

# 1 Rice

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## 1.1

### Introduction

Rice is the world's single most important crop and a primary food source for half of the world's population. Rice, wheat, and maize provide 49% of the calories consumed by the human population. Of those 23% are provided by rice, 17% by wheat and 9% by maize. Thus almost one fourth of the calories consumed by the entire world population come from rice. More than 90% of the world's rice is grown and consumed in Asia, where 60% of the earth's people live. Rice is planted to about 154 million hectares annually, or on 11% of the world's cultivated land. World rice production was 600 million tons in 2000. India has the largest area under rice (45 million hectares), and China is the largest producer of rice (190 million tons). Other major rice-producing countries are Indonesia, Bangladesh, Vietnam, Thailand, Myanmar, Japan, and the Philippines (Table 1). The importance of rice in the diet varies among countries. It accounts for over 70% of the daily calories intake in countries such as Bangladesh, Cambodia, Laos, Myanmar, and Vietnam but drops to about 40% in countries such as China and India, whose northern areas consume primarily wheat.

#### 1.1.1

#### Taxonomy and Origin of Cultivated Rice

Of the two cultivated species, Asian cultivated rice, *Oryza sativa*, is grown worldwide. *Oryza glaberrima*, the African cultivated rice, is grown on a limited scale in West Africa. Like other cereals such as wheat, maize, barley, sorghum, oats, and rye, which feed the world, rice belongs to the grass family Gramineae. The genus *Oryza*, to which cultivated rice belongs, probably originated at least 130 million years ago and spread as

a wild grass in Gondwanaland, the super continent that eventually broke up and drifted apart to become Asia, Africa, Australia, and Antarctica (Chang 1976). This explains the distribution of *Oryza* species on all of these continents except Antarctica (Table 2).

There are 22 wild species of genus *Oryza*. Nine of the wild species are tetraploid. The remaining wild species and the two cultivated species are diploid. Ten different genomes (Table 2) have been assigned to the different species based on chromosome pairing in interspecific hybrids or based on total DNA hybridization and molecular divergence.

The common rice, *Oryza sativa*, and the African rice, *Oryza glaberrima*, are thought to be examples of parallel evolution in crop plants. The wild progenitor of *O. sativa* is the Asian common wild rice, *O. rufipogon*, which shows a range of variation from perennial to annual types. Annual types, also given the specific name of *O. nivara*, were domesticated to become *O. sativa* (Khush 1997). In a parallel evolutionary path, *O. glaberrima* was domesticated from annual *O. breviligulata*, which in turn evolved from perennial *O. longistaminata* (Fig. 1).

Domestication of wild rices probably started about 9,000 years ago. Development of annuals at different elevations in East India, northern Southeast Asia, and western China was enhanced by alternating periods of drought and variations in temperature during the Neothermal Age about 10,000 to 15,000 years ago (Whyte 1972). Domestication in Asia could have occurred independently and concurrently at several sites within or bordering a broad belt that extends from the plains below the eastern foothills of the Himalayas in India through upper Myanmar, northern Thailand, Laos, and Vietnam to southwestern or southern China (Roschevitz 1931; Chang 1976). The earliest and most convincing archeological evidence for domestication of rice in Southeast Asia

**Table 1.** Total area planted, coverage of high-yielding varieties, and increase in rice production in selected countries in Asia

Country	Total area planted (million ha)		Area planted with HYVs (%)	Production (million tons)		Increase in production (%)
	1966	2000		1966	2000	
Bangladesh	9.1	10.7	65	14.3	35.8	150
China	31.3	30.5	100	98.5	190.1	93
India	35.2	44.6	73	45.6	134.1	194
Indonesia	7.7	11.5	77	13.6	51.0	275
Myanmar	4.5	6.3	72	6.6	21.3	222
Pakistan	1.4	2.3	42	2.0	7.0	250
Philippines	3.1	4.0	89	4.1	12.4	202
Sri Lanka	0.5	0.8	91	1.0	2.8	180
Thailand	7.3	10.0	68	13.5	23.4	73
Vietnam	4.7	7.6	80	8.5	32.5	282

was discovered by Welhelm G. Solheim II in 1966 (Solheim 1972). Pottery sherds bearing the imprints of grain and husks of *O. sativa* were discovered at Non Nok Tha in the Korat area of Thailand. The remains were dated to about 4000 BC. The oldest carbonized grains found in India date to about 6750 BC (Sharma and Nanda 1980). The oldest remains of cultivated rice in China date to five centuries before Christ. Carbonized rice grains from Tongxiang County of Zhejiang province were identified as being 7,040 years old.

