conditions, to develop varieties capable of withstanding stress without compromising with yield and rather achieve higher yield. Integrated molecular approaches and OMICS are fruitful to explore the candidate genes/loci, proteins, metabolic processes and pathways that are involved in crop improvements (Rana et al. 2020). Some of these approaches are QTL identification, transcriptomics analysis, proteomics and transgenic approach that are helpful to develop the abiotic tolerance varieties.

2 *Brassica napus*: An Oilseed Crop

Brassica napus L. commonly known as rapeseed or canola (2n = 4x = 38, AACC), is a member of the family *Brassicaceae* (Fig. 1). The family *Brassicaceae*, also known as the mustard family includes 419 genera and 4130 species some of which are *Arabidopsis thaliana, B. rapa, B. oleracea* and *Eruca sativa.* Furthermore*, B. napus* is an allotetraploid that has arisen from the hybridization of genomes of *B.rapa* and *B. oleracea*, each contributing genome A and C respectively (Cheung et al. 2009). It is mainly grown in Europe, China and Canada for its edible oil content, industrial derivatives and source of food for livestock. It is an economically important crop that adds to commercial value by producing high-grade vegetable oil, therefore ranking second in global oil production after soybean (Raza 2021). The oil obtained from rapeseed accounts for 30.6–48.3% of the dry weight and is rich in essential fatty acids like linoleic acid (17.11–20.92%), oleic acid (56.80–64.92%) and palmitic acid (4.18–5.01%) (Raza et al. 2021). Brassica plant has a yellow colour flower (Fig. 1) and its inflorescence has a high content of carbohydrates, sugars (fructose, glucose, raffinose and sucrose), essential n-3 fatty acid, α-linolenic acid, n-6/n-3 fatty acids and phytochemicals like tocopherols, lycopene, phenols, flavonoids and also the highest antioxidant properties. It is also a source of biodiesel fuel and contributes to food for animals. Edible oil obtained from *B.napus* accounts for nearly 12% of the total market worldwide (Paterson et al. 2001). Its agronomic importance is of particular interest for researchers to enhance its yield by genetic improvement. Advancement in high throughput sequencing techniques and phenomics has enhanced the reservoir of available genetic information of this species.

Fig. 1 Representation of *Brassica* crops growing in School of Agricultural Sciences, Sharda University, Greater Noida

3 Environmental Stresses

Agriculture produce is greatly dependent on prevailing environmental conditions to the extent that changes in environmental or climatic conditions affect the quality as well as quantity of produce. Fluctuations in climate pose serious stress to the normal growth of a plant. Deviations from optimum temperature, water availability, soil pH are the main factors of abiotic stresses. Major abiotic stresses concerning crop productivity are heat, drought, cold, salinity, alkalinity and waterlogging. According to USDA-FAO reports, salinity and drought stress respectively affect 20% and 26% of agricultural land (American Geophysical Union; https://sites.agu.org). Among the aforesaid abiotic stresses, salt stress is the second most limiting stress for crop production affecting agricultural land mainly in arid and semi-arid regions of the world. Abiotic stress induces adverse effects on plant physiology, metabolism, biochemical and molecular processes.

The impact of several abiotic stresses like temperature (Du et al. 2016) and waterlogging (Lv et al. 2016; Xu et al. 2015) has been studied in several crops including rapeseed (Raza et al. 2021). Changing climate due to advancements in urbanization and industrialization is a major threat to crop productivity. Like other crops, rapeseed is also subjected to stressful conditions that interfere with biochemical, physiological and molecular aspects of plant growth, subsequently affecting the yield. Adopting strategies to produce plants with improved abiotic stress tolerance and enhanced oilseed production is the fundamental aim.

Environmental stress is perceived by sensors or receptors of plants eliciting the downstream components of the stress-responsive pathway (Osakabe et al. 2013). The earliest response upon stress perception involves the production of Reactive Oxygen Species (ROS), Ca^{2+}/ Calmodulin complex and accumulation of stress regulating plant hormones (Mohanta et al. 2018). Further, these relay the stress response via secondary messengers that include Protein kinases (PKs), Protein Phosphatases (PPs), Calcium-dependent protein kinases (CDPKs), Mitogen-activated protein kinase (MAPKs) and CBL-interacting protein kinase (CIPKs) (Mohanta et al. 2018). These secondary messengers work by regulating Transcription Factors (TFs) and the expression of stress-responsive genes. Further, TFs and stress-responsive genes help to adjust or overcome stress by modulating metabolic, biochemical and molecular mechanisms.

4 Integrated '*OMICS*' Approaches for Abiotic Stress Management

OMICS approach is the combined associative analysis of multiple approaches that include genomics, epigenetics, QTL mapping, transcriptomics analysis, proteomics and transgenic study (Fig. 2). This integrated approach would be fruitful to explore the candidate genes/loci, proteins, metabolic processes and pathways which has been explained below:

4.1 QTL Mapping for Identification of Candidate Genes for Abiotic Stress Tolerance

Quantitative traits responsible for plant adaptability to various abiotic stresses need to be genetically evaluated to develop tools or approaches directed towards improving a plant's capacity to adjust to environmental stress and enhance productivity (Gad et al. 2021). Since the response of plants under undesirable environmental conditions is a net result of interactions between genes and environment, identification and analysis of Quantitative Trait Locus (QTLs) give an insight into the quantitative traits that may regulate one or more phenotypic traits. This approach has been already used in common bean (Sandhu et al. 2018), rapeseed (Zhou et al. 2014), peanut (Zhao et al. 2016) and wheat (Wang et al. 2018). A quantitative trait locus corresponding to a particular phenotypic variation could be identified and employed for improving phenotype. Drought tolerance in many crops like *Arabidopsis*, *Oryza sativa*, *Triticum aestivum* and *Glycine max* had been studied using QTL maps.

Germination-related traits under drought stress have been studied in detail in *B. napus* to understand the effect of drought on seed germination (Gad et al. 2021). Germination percentage (GP), root and shoot length (RL and SL), root to shoot length ratio (R/S), fresh weight (FW) and drought stress index (DSI) of these traits were investigated. Based on the QTL maps in *B. napus*, the genetics governing seed germination under drought stress was dissected. Further, the candidate genes in the QTLs linked with drought tolerance at the germination stage have also been identified. This study also highlighted the importance of root-to-shoot length ratio (R/S) in the phenotypic analysis for drought tolerance at the seedling stage. Similar results have been reported in wheat by Dhanda et al. (2004). Therefore, R/S may be regarded as an important morphological trait to study the effect of drought stress. Thirty-nine QTLs were identified for studied germination-related indexes in this study and were compiled into 36 consensuses QTLs. Out of these consensus QTLs, 18 QTLs affected DSI of four traits notably GP, RL, SL and R/S. Many of these QTLs were found clustered on chromosome 1 and chromosome 9. Studies in tomato (Foolad et al. 2003) and wheat (Wang et al. 2009) have also identified QTLs for drought tolerance at seed germination and early growth stages, respectively.

Colinearity between the physical and genetic maps of *B. napus* facilitated the identification of 256 candidate genes, of

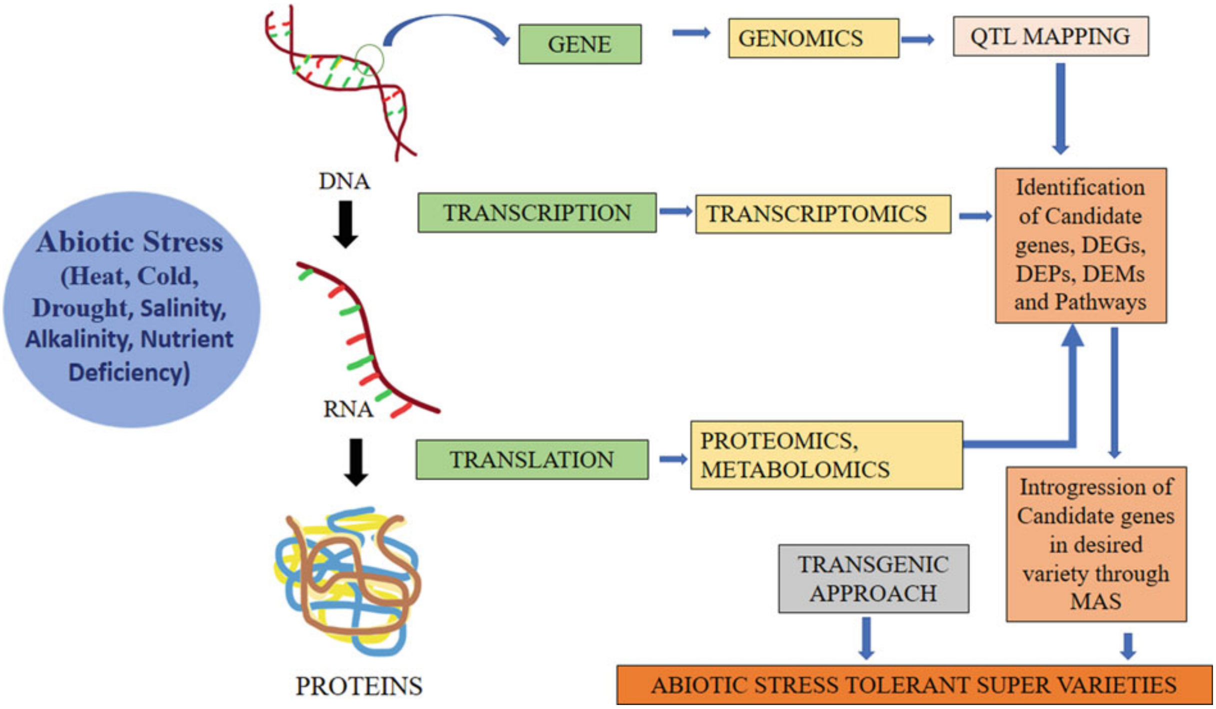

Fig. 2 Interaction of environmental stress (like heat, cold, salinity, alkalinity and nutrient deficiency) with the plant causes alteration in its genetic material, i.e. DNA. These alterations occur in specific genes that are responsible for stress amelioration in plants. According to the central dogma, the changes from DNA are passed on to the RNA transcripts and further to the proteins (expression molecules) and metabolites produced from these genes and transcripts. The development of OMICS techniques including Genomics, Transcriptomics, Proteomics and Metabolomics has allowed understanding the modulations in gene architecture. Genomics allows the identification of the QTLs underlying a specific stress response and furthers the candidate genes in these QTL regions. Transcriptomics studies the changes in RNA transcripts through techniques like SAGE and RNA sequencing to identify the differentially expressed genes (DEGs) under stress conditions which allow for the identification of candidate genes and key pathways through KEGG analysis. The changes at the gene level are expressed via proteins and metabolites which are studied through Proteomics and Metabolomics studies. The differentially expressed proteins (DEPs) and differentially expressed metabolites (DEMs) are identified with the help of these two techniques which further facilitate the identification of important metabolic pathways that play an important role under stress conditions. The candidate genes may be introgressed in desired variety through Marker-Assisted Selection (MAS), likewise, gene manipulation through transgenic approaches may lead to the development of abiotic stress-tolerant varieties

which 128 genes had SNP/InDel variations. Functional annotation of candidate genes highlighted *BnaC03g44440D* gene on QTL qR/S-13-1 to be associated with R/S, having orthologous gene *XERICO* in *A. thaliana*. Upregulation of *XERICO* enhanced tolerance to drought in *A. thaliana* (Ko et al. 2006). Similarly, *A. thaliana* DREB2 gene ortholog *BnaC03g37030D* was also detected in QTL qR/S-13-1. Overexpression of *A. thaliana* DREB2 gene has been reported to increase tolerance to drought in tobacco, apple and *A. thaliana* (Liao et al. 2017; Sharma et al. 2019; Chen et al. 2016).

Salt tolerance-related QTLs, and genes were also determined in *B. napus* (Lang et al. 2017). Further, the structure and expressions profile of the identified candidate genes has been studied and a new set of markers for salt tolerance to be used for Marker-Assisted Selection (MAS) has also been developed. Using 532 of the developed molecular markers a linkage map spanning 1341.1 cm distance was constructed to mine salt tolerance-related loci. A large number of these QTLs (i.e. 45), associated with the morphological and physiological parameters and accounting for a Phenotypic Variation (PV) of 4.80–51.15% were found in $F_{2:3}$ populations. Additionally, QTL—qSPAD5 linked with chlorophyll was found on linkage group 5 and *Bra003640* was identified as the primary gene responsible for salt tolerance. Specific to this QTL region two Intron polymorphic (IP) markers were developed and the QTL location was narrowed down to 390 kb region.

Similarly, cold resistance-related QTLs and candidate genes in the QTL region using *B. napus* genetic map was determined (Huang et al. 2018). Further, they designed cold resistance-related markers to aid in MAS. SSR marker derived genetic linkage map covering 1317.70 cM distance was hence constructed and 11 QTLs (PV—1.09–42.50%) for desired traits were mapped (Huang et al. 2018). The identified QTLs were majorly mapped on linkage group

(LG) 6 (qSPADYL-6, qMDAYS-6 and qSPADYS-6), LG3 and LG7 with a possibility that the same gene controls these QTLs. The study identified two candidate genes viz. *BnaA08g05330D* and *BnaA08g15470D* known to code for cold-regulated proteins (Huang et al. 2018). These genes were similar to stress-responsive proteins, namely, Bra039858 and Bra010579. The development of SSR markers related to cold resistance in rapeseed has helped distinguish cold-resistant varieties from cold-sensitive varieties.

Genetic mechanisms involved in waterlogging tolerance (WT) and corelation between WT and seedling biomass has also been deciphered in *B. napus* (Ding et al. 2020). This study involved the identification of QTLs related to WT and seedling biomass, along with the identification of stable QTLs and associated candidate genes. A total of 1468 Single Nucleotide Polymorphisms (SNPs) were identified in GIL population (GH01 recurrent parent) and 1450 SNPs in ZIL population (ZS9 recurrent parent). Out of the 66 QTLs identified for WT, 20 QTLs were common to both genetic backgrounds and were combined into 6 QTL clusters. Similar findings have been reported for QTLs related to branch number and spikelet number per panicle in Reciprocal Inbred Line (RILs) in rice (Mei et al. 2006). Interestingly, 12 candidate genes were identified in 6 QTL clusters some of which had a role in the degradation of RNA or protein or oxidation–reduction reactions (Ding et al. 2020). Moreover, 6 QTLs, namely, qWTA7-1, qWTA7-2, qWT7-1, qWTC7-2, qWTC1 and qWTC6 were detected in both genetic backgrounds suggesting that they can be applied in MAS breeding programmes for enhanced WT. Molecular mechanisms governing waterlogging stress in important crops like rice (Lasanthi Kudahettige et al. 2007), cotton (Christianson et al. 2010), *A.thaliana* (Voesenek and Bailey-Serres 2013) and rapeseed (Zou et al. 2015) have already been worked out.

4.2 Transcriptomics Analysis to Explore the Differentially Expressed Genes (DEGs)

Transcriptomics provides an understanding of how abiotic stress is regulated in plants, novel genes and other regulatory pathways involved in stress response with the help of transcriptome profiling. Next-Generation Sequencing (NGS) technology, RNA-Seq profiling, microarray, Serial Analysis of Gene Expression (SAGE), Expressed Sequence Tags (ESTs) are some techniques that are generally used for studying gene expression profiles to identify candidate genes, their functional annotation and key regulatory pathways.

Despite, studies on the regulation of abiotic stress response at the transcriptional level in several crops, the understanding of transcriptional regulation to multiple abiotic stress in response in rapeseed is still enigmatic. Therefore, to unravel the molecular mechanisms involved in the response of rapeseed to multiple abiotic stress, the transcriptome dynamics have been investigated. The key genes regulated in response to dehydration, salt (NaCl), cold and Abscisic Acid (ABA) stress in rapeseed have been investigated and 30,908 differentially expressed genes (DEGs) have been identified (Zhang et al. 2019). Out of these, 2568 DEGs were upregulated while 4376 DEGs were downregulated under all the four abiotic stresses whereas,225 upregulated and 295 downregulated genes were associated with Transcription Factors. Core genes identified to be regulated by all four stress conditions were *ERD15, LEA14, RAB18* and transcription factors of ERF, MYBR1 and bZIP families. However, NaCl and ABA stress shared genes belonging to the glyoxalase 1 family (Zhang et al. 2019). Further, Gene Ontology (GO) enrichment of upregulated and downregulated DEGs showed the importance of biological processes like water deprivation, osmotic stress, response to oxygen-containing compounds and lipids in abiotic stress response. This is in concurrence with the fact that a major part of the transcriptome is regulated by four abiotic stresses, namely, dehydration, salt, cold and abscisic acid (Coolen et al. 2016). The two unannotated genes *BnaAnng17910D* and B*naCnng23520DA* identified by Zhang et al. (2019) in their study, correspond to the *Arabidopsis* At1g01470.1 gene (a member of LEA14 family). Both these genes were found to be upregulated in all four stress conditions. Kimura et al. (2003) have reported similar results under cold, drought, light and salt stresses in *Arabidopsis*. Studies have also reported the role of dehydrin proteins in salinity, drought and extreme temperature conditions (Lv et al. 2018; Hara et al. 2013). Upregulation of dehydrin encoding genes points towards their similar roles in rapeseed (Zhang et al. 2019). Induction of genes of the ERD15 family under dehydration conditions has also been reported by Kiyosue et al. (1994). Studies have reported the role of this family as a regulator of many stress-related signaling pathways like salicylic acid-dependent defense pathway, ABA response, drought, wounding and cold (Kariola et al. 2006; Alves et al. 2011; Yu et al. 2017).

Differential cold tolerance in two early maturing rapeseed varieties, subjected to cold shock, i.e. chilling at 4 ºC and freezing at −4 ºC temperatures, followed by cold acclimation has been studied (Xin et al. 2019). With the help of RNA sequencing, a total of 47,328 DEGs were investigated in early maturing varieties of rapeseed. The further analysis enabled the identification of conserved as well as novel genes and pathways involved in eliciting plants' response to cold shock. KEGG pathway analysis provides an understanding of the functions of different genes (Kanehisa et al. 2007). This analysis showed enrichment of primary metabolism, hormone signal transduction pathway (conserved), circadian rhythms and plant–pathogen interaction pathways (novel) in the transcripts found to be differentially expressed. Many studies have reported the importance of hormone signaling pathways in plants' response to abiotic stress (Verma et al. 2016; Sharma et al. 2017).

Since, few studies have been reported on the interplay of regulatory networks involved in cold resistance, at the transcriptional and metabolome levels in rapeseed. The study reported by Jian et al. (2020) analysed the candidate genes and metabolome dynamics in response to low-temperature stress in various rapeseed ecotypes (spring and winter) through metabolome and transcriptome analysis. This study involved five lines of each, spring and winter ecotype and concluded spring ecotype to be comparatively more sensitive to low temperature than the winter ecotype. Several responsive genes and metabolites were identified out of which the common ones exhibited higher fold change in the winter ecotypes. After cold treatment, 28,512 DEGs and 47 Differentially Expressed Metabolites (DEMs) were found in the winter ecotype whereas 25,460 DEGs and 41 DEMS were found in the spring ecotype. Of these, a significant proportion of 46.2% DEGs and a small proportion of 6 DEMs were common in both the ecotypes. Further, 81 of the DEMs corresponded to primary metabolites—sugars, amino acids and organic acids. Identification of a significant number of metabolites and stress-responsive genes in this study by Jian et al. (2020) provides evidence for the presence of a complex regulatory network in cold tolerance in rapeseed. The data obtained in this study also suggests the distinct role of secondary metabolism, ABA, signal transduction, transcription factors and lipids in cold stress in the two rapeseed ecotypes.

Associative transcriptomics (AT) allows researchers to combine transcriptomics with association mapping, to understand the genetics governing complex traits. This strategy has been exploited in a considerable number of allopolyploid crops like wheat and rapeseed to generate markers for Marker-Assisted Breeding (MAB). In a study AT, was used to elucidate the candidate genes linked with freezing or low temperature (LT) tolerance in 123 accessions of *B.napus* (Huang et al. 2020). Considering photosynthetic efficiency to be the key determinant of LT tolerance, the genetic loci for photosynthetic gas exchange parameters including net photosynthetic rate (An), internal carbon dioxide concentration (Ci), stomatal conductance to water vapour (Gsw) and transpiration rate or evapotranspiration (E) were studied. Based on 201 SNPs and 147 Gene Expression Markers (GEMs) detected twenty-two candidate genes were identified. Among these candidate genes, the Cab026133.1 gene (ortholog of *Arabidopsis* AT2G29300.2) coding for tropinone reductase (BnTR1) was found to be linked with transpiration rate. Ectopic expression of this gene enhanced transpiration rate, alkaloid content and LT tolerance in transgenic *Arabidopsis* plants (Huang et al. 2020). Photosynthesis in rapeseed is influenced by C-repeat-binding factors (CBFs), particularly CBF5 and CBF7 improve energy conservation at low temperature (Dahal et al. 2012; Savitch et al. 2005). Among the dehydration-responsive element-binding factors (CBF1–CBF3), CBF-2 negatively regulates response to low temperature while CBF-1 and CBF-3 regulate it positively in *Arabidopsis* (Novillo et al. 2004, 2012). BnTR1 transgenic lines showed enhanced expression of positive regulators and repressed expression of a negative regulator. In concurrence with earlier studies on the accumulation of important metabolites under stress (Thalmann and Santelia 2017), alkaloid levels were found to be high in transgenic lines under control and low temperature conditions in comparison to wild type (Huang et al. 2020).

4.3 Proteomics Approach for Abiotic Stress Tolerance in Brassica Napus

Proteome encompasses the complete set of expressed proteins in an organism at a specific time (e.g. under stress conditions) in a particular cell or tissue. Advancements in whole-genome sequencing (WGS) and Mass spectrometry (MS) approaches have enabled understanding of the proteome of a plant species.

As discussed in previous sections, stress induces alterations at the genome and transcriptome level. Alterations at these levels are expressed in proteins synthesized under stress conditions. To gain an insight into physiological processes involved in salt tolerance at the seedling stage in rapeseed, proteomic analysis was employed to identify the changes that the structural proteins and enzymes undergo when exposed to salinity stress (Dolatabadi et al. 2019). Further, the key proteins, molecular pathways and candidate genes involved in conferring salinity tolerance were determined by LC–MS/MS mass spectrometry. While significant differences (at 5% probability) were observed in various physiological traits studied under salinity stress, the highest and lowest proline content was found in 300 mm and 0 mm concentrations of sodium chloride (NaCl), respectively. Further protein identification by 2-DE and PDQuest software revealed 110 repeatable protein spots. Out of these 110 repeatable spots, 44 spots had significantly changed as determined by the IF index, while 7 spots showed significant change on basis of the student's *t*-test (at 5% probability). Proteins identified by LC–MS/MS mass spectrometry were found to be associated with photosynthesis and energy production. Under salinity stress, spots corresponding to enzyme Phosphoribulokinase (PRK) known to be involved in carbohydrate metabolism (Caruso et al. 2008), alpha and beta chloroplast ATP synthase, Triosephosphate isomerase (TPI), glyceraldehyde 3-phosphate dehydrogenase and RuBisCo was increased in abundance (Dolatabadi et al.2019). Enzyme TPI is known to have a role in energy production pathways like gluconeogenesis, pentose-phosphate pathway and fatty acid biosynthesis (Sharma et al. 2012), glyceraldehyde 3-phosphate dehydrogenase and RuBisCo have a major role in carbon fixation (Guo et al. 2012; Tanou et al. 2009). Contrary to the above-discussed study, previous studies have reported a decline in the activity of Calvin cycle enzymes like PRK as a strategy to cope up with stress (Bandehagh et al. 2011; Podda et al. 2013). However, elevated levels of PRK observed in the study by Dolatabadi et al. (2019) could be an indicator of this genotype's sensitivity to salt stress. A similar decrease in the activity of alpha and beta subunits of enzyme ATP synthase, pivotal for conversion of ADP to ATP along a proton gradient has been reported under salt stress (Kang et al. 2012, Banaei-Asl et al. 2015), specifically in sensitive genotypes (Huseynova et al. 2007). A similar reduction in TPI concentrations has also been reported under stress conditions resulting in the production of free radicals (Sharma et al. 2012). Proline is synthesized as an osmoprotectant in plants exposed to high salt concentrations, its elevated concentrations observed in plants exposed to stress can be attributed to reduced activity of oxidative enzymes (Parihar et al. 2014). Although some studies have documented an increase in the concentration of sodium ion and sodium to potassium ratio in roots as well as shoots on salinity exposure (Dolatabadi et al. 2012), there are several reports on reduced levels of potassium ions in roots and shoots of plants under salt stress has been which can be due to antagonistic relationship between sodium and potassium ions (Parida and Das 2005).

The research gap in the studies concerning proteomic changes in *B. napus* roots under salt stress has been addressed by Kholghi et al. (2019) in their study on screening of 14 genotypes for their comparative salt stress tolerance. Salt stress-responsive proteins were isolated from roots of most tolerant (Safi-7) and susceptible genotypes (Zafar), by Polyacrylamide gel electrophoresis (PAGE) and differentially expressed proteins (DEPs) were determined by. Salt stress resulted in a decrease in dry weight of root as well as shoots and root potassium content in both the genotypes with more pronounced effects in the sensitive cultivar. While the chlorophyll content reduced significantly only in the sensitive genotype, electrolyte leakage and sodium content increased in stressed plants, both being lower in Zafar as compared to Safi-7. Reduction in biomass was attributed to disturbed physiological and biochemical activities under stress, which could have resulted in a reduction in leaf number and leaf area (Craine 2005; Yunwei et al. 2007). Another reason for the decrease in biomass could impede the breaking down of reserved nutrients following their translocation to growing parts (Xu et al. 2008). Salinity can cause burning of plant leaves and other parts resulting in degradation of photosynthetic pigment chlorophyll as evident from the SPAD value indicating reduced chlorophyll content in sensitive genotype. Electrolyte leakage is used as a measure of damage to the cell membrane under stress conditions (Thiaw and Hall 2004). Content of sodium ions was higher in plants exposed to stress which can be the primary reason for reduced plant growth as a high concentration of Na ion interferes with K ion uptake, hindering the activity of various cytoplasmic enzymes resulting in impaired metabolism (Xiong et al. 2002; Hasegawa et al. 2000). Approximately 60 differentially abundant spots were explored and 35 proteins were identified in roots of Zafar and Safi-7 cultivars by MALDI-TOF MS analysis. The occurrence of one protein at more than one spot in the gel can be explained due to post-translational modifications like phosphorylation and glycosylation which change the charge and molecular weight of proteins. The presence of more protein spots in the tolerant cultivar under salt stress in comparison to control conditions shows that the root proteome of the tolerant cultivar (Safi-7) is more active under salt stress. Functional categorization of proteins enabled the identification of proteins involved in the metabolism of amino acids, glycolysis, various heat shock proteins (HSP 70 and HSP90-2), mitochondrial electron transport chain, carbohydrate and nitrogen metabolism and redox regulation.

Waterlogging is known to affect *B. napus* at all developmental stages, significantly. Studies have defined Waterlogging tolerance coefficient (WTC) as a measure of waterlogging tolerance. Transcriptome analysis of the tolerant variety ZS9 under waterlogging stress revealed 4432 differentially expressed genes (DEGs) (Zou et al. 2013, 2014). Quantitative proteomic analysis approach—Isobaric tags for relative and absolute quantification-based quantitative proteomic analysis (iTRAQ) has been employed to determine more stress-responsive genes in the roots of tolerant—ZS9 and sensitive—GH01 cultivar, at germination stage (Xu et al. 2018). This study provided insight into the differentially expressed proteins under waterlogging conditions and if their expression was governed by genetic background.

Roots being the prime organs expected to be affected by waterlogging were phenotypically analysed and showed retarded growth in sensitive genotype under waterlogging conditions. This was further supported by cytological studies showing withered parenchyma cells in sensitive genotypes. Other physiological parameters like length of root and shoot and fresh weight were also found to be affected by waterlogging with more pronounced effects in the sensitive GH01 genotype, suggesting better adaptation of ZS9 to waterlogging stress. Several studies have reported that ZS9 has a better ability to grow and recover from waterlogging in field conditions at germination, seedling and maturity stage (Chen et al. 2006). Further, protein analysis through iTRAQ lead to the identification of 7736 proteins (Xu et al. 2018), of which 700 proteins showed varied levels of expression. The proteins that were commonly expressed at different time intervals were enriched with gene ontology studies. GO analysis showed these proteins to be involved in stress response, oxidation–reduction processes, transcription and hormone-induced responses. Some proteins were overlapping between the two genotypes having the same or different fold change tendency. KEGG pathway analysis of significantly accumulated or reduced proteins showed proteins enriched in hormone signal transduction, ribosomes, metabolism of starch and sucrose, oxidative phosphorylation, ribosomes, plant–pathogen interaction and amino acid biosynthesis. Proteins involved in the ethylene signaling pathway, phosphorylation of proteins and metabolism were also detected in both genotypes. Ethylene has been reported to be critical for waterlogging stress response in plants (Muller and Munne-Bosch 2015) as it influences the formation of aerenchyma or adventitious roots (Eysholdt-Derzso and Sauter 2019, Yamauchi et al. 2016). Earlier studies have also reported the importance of phosphorylation-mediated signaling mechanism in abiotic stress response as well as plant growth and development (Bonhomme et al. 2012, Hashiguchi and Komatsu 2016, Kline et al. 2010, Vu et al. 2018, Zhang et al. 2014).

The role of RGA homolog BnaA6.RGA in drought response has also been demonstrated (Wu et al. 2020). It has been found to act as a positive regulator of tolerance to water deficit by increasing sensitivity to ABA and resulting in a decrease in water loss due to stomatal closure (regulated by BnaA6.RGA) under drought conditions. Further, this homolog is also found to interact directly with *Arabidopsis* ABF2 ortholog BnaA10.ABF2 and regulate the expression of other drought-responsive genes. This study also highlighted the importance of Gibberellin (GA) and ABA pathway crosstalk in elucidating stress response. Gain of function mutant bnaa6.rga-D exhibited greater drought tolerance along with a hypersensitive response of its stomatal closure to ABA (Wu et al. 2020). In contrast, the quadruple mutant bnarga exhibited reduced tolerance to drought and reduced hypersensitive response to ABA. However, no significant difference in drought tolerance was observed in wild type and single BnaRGA mutant, indicating functional redundancy in BnaRGA genes involved in this process. Physical interaction between ABA signaling transcription factor BnaA10.ABF2 and BnaRGAs were also found. Further, expression levels of BnaC9.RAB18—a drought-responsive gene was enhanced by protein complex BnaA10.ABF2-BnaA6.RGA.

4.4 Implementation of Transgenic Technique for Abiotic Stress Tolerance

The transgenic technique has gained momentum for the development of stress-tolerant varieties. These methods rely on the genetic manipulation of genes involved in regulating the stress response. However, investigation of the transgenics under stress conditions and understanding the response of manipulated genes at a physiological and cellular level remains a challenge.

In an attempt to produce transgenic *B. napus* oilseed plants with improved tolerance to salt stress, *Arabidopsis* genes coding for cytosolic h-type Thioredoxin (Trx) proteins, namely, AtTrx-h2 and AtTrx-h3 were isolated to produce transgenics overexpressing Trx proteins (Ji et al. 2020). Thioredoxins (Trxs) are a group of proteins with antioxidant activity, encoded by a multigene family ubiquitously. H-type Trx proteins found in *Arabidopsis* are localized in the cytoplasm as well as other subcellular organelles. Their primary function is to elicit a response to pathogen attack and abiotic stresses. Transgenic lines overexpressing genes coding for cytosolic h-type Trxs (viz. AtTrx-h2 and AtTrx-h3) were generated. It was observed that transgenic lines expressing AtTrx-h2 in heterologous fashion had improved tolerance to saline conditions as evident from their chlorophyll content and higher fresh weight when grown in 50 mm NaCl. These plants also showed reduced levels of hydrogen peroxide and higher activity of enzymes with antioxidant activity like superoxide dismutase, catalase and peroxidase.

The role of flavonoids, including anthocyanin, has been reported in protecting plants from oxidative stress caused due to various abiotic stresses. In another study designed to assess whether enhanced anthocyanin levels improved salt tolerance in rapeseed, *Arabidopsis* gene coding for dihydroflavonol 4-reductase (DFR) was expressed in an ectopic manner (Kim et al. 2017). Shoots of transgenic *AtDFR-OX* displayed increased levels of transcripts of DFR, which was directly proportional to the accumulation of anthocyanin. *AtDFR-OX* shoots were found to have a lesser accumulation of reactive oxygen species (ROS) under high mannitol and NaCl concentration as compared to wild type showing the successful integration of the DFR gene in these transgenics. However, it was also found that shoots of the transgenic plants had improved tolerance to salt stress and higher chlorophyll quantities when compared to wild type grown under the same conditions.

Enzyme Serine Acetyltransferase (SAT) acts to limit Cysteine (Cys) biosynthesis in a rate-limiting manner (Rajab et al. 2019). This enzyme from tobacco is insensitive to feedback mechanism. NtSAT4 gene from tobacco was used in a study to create overexpression constructs targeted for expression in plastid, mitochondria and cytosol (Rajab et al. 2019). In this study, the *NtSAT4* gene was cloned and overexpressed in *B. napus* using cotyledonary explants via tissue culture technique. The gene was targeted for expression in cytosol, mitochondria and plastid. Experiments aimed to obtain stable transformants overexpressing the gene of interest and hence enhancing plants' ability to produce glutathione in response to heavy metals. To obtain stable transformants, various transformation techniques like tissue culture and floral dip methods were used, with a specific combination of phytohormones to induce callus, root and shoot formations accordingly. Shoots could be successfully regenerated on MS media supplemented with 3 mg/L BAP while 3 mg/L IBA contained in ½ strength MS media could induce root formation in OSCAR cultivar. The transgenic lines were selected on a selection media with a 50 mg/L concentration of antibiotic Kanamycin. Integration of NtSAT4 was confirmed by setting up PCR using gene-specific primers. Further, acclimatization of transgenic lines was done successfully by transferring them to soil and glasshouse environments. These lines exhibited the enhanced capacity to produce glutathione and cysteine conferring plant tolerance to a variety of abiotic stresses including heavy metals.

Cuticular wax is an important component of plant defense machinery for combating biotic as well as abiotic stresses, mainly water loss. Therefore, genetic manipulation of genes involved in the synthesis and modification of plant cuticular wax can reduce water loss and enhance efficiency to withstand water deficit. The synthesis of cuticular waxes is genetically controlled. The genes involved in their synthesis and modification are members of the KCS gene family having homologs in *A. thaliana,* namely, KCS1and CER1. In a study, homologs of KCS1 and CER1 genes in *B. napus viz.* BnKCS1-1, BnKCS1-2 and BnCER1-2 were isolated to characterize their expression patterns in cultivars (Zhongshuang 11-ZS11 and NoWAX) with varying wax traits (Wang et al. 2020). These genes were overexpressed in *B. napus,* to study their effects on the structure and components of cuticle wax and further interpret the importance of modifications in cuticular wax on plant growth and development as well as response to water deficiency in soil (Wang et al. 2020). The findings of this study by Wang et al. (2020) suggested that ABA and drought stress both induced formation BnKCS1-2 and BnKCS1-1 transcripts whereas BnCER1-2 transcripts were formed only under drought. On the other hand, the application of methyl jasmonate or exposure to cold resulted in retarded expression of all three transcripts. Transgenic lines with overexpression of these genes exhibited enhanced deposition of cuticular wax. Whereas, in non-transformed lines, BnKCS1-2 and BnKCS1-1 overexpression resulted in accumulation of high amounts of secondary alcohol, alkanes and aldehydes and reduced amount of ketones. BnCER1-2 overexpression in non-transgenic lines resulted in reduced levels of secondary metabolites, increased levels of alkanes and no pronounced effects on other components of wax. Transgenic lines showed deposition of wax crystals in much higher density due to overexpression of the three genes, as observed in Scanning Electron Microscopy (SEM) studies (Wang et al. 2020). These lines also showed improved tolerance to drought conditions and a lower water loss rate.

