Bir Bahadur · Manchikatla Venkat Rajam
Leela Sahijram · K.V. Krishnamurthy
Editors

Plant Biology and Biotechnology

Volume II: Plant Genomics and Biotechnology

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Foreword

While writing this Foreword, I was reminded of a quote attributed to Mahatma Gandhi: "The expert knows more and more about less and less until he knows everything about nothing." The quote illustrates the great dilemma that all of us face in modern times: but this is especially acute for those engaged in the pursuit of science. Compared to the times of Archimedes or Leonardo da Vinci or Antonie Philips van Leeuwenhoek, whose range of interests covered several disciplines (they looked at the world in its entirety), most of us have now become narrow specialists of one kind or another, knowing less and less about the wider world. Thus, edited monographs, proceedings of seminars and the like have become absolutely essential to keep us informed and engaged in research and teaching more meaningfully (such publications allow summarizing of recent researches at a more advanced level than is possible in ordinary textbooks).

Turning to plant sciences, the *Annual Review of Plant Biology,* started in the middle of the last century, continues to be an invaluable source of information on the broad advances of plant biology. Yet, it is necessary to have a more inclusive look at advances over a somewhat longer period and also have this information in a way more organized than the format of annual reviews allows. Thus, Prof. Bir Bahadur and his colleagues deserve our grateful thanks on undertaking an incredibly difficult task of summarizing advances on the very broad front of plant biology – the topics cover not only fundamental aspects of plant biology but also plant biotechnology, which is now growing almost as a separate discipline. I welcome their style of a historical approach (nearly every article follows this style). This approach is often neglected by specialists, but the fact is that this is the *only way* to genuine understanding and for a non-expert to easily discern major advances or milestones. This unity in overall planning and laying out the style has obviously been possible due to the fact that two of three co-editors are in fact former pupils of the senior editor (Prof. Rajam, the senior most of them, was, in a sense, a colleague while I was at Delhi University). Understandably, in the combined work on Volumes I and II, Prof. Bir Bahadur is author of nearly ten chapters and Prof. Rajam author of five chapters. Their two other colleagues Dr. Leela Sahijram and Prof. Krishnamurthy have also contributed several chapters. Nonetheless, the work has very valuable contributions also from several national and international contributors (in Volume 2, there are around

ten authors from outside India), which has immensely added to the value of this work.

I think that on the whole, a very laudable contribution has been made. The editors have managed to include almost all topics which are significant in modern plant biology. In Volume 1, I was delighted to see several chapters close to my interest, such as those relating to polyploidy, photosynthesis, apomixis and flower development. But in Volume 2, there is special emphasis on genomics and plant biotechnology, and there are many other chapters of current interest. Space is not adequate to mention all the chapters or their topics, but to me, those on genetic markers, doubled haploids, plant genomes and genomics (there are several on these topics), epigenetic mechanisms, bioinformatics and systems biology were of special interest. Also, I am very delighted that Volume 2 starts with an excellent chapter on *Arabidopsis thaliana*. Inspired by a lecture on Langridge's work by Prof. Arthur W. Galston, I undertook in 1960s to 'tame' a wild Indian strain of *Arabidopsis* by raising in vitro cultures. However, despite the fact that *Arabidopsis* is now the principal material for basic research in plant biology, there are many who have never seen a live *Arabidopsis* plant, and surely, the opening chapter of this volume will be valuable for all.

Although ably aided by his pupils, Prof. Bahadur remains the chief architect of this endeavour. And I am struck with the expanse of his canvas and the breadth of his interest – it seems to me that in part, it is due to his early association with Prof. J.B.S. Haldane, F.R.S., whose own interest covered many disciplines, from mathematics, biochemistry and genetics to animal and plant biology. The topics he and his colleagues cover are of both fundamental and applied interest. I have to admit that many of us in universities are a bit distant from fields and sometimes unfamiliar with the full potential of fundamental discoveries for biotechnological applications. This work will help focus due attention of readers on both aspects of plant biology.

When the chapters were first sent to me, I noticed many typographic mistakes than are normally present in finished manuscripts – it is true that English is not the mother tongue of many of us in India, but I hope these mistakes have been rectified.

