Narendra Tuteja
Sarvajeet Singh Gill *Editors*

Crop Improvement Under Adverse Conditions

Springer

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Professor Arturo Falaschi
(January 21, 1933–June 1, 2010)

Prof. Arturo Falaschi was born in Rome and graduated in Medicine in 1957 from Milan University. He undertook post doctoral trainings with J. Adler and Har Gobind Khorana (Nobel Prize in 1968 for deciphering the genetic code) in Wisconsin, USA (1961–1962), and later with Arthur Kornberg (Nobel Prize in 1959 for his studies on DNA replication) at Stanford (1962–1965). His main field of research was in the field of DNA replication and his contributions in this field are significantly important. His scientific work featured in the most prestigious international journals. Prof. Falaschi remains one of the few international researchers whose scientific activity is *documented throughout almost fifty years (from 1962 to 2010). Prof. Falaschi was responsible for the establishment of several research institutes and was a strong believer in the internationalization of science. Prof. Falaschi was very articulate and convinced several governments in the developed and the developing world to establish a 3-component International Centre for Genetic Engineering and Biotechnology (ICGEB), with one component in New Delhi, India, one in Trieste, Italy and one in Cape Town, South Africa. All these centres are devoted to research and training of young researchers from the developing world (www.icgeb.org). One of the focuses of ICGEB, New Delhi component is the development of crops resistant to various stresses. Prof. Falaschi was the mind and driving force in the founding and development of ICGEB, where he served as the Director General from 1989 to 2004. From 2004 to 2010, he worked as ICGEB Distinguished Scientist and Professor of Molecular Biology, Scuola Normale Superiore SNS, Pisa, Italy.*

This book is dedicated to the memory of Prof. Arturo Falaschi as a token of our appreciation and respect for him and his achievements.

Foreword

Plants are fundamental to life on Earth and they have been harnessed by humans for food, feed, fibre, fuel and fun. The need to increase crop production is becoming more urgent due to increasing population and diversion of crops to biofuels production. Furthermore, this needs to be done sustainably with reduced inputs and in the face of global environmental change. It is also notable that one-third of the world's food production is estimated to grow under irrigation—much of this irrigation is unsustainable, using water supplies that are overexploited and under threat from changing weather patterns resulting from global climate change. It is estimated that to meet the recent Declaration of the World Summit on Food Security target of 70 % more food by 2050, an average annual increase in production of 44 million metric tons per year is required, which is a 38 % increase over historical increases in production.

The gap between potential yield and actual yield is primarily due to the effects of abiotic stresses on crop production. It is therefore an imperative to improve our ability to maintain crop production in environments with suboptimal conditions, such as low water or nutrient supplies, or high salinity. This is, of course, required in addition to improving the efficiency of delivery of existing technologies into developing countries through improved education and outreach.

As such, the book edited by Dr. Narendra Tuteja and Dr. Sarvajeet Singh Gill provides a useful and timely compilation of up-to-date overviews of advances in the important area of plant sciences, "Crop Improvement Under Adverse Conditions". In this volume, a range of papers have been brought together which address both the technologies required to understand mechanisms of abiotic stress tolerance and the biological questions to which those technologies need to be applied. An understanding of the molecular and physiological aspects of plant function is provided in this book, and the emphasis on contributors from developing countries is very valuable—delivery of improved technologies and improved varieties of crops in such regions will have the greatest relative impact on global food production.

The editors and contributors are to be congratulated on their efforts, and readers are recommended to use this volume for a long time to come.

Mark Tester
Adelaide, Australia

Preface

Plant development and productivity are negatively regulated by various environmental stresses. Abiotic stress factors such as heat, cold, drought, salinity, wounding, heavy metals toxicity, excess light, flooding, high speed wind, nutrient loss, anaerobic conditions and radiations etc. represent key elements limiting agricultural productivity worldwide. The loss of productivity is triggered by a series of morphological, physiological, biochemical and molecular stress-induced changes. Such an unfavourable situation is in contrast with the increasing global food demand. World population is increasing at an alarming rate and is expected to reach more than nine billion by the end of 2050, whereas, plant productivity is being seriously limited by various abiotic stresses all over the world. Global climatic pattern is becoming more unpredictable with increased occurrence of drought, flood, storm, heat waves, and sea water intrusion. It has been estimated that abiotic stresses are the principal cause for decreasing the average yield of major crops by more than 50 %, which causes losses worth hundreds of millions of dollars each year. Therefore, to feed the world population maintaining crop productivity even under unfavourable environment is a major area of concern for all nations. Developing crop plants with ability to tolerate abiotic stresses is need of the day which demands modern novel strategies for thorough understanding of plant's response to abiotic stresses. Molecular breeding and genetic engineering have significantly contributed to expand the basic knowledge of the cellular mechanisms involved in stress response, suggesting new strategies to enhance stress tolerance.