5 Conclusion

Frequent changes in climate conditions that occur due to global warming are a major concern in the present scenario. The rapidly changing environment in the form of abiotic stress interferes with the normal growth and development of crop species including rapeseed, globally. As a consequence, the yield of several crops is drastically affected due to disturbance in physiological processes and cellular homeostasis of the plant. This causes impediments in meeting up the demand of food supply. To overcome these hurdles and maintain the requisite supply and demand chain, it is essential to understand the mechanism behind stress response. This would help identify the key players governing the ability of the plant to withstand a stressful environment. Manipulating these components of the molecular machinery of plants, using appropriate biotechnological tools can help develop varieties with desirable traits like abiotic tolerance and better or enhanced yield.

6 Future Thrust

As discussed in this chapter, 'OMICS' tools like genomics, transcriptomics and proteomics along with transgenic approaches have enabled the identification and development of useful genomics resources. The complex network of biological pathways governing response to various abiotic stresses in rapeseed has been unravelled to a great extent. Further, the status of the plant transcriptome, metabolome and proteome as modified under stressful environments has also been understood. With the help of QTL mapping and transcriptome analysis, the candidate genes and regulatory pathways involved in stress response have been deciphered. Identification of differentially expressed proteins through proteomic studies can help target potential proteins for better stress response. These genomic resources can lay the foundation for further work to gain in-depth knowledge of the molecular mechanisms. However, abiotic stress tolerant and high yielding rapeseed variety may be developed by amalgamation of available potential 'OMICS' techniques and 'Panomics' approach.

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Proteomics—A Powerful Tool for Understanding Saline Stress Response in Germinating Seed

Anup Kumar Sarkar and Sanjoy Sadhukhan

Abstract

Understanding the mechanism of seed germination in salt-affected habitats is very helpful to develop outstanding salt-resistant varieties with high seed vigour. Under a stressful condition, such as salinity, the efficiency of seed germination, and the development of a viable seedling, the critical drivers of plant species proliferation is hampered. Like other organisms, plants also rapidly adapt to environmental changes by modulating their protein content or activity at any stage of life from seed germination to its maturation. In the present scenario, proteins may be considered as the main effectors of biological responses to specific environmental conditions. For this reason, proteomics has become a powerful technique in biomolecular research and its uses as a tool for protein and peptide quantization is widely recognized by many researchers of Biology and Chemistry. In addition, it can also be used to quantify the activity of signaling and metabolic pathways in a multiplex and comprehensive manner. For a better understanding of how germinating seeds respond to salt stress, several researchers examined the changes that occurred in the proteome of various seeds during germination. Recently, several proteomic analyses of seed germination had been applied in several crop plants for the improvement of salt resistance or salt tolerance. In this chapter, the authors have summarized the development in proteomic investigations of seed germination under salt stress. Contemporary issues and future perspectives were also explored, which may prove useful in future research.

Keywords

Comparative proteomics • Imbibition • Post-translational modifications • Protein interactions • Salinity • Seed germination

Abbreviations

2-DE	Two-dimensional electrophoresis
2D-DIGE	Two-dimensional difference gel electrophoresis
2D-LC	Two-dimensional liquid chromatography
ABA	Abscisic acid
CBP	Calcium-binding protein
CBB	Coomassie brilliant blue
DNA	Deoxyribonucleic acid
GA	Gibberellic acid
HSPs	Heat shock proteins
LEA	Late embryogenesis abundant proteins
mM	Millimolar
IEC	Ion-exchange chromatography
NaCl	Sodium chloride
MALDI-TOF	Matrix-assisted laser desorption/ionization-time of flight
Mpa	Mega Pascal
mRNA	Messenger RNA
MS	Mass spectrometry
MudPIT	Multidimensional protein identification technology
PAGE	Polyacrylamide gel electrophoresis
RNA	Ribonucleic acid
ROS	Reactive oxygen species
SAS	Statistical analysis software
SDS	Sodium dodecyl sulfate
SDS-PAGE	Sodium dodecyl sulfate–polyacrylamide gel electrophoresis
SEC	Size exclusion chromatography
SPSS	Statistical package for the social sciences
SSPs	Seed storage proteins

A. K. Sarkar
Department of Botany, Dukhulal Nibaran Chandra College,
Aurangabad, Murshidabad, West Bengal 742201, India

A. K. Sarkar · S. Sadhukhan (✉)
Plant Molecular Biology Laboratory, Department of Botany,
Raiganj University, Raiganj, Uttar Dinajpur, West Bengal 733134,
India

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1 Introduction

Proteomics is an emerging discipline of biological science that is widely used for the quantitative and qualitative characterization of proteins as well as their interactions on a gene scale. Since its discovery, it has been extensively investigated to gain a better understanding of the biological process, including gene expression, post-translational modification, and interaction of proteins with other protein or non-protein molecules (Singh et al. 2018). Integration of proteomics in experimental plant science promotes a better understanding of metabolism related to many biological processes. It is a fact that the majority of the biological processes in plants are characterized by one or a few specific sets of proteins. The function of each protein depends on its molecular structure, subcellular localization and post-translational modifications. Proteomics is simply defined as the study of proteomes whereas the term "proteome" can be defined as the overall protein content of a cell that is characterized by its localization, interactions, post-translational modifications, and turnover, at a particular time (Aslam et al. 2017). Proteomics, in other words, is the study of a cell's entire protein composition, including its expression, structure, functions, interactions, and modifications at each given stage. Advancements in proteomics have been widely applied to the study of seed germination in recent years. Understanding of the physiology and metabolism of germination at the cellular and molecular levels has evolved at a rapid rate during the last decade due to outstanding advancement. Proteomic approaches have complemented experimental efforts to catalogue many physiological events of plants including germination events. Each stage of the seed-to-seed cycle of plant development including seed germination is characterized by a specific set of proteins (Oracz and Stawska 2016).

Proteins as the basic building block of cell and subcellular structure directly assert the potential function of genes via enzymatic catalysis, molecular signaling, and biophysical interactions in germinating seeds. Germination of seeds is a multistage process requiring the coordinated expression of numerous genes in different tissues (Potokina et al. 2002). Several investigators opined that changes in the gene expression at the transcript level do not always result in changes in protein level, and hence modifications of the proteome should be examined, as proteins act as direct plant response agents against stress (Gygi et al. 1999; Bogeat-Triboulot et al. 2007). Proteomic advancements have enhanced genetic and molecular understanding of responses in developing seeds under salt-induced stress.

2 Seed Germination

During seed germination, the quiescent embryonic cells shift into a metabolically active state in which complex biochemical and physiological changes occur (Sheoran et al. 2005). Germination commences when seeds are immersed in water, followed by disintegration of the endosperm cell walls, enzymatic digestion of starch and proteins to provide nutrients for the growing plant, and emergence of the radical from the seed (Osama et al. 2021). Both the embryo and endosperm have a crucial role in seed germination. From the embryo, initially the radical protrudes, followed by plumule, and eventually develops into a new plant. On the other hand, the endosperm provides nutrients to the growing embryo for seedling development. The embryo contains the vast majority of the genetic information that governs germination. Systematic interaction between embryo, seed coat, and intermediate endosperm is a prerequisite for successful germination. Following imbibition, the substrate and energy starvation influence the embryo to produce phytohormones, primarily Gibberellic Acid (GA), which initiates a signaling cascade that leads to the synthesis of α-amylases and other hydrolytic enzymes (He et al. 2015).

Proteins and peptides play a crucial role in regulating every step of seed germination starting from imbibition to autotrophic seedling formation. Imbibition of the seed with watermarks is a major change in protein metabolism. Large amounts of storage proteins are accumulated for use as an initial source of reduced nitrogen by the germinating seedling. For most plants, the transition from seed to seedling stage marks the transition from the stage of the life cycle most impervious to the stage most susceptible in respect to external environmental factors like drought, salinity, heat, water logging, etc. (Downie 2001). Seeds and young seedlings are frequently confronted with salinity than vigorously growing plants because germination usually occurs in the uppermost soil layers, which is the site with the highest accumulated soluble salts (Almansouri et al. 2001). The molecular mechanism of salt response during the germination stage is extremely complex. Promotion of fast germination under stress may seem to be desirable, although it exposes the newly sprouted seedling at risk of death if the adverse conditions persist or increase; as the embryo is exposed to the external environment with all of its reserves already depleted (Nanda et al. 2019). Seeds must adjust their physiology and development to assure their survival under changing conditions within a time range. Seed germination is typically associated with numerous metabolic, cellular, and molecular events, the majority of which are directly or indirectly dependent on proteins. During seed germination, which is a multistep process, proteolytic enzymes are required to break down the seed protein (Shutov and Vaintraub 1987). Different proteins, such as catalytic protein, germination-stimulating hormone, detoxification and defence-related proteins, and proteins involved in cell wall reinforcement, all of which stimulate seed germination (Dogra et al. 2013). To a certain extent, the protein content of seeds is influenced by the activity of the translation machinery, which constantly changes based on physiological state (Oracz and Stawska 2016). Thus, the integration of proteomic technologies is an effective strategy to promote a better understanding of mechanisms in response to environmental stresses.

Germination involves several events, including cell elongation, degradation of proteins, macromolecular synthesis, respiration, alterations of subcellular structure. Several researchers have reported the activity of some key enzymes of glycolysis, pentose phosphate pathway (PPP), tricarboxylic acid cycle (TCA cycle), and amino acid metabolism during germination. Metabolism-related proteins, particularly those involved in major and minor carbohydrate metabolism such as glycolysis, TCA cycle, fermentation, gluconeogenesis and glyoxylate cycle, and pentose phosphate pathway (PPP) are considered as the most abundant proteins in the germinating seeds (He and Yang 2013). Germination-specific proteins in the embryo that are catabolic and associated with the mobilization of food reserves from the endosperm also account for a significant percentage of seed proteins. Endogenous factors such as the proteinaceous plant hormones like abscisic acid (ABA) and gibberellins (GA) play a significant role in regulating early seed germination by countering the process of dormancy, which is a barrier to the completion of germination of a mature, intact, viable seed (Tuan et al. 2018). Proteins are essential for cellular function, and proteomics technology is an effective method for studying the total expressed proteins in an organism or cell type at a specific time. Cells and subcellular components of germinating seed must deal with a multitude of stimuli in the biotic and abiotic environment, which disrupt the water balance in the cytosol and affect several metabolisms, influencing the success of germination. The role of proteins in plant stress response is crucial since proteins are directly involved in shaping novel phenotypes by adjustment of physiological traits to an altered environment (Kosova et al. 2018). Protein-related features are widely recognized as a tool for studying the effect of abiotic stress because, in most cases, proteins can be altered by translocation or degradation or post-translational modification (Li et al. 2020; Ramazi and Zahiri 2021; Matamoros and Becana 2021). Numerous research studies have examined the use of proteomics to solve many unexplained aspects of seed germination. With the increasing availability of genome sequence data and the advancement of mass spectrometric (MS) technology, proteomics has been widely applied in analysing the mechanisms of the seed germination process under various abiotic stresses such as salinity and has proven to be very powerful. Plant abiotic stress response depends greatly on proteins for two reasons: firstly, by modulating physiological features to adapt to changes in the environment, proteins play a direct role in the establishment of novel plant phenotypes; and secondly, proteins are the critical executors of cellular mechanisms and key players in the maintenance of cellular homeostasis (Liu et al. 2015).

3 Salinity and Its Impact on Seed Germination

Soil salinity is a significant issue in agriculture, particularly since, the majority of crop plants have low salt tolerance. It is one of the major factors that are harmful to most plants due to its side effects in the form of osmotic stress and ion toxicity on growth and development (Ismail and Horie 2017). In general, the total amount of dissolved mineral salts in water and soil imparts salinity. These salts comprise electrolytes of anions (majorly CO_3^{2-}, SO_4^{2-}, Cl^-, NO_3^-, and HCO_3^-) and cations (majorly Ca^{2+}, K^+, Mg^{2+}, Na^+). As low as 40 mM NaCl generates an osmotic pressure of 0.2 MPa and this stress manifests shoot growth arrest and senescence in most salt-sensitive plants (Munns and Tester 2008). Salt induces osmotic stress by declining water potential and water availability in soil, which leads to dehydration at the cellular level; and is strongly associated with the production of reactive oxygen species (ROS). They are highly reactive and cytotoxic, which reacts with vital biomolecules, such as lipids, proteins, and nucleic acid (Abou Zeid and Hassan 2011; Kang et al. 2014).

Salt tolerance is a complex trait that involves different aspects of the genetic architecture, biochemistry, and physiology of the plant (Gandullo et al. 2021). Some plants involve the activation of various stress-regulated genes via integrated cellular and molecular responses that help cells to adapt and achieve cellular homeostasis (Jones 2007; Latif et al. 2016). Salt stress is developed from an excessive concentration of salts, especially sodium chloride (NaCl) in soil. Root triggers several cellular and molecular events in response to salt stress, such as (a) changes in carbohydrate and energy metabolism, (b) alterations in ion homeostasis and membrane trafficking, (c) ROS scavenging, and (d) dynamic reconfiguration of cytoskeleton and redistribution of cell wall components (Ghosh and Xu 2014). To survive, plants must respond appropriately to fluctuating environments both internal and external and these responses result from intricate coordinated changes in the quantities and activities of biomolecules including DNA, RNA, proteins, and other metabolites. The synthesis, modification, localization, and degradation of proteins in the cells are crucial for plants to survive under stressful environments, in which post-translational alteration of proteins increase the variations of gene products and influence almost all cellular processes (Fulzele and Bennett 2018).

Several workers have isolated and identified a large number of diverse proteins, which play pivotal roles in sustaining homeostasis and attaining stress resilience in plants (Kosova et al. 2018). Proteins involved in signal perception were found to be more abundant during the early stages of salt stress (Zhao et al. 2013). These include (a) receptors in the plasma membrane (PM) or the cytoplasm, (b) G-protein, (c) Ca^{2+} signaling protein or calcium-binding proteins (CBP), (d) phosphor-proteins involving activation of a kinase cascade, and (e) ethylene receptors (Ghosh and Xu 2014). For a particular protein-mediated trait, the total amount of that protein present under any specific conditions can affect its functional activities and the phenotype of its respective biological system. To fully understand cellular machinery, it is just not enough to identify the proteins that exist; it is also necessary to delineate all of their interactions. Recently described, networks of the protein interactions reflect a higher level of proteome organization than basic representations of protein networks (Cong et al. 2019). Several proteomic-based investigations have provided new insight into plant responses and adaptation against high salinity. Protein profiling or mapping of a cell, tissue, plant parts, or whole plant is critical for a functional recognition of each protein and its metabolic pathways in salt-induced stress conditions because it is a valuable natural genetic resource that may aid in the discovery of genes and gene products conferring tolerance to various stressful situations like salinity (Fig. 1).

The field of proteomics may be divided into three broad areas—*expression proteomics* (also called differential proteomics), *functional proteomics*, and *structural proteomics* (Graves and Haystead 2002). *Expression proteomics* is concerned with the study of overall changes in protein expression and provides information on specific changes in a biological system under various physiological and stress-induced conditions. *Functional proteomics* explains the understanding of the protein functions as well as unravels molecular mechanisms within the cell that depends on the identification of the interacting protein partners. Such proteomics often provides a detailed description of the cellular signaling pathways. *Structural proteomics* aids in understanding the three-dimensional conformation and structural complexities of functional proteins. Structural prediction of a protein is performed by directly determining the sequence of amino acids or from the gene with a method called homology modelling. With the help of this technique, it is possible to recognize all the proteins present in a complex system such as cell membranes, ribosomal subunits, and membrane-bound cell organelles and also to characterize all the protein interactions that are possible between these proteins and protein complexes (Agrawal et al. 2011; Fox 2012; Aryal et al. 2014).

4 Journey and Major Achievements of Proteomics

The terms "proteome" and "proteomics" were coined by Marc Wilkins and colleagues in 1994 (Ezzell 2002). Ever since, the field of proteomics has flourished at a fast pace, with significant advancements in the original methods/technologies making proteomic technologies more autonomous, high-throughput, robust, and dependable. Proteomics is a technical term that refers to the study of proteins using mass spectrometric (MS) technology. On the other hand, the proteome of an organism is technically defined as the sum of the proteins in existence either throughout its life cycle or in response to changing conditions or a specific abnormal state. In other words, it is a complex system, representing a result of interconnected dynamic properties of individual proteins (Larance and Lamond 2015). Proteomics has the potential to complement the information generated by genomics. Proteomics-based technologies are used in a variety of research settings, including the detection of various diagnostic markers, mechanisms related to pathogenicity, changes in expression patterns in response to various signals, and the interpretation of functional protein pathways in various diseases (Aslam et al. 2017). Seed proteome comprises a diverse collection of functionally distinct proteins that undergo highly dynamic qualitative and quantitative changes to meet seed requirements throughout the development and germination. Many post-translational changes, chemical interactions, and a plethora of proteins generated from alternative mRNA splicing contribute to the dynamic and complex nature of the seed proteome (Rajjou et al. 2011; Chaudhary et al. 2019; Tappiban et al. 2021). Proteomics is more reliable than transcriptomics to study plant stress responses as the transcribed gene may be differentially translated or even may not be translated. The primary goal of proteomics is to make an inventory of all proteins encoded in the genome and to investigate protein features such as expression level, post-translational alterations, and the ability to interact with other protein and non-protein molecules (Chandrasekhar et al. 2014; Feist and Hummon 2015). The generations of proteomics platforms (gel, label, gel-free/label-free, targeted) that have appeared in the last two decades are being exploited in describing protein profiles, post-translational modifications, and interactions (Komatsu and Jorrin-Novo 2021).

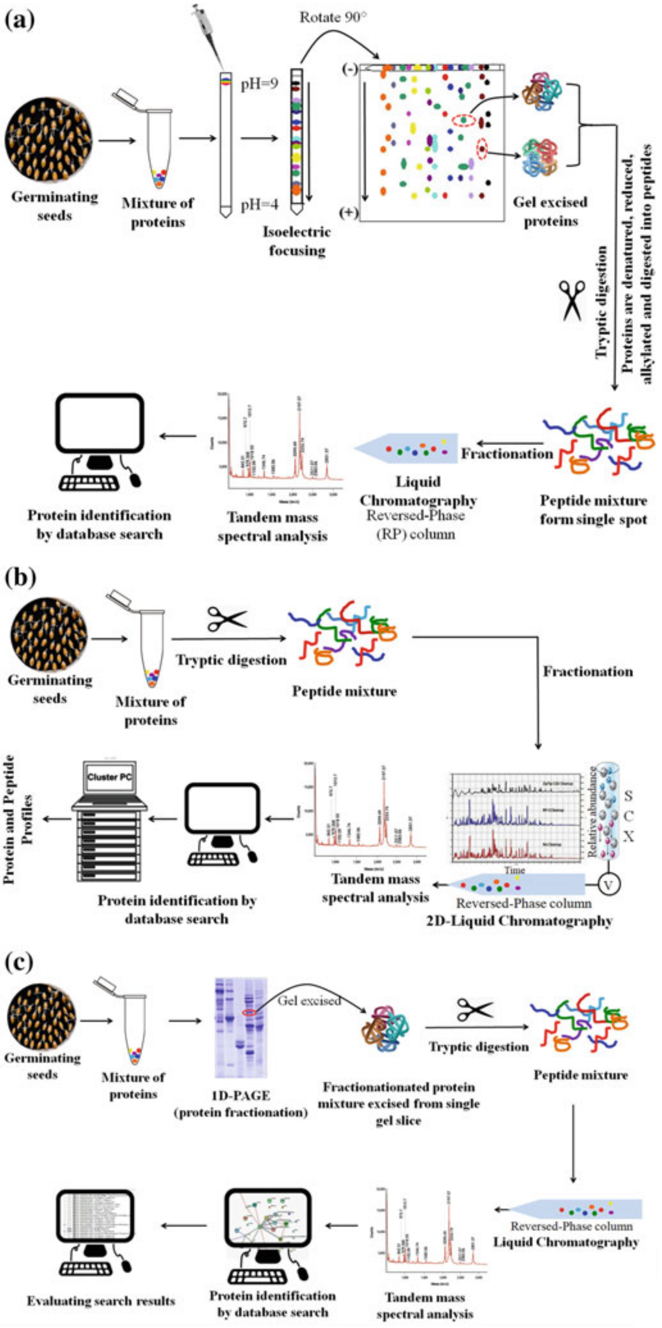

Fig. 1 Different methods of identification of proteins. **a** Proteomic workflow based on Mud-PIT, **b** 2D-liquid chromatography-based proteomic workflow, **c** 1D-Gel-LC–MS/MS-based proteomic workflow

5 Tools and Techniques Used in Proteomics

Proteomics is quite a complicated technique since it entails the analysis and categorization of the entire protein signatures of a genome. Following this, proteomics seeks to characterize the proteome qualitatively and/or quantitatively with a thorough understanding of the nature and complexity of a specific research target (Smolikova et al. 2020). Proteomics is significantly more difficult than genomics, since, although an organism's DNA remains relatively constant, the proteome differs in a spatio-temporal fashion in a cell. Distinct genes are expressed in distinct cell types, which means that the basic set of proteins synthesized in a cell even must be determined for a better understanding of proteomic research. The most common technologies used in proteomics are two-dimensional sodium dodecyl sulfate–polyacrylamide gel electrophoresis (2D SDS-PAGE) for protein separation, mass spectrometry (MS), and protein identification through manual interpretation or database correlation of mass spectra. The simulation of such steps is required for a successful proteome experiment, but it is dependent on precise knowledge of the factors affecting each step (Droit et al. 2005; Chandrasekhar et al. 2014; Mitra et al. 2016). With the advancement of technology, it is now possible to identify a considerable portion of a proteome's proteins. Proteomic techniques have become increasingly popular in recent years due to significant advances in sensitivity, accuracy. There are a few steps in proteomic analysis to identify a biomarker.

5.1 Collection, Pretreatment, and Preparation of the Samples

Proteome analysis in plants entails analysing proteins from a range of sources, including cell suspension cultures, various organs, tissues, organelles, and subcellular compartments. There is no universal protocol for protein extraction and solubilization due to the high level of diversity in source material and huge variations in composite proteins in contexts of cellular distribution, molecular weight, isoelectric point, hydrophobicity, and post-transcriptional modifications (Leimgruber 2005). Furthermore, in comparison to animal and fungal tissues, most plant tissues have low protein concentrations and high endogenous protease concentrations, which severely impede downstream protein separation and protein detection procedures (Hurkman and Tanaka 1986; Rose et al. 2004; Westermeier and Marouga 2005; Carpentier et al. 2008; Jorrin-Novo et al. 2009). Non-protein components found in plant cells and tissues, such as lipids, nucleic acids, polysaccharides, polyphenols, pigments, and secondary metabolites, interact with proteins during extraction (Carpentier et al. 2008). To achieve a better result, before analysing any previously uncharacterized proteome, protein extraction and solubilization processes must be optimized and validated for their effective extraction capacities while avoiding protein degradation and extraction of non-protein components (des Francs et al. 1985; Rabilloud 1996).

5.2 Purification and Separation of Proteins

The conventional techniques for the purification of proteins are chromatography based such as ion-exchange chromatography (IEC), size exclusion chromatography (SEC), and affinity chromatography (Gronberg et al. 2011). These techniques may be limited to the analysis of a few specific proteins but also incapable to determine protein expression level. To date, a large number of techniques have been used to separate and characterize various proteins in different plant species, including 2-dimensional liquid chromatography (2D-LC), polyacrylamide gel electrophoresis (PAGE), sodium dodecyl sulfate (SDS)-PAGE, Pro-Q Diamond stain, 2-D gel electrophoresis, mass spectrometry, Coomassie brilliant blue (CBB)-stained 2-DE, MALDI-TOF, fluorescence 2-D PAGE, non-gel-based LC–MS, ion-exchange chromatography (IEC), and 2-D difference GE (2D-DIGE) (Reuben-Kalu and Eke-Okoro 2020; Mustafa and Komatsu 2021). All these tactics have produced considerable results in protein characterization.

5.3 Identification of Proteins

Remarkable improvements in mass spectrometry have facilitated the identification of proteins by de novo sequencing without pre-existing knowledge of the relevant gene sequences (Chen et al. 2020; Ma et al. 2013). In the context of classical technique, mass spectroscopy provides a high-throughput strategy for large-scale protein identification when compared to other protein detection methods such as Edman degradation micro-sequencing (Rhee et al. 2006). Furthermore, a variety of protein sequencing and identification approaches have emerged intending to increase the sensitivity of proteomics at the single-molecule level and as an alternative to sequencing or identifying proteins, several of these techniques rely on fluorescence and nanopores for single-molecule detection (Alfaro et al. 2021).

5.4 Verification of Proteins

The identified peptides must subsequently be verified. There are several proteomic techniques to verify proteins, involving ELISA, and western blot (Liu et al. 2014; Wang et al. 2015a). Finally, verified proteins are searched against a particular protein database to obtain a list of proteins (Ghosh and Xu 2014).

5.5 Database Searching

There are several types of servers (Table 1) that can be used to check for biomarkers that have been discovered or identified by searching for proteins based on their data.

5.6 Protein–protein Interactions (PPIs) Analysis

Protein–protein interactions (PPIs) analysis is used to track the physical relationship between selected biomarkers and their interactions. STRING software (https://string-db.org) can be used to accomplish PPI analysis.

Table 1 List of different servers used in proteomics

Type of server	Name of the server	Link	References
Database	PIR	http://pir.georgetown.edu/	George et al. (1986)
	OWL	http://www.bioinf.man.ac.uk/dbbrowser/OWL/	Bleasby et al. (1994)
	TrEMBL	http://kr.expasy.org/sprot/	Boeckmann et al. (2003)
	SwissProt	http://kr.expasy.org/sprot/	
	UniParc	http://www.pir.uniprot.org/database/archive.shtml	Leinonen et al. (2004)
	UniProt	http://www.pir.uniprot.org/	Bairoch et al. (2005)
	RefSeq	https://www.ncbi.nlm.nih.gov/refseq/	Pruitt et al. (2005)
	UniRef	http://www.pir.uniprot.org/database/nref.shtml	Suzek et al. (2007)
	nr	http://www.ncbi.nlm.nih.gov/BLAST/	Yu and Zhang (2013)
BLAST	DELTA-BLAST	https://blast.ncbi.nlm.nih.gov	Altschul et al. (1997)
	PSI-BLAST	https://blast.ncbi.nlm.nih.gov	Altschul et al. (1997)
	PHI-BLAST	https://blast.ncbi.nlm.nih.gov	Zhang et al. (1998)
	TBLASTN	https://blast.ncbi.nlm.nih.gov	Gertz et al. (2006)
	BLASTP	http://blast.ncbi.nlm.nih.gov	Mahram and Herbordt (2015)
Protein domain servers	ScanProsite	http://us.expasy.org/tools/scanprosite/	Falquet et al. (2002)
	SIRW	http://sirw.embl.de/index.html	Ramu (2003)
	PATTINPROT	http://pbil.ibcp.fr/html/pbiljndex.html	Ziegler et al. (2003)
	ProWleScan	http://hits.isb-sib.ch/cgi-bin/PFSCAN	Huang et al. (2004)
	CD server	http://www.ncbi.nlm.nih.gov/Structure/cdd/cdd.shtml	Marchler-Bauer et al. (2007)
	InterProScan	http://www.ebi.ac.uk/lnterProScan/	Mulder and Apweiler (2007)
Motif-based alignment server	Match Box	http://www.sciences.fundp.ac.be/biologie/bms/help.html	Depiereux and Feytmans (1992)
	Dialign	http://bibiserv.techfak.uni-bielefeld.de/dialign/	Morgenstern et al. (1998)
	Gibbs	http://bayesweb.wadsworth.org/gibbs/gibbs.html	Thompson et al. (2003)
	BlockMakei	http://blocks.fhcrc.org/make_blocks.html	McEntyre and Gibson (2004)
	MEME	http://meme.sdsc.edu/meme/website/meme.html	Bailey et al. (2009)
Protein structure databases	PDB	http://www.rcsb.org/pdb/	Berman et al. (2000)
	SCOP	http://scop.mrc-lmb.cam.ac.uk/scop/	Lo Conte et al. (2000)
	MMDD	http://www.ncbi.nlm.nih.gov/Structure/	Chen et al. (2003)
	SwissModel	http://swissmodel.expasy.org/repository/	Schwede et al. (2003)
	CATH	http://www.biochem.ucl.ac.uk/bsm/cath/	Knudsen and Wiuf (2010)
	ModBase	http://alto.compbio.ucsf.edu/modbase-cgi/index.cgi	Pieper et al. (2014)
Protein structure analysis server	LigProt	http://bip.weizmann.ac.il/oca-bin/lpccsu	Sobolev et al. (1999)
	CASTp	http://sts.bioe.uic.edu/castp/index.php	Binkowski et al. (2003)
	ProtSkin	http://www.mcgnmr.ca/ProtSkin/intro/	Comeau and Krisch (2008)
	ConSurf	http://consurf.tau.ac.il/	Celniker et al. (2013)
Protein structure prediction sever	EBI	http://biotech.ebi.ac.uk:8400/	Rodriguez-Tome et al. (1996)
	O-GlycoBase	http://www.cbs.dtu.dk/services/NetOGIyc/	Gupta et al. (1999)
	PhosphoBase	http://www.cbs.dtu.dk/services/NetPhos	Kreegipuu et al. (1999)
	ESyPred3D	http://www.fundp.ac.be/urbm/bioinfo/esypred	Lambert et al. (2002)
	PredictProtein	http://www.embl-heidelberg.de/predictprotein	Rost et al. (2004)
	Whatlf	http://www.cmbi.kun.nl/gv/servers/WIWWWI	Sanchez-Pulido et al. (2004)
	SwissModel	http://www.expasy.org/swissmod	Waterhouse et al. (2018)

5.7 Statistical Analysis

The statistical study may be carried out using Statistical Analysis Software (SAS) or the Statistical Package for Social Sciences (SPSS) (Delwiche and Slaughter 2019; Lafler 2001). This programme is a sophisticated analytical technique that can save time when compared to traditional tools that take a lengthy period.

It is fact that proteomic analysis can rely either on top-down or bottom-up strategies (Jorrin-Novo et al. 2015; Lazarus et al. 2017). In the first case, ions of individual proteins with a molecular weight below 25 KDa are measured directly, including fragmentation and MS/MS acquisition of protein fragment ions. On the other hand, the bottom-up strategy includes proteolytic digestion of protein mixtures before MS and MS/MS analysis of the resulting proteolytic peptide-specific ions (Chmelik et al. 2009; Catherman et al. 2014; Gillet et al. 2016). Mass spectrometry with LC–MS-MS and MALDI-TOF/TOF being widely used equipment is the central among current proteomics (Aslam et al. 2017). Proteomic approaches allow for the identification of protein markers that can be used to determine optimal storage conditions (Baginsky 2009), which in turn provide information about physiological changes occurring during seed germination and seedling development.

Methodology and instrumentation have advanced significantly over the last three decades, and proteomics has emerged as a key focus in the field of biological research. Plant research has significantly profited from proteomics technology by analysing and discovering metabolic pathways and protein activities, as well as identifying protein–protein interactions in the model as well as crop plant systems (Fukao 2012). The workflow of a standard proteomics experiment is vital for the success of an experiment and it usually includes a good experimental design, an appropriate extraction/fractionation/purification protocol that considers the need of different samples (tissue/cells or organelle), a suitable separation protocol, protein identification, statistical analysis, and validation. Proteomics can be broadly divided into two areas viz. protein expression mapping and protein interaction mapping and the remaining areas of proteomics research work are post-translational modification, protein–protein interaction, structural proteomics, functional proteomics, proteome mining (Singh et al. 2018).

6 Proteomics in Plant Science

Proteomics is one of the most appealing areas with advanced techniques that are currently developing at a breakneck pace and deal with all aspects of plant sciences. Working on crop plants and well-known model plants, the technique has gained wide acceptance in plant science research. Technically, proteomics is the branch of functional genomics, which deals with the study of proteins including mRNA analysis and genomic analysis (Singh et al. 2018). In the case of plant physiology, this technology has been extremely useful in determining and identifying proteins, expression profile, post-translational modifications (PTMs), and protein–protein interactions under stress and non-stress conditions. Rapid upgradation in tools and methodologies of proteomics has enlightened newer insight in plant science. Proteins are now regarded as the workhorses of living cells of plants, and their abnormal abundance is regularly used to study stress responses. The creation of an extraction technique is the first major hurdle, and possibly the most result-determining phase in plant proteomics investigations. Different approaches in proteomics include protein extraction followed by separation of proteins either by gel-based method (2D electrophoresis, two-dimensional difference gel electrophoresis) or non-gel-based method (Isotope Coded Affinity Tag, Isobaric Tagging for Relative and Absolute Quantification, Stable Isotope Labelling by amino acid in Cell culture, Multidimensional Protein Identification Technique) (Fig. 1) and then quantification and identification using mass spectrometry and database comparison (Singh et al. 2018). Comparative proteome analysis leads to the detection of proteins involved in a variety of biological processes, such as protein synthesis, redox regulation, primary and secondary metabolism, or disease- and defence-related processes (Karmakar et al. 2019; Witzel et al. 2007). The proteome of an organism or a tissue is too complex to allow direct identification of the proteins. Therefore, developments along two routes were essential, a gel-based route and a gel-free route (Sergeant and Renaut 2010). Fluctuations in gene expression level can easily be determined by analysis of proteome to discriminate between two biological states of the cell. The use of proteomics in plant biology research has grown significantly in recent years, with advances in both qualitative and quantitative analysis inaugurating a new era of “Second Generation Plant Proteomics” (Jorrin-Novo et al. 2009). Plant proteomic studies were first conducted in *Zea mays* (Touzet et al. 1996). Protein expression patterns in plant tissues and organs have been used as a remarkable research tool that is mainly used to detect changes or assess the influence of environmental stresses on protein expression. In addition, it is frequently used to trace the alteration during plant–microbe interaction, events of pathogenesis, and breeding methods. Understanding proteomics at the cellular and subcellular levels allows for the identification of precise regulatory targets for plant immunity (Liu et al. 2019). The proteomic study of the salt-sensitive pathway revealed critical information about cellular and subcellular Na^+ transport (Lou et al. 2020). A lot of proteomic experiments enlightened the adaptive responses of the cell membrane to environmental stresses (Zamani et al. 2010; Takahashi et al. 2013; Chen and Weckwerth 2020). Some of the proteomic studies were also based on cell organelles like mitochondrion, chloroplast, nucleus, etc. A recent investigation in plants has recognized five categories of proteins viz. (a) heat shock proteins (HSPs), (b) late embryogenesis abundant proteins (LEA proteins), (c) osmolyte biosynthetic enzymes, (d) proteins involved in carbon metabolism, and (e) enzyme scavengers of ROS, which are directly related to salt tolerance mechanisms in plants and are present in varying abundance (Rodziewicz et al. 2014). Proteomics has evolved into a powerful tool to obtain protein-related quantitative data, especially for hydrophobic and low-abundant proteins in cells and organelles under different environmental conditions, such as salt stress, drought stress, virus-infected states, and heavy metal stress. Cao et al. (2016) have reported that more than 3900 proteins were present in highly purified rice plasma membranes. Proteomics can provide information regarding storage mobilization from endosperm to germinating embryos of seeds. In a proteomic analysis of endosperm in germinating *Jatropha curcas* seeds, it was shown that the oil mobilization was initiated during germination, and then the oil was consumed for early seedling development (Yang et al. 2009). The study also indicated the significant change in abundance of proteins during germination, most of which are associated with numerous storage lipid mobilization pathways including β-oxidation, glyoxylate cycle, glycolysis, citric acid cycle, gluconeogenesis, pentose phosphate pathway, etc. Components of signal transduction pathways have also been identified through this technique. Sakamoto et al. (2008) showed that a transmembrane protein with an ankyrin-repeat motif influences the abscisic acid-induced accumulation of ROS during salinity. Under salt stress, nuclear small ubiquitin-like modifier proteases are engaged in protein modification activities (Conti et al. 2008). Abbasi and Komatsu (2004) studied salt-responsive proteins in rice using a proteomic technique, which indicated that an oxygen-evolving enhancer protein expressed in the leaf sheath and leaf blade of rice showed a coordinated response to salt stress. With the help of proteomic and biochemical analyses, Zhang et al. (2021) revealed that protein abundance is related to several metabolic processes including chlorophyll biosynthesis, proline metabolism, and tricarboxylic acid cycle metabolism pathway in some cultivars of *Brassica napus*, which was greatly suppressed by salt stress. When it comes to biological sectors like agriculture and microbiology, proteomics is widely applied. There has been a lot of work, put into the development of salt-tolerant genotypes in agriculturally important crop plants, and conventional breeding has shifted towards the use of transgenics, large-scale transcript and protein profile data, and QTL discovery.

