

Breeding Field Crops: History, Current
Status and Introspections

K. K. Vinod, S. Gopala Krishnan, Manoranjan Senapati, and Ashok Kumar Singh

Abstract

Agriculture is the fundamental basis of human evolution and has evolved itself as the civilisations progressed. Crop breeding is a process in which the most chosen plant is selected for further cultivation. The science behind the genetics has paved the way to trait-based breeding, wherein desirable traits were selected over the undesired ones. The breeding work in India began mainly with the widespread evaluation of wheat genotypes for the improvement of grain, straw and rust resistance. This was followed by breeding for a number of crops including tobacco, sisal hemp, barley, flax and a few fruit tree species. In the year 1955, All India Coordinated Research Project (AICRP) was launched which has transformed the cultivar evaluation system and release in India. Even at the international level, there was an upsurge in the establishment of a number of crop-based non-profit research institutions. International Rice Research Institute (IRRI) was the first such institute which was opened in the year 1960 at Philippines. Breeding efforts in India is yet to venture deep into the genomicsassisted breeding including genomic selection and gene editing in majority of the field crops, although the research in this direction is progressing. Recent efforts towards the integration of technologies to translate breeding success into genetic gain are also discussed. With this backdrop, this chapter gives a brief about the key developments in the breeding history of field crops, particularly in India, during the last few decades. Also discussed are the future perspectives.

Crop improvement by breeding is a continuous process. Those who are engaged in this vital task have a hand in crop plant evolution and enjoy the pride and privilege of fighting the war against hunger - Anonymous.

K. K. Vinod \cdot S. Gopala Krishnan \cdot M. Senapati \cdot A. K. Singh (\boxtimes) Division of Genetics, ICAR-Indian Agricultural Research Institute, New Delhi, India

D. K. Yadava et al. (eds.), Fundamentals of Field Crop Breeding, [https://doi.org/10.1007/978-981-16-9257-4_1](https://doi.org/10.1007/978-981-16-9257-4_1#DOI)

Keywords

Breeding methods · Green revolution · Marker-assisted selection · Genomic selection · Genetic gain

1.1 Introduction

Agriculture is a tradition as old as human civilisation. Since time immemorial, agriculture was a gatherers' pursuit wherein the grains, roots, fruits and nuts were collected by the early hunters. Evidence for the use of cereal seeds such as sorghum grasses dating back to 0.11 million years in the Late Pleistocene was seen from the starch granule assembly on the surface of middel stone age tools (Mercader [2009\)](#page-35-0). Humans started organised agriculture much later in the Holocene, about 10,000 years ago, with the collective domestication of several grain species such as wheat, rice, barley and chickpea (Eckardt [2010](#page-33-0); Willcox et al. [2009](#page-36-0); Zuo et al. [2017\)](#page-37-0). However, the crop improvement by breeding began only in the late nineteenth century with the rediscovery of Mendel's research findings. In breeding, selection is the crucial step that requires a multitude of factors and methods to achieve the breeding objective. Starting from intuitive selection to genomic selection, the process requires diversity to choose from. Therefore, generating new varibility is crucial in crop breeding.

All the methods, be it for generating variability and/or for deciding to select, are fundamentally anchored to the science of genetics. Breeding crop varieties revolves around two elemental phenotypic dimensions, namely, quantitative and qualitative. Quantitatively, the need 'for producing more to feed more', is the primary dimension that safeguards the food security for the growing world population; while the second defines how well the crop produce serves as the food and feed. All other breeding objectives such as adaptation, tolerance to stresses, and resilience can be mapped onto these basic dimensions.

Unlike, during the early Holocene when agriculture was mainly in the subsistence mode, in the Anthropecene era, it has metamorphosised into an industry. Thereby another dimension of 'commercial' has been sandwiched between the two basic dimensions of crop breeding. This had brought in a dramatic evolution in agricultural research globally, particularly in crop breeding. The most historical outcome of this evolutionary transformation was the 'green revolution', which brought in a paradigm shift in the way modern cultivars are bred.