In this book "Crop Improvement Under Adverse Conditions", we present a collection of 17 chapters written by 55 experts in the field of plant abiotic stress tolerance and crop improvement. It is a timely contribution to a topic that is of eminent importance. The chapters provide a state-of-the-art account of the information available on abiotic stress tolerance and crop improvement. In this book, we present the approaches for crop improvement under adverse environmental conditions. Chapter 1 deals with the research, development, commercialization, and adoption of drought- and stress-tolerant crops, where the factors affecting adoption of stress-tolerant crops by farmers are explored which includes complementary technologies, competing technologies, appeal to first-time users, distribution and timing of benefits to users, and social perceptions of the technology. Chapter 2 uncovers the impact of extreme events on salt-tolerant forest species of Andaman and Nicobar Islands. Chapter 3 deals with greenhouse gases emission from rice paddy ecosystem and their management. The plant development path of mitigating greenhouse gases (GHG) from agriculture cropping systems is not yet well established. Therefore aggressive research strategies and field validations are needed for establishing 'plant development' as a sustainable tool for GHG mitigation in agriculture sector. Chapter 4 covers remote sensing applications to infer yield of tea in a part of Sri Lanka. Chapter 5 deals with the polyamines contribution to the improvement of crop plants tolerance to abiotic stress, where, mechanism of action of polyamines to protect crop plants from challenging environmental conditions has been discussed. Chapter 6 discusses the overlapping horizons of salicylic acid in different stresses. In this chapter, the indigenous accumulation and overlapping roles of SA under different environmental and physiological conditions highlighting its recently updated roles and regulations in plants is discussed. Chapter 7 focuses on the effects of oxidative stress within the nuclear compartment where DNA becomes the main target of the highly toxic reactive oxygen species (ROS). Chapter 8 deals with a fast and reliable approach for crop improvement through in vitro haploid production. This chapter will act as a guide to prospective scientists working in the area of haploid production intended for crop improvement. Chapter 9 discusses the strategy for the production of abiotic stress-tolerant fertile transgenic plants using androgenesis and genetic transformation methods in cereal crops. Chapters 10 and 11 deal with the control and remedy of plant diseases through nanotechnology and the scope and potential of nanobiotechnology in crop improvement. The use of mutifunctionalised nanoparticles as plant transgenic vehicle for developing disease and stress resistant transgenic plants is discussed. Nanotechnological approaches on plants allow more efficient and sustainable food production by reducing the chances of disease and pest incidence in plants. In Chap. 11, thorough studies and reliable information regarding the effects of nanomaterials on plant physiology and crop improvement at the organism level are discussed. Chapter 12 deals with the role of nematode trapping fungi for crop improvement under adverse conditions. Chapter 13 uncovers the role of sugars as antioxidants in plants. This chapter discussed that soluble vacuolar carbohydrates (e.g. fructans) may participate in vacuolar antioxidant processes, intimately linked to the well-known cytosolic antioxidant processes under stress. All these insights might contribute to the development of superior, stress-tolerant crops. Chapter 14 deals with chromium toxicity and tolerance in crop plants, where, the mechanism of phytotoxicity and phytotolerance under Cr stress is discussed. Chapter 15 deals with boron toxicity and tolerance in crop plants, where, attempts to improve crop yields under boron-toxic soils is discussed. Chapter 16 deals with the approaches for stress resistance and arsenic toxicity in crop plants. Chapter 17 uncovers the mechanism of cadmium toxicity and tolerance in crop plants.

The editors and contributing authors hope that this book will include a practical update on our knowledge of "Crop Improvement Under Adverse Conditions" and lead to new discussions and efforts to the use of various tools for the improvement of crop plants under changing environment.

We are highly thankful to Dr. Ritu Gill, Centre for Biotechnology, MD University, Rohtak for her valuable help in formatting and incorporating editorial changes in the manuscripts. We would like to thank Prof. Mark Tester for writing the foreword and Springer Science+Business Media, LLC, New York, particularly Editor, Plant Sciences, Amna Ahmad and Developmental Editor/Project Manager, Daniel L.A. Dominguez and Andy Kwan, for their support and efforts. We have dedicated this book to Prof. Arturo Falaschi, the mind and driving force in the founding and development of ICGEB.

Narendra Tuteja
Sarvajeet Singh Gill

Contents

The Editors

Narendra Tuteja was born in 1955. Currently, Dr. Tuteja is working as a Senior Scientist in Plant Molecular Biology Group, International Centre for Genetic Engineering and Biotechnology (ICGEB), New Delhi. Dr. Tuteja obtained his M.Sc., Ph.D and D.Sc. in Biochemistry from the Lucknow University in 1977, 1982 and 2008, respectively. He is fellow of the Academies of Sciences: FNASc. (2003), FNA (2007), FASc. (2009), FNESA (2009) and FTWAS (2012).