The African cultivar *O. glaberrima* originated in the Niger River delta. The primary center of diversity for *O. glaberrima* is the swampy basin of the upper Niger River and two secondary centers to the southwest near the Guinean coast. The primary center was probably formed around 1500 BC, while the secondary centers were formed 500 years later (Porteres 1956).

### 1.1.2

#### Dispersal of Cultivated Rice

From the Himalayan foothills rice spread to western and northern India, to Afghanistan and Iran and south to Sri Lanka. The date of 2500 BC has been established for Mohenjodaro in Pakistan, while in Sri Lanka rice was a major crop as early as 1000 BC. The rice crop may well have been introduced to Greece and neighboring countries of Mediterranean by returning members of Alexander the Great's expedition to India in 324 BC. However, in all probability rice did not become an established crop in Europe until much later,

perhaps in the 15th century. Rice was introduced from India to Madagascar, to East Africa, and then to countries of West Africa. Indica rices also spread eastward to Southeast Asia and north to China.

The japonica rice was most likely domesticated somewhere in northern parts of Southeast Asia or southern China. It moved north to become a temperate japonica. From China temperate japonicas were introduced into Korea and from Korea to Japan around the beginning of the first century. In the hilly areas of Southeast Asia, japonica rices were grown under upland culture as a component of shifting cultivation before the upland tribes moved into lowlands and introduced the japonicas into lowland culture. From mainland Southeast Asia, both indica and japonica rices were introduced into Malaysia, the Philippines, and Indonesia and from the Philippines to Taiwan. Migrating Malays from Indonesia introduced tropical japonicas to Madagascar in the 5th or 6th century. Portuguese priests introduced the tropical japonicas from Indonesia to Guinea Bissau, and from there they spread to other West African countries. Thus most of the upland rice varieties grown in West Africa are tropical japonicas. The Portuguese also introduced tropical japonicas and lowland indicas to Brazil, and Spanish-speaking people brought them to other Latin American countries. Thus in Brazil today most of the upland varieties are tropical japonicas and the lowland varieties are indicas (Khush et al. 2003). The first record of rice in the U.S. dates from 1685, and it was probably introduced from Madagascar with the slave trade.

**Table 2.** Chromosome number , genomic composition , and geographical distribution of *Oryza* species

Species	2n	Genome	Distribution
<b><i>O. sativa</i> complex</b>			
<i>O. sativa</i> L.	24	AA	Worldwide
<i>O. nivara</i> Sharma et Shastry	24	AA	Tropical and subtropical Asia
<i>O. rufipogon</i> Griff.	24	AA	Tropical and subtropical Asia, tropical Australia
<b><i>O. breviligulata</i> A. Chev. et Roehr.</b>			
<i>O. glaberrima</i> Steud.	24	AA	Africa
<i>O. longistaminata</i> A. Chev. et Roehr.	24	AA	West Africa
<i>O. meridionalis</i> Ng	24	AA	Africa
<i>O. glumaepatula</i> Steud.	24	AA	Tropical Australia
<b><i>O. officinalis</i> complex</b>			
<i>O. punctata</i> Kotschy ex Steud.	24, 48	BB, BBCC	South and Central America
<i>O. minuta</i> J.S. Pesl. ex C.B. Presl.	48	BBCC	Africa
<i>O. officinalis</i> Wall ex Watt	24	CC	Philippines and Papua New Guinea
<i>O. rhizomatis</i> Vaughan	24	CC	Tropical and subtropical Asia, tropical Australia
<i>O. eichingeri</i> A. Peter	24	CC	Sri Lanka
<i>O. latifolia</i> Desv.	24	CC	South Asia and East Africa
<i>O. alta</i> Swallen	48	CCDD	South and Central America
<i>O. grandiglumis</i> (Doell) Prod.	48	CCDD	South and Central America
<i>O. australiensis</i> Domin.	48	CCDD	South and Central America
<b><i>O. meyeriana</i> complex</b>			
<i>O. granulata</i> Nees et Arn. ex Watt	24	EE	Tropical Australia
<i>O. meyeriana</i> (Zoll. et (Mor. ex Steud.) Baill)	24	GG	South and Southeast Asia
<b><i>O. ridleyi</i> complex</b>			
<i>O. longiglumis</i> Jansen	48	GG	Southeast Asia
<i>O. ridleyi</i> Hook. F.	48	HHJJ	Irian Jaya, Indonesia, and Papua New Guinea
<b>Unclassified</b>			
<i>O. brachyantha</i> A. Chev. et Roehr.	48	HHJJ	South Asia
<i>O. schlechteri</i> Pilger	24	FF	Africa
	48	HHKK	Papua New Guinea

