Plant Physiology

New findings populate the enormous literature on plant physiology, almost on a daily basis. This text is a detailed introduction to the essential concepts of this rapidly advancing field of study; to important physiological aspects related to the functioning of plants. It covers a wide range of topics including water, absorption of water, ascent of sap, transpiration, mineral nutrition, fat metabolism, enzymes and plant hormones. Photosynthesis, respiration and nitrogen metabolism get discussed in separate chapters because their contribution towards food security, climate resilient farming and sustainable life needs highlighting. Unlike other books on the subject, this text lays due emphasis on the conceptual framework.

Our emphasis is on the concepts of water use efficiency (WUE) and nitrogen use efficiency (NUE), to lessen pressure and our dependence on our natural resources. A special feature of the book is a discussion on 'molecular mechanism of abiotic and biotic stresses'. Seminal contributions of an 'international group of plant physiologists' and 'implications of plant physiology in agriculture' would be of immense interest to the readers. Alongside its emphasis on theoretical concepts, this text details experiments relating to most topics/chapters. A structured approach including principle, procedure, discussion, results and observation, and precautions has been used to explain the experiments.

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Plant Physiology

Theory and Applications

2nd Edition

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Foreword

Plant Physiology is a rapidly advancing field of study where new findings are surfacing in the literature almost daily. The ways of teaching the subject at both undergraduate and postgraduate levels have undergone a sea change and there is now a far greater emphasis on the conceptual framework than there was some years ago. It has become increasingly difficult for students to keep abreast with the ongoing explosion of knowledge in this field.

This book on Plant Physiology – Theory and Applications is both authoritative and timely. The book focuses on in-depth analysis of wide-ranging topics included in the Plant Physiology syllabi of different universities in India and overseas. The textbook starts with water and concludes with experimental exercises, project works and physiological set-ups or demonstration experiments. The chapters dealing with photosynthesis, respiration, and nitrogen metabolism are important since an understanding of their role for sustaining life on earth is essential for food security and climate resilient farming. Experiments are underway to convert C3 plants like rice into C4 plants in order to improve their photosynthetic efficiency. Researches are underway to transfer nitrogen-fixing genes into cereal crops to lessen our dependence on nitrogenous fertilisers. I am confident that the students going through the book will be stimulated to undertake the innovative experiments which can help to shape the physiological rhythms of plants to the emerging era of global warming and climate change. The material is presented in a concise and lucid manner so that the readers can easily comprehend the conceptual complexities of recent achievements in the field. A discussion of Molecular Mechanism of Abiotic and Biotic Stresses would be of immense help to the students. In view of climate change, the authors have emphasised the concepts of water use efficiency (WUE) and nitrogen use efficiency (NUE). A feature of the book is the inclusion of Review Questions with answers at the end of each chapter. This would be of enormous help to the students preparing for their academic course work.

We are indebted to Dr S. L. Kochhar and Dr Sukhbir Kaur Gujral for their labour of love in presenting the secrets of life to young scholars in an easily understandable manner. I also compliment Cambridge University Press for publishing this book as a part of their commitment to make scientific knowledge available in an authentic manner at affordable prices to young university students. I hope the book will be read and used widely.

M. S. Swaminathan
Founder Chairman, M. S. Swaminathan Research Foundation
Ex-Member of Parliament (Rajya Sabha)

Preface to the Second Edition

The Foundation Imprint of our book, *Plant Physiology: Theory and Applications*, which was first published in 2017 by CUP, India, met with an overwhelming response and the stocks were exhausted within a year or so. In a large measure, the textbook succeeded very well in addressing the need for such a tome amongst students and scholars in the fields of botany and agricultural sciences. However, review inputs and advice from subject experts overseas and within the country, as well as suggestions offered to us by the editorial staff of the Cambridge University Press, led us to considerable soul-searching on how to enhance its value.