Jiang et al. (2007) conducted a proteome analysis of *Arabidopsis* roots stressed with 150 mM NaCl and found the regulation of 200 protein spots whereas Wang et al. (2008) found that 110 proteins were differentially expressed in contrasting wheat genotypes exposed to 200 mM NaCl. According to a survey of protein function based on homology, some proteins play an important part in numerous physiological processes of plants including germination. Proteomics is widely used to better understand how plants interact with other organisms. This technique is also commonly used to study the plant–insect interactions, which aid in the identification of potential genes involved in the plant's defence response to herbivores (Sangha et al. 2013; Rustagi et al. 2021). With the help of proteomic analysis, Vannini et al. (2021) have shown the underlying mechanism of modulation of growth and defence in plants by mycorrhizal fungus and plant growth-promoting bacteria. The applications of plant proteomics in scientific research are still in the budding stage.

7 Proteomics in Understanding Saline Stress Response in Germinating Seed

Salinity is globally one of the most formidable barriers to seed germination and many researchers reported that many proteins are intricately involved in salt stress responses in germinating seeds. Consequently, proteomics, under its capacity to yield definitive information on protein identity, localization, transcriptional and post-translational modification, and the accuracy of in silico gene model prediction in the plant, has become an integral component of all large-scale "omic" and systems approaches in understanding the rich complexity of physiology and biochemistry of seed germination under salinity (Table 2). Since proteins are associated with the majority of the metabolic events in the seed, and in addition to being crucial structural components in the cytoskeleton, membranes, cytoplasmic organelles, and cell wall, it makes perfect sense to analyse the proteome of a seed or a seed tissue or a specific cell type or even a subcellular compartment (Wang et al. 2015b). Proteins contribute to stress-adaptation mechanisms that involve changes in the cell cytoplasm, cytoskeleton, plasma membrane, and intracellular compartment combination, as well as changes in their biochemical activities (Bogeat-Triboulot et al. 2007; Lau et al. 2020; Sun et al. 2020). Protein accumulation changes in response to stress are intimately linked to the phenotypic response of the plant to stress (Bandehagh et al. 2021). Identification and characterization of salt-responsive proteins through research in high-throughput proteomics is a fundamental reason for producing salt-tolerant plant varieties. This technology aids in the investigation of adaptive

Table 2 Proteomic studies related to germinating seed and/or salt stress response

Name of the plant	The outcome of proteomic studies related to germinating seed and/or salt stress response	References
Abelmoschus esculentus L.	In proteomic studies, a total of 7179 proteins were identified from seedlings, with quantitative information available for 5774 of them. There were 317 differentially expressed proteins (DEPs) in the NaCl/control comparison group, with 165 proteins upregulated and 152 proteins downregulated in the presence of NaCl	Zhan et al. (2019)
Amaranthus cruentus L.	Root proteome revealed that plants exposed to salinity stress modify about 77 proteins, including enzymes involved in ROS scavenging, nucleotide metabolism, and fatty acid and vitamin production	Huerta-Ocampo et al. (2014)
Arabidopsis thaliana L.	Comparative proteomic analyses of roots showed changes in protein abundance in response to treatment with NaCl. Most of them are stress-responsive proteins and few are involved in ROS scavenging, signal transduction, translation, cell wall biosynthesis, protein translation, processing and degradation, and metabolism of energy, amino acids, and hormones	Jiang et al. (2007)
	Carbonylation of several important metabolic proteins, e.g. glycolytic enzymes, mitochondrial ATP synthase, and Rubisco increased during germination without any apparent ill effects on the seeds, which germinated at high rates and grew vigorously	Job et al. (2005)
	Proteomic analyses of seeds during germination revealed that the accumulation of cruciferin (the main seed storage protein in *Arabidopsis*) occurred by de novo synthesis during after-ripening to provide an additional source of amino acids and nitrogen to seedlings	Chibani et al. (2006)
	Methionine-related enzymes become abundant during seed germination	Gallardo et al. (2002, 2014, 2001)
	Measure differential protein expression and de novo protein synthesis. It was found that some proteins were not present in the mature seeds, but were synthesized during germination	Galland et al. (2014)
Beta vulgaris L.	Proteomic analysis of seed reported that 758 proteins which interfere and reconstruct the metabolic status	Catusse et al. (2008)
Brassica napus L.	Proteomic studies reported 130 differentially expressed proteins that were mainly involved in storage (23.4%), energy metabolism (18.9%), protein metabolism (16.2%), defense/disease (12.6%), seed maturation (11.7%), carbohydrate metabolism (4.5%), lipid metabolism (4.5%), amino acids metabolism (3.6%), cell growth/division (3.6%), and some unclear functions (2.7%)	Gu et al. (2016)
	Proteomic studies on seed recognized 323 proteins, where 233 proteins were identified with 3 unique peptides-2S albumins like napin seed storage proteins (SSPs), 11/12S globulin like cruciferin SSPs, and 7S globulin like vicilin SSPs	Rahman et al. (2021)
Cajanus cajan (L.) Millsp.	Proteomic analysis of seeds reveals the accumulation of 373 seed proteins and many of them are stress-related proteins	Krishnan et al. (2017)
Capsicum annuum L.	A total of 4,693 proteins were identified through proteomic study of seedlings, among which 3,938 were yielded quantitative information	Zhang et al. (2019)
Cicer arietinum L.	The proteomic analysis showed that dehydration induces the accumulation of more proteins related to photosynthesis, stress response, gene transcription, signaling, protein biogenesis, and protein degradation in tolerant genotypes in comparison to sensitive genotypes	Vessal et al. (2020)
Coffea arabica L.	Ten proteins have been found that appear to influence plant development in various ways, either directly or indirectly, by being involved in plant growth or as an intermediate in a metabolic pathway that could influence seed germination	Franco et al. (2009)
Cucumis sativus L.	Melatonin alleviates the inhibitory effect of high salinity on cucumber seed germination primarily by regulating energy production	Zhang et al. (2017)
Cyclobalanopsis gilva (Blume) Oerst	The β-amylase activity was four-fold higher in successfully germinated seeds compared to non-germinated seeds	Zaynab et al. (2021)
Helianthus annuus L.	Proteome analysis revealed an increase in proteins associated with metabolism and energy from the first hours of imbibition, followed by a decrease in proteins associated with protein metabolism and seed storage in germinating seeds compared to non-germinating seeds	Xia et al. (2018)

(continued)

Table 2 (continued)

Name of the plant	The outcome of proteomic studies related to germinating seed and/or salt stress response	References
Jatropha curcas L.	Proteomic analysis of endosperm provides information regarding mobilization of storage material in germinating seed	Yang et al. (2009)
Lepidium sativum L.	Proteomic characterization of the micropylar endosperm revealed the presence of proteins involved in protein folding, protein defence, and stability	Muller et al. (2010)
Leymus chinensis (Trin.) Tzvelev	A significant increase in reactive oxygen species (ROS) during after-ripening is one of the vital drivers to regulate seed dormancy release by modulating cytoskeleton and chromatin	Hou et al. (2019)
Nelumbo nucifera Gaertn	The proteome composition of lotus seed embryos, mature endosperm, and immature endosperm differed significantly, according to the proteomics study. Immature endosperm included 122 non-redundant proteins and the embryo contained 141 non-redundant proteins while mature endosperm contained 66 non-redundant proteins	Moro et al. (2015)
Nicotiana tabacum L.	Proteomic analysis showed the relationship between seed persistent syndrome and storage protein content and processing	Onelli et al. (2017)
Oryza sativa L.	The proteomic analysis reported several salt-responsive proteins in the root including ABA-responsive protein, ascorbate peroxidase, etc	Salekdeh et al. (2002)
	Salinity modulates several proteins associated with photosynthesis, photorespiration, signal transduction, regulation of metabolism, defence against oxidative stress, control of ion channel, and protein folding	Nohzadeh Malakshah et al. (2007)
	Existence of novel protein candidates associated with salinity stress	Yan et al. (2005), Jiang et al. (2007)
	In the proteomic studies abundance of 63 proteins was observed to decrease during germination, while the abundance of 69 proteins was increased (including 20 induced proteins)	Yang et al. (2007)
	Detection of alteration in protein phosphorylation	Chitteti and Peng (2007)
	Presence of salinity stress-responsive protein in root apoplast, which plays a putative role in stress signaling	Zhang et al. (2009)
	Cysteine and Methionine-related enzymes have been observed to change in abundance during the germination of seeds	Whitcomb et al. (2020)
	More than 800 phosphoproteins are identified, out of which, 149 changed in amount during germination. Most of them are involved in phosphorylation and influence reprogramming cellular metabolism in germinating seed	Han et al. (2014a, 2014b)
	Eleven genes in salt stress treated seeds were expressed early during the seed imbibitions and some of the expressed proteins are might be applicable for the improvement of seed germination under salt stress	Xu et al. (2017)
Pisum sativum L.	Seed germination in optimal conditions enhanced the accumulation of different proteins involved in glycolysis, Krebs cycle, synthesis of fatty acids, cell growth, cellular transport, and detoxification whereas osmotic stress decreased the aggregation of all of them except enzymes of Krebs cycle	Brosowska-Arendt et al. (2014)
	The abundance of SBP65 (belonging to group 3 of LEA proteins) continuously decreased after 18 h of germination coinciding with the loss of desiccation tolerance	Wang et al. (2012)
	Methionine-related enzymes become abundant during seed germination	
Triticum aestivum L.	Seed endosperm also responds to abiotic stressors like salinity by altering protein compositions	Yan et al. (2021)
	Proteomic investigations combined with mRNA analysis revealed that after-ripening seeds have lower levels of disulfide isomerase, which promotes proteolysis and, as a result, breaking of seed dormancy and initiation of germination	Gao et al. (2013)
	Proteomic analyses of dry and after-ripening seeds have demonstrated that imbibition of after-ripening seeds led to substantial repression of glucose/ribitol dehydrogenase compared to dry seeds, thus implying that suppression of glucose and ribitol dehydrogenase homologs 1 (GRDs) may be related to the germination	
	The abundance of methionine-related enzymes has been found to change during seed germination	Fercha et al. (2013)

(continued)

Table 2 (continued)

Name of the plant	The outcome of proteomic studies related to germinating seed and/or salt stress response	References
Vigna radiata (L.) R. Wilczek	The expression of a vast number of proteins involved in stress response and plant growth was affected by salinity. During seed germination, 111 proteins were upregulated and 149 proteins were down-regulated, according to quantitative evidence	Yu et al. (2020), Alharby and Hakeem (2021)
Zea mays L.	Proteomic studies have revealed that alterations in splicing factors and transcription factors are thought to be of crucial importance in response to early salt stress. The genes involved in ABA and GA have converged as principal targets for adjusting hormone balance non-germinated seed	Chen et al. (2021)

responses in germinating seeds and seedlings to abiotic stresses such as salinity (Fig. 2). At present, in the NCBI database, more or less one lakh forty thousand publications related to proteomics are indexed, of which nearly sixteen thousand publications are associated with proteome/proteomics stress studies and around six hundred publications mention proteome/proteomics research related to plant salinity stress (https://www.ncbi.nlm.nih.gov). Proteomics is considered to be the best way of establishing large-scale gene expression profiling during the germination and post-germination events because this methodology depends largely on storage proteins as well as proteins synthesized de novo from stored mRNAs (Rajjou et al. 2006, 2008; Catusse et al. 2008). Proteomics offers a broad array of applications in protein profile analysis under salt-induced stress conditions, but its primary function is to identify genes and proteins responsible for plant salinity stress response and tolerance mechanisms (Wang et al. 2014). Proteomics can also be used to compare the differential expression of proteomes between control (non-stressed) and stressed plants or between different species or varieties of any species. Many relevant studies have been conducted in many plants for the comparative analysis of proteomes (Table 2). Various proteomics studies of seed germination in recent years have revealed that some of the germination-specific proteins involved in energy production and cell structure

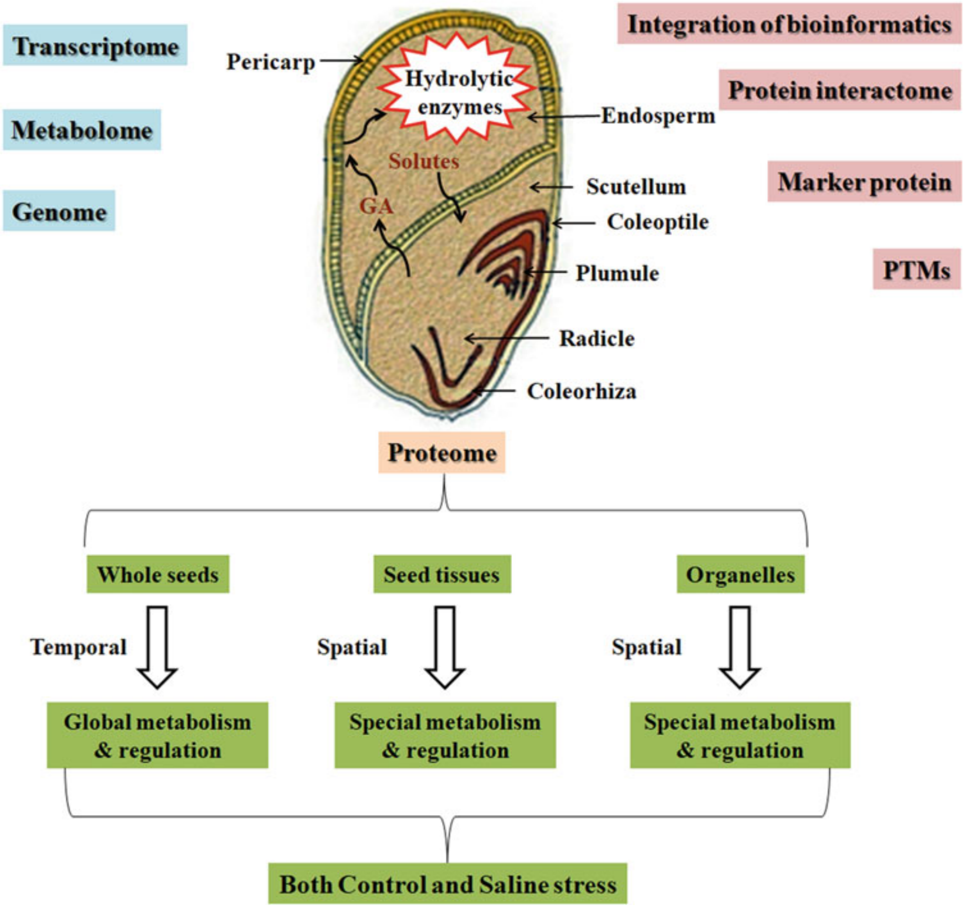

Fig. 2 Proteomics of seed germination under saline stress: accomplishments and future directions

maintenance are produced from long-lived mRNAs. Researchers often used comparative two-dimensional electrophoresis (2-DE) of complete germinating seeds of different species with a time course sampling to provide a broad picture of protein mobilisation during seed germination (Yang et al. 2007; He et al. 2011; He and Yang 2013; Mouzo et al. 2018). Mass spectrometric (MS) identification of unknown proteins in non-model species, is carried out by correlating sequences available in similar evolutionary origin or/and even the entire database and this identification methodology has been extensively recognized by modern researchers (Sobhanian et al. 2010; Li et al. 2011; Sinha and Chattopadhyay 2011; Yu et al. 2011; Debez et al. 2012). In any organism, data from the genome and inferred protein sequences can be used to recognize proteins and track sequential changes in protein expression within that organism under different physiological conditions. In the current scenario, the majority of proteomic research has focused on the unfavourable impact of influences on seed survivability and germination ability. The majority of this research has focused on a specific organ or tissue, such as whole germinating sprouts, seeds, endosperm, or embryos. Using proteomics, numerous essential proteins have been discovered in germinating seeds of many crop plants. A multitude of germination-related information was discovered in addition to their identification, enhancing our understanding of the germination process (Table 3). The physiological and molecular scenario of seed coat imbibition and mobilization of reserve foods can be provided through proteomic investigations. Proteomic analysis reveals that the enzymes involved in starch breakdown and mobilization, such as α-amylases and β-amylases increase significantly over three days following imbibition (Miernyk and Hajduch 2011). Nowadays, studies are performed to address various issues related to seed germination including the importance of differentially expressed proteins during germination (Teisseire and Guy 2000; Devi and Prasad 2005).

Plants are unable to escape unfavourable or stressful conditions due to their immobile nature, thus they require robust defence mechanisms to deal with unfavourable environmental changes such as salinity, drought, and heat stress. Under stressful conditions, plants usually activate signaling kinase cascades, regulate ion channels, accumulate reactive oxygen species, and secrete hormones, and when the stress is relieved, homeostasis is restored (Ahmad et al. 2010, 2012, 2016; Ahmed et al. 2013; Ashraf et al. 2014; Rejeb et al. 2014; Ziogas et al. 2015; Molassiotis et al. 2016). Every change for increased tolerance in plants is largely driven by the modification of gene expression and protein conformation that safeguards and preserves cellular components' function and structure. The significant number of biological issues about plant stress response remains unresolved even after the completion of genome sequencing. As many of the stress adaptations of cells or organisms are the responsibility of proteins and peptides, proteomic analysis can therefore resolve these unresolved concerns. Plants always experience a significant change in protein expression in response to abiotic stressors like salinity; therefore, a proteomic approach will be extremely valuable in explaining the role of protein accumulation under stress circumstances and its relationship to stress tolerance (Wang et al. 2019). Furthermore, because protein localization and activity vary depending on the situation, therefore, it will be critical to identify and understand the biological information included in protein expression study in many cell types and situations. Different proteins from different plants have been identified that serve key functions in support of homeostasis and salt stress tolerance in plants (Table 3). Since proteins can be widely acknowledged as direct effectors of the stress response, it is highly important to investigate changes in proteome level to recognize potential protein markers whose abundance could be associated with changes in physiological indices under salt-induced stress. Plant proteome responses to salt stress depend on its intensity, duration, and the organ examined (Ji et al. 2016; Wang et al. 2019). Much effort has also been put into cataloguing organellar and cellular proteins such as stress sensors, signal transducers, transcription factors, chaperones, and so on in a variety of salt-sensitive plant species. Shewry and Casey (1999) have revealed some amazing understanding of the seed proteome of legume crop plants, as well as their fluctuations in response to stressors, which may have a considerable impact on the quality and nutritional quality of these plants. Proteomics not only monitors protein abundance and protein interactions, but also recognizes translation and post-translation regulations so that new insights into plant modifications under abiotic stress like salinity are provided (Salekdeh et al. 2002). Seeds undergo some alterations in response to salinity, which may result in the accumulation or depletion of specific metabolites, resulting in the imbalance in the levels of a relatively small set of cellular proteins, which could increase, decrease, appear, or disappear after salt treatment (Kong-Ngern et al. 2005). Stress proteins could be used as important molecular markers for the improvement of salt tolerance and an approach to overexpressing these genes in different plants under controlled conditions has been quite successful (Soltabayeva et al. 2021). However, proteins produced under salt stress are not always associated with salt tolerance; consequently, using proteins as a salt tolerance indicator depends on the nature of the plant species or cultivar (Amini et al. 2007). To avoid the adverse effect of salinity plant evolves some modifications in gene expression which may lead to accumulation or depletion of certain metabolites resulting in the imbalance in the level of a relatively small set of cellular proteins (Jia et al. 2015; Mahmoodzadeh 2009). Such proteins may increase,

Table 3 Some saltresponsive proteins identified by proteomic analysis

Plants	Parts/Tissue	Protein ID	Status under salinity	Function	References
Amaranthus cruentus L.	Mesophyll and bundle sheath chloroplast	ATP synthase subunits	Accumulated	Promote salt tolerance	Joaquin-Ramos et al. (2014)
	Mesophyll and bundle sheath chloroplast	Electron Cycling Proteins			
Arabidopsis thaliana L.	Seed	HY5	Down regulated	Control seed germination through regulation of nucleo-cytoplasmic partitioning of constitutive photomorphogenesis 1	Yu et al. (2016)
		XIW1	Upregulated	Promote ABA responses and inhibiting seed germination	Cai et al. (2020)
	Seedling	Salt tolerance homolog 2	Upregulated	Positive regulator of photomorphogenesis	Datta et al. (2007)
Beta vulgaris L.	Seedling	Osmotin-like protein	Upregulated	Osmotic stress tolerance	Hajheidari et al. (2005)
		Glycine decarboxylase	Upregulated	Protection of membrane proteins and provide constitutive adaptation to the plasma membrane	Wakeel et al. (2011)
		Ferredoxin-NADP-reductase			
		Aminomethyl transferase			
Chenopodium quinoa Wild	Leaves	Desiccation-responsive protein 29B	Upregulated	Regulate stomatal movement and provide salt tolerance	Rasouli et al. (2021)
		Osmotin-like protein OSML13	Upregulated	Osmotic stress regulation by osmotic adjustment	
		Polycystin-1, lipoxygenase, alpha-toxin, and triacylglycerol lipase (PLAT) domain-containing protein 3-like	Upregulated	Osmotic stress regulation by osmotic adjustment	
Chenopodium quinoa Wild	Leaves	Dehydrin early responsive to dehydration (ERD14)	Upregulated	Play a regulatory role in stomata under salinity condition	
Glycine max L.	Hypocotyls/Root	LEA proteins	Upregulated	Protective roles in salt stress tolerance	Aghaei et al. (2009)
	Seed	LEA proteins		Seed and hypocotyls development	
		Glyceraldehyde 3-phosphate dehydrogenase		Protective roles in salt stress tolerance	Xu et al. (2011)
		Glutathione S-transferase 9		Protective roles in salt stress tolerance	
		Seed maturation protein PM36		Protective roles in salt stress tolerance	
Hordeum vulgare L.	Seedling	HvNHX1	Upregulated	Ion homeostasis and cell redox homeostasis	Wu et al. (2014)

(continued)

Table 3 (continued)

Plants	Parts/Tissue	Protein ID	Status under salinity	Function	References
Lactuca sativa L.	Leaf of Seedling	Superoxide dismutase	Upregulated	Provide salinity tolerance	Lucini et al. (2015)
Nicotiana tobaccum L.	Seedling	Osmotin	Upregulated	Osmotic stress tolerance	Abdin et al. (2011)
Nicotiana tobaccum L.	Seedling	Chitinases	Upregulated	Cell wall modifications during plan development	Dani et al. (2005)
Nicotiana tobaccum L.	Seedling	Germin-like protein	Upregulated	Cell wall modifications during plan development	
Oryza sativa L.	Leaf	LEA proteins	Upregulated	Prevention of water stress and seed dehydration	Chourey et al. (2003)
Oryza sativa L.	Seedling	Ascorbate peroxidase	Upregulated	Improved leaf sheath and leaf blade	Abbasi and Komatsu (2004)
Oryza sativa L.	Seedling	Dehydro ascorbate reductase	Upregulated	Improved leaf sheath and leaf blade	
Oryza sativa L.	Seedling	Superoxide dismutase	Upregulated	Improved leaf sheath and leaf blade	
Oryza sativa L.	Leaf	ROS detoxifying enzymes	Upregulated	Promote salt tolerance	Parker et al. (2006)
Oryza sativa L.	Leaf	ATP synthase beta subunit	Upregulated	Promote salt tolerance	
Oryza sativa L.	Leaf	RuBisCo activase	Upregulated	Promote salt tolerance	
Oryza sativa L.	Root	ROS detoxifying enzymes	Upregulated	Protect from oxidative damage	Salekdeh et al. (2002), Chitteti and Peng (2007)
Oryza sativa L.	Root	Caffeoyl CoA-Omethyltrasferase	Upregulated	Promote salt tolerance	Salekdeh et al. (2002)
Pisum sativum L.	Whole plant	Cu-ZnSOD-II	Upregulated	Protect from superoxide and H_2O_2-mediated oxidative damage	Hernandez et al. (1995)
Setaria italica (L.) P. Beauv	Seedlings	ATP synthase beta-subunit	Up-regulated	Enhancing plant salt tolerance	Veeranagamallaiah et al. (2008)
Setaria italica (L.) P. Beauv	Seedlings	Caffeoyl CoA-Omethyltrasferase	Upregulated	Enhancing plant salt tolerance	
Solanum tuberosum L.	Shoot	ATP synthase beta subunit	Upregulated	Enhancing plant salt tolerance	Aghaei et al. (2008)
Solanum tuberosum L.	Shoot	Heat shock proteins	Upregulated	Enhancing plant salt tolerance	
Solanum tuberosum L.	Shoot	Osmotin-like protein	Upregulated	Enhancing plant salt tolerance	
Sorghum bicolor L.	Seedlings	Malate dehydrogenase	Upregulated	ROS scavenging	Ngara et al. (2012)
Sorghum bicolor L.	Seedlings	Ascorbate Peroxidase	Upregulated	ROS scavenging	
Triticum aestivum L.	Seedlings	Glycine dehydrogenase	Upregulated	Improved protein biosynthesis	Caruso et al. (2008)
Triticum aestivum L.	Seedlings	Glutamine synthase	Upregulated	Improved protein biosynthesis	

(continued)

Table 3 (continued)

Plants	Parts/Tissue	Protein ID	Status under salinity	Function	References
Vigna radiate (L.) R. Wilczek	Seedlings	Oxygen-evolving enhancer protein 1	Upregulated	Improve photosynthesis-related proteins	Alharby and Hakeem (2021)
Vigna radiate (L.) R. Wilczek	Seedlings	RUBISCO	Upregulated	Keep their photosynthetic efficiency	
Vigna radiata (L.) R. Wilczek	Seedlings	Heat shock protein 70	Induced	Plays a great role in plants during salinity stress exposure	
Vigna radiata (L.) R. Wilczek	Seedlings	RUBP/oxygenase activase	Upregulated	Keep their photosynthetic efficiency	
Vigna radiata (L.) R. Wilczek	Seedlings	Rubber elongation factor protein (REF)	Upregulated	Promote salt tolerance	
Vigna radiata (L.) R. Wilczek	Seedlings	Pathogen related protein 10	Upregulated	HSP-involved signal transduction process	
Zea mays L.	Seedlings	NHX1	Upregulated	Ion transport	Neubert et al. (2005)

decrease, appear, or disappear during salinity (Kong-Ngern et al. 2005). Knowing the involvement of these stress-inducing proteins, the mechanisms of salt tolerance in plants would be easier to explain.

Protein markers can provide comprehensive knowledge about physiological changes occurring during seed germination and about the condition of the stored material of seeds. Proteomic approaches enable the evaluation of protein markers which can be useful in the determination of optimal conditions for germination. The proteomic technique has been used extensively in a recent study to investigate germination in salt-susceptible plants (Table 2). Proteomics is routinely employed in comprehensive profiling of complex protein extracts and delivers valuable qualitative and quantitative information on protein dynamics in plants including their seed biology. Seed proteins are classified as structural, storage, and physiologically active proteins and all of them have been found to play a role in germination under both ideal and stressful conditions (Table 3). Seed protein research is being conducted to better understand metabolic regulation at both the transcriptional and post-translational levels. Proteomic analyses of salt stress responses in germinating seeds are highly necessary to ensure a greater understanding of the entire process of germination and post-germination events because salinity is responsible for post-translation modifications, such as removal of signal peptides, phosphorylation, and glycosylation. Such studies are also important for understanding protein activities and subcellular localization (Yan et al. 2005). Till today, considerable proteomic works on seed germination in different plants has been performed, such as *Nicotiana tabacum* (Dani et al. 2005; Abdin et al. 2011; Onelli et al. 2017), *Lycopersicon esculentum* (Chen et al. 2009), *Thea sinensis* (Chen et al. 2011), *Fagus sylvatica* (Pawłowski 2007), *Acer platanoides* (Pawłowski 2009), *Arabidopsis thaliana* (Chibani et al. 2006; Rajjou et al. 2006), Cress (Muller et al. 2010), *Beta vulgaris* (Catusse et al. 2008), *Medicago truncatula* (Boudet et al. 2006), *Hordeum vulgare* (Finnie et al. 2004), *Glycine max* (Cheng et al. 2010; Ma et al. 2014), *Zea mays* (Fu et al. 2011), and *Oryza sativa* (He et al. 2011), etc.

Numerous proteomic investigations have been conducted on rice, maize, and Arabidopsis germinating seeds. Proteomic analysis revealed that the viability loss of *Arabidopsis* seed is related to protein changes in dry seeds and an inability of low-viability seeds to produce a normal proteome during germination (Rajjou et al. 2008). In a systematic proteomic analysis of NaCl-stressed germinating maize seeds, it was the expression of proteins that respond to abscisic acid signals increased in response to salt stress (Meng et al. 2014). Xu et al. (2017) conducted experiments to identify proteins that contribute to seed germination under salt stress and discovered 14 proteins involved in seed imbibition in rice. From the study, it was concluded that the early imbibition process is mediated by protein catabolism rather than by de novo protein synthesis and the majority of these proteins were involved in energy supply and storage. Cheng et al. (2017) reported that glucose-1-phosphate adenylyltransferase large subunit (GAS) protein in imbibed seed under salt stress as well as in water stress are expressed suggesting that these proteins are required for seed germination under various conditions including salinity. According to a proteomics study, salt stress causes downregulation of metabolically relevant proteins in the hypocotyl of soybean seedlings (Sobhanian et al. 2010). Proteomic analysis has revealed that MMDH1 (Mitochondrial malate dehydrogenase) was one of the 95 proteins that significantly accumulated during *Arabidopsis* seed germination (Fu et al. 2005). Melatonin increases seed germination under high saline conditions, as shown in a proteomics study. In a proteomics study, it was shown that the inhibitory effect of excessive salinity on cucumber seed germination was eased by the application of 1 μM melatonin (Zhang et al. 2014). Further study showed that during germination of cucumber seeds under salt stress, storage protein showed an increasing abundance after melatonin treatment, including two globulin-like proteins (P13744 and Q8W1C2) and two vicilin-like proteins (Q39651 and Q9ZWI3) (Zhang et al. 2017). Gu et al. (2016) conducted a proteomic study on the protein expression pattern of seed germination of *Brassica napus* by using differential fluorescence two-dimensional gel electrophoresis. The expression pattern of proteins showed that heterotrophic metabolism could be activated in the process of seed germination and that the onset of defence mechanisms might start during seed germination.

Protein function depends not only on the molecular structure of the protein but also on its subcellular localization and post-translational modifications (Kosova et al. 2018). Protein function is closely related to subcellular localization because different cell components provide different physiological and biochemical environments (such as pH and redox conditions) or potential acting substrates (Liu et al. 2019). Thus, in recent times, researchers have also set their focus on subcellular proteins during germination. Different gel-based and gel-free proteomics approaches are used to characterize mitochondrial proteomes of germinating seeds. Diverse methodologies have been used to track the changes in mitochondrial protein abundance during seed germination, including (a) a direct study of the global mitochondrial proteome variations using isolated organelles from germinating seeds (Howell et al. 2006; Wang et al. 2015b); (b) a targeted approach to study specific mitochondrial proteins in isolated organelles from germinating seeds (Logan et al. 2001; Taylor et al. 2010) (c) an indirect approach to describe the changes of mitochondrial proteomes in germinating seeds, using total seed protein extracts to identify and measure mitochondrial proteins (Law et al. 2012) (d) an indirect study to describe the variations in the total proteome in germinating seeds, in which mitochondrial proteins have been detected among many other proteins. The dynamics of mitochondrial protein abundance in germinating seeds have been observed in many plant species, such as *Oryza sativa* (Howell et al. 2006, 2007; Taylor et al. 2010; Han et al. 2014a), *Pisum sativum* (Wang et al. 2012), *Arabidopsis thaliana* (Gallardo et al. 2001; Fu et al. 2005; Law et al. 2012; Galland et al. 2014), and *Zea mays* (Logan et al. 2001). Tan et al. (2013) summarized the results from 13 different studies in which proteomics had been used to study the effect of a range of environmental conditions on the germinating seed proteome. The analysis also showed that the largest protein groups affected by abiotic stresses were proteins associated with glycolysis, storage protein mobilization, protein processing, osmotic homeostasis, and ROS scavenging. The characterization of protein–protein interactions is essential to the understanding of the molecular role of the cell in the execution of various biological functions including germination and stress responses. Proteomic studies also revealed that the radicle protrusion from imbibed seed requires only protein translation, implying that germination-specific proteins are translated from stored mRNAs (Sano et al. 2012).

8 Future Aspects of Proteomics in the Improvement of Salt-Resistant Seed Germination

Proteomics is growing rapidly in plant sciences, with numerous researches on seed germination having been conducted and published. This is an appealing method for investigating seed germination because it allows researchers to gather a large amount of data from a small amount of tissue. Large-scale gene expression analysis at both the mRNA and protein levels has been used to uncover the characteristics of seed germination in both normal and salt-induced stress conditions, due to considerable advances in omics technology. The investigation of salt-induced changes in the seed proteome would highlight important genes associated with germination owing to the advent of a high resolution of protein separation by two-dimensional gel electrophoresis (2-DE) and protein identification by mass spectrometry and database search. Though there have been major proteomic advances using several plant species, much of the knowledge gained on seed germination processes and salt stress response mechanisms have been gained from work using *Arabidopsis* and *Oryza* as their completed genome sequences are more or less publicly available (Jorrin et al. 2007; Jorrin-Novo et al. 2009). With the increasing availability of plant genome sequences and the advancement of mass spectrometry (MS) technology, proteomics has been widely applied in analysing the mechanisms of different biological processes including seed germination and proved to be a very powerful tool to study stress responses. Protein quantitative studies may expand by improvising new techniques, known as second-generation proteomics, that exceed a few limits related to technical analytical variability, delivering data with greater repeatability, and protein comparison in between different organs or among various growth stages (Roveda-Hoyos and Fonseca-Moreno 2011). Furthermore, improving the understanding of the identified key metabolic proteins involved in salt tolerance can be implemented into biotechnological applications, regarding recombinant/transgenic formation.