Since the onset of the twentieth century, there have been consistent efforts to control and understand the pattern of plant evolution. The contemporary birth of the new sceince of genetics has spearheaded artificial hybridisations resulting in identifying a better variant on a continuous scale facilitated by combining more than one desirable trait at a time. This has led to the refinement of the selection process in breeding. Besides, a weightage was attached to some traits such as yield

over the other, during the selection process. The breeding process has become more systematic, thanks to the laws of inheritance by Gregor J. Mendel, who demonstrated the possibility of predicting the occurrence of variation in a breeding population. Later into the century, heredity has seen its molecular definition through the discovery of deoxyribonucleic acid (DNA) structure by Watson and Crick in 1953. A parallel development in mathematical and statistical predictions, invented by R.A. Fisher, in combination with landmark genetic discoveries of T.H. Morgan, A. H. Sturtvent, W. Bateson, G.W. Beadle, E.L. Tautum, O.T. Avery, C.M. MacLeod, M. McArty, S. Benzer, J.B.S. Haldane, J. Lush, etc., laid out the foundation for the architecture of modern plant breeding.

Humans use only 0.03% of the total flowering species for food. Among the 347,298 known species of vascular plants worldwide (WCVP [2020;](#page-36-0) Cheek et al. 2020 , 50,000 are edible, but only \sim 120 are cultivated for food (FAO [1996\)](#page-33-0). Among these, just three crops, namely, rice, wheat and corn, supply more than 60% of the world's dietary energy. In addition, oilseeds, legumes and millets contribute more than 15% of the calories (Loftas [1995\)](#page-34-0). These crops, collectively known as field crops form the backbone of global food security. Majority of the field crops are annuals that produce staple grains in human food. They are cultivated in vast areas and occupy lands all around the world. Among the various species humans have domesticated, no other group of crops have undergone rigorous breeding efforts like that of field crops leading to significant changes in the trait forms making them amenable for intensive cultivation.

1.2 Chronicling Breeding for Improvement of Field Crops in India

The breeding efforts in food staples have been tremendous during the last century. Current estimates indicate that food demand will go up by 36–56% from the period between 2010 to 2050 and, meanwhile the people at risk of hunger will shift sharply from -91% to 8% (van Dijk et al. [2021](#page-36-0)). Crop breeding needs to be continuously impressive as it was, in the coming decades too to meet such a formidable challenge. This is highly relevant to India, which at present harbours 17.7% of the world human population with a meagre 2.4% land share (Kumar [2011](#page-34-0)), and having an alarming annual population growth rate of 1.0%. At the current rate, one per cent of the Indian population is about 14 million, more than half the size of the population in Australia, which means India adds more than one Australia every two years. Historically, India has always been at the forefront of agricultural development worldwide. A subcontinent that has been struggling to sustain agriculture since the beginning of the twentieth century with continuous famines and crop failures, India was almost absent in the world agricultural map at the beginning of the twentieth century.

Follwing the recommendations of Famine Commission of 1980, the Department of Agriculture under the Goverment of India was revived, alongwith setting up of several provincial agricultural departments. In 1903, the British Indian Government decided to establish a Central Agricultural Research Institute under the Department

of Agriculture to introduce scientific agriculture in India. Consequent inauguration of the Agricultural Research Institute and College in 1905 at Pusa in Bihar marked the beginning of organised agricultural research in India (Howard and Howard [1929\)](#page-34-0). Breeding research at the Agricultural Research Institute began with the extensive evaluation of wheat cultures, with a main emphasis on hybridisation to improve grain, straw and rust resistance. Breeding for other crops such as tobacco, sisal hemp, barley, flax and a few fruit trees was also taken up (ARIC [1909\)](#page-33-0). Agricultural Research Institute and College was later renamed as Imperial Agricultural Research Institute in 1919, and then as Indian Agricultural Research Institute (IARI).

Contemporarily, rice breeding research was initiated in Bengal and Madras provinces with the setting up of several research stations. The Royal Commission of Agriculture in 1928 proposed to scale up and coordinate the agricultural research pan India, by establishing an Imperial Council of Agricultural Research (GoI [1928\)](#page-33-0). The Imperial Council of Agricultural Research established in 1929 was rechristened as Indian Council of Agricultural Research (ICAR), and provided with extensive mandate on different crops. Understanding the immediacy of independent research, ICAR had established several crop-specific research institutes at different locations at different time (Table [1.1\)](#page-4-0).

