Ganesh K. Agrawal
Randeep Rakwal *Editors*

Seed Development: OMICS Technologies toward Improvement of Seed Quality and Crop Yield

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This book is dedicated to Dominique Job and Claudette Job in recognition of their contribution to the field of seed research and development

The secret of joy in work is contained in one word—Excellence. To know how to do something well—is to enjoy it
(Pearl Sydenstricker Buck)

Foreword

Dominique grew up partly in France and partly in several African countries. Having been trained in Physics and Mathematics, he obtained his Master's degree in Physics at the University of Dakar, Senegal. Back in France, he joined the laboratory of Plant Biochemistry at the *Centre National de la Recherche Scientifique* (National Center for Scientific Research; CNRS)/Marseilles University (Prof. Jacques Ricard) to prepare a thesis during which he studied the physicochemical and enzymatic properties of various hemeproteins from plants. He was recruited at CNRS as a Research Associate in the year 1970. It was then that he met with Claudette (Research Engineer at CNRS). Claudette was working in the same laboratory and wrote a thesis on the structure of these hemeproteins, notably through establishment of their amino acid composition. After their wedding, they spent most of their scientific careers at CNRS, working together in different laboratories in Marseilles (years 1970–1992) and Lyon (since 1992).

Early works of Dominique focused on studying the oxidation mechanisms of auxin, specifically indole-3-acetic acid (IAA), by several isoperoxidases isolated from horseradish and turnip toots. Thanks to the purification to homogeneity, from hundred kilograms of turnip roots, of such enzymes, these studies relied on the use of rapid kinetic techniques (stopped-flow; T-Jump relaxation) and of spectroscopic approaches at very low temperature to considerably slow biochemical reactions and then be able to follow step-by-step, like in a movie, the reaction cycle of the enzymes during catalysis. A general mechanism was proposed to explain the mode of action of IAA as a regulator of plant growth. This work was the subject of his doctoral thesis in 1975. In particular, he clarified the possibility of oxidative degradation of auxin by peroxidases, supporting their role as auxin oxidases. Until 1978, he was during a postdoctoral fellowship at the Department of Chemistry (Professor Brian Dunford), University of Alberta, Canada; at the University of Newcastle upon Tyne, Radiation and Biophysical Chemistry Laboratory (Dr. Peter Jones), UK; and then his return to Marseilles, involved in the study of the physicochemical properties of plant peroxidases, notably toward deciphering their reactivity toward hydrogen peroxide (H_2O_2) and diverse aromatic substrates. This work contributed to understanding the mechanism of action of these hemeproteins in peroxidation reactions. The oxidation rates of a series of aromatic substrates proved to follow

Hammett relationship, allowing proposing a general mechanism in which the substrate gives an electron to the enzyme and simultaneously loses a proton. Furthermore, the second order rate constants measured for aromatic substrate oxidation approached the diffusion-controlled limit for bimolecular reactions. These results are regularly cited 30 years after their publication, to explain the features of electron transfer occurring at the heme iron in peroxidation reactions. Another highlight was the characterization by ESR spectroscopy at very low temperature of a new oxidation state of peroxidases in their reaction with H_2O_2, that is a compound which they named Compound Y, and whose formation proved to precede that of Compound I, which was previously classically assumed to be the first intermediate in peroxidation reactions.

In the year 1980, he decided to reorient his scientific activity and initiated, with Claudette, a study of the mechanisms of transcription in plants. In particular, they succeeded in purifying to homogeneity the three classes of nuclear DNA-dependent RNA polymerases from wheat germ, although these enzymes are very low abundant, extremely fragile and possess complex structure, each being composed of more than a dozen subunits. Major findings of this research were the elucidation of the mechanisms contributing to the processivity of transcription RNA chain elongation, the factors influencing the balance between abortive and productive initiation, the mechanism of action of α-amanitin (a specific inhibitor of class II DNA-dependent RNA polymerases) and the influence of the sequence and conformation of the DNA template (e.g., right-handed DNA or B-DNA and left-handed DNA or Z-DNA) on the velocity and fidelity of transcription. Part of this work was done in collaboration with the Department of Molecular Biology of the Max-Planck Institut für Biophysikalische Chemie/Institute for Biophysical Chemistry (Dr. Tom Jovin), Gottingen, Germany.