Dr. Tuteja has made major contributions in the field of plant DNA replication and abiotic stress signal transduction, especially in isolating novel DNA/RNA helicases and several components of calcium and G-proteins signaling pathways. Initially he made pioneer contributions in isolation and characterization of large number of helicases from human cells while he was at ICGEB Trieste and published several papers in high impact journals including EMBO J. and Nucleic Acids Research. From India he has cloned the first plant helicase (Plant J. 2000) and presented the first direct evidence for a novel role of a pea DNA helicase (PNAS, USA, 2005) in salinity stress tolerance and pea heterotrimeric G-proteins (Plant J. 2007) in salinity and heat stress tolerance. Dr. Tuteja has reported the first direct evidence in plant that PLC functions as an effector for Gα subunit of G-proteins. All the above work has received extensive coverage in many journals, including Nature Biotechnology, and bulletins all over the world. His group has also discovered novel substrate (pea CBL) for pea CIPK (FEBS J. 2006). He has already developed the salinity tolerant tobacco and rice plants without affecting yield. Recently, few new high salinity stress tolerant genes (e.g. Lectin receptor like kinase, Chlorophyll a/b binding protein and Ribosomal L30E) have been isolated from Pisum sativum and have been shown to confer high salinity stress tolerance in bacteria and plant (Glycoconjugate J. 2010; Plant Signal. Behav. 2010). Recently, very high salinity stress tolerant genes from fungus Piriformospora indica have been isolated and their functional validation in fungus and plants is in progress. Overall, Dr. Tuteja's research uncovers three new pathways to plant abiotic stress tolerance. His results are an important success and indicate the potential for improving crop production at sub-optimal conditions.

Sarvajeet Singh Gill was born on January 21st, 1979. Dr. Gill obtained his B.Sc. (1998) from Y.D. College, Kanpur University and M.Sc. (2001, Gold Medalist), M. Phil. (2003) and Ph.D (2009) from Aligarh Muslim University. Presently, Dr. Gill is working as Assistant Professor in Centre for Biotechnology, MD University, Rohtak, Haryana.

Dr. Gill's main area of research includes Genetic Engineering, Stress Physiology and Molecular Biology (Development of abiotic stress tolerant crop plants, the physiological, biochemical and molecular characterization of agronomically important plants under abiotic stress factors, involvement of mineral nutrients and other biotechnological approaches in the amelioration of abiotic stress effects in crop plants, use of a combination of genetic, biochemical, genomic and proteomic approaches to understand the responses of various components of antioxidant machinery to abiotic stress and stress signaling and stress tolerance in crop plants. Dr. Gill has several research papers, review articles and book chapters to his credit in the journals of national and international repute and in edited books. He has edited four books namely Sulfur assimilation and Abiotic Stress in Plants; Eutrophication: causes, consequences and control; Plant Responses to Abiotic Stress, Omics and Abiotic Stress Tolerance and Improving Crop Resistance to Abiotic Stress, published by Springer-Verlag (Germany), IK International, New Delhi, Bentham Science Publishers and Wiley-VCH, Verlag GmbH & Co. Weinheim, Germany, respectively. Dr. Gill is a regular reviewer of National and International journals and grants. He was awarded Junior Scientist of the year award by National Environmental Science Academy New Delhi in 2008. With Dr. Tuteja, Dr. Gill is working on heterotrimeric G proteins and plant DNA helicases to uncover the abiotic stress tolerance mechanism in rice. The transgenic plants overexpressing heterotrimeric G proteins and plant DNA helicases may be important for improving crop production at sub-optimal conditions.

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Chapter 1
The Research, Development, Commercialization, and Adoption of Drought and Stress-Tolerant Crops

Gregory Graff, Gal Hochman and David Zilberman

1 The Importance of Stress-Tolerant Crops

Global crop production tripled over five decades from 1960 to 2010 (Fig. 1.1). In the next four decades from 2010 to 2050, global crop production must double yet again if supply is to keep up with expected growth in demand. For not only is global population growing—with basic food requirements thus expanding proportionately—but the burgeoning middle classes of Asia, Latin America, and Africa are consuming ever more livestock products and processed foods, thus amplifying those populations' demand for basic crop commodity output (Rosegrant et al. 2002). There is also growing demand for crops to produce biofuels, with numerous countries legislating ambitious renewable fuel standards (Rajagopal et al. 2007). These and other pressures have manifested in recent upward trends in agricultural commodity prices (Trostle 2008). Limited supplies and higher prices of food inevitably impact most the poorest and most food-insecure members of the human population, the billion or so who live on the equivalent of one or two dollars a day and spend a majority of their income on food, resulting in malnutrition, hunger, poor health, stunted growth, and entrapment in poverty.

