



*Advances in*

**PLANT  
PHYSIOLOGY**

**(from the Green to the Grain)**



**SESHADRI KANNAN**

# **Advances in Plant Physiology**

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**Seshadri Kannan**

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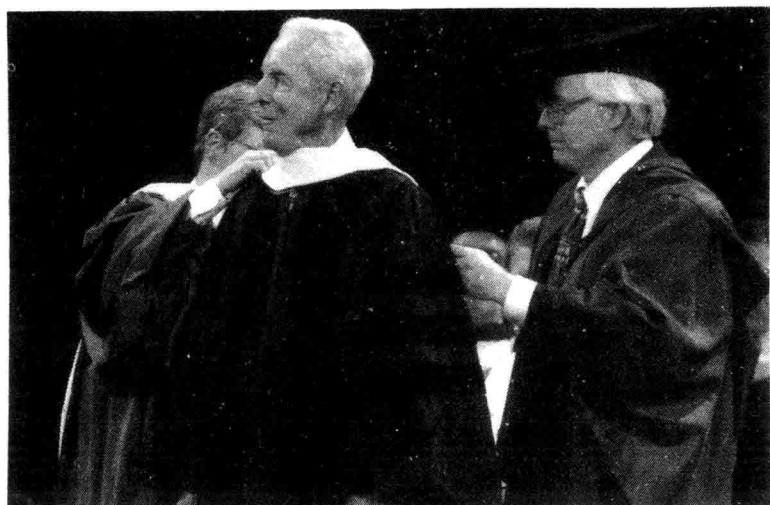
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**Advances in Plant  
Physiology**  
(From the Green to the Grain)

*Dedicated to*

**My Father Late G. Seshadri Aiyangar who  
inducted me to agriculture, and to Dr. Sylvan  
Harold Wittwer who is called "MSU Dynamo" and  
who taught me the true meaning of Karma and  
Reward as given in the Age-less Bhagawat Gita,  
"Karmanyéva Adikarasthé Maa Paleshu  
Kadáchanü". At 89, Sylvan loves plants,  
swimming, church and the fresh air at Logandale,  
Nevada, all the more so with family at the annual  
Xmas meet.**



**Michigan State University Commencement, December 6, 2002  
(L to R) Dr. Simon, Sylvan Wittwer & Paul Hunt**

Sylvan Wittwer received the honorary degree of Doctor of Agriculture, from the University where was professor of Horticulture, and Director of Agricultural Experiment Station. Though he had received many awards and honours from various universities this is conferred on him as a special one, not normally given to the faculty member of the same university. The citation runs as follows: You are a world renowned horticulturist committed through your teaching, research, and service to making the world a better place..... Because of your experience with international agriculture and your research on the effects of climate on food production, you were named the chair of the National Research Council's Board of Agriculture and Natural Resources"..... For your enormous energy, your integrity, and your intense focus on using your scientific expertise for the benefit of humanity, I am pleased to award the honorary degree....."

He had visited many countries, India, China, Africa, Europe and the Far East. The one visit which is the most memorable for the Indian agricultural scientists was his 'Coromandel Lecture' in Sept 4, 1979 at New Delhi.

## PREFACE

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Plant Physiology, is one of the earliest branches of biology. Today it has ramified into many branches and also assimilated many disciplines. During the last few decades, it has branched out so much as now indistinguishable from plant molecular biology, plant biochemistry and plant biotechnology. Its importance as a "whole Plant" physiology however is much more relevant now to agriculture than ever before. Significant contributions in the areas like photosynthesis, and plant nutrition are briefly described here.

Looking back, there were quite a few symposia on photosynthesis and plant nutrition, the one, "Gene to Genus" organized by the International Minerals and Chemicals Corporation, in 1965, and another by them "Harvesting the Sun". In these many scientists, like Albert Szent-György *von Nagyra polt* (a Nobel laureate) had presented talks, with reference to food production in general. Food shortages, and starvation of people in the developing countries like Africa were highlighted. Even after 40 years of those meetings, food is still dear to many, and there are countries where people are not adequately fed. Where food is in plenty, the purchasing power is on the decrease with the greater advancement in many fields of industry and technology. The responsibility of the scientists towards alleviating starvation by making food available to all, and providing a nutritious one, is very great. Plant biotechnology, and plant genetic engineering which includes the introduction of "genetically modified" crop plants are important and many break-throughs have been accomplished. If the earlier *Homo sapiens-erectus* of the "Olduvai Gorge" when these humans started walking on 2 legs, come back and look at us who

have made "Space-walking" and "Moon-Landing" a reality, perhaps they will be astonished and take us for the 'messengers' of gods from heaven.

