Plant Adaptation to Environmental Change

Significance of Amino Acids and their Derivatives

Edited by
Naser A. Anjum,
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and Ritu Gill

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Preface

Plants are fundamental to all life on Earth. They provide us with oxygen, food, fuel, fibre, medicines and even shelter, either directly or indirectly. However, plant-based food production has always been linked to environmental changes. To this end, both naturally and human activities-influenced changes in the physical and biogeochemical environments contribute to global environmental changes which cumulatively create sub-optimal conditions for plant growth. Being sessile in nature, plants, in a variably changing environment, have to cope with a plethora of sub-optimal (adverse) growth conditions where the majority of these conditions can delay growth and development and most importantly prevent them reaching their full productivity genetic potential. Nevertheless, in the complex field environment with its heterogenic conditions, global environmental changes-mediated potential anomalies in plants are further aggravated with various abiotic stress combinations. However, plants develop a battery of highly sophisticated and efficient strategies to acclimate, grow and produce under gradual change in their environment. Understanding of the global environmental change-led impacts on plants and also the exploration of sustainable ways to counteract these impacts have become thrust areas of utmost significance.

Through authoritative contributions, the present volume entitled *Plant Adaptation to Environmental Change: Significance of Amino Acids and their Derivatives* overviews varied amino acids and their derivatives' significance for plant stress adaptation/tolerance, discusses significant biotechnological strategies for the manipulation of amino acids and their major derivatives (hence to improve biotic/abiotic stress tolerance in crop plants), provides state-of-the-art knowledge of recent developments in the understanding of amino acids and their derivatives emphasizing mainly on the cross-talks on amino acids, peptides and amines, and fills the gap in the knowledge gained on the subject obtained through extensive research in the last one and half decades.

In particular, the role of important amino acids, peptides and amines as potential selection criteria for improving plant tolerance to adverse growth conditions has been critically discussed at length in different chapters contributed by experts from over the globe working in the field of crop improvement, genetic engineering and abiotic stress tolerance. Though occasional overlaps of information between chapters could not be avoided, they reflect the central and multiple aspects of major amino acids, peptides and amines-based strategies for enhancing tolerance to environmental change in the light of the advances in molecular biology.

Chapter 1 introduces major factors responsible for environmental change and its implication for plant growth and development, and amino acids and their important derivatives in context mainly with their significance for plant adaptation and/or tolerance to varied environmental stress factors.

Focusing on 5-aminolevulinic acid (5-ALA) Chapter 2 deals with the biosynthetic pathway and chemical synthesis of 5-ALA, the biosynthetic pathway of tetrapyrrole compounds from 5-ALA, industrial strains development for 5-ALA over-production and 5-ALA important biological activity significance in different stressed plants. Chapter 3 summarizes available data on the structure, occurrence, biosynthesis, regulation and significance of cysteine, peptides (glutathione, phytochelatins) and cysteine-rich, gene-encoded low-molecular weight proteins – metallothioneines in plant metabolism and stress defense as well. Considering the significance of legumes for both humans and animals as a source of protein-rich food Chapter 4 discusses transcriptomics and plastidic glutamine synthetase mutants for new insights in proline metabolism in drought exposed *Lotus japonicus*. In Chapter 5, information about physiological functions and regulations of proline in plant systems is summarized and diverse roles of proline including the signalling events involved in proline synthesis are presented. Chapter 6 reviews the knowledge that has been gathered over the last couple of decades with respect to glycine betaine and proline – extensively explored as target osmoprotectants for enhancing abiotic stress tolerance in crop plants.

The central focus of Chapters 7–11 is polyamines. In particular, Chapter 7 critically discusses polyamines as indicators and modulators in the abiotic stress in plants. By exploring the natural variation for polyamine levels, and how these interact with the environment, Chapter 8 looks for developing tools that will facilitate the manipulation of polyamine levels that can lead to practical applications in agriculture. Chapter 9 emphasizes the mechanism of polyamine metabolism and their multifunctional role in plants under major environmental stresses like salinity, drought and cold. In addition, in this chapter, the regulation of expression of genes, encoding polyamine-metabolizing enzymes under such stress conditions, their promoter structures and overexpression of such genes through transgenic approaches for enhanced tolerance is also highlighted. Chapter 10 summarizes some recent data concerning changes in polyamine metabolism (biosynthesis, catabolism and regulation) in higher plants subjected to a wide array of environmental stress conditions, and describes and discusses some new advances concerning the different proposed mechanisms of polyamine actions implicated in plants' responses to abiotic stress. Furthermore, this chapter also discusses progress made in genetic engineering in polyamine-induced stress tolerance in plants. Polyamines involvement in plant tolerance and adaptation to stress is discussed in Chapter 11. The role of polyamines in the biotic stress of plants as a result of plant–pathogen interaction with a note on current research tendencies and future perspectives is critically discussed in Chapter 12; whereas, Chapter 13 highlights the role of polyamines in the management of important stresses. Chapter 14 deals with polyamines significance in plant *in vitro* culture. Betaines and related osmoprotectants' significance in metabolic engineering of plant stress resistance is highlighted in Chapter 15; whereas, Chapter 16 throws lights on brassinosteroids' role for amino acids, peptides and amines modulation in stressed plants. Chapter 17 presents a critical appraisal of the manuscripts covered in the current book and also highlights important aspects so far less explored in the current context.