The greatest challenge in further increasing agricultural production, it is generally argued, is that agriculture already operates at or beyond the limits of available resources—including arable land, fresh water, energy inputs, carbon emissions, and the loading of excess nutrients and agrochemicals onto neighbouring and downstream ecosystems. Further expansions in agricultural production are not feasible,

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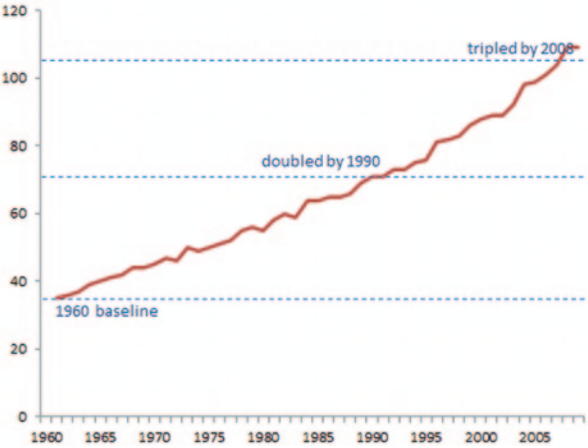

Fig. 1.1 Five decades of world crop production: 1960–2010 (Gross Production Index Number (2004–2006 = 100). (Source: FAOStat 2011)

not economical, or increasingly likely to cause irreversible environmental impacts, such as species extinction and climate change (Tilman et al. 2002). Climate change, moreover, threatens to further complicate the challenge of a sustainable increase in agricultural production—given increasing temperatures, shifting rainfall patterns, increasing variability, and greater frequency and severity of extreme weather events.

Such Malthusian views, however, are based on a linear conception of agricultural productivity growth and a static conceptualization of the nature of resource constraints. In the long run, the resource-use efficiency of agricultural production—the amount of land and water required per ton of harvested yield—has proven to be quite dynamic, and has improved markedly when measured over decades (Alston et al. 2010). Constraints of land or water use shift and recede before changes in technology, cropping, and cultural practices. Productivity growth is driven by several factors, and the most important include: (i) The quantity and the quality of the natural capital employed, particularly land and water, (ii) other physical capital employed, including mechanical equipment and irrigation infrastructure, (iii) suitability of other inputs and technologies employed, such as fertilization and pest control, (iv) the genetic traits and yield potential of the crops sown, and, finally, (v) the efficiency of allocations of agricultural inputs and outputs under the management of farmers and in response to price signals from markets. Moreover, all these factors can interact in complex, sometimes mutually reinforcing ways to improve agricultural productivity and, ultimately, its sustainability.

Of these factors, one of the potentially most significant for future increase in productivity will be the genetic improvement of crops to maintain yields under suboptimal conditions—such as drought or chronic water deficit, excessive salinity, extreme hot or cold temperatures, or other kinds of environmental stress or abiotic stress (Araus et al. 2008). Such conditions characterize—indeed, they define—those lands that are considered to be ‘marginal’, whether currently cultivated lands achieving lower and unstable yields or currently uncultivated lands, including those abandoned due to soil degradation by previous agricultural practices. Such yield-limiting conditions could even come to characterize some of today's prime agricultural lands, depending upon how scenarios of climate change unfold in the future.

1.1 Background of Stress-Tolerant Crop Genetics

Historically, tolerance of adverse environmental conditions was not a primary characteristic favored in the domestication of crop species and subsequent genetic selections in traditional agriculture. Indeed most domesticated crop species are largely incapable of prolonged survival in the wild (Gepts 2004). Many traits that enhance chances of plant survival under adverse environmental conditions—like small stature and large root systems, photosynthetic reductions, or accumulation of defensive proteins—come at physical cost of lower production of harvestable output under optimal growing conditions (Cattivelli et al. 2008). Selection and replanting by farmers has tended to trade-off between plants that apportioned more of their energy to harvestable product versus survival. Recalling also that, for most of history, subsistence agriculture was quite diversified and spatially diffused, it stands to reason that, all other factors being equal, as long as a better-yielding variety did not fail too often, farmers would favor its higher expected yields, in any given season, over other varieties with lower yields but better assurance against failure in the uncertain event of a poor season. Moreover, diversification across multiple crops and livestock, often supplemented with other food sources like hunting and gathering, meant that, if a harvest did fail, other sources could be depended upon. Moreover, in most regions over most of history, if soils in one location tended to hinder growth of favored varieties, they would be passed over or abandoned in favor of other areas with more suitable soils (thus, effectively relegated to the category known as 'marginal' lands). Crop survival mechanisms were not, in short, the primary genetic characteristics for which subsistence farmers were selecting historically.

With the advent of scientific breeding in the last century, this trade-off was, if anything, further accentuated, at least initially. Evidence shows that early Green Revolution varieties with greater yield gains, also experienced greater yield variances (Traxler et al. 1995). While improved varieties yielded significantly better than existing varieties under optimal growing conditions, under adverse conditions they did not necessarily perform better—and may have performed worse—than existing (usually locally adapted) varieties. The benefits from an improved variety's increased yield potential were realized by maintaining optimal growth conditions with other inputs, such as irrigation and nitrogen application, thus creating incentives for farmers to procure these complementary inputs. Especially where these complementary inputs were available at economical or even subsidized rates, Green Revolution farmers favored varieties with higher mean yields, not necessarily higher survival rates under stressful conditions. This trade-off, thus, lies at the root of contentions that the Green Revolution did not equitably help all farmers, particularly neglecting to benefit those farmers who are relegated to cultivating marginal lands (Hazell et al. 2002).