Once again, I wish to congratulate Prof. Bir Bahadur and his colleagues for a very unique monograph and insight in modern plant biology.

Satish C. Maheshwari

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Preface

The human population is increasing at an alarming rate and is expected to reach 11 billion by 2050. As there is a big gap between population growth and food production, food security for an ever-increasing population poses a major challenge for the present and future times. In fact, it will become necessary in the coming two decades or so to double food production with available arable land; else, it may precipitate great famines in some parts of the world. This is not achievable with just conventional strategies like plant breeding. However, the projected increase in food production may be achieved if traditional breeding methods are coupled with biotechnological approaches as the latter can offer novel ways for increasing productivity and quality of crops as also for producing an array of useful compounds including pharmaceuticals and biofuels. Indeed, during the past couple of decades, dramatic progress has been made in the field of plant genomics and biotechnology. Therefore, a need was felt for updating scientific developments in these areas.

Plant Biology and Biotechnology – Volume 2 was planned to present state-of-the-art scientific information on various basic and applied aspects of plant genomics. This volume comprises 37 chapters spanning various aspects of plant genomics and biotechnology and provides comprehensive and updated information on a wide variety of topics including *Arabidopsis* as a wonderful model system for plant research, plant–fungus interactions, microalgae in biotechnological applications, genetic markers and marker-assisted breeding, doubled haploids in breeding, DNA fingerprinting for plant identification, nuclear and organellar genomes, functional genomics, proteomics, epigenomics, bioinformatics, systems biology, applications of tissue culture in crop improvement and conservation of plant genetic resources, genetically modified crops for production of commercially important products and engineering abiotic and biotic stress tolerance, RNAi and microRNAs in crop improvement and environmental, marine, desert and rural biotechnologies. The book can serve as a good reference for plant molecular geneticists, plant biotechnologists, plant breeders, agricultural scientists and food scientists. Besides, it will also serve as a reference book for post-graduate students, researchers and teachers besides scientists working in agri-biotech companies.

Contributors of these volumes were selected from a wide range of institutions for introducing a diversity of authors. At the same time, these authors were selected based on their vast expertise in specific areas of their choice to

match the diversity of topics. These authors have a deep understanding of their subject to enable them not only to write critical reviews by integrating information from classical to modern literature but also to endure an unending series of editorial suggestions and revisions of their manuscripts. Needless to say, this is as much their book as ours.

We hope that these books will help our fellow teachers and a generation of students enter the fascinating world of plant genomics and biotechnology with confidence, as perceived and planned by us.

Hyderabad, Telangana, India — Bir Bahadur
New Delhi, India — Manchikatla Venkat Rajam
Bangalore, Karnataka, India — Leela Sahijram
Bangalore, Karnataka, India — K.V. Krishnamurthy

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We wish to express our grateful thanks to a number of friends and colleagues for their invaluable help in many ways and for their suggestions from time to time during the evolution of the two volumes. We also thank research scholars of Prof. M.V. Rajam (University of Delhi South Campus) – Shipra Saxena, Meenakshi Tetorya, Mahak Sachdeva, Bhawna Israni, Mamta, Manish Pareek, Anjali Jaiswal, Jyotsna Naik, Sneha Yogindran and Ami Choubey for their help in many ways.

We wish to express our appreciation for the help rendered by Ms. Surabhi Shukla, Ms. Raman, Mr.N.S. Pandian and other staff of Springer for their cooperation and invaluable suggestions. Above all, their professionalism, which made these books a reality, is greatly appreciated.

We wish to express our grateful thanks to our respective family members for their cooperation.

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Dr. Bir Bahadur, born 5 April 1938, studied at City College, Hyderabad, for 5 years including an Intermediate Course (Osmania University), graduated from Nizam College and postgraduated from University College, Osmania University, both in the first division. He obtained his Ph.D. in Plant Genetics from Osmania University. He was closely associated with late Prof. J.B.S. Haldane, F.R.S., a renowned British geneticist who encouraged him to study heterostyly and incompatibility in Indian plants, a subject first studied by Charles Darwin.