Paul de Kruif, a bacteriologist and a well-known science writer, had written one of the best-selling and most widely read science books of all time, around 1926, *Microbe Hunters*, which was translated into 18 languages and was the first book with a totally scientific theme to sell over a million copies. He described the work of Leeuwenhoek, Spallanzani, Pasteur, Koch and others, and also how the early microbiologists made lenses from glass for looking at small organisms. *Microbe Hunters* is credited with inspiring an entire generation of biological scientists to take up careers in research. Another book by Paul de Kruif published in 1928 entitled *Hunger Fighters*, which described about those of the 19<sup>th</sup> century who were the pioneers in agricultural revolution is very thought-provoking. Centuries have passed and today astronomers are looking for microbes in distant stars of far-off galaxies with telescopes which could not have been ever imagined by early microbe hunters. Again, with many millennia later from now, discoveries will grow beyond our imagination. Recently a new branch of plant biology has emerged, known as 'epigenetics' which embraces the mechanisms of gene arrangement in the chromosomes and their heritability between cell divisions and even across generations. For many of these branches, plant physiology serves as the basic science. These advances are to be harnessed for increasing the food production and improving the quality of life.

The FAO report on the global information and early warning system on food and agriculture, June 2002, gives details on the food crops and shortages in different countries. In Africa two successive poor harvest had led to severe food shortages since the drought of 1992. Due to insufficient rainfall, cereal production has fallen down in the North



African countries. In Afghanistan there was worst locust attack and floods which caused havoc. There are therefore serious concern on measures to increase food production and greater need for the plant scientists to evolve suitable strategies.

The information on the advancement in plant physiological research presented here will serve a useful purpose for those interested in plant physiology in general and food production in particular. Most of the reports included in this book were collections of papers and scientific articles published by the authors cited, and I am very much thankful to all of them who helped me in many ways including the supplying of reprints of their papers. Further, it is to be admitted no attempt has been made to cover the entire field of plant physiology which is so vast and highly specialized today, and thus it is limited to a few areas. Finally, below is reproduced an important advice for those involved in research and teaching:

Sarah C. Hake wrote on the FORUM in the Agricultural Research about cycles of learning: "ARS and Tomorrow's scientists". "You're a college sophomore who has just decided to take a job as a part-time research assistant at a nearby plant genetics research laboratory. It seems like a good opportunity and the research—genes and pollen—piques your interest. The lab turns out to be a great place to work. There's much to learn, and you're surrounded by people who enjoy what they do. Even better, your supervisor, a top researcher in the field, wants to nurture your interest in science... Seven years and one doctorate later, you return to the lab. But this time, you're the one who's training and mentoring novice undergraduates. As you introduce them to the world of laboratory research, you're determined that their experience will be as valuable as your first job there.....These learning cycles are formed, renewed, and strengthened every workday at ARS laboratories....The cycles foster newly emerging

talents and generate new discoveries. They educate, enable, and empower.....Established scientists who share their skills, energy, and empathy with those who are not yet as expert find that these mentorships can be among the most rewarding aspects of their professional lives." What is applicable to ARS is equally so for any good research laboratory and institution and must serve as a guide to the teachers of plant physiology. The greenness of the plant is vital to the development of the grain. Lack of it causes chlorosis and reduces photosynthesis. Soil and water degradation affect plant nutrients and then the yield.