9 Conclusion

Proteomic techniques have recently become extensively used in plant science research, and they may be useful to seed science research as well. It has gained huge attention worldwide due to the easy handling of the proteomic analysis tools and the accuracy of the results. It offers a new approach to discovering proteins and pathways associated with physiological phenomena and stress responses in plants. As proteins represent one of the important components of seed, critical for germination and seedling development; during the past decade proteomics has become an important tool of seed research. In addition, proteomics also makes it possible to address physiological changes by characterization of alteration in protein abundances (expression) simultaneously with an assessment of post-translational modification patterns, which might be informative in the sense of salt-induced alterations in germinating seeds. Seed germination and seedling development are largely dependent on the metabolic status of reserve substances, especially of storage proteins. Thus, knowledge of the seed proteome, as well as its dynamics in response to environmental and biological stressors, may be helpful for the understanding of the physiological process. Proteomics has aided our understanding of a variety of phenomena, yet it is still insufficient for a thorough comprehension of a biological system. This technology helps to promote stronger links between people working in different fields of science creating future concepts of crop improvement through seed biology.

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Role of Secondary Metabolites and Prospects of Engineering Secondary Metabolite Production for Crop Improvement

Rakhi Chakraborty

Abstract

Plant secondary metabolites impart significant contributions in defense, stress tolerance, reproduction and are also involved in plant growth regulation and crop yield. They are of diverse chemical nature and biological functions, depending on their biosynthesis within a plant cell. Major classes of plant secondary metabolites that help regulate plant growth and development include—phytohormones, phenolics, terpenoids, nitrogen-containing compounds (alkaloids, non-protein amino acids and cyanogenic glycosides) and sulphur-containing compounds (glucosinolates, phytoalexin, defensin, etc.). They are synthesized in a relatively small amount within plant cells and exert their specific functions through several complex signaling pathways. Large-scale production of plant secondary metabolites is thus considered as one of the important strategies for crop improvement. Application of physical (UV-rays, gamma radiation, etc.), chemical (salicylic acid, jasmonic acid, melatonin, etc.) and biological elicitors (cyanobacteria, fungal and bacterial species), induction of polyploidy, nanotechnological approaches, epigenetic modification (gene overexpression, gene silencing, histone modification, etc.), transgenesis (homologous or heterologous transfer of one or more genes of specific secondary metabolite biosynthetic pathway), transcriptional and post-transcriptional regulation, etc., have been successfully applied in several crop plants for the increased production of desired secondary metabolites. However, most of the studies remain confined to the laboratory scale due to several constraints, viz. altered expression pattern, genetic instability, bioavailability, bioactivity, lack of desired quality and quantity of the products, etc. In this chapter, specific functions of plant secondary metabolites regulating the growth and development of crop plants have been thoroughly discussed. Moreover, the engineering strategies for large-scale production of secondary metabolites along with the challenges have also been elaborated.

Keywords

Cellular signaling • Crop improvement • Genetic engineering • Metabolic regulation • Nanotechnology • Plant secondary metabolites

Abbreviations

ABA	Abscisic acid
AP2/ERF	APETALA 2/ethylene-responsive element binding factor
APX	Ascorbate peroxidase
BABA	β-Aminobutyric acid
BR	Brassinosteroid
CAT	Catalase
CRISPR/Cas9	Clustered regularly interspaced short palindromic repeat/CRISPR associated protein 9
DELLA	Aspartate-glutamate-leucine-leucine-alanine
DREB	Dehydration-responsive element-binding protein
2,4-D	2,4-Dichlorophenoxyacetic acid
ETR1	Ethylene receptor 1
ERS1	Ethylene response sensor 1
GABA	γ-Aminobutyric acid
GR	Glutathione reductase
GSA1	Grain size and abiotic stress tolerance1
HY5	Elongated hypocotyl 5
HLS1	Hookless 1
JA	Jasmonic acid
MYB	My elob lastosis
NO	Nitric oxide
ODC	Ornithine decarboxylase
ORCA3	Octadecanoid-derivative responsive Catharanthus APETALA2-domain

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R. Chakraborty (✉)
Department of Botany, Acharya Prafulla Chandra Roy
Government College, Himachal Vihar, Matigara, Siliguri, 734010,
West Bengal, India

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POX	Peroxidase
PVP	Polyvinyl pyrrolidone
ROS	Reactive oxygen species
SA	Salicylic acid
SBHA	Suberoyl-*bis*-hydroxamic acid
SOD	Superoxide dismutase
TIA	Terpenoid indole alkaloid
TILLING	Targeting induced local lesions in genomes
UDP	Uridine diphosphate

1 Introduction

Secondary metabolites in plants are defined as low molecular weight by-products of primary metabolism that are usually not directly involved in the primary growth of plants but play an immense role in crop protection or yield improvement by interacting with several biotic and abiotic factors. Secondary metabolites are produced from primary metabolites via various metabolic pathways under certain physiological conditions (Ahmed et al. 2017). According to Delgoda and Murray (2017), there are about 2,00,000 secondary metabolites of diverse chemical nature produced by different plants, though not all of them are biologically active. Their expression patterns are also differentially regulated by complex signaling pathways involving several enzymes and genes. Depending on their biological functions, secondary metabolites are grouped into several major classes. Plant growth regulators or phytohormones occupy an important group of secondary metabolites that can regulate growth and development and also aid in defense against a wide range of biotic and abiotic stresses (Erb and Kliebenstein 2020). Other major classes include nitrogen-containing compounds (alkaloids, cyanogenic glycosides and non-protein amino acids) terpenoids, phenolic compounds and sulphur-containing compounds (glucosinolates, defensin, phytoalexins, etc.) that directly or indirectly help in promoting crop improvement under several unfavourable environmental conditions. Diversity of plant secondary metabolites is also correlated with their multifaceted functional attributes, viz. protection against herbivores, pathogenic microorganisms and weeds, facilitating pollination and fertilization by attracting pollinators, establishing symbiotic association with mycorrhizal fungi and providing tolerance against environmental stress factors (Zhang et al. 2020a). Plant secondary metabolites also serve as excellent sources of pharmaceuticals, agrochemicals, food additives, flavouring agents, cosmetics and many other industrial products due to their effective antimicrobial, antioxidant, insecticidal and other beneficial properties (Tiwari and Rana 2015). The basic skeletons of all the secondary metabolites are synthesized via three major metabolic pathways, viz. shikhimic acid pathway, isoprenoid pathway or mevalonic acid pathway and the polyketide pathway, which are further modified by series of addition, deletion and substitution depending on the specific requirement (Teoh 2016). In general, plants produce secondary metabolites in very low concentrations, however, production increases under the adverse environmental condition that is attributed to increased stress tolerance. The complex interaction between several genes and transcription factors is known to be responsible for regulating the levels of secondary metabolite production in plants (Jan et al. 2021).

Crop production is influenced by a range of external and internal factors, viz. soil condition, temperature, light intensity, humidity, nutrient status, gene expression and regulation, signaling pathways, etc. Slight variation in any of these factors can cause significant alterations in the growth and yield of crops. Many advanced strategies have been adopted in the recent past to optimize crop yield throughout the year. Targeting secondary metabolite biosynthetic pathways is one such tool for yield improvement. Advancement in genetic engineering and biotechnological tools are being utilized to dissect the secondary metabolite biosynthetic pathways for decoding their specific functions in plants both in laboratory and field conditions. This review attempts to present an overview of major secondary metabolites in plants and their functions in plant growth and development. It also focuses on the advanced metabolic engineering techniques for their increased production and the problems for the implementation of these techniques in the agricultural sector.

2 Role of Secondary Metabolites in Plant Growth and Development

2.1 Phytohormones

Phytohormones play a significant role in plant growth and development (Table 1). They act as chemical messengers and target specific plant tissue to elicit certain physiological responses under several environmental conditions. For example, ethylene triggers the signaling pathway and interacts with other hormones for eliciting developmental responses. Ethylene is a gaseous hormone with a simple structure that regulates leaf development, flower development, fruit ripening, seed germination, etc. Dubois et al. (2018) showed that mutation in positive and negative regulators of the ethylene signaling pathway showed altered growth patterns. For example, the mutation in ethylene receptor proteins, viz. ETR1 and ERS1 showed decreased leaf growth, whereas overexpression of *Auxin-Regulated Gene involved in Organ Size* (*ARGOS*) and *ARGOS-LIKE* (*ARL*) caused a negative feedback regulation of ethylene

Table 1 An overview of the role of plant secondary metabolites in plant growth and development

Secondary metabolites	Role in plant development
Phytohormones	• Growth and development of vegetative organs, viz. stem, root and leaves • Flower initiation and development, fruit ripening, seed germination and post-germination developmental changes • Alleviation of environmental stresses by ROS scavenging, ion homeostasis, accumulation of osmoprotectants, increased activity of antioxidative enzymes, etc • Regulation of major metabolic pathways—photosynthesis, glycolysis, pyruvate metabolism, TCA cycle, shikimic acid pathway, alkaloid biosynthesis, etc.
Terpenoids	• Regulation of photomorphogenetic responses- choloroplast organization and chlorophyll biosynthesis, apical hook opening, expansion of cotyledons, root development, etc. • Increased insect pollination, decreased spread of weeds, increased resistance against pests, fungal and microbial pathogens • Biosynthesis of phytoalexins, prevention of oxidative damage, increased biomass production under stress condition
Coumarins	• Growth regulation of vegetative organs, increased nutrient uptake from the soil • Stimulate symbiotic association with mycorrhizae and growth of beneficial soil microflora • ROS scavenging, reduced lipid peroxidation and membrane destabilization, reduced Na^+ toxicity, increased activity of antioxidant enzymes under abiotic stress • Increased disease resistance
Flavonoids	• Growth promotion under stress condition • ROS scavenging, ion homeostasis, increased activity of enzymatic and non-enzymatic antioxidants, increased osmoregulation, reduced heavy metal toxicity • Enhanced resistance against insects, fungal and bacterial pathogens • Increased nutrient accumulation
Cyanogenic glycosides	• Accumulation and allocation of nitrogen in plants under stress condition • Stimulate growth and developmental responses under adverse environmental conditions • Increased defense against herbivores
Non-protein amino acid	• Reduce oxidative damage by preventing ROS formation, electrolyte leakage and lipid peroxidation • Confer stress tolerance by activation of antioxidative enzymes, maintaining osmotic balance and redox homeostasis, overexpression of heat-shock proteins • Increased chlorophyll content, photosynthetic efficiency, relative water content, regulation of carbohydrate and amino acid metabolism, regulation of expression of stress-responsive genes
Glucosinolates	• Promote root growth, chlorophyll content, biomass production • Increased osmoregulation, aquaporin synthesis, stomatal closure under drought condition • Increased resistance against fungal and bacterial pathogens

response and stimulated growth in *Arabidopsis* (Shi et al. 2015). Several reports are available depicting the complex interaction of ethylene with other phytohormones during growth and development. According to Iqbal et al. (2017), auxin stimulates endogenous ethylene biosynthesis and thereby regulates shoot apical meristem and leaf development in tomato and *Arabidopsis*. However, auxin-independent ethylene responses are also observed in common beans (*Phaseolus vulgaris*) (Keller et al. 2004). Ethylene also influences ABA sensitivity and acts synergistically with gibberellin during various stages of seed germination. Post-germination developmental changes, viz. apical hook formation, hypocotyl growth, root initiation, etc. are also found to be regulated by the combined interaction of phytohormones, viz. auxin, cytokinin, ethylene, jasmonic acid, salicylic acid and brassinosteroids via regulation of several genes and transcription factors like *YUCCA1*, *YUCCA5*, *HLS1*, HY5, MYC2, DELLA, etc. (Ahammed et al. 2020). Sami et al. (2019) reported the crosstalk between the phytohormones with glucose in modulating plant developmental responses via hexose-dependent and hexose-independent signaling pathways. ABA, BR, SA, auxin, ethylene and GA help to minimize the adverse effects of salinity stress by interacting with signaling molecules like

NO, ROS and Ca^{+2} and stimulate plant growth by maintaining ion homeostasis, reducing oxidative damage, upregulation of genes for secondary metabolite biosynthesis, accumulation of osmoprotectants, increased biomass production under several abiotic stress condition (Amir et al. 2019). Interaction of NO with phytohormones like cytokinin, ethylene and auxin resulted in increased salinity tolerance in *Lactuca sativa* by regulating Na^+ accumulation, antioxidant activities, mineral uptake and photosynthetic rate (Campos et al. 2019). Crosstalk between strigolactones and other phytohormone signaling pathways also led to plant growth promotion under normal and abiotic stress conditions by the formation of adventitious roots, regulation of shoot branching, inhibition of bud growth, promotion of secondary growth, leaf senescence, seed germination, internode elongation and nutrient uptake, etc. (Yang et al. 2019). Kumari and Parida (2018) showed that molecular crosstalk between ABA and JA brought about stomatal closure, reduced transpiration, regulation of major metabolic pathways, viz. glycolysis, pyruvate metabolism, TCA cycle, shikimic acid pathway, gluconeogenesis, alkaloid biosynthesis, etc. under saline condition. Exogenous application of gibberellic acid showed growth promotion in wheat cultivars by stimulating higher accumulation of proline along with the increased activity of Rubisco and antioxidant enzymes (peroxidase and superoxide dismutase) under saline conditions (Manjili et al. 2012).

2.2 Terpenoids

Terpenoids are the largest group of plant secondary metabolites and confer important roles in plant defense and crop vigour. Yu et al. (2018) reported the functional attribution of Terpenoid Indole Alkaloids (TIAs) during the process of photomorphogenesis in *Catharanthus roseus*. They observed the light stimulated activation of TIA biosynthetic enzymes and TIA accumulation (tabersonine, catharanthine, vindoline, vinblastine and vincristine) at the time of cotyledon opening. The combined interaction of auxin and cytokinin with terpenoid biosynthetic pathway in the morphogenesis and structural organization of chloroplasts in *Artemisia alba* has also been described by (Danova et al. 2018). Terpenoids were also known to improve the rate of plant reproduction and stimulate crop protection by increasing the rate of insect pollination, decreasing the spread of weeds and invader plants and reducing damages caused by pests and microbes in several agriculturally important crops, viz. apple, blueberry, tomato, etc. (Abbas et al. 2017). Terpenoid phytoalexins (zealexins and kauralexins) were known to induce root growth and biomass accumulation along with prevention of oxidative damage under various biotic and abiotic stress conditions (Akhi et al. 2021). Terpenes may also influence the expression of genes involved in plant defense mechanisms by acting as chemical messengers and regulating the adaptive features of plants under various biotic and abiotic stress (Zwenger and Basu 2008). For instance, 7-epizingiberene and R-curcumene were reported to increase insect resistance in tomatoes (Bleeker et al. 2011). β-caryophyllene could also induce resistance against microbial pathogens via jasmonic acid signaling, whereas isoprene and α- and β-pinene confer resistance via salicylic acid signaling in *Arabidopsis thaliana* (Frank et al. 2021). Wang et al. (2020) showed that sesquiterpenes secreted from glandular trichomes of wild tomato (*Solanum habrochaites*) could be responsible for conferring repellence against the potato aphid *Macrosiphum euphorbiae*. They highlighted the role of β-caryophyllene, α-humulene, α-santalene, α-bergamotene and β-bergamotene in affecting the survivorship and feeding behaviour of the aphid population. Capsidiol was known to be accumulated in *Nicotiana attenuata* in response to *Alternaria alternata* infection, and confer resistance against this fungal pathogen independent of jasmonic acid and ethylene signaling pathways (Song et al. 2019). Habash et al. (2020) evaluated the impact of a sesquiterpene, nootkatone against *Heterodera schachtii* parasitism on *A. thaliana*. They pointed out that nootkatone specifically decreased the number of nematodes and upregulated the defense-related genes involved in salicylic acid, jasmonic acid and ethylene biosynthetic pathways. The significance of terpenoids in plant growth and development is summarized in Table 1.

2.3 Phenolic Compounds

2.3.1 Coumarins

Coumarins are produced via phenylpropanoid pathway and involved in plant defense against pathogens, management of abiotic stresses and hormonal regulation. Coumarins along with reduced glutathione helped to ameliorate salinity stress and improve crop production in tomatoes by detoxifying ROS and methylglyoxal via enhancing the activities of glyoxalase enzymes (Table 1). Significant reduction in lipid peroxidation, membrane destabilization and Na^+ toxicity was also observed (Parvin et al. 2020). Sultana et al. (2020) also observed that the exogenous application of coumarin effectively enhances vegetative growth and antioxidant enzyme activities (catalase, ascorbate peroxidase and guaiacol peroxidase) in sorghum seedlings on exposure to different concentrations of NaCl. Conversely, regulation of seed germination by coumarins was also observed in *Brassica parachinensis* via the reduction in ROS accumulation and decreased GA biosynthesis (Chen et al. 2021). Coumarin accumulation was also shown to confer increased resistance in *A. thaliana* against soft rot causing bacteria

Dickeya spp. (Perkowska et al. 2021). Sarashgi et al. (2021) showed that coumarins present in root exudates of Brassicaceae plant species (*Brassica napus*, *Raphanus sativus* and *Sinapis alba*) play an important role in iron accumulation. Overexpression of genes involved in the coumarin biosynthetic pathway helped to mitigate the mycorrhizal incompatibility in *A. thaliana*. It was also experimentally proved that root secreted coumarins, especially scopoletin can improve pre-penetration signaling and established chemical communication between the host and the arbuscular mycorrhizal fungus *Rhizophagus irregularis* (Cosme et al. 2021). Coumarins were also known to promote lateral root growth in *A. thaliana* by inhibiting basipetal transport of auxin and altering microtubule cortical array organization (Bruno et al. 2021). Scopoletin exuded from roots could improve plant growth by establishing an association with rhizospheric microorganism *Pseudomonas simiae* and *Arabidopsis thaliana* (Stringlis et al. 2018). In vitro experiments with plant-derived coumarins showed improved soil characteristics and also stimulated the growth of beneficial soil microflora (Niro et al. 2016). Seed priming of *Vicia faba* with different concentrations of coumarin showed improved vegetative growth by the enhanced accumulation of primary and secondary metabolites, viz. carbohydrates, proteins, phytohormones, phenolics, etc. (Saleh et al. 2015). Abenavoli et al. (2004) showed that different concentrations of coumarin could affect root growth parameters in different types of maize seedlings in hydroponic cultures by regulating lateral root formation, root length and branching patterns. Coumarins also facilitate nitrate uptake from the soil, increased accumulation of nitrate in root cells and translocation of nitrates from root to shoot in durum wheat seedlings. The diameter of the xylem vessels of the root cells and the increased respiration rates were also found in response to coumarin treatment (Abenavoli et al. 2001).

2.3.2 Flavonoids

Flavonoids play a major role in plant growth in several adverse environmental conditions (Table 25.1). Liang and He (2018) experimentally demonstrated the protective role of nine anthocyanins, viz. pelargonidin 3-robinobioside, pelargonidin 3,5-di-(6- acetylglucoside), pelargonidin 3-(600-p-coumarylglucoside)-5-(6000-acetylglucoside), pelargonidin 3-(600-malonylglucoside)-7-(6000-caffeylglucoside), cyanidin 3-rutinoside, cyanidin 3-O-[b-DXylopyranosyl-(1->2)-[(4-hydroxybenzoyl)-(->6)-b-D-glucopyranosyl-(1->6)]-b-D-galactopyranoside], cyanidin 3-lathyroside, cyanidin 3-[6-(6-sinapylglucosyl)-2-xylosylgalactoside] and cyanidin 3,5-diglucoside (600,6000-malyl diester) during low nitrogen stress condition by enhancing seed germination rate in *A. thaliana*. Apigenin helped to mitigate the adverse effects of salinity stress by improving the activities of enzymatic (catalase and ascorbate peroxidase) and non-enzymatic antioxidants (carotenoids and flavonoids) and maintaining K^+/Na^+ homeostasis in rice seedlings (Mekawy et al. 2018). Li et al. (2019) observed that the MYB- stimulated enhanced synthesis and accumulation of flavonoids help to increase plant growth in *A. thaliana* under saline conditions. They elucidated that the overexpression of MYB transcription factor (MYB111) during salinity stress condition, in turn, activate the major enzymes of flavonoid biosynthesis, viz. chalcone synthase, flavanone carboxylase and flavanol synthase 1. Caliskan et al. (2017) have revealed the significance of phenolic compounds in salinity tolerance in *Hypericum pruinatum*. Their study showed increased accumulation of phenolics, viz. chlorogenic acid, rutin, hyperoside, isoquercetine, quercitrine and quercetine in salt-stressed plants. Similar enhancement in flavonoid biosynthesis was also observed in *Camellia sinensis* subjected to drought stress. The activation of enzymes, viz. chalcone synthesis1, cinnamate-4-hydroxylase, flavonoid 3′5′ hydroxylase and flavanone-3-hydroxylase lead to increased accumulation of a good number of flavonoids (myricetin, quercetin and kaempferol) that successfully ameliorate the adverse effects of drought and promote plant growth by maintaining cellular antioxidative status (Sun et al. 2020). Increased expression of three key enzymes of phenolic metabolism, viz. Shikimate Dehydrogenase (SKDH), Cinnamyl Alcohol Dehydrogenase (CAD) and Polyphenol Oxidase (PPO) associated with enhanced accumulation of phenolics could alleviate the adverse effects of Zn and Cd toxicity in *Kandelia obovata* (Chen et al. 2019). Phenolic acids and flavonoids (quercetin, catechin, apigenin, o-coumaric acid, luteolin, etc.) showed enhanced scavenging of free radicals like superoxide and peroxide anions, that in turn provide better insect resistance and antibiosis in winter triticale (Czerniewicz et al. 2017). Anthocyanin accumulation in leaves of *Euphorbia pulcherrima* showed higher antioxidant activities associated with tolerance against photo-oxidative stress (Moustaka et al. 2020). Oleuropein was known to protect salt-stressed olive plants by accelerating biomass production via increased antioxidative defense and osmoregulation (Petridis et al. 2012). Munné-Bosch and Alegre (2003) showed that the synergistic action of carsonic acid and α-tocopherol prevent oxidative damages and promote the growth of rosemary and sage plants under drought stress. A similar accumulation of anthocyanins and flavonols was observed in *A. thaliana*, which might be responsible for increased antioxidant activities in response to drought (Nakabayashi et al. 2014). UV-B LED light pre-treatment in lettuce showed enhanced accumulation of flavonoids that in turn helped to confer resistance against downy mildew (McLay et al. 2020). Constitutive expression of a UDP-dependent glycosyltransferase (OsUGT706C2) stimulated flavonoid biosynthesis in rice, which in turn contributed to UV-B tolerance and crop improvement

(Zhang et al. 2020b). Li et al. (2021) showed that increased flavonoid content helped to enhance antioxidant activity and crop yield in drought-affected maize plants. Overexpression of *GSA1* that encodes a UDP-glucosyltransferase which helped to regulate flavonoid accumulation, grain size and abiotic stress tolerance in rice (Dong et al. 2020).

2.4 Nitrogen-Containing Compounds

2.4.1 Cyanogenic Glycosides

Cyanogenic glycosides are by-products of amino acid metabolism and can produce toxic hydrogen cyanides by enzymatic hydrolysis. Siegień et al. (2021) showed that a higher accumulation of two major cyanogenic glycosides, namely linamarin and lotaustralin could function as nitrogen reservoirs in flax leaves under low nitrogen conditions. According to the studies of Sohail et al. (2020), dhurrin stimulated the rapid growth of germinating seedlings of sorghum and helped to adapt to dry climatic conditions by serving as a nitrogen source. In another experiment, Myrans et al. (2021) also showed that cyanogenic glycosides play a divergent role in the allocation of nitrogen according to their availability in wild and cultivated sorghum species that eventually contribute to plant defense against environmental stresses and also improve crop growth. However, according to Cuny et al. (2019), two cyanogenic glycosides (limanarin and lotaustralin) played a significant role in defense against herbivores rather than in growth promotion in *Phaseolus lunatus*.

2.4.2 Non-protein Amino Acids and Derivatives

Non-protein amino acids are generally referred to the amino acids other than the proteinogenic amino acids. γ-aminobutyric acid (GABA) is a well-known amino acid that rapidly accumulates in plant tissues under stress and known to regulate plant growth and development. GABA has been known to alleviate oxidative damage and denaturation of chlorophyll molecules under high-temperature stress by stimulating activities of antioxidant enzymes (SOD, CAT, POX, APX and GR), overexpression of heat-shock proteins, accumulation of osmolytes and by lowering electrolyte leakage and lipid peroxidation in *Agrostis stolonifera* (Zeng et al. 2021). Similar heat tolerance was also conferred by exogenous application of GABA in wheat seedlings by regulation of amino acid metabolism and maintenance of redox homeostasis that in turn help to grow the plants under such adverse environmental conditions (Wang et al. 2021). GABA signaling could modulate stomatal movement in leaves of *A. thaliana* and suffice optimum water resilience under drought stress. Overexpression of Glutamate Decarboxylase 2 gene (*GAD2*) in turn was found to be responsible for increased biosynthesis of GABA via Ca^{+2}/calmodulin signaling (Xu et al. 2021). Wu et al. (2020) also found that exogenous application of GABA into tomato plants helped to reduce Na^+ uptake and accumulation in roots and leaves, prevent ROS formation and lipid peroxidation and also improve plant growth under NaCl stress. Sita and Kumar (2020) pointed out the role of GABA in the alleviation of multiple abiotic stress factors in leguminous plants by modulating carbohydrate and amino acid metabolism and maintaining antioxidative mechanisms and membrane stability. In this context, Priya et al. (2019) also elaborated the thermo-protective effect of GABA on *Vigna radiata* by enhancement of reproductive function under high-temperature stress. Post-harvest exogenous application of GABA could mitigate the toxic impacts of low-temperature storage by reducing the activities of lipooxygenases and phospholipases and accelerating antioxidative activities of SOD and CAT in cucumber fruits (Malekzadeh et al. 2017). Dopamine, an amino acid derivative, could act as a signal molecule in plant growth and development and protect against various abiotic stresses by regulating the expression of major stress-responsive genes involved in senescence, chlorophyll degradation, nitrate transport, etc. (Liu et al. 2020). Dopamine application could increase biomass production of apple seedlings by enhancing the rate of photosynthesis and chlorophyll content and decreasing the accumulation of ROS under alkali stress (Jiao et al. 2019). Exogenous application of β-Aminobutyric Acid (BABA) has been shown to improve Relative Water Content (RWC), photosynthetic efficiency and antioxidant activities in *Vicia faba* through the over-expression of stress-responsive genes, *viz. VfGST, VfMYB, VfDHN, VfLEA, VfERF, VfNCED, VfWRKY, VfHSP* and *VfNAC* under drought stress (Abid et al. 2020). Kim et al. (2013) also studied the effect of BABA on seedling growth of Kimchi cabbage by inducing resistance against *Alternaria brassicicola* and *Colletotrichum higginsianum* (Table 1).

2.5 Sulphur-Containing Compounds

2.5.1 Glucosinolates

Glucosinolates are a group of plant secondary metabolites with S-β-d-glucopyrano unit anomerically connected to an O-sulphated (Z)-thiohydroximate (Blažević et al. 2020). Glucosinolates are found to be indirectly involved in crop improvement by increasing resistance against ZnO nanoparticle toxicity in *A. thaliana* (Tao et al. 2021). Tao and co-workers also showed that treatment with ZnO nanoparticles promoted increased accumulation of glucosinolates that in turn helped to mitigate the adverse effect of the nanoparticles on root growth, chlorophyll content and plant biomass. Glucosinolates like isothiocyanates, glucobrassicin, sinigrin, glucoiberin, etc. were known to confer greater resistance against a wide range of plant pathogens (*Rhizoctonia solani*, *Fusarium* sp., *Alternaria solani*, *Aspergillus flavus,* etc.) and indirectly involved in crop protection and improvement (Poveda et al. 2020). Eom et al. (2018) conducted a transcriptome analysis study to elucidate the role of glucosinolate metabolism in Chinese cabbage (*Brassica rapa* ssp. pekinensis) in response to drought stress. Differential expression of several drought-responsive genes, *viz. AP2/ERFs*, *bHLH*s, *NAC*s, *bZIP*s and particularly, *BrbZIP*s were found to be involved in improving plant tolerance by increased accumulation of glucosinolates in leaves and preventing water loss by inducing stomatal closure. In this connection, a marked increase in glucosinolate accumulation was also observed under the influence of drought and salinity stress in different Brassicaceae crops, *viz. Brassica rapa*, *B. juncea*, *B. oleracea*, *B. napus,* etc. (Essoh et al. 2020). It was also shown that the glucosinolates confer abiotic stress tolerance by the overexpression of *MYB* genes (especially MYB28 and MYB29), involved in increased aquaporin synthesis and osmoregulation (Essoh et al. 2020) (Table 1).

3 Strategies to Regulate Secondary Metabolite Production

Several strategies have been adopted to increase the production of secondary metabolites beneficial for crop growth and improvement (Fig. 1). A detailed account of these strategies is discussed in the following sub-sections and the major studies depicting the use of these elicitors in the improvement of crop plants are also enlisted in Table 2.

3.1 Chemical Elicitors

Exogenous application of plant growth regulators (salicylic acid and 24-epi-brassinolide) showed improved secondary metabolite production in *Brassica nigra* under salinity stress

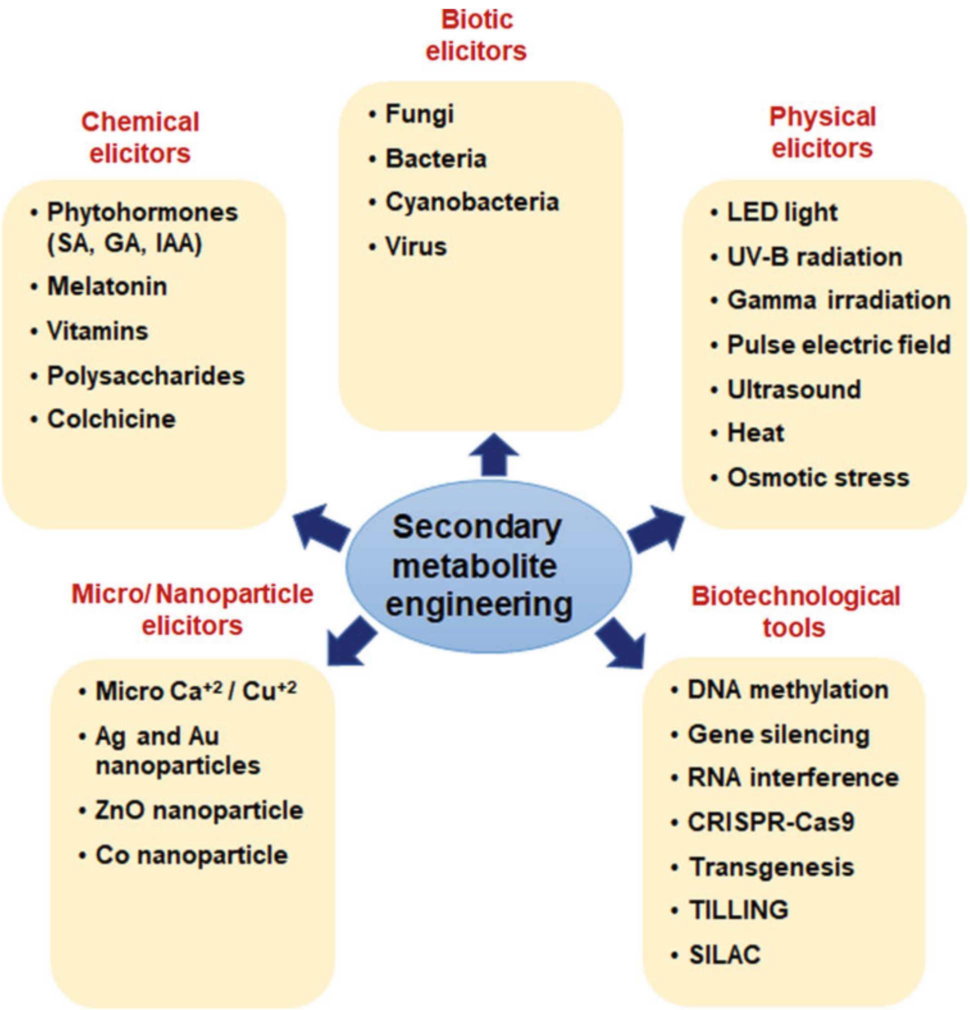

Fig. 1 Commonly known elicitors that are being used for the engineering of secondary metabolites in plants for the improvement of crop production

Table 2 Studies depicting the strategies to engineer secondary metabolite production in plants for crop improvement

Plant species	Approach used for elicitation	Effect on crop improvement	References
Arabidopsis thaliana	Overexpression of *TOGT1* gene	Enhanced scopoletin production	Wang and Hou (2009)
Arabidopsis thaliana	Complete pathway transfer of dhurrin biosynthesis from sorghum	Enhanced dhurrin production	Tattersall et al. (2001)
Arabidopsis thaliana	Heterologous overexpression of *PnJAZ1* gene from *Pohlia nutans*	Helped in seed germination and seedling growth under salt stress by regulating JA and ABA biosynthesis	Liu et al. (2019)
Arabidopsis thaliana	Heterologous overexpression of *CrUGT87A1*gene from *Carex rigescens*	Increased flavonoid accumulation, antioxidative activities and improved salinity tolerance	Zhang et al. (2021)
Atropa belladonna	Transgenesis and overexpression of *ODC* gene	Increased production of putrescine, N-methyl putrescine, hyoscyamine and anisodamine	Zhao et al. (2020)
Bambusa multiplex	Histone deacetylase inhibition by suberoyl bis-hydroxamic acid and trichostatin A	Increased production of 3-O-p-coumaroyl quinic acid and 3-O-feruloyl quinic acid	Nomura et al. (2021)
Brassica nigra	Exogenous application of gibberellic acid salicylic acid (1 mM) and 24-epi-brassinolide (0.1 μM)	Improved secondary metabolite production under salt stress	Ghassemi-Golezani et al. (2020)
Brassica rapa	Foliar application of thiamine (100 mM)	Enhanced secondary metabolite production, increased photosynthetic rate and antioxidant activity under drought stress	Jabeen et al. (2021)
Brassica rapa	Single amino acid modification of CAX1a transporter by TILLING technique	Increased IAA and GA content with improved salinity tolerance	Navarro-León et al. (2020)
Capsicum frutescens	Seed treatment with colchicine (300 mg/L) and oryzalin (30 mg/L)	Increased capsaicin production by tetraploid plants	Pilankong et al. (2017)
Catharanthus roseus	Application of PVP-coated cobalt nanoparticles (10, 15 and 20 mg/L)	Concentration-dependent increase in accumulation of alkaloids in cell suspension culture	Fouad and Hafez (2018)
Catharanthus roseus	Transgenesis and overexpression of geranyl diphosphate synthase and geraniol synthase	Increased accumulation of vindoline and catharanthine	Kumar et al. (2018)
Catharanthus roseus	Seed treatment with colchicine (0.2% aqueous solution)	Tetraploid explants showed increased production of terpenoid indole alkaloids along with an increased number of stomata and larger leaves	Xing et al. (2011)
Centella asiatica	Elicitation with *Colletotricum gloeosporioides*	Promotes biosynthesis of asiaticoside	Gupta and Chaturvedi (2019)
Convolvulus sepium, *Withania somnifera*, *A. thaliana*, *Tylophora tanakae*	Transgenesis and overexpression of fungal *crypt* gene	Enhanced biosynthesis of calystegine, withaferin, tylophorin, etc. in hairy root culture	Chaudhuri et al. (2009)
Coriandrum sativum	Regulation of photosynthetic photon flux density (300 μL) and root-zone temperature (30 °C)	Increased accumulation of phenolics and flavonoids and biomass production along with enhanced antioxidant activity	Nguyen et al. (2019)
Cuminum cyminum	Treatment with 2,4-D (2.5 mg/L) and kinetin (0.5 mg/L)	Increased essential oil synthesis and callus induction	Farvardin et al. (2017)
Datura metel, *Hyoscyamus muticus*	Transgenesis with tobacco *pmt* gene	Increased production of scopolamine (in *Datura*) and hyoscyamine (in *Hyoscyamus*) in hairy root culture	Moyano et al. (2003)
Dracocephalum forrestii	LED light (blue, red, blue + red and white) exposure	Increased phenolics and flavonoid content in shoot culture	Weremczuk-Jeżyna et al. (2021)
Echinacea purpurea	Exogenous application of gibberellic acid (0.025 μM)	Accumulation of caffeic acid and lignin in hairy root culture	Abbasi et al. (2012)