He made significant contributions in several areas, especially heterostyly, incompatibility, plant genetics, mutagenesis, plant tissue culture and biotechnology, morphogenesis, application of SEM in botanical research, plant asymmetry, plant morphology and anatomy and lately the biofuel plants Jatropha and castor.

He served as Lecturer and Reader at Osmania University, Hyderabad, and as Reader and Professor at Kakatiya University, Warangal. He also served as Head of Department; Chairman, Board of Studies; Dean, Faculty of Science; and Coordinating Officer/Dean, UGC Affairs at Kakatiya University. He has over 40 years of teaching and over 50 years of research experience. He has supervised 29 Ph.D. students and 3 M.Phil. students in both these universities and has published about 250 research papers/reviews, which are well received and cited in national and international journals, textbooks and reference books.

He was a postdoctoral fellow at the Institute of Genetics, Hungarian Academy of Sciences, Budapest, and worked on mutagenesis and chromosome replication in *Rhizobium.* He is a recipient of the direct award from the Royal Society Bursar, London. He also worked at Birmingham University (UK). He was conferred with the title of Honorary Research Fellow by the Birmingham University. He studied species differentiation in wild and cultivated solanums using interspecific hybridization and the enzyme-etched seeds technique in combination with scanning electron microscopy to assess the relationship among various *Solanum* species. At the invitation of the Royal Society, he visited Oxford University, Leeds University, Reading University and London University, including the Royal Botanic Gardens, Kew, and various research labs. He was invited for international conferences by the US Science Foundation at the University of Missouri, St. Louis, at the University of Texas, Houston (USA), and at the SABRO international conference at Tsukuba, Japan. He has extensively visited most countries of Eastern and Western Europe as well as Tanzania and the Middle East.

He has authored/edited ten books. One of his important books is entitled *Jatropha, Challenges for a New Energy Crop*, Vol. 1 and 2, published by Springer, New York, USA, 2013, jointly edited with Dr. M. Sujatha and Dr. Nicolas Carels. These books are considered significant contributions to bioenergy in recent times. He was Chief Editor, *Proceedings of Andhra Pradesh Akademi of Sciences*, Hyderabad, and Executive Editor, *Journal of Palynology* (Lucknow).

He is the recipient of the Best Teacher Award by the Andhra Pradesh Government for mentoring thousands of students in his teaching career spanning over 40 years. He was honoured with the Prof. Vishwambhar Puri Medal of Indian Botanical Society for his original contributions in various aspects of plant sciences. He has been honoured with the Bharat Jyoti Award at New Delhi for outstanding achievements and sustained contributions in the fields of education and research. He has been listed as one of the 39 prominent alumni of City College, a premier institution with a long history of about 90 years as per the latest update on its website. He has been chosen for distinguished standing and has been conferred with an honorary appointment to the Research Board of Advisors by the Board of Directors, Governing Board of Editors and Publications Board of the American Biographical Institute, USA.

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Dr. Manchikatla Venkat Rajam is currently Professor and Head, Department of Genetics, University of Delhi South Campus, New Delhi, India. He obtained his Ph.D. in Botany (1983) from Kakatiya University, Warangal, India. He was a postdoctoral fellow at the prestigious Yale University, New Haven (1984–1985), and also worked at BTI (Cornell University, Ithaca) for a couple of months as a visiting research associate. At Yale University, his work led to the discovery of a new method for the control of fungal plant infections through selective inhibition of fungal polyamine biosynthesis. This novel method has been adapted by several research groups globally for the control of a variety of fungal infections, and a large number of research articles have been published in this line of work. He returned to India to join as Pool Officer (CSIR) and worked for about 2 years (1986–1987) at Kakatiya University. Subsequently, he joined the University of Delhi South Campus, where he has been on the faculty since 1987. He had worked in ICGEB, New Delhi, for 6 months as a National Associate of DBT (1994). He made several short visits to various countries including France, Italy, China and Indonesia under the collaborative projects supported by the EU and Indo-French. He is a Fellow of the prestigious Indian National Science Academy (FNA); National Academy of Sciences, India (FNASc); National Academy of Agricultural Sciences (FNAAS); Andhra Pradesh Akademi of Sciences (FAPAS); and Association of Biotechnology and Pharmacy (FABAP) and is an elected member of the Plant Tissue Culture Association, India, since 1995. He was awarded the Rockefeller Foundation Biotech Career Fellowship in 1998 (but could not avail it); the 'Shiksha Rattan Puraskar' by the India International Friendship Society in 2011; Department of Biotechnology National Associateship in 1994; and National Scholarship for Study Abroad (Government of India) in 1984 and for Research in 1985 by the Rotary International Club of Hyderabad. He is serving as an Associate Editor and member of the editorial board of several reputed journals including *BMC Biotechnology* and the OMICS journal *Cell and Developmental Biology* and is a member of the advisory or other committees of some universities, institutions as well as other bodies. He has guided 28 Ph.D. students, 7 M.Phil. students and over 22

