GENETIC RESOURCES, CHROMOSOME ENGINEERING, AND CROP IMPROVEMENT SERIES

Volume 2

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Cereals

EDITED BY
RAM J. SINGH AND PREM P. JAUHAR

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Series Editor, Ram J. Singh

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Dedication

And, he gave it for his opinion that whoever could make two ears of corn or two blades of grass to grow upon a spot of land where only one grew before, would deserve better of mankind, and do more essential service to humanity, than the full race of politicians put together.

—Swift

Our efforts in the preparation of this volume are dedicated to our wives but for whose patience and sacrifice this volume would not have been completed.

—The Editors

Preface

Cereal crops — chiefly wheat, rice, maize, sorghum, and pearl millet — are the main food source for more than two thirds of the world population. From time immemorial humans have relied heavily on cereals for their dietary carbohydrates. Thus, cereals have had a profound impact on the development of human societies and influenced civilization — perhaps in more ways than any other group of crops. Ancient Egyptian tomb paintings depict cultivation of wheat and harvesting and grinding of wheat grain to make bread. Today, cereals supply over 80% of the dietary protein for most Asian and African countries. Being devoid of cholesterol, cereal grains provide wholesome food for human consumption, and there is an inverse association between intake of whole grains and cardiovascular disease (simin.liu@channing.harvard.edu). Severe protein malnutrition among the poor masses in Asian and African countries, where cereals constitute the staple human diet, is a serious problem of alarming proportions. Some 842 million people worldwide are malnourished (fao.org/newsroom/en/news/2004), and this number is likely to increase with the projected increase in human population from 6.1 billion to 8.0 billion by 2030. To meet the ever-increasing demand for food, genetic improvement of grain yields and nutritive value of cereal crops cannot be adequately emphasized.

Most improvement in cereal crops has been achieved so far through conventional breeding, aided to some extent by knowledge from agronomy, cytogenetics, plant pathology, entomology, and related disciplines. The improved wheat and rice cultivars in the 1960s and 1970s launched the Green Revolution, averting starvation among the poor masses in Asia. Sustained improvement in grain yields and nutritional quality must remain the ultimate goal of plant scientists to ensure global food security. Continued crop improvement will necessitate the employment of all available tools: germplasm collection and conservation, conventional breeding, cytogenetics, biotechnology, and molecular genetics, among others. Improving yields and nutrition of cereal crops have been the primary goals of international centers like the International Maize and Wheat Improvement Center (CIMMYT) in Mexico (maize and wheat); the International Rice Research Institute (IRRI) in the Philippines (rice); the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT) in India (sorghum and pearl millet); and the International Center for Agricultural Research in the Dry Areas (ICARDA) in Syria (barley and wheat). Because there is no consolidated account of cereal crop improvement using conventional and modern tools, we planned to assemble such a book that constitutes Volume 2 in the series "Genetic Resources, Chromosome Engineering, and Crop Improvement." This book is also an outgrowth of a symposium on "Alien Gene Transfer and Cereal Crop Improvement" that one of us (P.P.J.) organized and chaired at the Crop Science Society of America Meetings, Salt Lake City, Utah, in November 1999. We invited world-renowned scientists from several countries to contribute chapters on a cereal crop of their expertise. This volume consists of 13 chapters dealing with major cereal crops: wheat (durum wheat and bread wheat), rice, maize, oat, barley, pearl millet, sorghum, rye, and triticale.

The introductory chapter by Jauhar outlines the cytogenetic architecture of cereal crops, describes the principles and strategies of cytogenetic and breeding manipulations, and summarizes the landmarks of research done on various crops. Thus, the author has attempted to set the stage for the reader to comprehend the ensuing chapters. Each chapter generally provides a comprehensive account of the crop; its origin; wild relatives; exploitation of genetic resources in the primary, secondary, and tertiary gene pools through breeding and cytogenetic manipulation; and genetic enrichment using the tools of molecular genetics and biotechnology. Durum wheat, being the forerunner of bread wheat, is dealt with first by Ceoloni and Jauhar in Chapter 2. Chapter 3 by Mujeeb-Kazi provides details on the utilization of genetic resources for bread wheat improvement, while wheat genomics is covered by Lapitan and Jauhar in Chapter 4. In Chapter 5, Brar and Khush give a comprehensive account of genetic resources and chromosome engineering in genetic improvement of rice. Genetic enhancement of maize for yield and protein quality is dealt with in

Chapter 6 by Vasal, Riera-Lizarazu, and Jauhar. The subsequent chapters deal with oat, barley, pearl millet, sorghum, rye, and triticale.

Each chapter provides an authoritative account of the topic covered and was written by one or more experts in the field. We are privileged to have known the authors both professionally and personally and are very grateful to them for their invaluable contributions. Certain topics and research organisms are closely related, which has inevitably led to some overlap and duplication among chapters, although repetitions were minimized by giving cross-references. Each chapter can be read independently in this coherent volume on cereals.

We are also grateful to all the scientists who reviewed various chapters. Our communications with them were always cordial and friendly. We are particularly indebted to Charles Crane, Pierre Devaux, Sally Dillon, Pat Hayes, Eric Jellen, Daryl Klindworth, Mike McMullen, Richard Pickering, and Richard Cross for critically reviewing some of the chapters. Although every chapter has been appropriately reviewed by the editors and other experts in the field, the authors are ultimately responsible for the accuracy and completeness of their respective chapters. One of us (R.J.S.) expresses his gratitude to Dr. Steven G. Pueppke, Associate Dean and Research Director, University of Illinois, Urbana, for all his support and encouragement. Prem Jauhar is sincerely grateful to his wife, Raj Jauhar, for her help, patience, and understanding; she spent countless weekends and evenings at home alone when he was at work. But for her encourgement and unconditional support, this arduous journey would have been even more difficult.

This book is intended for scientists, professionals, and graduate students interested in genetic improvement of crops in general and cereals in particular. The book will be useful for plant breeders, agronomists, geneticists, cytogeneticists, taxonomists, evolutionists, molecular biologists, and biotechnologists. Graduate-level students in these disciplines with adequate background in genetics and a spectrum of other researchers interested in biology and agriculture will also find this volume a worthwhile reference. We sincerely hope that the information embodied in the book will help in the much-needed genetic amelioration of cereal crops to feed the ever-expanding human population. In addition, we hope that it helps to raise awareness of the importance of conserving wild genetic resources that may be exploited in improving their cultivated cereal relatives through cytogenetics and biotechnology.

Ram J. Singh
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The Editors

Ram Jag Singh, M.Sc., Ph.D., is an agronomist-plant cytogeneticist in the Department of Crop Sciences, University of Illinois at Urbana-Champaign. He received his Ph.D. degree in plant cytogenetics under the guidance of the late Professor Takumi Tsuchiya from Colorado State University, Fort Collins, Colorado. He benefited greatly from Dr. Tsuchiya's expertise in cytogenetics.

Dr. Singh conceived, planned, and conducted pioneering research related to cytogenetic problems in barley, rice, rye, wheat, and soybean. Thus, he isolated monotelotrisomics and acrotrisomics in barley, identified them by Giemsa C- and N-banding techniques, and determined chromosome arm-linkage group relationships. In soybean (*Glycine max*), he produced fertile plants with 2n = 40, 41, or 42 chromosomes, from an intersubgeneric cross between soybean and a wild species, *Glycine tomentella* (2n = 78), and obtained certain lines with resistance to the soybean cyst nematode (SCN). Singh constructed, for the first time, a soybean chromosome map based on pachytene chromosome analysis and laid the foundation for creating a global soybean map. By using fluorescent genomic *in situ* hybridization he confirmed the tetraploid origin of the soybean.

Singh has published 67 research papers, mostly in reputable international journals, including the *American Journal of Botany*, *Chromosoma*, *Crop Science*, *Genetics*, *Genome*, *Journal of Heredity*, *Plant Breeding*, and *Theoretical and Applied Genetics.* In addition, he summarized his research results by writing nine book chapters. His book *Plant Cytogenetics* is widely used for teaching graduate students. Dr. Singh has presented research findings as an invited speaker at national and international meetings. He is a member of the Crop Science Society of America and the American Society of Agronomy. In 2000, he received the Academic Professional Award for Excellence: Innovation and Creativity from the University of Illinois at Urbana-Champaign.

Prem Prakash Jauhar, M.Sc., Ph.D., is a senior research geneticist with the U.S. Department of Agriculture–Agricultural Research Service, Northern Crop Science Laboratory, Fargo, North Dakota. He also holds the position of professor of cytogenetics with North Dakota State University, Fargo. He is the principal investigator on the USDA project "Genomic Relationships in the Triticeae and Enhancement of Wheat Germplasm by Classical and Molecular Techniques."

Prem earned his Ph.D. from the Indian Agricultural Research Institute, New Delhi, in 1963 when he was appointed to the faculty of this institute, doing research and teaching cytogenetics to graduate students. From 1972 to 1975, he served as a senior scientific officer at the University College of Wales, Welsh Plant Breeding Station, Aberystwyth, Wales, U.K.

Prem Jauhar's research interests have centered on various facets of cytogenetics and biotechnology and their relevance to plant breeding. He has been particularly interested in chromosome pairing. In 1975, he discovered the regulatory mechanism that controls chromosome pairing in polyploid species of *Festuca* (*Nature* 254: 595–597, 1975) and originated the concept of hemizygous-ineffective genetic control of pairing — a phenomenon that has major implications in cytogenetics, plant breeding, and evolution. After establishing an efficient *in vitro* regeneration system for durum wheat, Jauhar's lab produced the first transgenic durum wheat and standardized the technology in 1996, paving the way for direct gene transfer into commercial durum cultivars. Jauhar is also involved in germplasm enhancement by genomic reconstruction through wide hybridization coupled with manipulation of homoeologous chromosome pairing. By transferring a part of a wild grass chromatin into the durum wheat genome, Jauhar produced durum germplasm with scab resistance.

Working on *Ph1*- and *ph1*-euhaploids in bread wheat (2n = 3x = 21; ABD genomes) and durum wheat (2n = 2x = 14; AB genomes) that he synthesized, Jauhar elucidated inter- and intragenomic relationships in these polyploid wheats. He demonstrated that the A and D genomes of bread wheat are more closely related to each other than either one is to B — a finding that contributed to the

understanding of the phylogeny of wheat. Jauhar's haploidy research produced the first clear evidence of sexual polyploidization via 2n gamete formation in durum wheat haploids (*Crop Science* 40: 1742–1749, 2000), demonstrating how polyploids are produced in nature.

Jauhar has published in international journals, including *Nature*, *Chromosoma*, *Theoretical and Applied Genetics*, *Genome*, *Journal of Heredity*, *Genetica*, *Plant Breeding*, and *Mutation Research*. He has 120 publications, including 90 research papers, 3 books (two authored and one coauthored and edited), and 17 invited book chapters. His research papers and books are used in graduate teaching and research worldwide. Jauhar has a keen interest in disseminating science and serving the scientific community. He has given invited seminars in 15 countries, organized and chaired symposia and scientific sessions at national and international conferences, and served on international advisory committees. Most recently, he was a keynote speaker at the National Symposium on Classical Cytogenetics and Modern Biotechnology organized by the Centre for Advanced Study in Cell and Chromosome Research, Calcutta University, January 24–25, 2005. He also delivered the Panchanan Maheshwari Memorial Lecture at the centennial celebrations of the legendary scientist's birth, held at Delhi University, February 15, 2005. Since 1991, Prem Jauhar has served as an associate editor of the *Journal of Heredity.*

Prem P. Jauhar has received several awards and professional recognitions. Some recent awards include his election as Fellow of the Crop Science Society of America (1995), the American Society of Agronomy (1996), and the American Association for the Advancement of Science (2002).

