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Achieving sustainable cultivation of rice

Volume 1: Breeding for higher yield and quality

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Introduction

Rice (*Oryza sativa* L.) is a principal food for 3 billion people, providing up to 23% of calorie requirements worldwide. Rice is cultivated in more than 100 countries across the world on around 154 million hectares annually, equal to 11% of the world's cultivable land. At present, the increase in rice production rate (at under 1% per year) is lower than the increase in population of 1.5% per year. The rice community faces the challenge of increasing rice production by 25-50% over the next thirty years, in the face of a rising population, plateauing rice yields, pressures on land and other resources available for rice cultivation and an unstable, changing climate. The two volumes of *Achieving sustainable cultivation of rice* summarise some of the key research addressing those challenges. This volume (Volume 1) reviews developments in breeding to improve yields as well as research on improving nutritional and other aspects of quality. Volume 2 focusses on developments in cultivation techniques and pest management in making production more efficient and sustainable.

Part 1 Rice breeding

While modern rice breeding has been tremendously successful in raising yields to help feed a growing population, breeding strategies of the past are no longer viable for the future. It is generally agreed that the Green Revolution resulted in a relatively small number of genetically related, high-yielding semi-dwarf rice varieties, largely replacing the mosaic of lower-yielding, but genetically diverse landraces that once characterised the rice production environments in those regions. As a result, it is estimated that the modern cultivars have retained only 10 to 20% of the genome diversity that was present in the progenitor species *O. rufipogon*. This narrower genetic base has made it more difficult to sustain increases in yields, and is also vulnerable to a range of biotic and abiotic stresses exacerbated by the effects of climate change.

To address the challenges to sustainability that come with the increasing instability of rice growing environments throughout the world, rice breeders need to expand the germplasm base with which they work and consciously bring in genetic variation from diverse sources to provide durable forms of pest and disease resistance as well as tolerance to a multitude of environmental stresses, including drought, flooding, salinity, extreme soil pH, micronutrient toxicity or deficiency. In addition, the pressures of a growing population mean adopting methods that allow for greater flexibility, reduced breeding cycle time and more efficient use of genetic variation than in the past.

Chapter 1 discusses sources of genetic diversity in rice and how breeders can utilise new tools and strategies to strategically access that diversity for variety improvement. As the chapter points out, within the *Oryza* genus, there are six species complexes, containing two domesticated species: Asian rice (*O. sativa*) and African rice (*O. glaberrima*), and over 20 extant wild species, which show wide variation in plant morphology, range of habitats and tolerance to biotic and abiotic stresses. There is further variation within each complex. As an example, the five different subpopulations of *O. sativa* demonstrate different levels of genetic variation and different alleles and allele combinations that contribute to local adaptation, stress tolerance and grain quality characteristics.

As discussed in more detail in Chapter 3, many studies have identified beneficial alleles in wild *Oryza* species. To better work with wild relatives, breeders have defined primary (*O. sativa* complex), secondary (*O. officinalis* complex) and tertiary gene pools based on species crossability. Gene banks serve as one of the most accessible sources of this genetic diversity. Up until now it has not been feasible to screen large numbers of accessions either genotypically or phenotypically to identify alleles that might contribute useful variation. However, with the rapid decline in the cost of next-generation sequencing and the establishment of high-throughput genotyping facilities capable of processing tens of thousands of breeding lines, it could soon be possible to genotype the majority of accessions used in variety improvement. Genotypic information can be used to provide a unique genetic tag for every accession in a gene bank, enabling scientists to index the bank's entire contents and develop an online database of genetic signatures. The purpose of such a database is to provide a unique identifier for each accession, to quantify the genetic relationships (kinship) among accessions, and to provide the basis for unravelling genotype–phenotype relationships which are key to the discovery of useful genetic variation for breeding.