### 1.1.3

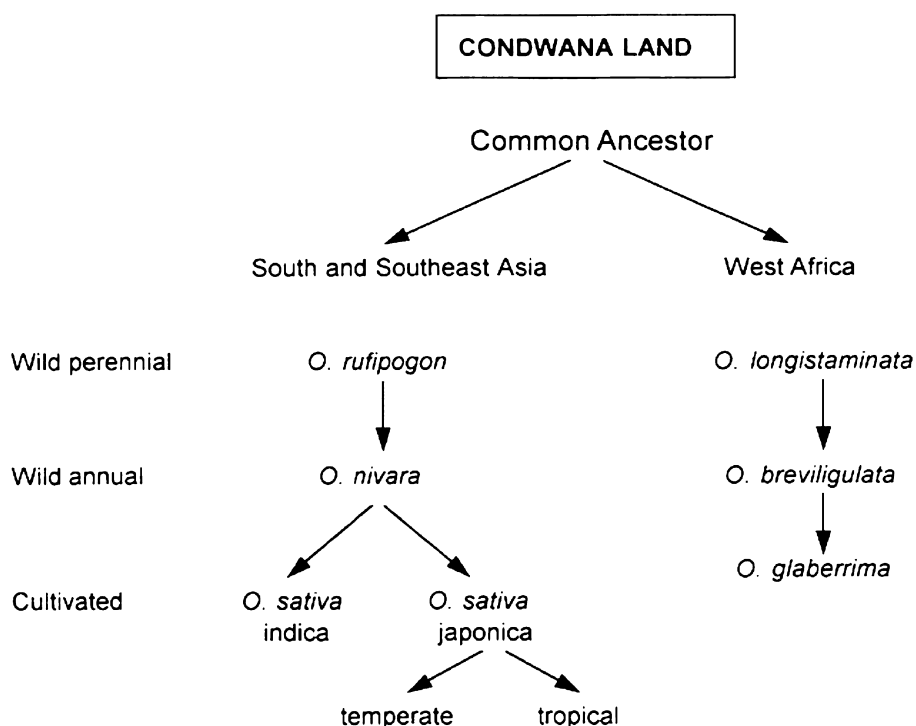
#### Varietal Diversity of Rice

From its subtropical origin rice is now cultivated between 55° N in China and 36° S in Chile. Cultivation and farmer selection for centuries under varied growing conditions have resulted in a myriad of rice varieties. An estimated 120,000 distinct rice varieties exist in the world. Approximately 80,000 are preserved in the Gene Bank of the International Rice Research Institute (IRRI) in the Philippines. China has about 40,000 and India about 25,000 in their gene banks. Other countries have smaller selections.

Rice varieties differ in numerous morphological and physiological traits and have been selected

for adaptation to different growing conditions. Some mature in less than 80 d from sowing. Others, like Rayada rices of Bangladesh, have a growth cycle of about 280 d. These are photoperiod-sensitive deep-water rices and are planted with the onset of rains in March and harvested in December. Rice varieties also differ in endosperm traits, which determine their acceptability to various consumer groups. While the vast majority of rice varieties are nonglutinous, glutinous varieties form the everyday diet of the people of Laos and northeast Thailand. Most of the major rice-growing countries have a few aromatic varieties that are prized on the market. Varieties differ in the level of cold tolerance and tolerance to other abiotic stresses such as drought, submergence, and salinity. There are

**Fig. 1.** Evolutionary pathways for two cultivated species of rice



differences in resistance to diseases and insects. In some countries, varieties are classified according to the season in which they are grown. For example, in Bangladesh, where rice is grown throughout the year, varieties have been selected for adaptation to following seasons (Khush 1997).