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Contents

CHAPTER 1

Cytogenetic Architecture of Cereal Crops and Their Manipulation to Fit Human Needs: Opportunities and Challenges

Prem P. Jauhar*

CONTENTS

Mention of trade names or commercial products in this publication is solely to provide specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

1.1 INTRODUCTION

Cereals are members of the grass family Poaceae (Gramineae), whose seeds are used for food. The word *cereal* is derived from *Ceres*, the Greek goddess of agriculture. Cereal grains have been the staple human diet since prehistoric times. The cultivation of cereals for human consumption began around 10,000 B.C., ranking them as the earliest cultivated staple food plants of many human societies. Their cultivation signified the dawn of the era of stable civilization, which replaced the primitive nomadic way of life. Common cereals are wheat (bread wheat, *Triticum aestivum* L., and durum wheat, *Triticum turgidum* L.); rice (*Oryza sativa* L.); maize (*Zea mays* L. ssp. *mays*); oats (*Avena sativa* L.); barley (*Hordeum vulgare* L.); sorghum (*Sorghum bicolor* L. Moench); pearl millet (*Pennisetum glaucum* (L.) R. Brown = *Pennisetum typhoides* (Burm.) Stapf et Hubb.); rye (*Secale cereale* L.); and the man-made cereal, triticale (*Triticosecale* Wittmack). The total world production of cereal crops was 1835.2 million tonnes in 2002–2003, and is estimated at 1886.6 million tonnes in 2003–2004 (http://faostat.fao.org). Total world acreage of major cereal crops and their production are given in Figure 1.1 and Figure 1.2, respectively. Wheat, rice, and maize are undoubtedly the most important cereals worldwide.

Currently, the cereal crops are the main food source for more than two thirds of the world population. In most Asian and African countries, cereals supply over 80% of the dietary protein. Severe malnutrition among the poor masses poses a serious problem; some 842 million people worldwide are malnourished (fao.org/newsroom/2003). To meet the ever-growing demand for food, genetic improvement of cereal crops cannot be overemphasized. Conventional breeding practiced for over a century has resulted in cultivars with high yields and superior agronomic traits. Thus, largely through exploitation of hybrid vigor, grain yields of maize, pearl millet, and sorghum registered a substantial increase from 1965 to 1990 (Khush and Baenziger 1996; Jauhar and Hanna

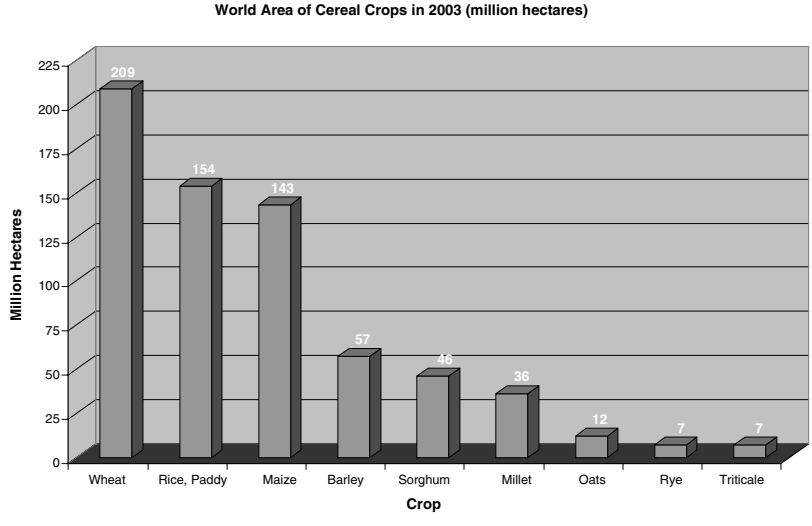

Figure 1.1 Total world area of major cereal crops in 2003. Note that wheat, rice, and maize are the most important cereals with the most acreage. Triticale, the new man-made cereal, occupies a small area. (*Source*: faostat.fao.org.)

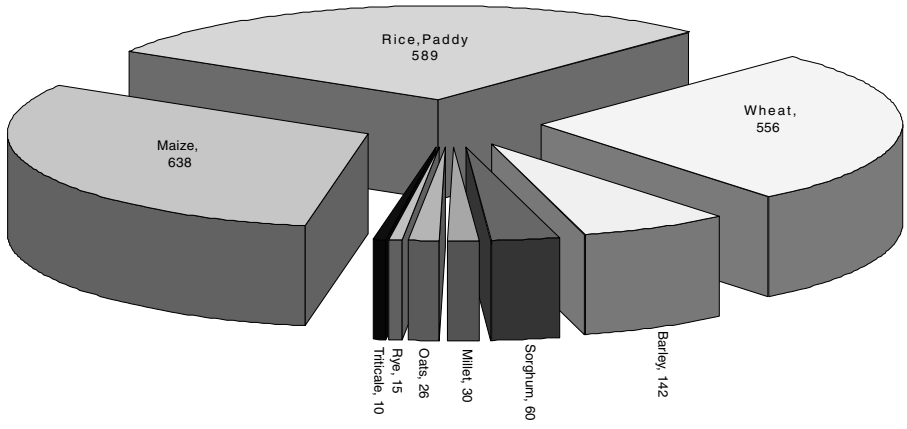

Figure 1.2 Pie diagram showing the world production of the major cereals in 2003. (*Source*: faostat.fao.org.)

1998). More remarkably, the development of semidwarf improved wheat and rice cultivars in the 1960s launched the most welcome Green Revolution in Asia, averting mass-scale starvation (Khush 1999). Sustained improvement of grain yields and nutritional status of cereal crops should remain the principal goals of crop scientists and agriculturists.

A full understanding of a crop — its genomic constitution and nature of its polyploidy, if any — is very helpful in planning breeding strategies and refining various tools for its genetic improvement. Bread wheat (AABBDD) and durum wheat (AABB) are natural hybrids, having resulted from hybridization between related wild species and doubling of chromosome number (Figure 1.3). Although their genomes (chromosome sets) are genetically similar (homoeologous), a gene, *Ph1*, on the long arm of chromosome 5B (chromosome number 5 of the B genome) ensures diploid-like pairing, i.e., pairing between homologous partners only (Riley and Chapman 1958; Sears and Okamoto 1958), which confers disomic inheritance. Oat is also an allohexaploid, and its cytogenetic architecture is similar to that of bread wheat, with genetic control of chromosome pairing (Rajhathy and Thomas 1972; Jauhar 1977) similar to the *Ph1* system of wheat. It is interesting that maize, rice, pearl millet, and sorghum have been shown to be diploidized cereals, having resulted from ancestral rounds of polyploidy (see Section 1.6). Appropriate chromosome engineering and cytogenetic manipulations have been used for the improvement of these crops.

An important threat to global food security is the occurrence of numerous diseases and pests and the emergence or introduction of new ones. Landraces and wild relatives of cereal crops are rich reservoirs of genes for resistance to diseases, pests, and abiotic stresses; these genes can be incorporated into cereal crops through hybridization. Cytogenetic manipulations, including the suppression of *Ph1*-pairing regulation for recombining desirable alien chromatin or genes into hexaploid wheat, have been termed chromosome engineering (Sears 1972, 1981). Durum wheat is less genetically buffered than bread wheat, and hence the former is less amenable to cytogenetic or chromosomal manipulation. Although other techniques of transferring alien chromatin into a crop like wheat are known, e.g., through X-irradiation (Sears 1993), the promotion of homoeologous pairing offers a more precise means of "chromosome surgery" to recombine chromosome segments, and hence a more desirable method of alien gene transfer. Some of the cytogenetic manipulations used in wheat have been fruitfully employed in hexaploid oat (see Chapter 7 by Jellen and Leggett in this volume).

This volume on cereals covers the improvement of important cereal crops utilizing all available tools: conventional breeding, chromosome engineering by interspecific hybridization coupled with manipulation of chromosome pairing, and use of molecular tools, including markers and genetic transformation. Each cereal crop has been dealt with by an expert in the field. In this introductory chapter, I have given an overview of the cytogenetic architecture of cereal crops and discussed the

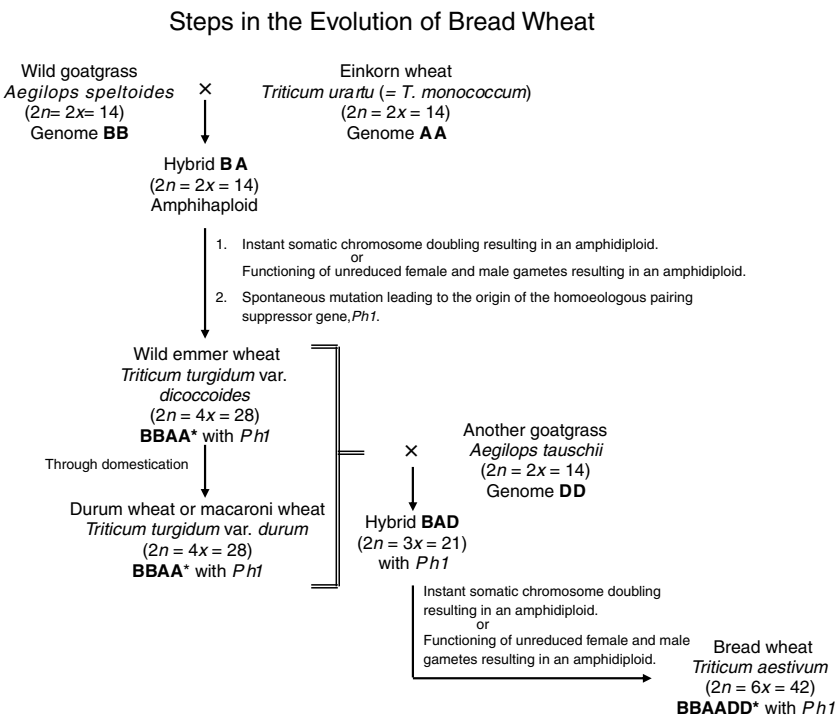

Figure 1.3 Diagram showing different steps in the evolution of bread wheat, with durum wheat as its forerunner. Note how allopolyploidy gave rise to our most important crop in a few steps of evolution.

attributes of their genomes, including size, gene density, and synteny with other cereal genomes. I have also summarized major landmark studies leading to the improvement of the major cereal crops. Subsequent chapters present the details.

1.2 CEREAL CROPS: A SOURCE OF SUSTENANCE TO HUMANKIND

Cereal crops occupy about two thirds of all cultivated land, and their importance lies in the fact that they have fair to good nutritive value and are relatively easy to grow, store, and transport. Although they are classified as carbohydrate-rich foods, they are also a major source of protein of fair to good quality in much of the world. They are in fact an important source of sustenance for humankind. Table 1.1 presents the food value (the energy, protein, and lipid content) of four important cereals compared to three major vegetable foods. Energy content depends mostly upon carbohydrate contents in these foods. Interestingly, in addition to energy figures, the protein content is higher in cereal grains than in potatoes or peas; these high values are, of course, partly due to the fact that cereal grains contain a much lower proportion of water than potatoes and peas. Even more importantly, cereals do not contain cholesterol, and there is an inverse relationship between intake of whole grains and coronary artery disease (Kushi et al. 1999). In a study over a period of 5.5 years, both total mortality and rate of occurrence of cardiovascular disease were found to be inversely associated with intakes of whole-grain but not refined-grain breakfast cereals (Liu et al. 2003).