And so, it gives us great pleasure in presenting to the readers an expanded and updated version whereby the readers can assimilate knowledge without undue effort as they imbibe; this self-contained textbook should, therefore, have a much wider appeal. The material is presented in a concise and lucid manner so that the readers can develop better understanding of the conceptual complexities in the field. We hope it will prove to be even more useful than the previous ones.

The salient features of this Second Edition are as follows:

The present edition is divided into 7 units, with a total of 23 chapters in all. In addition to the accurate and authoritative textual content in each chapter, we have endeavoured to present, through models and flow charts, more information about growth and development such as mode of action, physiological role, biosynthesis and inactivation of auxins, gibberrelins, ethylene and abscisic acid. The role of recently discovered hormones such as jasmonates, polyamines, salicylic acid and nitric oxide and others has been emphasised. The mode of action of phytochrome-mediated responses based on their requirements such as LFRs, VLFRs and HIRs finds a special mention. Included in the new edition are chapters on 'Concepts of Metabolism', 'Carbohydrate Metabolism', 'Sulphur, Phosphorus and Iron Assimilation in Plants', 'Plant Photoreceptors' and 'Ripening, Senescence and Cell Death' as well the work on *Arabidopsis thaliana* as an experimental tool and a model system for research in genetics and molecular biology, detailing its advantages over other plant material. A special feature of the chapter on Stress Physiology is an invited article on 'Molecular Mechanism of Abiotic and Biotic Stresses' which is being reproduced in the original. We have also included here, a discussion of Reactive Oxygen Species (ROS) and the Asada-Halliwell or Ascorbate-Glutathione Pathway.

Other useful additions are the inclusion of numericals dealing with pH, the molecular movement of water between cells, and energy transformation during respiratory and fat metabolism. We have laid due emphasis on the concepts of water use efficiency (WUE) and nitrogen use efficiency (NUE) to lessen pressures and dependence on our natural resources. Furthermore, we have devoted one chapter to the seminal contributions of an international group of plant physiologists whose discoveries have impacted the very fundamentals of this field. We have also dealt with classical experiments that have shaped its development. Another addition that should be of immense importance to readers is the chapter on 'Implications of plant physiology in agriculture'. And as a special for Indian readers, is the chapter on the development and status of plant physiology in India. Yet another significant addition is the inclusion of experimental exercises, project work and physiological set-ups or demonstration experiments. By engaging themselves in conducting such experimentation, students would not only hone their practical skills in plant physiology but would also imbibe aspects of the subject with greater thoroughness – so vital for their semester course work. The fact is that we have attempted to integrate into this compendium, relevant practical details, such as Requirements, Principle, Methodology, Observation, Discussion and Conclusions, et al. This approach should enable the students to have an access and a deeper insight into experimental working and how it has led to significant findings.

Another salient feature is the inclusion of Review Questions with answers at the end of each chapter which should be of much help to the students, preparing for their examinations, (including the competitive ones). A glossary is provided to assist students in reviewing both the new and the familiar terms. The compilation is profusely illustrated to enhance the clarity and the utility of the book. At the end of units, we have interpolated many high-resolution coloured images pertaining to the subject matter, besides over a hundred well-labelled line diagrams. The online resource material includes discussions like 'Various Laboratory Techniques' and 'Microchemical Tests for Major Food Constituents'.

Preface to the First Edition

Our earlier book, *Comprehensive Practical Plant Physiology*, was first published in 2012 and was very warmly received by students and teachers alike. In a large measure, the book succeeded in generating a lot of interest amongst students and scholars alike, in the field of Botany and Agricultural Sciences. However, the readers have urged us to restructure the text and update the information so that the book becomes self-contained in itself, matching other leading titles in the field of plant physiology.