(continued)

Table 2 (continued)

Plant species	Approach used for elicitation	Effect on crop improvement	References
Echinacea purpurea	Treatment with ZnO microparticles (150 mg/L) and ZnO nanoparticles (75 mg/L)	Increased biomass and flavonoid accumulation in in vitro callus culture	Karimi et al. (2018)
Glycyrrhiza uralensis, *Tropaeolum majus*, *Ocimum basilicum*	UV-B treatment (280–320 nm)	Stimulated secondary metabolite biosynthesis	Yavas et al. (2020)
Helianthus annuus	Application of biofabricated silver nanoparticles with *Euphorbia helioscopia* leaf extract (60 mg/L)	Enhanced growth and secondary metabolite production	Batool et al. (2021)
Hyoscyamus reticulatus	Treatment with ZnO nanoparticles (100 mg/L)	Growth promotion and increased synthesis of hyoscyamine and scopolamine	Asl et al. (2019)
Hypericum perforatum	Treatment with dextran, pectin and chitin (100 mg/L)	Increased biosynthesis of hypericin and pseudohypericin in shoot culture	Simic et al. (2014)
Hypericum perforatum	Elicitation with *Colletotrichum gloeosporioides*, *Aspergillus niger*, *Fusarium oxysporum*, *Saccharomyces cerevisiae*, and *Botrytis cinerea*	Enhanced accumulation of xanthones, flavonoids and phenolics	Shakya et al. (2019)
Hypericum perforatum	Elicitation with *Agrobacterium tumefaciens*, *A. rhizogenes* and *Stenotrophomonas maltophilia*	Increased accumulation of flavonols, flavanols, lignin, etc	Shakya et al. (2019)
Lactuca sativa	Chitosan-coated microcapsules combined with calcium and copper ions and *Trichoderma viridae*	Enhanced secondary metabolite production and increased antioxidant activities	Jurić et al. (2020)
Leucojum aestivum	Exogenous melatonin treatment (10 µM)	Increased alkaloid content in in vitro cell culture	Ptak et al. (2019)
Lithospermum erythrorhizon	*Agrobacterium*-mediated transformation of *ubiA* gene from *E. coli*	Promotes shikonin production	Boehm et al. (2000)
Mentha spicata	Silencing of *MSYABBY5* gene	Enhances terpene biosynthesis in peltate glandular trichomes	Wang et al. (2016)
Nicotiana benthamiana	Heterologous expression of *IbC4H* gene from *Ipomoea batatas*	Enhanced polyphenol biosynthesis and increased antioxidant activity	Wang et al. (2017)
Nicotiana tabacum, *A. thaliana*	Overexpression of *PAP1* gene	Increased accumulation of flavonoids	Gantent and Memelink (2002)
Ocimum basilicum, *Origanum vulgare*	Exogenous application of IBA (0.1 mg/L) and BA (2 and 4 mg/L)	Increased phenolic content in vitro shoot culture	Karalija et al. (2016)
Panax ginseng	Exogenous application of linoleic acid and α-linolenic acid (5 µM/L)	Increased biosynthesis of ginsenoside along with biomass production	Wu et al. (2009)
Papaver somniferum	Silencing of *4'OMT2* gene	Increased biosynthesis of benzylisoquinoline alkaloids	Alagoz et al. (2016)
Papaver somniferum	Elicitation with poppy mosaic virus	Stimulates production of alkaloids—codeine, papaverine, narcotine, etc	Zaim et al. (2014)
Passiflora edulis	Elicitation with TMV, telosma mosaic virus and cucumber mosaic virus	Increased biosynthesis of polyphenols and flavonoids	Mishra et al. (2020)
Pelargonium spp., *Withania somnifera*	Homologous and heterologous overexpression of *DXS* gene from *Pelargonium*	Increased biosynthesis of essential oil (in *Pelargonium*) and withanolide (*Withania somnifera*)	Jadaun et al. (2017)
Prunella vulgaris	Application of silver and gold nanoparticles	Enhanced phenolic and flavonoids accumulation and increased antioxidant activity	Fazal et al. (2016)
Psoralea corylifolia, *Capsicum annum*, *Stevia rebaudiana*, *Panax ginseng*	Gamma irradiation (20 kGy)	Enhanced production of psoralen, capsaicinoids, stevioside and ginsenoside, respectively	Vardhan and Shukla (2017)

(continued)

Table 2 (continued)

Plant species	Approach used for elicitation	Effect on crop improvement	References
Rubia cordifolia	Transgenesis with *rol* genes	Stimulates increased biosynthesis of anthraquinones	Bulgakov et al. (2010)
Salvia dolomitica	Controlled exposure to drought	Increased production of terpenoids, phenolics and flavonoids	Caser et al. (2019)
Salvia miltiorrhiza	Inhibition of DNA methylation by 5-azacytosine (10 μM)	Increased phenolic acid biosynthesis in hairy root culture	Yang et al. (2018)
Salvia miltiorrhiza	CRISPR/Cas9 mediated targeted mutagenesis of *SmRAS* gene	Increased production of rosmarinic acid	Zhou et al. (2018)
Saussurea involucrata	Transgenesis and overexpression of *chi* gene from *Saussurea medusa*	Increased production of naringenin, apigenin and total flavonoid in hairy root culture	Li et al. (2006)
Solanum chrysotrichum	Cell immobilization within calcium-alginate gel beads (0.1 to 0.8 mol/L Ca and 1–1.5% w/v alginate)	Enhanced spirostanol production	Charlet et al. (2000)
Solanum tuberosum	Transgenesis and overexpression of *RIP* gene	Increased production of sesquiterpenes and glycoalkaloids	Matthews et al. (2005)
Solanum tuberosum	Induction of polyploidy by colchicine and oryzalin	Increased sesquiterpene production by tetraploid plants in vitro	Cara et al. (2020)
Stevia rebaudiana	Seed treatment with colchicine (0.6% aqueous solution)	Tetraploid plants showed increased stevioside production along with increased leaf size and chlorophyll content	Yadav et al. (2013)
Tanacetum parthenium	Treatment with ZnO nanoparticles (2000 ppm)	Increased production of terpenolide and essential oil, mineral absorption and crop yield	Shahhoseini et al. (2020)
Taxus chinensis	Application of pulse electric field (50 Hz, 10 V/m)	Enhanced taxuyunnanine C production	Ye et al. (2004)
Tripterygium wilfordii, Catharanthus roseus	Homologous and heterologous overexpression of class I TGA transcription factor from *Tripterygium wilfordii*	Stimulates biosynthesis of sesquiterpene and pyridine alkaloids	Han et al. (2020)
Vitis vinifera	Exogenous melatonin treatment	Promotes endogenous melatonin and flavonoid level coupled with fruit ripening	Xu et al. (2017)
Vitis vinifera	Elicitation with Grapevine red blotch-associated virus	Increased biosynthesis of flavonoids and anthocyanin	Blanco-Ulate et al. (2017)

(Ghassemi-Golezani et al. 2020). Application of Gibberellic Acid (GA_3) in hairy root cultures of *Echinacea purpurea* showed enhanced accumulation of caffeic acid derivatives and lignin (Abbasi et al. 2012). Indole Butyric Acid (IBA) and Benzyladenine (BA) also showed elevation in the accumulation of phenolics and flavonoids along with increased antimicrobial activity in *Ocimum basilicum* and *Origanum vulgare* (Karalija et al. 2016). 2,4-D and kinetin also showed increased essential oil synthesis in *Cuminum cyminum* (Farvardin et al. 2017). Exogenous application of melatonin has been shown to stimulate biomass production and accumulation of many Amaryllidaceae alkaloids (especially lycorine and galanthamine) in in vitro cell cultures of *Leucojum aestivum* (Ptak et al. 2019). Melatonin could also enhance phenolics and flavonoid content and antioxidant activity by upregulation of the *STS* gene and ethylene signaling in grape berries (Xu et al. 2017). Foliar application of vitamin B_1 (thiamin) also stimulated secondary metabolite production, antioxidant activity and growth promotion in *Brassica rapa*, subjected to drought stress (Jabeen et al. 2021). Polysaccharides such as dextran, pectin and chitin also acted as elicitors for the biosynthesis of phenolics, flavonoids and napthodianthrones (hypericin and pseudohypericin) in *Hypericum perforatum* shoot cultures (Simic et al. 2014). Exogenous application of essential fatty acids (linoleic acid and α-linolenic acid) also helped to elicit the production of phenolics, flavonoids and ginsenoside along with increased biomass production and antioxidant activity in *Panax ginseng*, cultured in bioreactors (Wu et al. 2009). Immobilization of cells of *Solanum chrysotrichum* within the calcium-alginate gel matrix showed significant enhancement in the production of antimycotic saponin—spirostanol (Charlet et al. 2000). Salicylic acid, jasmonic acid and methyl jasmonate also act as regulators of secondary metabolite biosynthesis in *Withania somnifera*, *Gymnema sylvestre*, *Panax ginseng,* etc. (Chodisetti et al. 2015; Sivanandhan et al. 2013; Thanh et al. 2005). According to Gantait and Mukherjee (2021), inhibition of spindle fibre formation or induction of polyploidy can also be considered effective in manipulating secondary metabolite production in several plants. They showed that treatment with colchicine and oryzanol in different culture conditions can significantly increase biosynthesis of alkaloids (capsaicin, vincristine, etc.), terpenoids (andrographolide, α-gualene, limonene, etc.), glycosides (stevioside, rebaudioside, bacoside etc.), lactones (artimisinin, wedelolactone, etc.) total phenolics, flavonoids (quercetin, kaempferol, chlorogenic acid, etc.) in several polyploid plant species—*Catharanthus roseus*, *Capsicum fruitescens*, *Aquilaria malaccensis*, *Sphagneticola calendulacea*, *Andrographis paniculata*, *Stevia rebaudiana*, *Bacopa monnieri*, *Eucommia* sp., *Citrus limon,* etc.

3.2 Physical Elicitors

Induction of light stress by exposure with LED lights of different wavelengths (blue, red, blue-red 30%:70% and white; λ = 430 nm, 670 nm, and λ€ = 430–670 nm) showed significant enhancement in the biosynthesis of phenolic and flavonoid derivatives (chlorogenic acid, caffeic acid, salvianolic acid, apigenin *p*-coumarylrhamnoside, methyl rosmarinate, etc.) in in vitro shoot culture of *Dracocephalum forrestii* (Weremczuk-Jeżyna et al. 2021). UV-B radiation was also found to induce biosynthesis and accumulation of flavonoids, tannins, isoprenoids, glucosinolates in *Glycyrrhiza uralensis*, *Tropaeolum majus*, *Ocimum basilicum* and many others (Yavas et al. 2020). Gamma irradiation also showed similar enhancement in biosynthesis and accumulation of psoralen in *Psoralea corylifolia*, capsaicinoids in *Capsicum annum*, stevioside in *Stevia rebaudiana*, ginsenoside in *Panax ginseng* by activating the key enzymes of secondary metabolism, viz. phenylalanine ammonia-lyase, chalcone synthase, squalene synthase, etc. (Vardhan and Shukla 2017). Ye et al. (2004) elucidated the efficiency of pulse electric field for stimulation of secondary metabolite biosynthesis in *Taxus chinensis*. Regulation of photosynthetic photon flux density and root temperature was shown to stimulate the biosynthesis and accumulation of total flavonoids, chlorogenic acid, rutin, trans-2-decenal in addition to increased antioxidant activity and crop yield in coriander (Nguyen et al. 2019). Caser et al. (2019) reported the implication of controlled drought conditions could modulate terpenoid, phenolics and flavonoid biosynthesis in *Salvia dolomitica*. Narayani and Srivastava (2017) reported similar elicitation of secondary metabolite production by several abiotic (heat shock, osmotic stress, ultrasound, ozone exposure, etc.) and biotic factors (extract of algae, fungi, bacteria, microbe-derived chitosan, pectin, cyclodextrin, etc.) in in vitro cell culture.

3.3 Microparticles and Nanoparticles as Elicitors

Sustainable utilization of chitosan-coated microcapsules combined with calcium and copper ions and *Trichoderma viridae* on the enhanced production of secondary metabolites and significant increments in antioxidant activities was observed in *Lactuca sativa* (Jurić et al. 2020). Application of silver and gold nanoparticles in callus culture of *Prunella vulgaris* showed enhanced production of phenolics and flavonoid content along with increased antioxidant activity (Fazal et al. 2016). Seedling treatment of *Tanacetum parthenium* with zinc oxide nanoparticles showed improved crop yield, mineral absorption along with the biosynthesis of essential oil and sesquiterpene lactones (parthenolide) (Shahhoseini et al. 2020). Nano ZnO also helped to increase root growth coupled with increased phenolic content, antioxidant activity and increased accumulation of tropane alkaloids (hyoscyamine and scopolamine) by upregulation of hyoscyamine-6-beta-hydroxylase (*h6h*) gene in *Hyoscyamus reticulatus* (Asl et al. 2019). Application of different concentrations of ZnO nanoparticles and microparticles on the *Echinacea purpurea* callus extract showed enhanced accumulation of flavonoids, which could be correlated with its anticancer activity (Karimi et al. 2018). Biofabrication of silver nanoparticles with the leaf extract of *Euphorbia helioscopia* showed enhanced growth parameters and secondary metabolite production in *Helianthus annuus*, in different developmental stages (Batool et al. 2021). Polyvinyl Pyrrolidone (PVP) coated cobalt nanoparticles also stimulated alkaloid biosynthesis in cell suspension culture of *Catharanthus roseus* under oxidative stress conditions (Fouad and Hafez 2018).

3.4 Biotic Elicitors

Elicitation of secondary metabolite production with the help of microbial extract was found to be useful in *Hypericum perforatum* (Shakya et al. 2019). The addition of cell culture filtrates of *Colletotrichum gloeosporioides*, *Aspergillus niger*, *Fusarium oxysporum*, *Saccharomyces cerevisiae*, and *Botrytis cinerea* have shown increased accumulation of xanthones, flavonoids and phenolic substances in shoot and suspension culture of *H. perforatum*. Apart from the fungal elicitors, several bacterial species, *viz. Agrobacterium tumefaciens*, *A. rhizogenes* and *Stenotrophomonas maltophilia* also showed the enhanced synthesis of flavonol, flavanol, lignin and other phenolics in *H. perforatum* (Shakya et al. 2019). A Co-cultivation system using an endophytic fungus *Colletotrichum gloeosporioides* stimulated the biosynthesis of asiaticoside content in *Centella asiatica* (Gupta and Chaturvedi 2019). Many cyanobacterial genera, viz. *Synechocystis*, *Synechococcus* and *Anabaena* are successfully transformed with plant-derived genes to produce important secondary metabolites like- limonene, p-coumaric acid, caffeine, carotenoid, etc. (Xue and He 2015). Viral infection often acted as elicitors for secondary metabolite production in the host plants. For example, cucumber mosaic virus elicits the production of polyphenols and flavonoids in *Passiflora edulis,* Grapevine red blotch-associated virus elicits flavonoid and anthocyanin synthesis in *Vitis vinifera*, poppy mosaic virus elicits alkaloid production in *Papaver somniferum*, etc. (Mishra et al. 2020).

3.5 Biotechnological Approaches

3.5.1 Regulation at DNA Level

Epigenetic regulation (DNA methylation, histone modification, RNAi transcription) of selected metabolic pathways was also found to be significant for modulation of secondary metabolites production in the plant cell (Brzycki et al. 2021). Yang et al. (2018) have confirmed the role of a DNA methylation inhibitor (5-azacytosine) in increasing the expression of major genes involved in phenolic acid biosynthesis in *Salvia miltiorrhiza*. However, the opposite result was observed when a donor for DNA methylation, SAM (S-adenosyl methionine), was added. Similarly, treatment of suspension culture of *Bambusa multiplex* cells with two histone deacetylase inhibitors (SBHA and trichostatin A) showed enhanced biosynthesis of cryptic secondary metabolites (Nomura et al. 2021). Gene silencing approaches through RNA interference are also extensively used to enhance the production of plant secondary metabolites for crop improvement (Rajam 2020). The silencing of a novel gene (*MSYABBY5*) showed increased terpene biosynthesis in the peltate glandular trichome of *Mentha spicata*. On the contrary, heterologous expression of *MSYABBY5* repressed secondary metabolite production in *Ocimum basilicum* and *Nicotiana sylvestris* (Wang et al. 2016). Attempts have also been made through gene silencing via RNA interference by topical application of dsRNA (Deguchi et al. 2020).

3.5.2 Transcriptional Regulation and Transgenesis

Transcriptional regulation of *MYB* and bHLH protein-encoding genes (*C1* and *R*), AP2/ERF-domain transcription factor ORCA3, DREB2A and DREB2B proteins are also being successfully implemented in *Catharanthus roseus*, *Arabidopsis thaliana* and several other plants for engineering biosynthesis of anthocyanins, flavonoids, terpenoid indole alkaloids, etc. (Memelink et al. 2001). Overexpression of genes of secoiridoid pathway (geraniol synthase and geranyl diphosphate synthase) stimulated the accumulation of commercially important monoterpene indole alkaloids (vindoline and catharanthin) in transgenic *C. roseus* (Kumar et al. 2018). Similar overexpression of ornithine decarboxylase (*ODC*) gene showed increased biosynthesis of tropane alkaloids, *viz*. putrescine, N-methyl putrescine, hyoscyamine and anisodamine in *Atropa belladonna* hairy root cultures. Transcriptional and post-transcriptional regulation of several transcription factors, viz. WRKY, MYB, bHLH, APETALA2/Ethylene Responsive-Factor (AP2/ERF), Jasmonate-responsive ERF (JRE), Basic Leucine Zipper (bZIP), SQUAMOSA Promoter-binding protein-Like (SPL), etc. could help modulate the biosynthesis of several classes of terpenoids and flavonoids—monoterpenes, sesquiterpenes, diterpenes, triterpenes, steroidal lactones, etc. in several crop species (Nagegowda and Gupta 2020). Similarly, homologous and heterologous overexpression of class I TGA transcription factor from *Tripterygium wilfordii* stimulated the biosynthesis of sesquiterpene and pyridine alkaloids (Han et al. 2020). *Agrobacterium*-mediated transgenesis of cannabinoid-synthesizing genes was also successfully applied for increased metabolite production in hemp (*Cannabis sativa*) in tissue culture. Manipulation of the shikonin biosynthetic pathway with the introduction of the 4-hydroxybenzoate-3-polyprenyltransferase (*ubiA*) gene from *E. coli* had successfully enhanced shikonin production in *Lithospermum erythrorhizon* (Boehm et al. 2000). Activation of cryptic gene clusters by co-cultivation or epigenetic modification of several endophytes (*Fusarium mairei*, *Trichoderma atroviridae*, *Enterophosphospora* sp., etc.) also helped in large-scale production of high-value plant secondary metabolites like taxol, berberine, camptothecin, vincamine (Venugopalan and Srivastava 2015).

According to Chandra and Chandra (2011), the formation of hairy root lines by the transformation of T-DNA from *Agrobacterium rhizogenes* could offer a useful strategy for the increased production of secondary metabolites. For instance, incorporation of the chalcone isomerase (*chi*) gene from *Saussurea medusa* into the genome of *Saussurea involucrata* showed increased production of naringenin, apigenin and total flavonoid content. Moreover, binary vectors formed by combining the T-DNA of the Ri-plasmid and putrescine N-methyltransferase (*pmt*) gene showed enhanced production of scopolamine and hyoscyamine by upregulation of tropane alkaloid biosynthetic pathway in *Datura metel* and *Hyoscyamus muticus* (Moyano et al. 2003). Transformation of *Rubia cordifolia* hairy root cultures with *rol* genes boosted the plant cells for increased production of secondary metabolites (Bulgakov et al. 2010). Transgenic *A. belladonna* also showed enhanced biosynthesis of hyoscyamine and anisodamine due to overexpression of the *ODC* gene (Zhao et al. 2020). Transgenic mimicry of pathogen attack could also lead to increased secondary metabolite production in several crop species, suggesting a suitable method for eliciting defense responses in plants. *A. rhizogenes* mediated transfer of fungal β-cryptogein gene (*crypt*) resulted in improved growth and enhanced accumulation of calystegine, polyphenols, withaferin, tylophorin, etc. in *Convolvulus sepium*, *Withania somnifera*, *A. thaliana* and *Tylophora tanakae* (Chaudhuri et al. 2009). Genetically modified potato cultivars constructed using Ribosome-Inactivating Protein-coding gene (*RIP*) from maize, showed enhanced synthesis and accumulation of sesquiterpenes and glycoalkaloids under a range of biotic and abiotic stress conditions (Matthews et al. 2005). Adventitious root culture using bioreactors is considered useful for large-scale production of plant secondary metabolites, viz. ginsenoside, resveratrol, camptothecin, vindoline, etc. (Kumar 2015). Catalytic synthesis of glycoconjugate involving the multigene superfamily of glycosyltransferases can also be employed in the production and modification of plant secondary metabolites. For instance, reduced expression of Tobacco Glycosyltransferase (TOGT) in transgenic tobacco plants showed decreased glycosylation of scopoletin that impaired resistance against TMV. Whereas overexpression of the *TOGT1* gene led to increased resistance against Potato Virus Y by enhancing scopoletin synthesis (Wang and Hou 2009). Transgenic overexpression of *1-deoxy-D-Xylulose-5-phosphate Synthase* (*DXS*) gene from *Pelargonium* spp. showed enhanced production of secondary metabolites in both homologous (essential oil in *Pelargonium* spp.) and heterologous conditions (withanolide in *W. somnifera*) (Jadaun et al. 2017). Heterologous expression of cinnamate 4-hydroxylase gene from *Ipomoea batatas* (*IbC4H*) showed enhanced drought tolerance associated with increased polyphenol biosynthesis and antioxidative activities in transgenic tobacco (Wang et al. 2017). Liu et al. (2019) showed that overexpression of a jasmonate ZIM-domain gene from a moss *Pohlia nutans* (*PnJAZ1*) in *A. thaliana* regulated ABA signaling pathways and induced seed germination and seedling growth under salinity stress. Overexpression of an anthocyanin-producing gene (*production of anthocyanin pigment 1*, *PAP1*) showed enhanced accumulation of anthocyanin by regulating the enzymes of flavonoid biosynthetic pathways in *Nicotiana tabacum* and *A. thaliana* (Gantet and Memelink 2002). Ma et al. (2019) reported the efficient application of a fungal host *Yarrowia lipolytica* for the heterologous synthesis of plant terpenoids by the introduction of terpene synthase and modifying the mevalonate pathway. Nascimento and Fett-Neto (2010) pointed out the effective transformation of entire plant-derived metabolic pathway genes from one species to another. For instance, complete pathway transfer of cyanogenic glycoside dhurrin from *Sorghum bicolor* to *Arabidopsis thaliana* was carried out successfully for increased herbicide resistance (Tattersall et al. 2001). Zhang et al. (2021) reported that overexpression of a UV-B responsive UDP-sugar glycosyltransferase gene from *Carex rigescens* (*CrUGT87A1*) showed increased salinity tolerance in *A. thaliana* by stimulating flavonoid biosynthesis and antioxidative activity. Bleeker et al. (2012) successfully transfer the biosynthetic pathway to produce a sesquiterpene (7-epizingiberene) from the wild tomato into a greenhouse cultivated variety for enhanced herbivore resistance.

3.5.3 Molecular Engineering Techniques

Several reports are depicting the significant contributions of molecular engineering approaches in the modulation of secondary metabolite biosynthesis for crop improvement. Sabzehzari et al. (2020) have demonstrated the significance of Clustered Regularly Interspaced Short Palindromic Repeat (CRISPR)-mediated transcriptional regulation of secondary metabolite production in several crop plants by silencing the enzymes of biosynthetic pathways. In this context, genome editing of *4′OMT2* (3′-hydroxyl-N-methylcoclaurine 4′-O-methyltransferase) gene by CRISPR/Cas9 system helped in mass production of bioactive benzylisoquinoline alkaloids (papaverine, codeine, thebaine, laudanosine, noscapine, s-reticuline and morphine) in *Papaver somniferum* by converting them into biofactories (Alagoz et al. 2016). Genome editing of *SmRAS* (rosmarinic acid synthase) gene through CRISPR/Cas9 helped in regulating the biosynthetic pathway in *Salvia miltiorhiza* (Zhou et al. 2018). Genetic manipulation of Morphogenic Regulator (*MR*) gene during somatic embryogenesis was found to be helpful in increased production of cannabinoids in vitro. Targeting Induced Local Lesions In Genomes (TILLING) mutation technique of cation/H^+ exchangers transporters showed improved salinity tolerance and crop growth in *Brassica rapa* by influencing phytohormone signaling and ion homeostasis (Navarro-León et al. 2020). Stable Isotope Labelling by Amino acids in Cell culture (SILAC) approach was successfully employed for enhancing the secondary metabolism pathways in plants (Martínez-Esteso et al. 2015). Multiple Reaction Monitoring (MRM) would also be an innovative approach in targeting the key enzymes and transporter proteins of plant secondary metabolic pathways for enhanced production and crop improvement (Martínez-Esteso et al. 2015). Isolation of plant extracellular vesicles and nanovesicles from different plant sources have also been proved to be useful for plant bioprocess engineering of secondary metabolite production (Woith et al. 2021). Wany et al. (2014) mentioned the significance of functional genomic approaches for enhancing secondary metabolite production via antisense- or sense gene suppression of metabolic pathways, production of novel compounds, regulation by compartmentalization in many plants (*A. thaliana*, *Ocimum americanum*, etc.). Jain et al. (2013) mentioned that cell suspension culture in bioreactors could be helpful for large-scale bioproduction of saponins from *Bacopa* *monnieri*. Biotechnological approaches were applied to identify and characterize the genes responsible for climate resilience (*SiATG8a*, *SiASR4*, *SiMYB56*, *EcbZIP17*, *EcGBF3*, *PgNAC21*, *PgeIF4A,* etc.) in millets and were successfully introduced into several crop plants (tobacco, rice, *Arabidopsis,* etc.) for improved stress tolerance and crop performance (Singh et al. 2021). Ferrari (2010) summarized the importance of the data pool retrieved from transcriptomics, proteomics and metabolomics for developing novel techniques of secondary metabolite production. Careful dissection of the signaling network could offer a detailed understanding of elicitor induction for the modulation of metabolic pathways.

4 Constraints of Plant Secondary Metabolite Production and Future Prospects

A large number of external and internal factors regulate the biosynthesis of secondary metabolites in plants. Verma and Shukla (2015) have classified the factors into four broad categories—genetic, ontogenic, morphogenetic and environmental factors. The complex interplay between these factors, in turn, affects plant secondary metabolism in several different manners. Metabolic engineering of secondary metabolite biosynthetic pathways has faced some challenges regarding the desired concentration, bioavailability, absorption criteria and bioactivity of the compounds specifically used as food products (Davies and Espley 2013). In this connection, Nascimento and Fett-Neto (2010) pointed out some major drawbacks of developing novel engineering strategies for plant secondary metabolite production. These include—lack of availability of sustainable plant sources, constraints regarding transformation and regeneration, proper evaluation of synthesis and accumulation in different developmental and environmental conditions, problems in proper identification of metabolic intermediates, difficulties in separating the actual plant metabolic reactions from that of the endophytes or plant–endophyte interaction and the lack of knowledge regarding the intracellular and intercellular transport mechanism of secondary metabolites in the plant. Plant tissue and organ culture have been successfully employed for large-scale production of medicinally important plant secondary metabolites for many years. However, the culture conditions, media requirements, cultivation techniques showed great variation in yield and quality of the final products (Isah et al. 2018). Large-scale production of secondary metabolites is still not obtained by using cyanobacterial biofactories due to the absence of specific proteins and transcription factors required for post-translational modifications of some enzymes involved in plant secondary metabolism (Xue and He 2015). Tiago et al. (2017) pointed out several limitations regarding the production of secondary metabolites in plants, viz. complex interaction of soil and environmental factors on the biosynthesis of secondary metabolites, pleiotropy of genes encoding the biosynthesis of secondary metabolites, multiple regulations of biosynthetic genes, obtaining superior genotypes, toxicity symptoms, etc. According to Brzycki et al. (2021), a combination of traditional approaches such as metabolic engineering and cellular engineering techniques with modern targeted epigenetic engineering could overcome the production deficit of secondary metabolites in plants. Recently, the extensive use of mathematical modelling approaches like Response Surface Method (RSM), Artificial Neural Network (ANN), Kriging and the ANN-RSM combined approach in plant biotechnology helped to maximize the yield of secondary metabolites by selecting high-performance cell lines, optimizing the culture conditions and improving cell permeability (Amdoun et al. 2021). Decoding the mechanism of induction of plant secondary metabolite production in response to environmental stresses and increased resistance against herbivores would help to optimize the targeted gene manipulation for achieving enhanced crop yield (Kessler and Kalske 2018).

5 Conclusion

Secondary metabolites play a significant role in plant growth and affect crop production in various ways. Biosynthesis and the function of plant secondary metabolites are tightly regulated by several genes and transcription factors that are involved in complex crosstalks between them. Biotic and abiotic elicitors stimulate the biosynthesis of secondary metabolites by different molecular mechanisms. Overexpression of these transcription factors by differential expression of these genes, modification at the transcriptional and translational level, induction and maintenance of polyploidy, production of new transgenic crops, use of nanoparticles, etc. are considered effective engineering approaches in increasing secondary metabolite production for crop improvement. Although there are some concerns regarding the sensitivity and specificity of these techniques, several reports are available citing successful implementations of genetic engineering approaches towards crop improvement. Future scope lies in a detailed understanding of the signaling cascade of the secondary metabolites and their specific molecular interaction with the other components responsible for plant growth and development.

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Interventions of Nanotechnology for the Growth and Stress Tolerance in Crop Plants

Mahima Misti Sarkar, Ashis Sarkar, and Swarnendu Roy

Abstract

Agriculture is one of the important sources to fulfill the demand of human food requirements. The conventional methods of increasing crop production presently depend upon chemical substances, which are harmful to the environment as a major proportion of the applied chemicals get accumulated in the environment. Therefore, a sustainable and environment-friendly method to produce food from comparatively diminishing agricultural fields to feed the rapidly growing world population is the need of the hour. To address the present scenario, nanotechnology has emerged as a potential tool for the development of sustainable and productive agricultural systems. Nanoparticles owing to their tiny size and surface chemistry are relatively easier to be absorbed by plants and most importantly impart negligible toxic effects on the agricultural system. The other advantages of using nanoparticles lie within their flexibility in shape, size, solubility, and other features, which make them a suitable carrier for beneficial agrochemicals. Therefore, this chapter will focus on the different types of nanoparticles available, their mechanism of uptake, and their potential to stimulate crop improvement either by directly boosting the plant growth or by indirectly managing the losses incurred due to the effects of abiotic or biotic stresses.

Keywords

Abiotic stress • Biotic stress • Crop yield • Functionalization • Nanotechnology • Surface chemistry

Abbreviations

AgNPs	Silver nanoparticles
APX	Ascorbate peroxidase
CAT	Catalase
CBN	Carbon-based nanomaterials
EL	Electrolyte leakage
HANPs	Hydroxyapatite nanoparticles
MDA	Membrane lipid peroxidation
MgONPs	Magnesium oxide nanoparticles
MSI	Membrane stability index
MWNTs	Multi-walled nanotubes
NPK	Nitrogen–phosphorus–potassium
NPs	Nanoparticles
PAL	Phenylalanine lyase
POX	Peroxidase
PPO	Polyphenyl oxidase
PR	Pathogenesis-related gene
ROS	Reactive oxygen species
RWC	Relative water content
SA	Salicylic acid
SiNPs	Silica nanoparticles
SOD	Superoxide dismutase
STE	Sieve-tube elements
SWNTs	Single-walled nanotubes
TiO_2NPs	Titanium dioxide nanoparticles
TMV	Tobacco mosaic virus
ZnONPs	Zinc oxide nanoparticles

1 Introduction

The transition of the human race from hunter-gatherers to builders of modern hi-tech cities came along in centuries and we as humans have been constantly driving life-changing innovations to improve every aspect of our life. Among these, the introduction of agriculture has been certainly decisive in ensuring food security and thus has greatly influenced the development of human civilization (Balkrishna et al. 2021). Although a steady and ascending advancement has been inducted since the beginning of

M. M. Sarkar · A. Sarkar · S. Roy (✉)
Plant Biochemistry Laboratory, Department of Botany, University of North Bengal, Raja Rammohunpur, Darjeeling, India
e-mail: swarnendubotany@nbu.ac.in

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agriculture, the past century has witnessed very fast agricultural innovations like mechanization, marker-assisted breeding, and the development of transgenic crops (Moulick et al. 2020). By 2050, the human population is expected to touch the 10 billion mark, therefore, approximately 50% more food would be required to sustain the global population (Mora et al. 2020). The current agricultural approaches seem to be non-supportive for feeding this ever-growing human population due to various rising concerns, viz. continuous reduction of soil fertility, water availability; increased proliferation of pathogens and pests, toxic chemicals in soil, climate change, etc. (Moulick et al. 2020). To counteract these adversities researchers have focused on improving the soil health, microbiome, biofertilizers, biopesticides, bio fungicides, etc. In this connection, the "smart agriculture" approach is gaining importance which advocates for the development of safer and potent pesticides, remote sensors, next-generation bio-sensors to monitor soil health, satellite technology, etc. (Moulick et al. 2020; Mora et al. 2020).