The chapter discusses initiatives to achieve this outcome such as the *Oryza* Map Alignment (OMAP) project to sequence wild relatives of rice and other projects focussed on the sequencing of diverse varieties of *O. sativa* and, in particular, *O. glaberrima* as an underexploited source of natural variation. However, it is clear that individual projects have resulted in duplication of effort and information. As the chapter argues, a public repository of rice genomic information is urgently needed to document molecular variation, to link genotypes with specific germplasm resources, and to help annotate the functional significance of discrete molecular variants. To make genomic information useful for applications in plant improvement, a significant investment in phenotyping will also be required as well as investment in a database linking the phenotypic information to specific germplasm accessions and genotypes in a way that is easily searchable. Strategic phenotyping will provide the foundation for establishing genotype–phenotype relationships and predictive models for trait improvement. A recent initiative to take this forward is the 3000 Rice Genomes Project which re-sequenced 3000 rice accessions from 89 countries to allow large-scale investigation of novel alleles by researchers around the world.

An important strategy for broadening the genetic base of breeding populations is the establishment of large, pre-breeding programmes. Pre-breeding refers to the development of new base populations or intermediate breeding populations derived from wide crosses between wild or exotic germplasm and elite breeding materials. The purpose of pre-breeding programmes is to facilitate the screening and selection of favourable recombinants in advanced breeding backgrounds without disrupting the normal breeding programme. These programmes can be accomplished using a combination of conventional and molecular plant breeding strategies, including tissue culture. Marker-assisted selection (MAS) techniques have been invaluable in pre-breeding programmes for selecting recombinant individuals that retain only very small pieces of exotic donor chromosomes, thus vastly reducing linkage drag and the overall time required for pre-breeding. The chapter also reviews the most common types of structured population crosses used for recombining natural variation, including bi-parental quantitative trait loci (QTL) mapping populations, interspecific advance backcross-QTL populations (BC-QTL/near-isogenic lines/NIL populations), chromosome segment substitution line populations and multi-parent advanced generation inter-cross (MAGIC) populations.

In rice, most traits are governed by a combination of a few genes of large effect and many genes of small effect. Historically, rice breeders have concentrated trait-based selection on favourable alleles of large effect, either via traditional pedigree breeding, phenotypic backcrossing or MAS. However, with the advent of next-generation sequencing, high-resolution genotyping and big data analysis methods, the contribution of small effect alleles to quantitatively inherited phenotypes is gaining recognition. The potential to methodically recombine many alleles of small effect using genomic selection (GS) is rapidly gaining traction as a way of enhancing the rate of genetic gain in many crops, including rice. GS offers an alternative to traditional MAS by allowing for selection based on an infinite number of loci across the genome. It has the potential to reduce breeding time by increasing the proportion of high-performing offspring in a breeding population, thus accelerating gain from selection.

Building on Chapter 1, Chapter 2 discusses developments in MAS in more detail. As the chapter shows, the sequencing of the rice genome is allowing rice geneticists and breeders to unlock the biological functions of more than 50,000 predicted genes in order to revolutionise rice breeding in the twenty-first century. The advent of molecular markers has made it possible to dissect the genetic basis of more complex traits and use functional DNA markers to monitor the introgression of the gene of interest into target cultivars for improvement. The chapter begins by reviewing the development of different types of markers, including the use of high-density single-nucleotide polymorphism (SNP) markers to locate the position of QTLs for particular traits. As the chapter shows, thousands of QTLs have been identified for traits such as grain number and size, panicle architecture, stem/lodging tolerance, submergence and drought tolerance. Developments such as SNP chips, DaRT and genotype-by-sequencing technologies facilitate precise transfer of the genes with greater efficiency in less time.

MAS involves the indirect selection of target traits using molecular markers linked to genes responsible for an agricultural trait. The applicability of DNA markers in MAS depends on the reliability of the marker, template DNA requirement, means of marker assay, level of polymorphism and costs. Given the advantages of MAS compared to phenotypic screening, it has found several applications in rice including genotype identity testing, genetic diversity analysis of breeding materials, gene surveys in parental material, marker-evaluated selection, marker-assisted backcrossing (MABC) and marker-assisted pyramiding (MAP). The chapter reviews developments in MABC and MAP in particular. To date, MAS has been successfully used in rice breeding to selectively transfer major genes/QTLs controlling abiotic stress tolerance including salt, drought and submergence tolerance, pest and disease resistance, yield and grain quality.