I have included excerpts from the articles in *Annual Reviews of Plant Biology* Giordano *et al.* 2005 (56:56:99-131) and Edwards *et al.* 2004 (55:173-196) and I am grateful to Laura Folkner, the permissions department *www.AnnualReviews.org*" for granting permission for the same. I am thankful to the Director of Publications Nancy Winchester, for according permission to use excerpts from the articles in *Plant Physiology* 1995, 108:883; 1996, 114:1-2; 1997, 114:399-400; and specially for the forward to the first issue of *Plant Physiology* vol 1:1-2 by Charles A. Shull (1926); American Society of Plant Physiologists, (article by Epstein, 1997); to the executive editor, National Academy of Sciences, USA, for the excerpts from the articles by Dyson (1999) *PNAS* (USA) 96:5929-5936 (© 1999), and Hansen (2000) *PNAS* (USA) 97:9875-9880 (© 2000), and to the Rights & Permissions department, CSIRO, for using passages from the paper of Osmond (1997) *Aust J Plant Physiol* 24:409-412. The articles in the journal (can be accessed from the website <http://www.publish.csiro.au/journals/fpb> as also the full text *via* subscriptions or pay-per view services). "The University of Chicago Press has granted permission to use excerpts from the article by Keeley and Rundel, *Internatl J Plant Sci* (2003), 164 (Suppl) S55-S77. I am thankful to the UCP permissions department and to the authors of the article. I am indeed very grateful to Arthur Wallace for

including the passages and a figure from his very valuable book, *Closing the Crop Yield Gap through Better Soil and Better Management, The Law of the Maximum* (A. Wallace and G. Wallace 2003), to Sherwood Idso from the articles from the weekly reports, *www.co2.org*, vol 7:22 September 2004, and 9: 11 January 2006, to Bernard Switalski to use the information in his paper 2001, and 2002 on global warming. A few passages and information from the book published by the International Food Policy Research Institute especially from "World Water and Food to 2025 dealing with Scarcity" 2002, have been incorporated in the present book with due acknowledgement to the IFPRI as also a reference to the discovery of phytochrome which appeared in the "Agricultural Research" Beltsville, Maryland. I wish to record my gratitude to Dr. Emanuel Epstein, who by his being active at the young age of 88, published a revised edition on plant nutrition along with A.J. Bloom, calls others as 'youngsters'. He has published 34 research papers since retirement. My close association with him over 3 decades has been very rewarding. Here is what is written by Clifton B. Parker, in *DATELINE UCDAVIS*, January 17, 2003: Since his so-called retirement in 1987, Epstein, a plant physiologist and professor emeritus, is still learning and researching. He's deep into the life of the mind – for the long haul. Epstein said, "It's a passion, a commitment to take yet another step to advance science and understand nature's secrets.... Higher education needs to be more progressive in letting elderly scholars continue their full-time status.... Many of us can still make an impact". This gives me enormous encouragement. I am indebted to Md Masroor A. Khan of the Aligarh Muslim University, Aligarh for his valuable suggestions in the preparation of this book. I am thankful to my sons Sriram and Seshadri who so kindly thrust on me a computer and remained a constant prompter to my writing, and to the granddaughters Sanjana and Anjali who were serious to force me learn computer games, besides

word processing. It is my responsibility to thank my wife Kalpakam who has all the patience till my completion of this work.

Finally, publishing a book, small or big, demands the same skill and attention. I record my sincere appreciation and thanks to the APH Publishing Corporation for rendering an excellent job in this publication.

**Seshadri Kannan**

# CONTENTS

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<i>Preface</i>	v
<b>1. Plant Physiology has become Plant Biology: "A Cross-Disciplinary Science"</b>	1
(a) Photosynthesis: $C_3$ , CAM, $C_4$ , $C_3$ - $C_4$ Intermediates:	
(b) Photosynthetic mechanisms in algae	
<b>2. Carbon Dioxide</b>	15
(a) Atmospheric concentration of $CO_2$ is expected to rise from a current 372 $\mu$ mole/mole to 550 $\mu$ mole by the middle of this century.	
(b) Photosynthesis and carbon dioxide	
<b>3. Flowering</b>	31
(a) Photoperiodism	
(b) Flower Development	
(c) Photomorphogenesis	
(d) Vernalization	
(e) Self-Incompatibility in Plants	
<b>4. Plant Hormones</b>	45
(a) About Abscission	
(b) Climacteric	
<b>5. Water Transport in Rice</b>	55
<b>6. Salt Tolerance</b>	59
<b>7. Nutrient Uptake and Transport</b>	67
(a) Foliar Uptake, Cuticles and Stomates	