However, the trade-off between higher yield and yield stability is not a rigid one, and post-Green Revolution, public breeding programs as well as commercial breeding programs have met with some success in achieving greater yield stability while breeding for higher yields (Cattivelli et al. 2008; Traxler et al. 1995). A 1998 survey to assess gene pool enrichment in the US summarized the objectives of 280 breeding projects, largely by public-sector breeders at the State Agricultural Experiment Stations (SAES) associated with the state Land Grantre search universities and the US Department of Agriculture's (USDA) Agricultural Research Service (ARS) in the US (Frey 1998). Out of the total number of breeding projects surveyed, 33 projects—representing just 12 %—reported an objective related to abiotic stress tolerance. Of these 33 stress-tolerance projects, seven had not produced successful results and five more were still uncertain. Considering breeding projects by type of crop, emphasis on stress-tolerance objectives was highest among temperate fruit and nut crops, with 14 out of 44 projects (32 %) related to improving cold hardiness, winter hardiness, heat tolerance, or drought-tolerance—with these concentrated primarily in blueberry, strawberry, and grape. Emphasis on stress-tolerance objectives was also higher in forage grasses, where four out of 29 projects (14 %) were breeding for drought and salt tolerance. By contrast, in grains, only four out of 52 (8 %) of reported projects related to stress tolerance; all of which were in wheat. In the majority of crop categories—including fiber crops, forage legumes, root crops, and oilseeds—stress tolerance objectives were all but absent. While stress tolerance has been targeted in breeding programs, it has been a minor emphasis relative to other types of objectives, and more difficult to achieve.

1.2 Recent Advances at the Molecular Level

Over the last two decades, rapid advances in plant molecular biology have opened up new opportunities to enhance stress tolerance while also increasing or at least preserving mean yields. The tools of molecular biology have enabled the identification of hundreds of genes involved in plant stress response and elucidated plants' complex stress response mechanisms as well as the interrelationships amongst them. This rapidly expanding knowledge base has enabled molecular breeding programs and transgenic strategies for drought and stress tolerance. Such knowledge can be used in molecular breeding programs to identify and bring multiple genes involved in stress response into elite germ plasm (Araus et al. 2008; Cattivelli et al. 2008; Liu and Chen 2010; Salekdeh et al. 2009; Sinclair 2011; Jenks et al. 2007). The molecular breeding approach has, for example, resulted in new varieties of hybrid maize released for the North America 2011 growing season that are marketed specifically as 'drought tolerant', including Syngenta's *Agrisure Artesian* maize, released in Colorado, Kansas, and Nebraska (Syngenta rolling out drought-tolerant corn 2011), and Pioneer Hi-Bred's*Optimum AQUAmax* maize, released in Colorado, Kansas, Nebraska, and Texas (Bennett 2011).

Alternatively, transgenic strategies allow individual stress response genes to be discretely added to high-yielding varieties, without compromising the transformed variety's yield potential as well as being stacked together with other transgenic traits—such as herbicide tolerance or insect resistance—that are already widely desired by farmers. Transgenic drought-tolerant maize varieties are in advanced field trials and being reviewed by regulators in the United States, Europe, Australia, and several other countries, including Monsanto's and BASF's jointly—developed MON 87460 event, with the cold shock protein B (*CspB*) from *Bacillus subtilis*. The same transgene is being adapted to African maize varieties by the Water Efficient Maize for Africa (WEMA) initiative, coordinated by the African Agricultural Technology Foundation (AATF), and consisting of a publicprivate partnership between Monsanto and several public sector agricultural research institutions in Africa, with funding from the Bill and Melinda Gates Foundation and the Howard G. Buffett Foundation.

1.3 Research and Development and the Commercialization of New Crop Varieties

Regardless whether a breeding or a transgenic approach is taken to improve crop genetics, doing so involves a research and development process followed by the commercialization of the successfully developed crop variety or other related technology. Today, these processes constitute the primary pathway by which fundamental knowledge of plant biology is translated into human benefit.

It is important to clarify that *any* release of a new crop variety—whether done by a company or a public-sector organization—can be understood as the commercialization of that variety for that is the point at which it leaves the controlled environment of the laboratory, greenhouse, or test plot and enters the much less controlled environment of human commerce. Moreover, varietal release occurs in the context of markets in virtually all cases. There is little dispute this is the case when a company makes the release. Indeed, however, it is exceedingly rare that seeds are freely handed out directly by governments or non-profit organizations to farmers. Even in those cases when they are, the released seeds are intended as inputs for (essentially commercial) agricultural production, or may be sold on the secondary market. In the more common case of a 'public' release of a new variety by a publicsector breeding program, the new variety is still very much entering commerce. Typically it is taken up by local seed companies or nurseries, either to be crossed into local varieties or simply to be multiplied and sold to farmers. Even when small scale or small profit margins dissuade companies from taking on this role, farmers themselves will grow and sell their surplus seed to other farmers for use in subsequent seasons. Finally, the very act of any farmer taking up or adopting a new crop variety is an economic decision, taken with due consideration of its economic implications for that farmer's production and household.