To illustrate its contribution, the chapter includes a case study on improving flood tolerance in rice. As early as the 1970s, landraces such as FR13A and FR43B were identified to have tolerance to transient complete submergence. Use of DNA markers and linkage mapping identified a locus for submergence tolerance, designated as *Sub1*, near the centromeric region of chromosome 9 of FR13A. High-resolution mapping identified ethylene response factor-like genes such as *Sub1A*, which could then be introduced into target varieties by MAS. Before the identification of the *Sub1* locus, conventional breeding for submergence tolerance from FR13A to target varieties have been slow (up to 10 years) and had limited success. Identification of *Sub1A* made identification of lines carrying the target trait possible even at early generations, reducing the number of plants for backcrossing and accelerated the selection process to around two years, thereby increasing genetic gain per unit time.

Echoing Chapter 1, the chapter concludes by discussing genome-wide association studies (GWAS) and GS as two emerging genomics-based breeding strategies that promise to take breeding to the next stage of development. Both methods have the potential to deliver genetic gains by speeding the whole process of varietal improvement and dissemination to target regions. GWAS has emerged as an alternative to traditional linkage analysis by using a set of diverse, unrelated germplasm to identify associations between markers and traits of interest. In rice, the availability of a high-quality reference genome, abundance of germplasm and self-fertilising nature of the crop make it an ideal candidate for GWAS applications. With GWAS application becoming commonplace in gene/QTL discovery and mapping, the challenge for breeders now is in determining how information derived from such studies can be directly utilised for MAS and/or GS in applied breeding programmes.

As indicated in Chapter 1, the application of MAS in rice breeding has been mostly effective in the incorporation of traits that are controlled by major genes or QTLs with a known association to a marker. However, not all traits of agronomic importance are controlled by major genes/QTLs but by many genes with small, additive effects. Unlike MAS which utilises a defined set of markers associated with a trait for selection, GS uses all available marker (i.e. SNP) data across the genome and feeds it into a prediction model that would then estimate the genome-estimated breeding value of an individual in a breeding population. To date, results of GS simulation and cross-validation studies have not been evaluated in actual rice breeding programmes. The shift to practical application will require significant investment in resources to set up both genotyping and phenotyping pipelines needed for genome-wide selection.

Building on both Chapters 1 and 2, Chapter 3 focusses specifically on ways of improving rice yields, providing a context for Chapters 4 and 5. Yield gain can be significantly enhanced by fine-tuning aspects of plant architecture such as height, productive tiller number and main culm/stem diameter. The chapter reviews research identifying genes such as *SPL14* for primary and secondary branching of the panicle and panicle length; *SCM2* for increasing stem diameter; and the *Gn1a*, *DEP1* and *DEP3* genes for grain number and panicle size. Echoing Chapter 1, the chapter points out the particular importance of wild rice species as a source of these beneficial traits, and research to identify yield-related traits such as culm/stem length, panicle length and number, spikelets per panicle as well as grain thickness, weight and length. The chapter then focusses on genes relating to three traits which particularly influence yield: grain size and weight, number of grains per panicle and number of panicles per plant. As an example, it explores how researchers have pyramided different QTLs (including the gene *GS5*, which affects grain size, filling and weight), with F3 and F4 plants, using a set of SSR and InDel markers and NGS data, demonstrating better yield than the elite parents.

The chapter looks at developments and challenges in hybrid breeding as one method for exploiting wild varieties. Research suggests the potential to increase heterosis if more diverse parents are crossed. The chapter reviews research addressing limitations such as partial hybrid sterility and loss of vigour in future generations, requiring fresh F₁ seeds to be produced each season to maintain a high level of heterosis and the need to maintain two or three separate populations to produce hybrid seeds. The chapter discusses developments such as the identification of wide compatibility alleles and embryo rescue techniques to improve the success of wild *Oryza* breeding programmes. Other developments include the use of SNP chips and MAGIC populations to increase genetic variation and diversity through shuffling a wide range of genomes to promote identification of beneficial alleles.