During the course of reorganisation, we were greatly influenced by the feedback reviews we received from the many experts based within the country and in Southeast Asia, as well as the suggestions offered to us by the editorial staff at Cambridge University Press, India. We are much pleased to present to our readers an altogether new book, in which we have ensured a continuous flow of information so that the readers can assimilate the knowledge without too much effort. The material is presented in a concise and lucid manner, so that the readers can comprehend the conceptual complexities, come to know about the recent achievements in the field, and share the joy that we feel for this subject.

Salient features of this edition are as follows:

In addition to the generalized and well-informed textual content in each chapter, we have attempted to highlight the important information through models and flow charts; such as the information in the chapter on 'growth and development' regarding various topic like, mode of action, physiological role, biosynthesis and inactivation of auxins, gibberellins, ethylene, and abscisic acid. The role of the recently discovered hormones such as jasmonates, polyamines, salicylic acid and nitric oxide, etc., has also been emphasised upon appropriately. The mode of action of phytochrome-mediated responses based on their requirements such as LFRs, VLFRs and HIRs, also finds a special mention. Included also in the discussion is the work on *Arabidopsis thaliana* as an experimental tool and model system for research in genetics and molecular biology, enumerating its advantages over other plant materials. We have also included a discussion on Reactive Oxygen Species (ROS) and Asada-Halliwell or Ascorbate-Glutathione Pathway in the chapter 'Stress Physiology and Secondary Metabolites'.

Another striking feature is the inclusion of numerical questions dealing with pH, molecular movement of water between cells and energy transformation during respiratory and fat

metabolism. Furthermore, we have consolidated in a single chapter the seminal contributions of an international group of plant physiologists whose discoveries impacted our fundamental thoughts. We have not hesitated to include the classical experiments that had a revolutionary impact on the development of the subject. A chapter on the development and status of plant physiology in India will be of special interest to the Indian students. Another significant addition is the inclusion of Experimental Exercises, Project work and Physiological set-ups or Demonstration Experiments. This is an attempt to make students feel comfortable with their semester course work and hone their practical skills in plant physiology. In fact, we have tried to integrate the practical details, such as Requirements, Principle, Methodology, Observation, Discussion and Conclusions, etc., for the very same reason. This approach should enable the students to have not just an access but a deep insight into the various experimental working and findings.

Another salient feature of the book is the inclusion of Review Questions along with their answers at the end of each chapter, which would be of great help to the students preparing for their examinations. A glossary is provided to help students in reviewing both new and familiar terms. The book is profusely illustrated to enhance the clarity and utility of the book.

The online resource material includes chapters like, The Status and Development of Plant Physiology in India and Various Laboratory Techniques; and several appendices like, Microchemical Tests for Major Food Constituents, Concepts of Thermodynamics, The Laws of Thermodynamics, Redox Reactions, Chemosynthesis, ATP: The Energy Currency of the Cell, Coupled Reactions and Metabolic Pathways.

We wish to express our deep gratitude to Professor M. S. Swaminathan FRS, World Food Laureate, Founder Chairman and Mentor, M. S. Swaminathan Research Foundation, Chennai, not only for his kindness in writing the Foreword to the book but also for his great encouragement and continued interest in this project. We are also thankful to his Foundation for sending us pictures of *Rhizophora mucronata* – a component of the mangrove ecosystem.

We wish to offer our gratitude to Professor S. C. Maheshwari, well-known for his pioneering work on haploid from pollen, for permitting us to use pictures of some leading physiologists appearing in his article and also for sending his photograph to be included. The authors are highly indebted to Dr Govindjee, Professor Emeritus, University of Illinois, Urbana-Champaign, USA, for sending us his research contributions as well as his photograph. Additionally, we are grateful to Professor R. C. Sachar, formerly of Delhi University for sending us a write-up about his research contributions. Our sincere thanks are also for Professors A. K. Bhatnagar, formerly of Delhi University; Professors R. R. Singh and Nirmala Nautiyal of Lucknow University; Dr H. N. Krishnamoorthy, formerly of HAU, Hisar; Dr Alok K. Moitra, Executive Secretary, INSA, Delhi, for arranging pictures of some Indian physiologists. The authors express their gratitude to Dr P. S. Deshmukh (Emeritus Scientist), Dr M. C. Ghildyal, Professor Raj Kumar Sairam, Professor G. S. Sirohi and Dr Ajay Arora of the Division of Plant Physiology, IARI, New Delhi, for their help and cooperation.

