Sulphur in Plants

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PREFACE

Sulphur (S) plays a pivotal role in various plant growth and development processes being a constituent of sulphur-containing amino acids, cysteine and methionine, and other metabolites viz., glutathione and phytochelatins, co-factor of enzymes which contribute to stress repair and amelioration of heavy metal toxicity. Besides, a number of S-containing components are biologically active and, thus, a source for use as medicinal value.

The basic global issue before the agricultural scientist and world community is to evolve cultivars and develop methodologies for efficient use of inputs to enhance agricultural productivity. This is particularly true of the developing countries which are going to see maximum rise in population with changing food demands and declining availability of land. Amongst the inputs, nutrients play a crucial role. The major requirement is for N, P and K followed by several micro-nutrients. In this context reports of world-wide S deficiency in the agricultural systems are relevant. The reasons are many. Broadly speaking reduction in S emission, use of S-free N, P and K fertilizers and higher biomass production contributed the maximum. Despite the need for sulphur as an essential plant nutrient and the substantial returns expected from its use, very little attention has been given to fill the gap between supply and demand of S.

During the recent past, there has been spurt in research activity in various aspects of S utilization by crops. These range from an understanding of the global S cycle to the biotechnological approaches to improve the utilization efficiency of not only S but also its role in balanced use of fertilizers. This is to contribute to efficient use of nutrients and, thus, development of sustainable agricultural practices.

In this book, the editors have attempted to put together the research contributions by experts in their respective fields to elaborate the various aspects of sulphur to be considered from the agricultural point of view.

In chapter 1, a general introduction of the S, its global inventory and the expected changes concerning its turnovers on a global scale within the next 15 years are discussed comprehensively; the S cycle of upland, wetland and limnic ecosystems are examined, and S balances at different scales from landscape over sub-field down to plant level are presented.

Chapter 2 deals with the food requirement scenario keeping in view the increase in population, income level, urbanization and, thus, the changing food habits, and need to remedy the under-nourishment and malnutrition prevailing amongst the teeming millions in some regions of the world. This is followed by discussion on prevalence of S deficiency, its causes and the present and future scenario of fertilizer demand and supply.

Chapter 3 deals with managing sulphur (S) in agroecosystems. In the first part of this chapter global biogeochemical S cycle, S sources and transformation processes in the environment are dealt. The second part deals specifically with the

management of S in agroecosystems.

Chapter 4 summarizes what is known about the uptake and transport of sulphate in plants. The physiological and biochemical background on sulphate transport characteristics are summarized together with a critical appraisal of current molecular approaches in this research area. A model of a 'highly regulated circuit' controlling sulphate uptake and assimilation, mediated by feedback loops involving key metabolites of cysteine biosynthesis has been proposed.

In chapter 5, the newly obtained information for the current view on the pathway of assimilatory sulphate reduction are presented. A brief historical account of investigations of sulphate assimilation is followed by biochemical and molecular characterisation of the enzymes and their regulation. Finally, a summary of the remaining open questions and directions for future research is given.

Chapter 6 deals with the sulphur distribution and redistribution in vegetative and generative plants. In the first part, evidence for the reallocation of S, factors that influence reallocation changes in mobility and sinks with respect to plant development, and mechanisms for loading sulphate and organic-S into the phloem are discussed. In the second part, pattern of distribution and redistribution of sulphur in vegetative plants in monocots and dicots, pathways for the importation of S into developing grains in monocots and dicots and forms of S imported by developing cereal grains and incorporated into grain proteins are given.

Chapter 7 deals with the biosynthesis of cysteine and methionine.

Chapter 8 focuses on the recent advances in the elucidation of glucosinolate biosynthesis. Finally, future research need on identification of regulators of glucosinolate biosynthesis to make it possible to metabolically engineer glucosinolate profiles in a tissue specific manner to improve disease resistance and nutritional value is given.

Chapter 9 and 10 deal with ecophysiological and molecular aspects of metallothionine (MTs) and phytochelatins (PCs). In chapter 9, emphasis is placed on their role in metal detoxification, metal specific genetically defined tolerance (hypertolerance) and the possible use of PCs as biomarkers of heavy meal toxicity, and chapter 10 reviews our current understanding of the biosynthesis, expression, regulation and functions of MTs and PCs, drawn from a range of physiological, biochemical, genetic and molecular biological approaches to their study.

In chapter 11 occurrence, localization, coding gene, metabolism and function of a higher plant sulpholipid, sulphoquinovosyl diacylglycerol (SQDG), are given in 1-5 sections. In 6th sections, a number of different stress responses were considered, and tried to evaluate whether SQDG can play a role in adaptation. The future looks very interesting for research on this unique membrane lipid!

Chapter 12 discusses the role of thiol compounds (with special emphasis on GSH redox system) in the defense systems and their involvement in plant responses to environmental stress.

In chapter 13, an extensive review of genetic engineering strategies used to modify stress tolerance is presented. Main focus is given on the changes in the content and redox state of glutathione, a major low-molecular-weight thiol-containing compound and a scavenger of reactive oxygen species.

In chapter 14 detail mechanisms of H_2S emission and utilization by plants that will help to develop strategies for usefulness of the channelling of extra sulphur into specific sulphur pool in order to improve crop quality by using molecular biology tools are described.