Another important factor contributing to the worldwide importance of cereals is the large number of diverse species that can grow in different parts of the world, including temperate and tropical

Table 1.1 Comparative Values of Energy Provided, and the Total Content of Protein and Lipid in 100 g of Cereal Grains and Other Common Foods

Food Crop	Energy (kJ)	Protein (g)	Lipid (g)
Wheat	1420	12.0	2.0
Rice	1296	8.0	2.0
Maize	1471	10.0	4.0
Sorghum	1455	10.0	5.0
Potatoes	347	2.0	0.1
Peas	293	4.9	0.4
Lettuce	63	1.2	0.2

Source: http://www.cix.co.uk/.

climates, and humid and arid or semiarid regions. Thus, bread wheat, durum wheat, barley, oats, and rye are cultivated in temperate regions throughout the world. Maize grows best in hotter regions and is important in tropical and subtropical areas. Rice is mainly a crop of the wet tropics, whereas sorghum and pearl millet can survive in hot, dry conditions, such as the drought-prone Sahel of Africa. As stated above, cereal crops are of diverse origins; some are diploid while others are allopolyploids that enjoy the benefits of polyploidy and hybridity. Thus, rice, maize, barley, sorghum, pearl millet, and rye are diploid or diploidized crops, whereas bread wheat, durum wheat, and oats are obvious polyploids (allopolyploids, to be precise) (see below).

1.3 POLYPLOID CEREALS: THEIR CYTOGENETIC ARCHITECTURE

Polyploidy is recognized as a dominant factor in plant speciation (Masterson 1994; Leitch and Bennett 1997; Soltis and Soltis 1999; Jauhar 2003a). Some plant groups seem to have undergone several cycles of chromosome doubling. The proportion of angiosperms that have had one or more events of polyploidy somewhere in their ancestry lies between 50 and 70% (Stebbins 1971; Lewis 1980; Masterson 1994). Allopolyploidy or amphidiploidy, resulting from interspecific or intergeneric hybridization coupled with chromosome doubling, has in fact produced the majority of our most important crop plants, including the cereal crops — bread wheat, durum wheat, and oats.

1.3.1 Polyploid Wheats: A Model for Evolution by Allopolyploidy

Allopolyploids enjoy the benefits of both polyploidy and stable hybridity and are highly adaptable to adverse environmental conditions. The enzyme diversity coded by related genes in different genomes seems to contribute to their selective advantage and fitness (Adams and Allard 1977; see also Jauhar 2003a). Sexual polyploidization, which results from functioning of meiotically unreduced gametes, is a significant source of allopolyploids in nature (Harlan and de Wet 1975; Jauhar et al. 2000; Jauhar 2003a). Since corresponding chromosomes of different genomes are genetically similar (or homoeologous) and hence capable of pairing with one another, a genetic control restricting pairing to homologous partners would be necessary for meiotic regularity and reproductive stability of allopolyploids. Thus, sexual polyploidization and genetically regulated chromosome pairing promote the founding of successful allopolyploid species (Jauhar 2003a). Wheat offers an excellent example of evolution by allopolyploidy.

That the successful establishment of a sexually reproducing allopolyploid depends upon the integration of constituent genomes into a meiotically and reproductively stable form is well exemplified by bread wheat with its three related genomes. Hexaploid bread wheat (2n = 6x = 42; AABBDD genomes) and its tetraploid forerunner, durum wheat (2n = 4x = 28; AABB genomes),

are stabilized natural hybrids of wild diploid species. The steps in the evolution of polyploid wheats are outlined below and in Figure 1.3.

1.3.1.1 Durum Wheat: A Forerunner of Bread Wheat

Tetraploid durum wheat (macaroni wheat) is a predecessor of hexaploid bread wheat. Its two genomes, A and B, came from two diploid wild grasses. The donor of the A genome is *Triticum urartu* Tumanian (Nishikawa 1983; Dvořák et al. 1993), a species closely related to einkorn wheat (*Triticum monococcum* L.), which was domesticated in southeastern Turkey about 12,000 years ago (Heun et al. 1997). The B genome was probably derived from *Aegilops speltoides* Tausch (Sarkar and Stebbins 1956; Wang et al. 1997; Dvořák 1998). The two progenitors, both native to the Middle East, hybridized in nature about half a million years ago (Huang et al. 2002) and gave rise to tetraploid wild emmer wheat (*T. turgidum* var. *dicoccoides* Körn), presumably in one step as a result of somatic chromosome doubling in the BA hybrid during premeiotic mitotic divisions or by meiotic nonreduction. Unreduced (2n) gametes could arguably have functioned in both progenitors, thereby producing an instant amphidiploid, which became emmer wheat. However, 2n gametes occur very rarely, if at all, in diploid species. Chromosome doubling most plausibly occurred via fusion of unreduced gametes in the BA hybrid (amphihaploid), since such gametes are known to occur in interspecific and intergeneric hybrids (see also Chapter 2 by Ceoloni and Jauhar and Chapter 3 by Mujeeb-Kazi) rather than in diploid parents. This step of evolution can in fact be recreated by inducing BA haploids (amphihaploids, to be precise) of durum wheat (see Figure 1.3). It has been shown that synthetic durum haploids produce unreduced gametes by first division restitution (FDR), resulting in a viable seed set and then tetraploid (disomic) durum plants (Jauhar et al. 2000). As noted by these workers, the *Ph1*-induced failure of homoeologous pairing may be a prerequisite for the formation of FDR nuclei (Jauhar 2003a), implying that *Ph1* was likely present in the hybrid that inherited it from its B- or the A-genome parent. If one of the diploid progenitors of emmer wheat did harbor *Ph1*, then what regulatory function, if any, it would have played there is a matter of speculation. But then, if *Ph1* had not been present in the BA hybrid, the derived wild emmer and durum wheat would be expected to show a number of B/A translocations at homoeologous breakpoints. However, we do not find such translocations, implying that the two genomes maintained their meiotic integrity perhaps through *Ph1* regulation. One might speculate, therefore, that the hybrid had somehow acquired *Ph1*, although its precise origin remains enigmatic.

If the BA hybrid did not have the benefit of FDR or some similar mechanism of forming 2n gametes, it would perhaps not have survived in nature. The establishment of *Ph1* regulation was also vital for the survival and success of the derived amphidiploid BBAA (Figure 1.3). Because *Ae. speltoides* (BB) functioned as the female parent (Wang et al. 1997), the correct genomic designation for emmer wheat would be BBAA, although it is generally given as AABB.

Wild emmer was domesticated in the Fertile Crescent, where it acquired the *Q* gene for free threshing (Muramatsu 1986) and gave rise to cultivated emmer or durum wheat, which is one of the earliest domesticated crops. The acquisition of *Q* gene marked the dawn of human civilization in the Near East. Emmer was the main crop during the spread of Neolithic agriculture from the Fertile Crescent to Eurasia and Africa.

1.3.1.2 Establishment of Genetic Control of Chromosome Pairing

The corresponding chromosomes of the A and B genomes are closely related genetically and are referred to as homoeologous chromosomes, their own partners being homologous. Because homoeologous chromosomes, e.g., 1A and 1B, are genetically similar and hence capable of pairing with one another, some sort of regulation of pairing would be necessary for meiotic regularity. Therefore, either *Ph1* was acquired at the BA hybrid level (see Section 1.1 above),

or it can be hypothesized that at (or before) the origin of the tetraploid wild emmer, a spontaneous mutation gave rise to the homoeologous chromosome pairing suppressing gene, *Ph1*, located in the long arm of chromosome 5B. Thus, *Ph1* permitted pairing only between homologous partners, ensuring diploid-like pairing and disomic inheritance, and has helped to maintain the meiotic integrity of the A and B genomes. But for this rigid regulation of chromosome pairing, the two genomes would have converged during the period of about 500,000 years that they have been together. However, some intergenomic rearrangements, such as those involving chromosomes 4A, 5A, and 7B, have occurred both in bread wheat (Naranjo et al. 1987; Naranjo 1990) and durum wheat (Naranjo 1990; Doğramaci-Altuntepe and Jauhar 2001; see Figure 2.3). This cyclic translocation seems to confer some selective advantage and appears to be the evolutionary signature of polyploid wheats.

1.3.1.3 Origin of Bread Wheat: An Important Evolutionary Step

Another cycle of spontaneous hybridization (see Figure 1.3) took place between tetraploid wheat and diploid goatgrass (*Aegilops tauschii* Coss., 2n = 2x = 14, DD genome) (McFadden and Sears 1946) about 8000 years ago (Huang et al. 2002) and gave rise to hexaploid bread wheat that sustains humankind. It is likely that, as a result of hybridization between durum wheat and *Ae. tauschii*, a triploid hybrid ABD was first formed, which produced unreduced male and female gametes and a set hexaploid seed, giving rise to bread wheat (Matsuoka and Nasuda 2004). This parallels the events in durum haploids (amphihaploids BA) that set seed (Jauhar et al. 2000).

The *Ph1*-regulated diploid-like pairing that was established in its ancestral allotetraploid conferred meiotic regularity, and hence reproductive stability, to hexaploid wheat also. The three genomes, AA, BB, and DD, have since maintained their meiotic integrity. But for this stringent regulation of chromosome pairing, the wheat crop would not have evolved and human civilization would perhaps not have progressed the way it has.

1.3.2 Cytogenetic Makeup of Hexaploid Oat

Common oat (*Avena sativa* L.) and red oat (*Avena byzantina* C. Koch) are allohexaploid species with three genomes (2n = 6x = 42; AACCDD genomes), although only the allotetraploid progenitor has been identified so far. Unlike wheat, discrimination between two of the oat genomes, A and D, has been problematic (Linares et al. 1998; Drossou et al. 2004). It is clear, however, that diploid-like pairing in hexaploid oats is under genetic control (Rajhathy and Thomas 1972, 1974; Jauhar 1977), which is hemizygous effective, as evidenced by lack of pairing in oat polyhaploids with one dose of the diploidizing gene(s) (Nishiyama and Tabata 1964), and genetically repressible, as in hexaploid bread wheat (Table 1.2). Based on chromosome pairing in oat polyhaploids and several amphiploids (Thomas and Jones 1964; Rajhathy and Thomas 1974), Jauhar (1977) concluded the presence of a rigid and complex genetic control of chromosome pairing in oat. He further hypothesized that the diploidizing gene(s) was located in the A genome and that multiple copies of these genes in the AAAABBCCDD decaploids (Thomas and Jones 1964) drastically reduced the frequency of multivalents (Jauhar 1977). Although the pairing control mechanism in hexaploid oat has not been fully elucidated so far, genetic suppression of homoeologous pairing is an important consideration in alien gene transfers into this cereal.