The outcome of the present treatise will be a resourceful guide suited for scholars and researchers exploring sustainable strategies for crop improvement and abiotic stress tolerance.

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Abbreviations

Abbreviation	Name or term in full
AAME	adipic acid monoethyl ester
ABA	abscisic acid
ADC	arginine decarboxylase
AG	aminoguanidine
AIH	agmatine iminohydrolase
AMF	arbuscular mycorrhizal fungus
AOs	amine oxidases
arg	arginine
AS	asparagine synthetase
asn	asparagine
BA	benzyladenine
CEVd	citrus exocortis viroid
CHA	cyclohexylamine
CMV	cucumber mosaic virus
CMV-Y	CMV-yellow
CP	clover phyllody
CPA	N-carbamoylputrescine amidohydrolase
CuAO	copper binding diamine oxidases
DAO	diamine oxidases
DAP	diaminopropane
DCHA	dicyclohexylamine
DFMA	α-difluoromethylarginine
DFMO	α-dl-difluoromethylornithine
DFMO	α-difluoromethylornithine
DW	dry weight
Epi	epinastic
ER	endoplasmic reticulum
Fd-GOGAT	ferredoxin-dependent glutamate synthase
FDR	false discovery rate
GA	gibberellic acid
GABA	gamma aminobutyric acid
GC-MS	gas chromatography-mass spectroscopy
GDC	glutamate decarboxylase
GDC	glycine decarboxylase
GDH	glutamate dehydrogenase
gln	glutamine
GLRaV	grapevine leafroll associated viruses
glu	glutamate
GO	glycolate oxidase
GS	glutamine synthetase
GSH	glutathione (reduced)
GS1	cytosolic glutamine synthetase
GS2	plastidic glutamine synthetase
GSSG	glutathione (oxidized)
HCAs	hydroxycinnamic acid amides
HPR	hydroxypyruvate reductase
hprol	hydroxyproline
HR	hypersensitive response
IAA	indole-3-acetic acid
IBA	indole-3-butyric acid
JA	jasmonic acid
LDC	lysine decarboxylase
MGBG	methylglyoxal bis-(guanylhydrazone)
MIPKs	mitogen-activated protein kinases
MJ	methyl jasmonate

mROS	mitochondrial reactive oxygen species
MTs	metallothioneins
NAA	naphthaleneacetic acid
NO	nitric oxide
NR	nitrate reductase
OAT	ornithine-delta-aminotransferase
ODC	ornithine decarboxylase
orn	ornithine
P5C	pyrroline-5-carboxylate
P5CDH	pyrroline-5-carboxylate dehydrogenase
P5CR	pyrroline-5-carboxylate reductase
P5CS	pyrroline-5-carboxylate synthetase
PA	polyamine
PAL	phenylalanine ammonia lyase
PAO	polyamine oxidases
PCs	phytochelatins
PCD	programmed cell death
PDH	proline dehydrogenase
pglu	pyroglutamate
PR	pathogenesis-related
pro	proline
Put	putrescine
ROS	reactive oxygen species
RWC	relative water content
SAM	S-adenosylmethionine
SAMDC	SAM decarboxylase
Spd	spermidine
Spm	spermine
TMV	tobacco mosaic virus
UPR	unfolded protein responses
WIPK	wound-induced protein kinase

Contents

1 Environmental Change, and Plant Amino Acids and their Derivatives – An Introduction

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1.1 Background

Being sessile in nature, plants, in a variably changing environment, have to cope with a plethora of adverse growth conditions (hereafter called stress) where the majority of these conditions can delay growth and development and most importantly prevent them reaching their full genetic potential in terms of productivity. Therefore, identifying the major factors responsible for environmental changes and understanding their cumulative potential effects on plant growth would be promising in sustainably protecting the agricultural ecosystem, and hence extract enough food for the burgeoning global population. The interactions between plants and environmental stresses reflect a complex system where plant stress responses occur at all levels of organization. At the cellular level, though a variety of reactive oxygen species (ROS), including hydrogen peroxide (H_2O_2), superoxide (O_2^-) and hydroxyl radical (OH-), are by-products of the normal aerobic plant cell metabolism, varied adverse growth conditions lead to significantly elevated generation of ROS and its reaction products (Apel and Hirt, 2004; Gill and Tuteja, 2010b). Subsequently, an imbalance between the pro-oxidants (ROS and its reaction products) generation and their antioxidants-mediated metabolism/scavenging occurs leading to a physiological condition called oxidative stress. Unmetabolized ROS and its reaction products are highly toxic due to their capacity to induce oxidative damage to vital cellular organelles, lipids, proteins, nucleic acids and pigments leading ultimately to cellular metabolism arrest.