postdoctoral fellows and has published over 120 papers (80 research articles in peer-reviewed journals, 15 review articles, 20 book chapters and general articles). He has one Indian patent to his credit. He has vast experience in plant biotechnology and RNA interference and has handled over 22 major projects in these areas.

Dr. Leela Sahijram

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Her team pioneered the micropropagation of banana (globally, the leading tissue culture–propagated fruit crop), which has spawned a multibillion-dollar industry worldwide. In 1990, she successfully demonstrated over 20 choice clones of banana from across India to be 'micropropagatable', including cultivars of the Cavendish Group. She was member of the Task Force for the rehabilitation of Nanjangud Rasabale (Pride of Karnataka) syn. Rasthali, 'Silk' group – a clone threatened with extinction. She has also worked extensively on micropropagation and 'specific-pathogen-free' (SPF) plantlet production through meristem culture/micrografting in crops like citrus, caladium, bougainvillea and chrysanthemum besides bananas and plantains. She specializes in hybrid embryo rescue in perennial horticultural crops (intergeneric/interspecific/intervarietal crosses), particularly in fruit crops, namely,

mango, seedless grapes/citrus, banana and papaya. In 2000–2001, she pioneered hybrid embryo culture and *ex vitro* grafting in controlled crosses of mango.

She was conferred with the Dr. Vikram Govind Prasad Award 1999–2000 for research on molecular diagnostics of viruses in micropropagated bananas. She was also honoured with the Horticultural Society of India Award 2006–2007 for research on hybrid embryo rescue in seedless grapes and with the Rashtriya Samman Award 2007 for developing biotechnologies for horticultural crops. She has been editing the *Journal of Horticultural Sciences*, an international journal, for the past 9 years as a Founder Editor. She has also edited a book entitled *Biotechnology in Horticultural and Plantation Crops*. She has several book chapters in national and international publications to her credit. She is the author of many technical and semi-technical popular articles and a laboratory manual besides having trained hundreds of personnel from development departments for setting up commercial plant tissue culture laboratories. She has travelled widely.

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Dr. K.V. Krishnamurthy is currently an Adjunct Professor at the Institute of Trans-Disciplinary Health Science and Technology (IHST), Bangalore, India, and offering consultancy services in Ayurvedic Pharmacognosy. He obtained his M.Sc. in Botany with University First Rank from Madras University, Chennai, in 1966 and his Ph.D. in Developmental Plant Anatomy from the same university in 1973. After a brief stint in government colleges in Tamil Nadu, he joined the present Bharathidasan University, Tiruchirappalli, in 1977 and became a Full Professor in 1989. He has an overall teaching and research experience of more than 47 years and has guided 32 Ph.D. scholars, more than 50 M.Phil. scholars and hundreds of master's degree holders. He has published more than 180 research papers and 25 books including *Methods in Cell Wall Cytochemistry* (CRC Press, USA) and a textbook on biodiversity (Science Publishers, USA), *Bioresources of Eastern Ghats: Their Conservation and Management* (with Bishen Singh Mahendra Pal Singh, Dehradun). His major research areas include plant morphology and morphogenesis, biodiversity, wood science, cytochemistry, plant reproductive