In the year 1992, Dominique and Claudette wished to move to the UMR041 CNRS/Rhône-Poulenc, a public-private joint laboratory (Prof. Roland Douce), Lyon, France, now the UMR5240 CNRS/Bayer CropScience. At the request of the Directorate of Research and Development of Rhône-Poulenc, they created a small research team on the biology of seed development, particularly on germination and initial seedling growth. The idea was to gain information on the seed system, in the context of the rapid development of commercial seed treatments to increase crop yields. Highlights of this research were the discovery of a new class of biotinylated proteins (SBP65, Seed Biotinylated Protein of 65 kDa), which belongs to the family of LEA (Late Embryogenesis Abundant) proteins and that is specifically expressed in seeds, as well as a mechanism of structural reorganization of the 11S globulin, a main storage protein present in seeds of dicotyledonous plants.

By that time, Dominique continued to be interested in enzymology and was involved, with several colleagues of the CNRS/Rhône-Poulenc joint laboratory, in several studies dealing with the characterization of the enzymatic pathways that in plants are responsible for essential amino acids (sulfur amino acids, branch chain amino acids) and vitamin (biotin) metabolisms.

More recently, in 1999, realizing the invaluable potential afforded by the knowledge of the first genome sequence of a plant, namely that of *Arabidopsis*, Dominique

and Claudette decided to broaden the scope of their research toward the global elucidation of the germination process by a systematic study of the proteome and transcriptome of this model plant. Their publication in 2001 in Plant Physiology on the *Arabidopsis* seed proteome was probably one of the leading publications in plant proteomics combining two-dimensional gel electrophoresis and mass spectrometry. The development of reference protein maps then allowed approaching several questions important in seed biology, as to the role of gibberellins in seed germination, the influence of abscisic acid on seed dormancy, and the role of protein oxidation (carbonylation) in plants and seeds during development. In addition, an important discovery dealt with the role during germination of messenger RNAs that have been stored in the dry mature seeds during their maturation on the mother plant. This work showed that germination was insensitive to α-amanitin and therefore can occur in the absence of *de novo* transcription[1]. This feature, being originally documented in *Arabidopsis*, has now been extended by other authors to other species, including rice.

Dominique and Claudette were also always willing to translate their work from model to crop seeds. To this end, they developed programs in close collaboration with industry and the seed sector. The benefits of this research have included the development of biochemical markers for monitoring priming (an invigoration treatment of low-vigor seedlots widely used in the seed industry) and patents have been filed.

In parallel to these research activities Dominique was successively deputy head and head of the joint laboratory CNRS/Rhône-Poulenc then CNRS/Bayer CropScience. Since 2000, he was also heavily involved in collective tasks. Thus, he has been for several years the scientific coordinator of the Genoplante programs, the French program in plant genomics. Soon, he was willing to establish cooperation with other plant genomics programs. In 2000, he set up together with Jens Freitag the first joint GABI-Genoplante programs (GABI is the German plant genomics program funded by the BMBF). A few years later, with the enthusiastic help of Pablo Vera, they set up trilateral programs in plant genomics, gathering together France, Germany, and Spain, with the idea of strengthening public-private partnership. In particular, these actions resulted in the creation of the ERA-NET PG (European Research Area in Plant Genomics; an instrument of the EU to promote joint research in Europe), which brought together 16 European member states and Canada. However, the trilateral projects between France, Germany, and Spain continued to exist, giving rise to the Plant-KBBE program, in which now Portugal and Canada are partners. Altogether, these activities have enabled the selection and the funding of hundreds of plant genomics projects and helped strengthening this discipline in France and Europe, which is important in the context of the development of novel uses of plant products and the necessity to increase crop yields in a more sustainable agriculture. These initiatives also allowed creating a series of international conferences on plant genomics, the Plant GEMs (Plant Genomics European Meetings), of

[1] Rajjou, L, Duval M, Gallardo K, Catusse J, Bally J, Job C, Job D (2012) Seed Germination and Vigor. Annu Rev Plant Biol 63:507–533.

which Dominique organized in Lyon the third meeting (22–25 September 2004), which brought together 650 participants. None of these actions could have been developed without the constant support of Research Ministries and Funding Agencies. Yet, they demonstrated the power of combining bottom-up and top-down approaches.