1. Boro: Winter rice, transplanted, cold tolerant, grown December to May
2. Aus: Summer rice, broadcast, sown, drought tolerant, short life cycle, grown April to July
3. Transplanted Aman: Autumn sown, transplanted, photoperiod sensitive, grown July to December
4. Broadcast Aman: Deepwater, photoperiod sensitive, grown March to December
5. Ryadas: Deepwater, photoperiod sensitive, very long duration, grown March to December
6. Ashina: Deepwater aus, broadcast sown, grown April to August
7. Hill Rice: Grown on upland fields, usually on sloping hillsides, direct seeded, grown June to September

Similar varietal differentiations exist in southern India and Sri Lanka, where rice is grown throughout the year.

#### 1.1.4

#### Rice Varietal Improvement

Since its domestication about 10,000 years ago, rice has undergone tremendous modifications so much as a result of human selection for improved traits that domesticated rice varieties can no longer survive in the wild state. The simple acts of reaping and sowing are selective. Our ancestors may not have known it, but they started the first rice-breeding programs when they began to grow rice plants for their use. Most farmers have a keen eye and a sensitive feeling for plants. Millions of farmers have applied this keen insight and sensitivity for thousands of years to select diverse varieties. Selection was first practiced on the variable and heterogeneous wild and semiwild populations, which must have narrowed the genetic variability. However, several mechanisms in primitive agriculture, such as the introduction of varieties from one region to another and occasional natural crosses, enhanced variability for further selection. Natural crosses between domesticated crop and the weed complexes were another source of variability. The third source of variability was varietal mixtures that primitive agriculturists grew as a protection against disease epidemics. Occasional intercrosses between component varieties generated variability. This

conscious and unconscious selection by humans led to the development of over 120,000 rice varieties grown around the world.

Thus farmers themselves were responsible for most rice improvement from the time of its domestication to about 1900. The best known examples are the “rono” varieties such as “Shinriki” that Japanese farmers selected in the 1890s. The rono varieties are shorter and therefore responded to nutrient inputs with higher yields. Rice-breeding stations were established in China, India, and Japan in the early 20th century. Rice breeders’ initial activities were the purification of existing varieties (landraces) through pure line selection. This resulted in pure line varieties. Up to the 1960s rice farmers in tropical and subtropical Asia grew thousands of landraces or pure line varieties, and few had been touched by modern agricultural science. These varieties were tall and weak stemmed and late maturing. When nitrogenous fertilizer was applied at rates exceeding 40 kg/ha, traditional varieties tillered profusely, grew excessively tall, lodged early, and yielded less than they would have with lower fertilizer inputs.

The International Rice Research Institute (IRRI) was established in 1960 in the Philippines to address the problems of stagnant yields. A major breakthrough in raising the yield potential of tropical rice came with the development of IR8 at IRRI in 1966, which resulted in a doubling of the yield potential of rice. IR8 has a short stature and a combination of several other agronomic traits such as sturdy stems for lodging resistance, dark green and erect leaves, and high tillering capacity. Because of lodging resistance it is highly responsive to fertilizer. Since the development of IR8 a series of improved rice varieties have been developed at IRRI and by the National Agricultural Research Systems (NARS). These varieties have been improved in many other traits such as grain quality, disease and insect resistance, growth duration, and tolerance to abiotic stresses. More than 300 varieties have been selected from the breeding materials developed at IRRI (Khush and Virk 2002). These and others developed by NARS are now planted on 80% of the world’s rice land. Because of widescale adoption of these varieties and associated technology, world rice production increased 135% in a 35-year period from 257 million tons in 1966 to 600 million tons in 2000, and, during the same period, average rice yield increased from 2.1 t/ha to 3.9 t/ha. Most of the major rice-growing countries achieved self-sufficiency in rice.

During this intensive breeding effort rice varieties have been developed that have genes from various ecotypes of rice. Even the genes from wild species have been introduced into modern varieties. Thus the ecotypic differentiation present in the landraces of rice no longer exists in the improved varieties. Genes from numerous landraces have been incorporated into new varieties. For example, widely grown IR64 has 20 landraces in its ancestry (Khush 1987).

### **1.1.5 Rice-Breeding Challenges in the 21st Century**

World population continues to increase by 75 million people a year, an annual growth rate of 1.3%, with 90% of this increase occurring in the developing countries of Asia, Africa, and Latin America. Providing for population growth now requires an expansion in world grain production of 26 million tons per year. Moreover, owing to rising living standards, food habits are changing in many countries, particularly in Asia, and people are eating more high-value foods such as meat, eggs, and milk. This is driving the demand for grain at a rapid rate. A kilogram of beef produced in the feedlot requires 7 kg of grain, a kilogram of pork needs 4 kg, and a kilogram of poultry needs just over 2 kg (Brown 1997).