biology and ecology, tissue culture and herbal medicine and pharmacognosy. He has operated more than 15 major research projects so far. He has been a Fulbright Visiting Professor at the University of Colorado, Boulder, in 1993 and has visited and lectured in various universities in the UK in 1989. His outstanding awards and recognitions include the following: INSA Lecture Award 2011; Prof. A Gnanam Endowment Lecture Award 2010; President 2007, Indian Association for Angiosperm Taxonomy; Prof. V. Puri Award 2006 by the Indian Botanical Society; Rashtriya Gaurav Award 2004 by India International Friendship Society, New Delhi; Scientist of the Year Award 2001 by the National Environmental Science Academy, New Delhi; Tamil Nadu State Scientist Award 1997–1998 in the Field of Environmental Science; Dr. V.V. Sivarajan Gold Medal Award by the Indian Association for Angiosperm Taxonomy for Field Study in the year 1997–1998; Prof. Todla Ekambaram Endowment Lecture Award, Madras University, 1997; Prof. G.D. Arekal Endowment Lecture Award, Mysore University, 1997–1998; Prof. V.V. Sivarajan Endowment Lecture Award, Calicut University, 1997; Prof. Rev. Fr. Balam Memorial Lecture Award, 1997; 1984 Prof. Hiralal Chakraborty Award instituted by the Indian Science Congress in recognition of the significant contributions made to the science of botany, 1960; Dr. Pulney Andy Gold Medal awarded by Madras University as University First in M.Sc. Botany, 1966; Dr. Todla Ekambaram Prize awarded by Madras University for standing first in M.Sc. Plant Physiology, 1966; Maharaja of Vizianagaram Prize awarded by Presidency College, Madras, for outstanding postgraduate student in science, 1965–1966; and Prof. Fyson Prize awarded by Presidency College, Madras, for the best plant collection and herbarium, 1965–1966. He has been the following: Fellow of the National Academy of Sciences of India (FNASc); Fellow of the Linnean Society, London (FLS); Fellow of the Indian Association for Angiosperm Taxonomy (FIAT); Fellow of the International Association of Wood Anatomists, Leiden; Fellow of the Plant Tissue Culture Association of India; and Fellow of the Indian Botanical Society. He has been the Editor and editorial member of many journals in and outside India and has also been reviewer of research articles for many journals. He has also served in various committees, the major funding organizations of India and several universities of India. He has been the Registrar and Director, College and Curriculum Development Council; Member of Syndicate and Senate; Coordinator of the School of Life Sciences and Environmental Sciences; Head of the Department of Plant Sciences; and a Visiting Professor in the Department of Bioinformatics at Bharathidasan University, Tiruchirappalli, before assuming the present job after retirement.

Arabidopsis thaliana: A Model for Plant Research

1

R. Sivasubramanian, Nitika Mukhi, and Jagreet Kaur

Abstract

Arabidopsis thaliana, a small, flowering, self-pollinating weed, has been developed into an elegant model system. Concerted effort from the plant research community has led to development of extensive genomic resources, tools, and techniques. Advances in high-throughput (omics-based) approaches and their application in *Arabidopsis* research have provided ample understanding of basic biological processes in plants. Further, bioinformatics platforms allow for integration of the multiple "omics" data, thus, enhancing our appreciation of biological interactions at an organismal level. Taken together, *A. thaliana* has emerged as an excellent reference source for functional and comparative genomic analysis. In this chapter, we summarize advances made in the field of *Arabidopsis* research and resources, tools, and technologies available to the plant scientific community. In addition, we briefly discuss ways in which knowledge gained from this model system can be harnessed for effective deployment in crop improvement.