Teaching Plant Physiology together at the college for over 25 years has strengthened our ties at a familial level and we both are indebted to our families, especially Urmil Kochhar and Jasbir Singh Gujral, without whose support and continued interest this book would not have materialised. We value our association with our former colleagues Dr G. N. Dixit and Dr S. Bala Bawa with whom we shared the joy of teaching plant physiology at the college.

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We wish to express our deep gratitude to the editorial and production team at the Cambridge University Press, India, for their courtesy, cooperation and technical guidance about details, and for their meticulous efforts in bringing out this edition well in time and in the best possible format.

We would highly appreciate receiving suggestions from our colleagues in India and overseas for the improvement of this new edition.

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Teaching Plant Physiology together at the college for over twenty-five years has strengthened our ties at the family level and we are indeed indebted to our families especially Mrs Urmil Kochhar and Mr Jasbir Singh Gujral, without whose support and constant encouragement, the book would not have materialised. Sincere thanks are also due to our children for their deep interest, support and genuine concern about its Cambridge edition. A special word of appreciation goes to our beloved grandchildren as they waited with keen anticipation over the years to see the book in print.

We indeed value our association with our former colleagues Dr G. N. Dixit and Dr (Mrs) S. Bala Bawa with whom we shared the joy of teaching plant physiology at college. Our thanks are due to Drs Inderdeep Kaur and Surinder Kaur, Associate Professor, Khalsa College, University of Delhi for their many helpful suggestions from time to time. Our special thanks are due to Dr Jaswinder Singh, Principal of Khalsa College for his continued interest in our project. Sincere gratitude is due to Saurabh Kochhar for his support in gathering information from multiple sources and his assistance with computer applications.

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We would indeed appreciate receiving suggestions from our fellow botanists in India and overseas for the further improvement of this second edition.

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Delhi.

S. L. Kochhar
Sukhbir Kaur Gujral

Some Common Abbreviations used in the Text

2,4,5-T	2,4,5-Trichlorophenoxyacetic acid
2,4-D	2, 4-Dichlorophenoxyacetic acid
4-CPA	4-Chlorophenoxyacetic acid
ABA	Abscisic acid
ABC proteins	ATP binding cassette proteins
ACC	1-aminocyclopropane-1-carboxylic acid
ACO	ACC oxidase
ACP	Acyl carrier protein
ACS	ACC synthase
ADH	Alcohol dehydrogenase
ATP	Adenosine triphosphate
BR_S	Brassinosteroids
BSA	Bovine serum albumin
CAC	Citric acid cycle
CAM	Crassulacean acid metabolism
cAMP	Cyclic adenosine monophosphate
COP gene	CONSTITUTIVE PHOTOMORPHOGENESIS gene
DAG	Diacyl glycerol
DCPIP	2,6-Dichlorophenol indophenol
DCMU	3,4-dichlorophenyl-1,1-dimethyl urea
DNP	2,4-Dinitrophenol
DRE	Dehydration response elements
EC	Enzyme commission
EDTA	Ethylenediaminetetraacetic acid
ETS	Electron transport system
EXPA	α-expansins
FCR	Folin-Ciocalteau reagent
Fd	Ferredoxin