Among the current scientific progressions, nanotechnology has emerged as an impending tool for solving the global food crisis. Nanotechnology essentially refers to the study of nanosized (1–100 nm) materials, which can exist in liquid, gaseous, or solid states (Buzea et al. 2007; Ghosh and Pal 2007). The nanosized materials usually exhibit some unique properties due to their "small size effect", "quantum effect", "macroscopic quantum tunnelling effect", and "surface effect" (Hu and Xianyu 2021). Nanomaterials hold some exclusive physicochemical properties and great flexibility to associate with various biomolecules along with other nanomaterials (Sanzari et al. 2019). The term "nanoparticles" has been introduced by Norio Taniguchi in the early 1970s, whereas the traces of nanoparticles (NPs) in nature can be found as early as thousand years back (Pramanik et al. 2020). In recent times, NPs are gradually gaining attention for their variety of agronomical applications and their role in the improvement of crop productivity. Several studies have reported that the metal-based NPs have been extensively used in agriculture as fertilizers, antimicrobial and antifungal agents to increase crop yield (Panáček et al. 2009; Rizwan et al. 2017; Rajput et al. 2018a; Huang et al. 2018). The role of NPs in abiotic stress management has also been well studied in many plants and has shown promising results, e.g., NPs of zinc oxide, copper oxide, silicon dioxide, etc. potentially improved crop productivity by reducing the negative effects of heavy metals and drought stress (Biju et al. 2017; Cui et al. 2017; Hussain et al. 2018; Rajput et al. 2018b). Recent advancements in analytical techniques and bioinformatics tools or "omics approaches" gave insight into the molecular mechanisms and also bestowed the status of metabolites, proteins, and genes in plants under biotic and abiotic stress (Kumar et al. 2015). The application of engineered nanomaterials in "omics"-based approach or system biology can deliver illustrious output in agronomical research via sensitive and precise screening of the biomolecules like metabolites (metabolomics), proteins (proteomics), mRNA (transcriptomics), and genes (genomics) in an organism (Quanbeck et al. 2012; Majumdar and Keller 2020).

Several studies have suggested that the interaction between plants and NPs is immensely complex and dynamic. The effect of NPs on plants depends on several factors such as the method of administration, stability, transformation, bioavailability, aggregation, application media, interaction efficacy of NPs with plant and soil, toxicity, and the fate of NPs in the environment (Bradford et al. 2002; Hotze et al. 2010; Lin et al. 2010a, b; Amde et al. 2017; Yadav et al. 2018). The uptake, translocation, and accumulation of NPs inside the plant deeply rely on various aspects like size and shape of NPs, physicochemical properties of the NPs, application methodologies, environmental components (soil, water, microbes), plant physiology, and anatomy (Pérez-de-Luque 2017; Sanzari et al. 2019). Besides, the location of applied NPs and their positive roles in plants has been elucidated through advanced imaging techniques e.g., single particle inductively coupled plasma mass spectrometry (sp-ICP-MS) and synchrotron-based imaging, advanced electron microscope (Castillo-Michel et al. 2017; Keller et al. 2018; Avellan et al. 2019). This book chapter provides an overview of the types of agronomically useful NPs, their current status, applications in crop improvement under stress, and futuristic applications.

2 Status of the Use of Nanotechnology in Crop Improvement

Nanotechnology is emerging in its great role to fulfill the nutrition needs of crops. Nowadays, nanonutrition is emerging as a promising tool in the agricultural sector and thus exploring the potential of nanoparticles in this context is of great interest (Ditta and Arshad 2016). Nanoparticles have been examined to have a tremendous impact on plant growth by regulating the primary and secondary metabolism (Jasim et al. 2017). In the agricultural field, nanotechnology is emerging as an alternative tool to reduce agricultural inputs, enhance food value, improve shelf life with improved nutrient contents, maintain freshness and quality of food, enhance micronutrients, and antioxidant absorption (Kanjana 2015). Nanoparticles are believed to confer novel applications in various aspects like crop management, crop improvement, protection of crops through genetic modulations, controlled release of agrochemicals (nutrients, fertilizers, pesticides, herbicides), target-specific delivery of biomolecules, detection of diseases and pests, seed management and their protection from pathogens (Chinnamuthu and Boopathi 2009). The advancement of nanotechnology is currently directed toward the development of nanosensors for monitoring soil conditions, nutrition availability, management of pathogen and pests, detection of hazardous or toxic substances, and also other environmental factors associated with plant growth and development (Cheng et al. 2016). Nanosensors can be used effectively to deliver fertilizers, microelements, growth-promoting biomolecules, pesticides, etc. to ensure healthy crop production without compromising product quality and also assuring the development of sustainable agricultural practices (Cheng et al. 2016). Nanosensors are also used as a detecting agent of plant pathogens using DNA, antibody, and volatile compounds as biosensing receptors. Nanosensors are a reliable method of disease detection because it is nondestructive, economical, minimally invasive, and easy-to-use systems with enhanced detection limit, specificity, sensitivity, and on-site detection of plant pathogens (Kashyap et al. 2019). Nano fertilizers can be synthesized either by the encapsulation of nutrient molecules within porous nanomaterials or by surface coating of nanomaterials by nutrient molecules. Nanopesticides or nanoplant protectors are nanomaterial-based developments that confer plant protection against pathogens, insects, and weeds, increasing their effectiveness and durability (Kumari et al. 2020). Nano formulation of any substance prevents undesirable loss by avoiding their interaction with soil, air, water, and microorganisms and thus prevents the leaching, evaporation, or even the degradation of the substances outside the plant body (Shang et al. 2019). But for the vast application of nanoformulation, further ecotoxicological studies along with a correct and safe application strategy of nanomaterials in agriculture need to be formulated (Bratovcic et al. 2021).

3 Nanoparticles and Their Types

Commonly studied nanomaterials are commercially produced by humans, while some nanoparticles are also unintentionally created during various natural processes such as degradation by the volcanic eruption, water, wind current, etc. (Panpatte et al. 2016). The formation of nanomaterials commonly follows two major processes, i.e., "top-down" (creation of nanomaterials from macro-size materials by physical method) and "bottom-up" (atomic and molecular rearrangement which gives rise to nanoscale materials by chemical or biological method) (Das and Das 2019). These nanoscale materials can be present in various shapes (tubular, spherical, or asymmetrical), form (one, two, or three dimensions), arrangement (solitary, multiple, or aggregated), and surface chemistry (presence and absence of charge or free groups). In general, the nanoparticles can be categorized into three major groups, i.e., polymeric, metals, and nonmetals (Fig. 1).

3.1 Polymeric NPs

3.1.1 Liposomes and Micelles

Liposomes are lipid-based vesicles commonly synthesized by hydration of dry phospholipids and can be created in various sizes, structures, and compositions. The foremost aim to use liposomes is their competency to fuse with cell membranes and deliver their fillings directly inside the cytoplasm (Ealia and Saravanakumar 2017). Thus, different therapeutic molecules (both hydrophobic and hydrophilic) can be filled inside the hollow core of the lipid layer and delivered to the targeted site (Oberholzer and Luisi 2002; Patil and Jadhav 2014). There are major three types of liposomes, i.e., small unilamellar, large unilamellar, and multilamellar classified based on the number of lipid bilayers. Furthermore, the feasibility of surface modifications with other polymers or polyethylene glycol (PEG) chains gives an upper hand in the target-specific efficient delivery of different molecules (Gabizon et al. 1994). Apart from liposomes, a few other nanostructured polymeric NPs, e.g., micelle, microemulsions, nanoemulsions have been currently gaining attention in agronomical research due to their commendable role as a nanodelivery system for different molecules like enzymes, nutrients, food antimicrobials, nutraceuticals, etc. (Srinivasan et al. 2019).

3.1.2 Dendrimers

Dendrimers are organic polymers (polyamidoamine, polypropylene imine, polyether-copolyester, peptide) and well-studied NPs for their unique features like higher monodispersity, hyper branching, compartmental structures, etc. Their branch number can be adjusted and ranges in size from 1 to 5 nm (Caminade et al. 2012; Ealia and Saravanakumar 2017). In recent times, these polymeric NPs have been extensively used in various therapeutic approaches. Moreover, some assembled dendrimers are capable of encapsulating various biologically active components and delivering them to the targeted sites to enhance disease resistance and stress tolerance to improve agricultural productivity (Chauhan et al. 2020; Sikder et al. 2021).

3.1.3 Nanogels

Another polymeric or nonfluid colloidal nanomaterial (based on amphiphilic polysaccharides, cholesterol, etc.) that swells and forms gels when it comes in contact with fluids, is regarded as nanogels. The diameter of nanogels typically lies

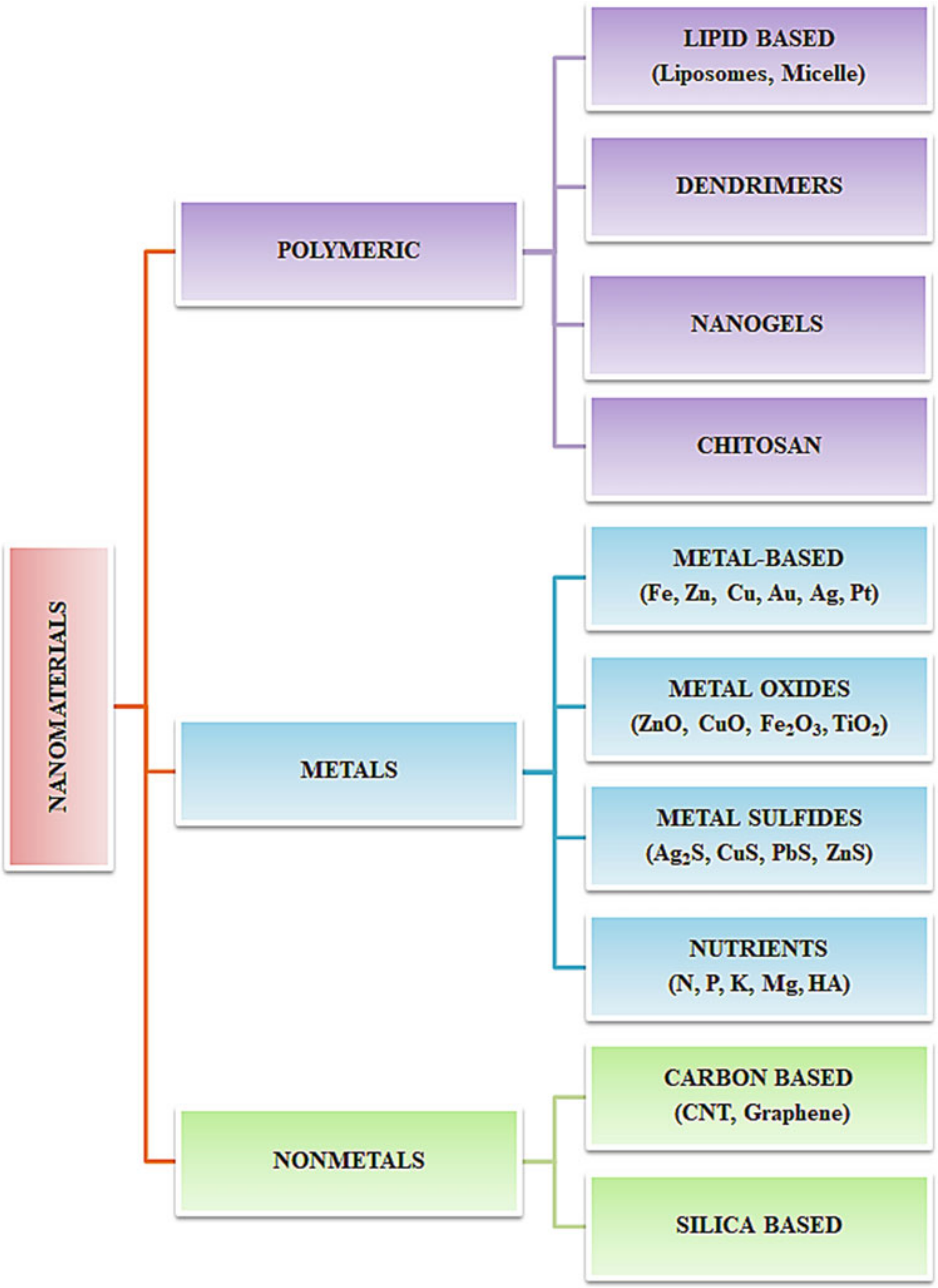

Fig. 1 Agronomically important nanoparticles and their classification

under 100 nm and shows unique properties like swelling ability, size flexibility with much higher water content, and formation of natural or synthetic polymers (Alemán et al. 2007; Tahara and Akiyoshi 2015). The use of nanogels is widespread in cell culture, biosensors, molecular delivery, etc. (Tahara and Akiyoshi 2015; Sharma et al. 2016; Neamtu et al. 2017). A recent study suggested that alginate-based nanogels can potentially deliver small molecular pesticides, which improves plant resistance against tobacco mosaic virus (TMV) and enhance the growth in N. *benthamiana* (Lv et al. 2021).

3.1.4 Chitosan

Chitosan is a polysaccharide-based biopolymer generally found in the exoskeleton of Crustaceans. Chitosan-based nanostructures show lower toxicity, higher surface-to-volume ratio, easier availability, enhanced mobility, etc. making them one of the effective polymer-based NPs for agronomical research (Kashyap et al. 2015; Mohammed et al. 2017). Chitosan nanoparticles also established some essential properties like biodegradability, biocompatibility, greater permeability, good capability to form film, etc., and also can be employed as a dynamic delivery vehicle (Shukla et al. 2013).

In addition, these NPs may also interact with different metal-based NPs (Ag and Cu) and serve as a possible therapeutic agent against pathogenic microbes and improve crop productivity (Agnihotri et al. 2012;Brunel et al. 2013).

3.2 Metal-Based NPs

3.2.1 Metals

In recent times, metals-based NPs like gold, platinum, silver, zinc, copper, cadmium, cobalt, iron, and others are gaining attention due to their role in countless biological applications. These nanoparticles can be synthesized practically from all metals by both "top-down" as well as "bottom-up" methods (Salavati-niasari et al. 2008). The NPs hold some unique physiochemical characteristics such as nanoscale size (10–100 nm), shapes (cylindrical or spherical), surface features (pore size, high surface area to volume ratio, surface charges, etc.), structure (crystals or amorphous), color, and stability under various environmental factors (Ealia and Saravanakumar 2017). Among the metal-based NPs, the noble metals (gold, silver, platinum) have shown promising competence in functionalization with many functional groups, e.g., polymers, peptides, RNA, or DNA (Fan et al. 2018). These functionalized NPs can potentially target diverse groups of plant cells and improve plant growth via increasing cellular penetration, biomolecular recognition, gene or drug delivery, tissue engineering, etc. (Fan et al. 2018).

3.2.2 Metal Oxides

Nanoparticles of metal oxides are the modified form of metal-based NPs, synthesized from the respective metallic NPs via altering their properties, for example, at room temperature in presence of oxygen, iron nanoparticles (Fe) instantly form iron oxide (Fe_2O_3) by oxidation (Sanchez-Moreno et al. 2016). Few frequently synthesized metal oxide NPs are zinc oxide (ZnO), titanium dioxide (TiO_2), iron oxide (Fe_2O_3), magnetite (Fe_3O_4), copper oxide (CuO), aluminum oxide (Al_2O_3), etc. Some advantages of using metal-based oxides are easy producibility, higher stability, simpler engineering to prepare required shape, size, and porosity, easier integration or functionalization with various molecules, etc. (Sanchez-Moreno et al. 2016).

3.2.3 Metal Sulfides

Another leading form of metal-based NPs is metal sulfides. The transformation of metal or metal oxide NPs into metal sulfides is facilitated by reshaping the chemical arrangement called sulfidation, thereby, reducing the hazards of using metal-based NPs (Devi et al. 2015). Some well-studied and agronomically important metal sulfides are silver sulfide (Ag_2S), copper sulfide (CuS), zinc sulfide (ZnS), cadmium sulfide (CdS), iron sulfide (FeS), and lead sulfide (PdS) NPs. A current study suggested the use of iron sulfide NPs can elevate plant growth and crop yield by improving iron content, redox status, expression of *Rubisco*, *GS*, and *GOGAT* genes in *Brassica juncea* (Rawat et al. 2017).

3.2.4 Nutrient Based

The growth and development of plants are directly regulated by the availability of both macroelements (nitrogen, phosphorus, and potassium) and microelements (zinc, copper, iron, manganese, etc.) in the soil. Thus, an introduction of nanostructured macro and microelements has shown a promising result in sustainable agricultural production (Kalia et al. 2019). The nanoformulation of nutrients transforms the physical properties like shape, size, crystallinity, dimensions, topography, etc., which positively progresses the uptake of nanosized nutrients by plant roots via interaction with soil components (Kalia et al. 2019). Further, the surface of nanofertilizer permits a large number of modifications using various types of biomolecules along with other NPs. The seed priming and foliar application of engineered nanofertilizers (surface modification by nanochitosan and CNTs) significantly improved the growth and yield as well as reduced harvesting duration of French beans (Abdel-Aziz et al. 2019). Among the nutrient-based NPs, hydroxyapatite (HA) has emerged as a well-known biomaterial. Though it has been extensively studied for biomedical applications, HA can serve as a potential nutrient source for phosphorous to improve plant biomass and crop yield (Madanayake et al. 2021). The HANPs offer greater flexibility to transform the surface and can be attached with various other nutrients or NPs. Some surface-modified HANPs have shown sustained discharge of several nutrients or metabolites (amino acids, chitosan, carboxymethyl cellulose, etc.) and established higher agricultural productivity (Kottegoda et al. 2011; Marchiol et al. 2019; Madanayake et al. 2021).

3.3 Nonmetal NPs

3.3.1 Carbon Based

A well-defined arrangement of carbon atoms in different shapes and sizes gives rise to various types of NPs like fullerenes, graphene, carbon nanotubes, carbon black, carbon fibers, etc. Fullerene is a spherical arrangement of carbon molecules (C_{60}), where approximately 28–1500 carbon atoms adhere together by sp_2 hybridization and forms globular assembly with diameters up to 4–36 nm (Ealia and Saravanakumar 2017). Another well-studied carbon-based nanostructure is graphene. Graphene is a hexagonal allotropic structure of carbon atoms and it is a honeycomb-like assembly in a 2D planar surface with an estimated thickness of 1 nm (Ealia and Saravanakumar 2017). These honeycomb-like graphene foils further give rise to carbon nanofibers and carbon nanotubes. Graphene nanofoils are further twisted in a cup or cone shape to produce carbon nanofiber. Whereas, the graphene nanofoils are wrapped or coiled into a hollow cylindrical shape to form nanotubes (Iijima 1991). Based on the configuration of graphene foil layers in carbon nanotubes (CNT), it can be classified as single-walled nanotubes (SWNTs) and multi-walled nanotubes (MWNTs). The thickness of SWNTs and MWNTs are 1 nm and 100 nm respectively with a few millimeters in length (Ealia and Saravanakumar 2017). Among nonmetallic NPs, carbon nanotubes have shown great potential as a therapeutic agent for their variable size and stable geometric shapes (Yetisgin et al. 2020). Carbon black is an amorphous or globular-shaped (20–70 nm diameter) material, fabricated from carbon molecules, and generally the particles aggregate due to their higher interaction between themselves (Ealia and Saravanakumar 2017).

3.3.2 Silica Based

In recent times, silica-based NPs have gained attention in agronomy for their diversified application, flexibility, and cost-effectiveness. Also, their physiochemical characters, surface-to-volume ratio, porosity, ability to functionalize a wide variety of molecules make silica-based NPs a potent therapeutic agent and delivery vehicle for a large number of agronomically useful molecules (Yetisgin et al. 2020). A large surface area of silica-based NPs is enclosed with polar silanol groups, which helps in water adsorption and further improves its solubility. Moreover, silica-based NPs have shown the capability of delivering molecules at targeted sites, e.g., pesticides, phytohormones, nucleic acids, etc. (Zhao et al. 2017; Sun et al. 2018; Khan et al. 2020).

4 Nanomaterials and Their Mechanism of Action

4.1 Uptake

The uptake of NPs by plants relies on many factors such as size, shape, stability, physicochemical properties, surface charge, and surface functionalization of the nanoparticles, type of application, and environmental factors like soil, water, microbial partners, etc. Moreover, the complex physiology and anatomy of the plants immensely contribute to the process of NPs uptake and transformation (Pérez-de-Luque 2017; Sanzari et al. 2019). The uptake mechanism of most nanomaterials has been well studied in plants. The NPs with good solubility are majorly applied in the form of solutions at both plant roots, leaves, and other aerial parts. However, the uptake of NPs largely takes place via root hairs and leaf surfaces, while a low absorption rate was reported via other parts (Ali et al. 2021a).

The dynamics of NPs uptake seem to be a comparatively complex process from the soil than that of the aerial absorption by plants. Many aspects like the amount of soil organic matter, the occurrence of symbiotic partners, secretion of mucilage, and root exudates may influence the NPs absorption from the soil. For example, root secreted mucilage and exudates are found to play a dual role in NPs uptake by upholding NPs attachment at the root surface, which improves the rate of NPs internalization and plays a similar role in trapping and aggregation of NPs (Avellan et al. 2017; Milewska-Hendel et al. 2017). A superior rate of NPs absorption was reported at the root tips and adjacent to lateral branch junctions in the case of root-specific uptake, however, a higher deposition of suberin in upper parts blocks the infiltration of NPs (Chichiriccò and Poma 2015). Nanoparticles generally interact with plant roots and are absorbed by root hairs, subsequently translocated to the above-ground parts, and finally accumulated in cellular or subcellular organelles of the plant body (Ali et al. 2021a). The entrance of NPs through the stomata or pores of the cell wall is directly correlated with the size of NPs, which also determines the successive transportations of NPs inside cells or cellular organelles, accumulation, transport kinetics, and toxicity (Tripathi et al. 2017). Moreover, a few other parameters are found to be crucial, e.g., surface area, hydrophobicity, charge, reactivity, agglomeration for the uptake and translocation of NPs in plants (Wang et al. 2013; Kaphle et al. 2018).

Another well-studied mechanism of NPs uptake is absorption via vegetative parts (preferably foliar uptake). Application of NPs on the exterior passively uptakes NPs through natural openings like stomata, hydathodes, or cuticles (Eichert et al. 2008; Kurepa et al. 2010). Furthermore, some aspects of plant physiology and anatomy need to be considered to gain better insights into the dynamics of plant–NPs interactions. For instance, the above-ground parts of plants are commonly found to be shielded by a layer of cuticles along with some waxes, which mainly functions as a protective barricade for above-ground organs, however, the natural openings remain uncovered and permit the passage of NPs inside (Sanzari et al. 2019). There are very few studies that inspected the uptake of NPs via an almost impermeable cuticle layer, however, studies reported that TiO_2, Ag, and Pb NPs (4–100 nm) can induce holes in the cuticle layer and infiltrates through it (Schreck et al. 2012;

Larue et al. 2014; Schwab et al. 2016). The presence of trichomes on plant organs is generally found to entrap NPs and allows more time for the internalization of NPs inside plant tissue (Sanzari et al. 2019). Studies suggested that wounds and injuries in plant aerial surfaces and hypogeal parts may serve as a potential route for NPs uptake (Al-Salim et al. 2011).

4.2 Translocation

The NPs absorbed via aerial and hypogeal parts of the plants once infiltrated the outer protective layer are generally mobilized either apoplastically (movement through the cell wall and extracellular spaces) or symplastically (movement through cytoplasms which are connected by a large number of plasmodesmata). In the case of foliar or aerial absorption, after NPs pass through the cuticle layer, the translocation toward the vascular bundles involves a few other obstructions (Bird and Gray 2003; Avellan et al. 2019). The tightly packed outermost layer of epidermal cells poses the very first blockade. Beneath the epidermis, chloroplast containing photosynthetic leaf tissue or mesophyll tissues impedes easy translocation of NPs (Schwab et al. 2016; Avellan et al. 2019). The movement of NPs can be either symplastic or apoplastic toward sieve tubes of phloem via the bundle sheath cells and companion cells. Nanoparticles can move through symplastic or apoplastic pathways to the bundle sheath cells that are connected to companion cells and advance toward sieve-tube elements (STE) of the phloem (Fig. 2) (Avellan et al. 2021). A similar mechanism of NPs movement through the plasmodesmata has been described in some popular plant species like *Arabidopsis* and rice (Lin et al. 2009; Geisler-Lee et al. 2013). Moreover, some studies have also reported that the internalization of NPs inside cells takes place via endocytosis, pore formation, protein carriers, etc. (Nel et al. 2009; Lin et al. 2010a, b; Wang et al. 2012; Palocci et al. 2017).

The root-specific absorption of smaller NPs (3–5 nm) generally takes place via capillary action, osmotic pressure, or direct passage through the root epidermal cells (Du et al. 2011; Pérez-de-Luque 2017). The cell wall of root epidermal cells usually shows semi-permeable nature and contains small pores, which allows smaller NPs whereas restricts the entry of relatively larger NPs (Ali et al. 2021a). Once, NPs cross the root epidermal cells, they are transported apoplastically through the extracellular spaces toward vascular bundles. On the other hand, they cross the endodermis layer symplastically to reach the central vascular cylinder due to the presence of the Casparian strip and are transported through the xylem vessels to move unidirectionally to different parts of the plant body (Ali et al. 2021a).

4.3 Accumulation

The fate or bioaccumulation of NPs is predominantly influenced by the physicochemical properties of NPs and the plant species. Furthermore, the accumulation of NPs is regulated by many other factors, which influence the uptake and translocation. For instance, a study had suggested that the accumulation of quantum dots (CdSe/ZnS) specifically takes place inside the cytoplasm and nucleus of the *M. sativa* cells (Santos et al. 2010). Another study described that hydrophilic NPs with a size ≥ 40 nm can enter through the natural openings like stomata and the foliar application of such NPs results in accumulation of NPs in the stomata and skips the vascular routes, and eventually gets distributed to the different parts of the plant body (Eichert et al. 2008). Other nanoparticles such as nanosilicon are distributed via xylem vessels to the different parts of the plant body including the leaves and deposited under the cell wall in the form of silica (Ma and Yamaji 2006; Sahebi et al. 2015; Nawaz et al. 2019). Some other studies suggested that the internalized NPs can be transported through phloem sieve tubes besides major transport molecules, i.e., sugars and NPs also show the bidirectional movement inside phloem, thus NPs can be effectively accumulated inside various potent sinks (e.g., young leaves, roots, stems, fruits, grains, etc.) (Wang et al. 2013; Raliya et al. 2016; Tripathi et al. 2017; Ruttkay-Nedecky et al. 2017). Nanoparticle dissolution also plays an important part in deciding the fate of nanoparticle accumulation. Dissolution occurs in two ways firstly the NPs can dissolute in their ionic form outside the roots when it comes in contact with the root exudates, and in the other case NPs can dissolute after entering inside the plant body. For example, ZnO NPs get ionized when comes in contact with root exudates on the root–soil interface and accumulate as their ionic form in the nuclei, cytoplasm, apoplast of the endodermal cells, and the vascular bundles (Singh et al. 2018). In a different study, it was observed that both $Cu_3(PO_4)_2 \cdot 3H_2O$ and CuO NPs, release Cu ions after they enter the plant tissues and come in contact with the xylem sap (Borgatta et al. 2018). After entering the plant body, NPs interact with some biologically active molecules in the cells and intercellular spaces. Lv et al. (2015) reported that Zn could be uptaken in the form of Zn^{2+} released from ZnONPs, and gets accumulated in the form of $ZnPO_4$ in maize root

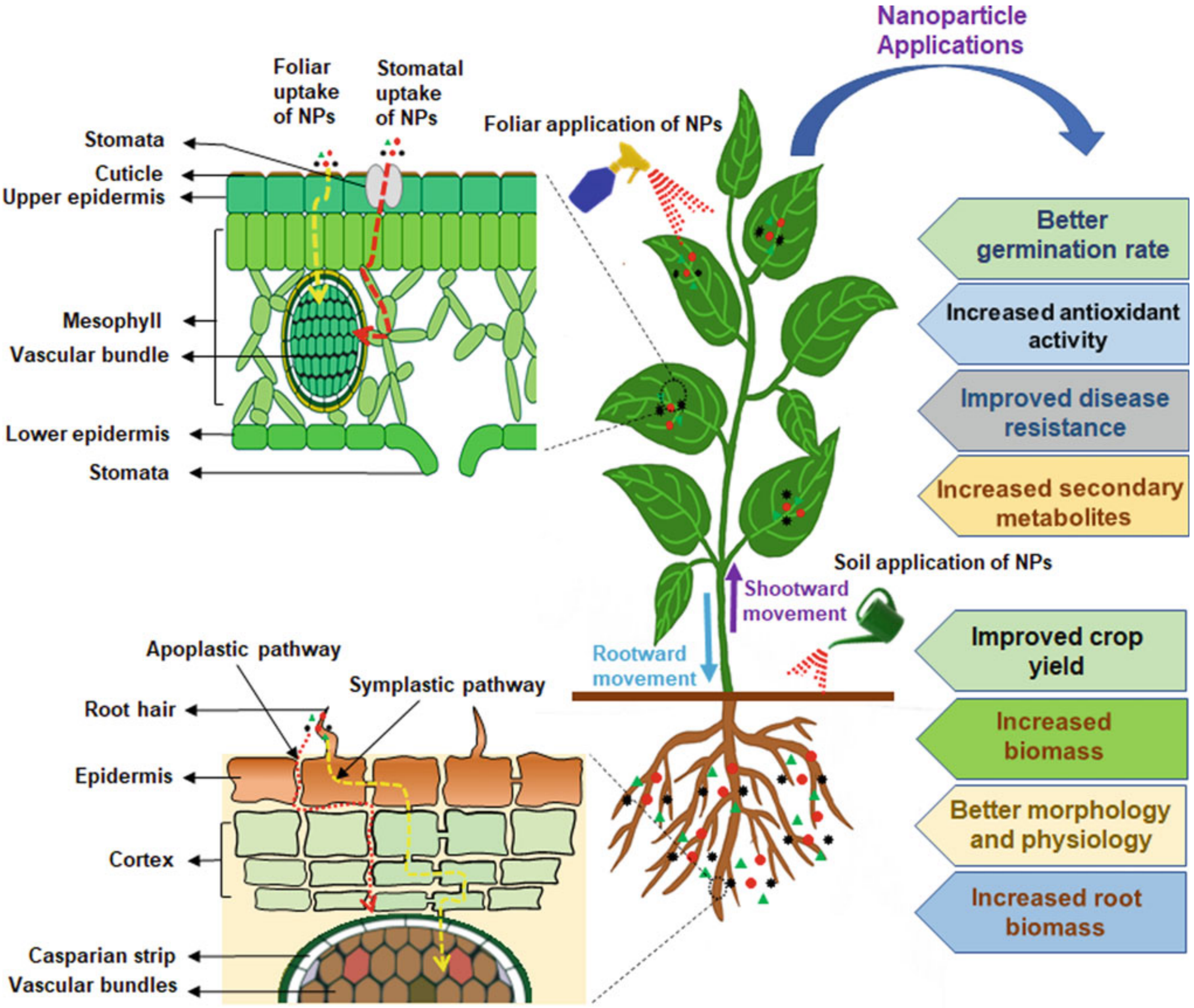

Fig. 2 Schematic representation of different approaches of nanoparticle applications. The proposed mechanisms of nanoparticle uptake and translocation by plants through different routes in different organs. Movement of nanoparticles inside plant body through apoplastic and symplastic pathways. The positive effects of nanoparticle application on plant morphology and physiology

cells following biotransformation inside the plant cells. Nanoparticles can also penetrate any cells and accumulate inside the organelles like chloroplast and mitochondria (Ahmadov et al. 2020).

5 Nanoparticles in Crop Improvement

5.1 Zinc Oxide Nanoparticles (ZnONPs)

Zinc is one of the essential micronutrients required for the proper growth and development of plants. Zinc deficiency in plants is observed in the form of retarded growth and low yield (Merchant 2010). Zinc oxide nanoparticles are considered a “biosafe material” for all living organisms. They are known to stimulate seed germination and plant growth and provide disease resistance and plant protection through antimicrobial activity (Faizan et al. 2020). Green-synthesized ZnONPs were observed to increase plant growth parameters in a better way than the chemically synthesized ones (Singh et al. 2019). In this connection, the green-synthesized nanoparticles were smaller in size than the chemically synthesized nanoparticles, therefore, it was concluded that the smaller sized nanoparticles have greater potential than the larger ones (Singh et al. 2019). In a different study, when the tomato plant roots were dipped in ZnONPs solution and transplanted in pots, the plants showed increased shoot and root length, fresh and dry mass of root and shoot, leaf area along with better antioxidant activity, higher accumulation of proline, and increased photosynthetic rate (Faizan et al. 2018). Pretreatment of seeds with ZnONPs also resulted in increased seed germination rate and early seedling growth of chili. A significant increase in root length, shoot length, and the total height of chili seedlings indicated the positive impact of ZnONPs (Afrayeem and Chaurasia 2017). Phyco-synthesized ZnONPs using a green macroalga (*Halimeda tuna*) when applied to the cotton (*Gossypium hirsutum* L.) plants, an increase in growth and total biomass of the plants was observed. Additionally, an increase in photosynthetic pigment content, reduction in MDA content, and improved antioxidant defense were also observed in nanoparticle-treated plants in comparison to the control plants (Venkatachalam et al. 2017). Transcriptomic and metabolomic analysis of iron-deficient tomato plants treated with ZnONPs foliar spray revealed a significant increase in the expression of the antioxidative enzyme encoded genes, transporters, and the enzymes/regulators involved in secondary metabolism and carbon/nitrogen metabolism. In this way, ZnONPs improved the levels of antioxidants, sugars, and amino acids, thus, improving plant health (Sun et al. 2020). These studies, therefore, reveal the potential of ZnONPs in supporting plant growth and development in a better way.

5.2 Magnesium Oxide Nanoparticles (MgONPs)

Magnesium is a metal, alkaline in nature, and an essential element for all living organisms. The ionic state of Mg has important roles in the formation of biological polyphosphate compounds like DNA, RNA, and ATP. It is a common additive to commercial fertilizers because Mg is the crucial central element in photosynthetic pigments like chlorophylls (Ramadan et al. 2020). Mineral nanoparticles have the potential to enhance the growth and development of plants along with the amelioration of the negative effects of soil hazards. For example, foliar application of magnesium and iron oxide nanoparticles to soybean plants resulted in the improvement of growth parameters (Ramadan et al. 2020). The application of MgONPs also increased the growth of tobacco plants by increasing the chlorophyll content and activity of antioxidant enzymes like POX and SOD when compared to the bulk Mg-treated plants (Cai et al. 2018). Green-synthesized magnesium hydroxide nanoparticles synthesized using *Aspergillus niger* filtrate when applied to *Zea mays* in both in vivo and in vitro conditions improved plant growth, where shoot height and root length were increased significantly along with minimum dissipation of chlorophyll as compared to the bulk Mg-treated plants and the control plants (Shinde et al. 2020). In another study, foliar application of MgNPs synthesized from *Aspergillus brasiliensis* TFR 23 to wheat plants significantly increased the activities of enzymes like dehydrogenase, esterase, alkaline phosphatase, acid phosphatase, nitrate reductase, which eventually leads to increased uptake and mobilization of nutrients. Also, the root length and root biomass were significantly increased indicating the positive role of MgNPs in crop improvement (Rathore and Tarafdar 2015).