Picking up from Chapter 3, Chapter 4 reviews ways of improving photosynthesis in rice. This is an important area of research not just in improving plant efficiency and yields but also in helping rice to adapt to increases in atmospheric CO₂ associated with global warming. As the chapter shows, with recent advances in the understanding of the photosynthetic biochemistry and physics of light harvesting, new strategies for improving photosynthesis are being evaluated in numerous C₃ crops, including rice. In particular, with improved understanding of photosynthetic limitation, it is now possible to target those genes that overcome these limitations. The chapter starts by summarising research on the biochemical limitations establishing the demand for CO₂ within C₃ leaves. Demand-based biochemical limitations include capacity limitations in the enzyme Rubisco which catalyses the fixation of CO₂, regeneration of ribulose biphosphate (RuBP) and the effects of photorespiration. Supply-side limitations include impediments to CO₂ diffusion through the boundary layer to the chloroplast.

The chapter goes on to review three key strategies in development for improving photosynthesis in C₃ plants. The first is to exploit existing variation in rice using QTL analysis in order to identify genetic regions that increase photosynthetic capacity. This approach is already showing promise and may lead to discoveries of unknown regulatory and development genes that could enhance photosynthesis and whole plant performance. The chapter explores developments in identifying QTL by either direct measurement of photosynthesis or indirect determination of phenotypic values of traits related to photosynthesis. These include 'phenomic' platforms which use sensors and imaging programmes to measure attributes such as leaf fluorescence, colour and temperature, and plant size and morphology which can be related to photosynthetic performance.

Since C₃ plants underperform at elevated CO₂ levels, a second strategy is to re-engineer C₃ photosynthesis in the rice plant in order to adapt it to the predicted increase in atmospheric CO₂. Approaches here include reducing Rubisco expression and overexpressing RuBP regeneration components. The final strategy reviewed is the significant challenge of introducing C₄ photosynthesis into rice. Engineering the C₄ pathway into C₃ plants has long been a dream of photosynthetic biologists since C₄ plants have been shown to demonstrate yield enhancements and resource use efficiency improvements of 40–60% relative to C₃ plants. As such, successfully engineering C₄ photosynthesis into rice represents a giant leap that could meet the world's rice demands well into the future. However, as the chapter points out, C₄ engineering is a considerable challenge given the complexity of the genetic controls over the C₄ pathway, many of which are not fully understood. To fully implement the C₄ pathway into a C₃ species such as rice, a range of changes will be required to leaf and organelle structure, metabolism and transport capabilities. The chapter reviews achievements so far such as successfully stacking the C₄ cycle genes into rice, developing a working model of Kranz leaf development, putting in place a multi-pronged gene discovery effort using the latest sequencing technologies and developing C₄ plants that can serve as genetic models. There is good reason to believe it will be possible to engineer a C₄-Rice prototype within the next decade.

Sustainable rice production requires new types of rice cultivars in specific target population environments (TPE) that combine high yield potential with greatly improved nutrient and water use efficiency (WUE) and tolerance/resistance to multiple abiotic/biotic stresses specific to each TPE. First proposed in China, Green Super Rice (GSR) is defined as rice cultivars able to produce high and stable yield with less inputs. Early breeding initiatives focussed primarily on drought tolerance/WUE and N/P use efficiency, but the scope has been broadened to promote high overall resource use efficiency to achieve more sustainable cultivation.