Chapter 15 deals with the consequences of SO_2 influx in plants.

Chapter 16 describes the very important role plants play in providing the protein required in animal diets. Mechanisms by which the plant regulates the relative abundance of these two protein classes are proposed. Also, efforts to enhance the relative abundance of the sulphur amino acids in seed storage proteins are described.

Chapter 17 is concerned specifically with impact of S on processing quality of wheat. An overview of the distribution of S deficiency, its amelioration, effect of other plant nutrients on S uptake is also given.

Chapter 18 examines the effect of sulphur on yield and quality of oilseed rape and also describes the relationship between sulphur nutrient status within the plant and disease development.

Chapter 19 synthesizes the available information on the responses of field crops, both in terms of yield and quality to S fertilization in monoculture and cropping systems that are prevalent in different states of India, and the role of S in optimizing crop production and reducing environmental risks.

Chapter 20 deals with the interaction of S with other nutrients which is relevant to considering/developing strategies for balanced use of fertlizers.

Chapter 21 discusses the biological profile of some of the sulphur compounds of plant origin, and rationale for their possible use in the form of medicine.

Thus, this book has presented an authorative review of present status of knowledge of sulphur and its availability for crop production and quality, and identified further research areas to be explored. We believe that this book, written by experts in different areas of research, will be useful for under-graduates, graduates, professors, scientists in biology and agronomy.

We are thankful to the authors for their time and efforts. We express our sincere gratitude to Mr. Siraj Hussain (IAS, Vice-Chancellor) and Professor Muhammad Iqbal (Head, Department of Environmental Botany) of Hamdard University for their constant encouragement and for providing us necessary facilities to effectively carry out this work. Financial supports from Indian National Science Academy (under Honorary Scientist Scheme) and Department of Science and Technology (under SERC Fast Track Young Scientist Scheme), Govt. of India are gratefully acknowledged.

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ABBREVIATIONS

γ ECS	γ-glutamyl-cysteine synthase
γGluCys	γ-glutamylcysteine
ADP	Adenosine diphosphate
AOS	active oxygen species
APK	APS kinase
APR	APS reductase
APS	adenosine 5'-phosphosulphate
APSST	APS sulphotransferase
APX	ascorbate peroxidase
APXs	Ascorbate peroxidases
ATPS	ATP sulphurylase
BSO	buthionine sulphoximine
CAT	catalase
CDPK	calcium dependent protein kinase
COS	carbonylsulphide
CP	chlorophyll-protein
CS_2	carbon disulphide
CHS	chalcone synthase
CYP	cytochrome P450
Cys	cysteine
DAG	diacylglycerol
DAP	diammonium phosphate
DGDG	digalactosyldiacylglycerol
DHA	dehydroascorbate
DMBA	9,10-Dimethyl 1,2-Benzanthracene
DMDS	dimethyl disulphide
DMS	dimethyl sulphide
dpa	days post anthesis
ESP	epithiospecifier protein
GC	gas chromatography
GCS	γ-glutamylcysteine synthetase
GPX	glutathione peroxidase
GR	glutathione reductase
GS	glutathione synthase
GSH	glutathione
GSH-S	glutathione synthetase
GSL	glucosinolate
GSNO	nitroso-glutathione
GST	glutathione-S-transferases

GUS	β-glucuronidase
H_2O_2	hydrogen peroxide
H_2S	hydrogen sulphide
hGSH	homoglutathione
HMW	high molecular weight
HMW-GS	high molecular weight glutenin subunits
hmPC	hydroxylmethyl PC
hPCs	homo-PCs
HSO_3^-	bisulphite
IAA	indole-3-acetic acid
IAAld	indole-3-acetaldehyde
IAN	indole-3-acetonitrile
IAOx	indole-3-acetaldoxime
ICP-OES	inductively coupled plasma-optical emission spectroscopy
kDa	kilo Daltons
LMW	low molecular weight
LMW-GS	low molecular weight glutenin subunits
MAPK	mitogen activated protein kinase
MDA	malondialdehyde
MDHA	monodehydroascorbate
Me	methyl
Met	methionine
MGDG	monogalactosyldiacylglycerol
MIC	minimum inhibitory concentration
MMT	*S*-adenosylmethionine methyltransferase
MOP	muriate of potash
MS	Mass Spectrometry
MSDs	membrane spanning domains
MTs	metallothioneins
MV	methyl viologen
O_2	superoxide radical ion
OAS	*O*-acetyl-L-serine
OAS-TL	O-acetylserine(thiol) lyase
OTC	L-2-oxothiazolidine-4-carboxylic acid
PAL	phenylalanine ammonia lyase
PAPS	adenosine 3'-phosphate 5'-phosphosulphate
PCs	phytochelatins
PhG	phenylglyoxal
PHGPX	phospholipid hydroperoxide glutathione peroxidase
PHLOH	phospholipid alcohol
PHLOOH	phospholipid peroxide
PLA_2	lipid-activated phospholipase A_2
PxV	potato potevirus
ROS	reactive oxygen species

QTL	quantitative trait locus
S-GT	UDPG:thiohydroximic acid glucosyltransferase
ST	sulphate transporter
TPX	thioredoxin peroxidase
UPP	unextractable polymeric protein