5.3 NPK NPs

The productivity of grain crops is directly influenced by the abundance and availability of essential nutrients like NPK in the soil because it is essential for plant growth and development. Nitrogen is the main component of proteins and protoplasm and thus has a great role in plant biomass production (Meharg and Marschner 2012). Phosphorus is involved in important physiological processes such as photosynthesis, cell division, stimulating root growth, grain formation, production of energy compounds, nucleic acids, and protein (Havlin et al. 2005). Potassium also has an important and essential role in enzyme effectiveness, photosynthesis, protein synthesis, osmotic regulation, ion balance, energy transfer, stomatal movements, and stress resistance in the plant (Marschner 2011). Nowadays, modern techniques to utilize nano-NPK is increasing the value of the agricultural product and reducing the wastage of the traditional NPK fertilizer, which is also responsible for soil and water pollution (AL-Gym and Al-Asady 2020). NPK nanoparticle treatment by spraying and mixing with soil on yellow corn (*Zea mays* L.) has resulted in a significant increase in vegetative growth and yield by significantly increasing plant mean height, the total number of leaves, total chlorophyll content, number of grains per cop, weight per 500 grains, grain yield and biological yield (AL-Gym and Al-Asady 2020). Foliar application of Zn, Fe, and NPK nanofertilizer on chickpea plants resulted in a significant increase in plant height, the number of branches, seed weight, biological yield, and seed yield than the untreated control plants (Drostkar et al. 2016). Nano-formulated and sulfate-supplemented NPK fertilizer (CS-NPKS) resulted in an increase in plant height, the number of leaves, stem diameter, and chlorophyll content than the untreated and normal NPK, NPKS treated plants (Dhlamini et al. 2020).

5.4 Silver Nanoparticles (AgNPs)

Silver nanoparticles have been used for improving crop growth and productivity in recent years. Various reports have indicated that appropriate concentrations of AgNPs can play an important role in improving seed germination (Shelar and Chavan 2015), plant growth (Kaveh et al. 2013; Sharma et al. 2012; Vannini et al. 2013), photosynthetic efficiency, and chlorophyll content (Sharma et al. 2012; Hatami and Ghorbanpour 2013). For example, foliar application of AgNPs on fenugreek plant (*Trigonella foenum graecum*) resulted in improved growth parameters, increased biochemical aspects such as photosynthetic pigment, indole acetic acid contents, and thus enhanced the crop yield. Further, the quality of seeds (increased percentage of protein and carbohydrate, flavonoids, phenolics, and tannins contents) was also improved along with increased antioxidant activity (Sadak 2019). Not only improved growth but AgNPs was observed to increase the production of a major phytochemical—diosgenin in the fenugreek plant, which has medicinal properties (Jasim et al. 2017). Improved germination parameters like longer shoot and root length, increased dry mass, and germination speed of lentils was observed when treated with AgNPs compared to the plants treated with bulk silver (Hojjat and Hojjat 2016). AgNPs along with *Bacillus cereus* LPR2 application in maize plants resulted in better root and shoot growth than the control plants (Kumar et al. 2020). AgNPs synthesized using the culture filtrate of an endophytic fungus (*Fusarium Semitectum*) when applied to mung bean, pigeon pea, and chickpea seeds improved the germination percentage, germination index, root length, and shoot length (Singh et al. 2016). Similarly, treatment with AgNPs, synthesized from *Berberis lycium* root bark extract resulted in better growth and yield of *Pisum sativum*. The yielded seed from treated plants was greater in protein and carbohydrate content than the untreated control plants (Mehmood and Murtaza 2017).

5.5 Titanium Dioxide Nanoparticles (TiO_2NPs)

Titanium dioxide (TiO_2) is considered a beneficial element for plant growth and development and is also widely used in the agriculture sector. The application of TiO_2 was reported to improve crop performance by stimulating enzyme activity, increasing chlorophyll content and photosynthesis, nutrient uptake, stress tolerance, and crop yield and quality (Chaudhary and Singh 2020). Titanium dioxide nanoparticles are considered an essential nutrient for plant growth and development (Khot et al. 2012; Fraceto et al. 2016). It was also reported to increase chlorophylls, carotenoid, and anthocyanin contents and thus, improved plant growth, development, and yield (Morteza et al. 2013). The application of TiO_2NPs imparted a positive role in the growth of plants such as *Brassica napus* (Mohammadi et al. 2013), *Solanum lycopersicum*, and *Vigna radiata* (Singh and Lee 2016). Also, 50 mg/L TiO_2NPs-treated coriander plants imparted the accumulation of higher amounts of micronutrients (K, Ca, Mg, Fe, Mn, Zn, and B) without exerting any toxic effects and therefore, resulted in increased root and shoot biomass (Hu et al. 2019). Aerosol or soil-mediated application of both ZnONPs and TiO_2NPs was also shown to impart their positive effects on tomato plants in a dose-dependent manner. They caused varying effects on plant phenology, chlorophyll contents, fruit yield, and nutritional quality (Raliya et al. 2015).

5.6 Silica Nanoparticles (SiNPs*)*

Silicon is not considered an essential element for plants but it is beneficial for plant growth and development. Silicon is considered a quasi-essential element that may not be required for plant growth but its absence can impart a negative impact on plant growth, development, and reproduction (Rajput et al. 2021). The major problem of using commercial silicon fertilizer is its low bioavailability, however, the use of silica nanoparticles can reduce this problem by increasing bioavailability (Rajput et al. 2021). In recent years, SiNPs have been explored to improve plant growth and development even in the presence of unfavorable environmental conditions. The impact of SiNPs directly or indirectly depends upon their shape, size, and other features (Rastogi et al. 2017). Both the soil application and foliar application resulted in enhancement of plant bio-metrics, physiology, and properties of flowers, which were strongly linked to the leaf Si content (Attia and Elhawat 2021). Moreover, all the germination parameters (germination percentage, germination speed, vigor index, coefficient of velocity of germination, germination index, mean germination time) and growth characteristics (fresh and dry weight, shoot and root length, relative water content) was reported to enhance significantly when *Cucumis sativus* plants were treated with an aqueous solution of SiNPs (Alsaeedi et al. 2019). A lower concentration of SiNPs was reported to increase hypocotyl length and flowering of *Vicia faba* (Roohizadeh et al. 2015). All the reports supported the ability of SiNPs in supporting sustainable agricultural practices.

5.7 Chitosan NPs

Chitosan is a biodegradable, biocompatible, and nontoxic polymer and it has multiple important and beneficial applications in the field of biomedical sectors as well as in agriculture. It has antimicrobial, antioxidant, and chelating properties along with modifiable functional groups which makes it versatile to be used in various applications (Jiménez-Gómez and Cecilia 2020). Chitosan-based nanoparticles have also promising characteristics for the development of sustainable agricultural practices (Bandara et al. 2020). To enhance rapid seedling growth, seed priming/treatment with chitosan nanoparticles has proved to be effective

(Kumaraswamy et al. 2018). Foliar application of chitosan nanoparticles on coffee seedlings showed promising results on various growth parameters (plant height, stem diameter, leaf area) along with improved biochemical characteristics (photosynthetic intensity, chlorophyll content, stomatal conductance, CO_2 concentration in stomata, and nutrient uptake) (Nguyen et al. 2019). Foliar application of chitosan nanoparticles synthesized from chitosan of the fungal cell wall to tomato plants resulted in an improved number of flowers per plant, number of fruits set per plant, and fruit fresh weight (Sathiyabama and Parthasarathy 2016). Chitosan nanoparticles when applied to the *Robusta coffee* seedlings also increased the nutrient uptake compared to the application of bulk chitosan. Also, there was a significant improvement in vegetative growth, chlorophyll content, and photosynthetic rate (Van et al. 2013). The effectiveness of bulk NPK fertilizer was enhanced when it was nanoformulated with chitosan nanoparticles. Nanoformulated NPK resulted in improved plant height, spike weight, crop yield, and harvest index (Abdel-Aziz et al. 2016). Chitosan nanoparticles appear to activate the hydrolytic enzymes, which help in the breakdown of reserve food material such as proteins, thereby, improving the rate of cell division by stimulating the phytohormones like auxin and cytokinin and nutrient uptake efficiency (Kumaraswamy et al. 2018).

5.8 Carbon-Based Nanomaterials (CBN)

Carbon-based nanomaterials are mostly explored in the field of nanopharmacology, nanomedicine, public health, where they are used as drug carriers and for targeted delivery (Niazi et al. 2014; Mohajeri et al. 2019). In-plant systems also, CBN can be used as germination and growth enhancers, pesticides, and as a carrier of molecules (DNA, phytohormones, herbicides, fertilizers) to the plant cells (Verma et al. 2019). However, the full potential of CBN is yet to be realized in the field of sustainable agriculture (Saxena et al. 2014). Carbon-based nanomaterials such as graphene and multi-walled carbon nanotubes (CNTs) treated sorghum and sweetgrass seeds were reported to have germination status (Pandey et al. 2018). Similarly, soil application of CNTs has resulted in better water absorption by seeds leading to better germination percentage and seedling growth (Yatim et al. 2015). Multiwalled-CNTs-treated *Phoenix dactylifera* plants also showed improved callus growth, accelerated seedling growth, increased shoot length and leaf number, and enhanced root number, root length, plantlet length, and hairy roots along with better adsorption or transportation of nutrients into the plants (Taha et al. 2016). Application of carbon nanoparticles on *Vigna radiata* seedlings resulted in a significant increase in chlorophyll and protein content and plant biomass. Moreover, the activities of antioxidant enzymes like SOD, GOPX (guaiacol peroxidase), APX, and proline were also increased (Shekhawat et al. 2021).

5.9 Other Nanoparticles in Crop Improvement

Except for the above-described nanoparticles, several other nanoparticles are being evaluated for crop improvement. For example, a low concentration of FeNPs was observed to promote plant growth by altering the leaf organization, regulating the development of vascular bundles, and increasing the chloroplast number and grana stacking (Yuan et al. 2018). Similarly, a low concentration of AuNPs was observed to improve free radical scavenging potential and antioxidant enzyme activity along with the alteration in micro RNAs expression which can regulate different morphological, physiological, and metabolic processes in plants (Siddiqi and Husen 2016). The gold nanoparticle was also observed to induce the growth of tomato plants without imparting any negative impacts (Thakur et al. 2018). Also, the application of cerium NPs to *Calendula officinalis* in low concentration resulted in enhanced antioxidant enzyme activities, osmolytes content, and chlorophyll content (Jahani et al. 2019). Similarly, the application of selenium nanoparticles was also observed to increase seed germination of *Hordeum vulgare* without imparting any toxicity (Siddiqui et al. 2021).

6 Nanomaterials in the Alleviation of Abiotic and Biotic Stresses

6.1 Abiotic Stress

Plants are often exposed to harsh environments from their very first day of emergence. There are a large variety of unfavourable factors which can hamper a plant's normal growth, development, and reproduction. These factors include high salinity, high or low temperature, deficit or over water availability, heavy metal, UV radiation, etc. These factors are collectively referred to as abiotic stresses which can lead to huge losses in crop yield (He et al. 2018). Several strategies are already implicated to overcome the adverse stress effect of abiotic stresses on plants, among them, nanotechnology is presently emerging to its greater potential (Elsakhawy et al. 2018). In this connection, various nanoparticles have already been explored for the improvement of crops by negating the impacts of abiotic stresses (Fig. 3).

Salinity stress mainly hampers plant growth by causing oxidative damage due to the accumulation of Na^+ and Cl^- in the plants. Application of AgNPs was reported to reduce the effects of salinity stress by reducing oxidative damage and

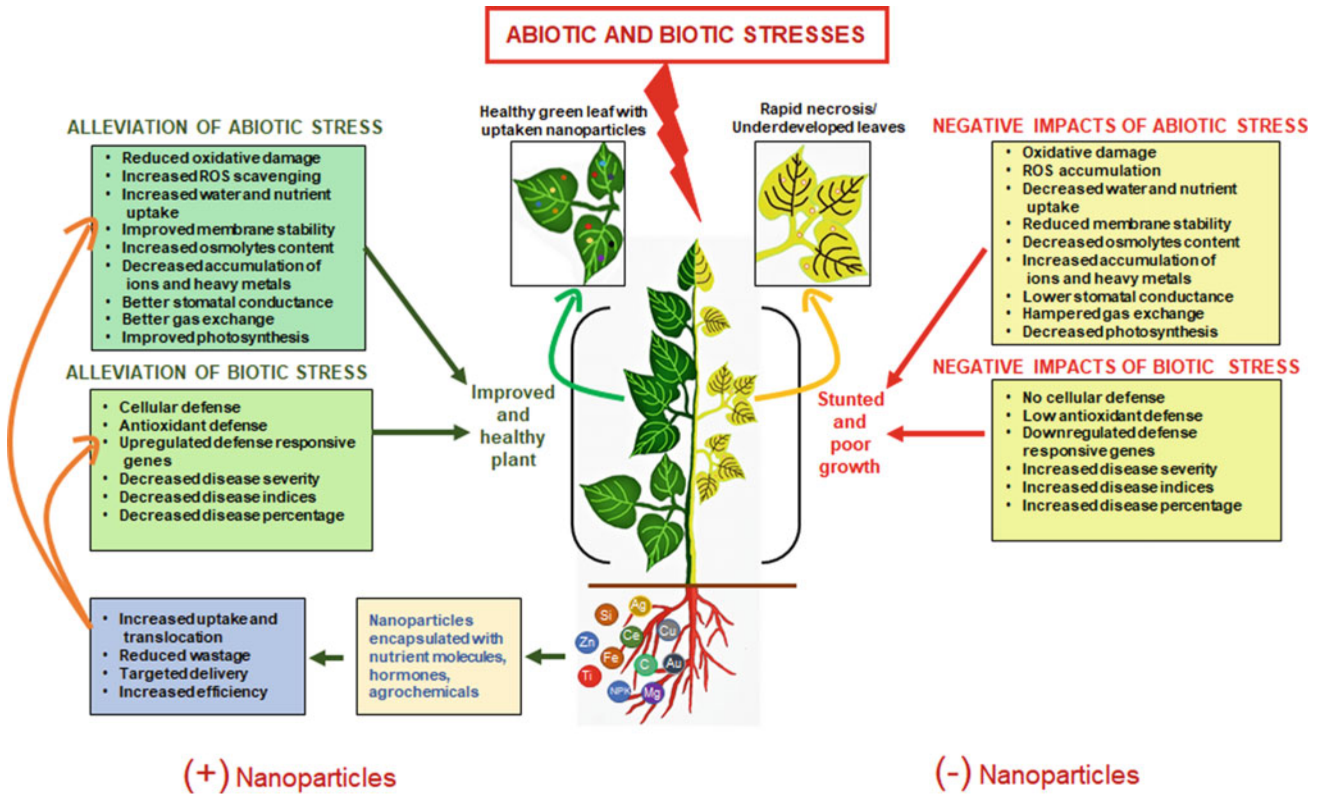

Fig. 3 Proposed mechanism of negative impacts of abiotic and biotic stresses on plant body and alleviation of those stresses by using nanotechnology. On the right side of the plant, there is no implementation of nanotechnology (nanoparticles) which causes severe physiological, biochemical, and molecular level damage to the plant under stressed conditions. But on the left side in the presence of nanoparticles (native/functionalized) plants showing to have better growth and development along with improved physiological, biochemical, and molecular status

accumulation of Na^+ and Cl^- and enhancing antioxidant activities (Khan et al. 2020). ZnONPs when applied to the seawater-stressed okra (*Abelmoschus esculentus*) plants, amelioration effects could be observed due to a significant increase in photosynthetic pigments, antioxidant enzyme activity (CAT, SOD), and decrease in proline and total soluble sugars (Alabdallah and Alzahrani 2020). Similarly, 100 mg/L TiO_2NPs and 20 mg/L selenium functionalized chitosan nanoparticles were observed to ameliorate the adverse effects of salinity stress in *Stevia rebaudiana* plants by supporting their growth through increased photosynthetic performance and antioxidant enzyme activity and decreasing the contents of H_2O_2, malondialdehyde (MDA), and electrolyte leakage (EL) (Sheikhalipour et al. 2021). Most importantly, the essential oil content, stevioside, and rebaudioside A content were also increased in stressed plants when treated with nanoparticles (Sheikhalipour et al. 2021). Chitosan nanoparticles were also observed to reduce the negative effect of salinity stress of *Catharanthus roseus* by activating antioxidant defense, which helps to scavenge the ROS and by increasing the expression of mitogen-activated protein kinases (MAPK3), geissoschizine synthase (GS), and octadecanoid-derivative responsive AP2-domain (ORCA3) genes, which facilitated higher alkaloid accumulation and provided better protection against salinity stress (Hassan et al. 2021). ZnONPs, SiNPs, TiO_2NPs, and ferric oxide nanoparticles when applied to the salinity-stressed *Linum usitatissimum* plants, showed improved growth, carbon and nutrient assimilation, and higher antioxidant activity, thus preventing the negative effects caused by salinity stress (Singh et al. 2021a, b).

Application of iron oxide nanoparticles and hydrogel nanoparticles on drought and cadmium-stressed rice plants resulted in increased biomass, photosynthetic activity, antioxidant activity, nutrient accumulation parallelly with the decreased ROS accumulation than the untreated plants (Ahmed et al. 2021). Further, the cadmium transporter genes like *Oryza sativa* heavy metal ATPase 2 (*OsHMA2*), *OsHMA3*, and *Oryza sativa* low-affinity cation transporter1 (*OsLCT1*) were found to be downregulated due to the application of nanoparticles which reduced the uptake of the toxic metal (Ahmed et al. 2021). Cadmium-induced toxicity in wheat plants was found to be reduced with the treatment of SiNPs, which resulted in enhanced gas exchange capacity, chlorophyll content, antioxidant activity, and reduced electrolyte leakage, and accumulation of Cd (Ali et al. 2019). Arsenate toxicity was also observed to be ameliorated by the use of SiNPs. In this context, the application of SiNPs was shown to reduce the accumulation of As and enhance the components of the ascorbate–glutathione cycle, which is involved in counter-balancing ROS-mediated damage to macromolecules (Tripathi et al. 2016). Similarly, cadmium and arsenic toxicity in *Solanum nigrum* was reduced by the application of multi-walled carbon nanotubes (MWCNT). MWCNT application enhanced the accumulation of cadmium and bioconcentration of arsenic and thus negated the co-contamination-induced toxicity along with a significant increase in plant growth, mineral accumulation, and antioxidant defense (Chen et al. 2021).

ZnONPs were also observed to enhance drought stress tolerance of eggplant (*Solanum melongena*) by increasing photosynthetic efficiency, membrane stability index (MSI), and relative water content (RWC) (Semida et al. 2021). AgNPs and CuNPs were also observed to reduce drought stress of wheat plants by enhancing stomatal conductance, chlorophyll stability index, leaf succulence, and leaf K content (Ahmed et al. 2020). Chitosan nanoparticles were also observed to reduce the negative impact of drought stress by increasing proline accumulation, antioxidative defense, and reducing H_2O_2 and MDA content in *Catharanthus roseus* plants (Ali et al. 2021b). Heat stress of plants was also reduced by the application of nanoparticles. For example, AgNPs were reported to mitigate the negative effects of heat stress by significantly increasing root length, shoot length, root number, fresh weight, and dry weight (Iqbal et al. 2017). Similarly, the negative effect of heat stress on sorghum plants was reported to be mitigated by the application of Se nanoparticles. Nanoparticle application increased pollen germination, seed yield, antioxidant defense along with the decrease in signature oxidants (Djanaguiraman et al. 2018). There are several reports on the efficacy of different nanoparticles in the alleviation of abiotic stresses in plants, some of which are listed in Table 1.

6.2 Biotic Stress

This has been estimated that 20–40% of crop production is reduced due to pathogenic attacks (Rahman et al. 2017). Current disease management is tremendously dependent upon the application of chemical fungicides, bactericides, and nematicides, but 90% of the used chemicals are lost in the environment during or after application in the agriculture field which ultimately contaminates the environment (Sai et al. 2018). Nanotechnology can be used as an advanced option to reduce pesticide toxicity by improving its shelf-life and solubility. There are two ways of using nanoparticles for agricultural disease management—either the nanoparticles themselves can act as a disease protectant or they can be used as a nanocarrier for various kinds of insecticides, fungicides, herbicides (Worrall et al. 2018). Nanoparticles themselves can directly kill plant pathogens like bacteria and fungi (Fig. 3). For example, foliar application of iron oxide nanoparticles to *Nicotiana benthamiana* plants imparted resistance against tobacco mosaic virus (TMV). In this context, the iron oxide nanoparticles were found to increase the fresh and dry weight of plants, activate antioxidant defense, and most importantly upregulate salicylic acid (SA) biosynthesis and the expression of SA-responsive pathogenesis-related (PR) genes (Cai et al. 2020). Similarly foliar application of MgONPs suspension to the *Ralstonia solanacearum* infested tomato plants induced systemic resistance in the plants against the bacteria by upregulating some of the defense-related genes like salicylic acid-inducible *PR1*, jasmonic acid-inducible *LoxA*, ethylene-inducible *Osm*, and systemic resistance-related *GluA* (Imada et al. 2016). ZnONPs were also observed to increase the plant growth, number of pods, chlorophyll, carotenoid contents, and nitrate reductase activity in lentil plants inoculated with several pathogens (*Alternaria alternata*, *Xanthomonas axonopodis* pv. *phaseoli*, *Fusarium oxysporum* f. sp. *lentis*, *Pseudomonas syringae* pv. *Syringae* and *Meloidogyne incognita*). Most importantly, the application of ZnONPs reduced the formation of galls, wilt, blight, nematode multiplication, and leaf spot disease (Siddiqui et al. 2018b).

Seed priming with nanoparticles is also an efficient technique to stimulate plant resistance against biotic agents. In this connection, priming with myogenic selenium nanoparticles resulted in a 72.9% reduction in the late blight disease of tomatoes (Joshi et al. 2021). Priming resulted in significant improvement in cellular and biochemical defenses against *Phytophthora infestans*, which could be attributed mainly to the accumulation of lignin, callose, and an increased level of phenylalanine lyase (PAL), lipoxygenase (LOX), *β*-1,3-glucanase (GLU), superoxide dismutase (SOD) (Joshi et al. 2020). Similarly, seed priming with SiNPs in pathogen (*Meloidogyne incognita*, *Pectobacterium betavasculorum*, and *Rhizoctonia solani* disease complex) inoculated beetroot (*Beta vulgaris*) plants resulted in better disease suppression than the foliar application. Application of SiNPs in this context enhanced root and shoot dry weight, chlorophyll content and its fluorescence characteristics, and antioxidative defense (SOD, CAT, polyphenol oxidase (PPO), and PAL) (Khan and Siddiqui 2020). But in another study, the foliar application was more effective than the seed priming of tomato plants in the presence or absence of pathogens (bacterial pathogens—*Pseudomonas syringae* pv. tomato, *Xanthomonas campestris* pv. *vesicatoria*, *Pectobacterium carotovorum* subsp. *Carotovorum* and *Ralstonia solanacearum*; fungal pathogens—*Fusarium oxysporum* f. sp. *Lycopersici*, and *Alternaria*

Table 1 Recent experiments reporting the efficacy of nanoparticles in the alleviation of abiotic stresses

Type of nanoparticles	Stress	Name of the plant	Alleviating effects	References
ZnONPs + SiNPs	Salinity	*Mangifera indica*	Increased plant growth, nutrient uptake, carbon assimilation, decreased flower malformation, increased annual fruit yield, and physiochemical characteristics	Elsheery et al. (2020)
ZnONPs + melatonin	Arsenic stress	*Glycine max*	Better growth, increased photosynthesis, low ROS accumulation, decreased MDA, and H_2O_2 content	Bhat et al. (2022)
ZnONPs	Salinity	*Lycopersicon esculentum*	Increased shoot and root length, biomass, leaf area, increased chlorophyll content, photosynthetic attributes, enhanced protein content, antioxidative defense	Faizan et al. (2021)
SiNPs	Mercury (Hg) stress	*Glycine max*	Inhibited immobilization and accumulation of Hg, increased chlorophyll content, decreased antioxidant activity	Li et al. (2020)
SiNPs	Fluoride toxicity	*Oryza sativa*	Improved rice health, seed germination, decreased root ion leakage, proline content, increased photosynthetic content	Mishra et al. (2021)
AgNPs + *Comamonas testosterone* (bacteria)	Salinity	*Linum usitatissimum*	Elevated photosynthetic pigments, increased sugar, proline, and protein content, decreased H_2O_2, MDA, increased enzymatic and non-enzymatic antioxidant defense	Khalofah et al. (2021)
AgNPs	Salinity	*Pennisetum glaucum*	Reduced oxidative stress and Na and Cl uptake, maintained ionic balance of cell (Na^+, K^+, and Na^+/K^+ ratio), improved antioxidant defense, reduced H_2O_2 and MDA content	Khan et al. (2021)
S-nitrosoglutathione loaded chitosan nanoparticle	Drought	*Saccharum officinarum*	Increased photosynthetic rate, root/shoot ratio, delayed release of nitric oxide, increased biomass allocation to the root system	Silveira et al. (2019)
Glycol Chitosan coated selenium nanoparticles	Oxidative stress	*Panax ginseng*	Reduced ROS accumulation, upregulated antioxidants' genes, increased ginsenoside	Abid et al. (2021)
Chitosan nanoparticle loaded *N*-acetyl cysteine	Ozone + oxidative stress	*Triticum aestivum*	Increased leaf antioxidants pool, mainly ascorbic acid, reduced symptom severity, increased seed weight	Picchi et al. (2021)
Chitosan-functionalized selenium + TiO_2NPs	Salinity	*Stevia rebawdiania*	Increased growth, photosynthetic attributes, antioxidant enzyme activities, decreased H_2O_2 NDA and EL, increased essential oil, stevioside, and rebaudioside A content	Sheikhalipour et al. (2021)
TiO_2NPs + *Funneliformis mosseae* (AMF)	Salinity	*Phaseolus vulgaris*	Increased salinity tolerance, increased molecular intensity ratio and relative density of chitin synthases gene, increased colonization	El-Gazzar et al. (2020)
FeNPs	Cadmium contamination	*Triticum aestivum*	Improved morphological parameters, photosynthetic pigments dry biomass, increased antioxidative enzyme activities, reduced EL, decreased Cd concentration in tissues and grains	Hussain et al. (2019)
FeNPs	Cadmium + salinity	*Triticum aestivum*	Increased nutrient uptake, decreased Na^+, Cl^-, and Cd uptake, improved plant growth and morphophysiological state	Manzoor et al. (2021)
FeNPs	Salinity	*Eucalyptus tereticornis*	Increased shoot length, chlorophyll content, SOD activity, soluble sugar content, reduced MDA content, upregulated salt responsive genes (*HKT1*, *SOS1*, *NHX1*)	Singh et al. (2021a, b)

solani) (Parveen and Siddiqui 2021). Application of ZnONPs and TiO_2NPs also induced disease suppression in beetroot plants inoculated with bacterial pathogens (*Pectobacterium betavasculorum*, *Xanthomonas campestris* pv. *beticola*, and *Pseudomonas syringae* pv. *aptata*). Though the ZnONPs were more efficient than the TiO_2NPs, their combined application improved chlorophyll, carotenoid, SOD, CAT, APX, PAL, GSH, proline, and H_2O_2 contents and decreased MDA content (Siddiqui et al. 2018a). Exogenous application of TiO_2NPs on fungus (*Bipolaris sorokiniana*) infected wheat plants was observed to reduce the disease incidence, percent disease index, and disease severity by modifying agro-morphological (root and leaf surface area, fresh and dry weight of plants, and yield parameters), agro-physiological (chlorophyll content, relative water content and membrane stability index), and non-enzymatic metabolites (protein, soluble sugar, soluble phenol, and flavonoid) (Satti et al. 2021).

Besides the direct action against pathogens, nanoparticles are also able to carry and deliver agrochemicals in a targeted way which makes the nanoparticles more efficient toward plant disease management, simultaneously reducing the wastage and negative environmental effects of agrochemicals (Fu et al. 2020). For example, polymerized citric-acid-functionalized multiwalled carbon nanotubes were used to encapsulate pesticides like zineb and mancozeb which were used as nanopesticide against *Alternaria alternata*. It has been observed that this nanohybrid material was more efficient in terms of toxicity against the fungus than the bulk pesticide (Sarlak et al. 2014). Mesoporous organosilicon nanoparticles with calcium carbonate as a capping agent were used to encapsulate prochloraz (a fungicide) for the management of Sclerotinia disease. This technique of fungicide application resulted in intelligent delivery of the fungicide and protected the potted rapeseed plants from Sclerotinia disease (Gao et al. 2020). In another case, mesoporous SiNPs were used for encapsulation of a pesticide spirotetramat for the improved deposition, uptake, and translocation into cucumber plants, which also ensured lower accumulation of pesticide in the edible part of the plants (Zhao et al. 2018). Avermectin-loaded lanthanum-modified chitosan oligosaccharide nanoparticles were used against the rice blast disease. Results showed that the functionalized nanoparticles not only increased the disease resistance but also improved the growth parameters like plant height and fresh weight (Liang et al. 2018a). Prochloraz loaded mesoporous SiNPs capped with chitosan on the surface can be used as a gatekeeper to protect the citrus disease at the pre-harvest stage. The use of the pesticide in this way possessed a longer duration and a better antifungal activity (Liang et al. 2018b). So, from the above studies, it is clear that nanoparticles are also able to provide resistance against various kinds of biotic agents without hampering plant health, some of the studies are also enlisted in Table 2.

Table 2 Recent experiments reporting the efficacy of nanoparticles in the alleviation of biotic stresses

Type of nanoparticles	Name of the plant	Disease-causing agent	Alleviating effects	References
Bio-fabricated ZnONPs	*Pennisetum glaucum*	*Sclerospora graminicola*	Plasmolyzed and inhibited spore germination of the pathogen, reduced disease incidence, increased lignification, callose deposition, antioxidative enzyme activity, increased defense enzyme related gene expression, and induced systemic resistance	Nandhini et al. (2019)
Graphene oxide NPs, ZnONPs	*Daucus carota*	*Pectobacterium carotovorum*, *Xanthomonas campestris*, pv. catotae, *Meloidogyne zavanica*, *Alternaria dausi*, *Fusarium solani*	Increased plant growth, chlorophyll, carotenoid and proline content, reduced galling and nematode multiplication, reduced soft rot, leaf spot, root rot indices, bacterial leaf blight	Siddiqui et al. (2019)
Biogenic ZnONPs from *Mentha spicata*	*Datura stramonium*	Tobacco Mosaic Virus	Reduced viral accumulation level, disease severity, upregulated *PAL*, *PR-1*, *CHS*, *POD* genes	Abdelkhalek and Al-Askar (2020)
ZnONPs based hydrogel	*Capsicum annuum*	*Fusarium oxysporum*	Reduced wilt disease symptoms incidence, enhanced photosynthetic pigments, soluble sugar, soluble proteins, total phenols, increased density of polypeptide peroxidase and polyphenol oxidase enzymes	Abdelaziz et al. (2021)

(continued)

Table 2 (continued)

Type of nanoparticles	Name of the plant	Disease-causing agent	Alleviating effects	References
ZnONPs and TiO_2 NPs	*Solanum lycopersicum*	*Bactericera cockerelli* Sulc. (Hemiptera: Triozidae)	Toxic effect of nanoparticles towards *B. cockerelli* nymphs resulted in a high mortality rate up to 100%	Gutiérrez-Ramírez et al. (2021)
SiNPs	*Oryza sativa*	*Fusarium fujikuroi*	Decreased disease severity index, improved silica content and peroxidase activity, increased grain yield	Elamawi et al. (2020)
SiNPs with *Saccharomyces cerevisiae*	*Capsicum annuum*	*Xanthomonas vesicatoria*	Reduced disease severity, improved vegetative growth, mineral contents, stimulated polyphenol oxidase activity, enhanced food yield quality parameters	Awad-Allah et al. (2021)
SiNPs	*Arabidopsis thaliana*	*Pseudomonas syringae*	Induced systemic acquired resistance, increased defense related hormone SA	El-Shetehy et al. (2021)
Biogenic AgNPs from *Melia azedarach*	*Solanum lycopersicum*	*Fusarium oxysporum*	Increased plants growth parameters, prominently damaged fungal cell wall and spores, damaged and dead cells with disintegrated cellular membranes of fungal hyphae	Ashraf et al. (2020)
Biogenic AgNPs from *Cladophora glomerata*	*Solanum lycopersicum*	*Meloidogyne javanica*	Significantly reduced galls number, egg masses, females per root system/plant, mortality of juveniles, increased expression of *PAL* and *PPO* gene expression	Ghareeb et al. (2020)
AgNPs augmented *Calothrix elenkinii*	*Lycopersicon esculentum*	*Alternaria alternata*	Reduced disease severity, increased leaf chlorophyll, carotenoid content, and polyphenol oxidase activity, increased antioxidant enzyme activity, high yield	Mahawar et al. (2020)
Chitosan coated mesoporous SiNPs	*Citrullus lanatus*	*Fusarium oxysporum* f. sp. *niveum*	Enhanced innate defense mechanism, reduced disease severity, and stress-responsive gene expression, increased fruit yield	Buchman et al. (2019)
Chitosan nanoparticles	*Solanum lycopersicum*	*Fusarium andiyazi*	Inhibited radial mycelial growth, upregulated expression of *β*-1,3-glucanase, chitinase, *PR-1* and *PR-10* genes	Chun and Chandrasekaran (2019)
Chitosan/SiNPs	*Vitis vinifera*	*Botrytis cinerea*	Reduced gray mold disease incidence and severity, significantly increased antioxidant activity, total phenol and flavonoid content	Youssef and Roberto (2021)
Copper sulfide nanoparticles (CuS NPs)	*Oryza sativa*	*Gibberella fujikuroi* (Bakanae disease)	Significantly reduced disease incidence, modulated nutrition, and phytohormone (SA, JA) production	Shang et al. (2020)

7 Conclusion

In the current scenario, a precise and sustainable innovation is required in agronomical research to fulfill global food demand. Among present agricultural innovations, nanotechnology is considered a novel approach and exhibited the capacity to improve plant growth and development by governing plant morphology, physiology, and molecular levels. The studies suggested that NPs can be used in the development of various plant growth promoters, biosensors, insecticides, pesticides, and various stress alleviators. Nanoparticles have been opened the passage to develop “precision farming” and improve agricultural productivity through the utilization of nanofertilizers, which are also known as “magic bullets”, and also reducing the usage of harmful chemical-based fertilizers, insect and pest repulsive products. Moreover, specified application of nanoparticles in crop protection from specific pathogens has been shown promising results. The studies revealed that the application of NPs helps plants in the elicitation of antioxidative defense mechanisms, which further assist in controlling the generation of excess ROS. The usage of NPs improved plant growth and productivity via overcoming the biotic and abiotic stress. Furthermore, nanoparticle-based plant advancement revealed a similar fitness to that of genetically modified plants, which opens a new scope for crop improvement. Soon, nanobionic plants (disease-resistant, stress-tolerant, photosynthetically efficient plants) may be introduced due to the versatility of nanotechnology.