More recently, Randeep Rakwal, Ganesh Kumar Agrawal, and Dominique have been active toward the establishment of an International Plant Proteomics Organization (INPPO)[2] to which have now joined many colleagues around the world (http://www.inppo.com/). The common goal is to establish the complete proteome of several plants, models and crops, as in being done in HUPO for the human proteome (http://www.hupo.org/). It is anticipated that this will help toward establishing sustainable agriculture in the context of an increasingly growing world population.

Dominique is a member of the Editorial Board of Molecular & Cellular Proteomics, Seed Science Research, and Associate Editor of Frontiers in Plant Proteomics. Together with Paul A. Haynes and Michel Zivy, he was the guest editor of a Special issue of PROTEOMICS dedicated to plant proteomics, which was published in May 2011. He is consulting professor at AgroParisTech and associate member of the French Academy of Agriculture.

Among the many successful collaborations that Dominique and Claudette have developed over the years, none have proved more successful and rich, both with respect to results and the work as a team, than those with their Ph.D. students and postdoctoral fellows: Jacques Dietrich, Laure de Mercoyrol, Yves Corda, Alain Kersulec, Manuel Duval, Bertrand Gakière, Karine Gallardo, Loïc Rajjou, Lucie Miché, Georgia Tanou, Julie Catusse, Rafika Yacoubi, and Julia Bally.

Still today, Dominique and Claudette continue their scientific journey toward '*nothing less than the excellence in their chosen fields of study*'. Last but not the least, their contributions to seed biology research and development will be remembered for many, many years to come.

[2] Agrawal GK, Job D, Zivy M, Agrawal VP, Bradshaw R, Dunn MJ, Haynes PA, van Wijk KJ, Kikuchi S, Renaut J, Weckwerth W, Rakwal R (2011) Time to articulate a vision for the future of plant proteomics—a global perspective. An initiative for establishing the international plant proteomics organization (INPPO). Proteomics 11:1559–1568.

Preface

The beginning of the twenty-first century is certainly a great time for plant biology research. The beginning of the new millennium has placed an ever growing amount of sophisticated technologies at the disposal of the modern scientist to the benefit of all. The research performed with these technologies has the potential to provide the answers to important and complex biological questions and problems (especially those relating to crop plants and the human food supply) within reach.

Of those technologies, transcriptomics, proteomics, and metabolomics are increasingly being utilized for the near complete understanding of plant biology including seed development. These technologies are also loosely called the twenty-first century omics technologies, which have revolutionized the way research was being performed in the past in the field of seed developmental biology. Since the year 2000 these technologies have been largely optimized for model and nonmodel plants. As far as seed development is concerned, these technologies have already generated huge amount of data and continue to do so with astonishing pace. Those data have been organized and integrated in an efficient and confident manner using systems biology approaches. Generated data are being exploited for seed and yield improvement by combing these technologies with breeding and other classical molecular approaches. Indeed, when one looks at the progress achieved to date in the field of seed development and its overall impact on biological research, it is clear just how essential these technologies are to our understanding of the physiology and biology of any organism. It would not be far from the truth to say that the "power of technologies" (and indeed the omic sciences as a whole) is one of the driving forces of the twenty-first century seed biology research. The principles of good science are as true in this age of omics still hold true today and the disciplined scientist must keep these principles in mind to avoid rushing blindly into the field (intentionally or unintentionally) without first obtaining a thorough understanding of its fundamental principles.

When one looks at the impressive progress of above mentioned technologies in seed development as well as its immense importance in biological sciences as a whole, it is clear that there was a need for a textbook of the subject to translate/disseminate the knowledge acquired by leading experts in the field to the wider scientific community for some time. This was the impetus for the book you are

currently reading. Though we knew that such a project would be a formidable challenge, we also knew that it would bring us the opportunity to work closely with the leading experts of the field. What we did not fully appreciate when we started was how much of a truly unparalleled experience it would be to work with each and every one of the contributors of this book, whom we genuinely thank for being part of this ambitious endeavour.