More than a billion people in developing countries live below the poverty line and have poor access to food. As poverty-alleviation programs in developing countries make an impact, the purchasing power of poor people will increase, as will the demand for food grains. Based on population projections and improved consumption patterns in developing countries, it is estimated that rice production must increase by 40% during the next 20 to 25 years or at the rate of about 1.1% a year. This increase will have to be achieved from less land, with less water, less labor, and fewer chemicals.

To feed 5 billion rice consumers in 2025, we have to develop rice varieties with higher yield potential and greater yield stability. Crop cultivars with higher yield potential are the key to increased productivity. Conventional hybridization and selection procedures will continue to be employed, but breakthroughs in cellular and molecular biology will be increasingly used in rice improvement. Transformation techniques allow us to introduce novel genes from unrelated sources to accomplish breeding objectives not possible through conventional breeding approaches. For example, none of the rice varieties or related wild species has beta

carotene, a precursor of vitamin A, and rice varieties with vitamin A could not be developed. Ye et al. (2000) introduced three genes, two from the daffodil (*Narcissus pseudonarcissus*) and one from the bacterium *Erwinia uredovora* into rice variety Taipei 309. This led to the establishment of a biosynthetic pathway for the production of beta carotene in rice endosperm. This so-called “golden rice” will have a great impact in alleviating vitamin A deficiency among poor rice consumers.

## 1.2 Construction of Molecular Linkage Maps in Rice

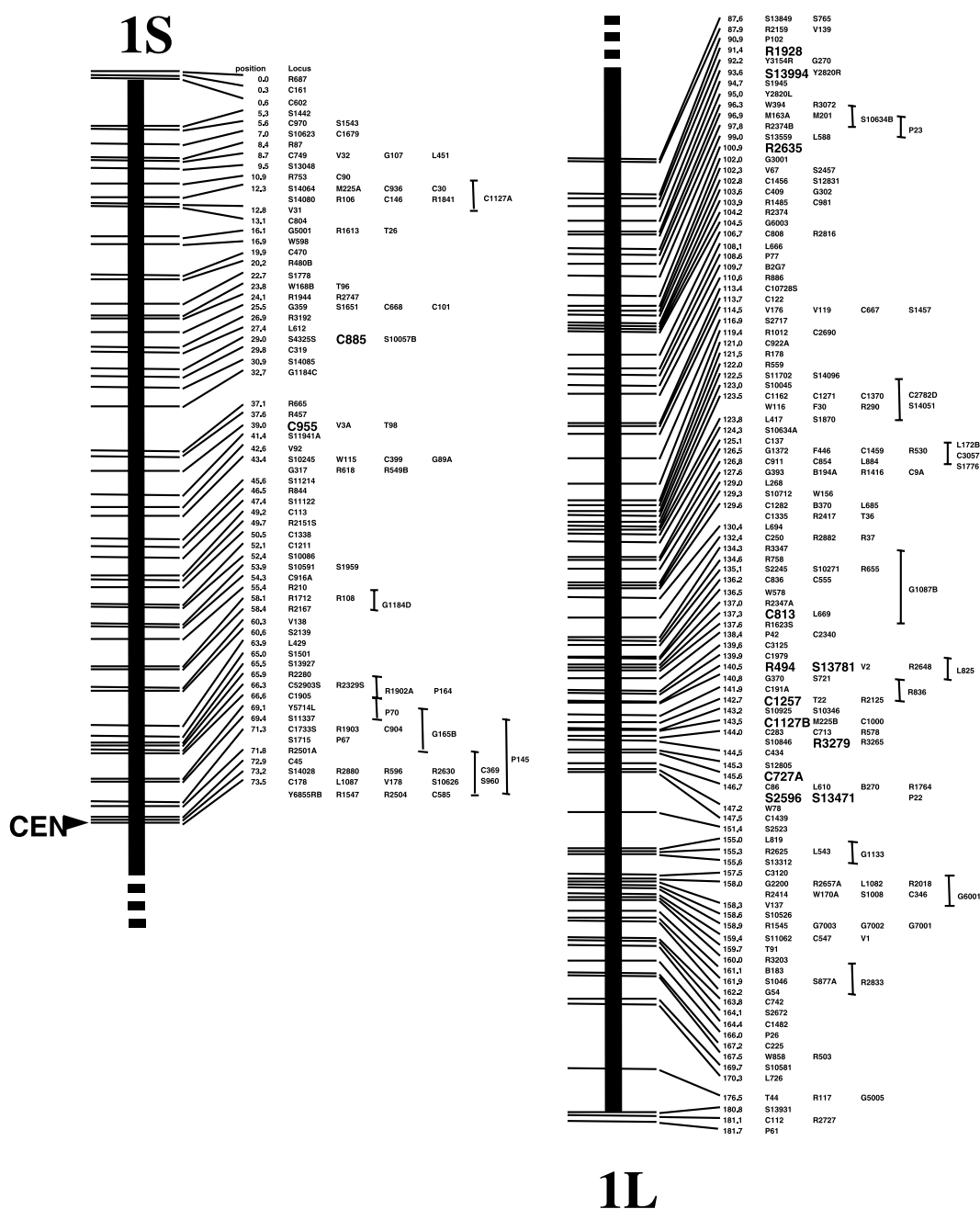
Genetic mapping means the identification of the location of polymorphism between parental lines that generate progenies used for statistical analysis of recombination frequency. The polymorphisms used are observed both in appearance and nucleotide sequence in genomic DNA. It is well known that Gregor Mendel succeeded in establishing the law of inheritance because he used nearly genetically pure common pea lines for target traits such as plant height or roundness of seed in his experiments. For genomewide mapping using polymorphisms in the nucleotide sequence, the parental lines must be genetically pure or homogeneous as well in terms of the target loci. In the case of rice, homogeneity in the genetic background of the parental lines can be achieved by repeated self-pollination for 5 to 6 generations. In non-self-pollinating plant species, genetic analysis can be performed by a pseudotest cross-analysis method using  $F_1$  siblings. The basic idea in generating genetic maps of both self-pollinating and non-self-pollinating plants is to detect recombination between markers of phenotype or DNA. This chapter focuses on the genetic analysis of rice, which is a purely self-pollinating plant.