1.4 GENETIC CONTROL OF CHROMOSOME PAIRING: MAJOR IMPLICATIONS

Allopolyploidy, resulting from interspecific or intergeneric hybridization coupled with chromosome doubling, and in conjunction with genetic regulation of chromosome pairing, has been instrumental in the production of many of our important grain, forage, and fiber crops. Thus, a

Table 1.2 Comparison of the Chromosome Pairing Control Mechanisms in Polyploid Grasses

Features	5B Control	Reference	A Control	Reference	C Control	Reference
Species in which chromosome pairing is regulated	Tetraploid and hexaploid wheats	Okamoto 1957; Sears and Okamoto 1958; Riley and Chapman 1958	Tetraploid and hexaploid species of *Avena*	Rajhathy and Thomas 1972	*Festuca arundinacea*, *Festuca rubra*, and other polyploid fescues	Jauhar 1975a,b
Location	5BL	Sears and Okamoto 1958; Riley 1960	A genome?	Jauhar 1975c	C genome?	Jauhar 1975c, 1977
Effectiveness	Hemizygous effective	Riley and Chapman 1958; Riley 1960	Hemizygous effective	Nishiyama and Tabata 1964; Rajhathy and Thomas 1972	Hemizygous ineffective	Jauhar 1975a,b
Dosage effect	Yes	Feldman 1966, 1968; Martinez et al. 2001	Yes	Jauhar 1975c; Ladizinsky 1973	Yes	Jauhar 1975c
Genetically repressible	Yes	Riley 1960; Dvořák 1972	Yes	Rajhathy and Thomas 1972, 1974	Yes	Jauhar 1975b,c, 1977
Species/genotype suppressing control	*Aegilops speltoides*	Riley et al. 1961	*Avena longiglumis* Accession CW57	Rajhathy and Thomas 1972	Diverse ecotypes of tall fescue	Jauhar 1975c, 1991

Source: Paraphrased from Jauhar, P.P., *Theor. Appl. Genet.*, 49, 287–295, 1977.

combination of sexuality, polyploidy, and genetic control of chromosome pairing provides an ideal recipe for evolution of successful plant species (Jauhar 2003a). Polyploid wheats and the more recent man-made cereal, triticale, provide excellent examples of cataclysmic evolution or evolution by large quantum jumps. Although most allopolyploids in nature may have developed genetic control of chromosome pairing, the mechanism has been clearly elucidated in bread wheat and durum wheat (Okamoto 1957; Sears and Okamoto 1958; Riley and Chapman 1958), and to some extent in hexaploid oat (Rajhathy and Thomas 1972, 1974; Jauhar 1977) and hexaploid tall fescue, *Festuca arundinacea* Schreb. (2n = 6x = 42; AABBCC) (Jauhar 1975a–c, 1991). Such a control results in diploid-like chromosome pairing, which in turn ensures disomic inheritance. It is likely that disomic polyploidy and sexuality may not coexist in nature without such a regulatory mechanism (Jauhar 1975d, 2003a). However, polysomic polyploids like *Medicago sativa* and potato are successful species.

When one dose of the pairing control gene(s) is enough to enforce diploid-like chromosome pairing, such a gene(s) is hemizygous effective. As evidenced by the absence of homoeologous chromosome pairing in their polyhaploids, the genetic control of chromosome pairing is hemizygous effective in durum wheat (Figure 1.4), bread wheat (Figure 1.5), and hexaploid oat, whereas it is hemizygous ineffective in hexaploid tall fescue (Jauhar 1975a,b). Thus, one dose of *Ph1* effectively suppresses homoeologous pairing in durum haploids (Figure 1.4B**;** Jauhar et al. 1999) and bread wheat haploids (Figure 1.5A**;** Jauhar et al. 1991), whereas absence of *Ph1* results in extensive homoeologous pairing in both durum (Figure 1.4C–G) and bread wheat (Figure 1.5B) *ph1b* haploids. The similarities and differences among the three regulatory mechanisms are given in Table 1.2. Genetic pairing regulation has important implications in cytogenetics, evolution, and plant breeding (Jauhar 1975c).

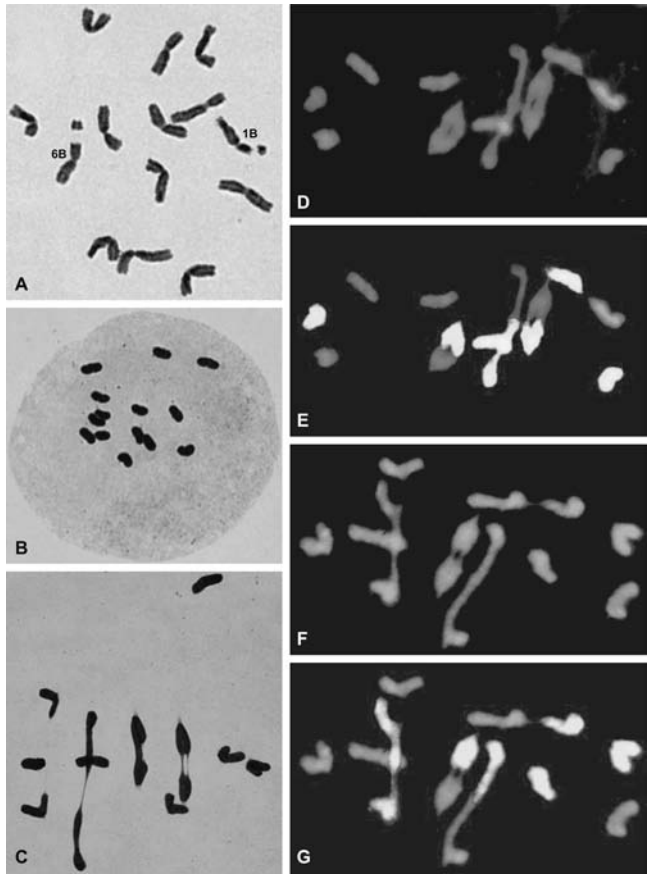

Figure 1.4 **(See color insert following page 114.)** Somatic (A) and meiotic (B–G) chromosomes of durum haploids derived by hybridization with maize: a pollen mother cell (PMC) from a haploid with *Ph1* (B) and PMCs from haploids without *Ph1* showing high homoeologous pairing (C–G). A: 14 somatic chromosomes; note one dose each of the satellited chromosomes 1B and 6B. B: A PMC with 14 univalents; note the total absence of pairing in the presence of *Ph1*. C: Four bivalents (two ring II and two rod II) + six univalents; note high pairing in the absence of *Ph1*. D, E: Fluorescent genomic *in situ* hybridization (fl-GISH) analysis of chromosome pairing: two ring II + one rod II counterstained with propidium iodide (PI) (D) and the same cell as D probed with biotinylated A genome probe (E); the preparation was blocked with the genomic DNA of *Ae. speltoides* (B genome) and the probe was detected with FITC. The A genome chromosomes are brightly lit in green color. Note pairing between the A genome chromosomes and the B genome chromosomes. F, G: Fl-GISH analysis of chromosome pairing: one ring II + two rod II counterstained with PI (F) and same cell as F after probing with the A genome probe (G). Note the intergenomic ring bivalent involving an A- and a B-genome chromosome, an intergenomic rod bivalent, and an intragenomic (within the A genome) bivalent.

1.4.1 Cytogenetic and Evolutionary Implications

1.4.1.1 Usefulness in Genome Analysis

The *Ph1* gene of wheat suppresses pairing between less related (homoeologous) chromosomes. Therefore, pairing or lack of pairing between chromosomes of two genomes in the presence of *Ph1* in the wheat background would generally provide a stringent test of their relationship (Jauhar and Joppa 1996). Adopting this approach, it was found that the seven chromosomes of the J genome of diploid *Thinopyrum bessarabicum* and seven of the E genome of diploid *Lophopyrum elongatum*

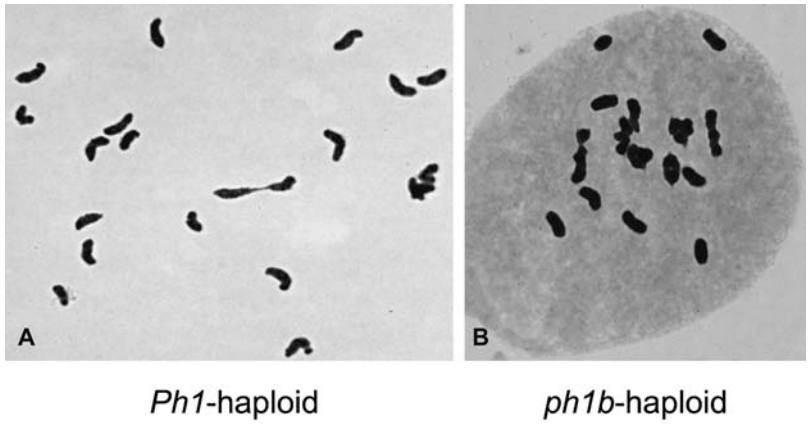

Figure 1.5 Chromosome pairing in PMCs of bread wheat haploids with and without *Ph1*. Note that one gene can make such a difference. A: One rod II + 19 I in the presence of *Ph1* in a *Ph1* haploid. B: Six II (three ring II + three rod II) + nine I. Note extensive pairing in the haploid with the *ph1b* allele.

in the AABBDDJE amphiploids (Forster and Miller 1989) showed no pairing in the presence of *Ph1*, clearly indicating that the J and E genomes are not closely related (Jauhar 1990a,b).

1.4.1.2 Gene Introgressions and Changes in Base Chromosome Numbers

The hemizygous ineffectiveness of the genetic control of chromosome pairing in hexaploid tall fescue and other polyploid fescues is of evolutionary significance in that it allows gene flow from one species to another (Jauhar 1975d), which would explain the widespread introgression of characters among taxa. Such a regulatory mechanism could have played a role in bringing about changes in base chromosome numbers of the type present in the genus *Pennisetum* (Jauhar 1981b; see also Chapter 10 in this volume) and numerous other taxa (Jauhar 1975d). Hemizygous-ineffective control would produce irregular meiosis with multivalent formation, which would result in loss or gain of chromosomes in hybrids. Subsequent spontaneous chromosome doubling of such hybrids could have produced aneuploid taxa; such taxa may not compete their euploid relatives, and hence become apomictic (Jauhar 1975c, 2003a).

1.4.2 Breeding Implications: Homoeologous Pairing, the Key to Gene Transfer

As stated above, the regulator of chromosome pairing, e.g., the *Ph1* gene in bread wheat, suppresses homoeologous pairing, resulting in diploid-like pairing involving homologous partners only and ensuring meiotic regularity and reproductive stability of the polyploid species. The function of *Ph1* is to discipline chromosomes and prevent "adultery" among them, i.e., suppress recombination between less related chromosomes, and thereby ensure disomic inheritance. Because of its function as a regulator of chromosome pairing, I called *Ph1* a policeman. Although there are other genes with some regulatory effect on pairing, *Ph1* is the principal regulator.

Ph1 suppresses pairing between unrelated or less related chromosomes and may inhibit pairing between wheat chromosomes and alien chromosomes in wheat × alien species hybrids, thereby impeding alien gene transfers into wheat. Because plant breeding depends on adultery among wheat and alien chromosomes to capture desirable segments or to trim off alien chromosome segments that bear unwanted genes, methods of promoting homoeologous pairing through cytogenetic manipulation must be adopted.