1.4 Roles of the Public Sector and the Private Sector

Both publicsector (government or non-profit) and private-sector (business) entities—as well as publicprivate partnerships between the two—are deeply engaged in R&D for crop improvement and in the commercialization of new varieties. The history of public support to crop breeding is primarily due to the genetic nature of such innovations. Seeds or other planting materials historically have been easily replicable, and therefore entrepreneurs have had little assurance, regardless of crop, that a genetic innovation they might introduce would not become widely copied at merely the cost of reproduction and transportation. Such imitators, because they invest nothing into R&D or breeding programs, can undercut the prices that the innovative entrepreneur must charge to recoup the value of his initial R&D investment plus interest (Baumol 2010).

Even when private entrepreneurs can manage to appropriate at least some returns above the marginal costs of reproducing and reselling a crop variety, they inevitably calibrate their levels and types of R&D efforts based only upon their expected profits from those appropriated returns: They are thus not induced to take into consideration any other benefits that their innovations might bring to others within the society. Such R&D can include the benefits of improved nutrition or food security that accrue to food consumers, improvements in environmental quality or public health, or technology spillover effects improving and accelerating the innovation efforts by other breeders or seed companies. For these reasons governments, non-profit philanthropies, and aid agencies have taken the lead and intervened in the missing or underperforming markets for innovation in agriculture (Sunding and Zilberman 2001).

The first real increase in private sector involvement in crop genetics began in the 1930s with changes initiated by the development of hybrids. The fact that hybrids would not breed true variety, introduced a physical mechanism of appropriability into the market for improved seeds. Breeders would only release seed for the hybrid progeny on the market while holding their foundational or parental breeding lines as trade secrets. As hybrid corn became commonplace in the 1930s and 1940s, private investment in corn breeding and the improvement of hybrid corn genetics took off.

At roughly the same time, in 1930, a new legal mechanism was introduced in the US: the '*plant patent*'. It was intended to enhance the appropriability of genetic innovations in asexually propagated crops, in order to encourage more privatesector investment in varietal improvement. Later, by the 1960s, yet another form of intellectual property over crop genetics—plant variety protections (PVP) or plant breeders' rights (PBR)—began to be developed in Europe and elsewhere, and was later coordinated internationally under the International Union for the Protection of New Varieties of Plants (UPOV) convention (Lesser 2007).

Much more significant privatization of crop genetics has come with the rise, since the 1980s, of recombinant DNA, cell and tissue culture, and plant transformation technologies. With the tools of biotechnology, the cost of making genetic improvements increased, while at the same time the potential value of (at least some) new traits increased too. Costs increased due to the much greater perceived needs for translation, testing, and regulatory oversight to control for potential bio-safety risks. At the same time, the primary factor that has made the large investments by the private sector economically feasible has been the adaptation of patent law so that patents can be used to protect inventions in crop genetics. With patents, the value of a much wider range of genetic improvements can begin to be appropriated in a way that resembles the hybrid varieties, and thus the private sector is much more likely to invest. Moreover, tools of molecular biology made it technically much easier to detect and enforce breaches of trade secrets, patents, and other means keeping breeding lines and other genetic materials proprietary, as was vividly illustrated in a 1994 US federal case between Pioneer hi-bred and Holden foundation seed (Pioneer Hi-Bred International v. Holden Foundation Seeds Inc 1994).

Despite the extent to which private involvement in crop genetic development has increased, it is most accurate to describe today's relationship between the public sector and the private sector as one of interdependence. The public sector continues to make significant contributions, especially in the more basic areas of biological research, but it is typically not able to justify the dedication of resources necessary for advanced testing, commercial scaling, and market deployment, including, in the case of transgenic varieties, the costs of obtaining regulatory approvals. The private sector has a comparative advantage in managing the riskier financial arrangements needed for these processes.

The resulting interdependence between the public and private sectors and the role of patents in inducing follow-on private investment in development and commercialization is reflected in the newer process of technology transfer between public sector agricultural research and the private sector. Today, patents or PBRs are often taken out by universities and government agencies when they make potentially useful inventions in crop genetics. The purpose of such intellectual property protection taken by public sector organizations is not to provide incentives to public sector research in the first place nor to generate financial support for them by way of royalties earned but, rather, its purpose is primarily to induce follow-on private investment of the magnitude necessary to further test the viability of inventions that have resulted from publicly funded research, and for those that prove feasible, to bring them the rest of the way through the R&D pipeline to commercialization. Thus, while the private sector depends upon the public sector as a source of new ideas, the public sector depends upon the private sector as a source of capital and expertise for development and commercialization.