Historically, mapping of rice was tried first by linkage analysis of appearance, or phenotype (Nagao and Takahashi 1963). Several phenotypes that could be easily identified and evaluated, such as waxy, dwarfism, chlorosis, or disease resistance, were chosen for genetic mapping, which led to the development of the 12 linkage groups of rice. After this remarkable work, improvement of the linkage map was achieved using isozymes such as esterase instead of phenotypes (Nakagahra 1977). The use of isozyme was the first step in innovating the linkage map by molecular tools.

The correspondence of linkage groups and chromosomes was achieved by using trisomic rice plants with representative phenotype (Iwata and Omura 1984; Khush et al. 1984). The current numbering of chromosomes and linkage groups was unified in 1990 at the 2nd International Rice Genetics Conference (Khush 1990).

In 1986, the utility of polymorphism in genomic nucleotide sequences was first shown to be effective in tagging the human inheritable disease Huntington's disease (Botstein et al. 1980). This linkage analysis of phenotype with DNA markers led to the success in identification of the gene controlling the corresponding phenotype. Subsequently, several efforts focused on detecting polymorphisms of nucleotide sequence to generate many DNA markers distributed all over the genome of a target species. The most reliable polymorphism is restriction fragment length polymorphism (RFLP) because it can be detected as a codominant trait in Southern hybridization. Other conventional polymorphisms such as random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP), which are less time consuming but costly and less reliable as compared to RFLP, are more widely used in linkage analysis. In the case of rice, the first molecular linkage map with 135 loci defined by RFLP markers was published in 1988 using 50 progenies derived between a cross of japonica and indica cultivars of *O. sativa* (McCouch et al. 1988). This pioneered the possibility of molecular genetic analysis of the rice genome further promising the gene identification corresponding to phenotype.

After this first endeavor, several groups in Japan continued the effort to increase the number of RFLP markers for a more detailed and accurate genetic anatomy of the rice genome. In Japan, one of the countries where rice is a main staple, a pilot project of development of genetic maps with genomic RFLP markers (Saito et al. 1991) was immediately followed in 1991 by a large-scale and systematic construction of a map with high-density DNA markers mainly of RFLP. The analyzed population was 186  $F_2$  plants obtained by a cross between japonica cultivar Nipponbare and indica cultivar Kasalath, and the first map constructed carried a total of 883 markers (Kurata et al. 1994). The markers were mainly derived from rice cDNAs randomly selected from several libraries and partially sequenced from both ends. These markers, which correspond to expressed genes from the rice genome, are more advantageous than random genomic DNAs because their mapped positions will