This book is composed of seven sections including appendix in the following order: introduction to seed development and omics technologies/transcriptomics/proteomics/metabolomics/towards systems biology/and discovery-driven seed and yield improvement. There are 26 chapters which between them provide excellent coverage of almost all the studies conducted to date on seed development toward improvement of seed quality and crop yield. Each chapter also provides basic knowledge tightly associated with that particular topic. Seed physiology and developmental patterns have been discussed for most of the crops that are being widely utilized as research material; one might think of redundancy but we believe that those detailed descriptions are necessary for observed/recorded subtle differences, if any, associated with different seed species and to avoid any confusion especially for students. More than 1,000 references serve as a great resource for the academic and nonacademic communities. We hope this book will be beneficial in scope and practical knowledge to you the readers, whose response will be the final judge on the validity of the work. Moreover, the editing and organization of book have been done in a way that the book and its contents can also be used as text book for all level of students. This book is also dedicated to Dominique Job and Claudette Job in recognition of their contribution to the field of seed research and development (Foreword).

We also wish to thank our colleagues and collaborators around the world with whom we have struggled to do “good science”, forming new partnerships and friendships in the process. Though during our long journey in science many persons had an effect on us, but Masami Yonekura (Ibaraki University, Japan), Shigeru Tamogami (Akita Prefectural University, Japan), Akihiro Kubo (National Institute of Environmental Sciences, Japan), Nam-Soo Jwa (Sejong University, South Korea), Oksoo Han and Kyoungwon Cho (Chonnam National University, South Korea), Shoshi Kikuchi (National Institute of Agrobiological Sciences, Japan), Yu Sam Kim and Hyung Wook Nam (Yonsei University, South Korea), Kyu Young Kang and Sun Tae Kim (Gyeongsang National University and Pusan National University, South Korea), and Oliver A.H. Jones (University of Cambridge, UK) deserve both mention and appreciation. We would also like to acknowledge two young people, Abhijit Sarkar (Banaras Hindu University, India and Administrative Officer at International Plant Proteomics Organization—INPPO, www.inppo.com) and Raj Agrawal (Computer Programmer and Webpage Administrator at INPPO) for their constant support in our scientific achievements. We would especially like to thank Prof. Vishwanath Prasad Agrawal (RLABB, Kathmandu, Nepal) for his directions and guidance in our research (this is especially true for Ganesh who started his research under Prof. Vishwanath’s watchful eyes).

It is without doubt that the support of the Editorial Team (Scientific, Technical, Medical, and Scholarly Division) at Springer (The Netherlands), especially the Editorial Director, Jacco Flipsen and the Publishing Assistant, Ineke Ravesloot, was instrumental in bringing this book out to light. We greatly appreciate their professional support and patience with our queries and correspondence.

Finally, to this long list of supporters, we must add our thanks for the personal sacrifices by our families, especially our wives [Mrs. Nitu Agrawal for Ganesh Kumar Agrawal; Mrs. Junko Shibato Rakwal for Randeep Rakwal] and children [Mr. Dakshit Agrawal (son) and Ms. Divya Agrawal (daughter) for Ganesh Kumar Agrawal; Mr. Aryan Shibato Rakwal (son) for Randeep Rakwal], who have allowed us to devote time meant for them into efforts for completing this project. Randeep's wife Junko Shibato has also contributed greatly with the technical aspects of the book at both laboratory and home. Our parents [Mrs. Savitri Devi (mother) and Late Sri Gajanand Madwari (father) for Ganesh Kumar Agrawal; Mrs. Meera Rakwal (mother) and Brigadier (retd.) Om Parkash Rakwal (father) for Randeep Rakwal], who brought us into this world and taught and inspired us to contribute to the society and do our job well and in the right way under any circumstances, also deserve special mention.

To you the reader we also extend our thanks and appreciation. We hope this work will be useful to you.