2 The Stages of the R&D Process

The research and development process always starts from new knowledge—whether a newly identified trait, the characterization of a promising new collection accession, or an insight about a better way of achieving an outcome. The R&D process, if completed successfully, results in the introduction of a new innovation, whether a product or a proces, to a marketplace. The R&D process is not necessarily linear—i.e. proceeding from basic science, to applied research, and on to development—and may even begin with users of the technology. Yet, it typically does follow a causal sequence of operational steps. The term 'R&D pipeline' is commonly used in industry to describe the full set of candidate innovations currently being worked on and therefore likely to be forthcoming from the R&D process in the foreseeable future. A typical characterization of stages in the R&D pipeline for the crop breeding and biotechnology industry includes: (a) discovery, (b) proof of concept, (c) early development, (d) advanced development, and (e) regulatory submissions, and (f) market launch. Of course, not all of these steps are necessary under both the breeding and transgenic approaches.

The 'discovery' stage includes identification of potentially desirable genes or plant characteristics with methods such as high throughput screening, model crop testing, or participatory breeding. Potentially useful identifications can be made in university, government, and industry laboratories. Basic research can be very important for generating such discoveries, particularly in agriculture. Indeed, innovations are one set of important byproducts of basic research. Yet, discoveries also may arise from the watchful eyes of farmers who grow diverse varieties, such as land races cultivated near the center of origin for a given crop.

Next, the genetics underlying a trait, whether from a land race or another type of organism, must be moved into breeding material. This occurs in the 'proof of concept' and 'early development' stages, in which crosses or crop transformations are made. Particularly when the approach is transgenic, additional work is required to evaluate the viability of the transformation event, improve expression, and test performance in greenhouse and controlled field conditions. The 'advanced development' stage includes combining (or stacking) the new trait(s) with other valued traits, field testing, agronomic evaluation, and, for transgenic varieties, generation of necessary regulatory data. When a significantly novel trait, or a transgenic trait, is involved, bio-safety or environmental impact may be the concerns. In order to comply with legal requirements controlling the environmental and market release of novel traits and transgenes, submissions are made in the 'regulatory' stage for review and approval by regulators.

Finally, at the 'market launch' stage, a successful launch can depend upon integration into production and distribution systems and a sufficient quantity of stocks in preparation for distribution and expected sales. Often an initial release is done in a smaller, controlled manner in regional test markets, in order to collect market data to guide a subsequent full rollout, as well as to minimize losses in the event the crop fails to perform as expected. Other work after commercialization includes marketing, the informing of potential adopters about the new variety and its characteristics. For more novel traits, additional work may need to be done together with growers to help them learn how to manage the crop with the novel trait.

The notion of an unimpeded flow, as suggested by the image of a 'pipeline', is perhaps misleading. Better metaphors still capturing the notion of a dynamic flow might be an 'R&D funnel' or an 'R&D sieve'. The R&D process—whether in crop breeding or biotechnology or, really, any field of technology—consists of progressive acts of selection. The initial large set of potential innovations considered early in the R&D process is, throughout the process, continually winnowed, filtered, and narrowed down.

2.1 Managing R&D Risks

Decisions are routinely made by scientists, managers, and their fund-providers—both in the private sector and in the public sector—as to whether to proceed with, modify, or terminate particular innovations at each successive stage of R&D. Those who are responsible for making such decisions—again, in both private and public sectors—are essentially engaged in an exercise of calculating the expected net benefits (expected benefits minus expected costs, to all relevant stakeholders) of moving the innovation one more step closer to commercialization. As a result, making a decision, either way, involves risk. At a minimum, if the decision is made to terminate, potentially large future private and social returns may be foregone (had the commercialization of the innovation succeeded). On the other hand, if the decision is made to proceed further, those further investments may be lost (if the innovation is later terminated or its commercialization does not succeed). In addition, liabilities may be incurred if the innovation somehow causes damages or losses to others.

Typically, the degree of uncertainty confronted is greatest early in the R&D process and decreases as the innovation progresses towards market and more is learned. There may be significant value gained in moving an innovation one step closer to market, precisely because of the learning that results in thereby reducing risk, sometimes referred to in the business world as ‘buying down the risk’ of a larger stream of future investments. There may also be value in simply ‘buying time’ for an innovation and keeping options open. This is particularly true if stopping and re-starting an R&D project and the associated redeployments of key personnel and physical resources, is costly or unfeasible. Finally, it should be noted that, at any given point in time, risk calculations about whether to further invest in or to terminate an R&D project, are made looking forward and considering future risks and opportunities for the innovation. R&D managers should not regard the size of prior investment that has already been made to bring the innovation to its current stage. These are ‘sunk’ costs. Of course, without them, the innovation would not have been brought this far, but having done so, they should no longer factor into how much further there is to go. Nor do past investments factor into the uncertainties faced further down the pipeline.