To address the challenge of breeding for multiple traits, the chapter describes the development of a modified backcross (BC) breeding procedure which can be easily adopted by small breeding programmes. This approach has allowed the development within a period of 5 years of large numbers of promising GSR lines with good tolerance to multiple abiotic/biotic stresses (in both rainfed and irrigated condition) from a small number of breeding populations. The shuttle breeding and molecular recurrent selection breeding strategy involves four major activities: (1) developing segregating BC populations by crossing elite widely adaptable recipients with a diverse set of donors, (2) strong phenotypic selection and progeny testing of the BCF_2 populations under multiple stresses, (3) QTL/QTL network discovery by genetic characterisation of selected introgression lines using high-throughput genotyping and (4) development of superior GSR varieties by designed QTL pyramiding or by molecular recurrent selection. As the chapter shows, the superior performance of many GSR varieties has been well demonstrated in the field trials under both irrigated and rainfed conditions at the IRRRI and in many target countries across Asia and Africa. Amongst other things, this breeding strategy suggests there is sufficient diversity in the primary gene pool to improve abiotic stress tolerance, and that selecting appropriate recurrent parent(s) with high yield potential and wide adaptability to the target environments is the key for success for improving complex traits in a BC breeding programme, since a widely adaptable variety must have key adaptive traits and pathways to most environments.

The final chapter in Part 1 looks at the key topic of drought tolerance in rice. As a water-loving crop, rice can be severely affected by drought stress. It is especially sensitive to drought stress during reproductive growth and even moderate stress can result in drastic reduction in grain yield (GY). Drought resistance is a complex trait whose effect depends on the action and interaction of different morphological, biochemical and physiological responses. Research suggests that drought resistance in rice mainly relies on WUE that allows minimum water usage for maximum production and osmotic adjustment that enables plants to maintain turgor and protect the meristem.

The chapter reviews studies identifying major QTLs related to GY under water-limited conditions in rice. An example is *qDTY12.1* which has an effect on a range of traits such as flowering, plant height, biomass and panicle number which influence GY under drought conditions. Physiological parameters like maintenance of water potential using deeper rooting system, synchronised modulation of metabolic processes, and the level of osmolytes and antioxidants are also key factors in selection for drought tolerance, together with endogenous levels of phytohormones. The chapter reviews research identifying QTLs relating to deep rooting and drought-protective genes such as protein kinases, late embryogenesis abundant proteins, antioxidant enzymes and osmolytes. Research has also highlighted a central role for major phytohormones such as abscisic acid, cytokinin (CK), gibberellic acid, auxin, ethylene and jasmonic acid in regulating plant growth and development as well as drought stress response. Genetic engineering by transformation of rice plants using modified gene constructs has also provided genetic evidence of drought tolerance components that can serve as models for development of cultivars with improved yield potential. The chapter looks at a range of transcription factors related to drought tolerance, such as the AP2/ERF transcription factor, *HYR* (HIGHER YIELD RICE) associated with photosynthetic carbon metabolism. Overexpression of *HYR* enhanced photosynthesis, contributing to higher GY under drought stressed conditions. The chapter concludes by highlighting the need for more research on the mechanisms underlying drought response in rice.

Part 2 Rice nutritional and processing quality

Chapter 7 introduces Part 2 by providing an overview of the role of rice in nutrition, providing a context for Chapters 9 and 10, in particular. As the chapter points out, malnutrition includes both under- and over-nutrition. Under-nutrition refers to dietary deficiency of key nutrients, including calories and micronutrients. Many studies have shown that unpolished rice contains high levels of minerals, many essential vitamins and a host of other phytochemicals, but once the bran is removed and the grains are white, the mineral and vitamin content is very low. Research has therefore focussed on biofortification of polished rice which remains a staple in many countries, focussing on iron, zinc and β -carotene. Whilst there has been some success in using conventional breeding to fortify rice with zinc, for example, much research has focussed on the use of biotechnology. Examples include manipulation of the expression of NA synthase (*NAS*) genes to increase the iron content of rice grains or to increase β -carotene to combat the serious effects of vitamin A deficiency (VAD).

The chapter also highlights the less-studied area of rice's role in over-nutrition, a condition where adequate calories are available but their dietary quality is poor. In combination with other lifestyle factors, over-nutrition can lead to obesity, diabetes and a host of other chronic diseases. Factors such as the type of carbohydrate, glycaemic index (GI) and starch digestibility are all implicated in the prevention and management of chronic disease. Research suggests, for example, that there is diversity in the GI of different rice varieties, and that low GI rice leads to a smaller glycaemic response, but that little work has been done so far to explore varieties of rice that might assist with managing blood sugar status.