1.5 CYTOGENETIC MANIPULATION OF POLYPLOID CEREAL CROPS

1.5.1 Wheat

As stated above, the origin of a rigid regulatory mechanism in the form of *Ph1* was essential for suppressing homoeologous chromosome pairing, and hence for reproductive stability and survival of polyploid wheats. Because *Ph1* restricts pairing to identical (homologous) partners, it does not permit adultery among less related (homoeologous) chromosomes. However, since plant improvement is facilitated by adultery and recombination among related or even less related chromosomes, *Ph1* poses an obstacle to the incorporation of alien genes into bread wheat and durum wheat. Because chromosome pairing between related or less related chromosomes is the key to gene transfer across species, appropriate means of circumventing the *Ph1*-created barrier will need to be adopted. Elegant means of incorporating alien genes into wheat were devised by Sears and other wheat researchers. Cytogenetic manipulations, including those based on suppression or inactivation of the *Ph1* system, for engineering desirable alien chromatin into wheat were termed chromosome engineering (Sears 1972). A high-pairing mutation involving a small intercalary deficiency for *Ph1* was produced in bread wheat and designated *ph1b* (Sears 1977). Since this mutation raises the level of homoeologous pairing, it may be employed for alien gene transfers into wheat.

The use of the *ph1bph1b* mutant of wheat (as a female parent) provides one means of promoting homoeologous pairing. Use of 5B-deficient stocks such as the 5D(5B) substitution lines also promotes intergenomic chromosome pairing and intergeneric gene transfer. Such a strategy of alien gene introgression in wheat has been employed (Sears 1981; see Jauhar and Chibbar 1999).

The use of 5B-deficient stocks, such as the 5D(5B) disomic substitution line of durum wheat, has been successfully employed to promote intergeneric chromosome pairing, for example, in an intergeneric hybrid (Figure 1.6A) between durum wheat and a diploid wheatgrass, *Th. bessarabicum* (2n = 2x = 14; JJ). In the presence of *Ph1* there is no chromosome pairing or minimal pairing in the hybrid (Figure 1.6B), but in the absence of *Ph1* extensive homoeologous chromosome pairing occurs (Figure 1.6C), a welcome feature from the breeding standpoint. We are using the 5D(5B)

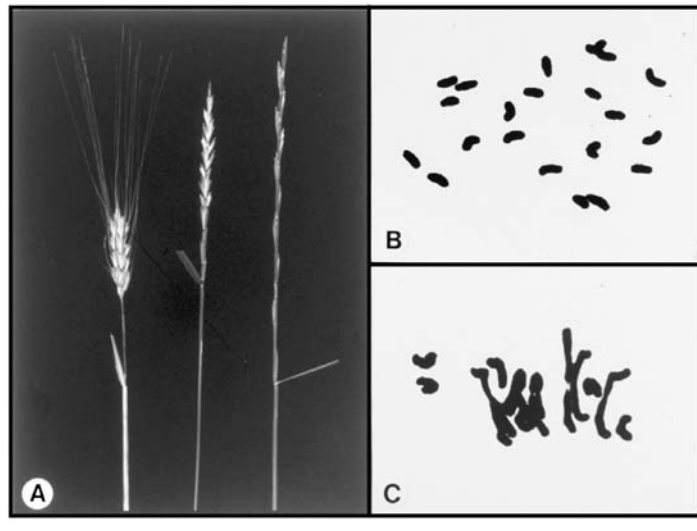

Figure 1.6 An intergeneric hybrid (2n = 3x = 21; ABJ) between durum wheat and a diploid wheatgrass, *Th. bessarabicum* (2n = 2x = 14; JJ). A: Spikes of durum parent, intergeneric hybrid, and the diploid wheatgrass. Note intermediate characteristics of the hybrid (the awns of durum parent missing). B: A PMC with 21 I. Note the absence of pairing in the presence of *Ph1*. C: A PMC with one III + one ring II + five rod II + six I. Note extensive homoeologous pairing in the absence of *Ph1*.

substitution line to promote homoeologous pairing and recombination between chromosomes of durum wheat and *Lophopyrum elongatum* (2n = 2x = 14; EE) (Jauhar and Chibbar 1999; Repellin et al. 2001).

Another and perhaps more suitable means of inducing wheat–alien species chromosome pairing is by crossing wheat with alien species that inactivate the homoeologous pairing suppressor *Ph1*. Certain genotypes of wild grasses, a potential donor of desirable genes, are known to inactivate *Ph1* at least partially (see, for example, Jauhar 1992; Jauhar and Almouslem 1998) and may be employed to promote homoeologous pairing and hence alien gene introgression. We are exploiting such genotypes in our wheat germplasm enhancement program (Repellin et al. 2001; Jauhar 2003b).

1.5.1.1 Specificity of Chromosome Pairing and Induction of Alien Integration into Wheat

Excellent means are now available for studying the nature and specificity of chromosome pairing in haploid complements and intergeneric hybrids (Jauhar et al. 1999, 2004). Thus, Jauhar (1992) combined both the E and J genomes with durum wheat in trigeneric hybrids with genomic constitution of ABJE and used fl-GISH to study the specificity of chromosome pairing: wheat–wheat, grass–grass, and wheat–grass (Jauhar et al. 2004). Wheat–grass pairing is, of course, essential for incorporation of alien segments into the wheat complement.

While introduction and integration of alien genetic material in the wheat genome is very important, its characterization (physical size and precise location) will also be very useful. Recently, we have witnessed a dramatic improvement in monitoring the alien transfer process in all its phases (Ceoloni et al. 1998). Thus, both molecular marker technology as well as molecular cytogenetic techniques, such as nonradioactive *in situ* hybridization, and such as fluorescent genomic *in situ* hybridization (fl-GISH), can effectively complement classical diagnostic tools for efficient and accurate characterization of introgression products (see Chapter 2 by Ceoloni and Jauhar in this volume). These procedures would also facilitate elimination of alien chromatin carrying undesirable traits of the wild donor. Details of the alien gene transfer work in polyploid wheats are given in Chapters 2 and 3 in this volume.

1.5.2 Oat

Hexaploid bread wheat (2n = 6x = 42; AABBDD) and hexaploid oat (2n = 6x = 42; AACCDD) have essentially similar genomic constitutions. (Note, however, that there is no correspondence between A genomes in the two Poaceae tribes to which wheat and oat belong.) As in bread wheat, the diploid-like pairing in oat is under genetic control. In both, the regulation is essentially similar (Table 1.2) and can be suppressed by appropriate genotypes of their wild relatives, leading to homoeologous pairing. In oat, a locus in the wild diploid *Avena longiglumis* CW 57 suppresses homoeologous pairing regulation. Through wide hybridization coupled with manipulation of chromosome pairing, some desirable genes have been transferred into cultivated oat. Thus, Thomas et al. (1980) transferred a mildew resistance gene from *Avena barbata* into oat. Jellen and Leggett present details of such transfers in Chapter 7 in this volume.

1.6 DIPLOID OR DIPLOIDIZED CEREALS: GENOMIC EVOLUTION

1.6.1 Cytogenetic Makeup and Ancient Polyploid Origin

Eukaryotic evolution is known to be accompanied by gene duplication. Duplications of genes, chromosomal segments, chromosomes, or whole genomes have played an important role in eukaryotic genome evolution (Koszul et al. 2004; Goffeau 2004). It has long been known that duplicated

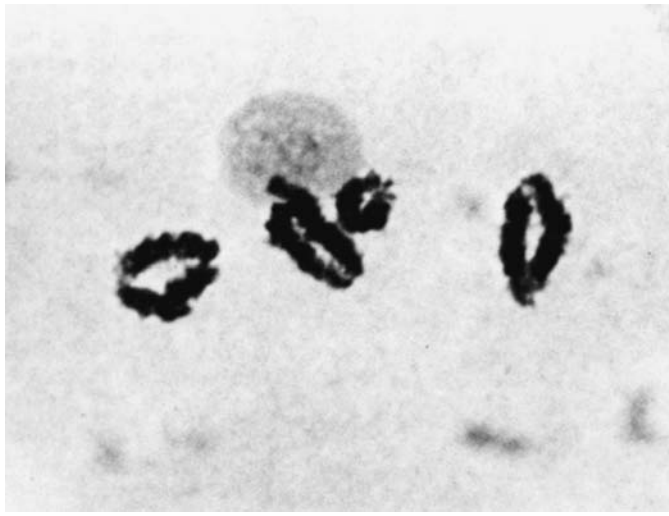

Figure 1.7 Meiotic pairing at a stage comparable to diakinesis in barley haploids (2n = x = 7). Note complete pairing: three large ring bivalents and fold-back pairing of the remaining univalent. (Courtesy of Sadasivaiah, R.S. and Kasha, K.J., *Chromosoma* 35, 247–263, 1971.)

genetic material confers adaptive advantage, and having extra gene copies is essential for an organism to evolve (Ohno 1970). Recent work has further shown that diversification of gene functions during evolution requires prior gene duplication (Dujon et al. 2004; Kellis et al. 2004).

Several of our crop plants are supposedly diploid. Genetic mapping studies have shown, however, that several crop species traditionally considered diploid are in fact diploidized polyploids derived from ancient polyploids through some sort of structural repatterning. Recent studies have shown that allopolyploidy-induced sequence elimination of low-copy DNA sequences or those in noncoding regions can occur in plant genomes (Feldman et al. 1997; Ozkan et al. 2001). Among these cereals, barley (2n = 2x = 14) is perhaps a typical diploid, although the formation of bivalents during meiosis in its haploids (2n = x = 7) (Sadasivaiah and Kasha 1971; Figure 1.7) would suggest chromosomal duplication. Haploids have half the normal somatic chromosome number and offer an excellent opportunity for studying inter- or intragenomic homologies, which are masked when every chromosome has an identical partner. Bivalent formation in haploid (monoploid, to be precise) barley suggests that the barley genome itself might have arisen from a lower basic chromosome number. Based on the presence of up to two bivalents in haploids (2n = x = 7) of pearl millet (Jauhar 1970), and on intergenomic and intragenomic chromosome pairing in its interspecific hybrids (Jauhar 1968, 1981a), it was inferred that the pearl millet complement was derived from an ancestral base chromosome number of x = 5 as a result of duplication during the course of evolution. Thus, Jauhar (1968) called pearl millet a secondarily balanced species (see Chapter 10 in this volume). From a study of restriction fragment length polymorphism (RFLP) linkage maps, Liu et al. (1994) provided corroborating evidence of the presence of duplicate loci in pearl millet.

Maize has long been considered to be an ancient polyploid having extensive chromosome duplications that were initially revealed from meiotic pairing in its haploids (Ting 1966), and by its ability to tolerate chromosome deficiencies. In diploid species, chromosome deficiency such as monosomy is not tolerated. In maize, however, 9 of the possible 10 monosomics (2n – 1 = 19) were produced along with some occasional double monosomics (2n – 1 – 1 = 18) and even triple monosomics (2n – 1 – 1 – 1 = 17) (Weber 1970, 1973, 1994), clearly suggesting maize to be "an ancient, secondarily balanced species with an extensive duplication (and probably redundance) of genetic information in the form of whole chromosomes" (Jauhar 1981b, p. 91). In this respect, surprisingly, there seems to be more genetic buffering in maize than in tetraploid durum wheat because in the latter, even simple monosomy for a chromosome is not well tolerated. The DNA

sequence data of Gaut and Doebley (1997) supported the polyploid origin of maize. They studied 14 pairs of duplicated loci and noted two different groups of coalescence times, which they attributed to ancestral tetraploidization between two diploids whose genomes were partially differentiated from each other. Thus, maize has clearly resulted from an ancient polyploidization event (Gaut et al. 2000; Wendel 2000; Gaut 2001).