2.2 Four Types of Uncertainties

There are four primary types of uncertainties to be managed in crop genetic R&D: technological, intellectual property, regulatory, and market. Properly managing each of these requires specialized expertise and tends to be the purview of different types of professionals. All four, however, interact extensively, thus requiring ultimately a comprehensive management strategy by those ultimately responsible for the R&D and commercialization of a new variety.

2.2.1 Technological Uncertainty

The first is technological uncertainty, not knowing whether the genetic innovation would work under increasingly realistic conditions and achieve desired performance parameters. Since this is the primary expertise of the molecular biologists, breeders, and agronomists at the core of any agricultural research organization or seed company, it is typically well addressed. Of course, until technical uncertainties are overcome, the R&D process does not progress, but once targeted technical issues are resolved, technological uncertainty can be greatly diminished in the later stages of R&D, unless IP or regulatory issues arise that require changes in the technology. New technological uncertainties can arise once a variety is commercialized and is being grown under more diverse field conditions and farming practices.

2.2.2 Intellectual Property Uncertainty

The second form of uncertainty involves intellectual property (IP) rights. The most fundamental concern whether a new variety—or a genetic component incorporated into a variety—might infringe another's IP rights and the likelihood that the owner would seek to enforce his IP rights against the infringing variety. If so, R&D or commercial use of the variety may need to be terminated, resulting in a loss of investments and potential benefits. However, it may be possible to negotiate a license to use the protected technology, but the outcomes of such negotiations, such as the terms of license and the cost of royalties, can be uncertain (Cahoon 2007; Nilsson 2007; Satyanarayana 2007). On the other hand, uncertainties also arise when seeking to obtain one's own IP rights over new technologies invented or new varieties developed or to enforce them. There are questions as to costs of pursuing IP rights, when or whether an application will be granted, as well as questions about the strength and enforceability of an IP right even if granted, as this can depend upon a range of legal issues (Livne 2007). Moreover, IP rights are country-or jurisdiction-specific. (Some regions, such as Europe, have multi-country patent offices). IP issues that arise in one market may not be relevant in another (Yin et al. 2007). Yet, such variations in IP coverage, can potentially affect international trade in agricultural products resulting from protected varieties (Binenbaum et al. 2003). Intellectual property uncertainty is of little concern in the early stages of R&D, particularly in the public sector, and, as such, many breeders and geneticists engaged in the discovery and proof-of-concept stages, tend to give it little consideration; however, IP becomes progressively more important as decisions are made to move a genetic innovation closer to market, particularly when larger investments are required to do so (Fenton et al. 2007). Moreover, public sector innovators may not have the legal expertise or resources needed to manage IP uncertainty, whether to thoroughly examine the extent to which an innovation enjoys freedom to operate with regards to others' IP rights (Krattiger et al. 2007), to make effective applications to obtain IP rights to support further private investment in a genetic innovation, or to assure public access to a new genetic innovation (Nelsen et al. 2007) depending upon the goals of the R&D organization.

2.2.3 Regulatory Uncertainty

The third type of uncertainty is *regulatory* uncertainty: This means not knowing when or whether an innovation will be approved by regulators for market release, or what costs may be incurred to meet the testing and data required for regulatory review. There also may be penalties imposed or liabilities incurred in the event of a regulatory violation. In one example, in 2001 the French-German company, Aventis, incurred hundreds of millions of dollars in fines, damages, and recall costs for releasing a transgenic *Bt* corn variety '*StarLink'* in the US market without having all the required regulatory approvals (Taylor and Tick 2001). Most countries regulate transgenic crops carefully, addressing bio-safety concerns such as environmental, human health, animal health, plant pest, as well as economic concerns such as value of exports (given that trade partners, also regulating such crops, may not accept some as imports). In the countries that have not yet adopted and implemented a functioning bio-safety regulatory framework, the presumption is effectively universal that no transgenic crops should be grown until the regulations can be implemented and transgenic varieties approved. Crop varieties developed using a breeding approach, confront far less regulations, thus greatly reducing if not eliminating regulatory uncertainty (and costs). In some countries, such as Canada, bio-safety regulations are being applied to novel traits resulting from other, non-transgenic methods such as mutagenesis.

2.2.4 Market Uncertainty

The fourth and ultimately most important type of uncertainty confronted in managing R&D is the one that arises from the market, reflecting a range of unknown factors that the resulting innovation will face once commercialized. In the marketplace, a new crop variety is subjected to the independent decisions of thousands of farmers. They ultimately are the decision-makers who decide whether or not the variety is appropriate for their farming operations. These decisions by farmers depend upon a host of technical, economic, legal, and other considerations that can only be partially anticipated during the controlled pre-market stages of R&D. How well will the variety actually perform? What will growing conditions be like? What will the weather be like? What competing varieties are in the market? The market exerts very real selective pressure of its own, whereby those varieties that prove unfit in