Building on Chapter 7, Chapter 8 looks in more detail at nutrients and phytochemicals present in rice. As it shows, the genetic differences between cultivated varieties of rice contribute greatly to variations in nutritional content, for example, carbohydrate content, concentrations of iron and zinc, lipid, vitamin E and phenolic acid content, with pigmented rice having higher concentrations than white rice, for example. The chapter reviews current research on the major health-promoting components in rice, including sterols, oryzanols, tocopherols, tocotrienols and phenolic compounds such as flavonoids. It also discusses newly discovered phytochemical compounds such as γ -oryzanol, isoferulic, syringic and chlorogenic acids. As research shows, the differential chemopreventive bioactivities of rice against chronic diseases such as cancer are positively correlated with the presence of phytochemicals such as phenols and flavonoids, especially in the bran and hull from pigmented rice.

The chapter also looks at ways of preserving or enhancing nutritional and nutraceutical properties of rice, including the use of both conventional and transgenic techniques for biofortification, a theme which is explored in more detail in Chapters 9 and 10. It also summarises research on the effects of growing conditions and cultivation techniques on nutritional content, for example, on the way the germinating process can increase the nutritional value of rice seeds, a theme which is picked up in more detail in Chapter 12. Finally, it assesses what we know about the effects of processing techniques such as dehulling and milling as well as cooking on the nutritional value of rice, emphasising the benefits of consuming whole rice or partially milled rice. As the chapter shows, there is still much more to be done in these areas and in better understanding of health benefits *in vivo*.

As Chapter 9 points out, VAD has been recognised as a significant public health problem for more than a quarter of a century. It has been estimated that a universally available source of vitamin A could, for example, save 23–34% of all deaths of children under 5 years globally. Whilst the varied diets in industrialised countries include sufficient sources of provitamin A carotenoids, many populations in the developing world are not able to access such balanced diets. The chapter reviews the various methods of supplementation, their strengths and weaknesses, before concluding that biofortification of a staple crop such as rice is the most sustainable option. It then reviews the alternatives for producing a provitamin A rice such as using traditional breeding or mutagenesis, none of which has proved viable, leaving the option of genetic engineering. It describes the origins and development of provitamin A Golden Rice to the stage of field trials. However, as the chapter points out, continued opposition to Golden Rice on the grounds that it involves genetic modification has proved a serious impediment to its final approval and use.

Chapter 9 is complemented by Chapter 10 which focusses on the development of rice varieties with improved grain iron content. Iron deficiency anaemia (IDA), together with vitamin A, iodine and zinc deficiencies, is the most common form of micronutrient malnutrition globally. IDA is widespread in both developing and developed countries. Several possible strategies have been suggested for combating the deficiency in affected populations. These include education about appropriate dietary habits, iron supplementation of specific groups at high risk, fortification of foods and biofortification (i.e. production of nutrient-enriched crops). The latter has been suggested as a sustainable approach to address micronutrient deficiencies worldwide. However, as indicated in Chapter 9, screening has shown that rice germplasm has a very low diversity for the key micronutrients. Given this insufficient natural genetic variation in the endosperm iron levels in rice, increasing iron levels through conventional breeding has not been possible, leading researchers to explore transgenic approaches.

The chapter starts by reviewing what we know about the molecular mechanisms controlling iron uptake and the transporters and chelators necessary for effective iron translocation within the plant. Gene technology approaches have focussed on transformation of genes involved in iron uptake, transport and storage in the endosperm. Different approaches have included increasing iron stores in the rice endosperm and improving bioavailability, modifying genes involved in iron uptake and translocation and strategies focussing on concerted expression of multiple genes. However, as the chapter points out, iron biofortification of rice endosperm has proved challenging, with the majority of approaches tested so far not generating rice lines that meet the target iron levels set by the HarvestPlus programme. Studies suggest the presence of strong physiological/molecular barriers that limit iron transport into the grain and/or endosperm. Research still needs to clarify the speciation of iron forms and chelators, the contribution of each type of transporter, and the precise iron flux for each translocation step. Biofortification strategies need to explore candidate genes that can increase the availability of free iron for transport and storage into the grains, in addition to promoting effective translocation within the plant.