Ganesh Kumar Agrawal and Randeep Rakwal

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Randeep Rakwal Ph.D. is a Professor of Graduate General Education Courses (GGEC) program at the University of Tsukuba (Tsukuba, Japan). Dr. Rakwal did B.Sc. (Hons.) Botany (Delhi University, 1989) and M.Sc. Agriculture (Plant Pathology) from G. B. Pant University of Agriculture & Technology (1992) in India. He completed Ph.D. in Biochemistry and Biotechnology (Tokyo University of Agriculture and Technology, Japan, with

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Abbreviations

ABA	abscisic acid
ABI/abi	abscisic acid insensitive
AB-QTL	advanced backcross QTL
ABRE	ABA response element
ACCase	acetyl-CoA carboxylase
ACP	acyl carrier protein
ADH	alcohol dehydrogenase
ADP	adenosine diphosphate
ADPG	adenosine diphosphate glucose
AdoMet	*S*-adenosylmethionine
AEP	Association Européenne des Protéagineux
AFP	aspartic acid family pathway
AFLP	amplified fragment length polymorphism
AGL	AGAMOUS
AGPase	ADP-glucose pyrophosphorylase
ANOVA	analysis of variance
ANR	anthocyanidins reductase
AP	APETALA
APCI	atmospheric pressure chemical ionization
AP-MS	affinity purification mass spectrometry
APPI	atmospheric pressure photoionization
APS	5'-adenylyl sulphate
APX	ascorbate peroxidase
ARA	arachidonic acid
ARF	auxin response factor
Arg	arginine
ASE	accelerated solvent extraction
Asp	asparagine
ATP-PFK	ATP-dependent phosphofructokinase
ATP	adenosine triphosphate
BAC	bacterial artificial chromosome
BAC1	basic amino acid carrier1

BAR	bio-array resource
BCCP	biotin carboxyl carrier protein
bHLH	basic helix-loop-helix
BIFC	bimolecular fluorescence complementation
BiP	chaperonin of the binding protein
BL-SOM	batch-learning self-organizing method
BN	blue native
bp	base pair
BR	brassinosteroid
Bt	*Bacillus thuringiensis*
BTPC	bacterial-type PEPC
BY	bright yellow
bZIP	basic leucine-zipper
C	carbon
Ca	calcium
CA	correlation-based analysis
CAM	crassulacean acid metabolism
CaMV	cauliflower mosaic virus
CAPS	cleaved amplified polymorphic sequence
CAT	catalase
CBA	constraint-based analysis
CCA	canonical correlation analysis
CE	capillary electrophoresis
Cd	cadmium
CDK	cyclin-dependent kinase
cDNA	complementary DNA
CDPK	calcium-dependent protein kinase
CGA	chlorogenic acids
C3'H	*p*-coumaroyl ester 3'-hydroxylase
C4H	cinnamate 4-hydroxylase
CHI	chalcone isomerase
CHS	chalcone synthase
CK	cytokinin
CL	4-Coumarate-CoA ligase
CLE	carbon labeling experiment
CLSM	confocal laser scanner microscopy
C-N	carbon-nitrogen
CNA	cell net analyzer
CNBr	cyanogen bromide
CO_2	carbon dioxide
C-O	carbon-oxygen
Co	cobalt
CoA	coenzyme A
COBRA	constraint-based reconstruction and analysis