Plants respond to the continuous environmental fluctuations with appropriate physiological, developmental and biochemical changes to cope with and/or acclimatize/adapt to these stress conditions. Plants exposed to stress factors often synthesize a set of diverse metabolites that accumulate to concentrations in the millimolar range, particularly specific amino acids (such as asparagine, histidine, proline and serine), peptides (such as glutathione and phytochelatins, PCs), and the amines (such as spermine, spermidine, putrescine, nicotianamine and mugineic acids). A credible number of studies have shown the significant

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changes in the contents of the majority of amino acids, peptides and amines, thus indicating their functional significance in the context of stress tolerance and/or adaptations. Multiple highly regulated and interwoven metabolic networks occur in plant cells where these networks largely play central regulatory roles in plant growth and development. Because the amino acids are vital for the synthesis of proteins and also serve as precursors for a large array of metabolites with multiple functions in plant growth and response to various stresses, the amino acids synthesis-related metabolic networks have gained considerable interest (Less and Galili, 2008).

This chapter introduces: (a) the major factors responsible for environmental change and its implication for plant growth and development, and (b) amino acids and their important derivatives in context mainly with their significance for plant adaptation and/or tolerance to varied environmental stress factors.

1.2 Environmental Change

Agricultural food production has always been linked to environmental conditions; however, growing demands for food in turn affect the global environment in many ways. According to recent estimates, global food security has been projected to face a severe threat from global environmental change, which includes naturally or human activities-influenced changes in the physical and biogeochemical environments (Steffen *et al.*, 2003; Carpenter *et al.*, 2009; Ericksen *et al.*, 2009; Liverman and Kapadia, 2010). Moreover, different elements of environmental change are interlinked through a complex set of physical, chemical and biological processes; where natural or human activities-led changes in one component can ramify for other components as well (IPEC, 2003).

Changes in atmospheric CO_2 concentration, increase in ambient temperatures and regional changes in annual precipitation are expected to significantly influence future agricultural production (Mittler and Blumwald, 2010). During the past two centuries the atmospheric CO_2 concentration increased significantly from ≈ 270 μmol/mol to current concentrations greater than 385 μmol/mol (Intergovernmental Panel Climate Change, 2007; Le Quéré *et al.*, 2009; reviewed by Mittler and Blumwald, 2010). Elevated atmospheric CO_2 generally increases plant productivity and alters nutrient element cycling. However, there is a report that experimental CO_2 enrichment in a sandy soil with low organic matter content can cause plants to accumulate contaminants in plant biomass, with declines in the extractable contaminant element pools in surface soils (Duval *et al.*, 2011). Combined ambient greenhouse gas concentrations (including methane, ozone and nitrous oxide) are now expected to exceed concentrations of 550 μmol/mol by 2050 (Raven and Karley, 2006; Brouder and Volenec, 2008). Moreover, atmospheric temperature is rapidly being changed with the climate change and global warming. To this end, the Intergovernmental Panel Climate Change (2007) has projected average annual mean warming increases of 3–5°C in the next 50–100 years due to the increase in greenhouse gases (reviewed by Mittler and Blumwald, 2010).

Seven percent of the electromagnetic radiation emitted from the sun is in the UV range (200–400 nm). A great reduction in and modification of UV radiation takes place as it passes through the atmosphere. Radiation of range 200–280 nm (UV-C radiation) is completely absorbed by atmospheric gases, 280–320 nm (UV-B radiation) is additionally absorbed by stratospheric ozone (thus only a very small proportion is transmitted to the earth's surface); whereas, the radiation of range 320–400 nm (UV-A radiation) is hardly absorbed by ozone (Frohnmeyer and Staiger, 2003). The depletion of the stratospheric ozone layer is leading to an increase in UV-B radiation reaching the earth's surface with serious implications for all living organisms. In this context, the release of anthropogenic pollutants such as chlorofluorocarbons has earlier been regarded as a major factor contributing a decrease of about 5% in ozone concentration observed during the last 50 years (Pyle, 1996). This has raised interest in the possible consequence of increased UV-B levels on plant growth and development and the mechanisms underlying these responses (Mackerness, 2000; Frohnmeyer and Staiger, 2003). Moreover, UV-B radiation has also been