Rice processing quality parameters are designed to assess the suitability of particular rice varieties in meeting processing and/or consumer quality traits. There are several common challenges to ensure rice processing quality parameters and testing are relevant and robust. These include an understanding of consumer needs and technology that satisfies needs across the industry. As Chapter 11 points out, the effective measurement of quality is critical to breeders and growers if the industry is to deliver a consistent product to the

consumer. As the chapter points out, there is often a relatively short period between rice harvest and rice sowing available to conduct rice quality evaluations and make selection decisions on the next generation of cultivars.

Rice quality characteristics typically assessed for uncooked grains include grain dimension, chalkiness, colour, composition and milling performance and, for cooked grains, include elongation, texture and digestibility. Composition of the grain is often limited to amylose content and nitrogen content as a proxy to protein content. Sulphur content is also measured. Functional parameters typically measured are viscosity, fragrance, texture and gelatinisation temperature, and more recently GI and antioxidant content. Chapter 11 reviews the development of newer techniques such as the use of capillary electrophoresis to determine amylose: amylopectin ratio in rice and the development of HPLC separation techniques able to distinguish varieties of different quality classes of rice. It also reviews ongoing challenges such as the need to improve measurement of protein and lipid content, and improve the assessment of physical grain quality. There is also a need to develop good phenotype screening across a broad range of parameters to fast track the development of new and resilient varieties.

As Chapter 11 points out, it has been long established that high growth temperatures can alter grain quality attributes including increased chalk, protein content and gelatinisation temperature, and decreased amylose content. Research also shows head rice yield is influenced by factors such as nitrogen fertilisation, harvest moisture and wet/dry cycles. Chapter 12 builds on Chapter 11 by reviewing how cultivation conditions affect rice quality. Cultivation practices include sowing, transplantation and harvesting dates, as well as irrigation, fertiliser use and tillage systems. As an example, delayed sowing and transplantation times can significantly influence leaf area index, light extinction coefficient and filled spikelets growth, and thus reduce GY. Delayed planting and transplanting also results in lower amylose and lipids content as well as pasting parameters such as decreased peak viscosity and lower grain hardness for textural quality. Chapter 11 reviews the effects of sowing, transplantation and harvesting dates; the impact of irrigation; fertiliser application; and other aspects of cultivation (such as planting density). It also assesses the potential effects of elevated temperature and other aspects of climate change (such as water availability elevated atmospheric levels of CO₂). Finally, it reviews the impact of organic cultivation on rice quality as an effective, sustainable technique for producing high-quality rice.

Summary

The chapters in this volume demonstrate the impressive range of research addressing how rice cultivation can continue to feed a growing population in a more sustainable way. They show the key importance of broadening the genetic base for rice in breeding, and the need for more coordinated documentation of molecular variation, linking of genotypes with specific germplasm resources and annotation of the functional significance of discrete molecular variants. They also show the advances that have been made in exploiting the broader genetic base, for example in the use of MAS to improve pre-breeding programmes or the use of molecular techniques in back crossing to produce improved varieties of GSR. They show the potential of newer techniques such as GS in improving traits determined by a number of genes with small additive effects. The chapters demonstrate the need for

a better understanding of these effects, and for more fundamental research to understand complex traits such as photosynthesis and response to drought in rice. There is clearly an urgent need for more research on ways of preserving and enhancing the nutritional and nutraceutical properties of rice to address both the problems of under-nutrition, in such areas as iron and VAD, as well as over-nutrition, an area which also takes in the wider debate about the use of genetic engineering in food production. Finally, chapters of this volume highlight key factors involved in achieving and maintaining consistent quality, including the role of cultivation. This theme is taken up in Volume 2.

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