Sorghum (2n = 2x = 20) has also been considered to be an ancient polyploid; the genus *Sorghum* has several extant species with 2n = 10. Using bacterial artificial chromosomes (BACs) in conjunction with fluorescent *in situ* hybridization (FISH), Gómez et al. (1998) found that a 45-kb sorghum BAC preferentially hybridized to centromeric regions of 5 of the 10 chromosomes of *Sorghum bicolor* (2n = 20), supporting earlier evidence of the tetraploid nature of this crop and also revealing two genomic sets of 5 chromosomes each. Clearly, several of the supposedly diploid crop plants have been shown to result from ancient polyploidization events. It will not be surprising if rye (2n = 14) also turns out to be paleopolyploid, like maize, sorghum, and pearl millet.

The diploid nature of rice (2n = 24) has long been questioned. Based on chromosome morphology and secondary associations in units of five at meiosis, Nandi (1936) hypothesized that rice is a secondarily balanced species. That rice has undergone an ancestral round (or perhaps more than one round) of genome duplication is borne out by recent studies. Because its chromosome complement (2n = 24) is not a multiple of x = 5, 7, 9, or 10 (the common base numbers reported in the Poaceae), it is likely that the present-day rice is an ancient aneuploid, having undergone perhaps only partial genome duplication. Interestingly, a systematic sequence analysis indicated that 15% of the rice genome is in duplicated blocks (Vandepoele et al. 2003). It is not surprising that intragenomic duplications have been revealed in rice. Earlier data on genetic and physical mapping demonstrated the presence of duplicated segments between chromosomes 1 and 5 (Kurata et al. 1994) and between chromosomes 11 and 12 (Wu et al. 1998).

Recently, the genome of subspecies *japonica* of rice was sequenced using a whole-genome shotgun approach. The availability of the draft sequence and the comparison of 2000 mapped cDNAs suggested that large-scale duplication had occurred during the evolution of rice (Goff et al. 2002). The recent release by the Institute of Genome Research of 12 rice pseudochromosome sequences has allowed the investigation of intragenomic duplications, showing that the rice genome contains extensive chromosomal duplication accounting for 53% of the available sequences (Guyot and Keller 2004).

1.6.2 Diversity of Origin of Cereal Genomes: Genomic Diversity and Synteny

The grass family Poaceae is an assemblage of diverse, widely adapted species (including cereals), which have been classified into two major clades based on molecular phylogenetic studies (Soreng and Davis 1998). One clade contains the subfamily Panicoideae, which includes the cereal crops maize, sorghum, and pearl millet. The other clade contains the subfamily Pooideae, which includes the cereal crops wheat, barley, oat, and rye. Minor clades include the subfamily Oryzoideae, which contains the model cereal — rice that is recognized as an early diverging lineage. The cereal genomes vary considerably in size, ploidy, and taxonomic affinity. The haploid nuclear genomes of sorghum, maize, barley, and wheat are estimated to be 1000, 3000, 5000, and 16,000 mega base pairs (Mbp), respectively, while rice has a much smaller genome of about 420 Mbp (Goff et al. 2002).

Despite the phylogenetic diversity and the consequent evolutionary distance among these cereal crop species resulting from millions of years of evolution, their genomes show a high degree of conservation, gene similarity, and genome synteny. Molecular mapping of the cereal nuclear genomes using RFLP has allowed the development of comparative chromosome maps (Devos and Gale 1997; Paterson et al. 2000; Ilic et al. 2003; Varshney et al. 2005). Synteny and gene homology between rice and the other cereal genomes are extensive; homologs of 98%

of the known maize, wheat, and barley proteins exist in rice (Goff et al. 2002; Yu et al. 2002). The high genetic colinearity of the rice genome with the larger cereal genomes makes rice the model genome for studying genome evolution and facilitating gene isolation from related cereals.

1.6.3 Cytogenetic Manipulation and Breeding Work in Diploid Cereals

Maize, barley, sorghum, pearl millet, and rye are diploidized to the extent that they behave as true diploids, despite the ancestral duplication of genetic material at least in some of them. Thus, they show disomic inheritance. These cereals are relatively easy to manipulate by tools of cytogenetics or by traditional breeding.

1.6.3.1 Rice: A Model Cereal Crop

Being the primary food source for more than a third of the world's population, rice is an extremely important cereal crop. It is the only cereal used almost exclusively for human consumption. Because of several desirable characteristics, including its diploidized nature with 2n = 24 chromosomes, availability of an extensive germplasm collection, availability of well-characterized cytogenetic stocks, and a large number of mutant markers, rice is a highly desirable organism for molecular cytogenetic and breeding research. However, with a symmetrical karyotype of small chromosomes, rice is not an attractive organism for traditional cytogenetic studies. Brar and Khush (Chapter 5 in this volume) provide a detailed account of its improvement via hybridization with wild species and by modern tools such as genetic transformation and functional genomics. Molecular markers have been employed to facilitate introgression of genes for resistance to diseases and pests (Gupta et al. 1999, 2002; Zhou et al. 2002; Somers et al. 2003; Liu and Anderson 2003; Adhikari et al. 2004; Dubcovsky 2004; Varshney et al. 2004; Zhou et al. 2004; Helguera et al. 2005).

As stated earlier, rice has a genome size of about 420 Mbp. Its small genome with high gene density, coupled with its synteny with other cereal crops, makes rice the standard model for cereal gene discovery.

1.6.3.2 Maize: A Cytogeneticist's Delight and a Breeder's Paradise

Because of its amenability to pachytene analysis and the availability of translocation stocks involving supernumerary chromosomes, maize is an ideal organism for basic studies in cytogenetics. Several basic phenomena in genetics, such as linkage, have been elucidated using maize as an experimental organism (e.g., McClintock and Hill 1931). Such eminent geneticists as Barbara McClintock spent their lifetime working on cytogenetics of maize. Unlike many other crops, genetic gains obtained through breeding have been consistent with maize, and the methodologies developed for maize have been applied to other crops (Duvick 1992). Through hybridization with other crops, followed by chromosome elimination, maize offers an excellent system for inducing haploids in unrelated cereals (e.g., Jauhar 2003c), facilitating their cytogenetic manipulation. Thus, using oat × maize crosses, maize chromatin has been added to the oat genome (Riera-Lizarazu et al. 2000; Kynast et al. 2002) and oat–maize addition lines (Kynast et al. 2001) have been isolated to facilitate work on functional genomics.

As a cross-pollinated crop, maize has tremendous genetic diversity (Figure 1.8). It offers enormous possibilities for heterosis breeding, which has considerably improved its yield and nutritional quality. The development of quality protein (high-lysine) maize is a landmark achievement that has helped to alleviate malnourishment among the poor who depend on maize as a primary food source (Vasal 2002; Chapter 6 in this volume).

Figure 1.8 **(See color insert following page 114.)** A collection of maize cobs showing a wide range of diversity. (From www.tropag-fieldtrip.cornell.edu/tradag/Maize.jpg.)

1.6.3.3 Pearl Millet: Poor Man's Bread: Heterosis Breeding

Pearl millet, another diploidized cereal, is a dual-purpose crop providing both grain and fodder. As a poor man's source of dietary energy, it sustains a large proportion of the population in hot, arid regions in Africa and Asia. With 2n = 14, large chromosomes, and other desirable attributes, pearl millet is well suited for basic research in cytogenetics (Jauhar and Hanna 1998). Moreover, like maize, pearl millet is an open-pollinated crop that responds very well to heterosis breeding. Single-cross hybrids yield about 25 to 30% more than open-pollinated varieties, and in 2001 more than 70 hybrids were cultivated on about 6 million ha of the total 10-million-ha pearl millet area in India (see Chapter 10 in this volume). Research on nutritional enhancement of pearl millet is also in progress.

Interspecific hybridization followed by cytogenetic manipulation has produced several desirable, heterotic hybrids with high fodder yield and quality (Jauhar and Hanna 1998; Chapter 10 by Jauhar et al. in this volume). Exploitation of hybrid vigor will continue to be the most important means of increasing both grain and fodder yield.

1.6.3.4 Barley, Sorghum, Rye, and Triticale

While sorghum does seem to have undergone a cycle of tetraploidization, there is no clear evidence of ancient genomic duplication in barley and rye, even though their haploids show meiotic pairing (Sadasivaiah and Kasha 1971; Levan 1942) indicating chromosome duplication. In terms of total production, barley ranks fourth among the cereal crops (Figure 1.1 and Figure 1.2). Genomic constitution of *Hordeum* species, germplasm resources as donors of desirable traits, and germplasm enhancement of cultivated barley are covered by Singh in Chapter 8 in this volume. Thus, tolerance to biotic and abiotic stresses has been transferred from its wild relative *Hordeum bulbosum* into barley (Pickering 2000). Because the bulbosum method of producing barley haploids is very reliable, the doubled haploid technique has been fruitful in producing several barley cultivars (Pickering

and Devaux 1992). Wheat-barley addition lines were produced by Islam and are being used in isolating wheat–barley recombinant chromosomes (Islam et al. 1981; Islam and Shepperd 1992, 2000). Barley is predominantly self-pollinated, and methods such as pedigree, backcrossing, and bulk breeding have been successfully employed for its improvement.

Sorghum is the world's fifth major cereal crop and is mostly grown in the semiarid tropics. It is primarily self-pollinated, but the discovery of cytoplasmic nuclear male sterility has facilitated the exploitation of hybrid vigor (Rooney and Klein 2000). Breeding for resistance to insect pests and diseases has produced excellent results. Marker-assisted selection has proved helpful in breeding for midge resistance (Henzell et al. 2002), although work in this area needs to be expanded. Development of high-lysine lines has improved the nutritional status of this important cereal for the benefit of the malnourished consumers. As in maize, the combination of high protein quality with high grain yield in sorghum will be highly welcome. Details of sorghum improvement using conventional and modern techniques, including transgenic technology, are given by Reddy et al. in Chapter 11 in this volume.

Rye is a relatively young cereal, with the world production amounting to about 30 million metric tonnes and the cool, temperate regions of Europe being the major growing areas. It is an outbreeder and shows inbreeding depression like pearl millet. However, suitable inbred lines with adequate vigor can be isolated for production of synthetics and exploitation of hybrid vigor. Hybrid varieties have been released in Europe and occupy 60% of the total rye acreage. The presence of cytoplasmic genic male sterility is necessary for making rye hybrids. Improvement in grain yield, protein content, insect pest resistance, and baking quality are among the goals of breeding. Varieties with large leaf mass would be suitable for green fodder.

Rye germplasm has also been used for wheat improvement. Hybridization between wheat and rye, coupled with intergeneric chromosome manipulation, led to the production of various combinations of genomes, wheat–rye addition lines involving individual rye chromosomes or chromosome segments (Schlegel 1990). Details of these cytogenetic manipulations are covered by Schlegel in Chapter 12 in this volume.