(b) Symplastic Transport of Ions	
(c) Apoplast and Plant Nutrition	
(d) Transpiration and Nutrient Uptake	
(e) Solute Transport between Vacuole and Plasma Membrane	
(f) Vesicular Transport in Salt Secreting Trichomes	
(g) Vesicles and Organic Acid and Sucrose Secretion	
(h) Vesicles and the Solute Transport from Guard and Motor Cells	
(i) Sucrose transport	
(j) Foliar application of nutrients	
(k) Plant endomembranes	
(l) Gaseous Nitrogen deposition on Plants	
(m) Fertilizer experiments	
(n) Nutrition	
(1) Iron	
(2) Magnesium	
(3) Boron	
(4) Nickel	
(5) Aluminium	
(6) Silicon	
(7) Cadmium	
(8) Selenium	
(o) Phytoremediation	
<b>8. Water Saving Agriculture</b>	<b>111</b>
<b>9. Crop Biotechnology</b>	<b>117</b>
<b>10. Genetically Modified Plants</b>	<b>127</b>
<b>11. Plants and Population</b>	<b>139</b>

<i>Contents</i>	xv
<b>12. Epilogue</b>	151
Water for Agriculture, Industry in the Developing Countries	
Plant Physiology—The Backbone of Horticulture	
Plant Physiology Research: Fundamental —Practical	
<i>Bibiliography</i>	161
<i>Annexure</i>	183
<i>Index</i>	185

## PLANT PHYSIOLOGY HAS BECOME PLANT BIOLOGY: A CROSS- DISCIPLINARY SCIENCE

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In an editorial Chrispeels, (1996) Editor-in-Chief of Plant Physiology, stated that "the tools of molecular biology, gene cloning and plant transformation have revolutionized the study of plants into a new plant biology. Now powerful molecular tools are available to help answer complex interdisciplinary questions". Chrispeels, in another editorial (1997), stressed the importance of biology as an increasingly exciting discipline in the last quarter of the 20th century and the ever-accelerating pace of new discoveries in the biological sciences is reflected in the pages of the journal. He states "although plant biologists have been interested in plant hormones for more than 50 years, questions that seemed intractable in the 60s and 70s, such as the identity of hormone receptors, or the identity of enzymes that catalyze steps in hormone biosynthesis, are suddenly tractable because molecular genetics has come to the aid of biochemistry to create a new research methodology. Such work spans the spectrum from whole-plant research to biochemistry to molecular biology, and often involves the characterization of mutants. We are now making progress in identifying hormone receptors, components of the signal transduction pathways, and the transacting factors that bind to promoter response elements to turn on the genes that encode the enzymes that modify plant growth". Long (1995) in another editorial in Plant Physiology, drew attention to the need to give graduate students training in broader areas and disciplines and that a developmental biologist should also



be trained in whole plant physiology. In other words, if one has to do creative work, one should be familiar with areas above and below the level of experimentation. A molecular biologist should have a thorough understanding of chemistry (i.e., micro- and macro-molecular biochemistry). And a cell biologist should know molecular biology and biochemistry and also organismal physiology. Persons working on whole organism physiology, should also know about plant development and cell biology, as also ecology and population biology. She quotes T.H. Huxley who divided the study of living things along these lines: "That part of biological science which deals with form is called *Morphology*—that which deals with function, *Physiology*." The new plant biology gives opportunity to ask questions that cut across several disciplines in order to derive correct answers. And "plant physiologists" are all fast becoming "plant biologists" whose science are interdisciplinary. Long states "We must keep up the good work, and we must ensure that plant biology doesn't drop out the middle; that quantitative physiology and biochemistry stay at the center of the field, providing both the tools for ecological study and the context for cell and molecular analysis."

Plant Physiology completed 75 years on January 2001 (Raikhel, 2001). It completed 48<sup>th</sup> year of publication in 1974 when a series of eight retrospective articles summarizing 50 years of progress in plant biology were published. During those years many groundbreaking and original discoveries were made. And yet the plant physiologists did not have sufficient understanding of various processes. In the 2001 issue 42 short commentaries were published summarizing the conceptual breakthroughs in the next 25 years. The three major technological advances which contribute to these are (1) the development of molecular tools, (2) the techniques evolved similar to the one in transforming plants using *Agrobacterium tumefaciens*, and (3) the extensive use of *Arabidopsis* as a model system.