**Fig. 2.** Rice molecular genetic map with 2,275 markers (Harushima et al. 1998) developed using 186 F<sub>2</sub> population from the cross Nipponbare × Kasalath

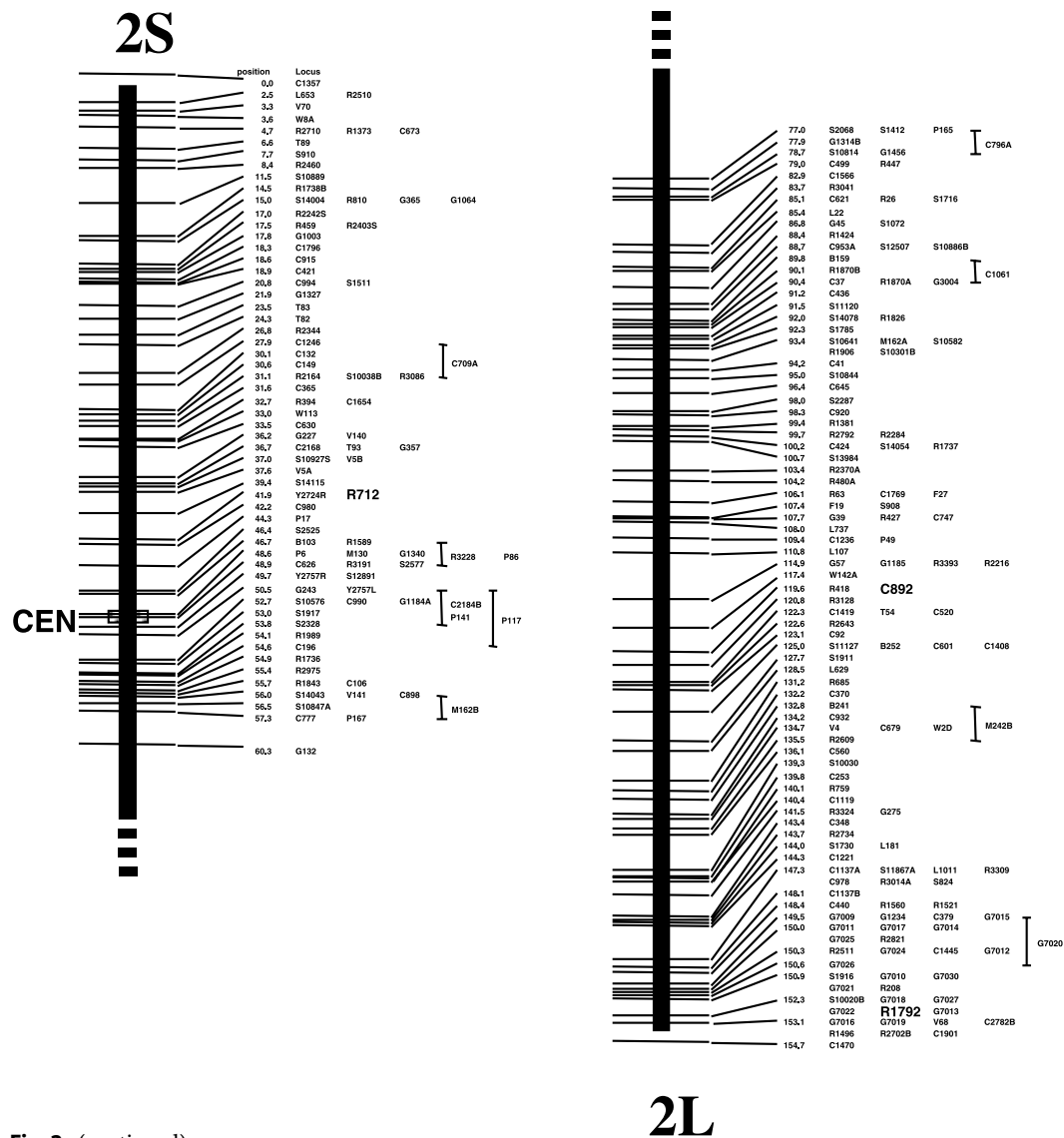


Fig. 2. (continued)





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Cereals and Millets

Kole, C. (Ed.)

2006, XXIII, 349 p., Hardcover

ISBN: 978-3-540-34031-7