Keywords

Arabidopsis thaliana • Model organism • Forward and reverse genetics • Functional genomics • Community resources • Crop plants • Plant biology

1.1 Passage to Glory: From "Tiny Weed" to a "Model Plant"

Mendel's seminal work on *Pisum sativum* (pea) and, later, *Zea mays* (maize) brought the two plants into the main foray as ideal systems for studying crop genetics. Maize, a major crop plant suitable for cytogenetic studies, played an instrumental role in providing valuable insights into

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various facets of plant biology. Horticultural plants like tomato (*Solanum lycopersicum*) and petunia (*Petunia hybrida*) were the other models being used by plant geneticists for studying biological processes. Despite being extensively used in plant biology, these crops failed to develop into ideal model systems for studies on molecular genetics. A major drawback with most of these crop plants being their long generation time and complex genomes. *Arabidopsis thaliana*, a dicot flowering weed belonging to the Brassicaceae family, was not given much importance until Friedrich Laibach included it in his search to identify a plant which had fewer numbers of large chromosomes suitable for cytogenetic analysis. But, due to the small-sized chromosomes, *Arabidopsis* was left out and was not mentioned in plant research for long (Meyerowitz 2001). Laibach refocused his attention on *Arabidopsis* in 1943 and proposed it as a genetic model owing to its short generation time, small size, large progeny, and self-pollinating lifestyle with possibility of outcrossing (Fig. 1.1). Laibach, along with Albert Kranz, further contributed to *Arabidopsis* research by collecting a large number of natural accessions (750) from around the world. George Redei, another plant geneticist, extensively worked towards standardizing mutagenesis protocols for *Arabidopsis* and generated a collection of X-ray induced mutants. Langridge, in 1955, described the first auxotrophic mutant in higher plants. Thereafter, the use of *Arabidopsis* mutants to dissect physiological and biochemical pathways underlying various biological processes gained momentum. Maarten Koornneef's group at Wageningen Agricultural University in Netherlands also started using *Arabidopsis* mutants in a major way and constructed its detailed genetic map, further facilitating research in *Arabidopsis* genetics (Koornneef and Meinke 2010). Around the same time, Estelle and Somerville (1986) used *Arabidopsis* mutants to characterize important biochemical processes like photorespiration, further emphasizing usefulness of this plant in genetic analysis. Pruitt and Meyerowitz (1986) demonstrated that *Arabidopsis* had a small genome relative to other crop models, thereby making mapping and gene cloning comparatively convenient. The next big step in *Arabidopsis* research was the discovery of

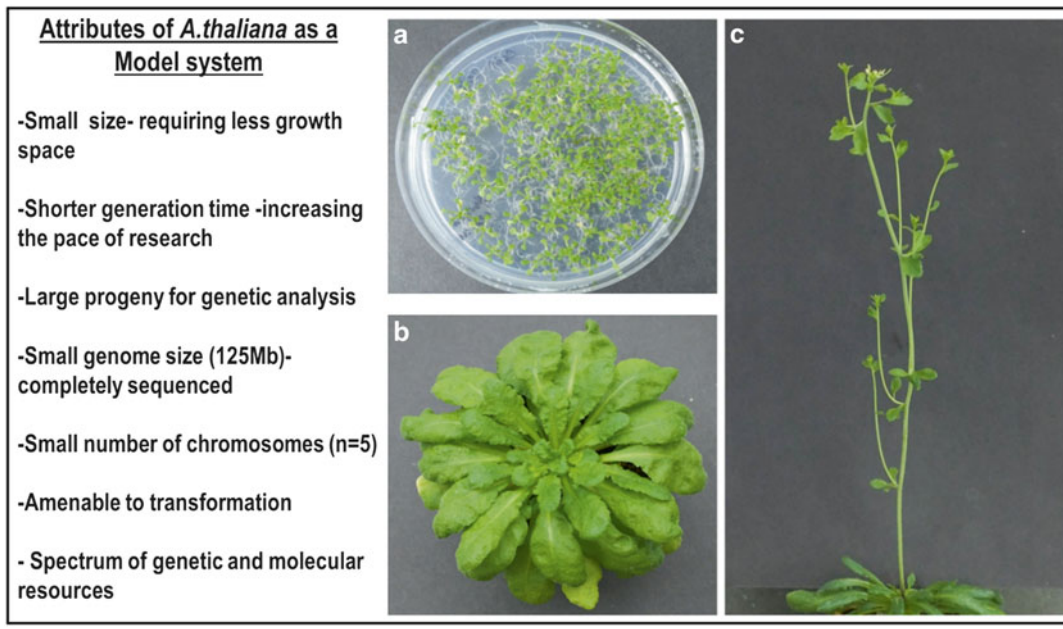

Fig. 1.1 (**a**) Large number of seeds can be grown on 90 mm petri plate. (**b**) Rosette of 4-week-old *Arabidopsis* (**c**) a 5-week-old *Arabidopsis* plant with the inflorescence flowers