Most interestingly, wheat × rye hybridization also resulted in a new man-made cereal, called triticale or *Triticosecale* Wittmack (AABBRR). Endowed with improved protein content, disease and pest resistance, and cold tolerance, hexaploid triticale promises to enlarge the spectrum of cereal crops for the benefit of humankind. An extensive coverage of this new cereal is given by Tamás Lelley in Chapter 13 in this volume. He describes triticale as a typically human inspiration, a remarkable feat of evolution.

1.7 PERSPECTIVES AND CHALLENGES

Cereal crops constitute the most important food source for humans, sustaining about two thirds of the world population. The current world population of about 6.1 billion is projected to reach 8.0 billion by 2030, posing a great challenge for plant scientists and agriculturalists to help cope with the ever-growing demand for food. According to FAO estimates, 842 million people worldwide were malnourished in 1999 to 2001, the most recent years for which figures are available. This total also includes 10 million people in the industrialized countries, 34 million in countries in transition, and 798 million in developing countries (fao.org/newsroom/news/2003). These alarming numbers underscore the need for increasing yields and upgrading the nutritional status of these important food crops, utilizing all available tools of conventional breeding, cytogenetics, molecular genetics, and biotechnology. Despite recent successes in improving cereal crop yields, which brought about the Green Revolution and thankfully saved numerous lives, the momentum of crop improvement must be maintained to ensure future food security.

The art of plant breeding was developed long before the laws of genetics became known. The advent of the principles of genetics and cytogenetics at the turn of the last century catalyzed the

growth of plant breeding, making it a science-based technology that was instrumental in substantial genetic improvement of crop yields. Grain yields of major crops, namely, wheat, rice, maize, sorghum, and pearl millet, have increased steadily since 1930, when principles of genetics were applied to plant breeding and heterosis breeding was adopted first in maize and later in pearl millet and sorghum. Although heterosis breeding has helped produce many superior hybrids in maize and pearl millet, the genetic base of such hybrids must be broadened to ensure protection against new pathogens (see Chapter 6 by Vasal et al. and Chapter 10 by Jauhar et al. in this volume). Apomixis could help maintain heterozygosity through seed production and perpetuate hybrid vigor. However, the potential of apomixis in harnessing hybrid vigor has not been exploited so far, although research on these lines has been under way for some time. If apomixis could be introduced in superior hybrids, they would clone themselves, thereby eliminating the need to produce commercial hybrids year after year. Exploitation of hybrid vigor will continue to be an important strategy in maize and pearl millet. Heterosis breeding could also prove very beneficial in other cereal crops, including the inbreeders, rice and wheat.

Alien genetic resources have been widely used to enrich cereal crops. Wide hybridization, coupled with manipulation of chromosome pairing, has been utilized to introgress desirable chromosome segments or genes from wild wheatgrasses into wheat. A novel technique of inducing crop–alien chromosome translocations involves the use of the chromosome-breaking action of gametocidal chromosomes (Endo 2003). Thus, certain *Aegilops* chromosomes become gametocidal when introduced into common wheat and induce chromosome breakage. By introducing these gametocidal genes into a wheat–alien addition or substitution line, random wheat–alien chromosome translocations have been recovered in the selfed progenies. Masoudi-Nejad et al. (2002) transferred rye chromosome segments into wheat by employing a gametocidal system. Structural changes in barley chromosomes added to wheat were induced by a gametocidal chromosome derived from *Aegilops cylindrica* (Shi and Endo 1999).

The availability of molecular markers has helped to map genes for superior agronomic traits, such as resistance to diseases and pests in wheat, and to identify quantitative trait loci. Both have accelerated breeding programs (Gupta et al. 1999; Buerstmayer et al. 2002; Anderson et al. 2003; Steiner et al. 2004). Discovery of more precise markers will aid genetic improvement of cereal crops. Recently, Hu and Vick (2003) developed a polymerase chain reaction (PCR)-based technique to target specific chromosome regions. The target region amplification polymorphism (TRAP) technique has been used on Langdon durum–*T. dicoccoides* substitution lines to generate chromosome-specific markers in wheat (Xu et al. 2003).

Since the mid-1980s, the availability of the tools of biotechnology, collectively termed genetic engineering, has helped to asexually incorporate into crop cultivars new traits that are otherwise very difficult to introduce by conventional breeding. Thus, this technology allows access to an unlimited gene pool for genetic enrichment of cereal crops. Most major crops have been genetically transformed by direct DNA delivery via microprojectile bombardment or other means (Jauhar and Khush 2002). The genetic transformation of cereal crops lagged behind other crops, mainly because *in vitro* regeneration techniques, a prerequisite for genetic transformation, were not available, and cereals also showed resistance to *Agrobacterium* infection. However, *in vitro* regeneration and transformation protocols have been developed for bread wheat (Vasil et al. 1992, 1993; see Repellin et al. 2001), durum wheat (Bommineni and Jauhar 1996; Bommineni et al 1997; He et al. 1999; Satyavathi and Jauhar 2003), and other cereals (see Chapters 5, 6, and 8 in this volume). Therefore, valuable genes can now be moved into elite varieties, further enhancing their quality, disease resistance, or productivity, to the limits of our understanding of the genetic basis of these traits. Using transgenic technology, it may be possible to asexually introduce value-added traits, including genes for disease resistance, into otherwise superior cereal cultivars. The transgenic production of golden rice, which is rich in vitamin A and iron, is a remarkable development (Ye et al. 2000) that has the potential of saving millions of lives and averting blindness among millions of children who

subsist mainly on rice (see Chapter 5 by Brar and Khush). Thus, *in vitro* approaches to gene transfer can effectively supplement conventional breeding programs.

The advent of molecular tools has helped in the understanding of crop genomes. Cereal crops being the most important, their genomes have been subjected to extensive analyses, ushering in the era of functional genomics. Rich germplasm resources of cereal crops are being tapped to identify valuable genes for crop enrichment. High-throughput genomics strategies are providing new, precise methods for identifying genes for disease resistance, abiotic stress tolerance, and improved nutritional value. New genomics information is also providing molecular markers to accelerate breeding programs and mapped sequences of candidate genes and the traits they control. Thus, cereal genomics is already aiding breeding programs (see Chapter 4 by Lapitan and Jauhar). Gupta and Varshney (2004) further discuss structural, functional, and comparative genomics, and marker-assisted selection, in relation to crop improvement.

Although cereals have evolved independently, perhaps from a common ancestral species, for some 50 to 70 million years (Kellogg 2001; Gaut 2002), and have developed drastically different genome sizes (see Goff et al. 2002), they display a remarkable degree of synteny (Gale and Devos 1998; Gaut 2002; Ilic et al. 2003; Sorrells et al. 2003). Thus, synteny and gene homology between rice and other cereal genomes is very high, and homologs of 98% of the known maize, wheat, and barley proteins are present in rice (Goff et al. 2002). By virtue of the synteny of cereal genomes, it makes more sense to conduct gene search studies on a model crop with the smallest genome. And with a genome of only 430 Mbp and high gene density, rice merits to be such a model crop. Thus, synteny permits gene searches in rice to be applied to other cereals, which is more efficient and better leverages resources than do direct searches in the larger genomes, as long as the trait of interest is shared by rice and other cereals.

Modern biotechnology has great potential to accelerate crop improvement, and the results obtained so far are very encouraging (Borlaug 2000; Swaminathan 1999; Cook 2000; Jauhar and Khush 2002). However, the new technology will augment, but not replace, conventional plant breeding. The old and new technologies should go hand in hand to accelerate cereal crop improvement to sustain global food security. Adoption of a combination of crop improvement tools would help in the sustained improvement of cereal crops that play such an important role in the sustenance and welfare of humankind. With continued improvement in cereal grain yields, nutritional value, and other desirable attributes, it should be possible to effectively feed the future generations of humanity, even if the projected population explosion were to occur.

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CHAPTER 2

Chromosome Engineering of the Durum Wheat Genome: Strategies and Applications of Potential Breeding Value

Carla Ceoloni and Prem P. Jauhar*

CONTENTS

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2.1 INTRODUCTION

The agricultural scene characterizing the onset of the third millennium appears to be profoundly different from that of a few decades ago, with concerns about natural resources increasingly acquiring a global dimension. So far, thanks to the widespread adoption of Green Revolution technology (Khush 1999), the demand for increased agricultural productivity has been met by combining genetic improvements with greater farming inputs and cultivation of more land. However, due to a progressive shortage of available farmland, water, and energy reserves, as well as to increased problems concerning the environment's capacity to assimilate the multiple forms of pollution generated by the economic growth, different food production methods need to be investigated. These will have to keep pace not only with the expanding human population's food needs (Braun et al. 1998; Khush 1999), but also with an array of newly arisen needs of environmental and socioeconomic relevance.

In this context, interventions aimed at enriching the seriously threatened genetic base of wheat cultivars with new variability from exotic sources may have great potential. The successful application of transgenic technology to bread wheat (*Triticum aestivum* L., 2n = 6x = 42; AABBDD) and durum wheat (*Triticum turgidum* L., 2n = 4x = 28; AABB) has recently opened up new and promising avenues by giving access to otherwise inaccessible gene pools (reviewed in Jauhar and Chibbar 1999; Jauhar 2001a). On the other hand, cytogenetic approaches, although unable to effect single-gene transfers, permit the engineering of the wheat genome with alien chromosomal introductions, thereby inspiring E.R. Sears to coin the term chromosome engineering (Sears 1972). Thus, wheat improvement can be brought about by these well-established methodologies (Sears 1972, 1981; Ceoloni 1987; Gale and Miller 1987) by exploiting diverse gene pools of Triticeae species (Feldman 1979, 1988; Feldman and Sears 1981). They represent an extremely rich reservoir of desirable genes that can significantly contribute to meet the present and future human needs to which the wheat crop is expected to respond.

The reason why we have been only modestly successful in taking advantage of alien genes for the development of improved wheats of commercial value does not reside in the lack of sufficient knowledge on the evolutionary and cytogenetic relationships between the wild and the cultivated wheat relatives or of proper transfer methods. Indeed, wheat cytogeneticists currently working on chromosome engineering are essentially following the footsteps of E.R. Sears, who highlighted and successfully exploited the main avenues that could lead to "transferring of segments of alien chromosomes carrying particular desired genes to wheat chromosomes" (Sears 1972, 1981, 1983).

Recently, we have witnessed a substantial improvement in monitoring the alien transfer process in all its phases (Ceoloni et al. 1998). To this end, both molecular marker technology and molecular cytogenetic techniques such as nonradioactive *in situ* hybridization — e.g., genomic *in situ* hybridization (GISH) and fluorescent *in situ* hybridization (FISH), or fluorescent GISH (fl-GISH) — can effectively complement classical diagnostic tools for efficient and accurate detection and characterization of introgression products. These procedures facilitate elimination of chromosomes carrying unfavorable traits of the wild donor and retention of only the most suitable ones for the target breeding goal(s).

Such a plentiful and diversified array of analytical methods is effectively assisting the work of wheat chromosome engineers, giving renewed and increased potential for meaningful practical achievements. This is particularly significant in the case of durum wheat, whose evolutionary history, as outlined below, is associated with an overall lower tolerance for genome alterations as compared to common wheat.