COS	castor oil seeds
COSY	correlation spectroscopy
CQA	caffeoyl quinic acid or caffeoyl quinate
CRTISO	carotenoid isomerase
Cu	copper
CW	cell wall
Cy	cyanine
Cys	cysteine
Da	dalton
DAF	days after flowering
DAGAT	diacylglycerol acyltransferase
DAHP	3-deoxy-D-arabino-heptulosonate-7-P
DAP	days after pollination
DArT	diversity arrays technology
DBE	debranching enzyme
DBPCFC	double-blind placebo-controlled food challenge
ddNTPs	dideoxy nucleoside triphosphates
DFR	dihydroflavonol 4-reductase
DG	diacylglycerol
1-D	one-dimensional
1-DGE	one-dimensional gel electrophoresis
2-D	two-dimensional
3-D	three-dimensional
2-DGE	two-dimensional gel electrophoresis
DHA	docosahexaenoic acid
DIGE	difference gel electrophoresis
DIMS	direct infusion mass spectrometry
DM	dry mass
DMSO	dimethylsulfoxide
DNA	deoxyribose nucleic acid
DOF	DNA-binding with one finger
DP	dirigent protein
DPA	days post anthesis
dsRNA	double-stranded RNA
DTT	dithiothreitol
DW	dry weight
DXR	1-deoxy-D-xylulose-5-phosphate reductoisomerase
DXS	1-deoxy-D-xylulose-5-phosphate synthase
EDTA	ethylenediaminetetraacetic acid
EEL	enhanced EM level
eFP	electronic fluorescent pictographic
ELISA	enzyme-linked immunosorbent assay
EM	electron microscopy

EMA	elementary modes analysis
EMM	elementary mode
EMS	ethyl methane sulphonate
EMU	elementary metabolite unit
ENR	enoyl-ACP reductase
EPA	eicosapentaenoic acid
EPA	extreme pathway analysis
EPSP	5-enolpyruvyl shikimate-3-P
ER	endoplasmic reticulum
EREBP	ethylene-responsive element binding protein
ERF	ethylene response factor
ESI	electrospray ionization
EST	express sequence tag
ETC	electron transport chain
eV	electron volt
EXP	expansin
FA	fatty acid
FAE	fatty acid elongase
FAH	ferulic acid 5-hydroxylase
FAIMS	field asymmetric waveform ion mobility spectrometry
FAO	Food and Agriculture Organization
FAS	fatty acid synthase
FAT	acyl-ACP thioesterases
FBA	flux balance analysis
FDR	false discovery rate
Fe	iron
F3H	flavonoid 3-hydoxylase
FFZE	free flow zonal electrophoresis
FHA	forkhead-associated
FID	flame ionisation detector
FQA	feruloyl quinic acid
FT-ICR	Fourier transform-ion cyclotoron resonance
FTIR	Fourier transform infrared spectroscopy
FUS	FUSCA
FVA	flux variability analysis
γ	gamma
GA	gibberellin
GA3	gibberellic acid
GABA	gamma-aminobutyric acid
GARE	GA-responsive element
Gbp	giga base pair
GC	gas chromatography

GES	genomic selection
GFP	green fluorescent protein
GGPPS	geranylgeranyl pyrophosphate synthase
GL	GLABRA
Glc	glucose
Glc-1-P	glucose-1-phosphate
Glc-6-P	glucose-6-phosphate
Gln	glutamine
Glu	glutamic acid
Gly	glycine
GM	genetically modified
GO	gene ontology
GOGAT	glutamate-oxoglutarate amino transferase
G-3-P	glycerol-3-phosphate
GPAT	glycerol-3-P acyltransferase
GPC	gel permeation chromatography
GRP	glycine-rich protein
GS	glutamine synthetase
GST	glutathione-*S*-transferase
GUI	graphical user interface
^{1}H	proton
HAP	heme-associated protein
HCA	hierarchical cluster analysis
Hcy	homocysteine
HD	3-hydroxyacyl-ACP dehydratase
HD-ZIP	homeodomain leucine zipper
HEAR	high erucic acid rapeseed
HEPES	4-(2-hydroxyethyl)-1-piperazineethanesulfonic acid
HI	harvest index
HILIC	hydrophilic interaction liquid chromatography
HMBC	heteronuclear multiple bond correlation
H_2O_2	hydrogen peroxide
HPLC	high performance liquid chromatography
HPR	hydroxypyruvate reductase
HQT	hydroxycinnamoyl-CoA shikimate/quinate hydroxycinnamoyl transferase
HR-MS	high-resolution mass spectrometry
HR-MAS	high-resolution magic angle spinning
H/S	hexose and sucrose
HSF	heat shock factor
HSP	heat shock protein
HSQC	heteronuclear single quantum coherence spectroscopy
HYD	hydroxylase enzyme