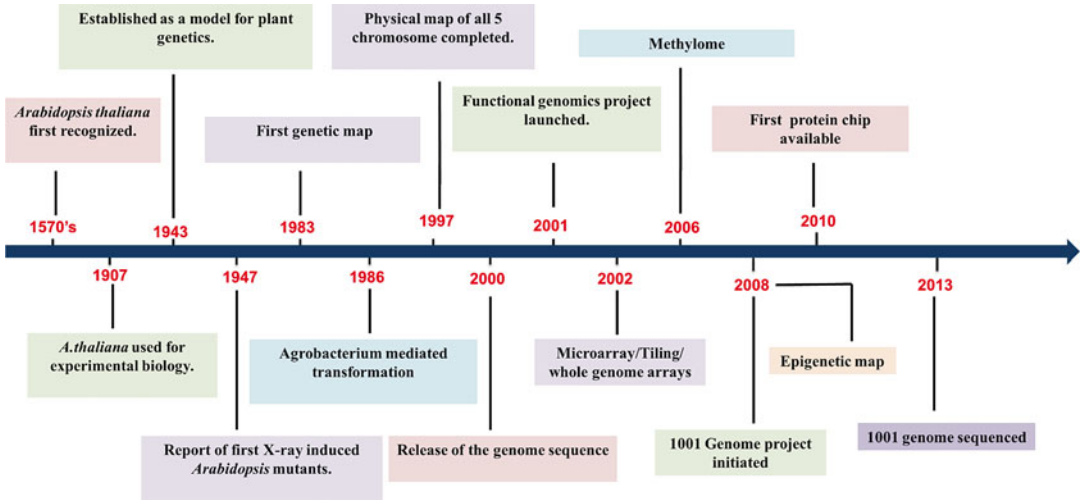

Fig 1.2 Milestones in *Arabidopsis* research

a simple, convenient *Agrobacterium tumefaciens*-mediated transformation of germinating seeds which opened the floodgates for developing various tools for genetic analysis (Feldmann and Marks 1987). Clough and Bent (1998) further simplified plant transformation by devising the "floral dip" method. All these advances, together, brought this weed into limelight as a model plant in the field of plant genetics (Fig. 1.2).

1.2 The *Arabidopsis* Genome: "Catalyst" for Plant Research

A relatively smaller genome size (approx. 125 Mb) was the simple reason *Arabidopsis* was chosen as a subject for the first plant genome sequencing project. By contrast, the genome size of related *Brassica napus* (rapeseed mustard) and *Brassica juncea* (Indian mustard) is about ten times that of *Arabidopsis*. Similarly, the genome of important cereals like rice, maize, and wheat is much more complex and roughly about 3×, 45×, 100×, respectively, compared to *Arabidopsis*. It was the first plant genome to be completely sequenced in the year 2000 under an international Arabidopsis Genome Initiative (AGI). Analysis of the genome using various gene-finding algorithms, along with supporting data from vast experimental evidences like EST sequences, MPSS tags, cDNA clones, etc. predicts about 33,000 gene models (TAIR 10). The genome analysis also revealed that it is enriched for genes with an average size of 5 Kb (Bevan et al. 1998). It was also observed that there is very little repetitive DNA compared to any other higher plant, which facilitates molecular studies and map-based cloning. Release of its genome sequence acted as a catalyst for commencement of various projects on functional genomics, leading to generation of a vast stockpile of resources discussed hereunder (Fig. 1.2).

1.3 Genetic Resources for Functional Genomics

Properties of a living organism are determined mainly by its genetic constitution and its interaction with the environment. With the ever-expanding wealth of genomic data produced by genome sequencing projects, the next essential step is to decipher the gene function. Multiple tools and techniques have been developed for *Arabidopsis* with a focus on dissecting and defining its gene function and interactions in a given biological process (Table 1.1).