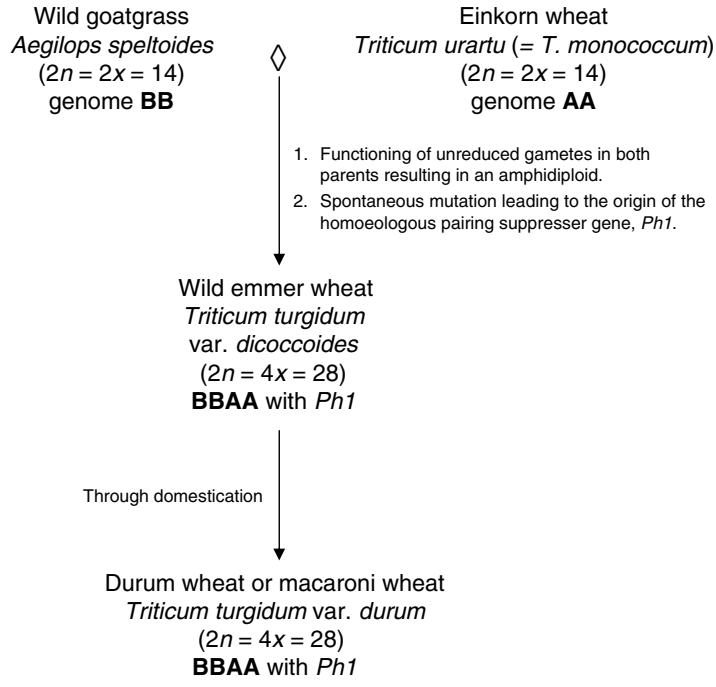

Figure 2.1 Steps in the evolution of durum wheat via functioning of unreduced gametes in both progenitors. (From Jauhar, P.P., *Euphytica*, 133, 81–94, 2003.)

2.2 THE EVOLUTIONARY PATHWAYS OF ALLOPOLYPLOID WHEATS

One of the most spectacular facets of the studies on plant and animal evolution has been the demonstration that it has not always proceeded by slow, even steps but that there have been "bursts of creative activity" (Anderson and Stebbins 1954). A salient factor in these evolutionary bursts is interspecific hybridization, followed or accompanied in some cases by the stabilizing force of chromosome doubling. These phenomena are well exemplified by the evolution of durum wheat (Figure 2.1 and Figure 2.2).

Durum wheat evolved in nature long before bread wheat. Its two genomes, A and B, were derived, respectively, from diploid wild grasses *Triticum urartu* Tum. (Nishikawa 1983; Dvořák et al. 1993) and *Aegilops speltoides* Tausch (Sarkar and Stebbins 1956; Wang et al. 1997). The two wild progenitors hybridized in nature about half a million years ago (Huang et al. 2002) and gave rise to tetraploid wild emmer wheat in one step because of functioning of unreduced gametes in both parents (Figure 2.1) or, alternatively, in the diploid AB hybrid (amphiploid), as illustrated in Figure 2.2 (Jauhar 2003a). The second route appears more plausible, because unreduced gametes are more likely to occur in the hybrid than in its diploid parents (see Chapter 1 by Jauhar in this volume). At the time of the origin of tetraploid emmer, a spontaneous mutation occurred to produce the homoeologous pairing suppressor gene *Ph1* that permitted pairing only among homologous partners, thereby ensuring diploid-like pairing and disomic inheritance (see Section 2.2.2).

It is through such an evolutionary pathway that cultivated polyploid wheats originated and became perhaps the most outstanding example of successful allopolyploids within the plant kingdom. Both the tetraploid and the later arisen hexaploid wheat are the outcome of hybridization–amphidiploidization events involving different diploid progenitors from the genera *Triticum* and *Aegilops* (Feldman et al. 1995; Jauhar 2003a).

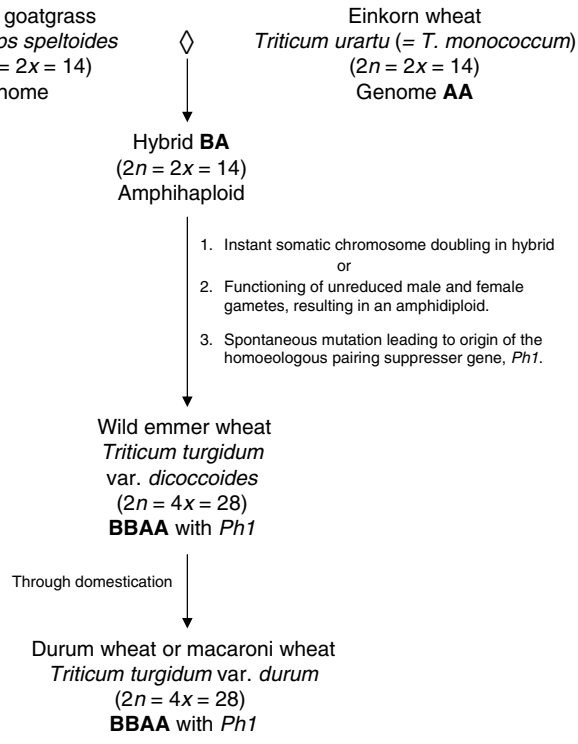

Figure 2.2 Steps in the evolution of durum wheat via instant somatic chromosome doubling or functioning of 2n male and female gametes in the BA hybrid (amphihaploid). (From Jauhar, P.P., *Euphytica*, 133, 81–94, 2003.)

2.2.1 Conservation of Intergenomic Relatedness

Polyploid wheats can be considered segmental rather than typical genomic allopolyploids (Feldman et al. 1995). Classical cytogenetic studies (Sears 1952, 1954, 1966) provided clear evidence for considerable genetic similarity shared by different genomes contributed by the diploid donors, with the partially homologous (homoeologous) chromosomes of the two (AB) or three (ABD) genomes falling into seven distinct groups of homoeology.

Comparative mapping analyses, extensively carried out in the last decade using a wide array of molecular markers and genes (Ahn et al. 1993; Devos and Gale 1997, 2000; Van Deynze et al. 1998; Keller and Feuillet 2000) have not only largely confirmed the significance of these first observations but also provided corroborating evidence for the concepts of intergenomic relatedness both within the tribe Triticeae and among diverse species of the grass family Poaceae (see also Chapter 1 in this volume). Recent phylogenetic (Kellogg 1998, 2001) and comparative genomic studies (Keller and Feuillet 2000; Feuillet et al. 2001; Feuillet and Keller 2002) have demonstrated the occurrence of many events of genome expansion, contraction, and rearrangements and, at the same time, the maintenance of a remarkable degree of overall conservation among the grass genomes. As for polyploid wheats, despite the existence of intergenomic rearrangements, such as those involving chromosomes 4A, 5A, and 7B of both *T. turgidum* (Naranjo, 1990; Jauhar et al. 2000; Doğramaci-Altuntepe and Jauhar 2001; see also Section 2.2.3, Figure 2.3) and *T. aestivum* (Naranjo et al. 1987; Anderson et al. 1992; Devos et al. 1995), a large body of evidence indicates that chromosomes belonging to each homoeologous group retained considerable gene orthology and colinearity during the course of evolution (e.g., Hart 1987; Anderson et al. 1992; Devos et al. 1993b; Van Deynze et al. 1995), with not only overall gene content but also physical location, structural organization, and gene density of gene-rich regions being similar among the component

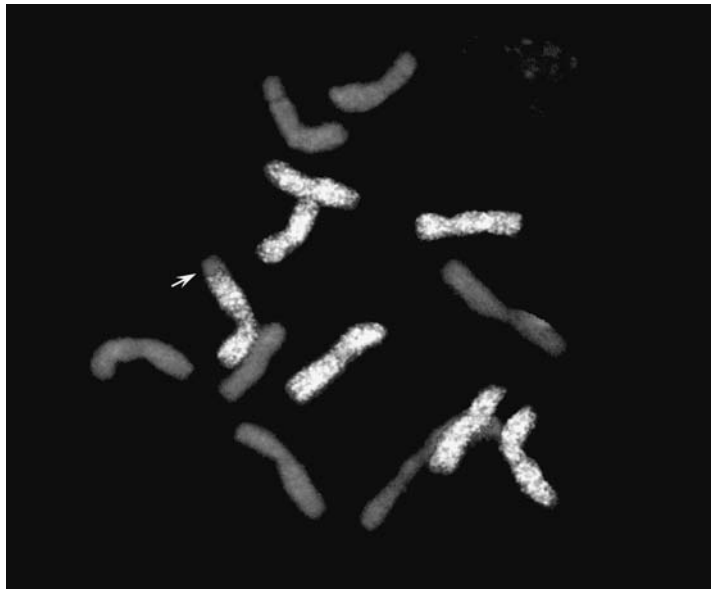

Figure 2.3 **(See color insert following page 114.)** Fourteen somatic chromosomes of a substitution haploid (derived from a D genome disomic substitution line 5D(5B) of Langdon durum wheat) after fluorescent genomic *in situ* hybridization. The brightly fluorescing (bright yellow) chromosomes belong to the A genome. (Chromosome 5D, partially hybridized with the A genome probe but masked by the propidium iodide counterstain, is not clearly seen in the photograph.) The six B genome chromosomes are in red. Note one dose of the 4A/7B translocation chromosome (arrow), which is a part of the evolutionary translocation 4A/5A/7B present both in durum and in common wheat; in this translocated chromosome, the distal segment of 7BS constitutes approximately 24% of the long arm of 4A. The 5A chromosome segment cannot be visualized because it stains the same as the 4A segment. (From Doğramaci-Altuntepe, M. and Jauhar, P.P., *Genome*, 44, 137–142, 2001.)

genomes (Keller and Feuillet 2000; Sandhu et al. 2001). As expected, the degree of such a structural and functional similarity turned out to be higher among Triticeae genomes than between these and the genomes of more distant grass species (Moore et al. 1995; Devos and Gale 2000).

2.2.2 Mechanisms of Diploidization and Their Effects at Different Ploidy Levels

Several different genetic and epigenetic mechanisms contributed to the successful establishment of allopolyploid wheats. Prevention of pairing between homoeologous chromosomes belonging to the constituent diploid genomes was an essential step, as exclusive bivalent pairing of homologous chromosomes ensured regular chromosome segregation and hence disomic inheritance and full fertility to the newly formed polyploid species. Since the early 1960s, several studies (e.g., Riley, 1960; Sears, 1976; Feldman, 1993) showed suppression of homoeologous pairing in wheat to be due to the action of a complex genetic system, with the *Ph1* gene, located in the long arm of chromosome 5 of genome B, exerting the strongest effect. Fixation of this gene in the primitive tetraploid wheat (and later of additional though less potent ones at the hexaploid level) represented an essential step in the cytological diploidization of the newly arisen polyploids. However, other mechanisms, being brought about concurrently with or immediately after the formation of the polyploids, probably provided the physical basis for the diploid-like meiotic behavior of polyploid wheats, later reinforced by the *Ph1* system (Feldman et al. 1997).

As inferred by recent studies on newly synthesized wheat allopolyploids (Feldman et al. 1997, Liu et al. 1998a,b; Ozkan et al. 2001; Shaked et al. 2001; Feldman et al. 2002; Kashkush et al. 2002), the mechanisms of polyploidization resulted in a variety of rapid genetic and epigenetic changes that affected, in a nonrandom and highly reproducible manner, both coding and noncoding