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Remote Sensing Technology—A New Dimension in Detection, Quantification and Tracking of Abiotic and Biotic Stresses

Papan Chowhan and Arka Pratim Chakraborty

Abstract

Plant stress results due to the lack of suitable and optimal conditions for ideal plant growth and development. Stress may be of any kind like abiotic or biotic that can cause many harmful effects to the plant. Remote sensing is a dynamic technique that records changes in electromagnetic radiation and assists in the quantification of different stresses. This technique has also been applied to monitor different abiotic and biotic stresses like nutrient, drought, salinity, pests and pathogen attack, etc. Numerous physiological, biochemical and structural crop characteristics can be measured through remote-sensing-based techniques and it is fast, cost-effective. Under both biotic and abiotic stresses, there are notable changes in photosynthetic ability and physical structure of the host plant at both tissue and canopy levels. Due to this, changes in light absorption pattern by the plant have been observed that in turn alter the reflectance spectrum. The study of the vegetative spectral reflectance helps us better understand the different physiological and chemical processes in plants due to the attack of pests and pathogens. Interestingly, remote sensing technology can be utilized to track the effect of various pathogens in different crops and for their better management. The present chapter aims to discuss the various applications of remote sensing in modern farming and their applications in the management of different abiotic and biotic stresses in crop plants.

Keywords

Agriculture • Disease management • Spectrum • Stress • Remote sensing (RS)

Abbreviations

AI	Aphid index
ARI	Anthocyanin reflectance index
BRI	Browning reflectance index
CASI	Compact airborne spectrographic image
CI	Chlorophyll index
CWSI	Crop water stress index
DSSI 2	Damage sensitive spectral index-2
DSSI	Damage-sensitive spectral index
DWSI-2	Disease water stress index 2
DWSI	Dynamic water stress index
ET	Evapotranspiration
F	Fluorescence
LAI	Leaf area index
LST-VI	Land surface temperature–vegetation index
MCARI	Modified chlorophyll absorption reflectance index
MLR	Multiple linear regression
MODIS	Moderate resolution imaging spectroradiometer
NDVI	Normalized difference vegetative index
NIR	Near-infrared REP–red edge position
nm	Nanometer
NPCI	Normalized pigment chlorophyll index
OSAVI	Optimized soil-adjusted vegetation index
PRI	Photochemical reflectance index
RS	Remote sensing
RVSI	Red-edge vegetation stress index
SAVI	Soil-adjusted vegetation index
SDI	Spectral disease indices
SIPI	Structure insensitive vegetation index
SMA	Spectral mixture analysis
TCARI	Transformed chlorophyll absorption reflectance index
UAV	Unmanned aerial vehicle
UV	Ultraviolet
VI	Vegetation index
VIs	Vegetation indices
WI	Water index

P. Chowhan · A. P. Chakraborty (✉)
Department of Botany, Raiganj University, Raiganj, Uttar Dinajpur, West Bengal 733134, India

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1 Introduction

Due to damage of plants by other living organisms such as different bacteria, fungi, viruses, parasites, insects, weeds etc. biotic stress occurs and abiotic stress is the negative effect of nonliving factors like water, soil moisture, heat etc. on the plant in a specific environment. The nonliving factors also influence the environment beyond its normal range to adversely affect the population performance or individual physiology of the plant in a significant way. It is difficult to diagnose the harmful effects caused by these living and nonliving factors even with close observation. Therefore, the determination of plant stress is very challenging as it looks similar and can be a combined result of water deficiency, disease infection, and others symptoms arising from different stress factors. For example, the browning of leaves of an oak tree due to drought or water deficit may look similar to the leaf browning caused by anthracnose, which is a minor leaf disease of an oak tree or leaf browning caused by oak wilt which is a vascular disease (Pritham 2015). Thus, remedial action for the affected plant or crop should not be done only by visual observation because it may result in an incorrect diagnosis. Abdulridha et al. (2019b) used remote sensing techniques for the detection of laurel wilt disease in the avocado (*Persea americana*) plant in presence of other biotic and abiotic stresses. The use of remote sensing or hyperspectral satellite data will help for better monitoring different biotic and abiotic stresses on a small or large area. Spectral reflectance measurements techniques are used to identify different types of plant stress by selecting wavelengths sensitivity. From previous studies, it was known that plant stress changed the spectral reflectance pattern both in the visible range (380–720 nm or F380–F720) and the infrared range (720–1500 nm or F720–F1500) (Mee et al. 2017). The magnitude of this change will vary at different wavelengths. This information helps us to early detect plant stress, particularly nutrient deficiency. Thus with the help of this method, we can able to lower the cost and increase the productivity of the crop. In recent years, many efforts have been made to develop new methods for the detection of plant stress. Remote sensing has become an important tool in agriculture, particularly, leaf temperature, which is an indicator of plant physiological status in response to both biotic and abiotic stress (Pineda et al. 2021).

2 Effect of Biotic and Abiotic Stresses in Agriculture

Biotic and abiotic stress caused massive economic losses to different crops and thus it is a major area of focus in agricultural research (Teshome et al. 2020). Both the economic decisions and practical development are affected by the relationship between biotic stress and crop production. Population dynamics, plant-stressor coevolution, and ecosystem nutrient cycling have been affected by the biotic injury on crop yield. The health of the horticultural crop and natural habitats ecology is also affected by biotic stress reported by Wang et al. (2003). It also has some major changes in the host plant because the stressed environment has an impact on the crops' growth and development, which leads to modifications of biochemical and morphological characteristics of the plant species (Oshunsanya et al. 2019). Plants are exposed to different biotic and abiotic stress factors such as water deficiency, high salinity, pathogens, or weeds, which reduce the crop yield or affect the quality of harvested products. *Arabidopsis thaliana* is most commonly used as a model plant to study the responses of plants to different factors of biotic and abiotic stress (Mittler 2006). Whereas biotic stress includes living disturbances, for example, bacteria, fungi, or pests. Abiotic stress factors are generally occurring naturally, such as intense sunlight or wind that cause harm to both plants and animals in a particular area and it is unavoidable. Abiotic stress factors affect animals, but plants are highly dependent on different environmental factors, so it is constraining. Regarding the growth and productivity of crops, abiotic stress is the most harmful factor worldwide. Fernando TM et al. (2004) reported that abiotic stressors were most harmful when they occurred together with combinations of abiotic stress factors. The most common of the stressors are the easiest for people to identify, but many other less recognizable abiotic stress factors affect the environments constantly (Wolfe 2007). The most basic stressors include high winds, extreme temperatures, and drought (Pritham 2015).

3 Application of Remote Sensing Technology for Monitoring Biotic and Abiotic Stress

Agricultural production has come through many changes in technology within the past few years. Farmers can utilize different advanced technologies such as site-specific applicators and remote sensing data to assist their decision-making for best crop management practices, which can improve productivity and also help to protect the environment (Sishodia et al. 2020; Huang et al. 2018). Plant stress can interfere with photosynthetic reactions within the plant and therefore affect the physical structure of the plant (Chaves et al. 2009) Thus, remotely sensed data is used to identify different levels of crop stress, and therefore it helps the producers by using this information to better crop management to maximize the crop production. Raikes and Burpee (1998) suggested that hyperspectral remote sensing was one of the advanced and effective techniques in mapping and disease monitoring in plants. However, the difficulty in discriminating disease from nutrient stresses hampers the practical use of this technique, because some common nutrient stresses like shortage or overuse of nitrogen or water could produce similar variations of biochemical properties and plant morphology and therefore generates similar spectral responses (Pritham 2015). However, there is a significant difference in the remedial procedures for stressed crops between disease and nutrient stresses. For example, applying fungicide to a water-stressed crop would lead to a disastrous outcome. Therefore, to discriminate yellow rust from common nutrient stresses is of practical importance to crop growers. Traditional methods like ground-based surveys require high labor costs and produce low efficiency. Thus, this method is unfeasible for a large area. But remote sensing technology can provide spatial distribution information of diseases and pests over a large area with relatively low cost than the traditional method (Pritham 2015; Zhang et al. 2012). The presence of diseases or insect feedings on plants or canopy surface of crops causes changes in pigment, chemical concentrations, cell structure, nutrient, water uptake, and gas exchange. These changes result in differences in color and temperature of the canopy and therefore affect canopy reflectance characteristics, which can be easily detectable by remote sensing technology (Raikes and Burpee 1998). Therefore, remote sensing technology provides a harmless, rapid and cost-effective method of identifying and quantifying crop stress from differences in the spectral characteristics of canopy surfaces affected by different biotic and abiotic stress agents (Wenjiang et al. 2012).

4 Detecting and Monitoring Plant Nutrient, Biotic and Abiotic Stress Using Remote Sensing Techniques

Plants require adequate nutrients in addition to water and sunlight for their proper growth. The plant requires macronutrients in greater amounts as compared to micronutrients, as both these macro and micronutrients are part of different substances in plant tissue. Shortage of any of these nutrients, mainly the macronutrients like nitrogen, potassium and phosphorus can result in different stress-induced responses in plants such as restriction of growth of shoots and roots, early defoliation of plant leaves and also decreased production of biomass. Nutrient surplus especially nitrogen, due to over-application of fertilizer may lead to losses via leaching and cause environmental pollution (Hawkesford et al. 2012). Thus, the nutrient requirement is also very important to ensure good health and the growth of plants. Therefore, in modern agriculture definite estimation of plant nutrients is based on different leaf optical properties such as fluorescence, reflectance and transmittance are gaining more importance and it can be done through different remote sensing techniques. The spectral reflectance data is related to the chlorophyll content of plant leaves and depend on the interaction between light penetration through the plant tissue and its absorption, reflection from the leaf surface or transmitted amount through the leaf (Ac et al. 2015; Gitelson et al. 2003). Zwiggelaar (1998) suggested that these optical spectra data were dependent on the pigment content of leaf of different absorption wavelengths as presented in Table 1.

The maximum absorption spectrum is generally found in the blue (400–500 nm or F400–F500) and red (660–680 nm or F660–F680) spectral region of the chlorophyll band (Mee et al. 2017). Healthy plants absorb more blue and red light, reflect most of the green and infrared light (Cetin et al. 2005). The yellow-green color of chlorosis in plants is due to the greater absorption of violet light and purple coloring of leaf margins and stems because of greater green light absorption by plants in phosphorus-deficient soil (Raun et al. 1998). Nitrogen deficiency reduces leaf chlorophyll content in plants and leads to lower absorption of light and higher reflectance in the visible and infrared range as studied on different crops like barley, wheat, and lettuce (Liu et al. 2004; Pacumbaba and Beyl 2011). Most findings suggest that the sensitivity of chlorophyll to physiological stress is effective in measuring the reflected spectra in identifying nutrient stress in different crop plants. However, spectral features are not useful in detecting plant stress where more than one factor is involved. Thus, this method is quite challenging when discriminating between different stress factors affecting a plant same time, which is more common in reality (Mee et al. 2017). Different stressors may affect the physiology of a plant in a similar way, for example, nutrient deficiency and disease cause similar changes in leaf pigment content, moisture, and canopy structure. Therefore, differentiation between crop disease and nutrient stress is difficult as similar spectral responses may be obtained.

Table 1 Absorption wavelengths of pigments (Mee et al. 2017)

Pigment/molecule	Absorption wavelengths (nm)
Chlorophyll a	435, 670–680, 740
Chlorophyll b	480, 650
α-carotenoid	420, 440, 470
β-carotenoid	425, 450, 480
Anthocyanin	400–550
Lutein	425, 445, 475
Violaxanthin	425, 450, 475
Water (molecule)	970, 1450, 1944

4.1 Nutrient Deficiency of Plants Detected by Using Chlorophyll Fluorescence

Precise information can be generated through chlorophyll fluorescence regarding different plant stresses by using the fluorescence emission pattern of leaves, tissues of the plants. The chlorophyll fluorescence is captured when parts of light energy are absorbed by the plant chlorophyll for photosynthesis and reemission of the light occurs when excited with UV-A (340–360 nm) or blue-green light (Maxwell and Johnson 2000). The blue-green light is much efficient and provides more detailed information as it can reach deeper layers of plant tissue than UV light, which is usually intercepted at the epidermal surface of leaves because very less amount of UV radiation can pass through the green mesophyll cells containing chlorophyll pigments which absorb the blue and red photons of light (Benediktyová and Nedbal 2009). The fluorescence ratios are a result of the simultaneous changes between the four wavelengths, i.e., blue (F440), green (F520), and red (F690, F740), which is commonly referred to as blue-green and red spectra. Usually, blue and green fluorescences are emitted by excitation with solar-induced light near the 440 and 550 nm spectral regions whereas fluorescence from the red region of 650–800 nm is given by the blue-green light excitation. The early detection of plant stress and nutrient availability depends on F440–F690 (blue-red) and F440–F740 (blue-red) whereas the ratio of frequently used chlorophyll content indicator is F690–F735 (blue-red) spectra (Buschmann et al. 2008; Chaerle and Van Der Straeten 2000). The fluorescence emission specific to different plant stresses was successfully detected on different plants, for example, deficiency of nitrogen and zinc on maize (*Zea mays*), heat and water stress on *Rhododendron* sp., etc. Cadet and Samson (2011) used fluorescence ratios to detect the deficiency of different nutrients like nitrogen, potassium, and phosphorus in sunflower (*Helianthus annuus*). To differentiate between nitrogen deficiency and disease infection in wheat plant (*Triticum aestivum*), fluorescence ratios can be used. Husna et al. (2015) used fluorescence sensing techniques to estimate the productivity and quality of palm oil from palm plants (*Elaies guineensis* Jacq.). The use of fluorescence imaging has been extended to different areas of agriculture like irrigation, water management, fertilization, and disease control of crops because of its potential in sensing plant stress induced by different factors like water deficit, nutrient deficiency, and disease infection.

4.2 Nutrient Deficiency Detection Using Thermography

Unlike fluorescence imaging, thermography has been used to visualize the stomatal movement without the presence of any light source (Vadivambal and Jayas 2011). The thermal signal is the change of temperature in the form of radiation reflected or emitted from the plant. Thermal intensity is detected by the surrounding temperature and the intensity of infrared radiation increases with the increase of temperature (Vadivambal and Jayas 2011). The change in leaf temperature of a plant generally occurs due to the opening and closure of stomata. The cooling process in plants is through the transpiration by stomatal opening and results in a decrease of temperature with heat loss to the atmosphere. However, the process of transpiration and stomatal regulation is usually determined by nutrient and water availability in soil. The transportation of dissolved nutrients and water from the soil to the plant is disrupted by the water or nutrient scarcity and nutrient uptake is limited by higher nutrient concentration in soil (Li et al. 2009). Therefore, as a result, loss of water is prevented due to closure of stomata and thus the temperature of the leaf surface increases. This is why nutrient deficiency affects stomatal regulation and leads to increased temperature within the plant. Chaerle et al. (2007) reported that thermal imaging of magnesium-deficient bean plants under controlled conditions showed higher leaf temperature. Thermography is passive, but it can be active with the introduction of a stimulus like light to induce a change in temperature of the targeted subject (Chaerle et al. 2007). Active thermography can help us to determine leaf internal heterogeneity in relation to any change or growth due to disease, whereas passive thermography assesses change of similar capacity through estimation of water evaporation (Chaerle and Van Der Straeten 2000). Thermography can detect plant stress, but it does not useful to differentiate between the different stressors. Thus, it should be used in combination with other remote sensing techniques such as chlorophyll fluorescence to determine and differentiate between different stresses simultaneously as reported by Chaerle et al. (2007).

4.3 Detection of Nutrient Deficiency Using Multispectral and Hyperspectral Imaging

Multispectral systems are useful to measure the reflectance in broad bands of 40 nm in the red, green, blue, and near-infrared regions and it can be extended to a maximum of ten wavelengths (Moshou et al. 2011; Mulla 2013). This is the main difference between hyperspectral and multispectral imaging techniques. Additional spectral bands are used in hyperspectral technique and it brings about higher spectral resolution or narrower bandwidth of about 10 nm or less in the visible and near-infrared band range. It provides more details with the broader aspect of functional and structural characteristics of vegetation (Blackburn 2007; Lee et al. 2010). Like thermography, the hyperspectral technique can be used together with chlorophyll fluorescence to differentiate between plant internal responses to stress-based changes in photosynthetic efficiency and spectral properties (Murchie and Lawson 2013). Different plant stress levels such as water content, disease and nutrient status of different crops have been effectively sensed using hyperspectral discrimination technique (Zhang et al. 2012; Zhang et al. 2006; Song et al. 2011; Cao et al. 2013). Zhang et al. (2013) reported that spectral reflectance was more effective at characterizing the distribution of nutrients such as nitrogen, phosphorus, and potassium in leaves of *Brassica napus*.

4.4 Development of Vegetative Indices by Using Multispectral Wavelengths

By using several selected bands within the visible (blue, green, and red bands) and near-infrared spectral regions in multispectral imagery different Vegetation Indices (VIs) were developed. VI is a dimensionless, radiation-based measurement derived from the spectral combination of remote sensing data (Prabhakar et al. 2012). These bands within the spectral regions are most responsive to the chlorophyll pigments where plant reflectance is found to be strongest (Blackburn 2007). The intensity of reflectance light in a plant is not dependent only on its chlorophyll concentration alone; several other factors such as leaf shape and geometry, canopy area, etc. may alter the depth of light absorption and reflectance (Blackburn 2007). The Normalized Difference Vegetative Index (NDVI) is the most frequently used index in multispectral imaging applications as compared to other Vegetative Index due to its practicality in detecting physiological variability of plants (Thomason et al. 2007; Tremblay et al. 2011). Generally, at an early stage of disease visible green range is useful in the detection of plant infection while reflectance in the near-infrared is more useful with the increasing severity of infection. Depending on which spectral region is used, the vegetative indices developed can be green NDVI (green and NIR), red NDVI (red and NIR), or red and green vegetation indices (Muñoz-Huerta et al. 2013; Navarro-Cerrillo et al. 2014) (Table 2). The red band in the vegetative index corresponds more to chlorophyll pigment, where radiation absorption is the maximum and the green band deals with the pigment region other than chlorophyll (Mulla 2013). Although NDVI is very useful in detecting plant stress, it comes with certain limitations in terms of sensitivity to higher chlorophyll content. Indices with narrower bands that develop particularly near 550 and 700 nm are most sensitive to pigment change (Table 3). Zhao et al. (2005) reported reflectance signal

Table 2 Narrow band vegetation indices used for abiotic and biotic stress detection (Prabhakar et al. 2012)

Index	Formula	References
Normalized pigment chlorophyll index (NPCI)	(R680 − R430)/(R680 + R430)	Penuelas et al. (1995b)
Structure insensitive vegetation index (SIPI)	(R800 − R445)/(R800 + R680)	Penuelas et al. (1995a)
Optimized soil-adjusted vegetation index (OSAVI)	(1 + 0.16) (R800 − R670)/ (R800 + R670 + 0.16)	Rondeaux et al. (1996)
Water index (WI)	R900 nm/R970 nm	Penuelas et al. (1997)
Red-edge vegetation stress index (RVSI)	(R714 nm + R752 nm)/2 − R733 nm	Merton and Huntington (1999)
Modified chlorophyll absorption Reflectance index (MCARI)	[(R700 − R670) − 0.2(R700 − R550)] (R700/R670)	Daughtry et al. (2000)
Transformed chlorophyll absorption reflectance index (TCARI)	3[(R700 − R670) − 0.2(R700 − R550) (R700/R670)]	Haboudane et al. (2002)
Disease water stress index 2 (DWSI-2)	R1660/R550	Apan et al. (2004)
Damage sensitive spectral index-2 (DSSI 2)	(R747 − R901 − R537 − R572)/ (R747 − R901) + (R537 − R 572)	Mirik et al. (2006a)
Aphid index (AI)	(R761 − R908)/(R712 − R719)	Mirik et al. (2006b)
Broccoli soft rot index	(D725 − D700)/(D725 + D700)	Datt (2006)
Bacterial leaf spot index	(R550 − R640)/(R550 + R640)	Datt (2006)
Sunburn index	(R450 − R680)/(R450 + R680)	Datt (2006)

R: Reflectance at the corresponding wavelength (nm); D: first-order derivative at the corresponding wavelength (nm)

Table 3 Sensitive bands and spectral indices used for detection of biotic stresses in different crops (Prabhakar et al. 2012)

Crop	Pest	Platform	Spectral resolution	Optimum bands (in nm)/ indices/technique used	References
Peanut	Leaf spot	Ground based	Multispectral	800 nm	Nutter (1989), Aquino et al. (1992)
Wheat	Cereal aphid	Ground based	Hyperspectral	NPCI	Riedell and Blackmer (1999)
Wheat	Yellow rust	Ground based	Hyperspectral	543, 630, 750, 861 ± 10 nm	Bravo et al. (2003)
Rice	Leaf blast	Ground based	Multispectral	(R550/R675), (R570/R675)	Kobayashi et al. (2003)
Cotton	Armyworm	Ground-based and airborne	Multispectral	NDVI	Sudbrink et al. (2003)
Sugarcane	Orange rust	Space borne	Hyperspectral	DWSI	Apan et al. (2004)
Rubber	Corynespora	Space borne	Multispectral (IRS 1 C)	NDVI	Ranganath et al. (2004)
Cotton	Spider mite	Airborne	Hyperspectral (AVIRIS)	SMA	Fitzgerald et al. (2004)
Tomato	Late blight	Ground-based airborne	Hyperspectral multispectral (ADAR)	5-index feature vector method	Zhang et al. (2005)
Wheat	Greenbug	Ground based	Multispectral	694, 800 nm	Yang et al. (2005, 2009)
Mustard	*Alternaria*	Space borne	Hyperspectral	DWSI	Dutta et al.(2006)
Cotton	Aphid, spider mite	Airborne, space borne	Multispectral (SAMRSS, QuickBird); hyperspectral (AV-NIR)	NIR is more sensitive	Reisig and Godfrey (2006)
Wheat	Green bug	Ground based	Hyperspectral	AI	Mirik et al. (2006a)
Wheat	Green bug	Ground based	Hyperspectral	DSSI	Mirik et al. (2006b)
Wheat	Aphid	Airborne	Multispectral	NDVI	Elliott et al. (2007)
Tomato	Leaf miner	Ground based	Hyperspectral	800–1100 nm, 1450 and 1900 nm	Xu et al. (2007)
Rice	Leaf folder	Ground based	Hyperspectral	757,445 nm	Yang et al. (2007)
Pine	Bark beetle	Space borne	Multispectral (Landsat)	LAI	Coops et al. (2009)
Conifer	Aphid	Space borne	Hyperspectral	ARI	Pena and Altmann (2009)
Rice	Bacterial leaf blight	Ground based	Hyperspectral	943 and 1039 nm, MLR	Yang (2010)

R: Reflectance

specific to nitrogen scarcity in *Sorghum bicolor* was found to be near the 555 and 715 nm wavelengths.

4.5 Using of Satellite and Airborne Platforms to Real-Time Monitoring of Crop Nutritional Status and Yield Prediction

It is important to track crop growth and development dynamics over time in the monitoring of crop conditions. This provides timely information which can help us to identify problematic areas affected by various vegetative factors such as water status, nutrient distribution, disease and weed encroachment, etc. Different satellite and aircraft platforms can be used for remote monitoring of crop condition, yield prediction and it can be achieved through the combining of their multiple image data with suitable process-based simulation models (Mosleh et al. 2015; Lobell 2013; Sims et al. 2013). For example, data derived from Moderate Resolution Imaging Spectroradiometer (MODIS) has been used to forecast crop yield of some crops like barley, *Brassica*, peas (*Pisum sativum*), wheat (*Triticum aestivum* L.) etc. (Mkhabela et al. 2011). The advancement of technology in recent years brought airborne sensors with both higher spatial, spectral resolutions and shorter revisit times, but some problems remain unsolved like data processing time and higher cost making them less operational and economically inefficient. Berni et al. (2009) suggested the use of Unmanned Aerial Vehicles (UAVs) mounted with cheaper thermal and multispectral sensors. Low-altitude Remote Sensing (RS) using UAVs is a very useful tool in precision agriculture (Messina and Modica 2020). Compact Airborne Spectrographic Imager (CASI) is used to detect weed infestation on corn (Goel et al. 2003).

5 Use of Remote Sensing Technology in Monitoring and Management of Biotic and Abiotic Stresses in Crop Plants and Its Applications in Agriculture

5.1 Water Management and Irrigation

Time and rate of irrigation are very important to reduce crop water stress and achieve maximum crop growth and yield. A variety of irrigation methods are used by farmers depending on many factors like water availability, water management infrastructure at the field (Pardossi et al. 2009). Many farmers used their farming knowledge and applied uniform irrigation at regular intervals based on soils and climate at the location (Boland et al. 2006) Large farmers often used soil moisture monitoring systems (wired or wireless moisture sensors) to irrigate (automatically or manually mode) their fields based on the data of soil moisture and plant water requirements. Different agencies also provide irrigation advisory services based on the climate and weather conditions in the area (Eching et al. 2002; Smith and Munoz 2002).

All of these conventional farming methods generally do not consider the variability within the field and use a uniform irrigation rate for the entire field. Remote sensing data can be used to apply a variable rate of irrigation with commonly used irrigation systems in the field. The variable rate of application helps to alleviate water stress due to extreme wet and dry conditions, achieve uniformly high yields in all parts of the field, and reduce the water and nutrient losses (Evans et al. 2013; McDowell 2017). Remote sensing images are generally collected multiple times during a growing season of a crop to determine various indicators of crop water demand such as Evapotranspiration (ET), soil moisture, and water stress, which are used to estimate the water requirement of the crop as well as schedule irrigation in the field.

Remote sensing products like optical, thermal, and microwave bands are used to develop and test multiple indices and techniques for water management (Amani et al. 2016). For example, NDVI and Soil Adjusted Vegetation Index (SAVI) were developed from optical images of remote sensing data and they can be used to detect water stress and soil moisture conditions for different crops. These indices, in combination with forecasted weather data of the area, can be used for irrigation scheduling in the field. Thermal remote sensing-based Crop Water Stress Index (CWSI) is another indicator that is used to estimate the irrigation water demand. CWSI is extensively used for irrigation management in many orchards (Egea et al. 2017; Maes and Steppe 2019). An autonomous multi-sensor (multispectral and thermal sensor) Unmanned Aerial Vehicle (UAV) system was used by Katsigiannis et al. (2016) to develop CWSIs maps for irrigation scheduling and water management in kiwi, pomegranate, and vine fields. However, more research and study are needed to establish climate–soil–crop-specific threshold values to enable irrigation scheduling in different crop fields by the use of CWSI. Zhang et al. (2019a, b) used UAV-based Multispectral Remote Sensing techniques for mapping water stress in maize (*Zea mays*).

5.2 Evapotranspiration

The major water flux from the Earth’s surface to the atmosphere is Evapotranspiration (ET). It is an important component of the hydrologic cycle and water balance on earth. Conventional methods of ET measurement (e.g., weighing lysimeter and eddy covariance) are very expensive and they do not provide spatially variable ET estimates resulting from the differences in land use, topography, soils of an area, and other hydrologic processes (Liou and Kar 2014; Verstraeten et al. 2008). Remote sensing data is often used to estimate ET, which is required to determine the crop water requirements to schedule irrigation and water management (Mendes et al. 2019; Barker et al. 2018). There are different methods of ET estimation by using remote sensing data and these methods can be grouped into three categories: (i) surface energy balance method, (ii) crop coefficient method, and (iii) the Penman–Monteith method (Mendes et al. 2019; Calera et al. 2017). Many studies provided a review of different remote-sensing-based ET estimation techniques (Liou and Kar 2014; McShane et al. 2017) including a review from Zhang et al. (2019a, b), which discussed the development theories of several ET estimation methods along with their advantages and disadvantages. The surface energy balance method is an extensively used for ET estimation in the past few years (Sishodia et al. 2020). Some studies also have been used as hybrid methods by combining the crop coefficient and energy balance method for ET estimation. In the surface energy balance method, the net radiation flux (Rn), soil heat flux (G), and sensible heat flux (H) are usually calculated from remotely sensed data in visible, near-infrared, and thermal infrared bands, while the latent heat flux (ʎET) is calculated as a reminder of the term in the energy balance equation (Barker et al. 2018; Calera et al. 2017).

A detailed review was provided by Liou and Kar (2014) and McShane et al. (2017) regarding various surface energy balance algorithms used for estimating landscape-scale ET at high spatial resolution and they discussed their physical basis, assumptions, and disadvantages. Surface energy balance techniques are a variety of empirical and physically based models to solve the energy balance equation fully or partially for ET estimation. Crop-coefficient-based methods for ET estimation are dependent on a statistical relationship between a vegetation index (e.g., NDVI, SAVI) and crop coefficient. There are numerous methods for the estimation of ET based on the remote sensing data, each having its advantages and disadvantages. Some surface energy balance methods like S-SEBI do not need any ground-based measurements and ET can be estimated only by using remote sensing data (Liou and Kar 2014). Further studies and research are needed for the development of remote-sensing-based ET estimation methods to identify and determine the spatial–temporal structure of uncertainties in ET estimation due to process errors, forcing errors, parameterization errors, etc.

5.3 Soil Moisture

Remote sensing data received in multiple bands, including optical, thermal, and microwave, is often used to estimate soil moisture (Verstraeten et al. 2008; Zhang and Zhou 2016). Thermal and optical remote sensing data are also used extensively for estimation of soil moisture and ET in a method called as “triangle” or “trapezoid” method or Land Surface Temperature-Vegetation Index (LST-VI) method (Zhang et al. 2016; Carlson 2007; Babaeian et al. 2018). This method is based on the physical relationship between the surface temperature of land and the characteristics of its vegetative cover. Soil moisture estimation by this method is done through the interpretation of pixel distribution in the LST-VI plot-space. If an image contains a sufficiently large number of pixels covering a full range of soil moisture, vegetation density and when cloud, surface water, and other outliers are absent, the LST-VI space looks like a triangle or trapezoid (Carlson 2007). One edge of the LST-VI triangle or trapezoid falling toward higher temperatures represent the dry edge and low content of soil moisture, while the opposite side of the triangle or trapezoid represents the wet edge with high soil moisture (Petropoulos et al. 2009). A newer generation of triangular models has been developed recently and they are tested for high spatial resolution mapping of soil moisture content in different agricultural applications (Babaeian et al. 2019; Sadeghi et al. 2017). For the application of these models in a diverse range of climatic, hydrologic, and environmental conditions, more studies are needed. Mohamed et al. (2019) used remote sensing data for mapping soil moisture content and their correlations with crop patterns in arid regions.

5.4 Disease Management

Different diseases of crop plants reduce the significant amount of crop production and farmer profits. Early detection of plant disease can help us to control the disease spread and reduce production losses. Conventional methods such as field scouting of disease detection are very time-consuming, labor-intensive, and subject to human error (Ehsani and Maja 2013) and it is difficult to detect the disease during the early stages with not fully visible symptoms by this method. Furthermore, some diseases do not show any noticeable visible symptoms at an early stage (Sladojevic et al. 2016). Due to the difficulties of mapping the spatial extent and disease severity with the conventional methods, remote sensing techniques can be used to monitor the disease at the early stages of development with much efficiency, as it is difficult to detect the signs of disease with the field scouting method. To improve the ability to detect different diseases and parasitic attacks at an early stage of disease development, we can use different sensors such as thermal sensors and the combination of their derived data with optical and multispectral sensors (Zhang et al. 2019a, b). Multiple techniques such as multispectral, hyperspectral, thermal, and fluorescence imaging are very useful to identify diseases in different crops (Mahlein 2016). Abdulridha et al. (2019a) used a machine learning method with vegetation indices generated from hyperspectral UAV images to detect canker disease of citrus plants with an accuracy of 96% at an early stage of disease development and stress due to late blight disease of tomato plant was detected by hyperspectral remote sensing technology (Zhang et al. 2003). The disease-specific Spectral Disease Indices (SDI) can provide more accuracy of disease detection than the typically used vegetation indices such as NDVI (Mahlein et al. 2013; Al-Saddik et al. 2017). By using SDIs, in place of typical VIs, we can reduce the complexity of disease detection and increase the system efficiency simultaneously. Remote sensing can also be used for fast and accurate forecasting of pests, subsequently reduction of pest damage and management costs (Marei 2020). Therefore, further studies are needed to develop more accurate methods for disease detection under diverse climatic conditions of field in the real world.

5.5 Crop Monitoring and Yield

Monitoring crop growth and yield are very important to understand the crop response to the environment and develop effective management plans for the fieldwork (Peng et al. 2019). Remote sensing data of crop growth and biomass yield can help us to obtain valuable information on site-specific properties such as soils, topography, management (e.g., water, nutrient) and different stressors such as diseases, weeds, water, nutrient stress etc. (Campos et al. 2019). Remote sensing data is also used for mapping differences in tillage and residue management (Yeom et al. 2019). Using hyperspectral images with various machine learning and classification techniques, we can map tillage and crop residue in agricultural fields (Hively et al. 2018; Salas and Subburayalu 2019). This information on crop conditions and tillage practices can help us to generate site-specific management plans like variable water, nutrient, and pesticide application in the field. Crop biophysical parameters or vegetation indices derived from remote sensing have a strong correlation with crop yield and biomass, having potential use in crop yield estimation (Peng et al. 2019). Spatial mapping of crop biophysical parameters or vegetation indices derived from multiple times remote sensing during a growing season is most likely to provide a better estimation of crop biomass yield. Toscano et al. (2019) used remote sensing data for mapping and yield assessment of durum wheat (*Triticum durum*). Remote sensing can also be used in weed mapping using 'Unmanned Aerial Vehicle' (Huang et al. 2020) and in pest management (Huang et al. 2012).

6 Conclusion

Remote sensing has many uses and advantages in agriculture such as crop yield estimation, monitoring crop growth, estimation of soil moisture, detection of different stresses and diseases, weather forecasting, etc. (Shanmugapriya et al. 2019). A lot of information has been generated in recent years on characterizing biotic and abiotic stress using remote sensing such as multispectral radiometry. Different management-related challenges along with abiotic and biotic stressors may be confronted by using remote sensing technologies to make better agricultural management decisions (Segarra et al. 2020). It is possible to better understand the crop stress induced by different pests and diseases with the help of remote sensing. The differentiation between biotic and abiotic stresses with much accuracy is also possible by using hyperspectral radiometry. Reflectance data derived from ground-based remote sensing technology provides important information for understanding spectral interactions between pests damage on the host plants. Remote sensing by satellite provides a sufficient amount of data for large-scale studies, but it has some disadvantages such as temporal or spatial resolution and availability of cloud-free data. Airborne systems have higher resolution, time flexibility, and can provide sufficient time for dissemination of crop protection advisory. Though the application of airborne remote sensing technology for detection of biotic and abiotic stress is popular in many developed countries, it is in its primary stages of usage in the developing countries because of its high cost, lack of availability of suitable sensors, small marginal farm holdings, and diverse range of cropping systems. Hence, it is quite difficult to use airborne hyperspectral remote sensing in these countries. In the past, there is limited availability of fine spatial resolution, near real-time data for the application of satellite remote sensing in agriculture but now this problem is not a matter of concern with the launch of new generation satellites. The narrow bands in hyperspectral sensors can detect the characteristic absorption peaks of different pigments of plants and other parameters more accurately and thus provide better information about plant health. But the availability of hyperspectral data from different satellite platforms is still in its early stage. Air and spaceborne remote sensing can provide spatial variability of biotic and abiotic stress of a large area. With the help of satellite and digital imaging methods, it is simple and cost-effective in monitoring the crop situation (Ennouri and Kallel 2019). Therefore, we can use remote sensing technology for getting much accurate and reliable information in crop protection and management.

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