FLC gene	FLOWERING LOCUS C gene
FT protein	FLOWERING LOCUS T protein
GA	Gibberellin
GA_3	Gibberellic acid
GAREs	GA response elements
GDH	Glutamate dehydrogenase
GLC	Gas–liquid chromatography
GOGAT	Glutamate synthase or glutamine-2-oxoglutarate-amino transferase
GPP	Gross primary productivity
GS	Glutamine synthetase
HIRs	High irradiance responses
HPLC	High performance (pressure) liquid chromatography
Hpt protein	Histidine phosphotransfer protein
HSF	Heat shock factor
HSPs	Heat shock proteins
IAA	Indole-3-acetic acid
IBA	Indole-3-butyric acid
IP_3	1,4,5-triphosphate inositol
IPP	Iso-pentenyl pyrophosphate
LAI	Leaf area index
LHb	Leghaemoglobin
LDH	Lactate dehydrogenase
LEA Proteins	Late embryogenesis abundant proteins
LFRs	Low fluence responses
LHC	Light-harvesting complex
NAA	Naphthalene acetic acid
NAD	Nicotinamide adenine dinucleotide
NADH	Nicotinamide adenine dinucleotide (reduced)
NADP	Nicotinamide adenine dinucleotide phosphate
NAM gene	NO APICAL MERISTEM gene
Nif genes	Nitrogen fixing genes
NiR	Nitrite reductse
NEDD	N-(1-naphthyl) ethylenediamine dihydrochloride
Nod genes	Nodulation genes
NPA	N-1-naphthylphthalamic acid
NR	Nitrate reductase
OAA	Oxaloacetate
OD	Optical density
OEC	Oxygen-evolving complex
OPCC	Oxidative pentose phosphate cycle
PAGE	Polyacrylamide gel electrophoresis
PAR	Photosynthetically active radiation
PC	Plastocyanin
PCD	Programmed cell death

PCK	PEP carboxykinase
PCMBS	p-chloromercuribenzene sulphonic acid
PCR	Photosynthetic carbon reduction cycle
PEP	Phosphoenolpyruvate
PEPcase	Phosphoenolpyruvate carboxylase (PEP carboxylase)
PFK	Phosphofructokinase
pmf	Proton motive force
PQ	Plastoquinone
PR-proteins	Pathogenesis-related proteins
PS	Photosystem
Q_{10}	Temperature coefficient
RCF	Relative centrifugal force
R_f	Relative front
RIA	Radio immunoassay
rpm	Revolutions per minute
RQ	Respiratory quotient
Rubisco	Ribulose-1,5-bisphosphate carboxylase/oxygenase
RUP proteins	REPRESSOR OF UV-B PHOTOMORPHOGENESIS proteins
SAGs	Senescence associated genes
SAM	S-adenosyl methionine
SAR	Systemic acquired resistance
SDS	Sodium dodecyl sulphate
SPAC	Soil–plant–air continuum (Soil–plant–atmosphere continuum)
TIBA	2,3,5-Triiodobenzoic acid
TLC	Thin-layer chromatography
TPP	Thiamine pyrophosphate
UVR8	Ultraviolet resistance 8
VAM	Vesicular-arbuscular mycorrhiza
VLFRs	Very low fluence responses
ZTL	Zeitlupe

Abbreviations for Units

%	per cent
A	Absorbance
Å	Angstrom
atm	Atmosphere
°C	Degree Celsius
cal	Calorie
cm	Centimeter
D	Dalton
[E]	Enzyme concentration
E	Extinction
E′°	Redox potential
emf	Electromotive force
g	Gram
h	Hour
ln	Logarithm to the base e
K	Kelvin
kcal	Kilocalorie
kD	Kilodalton
kg	Kilogram
Kj	Kilojoules
Km	Michaelis–Menten constant
L	Litre
log	Logarithm to the base 10
m	Molal (concentration)
M	Molar (concentration)
min	Minute
ml	Millilitre
mm	Millimeter

N	Normal (concentration)
nm	Nanometer
ppm	Parts per million
R	Gas constant
s	Second
[S]	Substrate concentration
S	Svedberg unit
T	Absolute temperature in Kelvin
V	Volt