Among the crops, rice pioneered in setting up of research establishments in India. Although the rice research had begun during the 1911–12 period, only Bengal and Madras provinces were endowed with research, until the establishment of ICAR. Further, several research stations were established, and by 1950, there were 82 research stations spread across 14 states (Ghose et al. [1960](#page-33-0)). The launch of the All India Coordinated Research Project (AICRP) in 1955 reformed the cultivar evaluation system and release in India. The major mandate of AICRP was to coordinate applied research on national and regional issues and to develop location-specific varieties and technologies in various crops. The first crop-based project was started for maize in 1957, and was named All India Co-ordinated Maize Improvement Project (AICMIP). Subsequently, the All India Coordinated Rice Improvement Project (AICRIP) was established in 1965. Later on, several cropbased coordination projects were initiated by ICAR at different crop research institutes. These institutes were provided with regional research stations covering all major production zones of the respective crops. Currently, every field crop has an independent AICRP system, that links several agricultural universities, institutes and private research organisations, who are involved in varietal/ technological development, evaluation and release. As a whole, AICRP has grown to be the single largest varietal evaluation and release system in the world. Additionally, to make agriculture support countrywide, state governments have opened several agricultural universities and research stations to cater for the need of local farmers and to provide agricultural education. Crop improvement by breeding is one of the major mandates of all crop-based research institutions.

Year	Institute	Location	Mandate $Crop(s)$
1905	Agricultural Research Institute and College ^a	Pusa	Wheat, barley, tobacco etc.
1937	Indian Agricultural Research Institute ^b	New Delhi	Wheat, barley, rice, legumes, Brassica, horticultural crops
1946	Central Rice Research Institute (presently National Rice Research Institute)	Cuttack	Rice
1976	Central Institute for Cotton Research	Nagpur	Cotton
1977	Directorate of Oilseeds Research ^c (presently Indian Institute of Oilseed Research)	Hyderabad	Oil crops
1978	Directorate of Wheat Research ^c (presently Indian Institute of Wheat and Barley Research)	New Delhi	Wheat
1979	Directorate of Groundnut Research ^c	Junagadh	Groundnut
1983	Directorate of Rice Research ^c (presently Indian Institute of Rice Research)	Hyderabad	Rice
1984	Directorate of Pulses Research ^c (presently Indian Institute of Pulses Research)	Kanpur	Grain legumes
1987	National Research Centre for Sorghum ^c (presently Indian Institute of Millets Research)	Hyderabad	Sorghum
1993	National Research Centre on Rapeseed and Mustard (presently Directorate of Rapeseed-Mustard Research)	Bharatpur	Brassica
1994	Directorate of Maize Research ^c (presently Indian Institute of Maize Research, Ludhiana)	New Delhi	Maize

Table 1.1 Establishment of major field crop-specific institutes in India under ICAR

a Renamed as Imperial Agricultural Research Institute in 1919

^bShifted to New Delhi following the destruction of IARI at Pusa in Bihar earthquake of 1935 c Instituted as AICRP, and later given independent research status

1.3 Role of International Centres in Strengthening the Breeding Efforts

Contemporary to the inception of agricultural research institutions in India, globally, there was a rise in installations of crop-based non-profit international research institutions. The first among these, the International Rice Research Institute (IRRI) was opened in 1960 at Los Baños, Laguna, in the Philippines. Subsequently, International Maize and Wheat Improvement Centre (CIMMYT) came into being in 1966, as a scientific and educational institution exclusively involved in wheat and maize research. The year 1967 saw the opening of two more institutions, the International Institute for Tropical Agriculture (IITA) in Nigeria and the International Centre for Tropical Agriculture (CIAT) in Columbia. Instituted in 1971 at Montpellier in France, the Consultative Group of International Agricultural Research (CGIAR) brought the international institutions under its governance. Currently, there are 15 research centres under CGIAR, of which seven works on tropical field crops. The major activity of these centres is breeding, besides other allied technological development.

As per the 2020 performance report of the CGIAR, 78% of its innovations were genetic with 66% impact directed to alleviate poverty and 15% directed to nutritional security (CGIAR [2020\)](#page-33-0). Sixty years into existence, international research organisations could transform agricultural research worldwide sowing the foundations of the green revolution in major cereals such as wheat and rice. The noble efforts of Dr. Norman E. Borlaug in developing high yielding, semi-dwarf and disease-resistant wheat varieties, which ensured food security in countries like India, Mexico and Pakistan have earned him the popular title of 'father of green revolution' as well as a Nobel peace prize in 1970 (Swaminathan [2009](#page-36-0)), besides several others. Aided by Dr. Norman Borlaug in wheat and IRRI in rice, Dr. M. S. Swaminathan spearheaded transformative research in India from the fields of IARI in 1966. The results were remarkable, a quantum jump of 42% increase in wheat production could be achieved in one year. Three genes governing plant height, namely, *rht1* and *rht2* from Norin 10 in wheat and sdl from Dee-Geo-Woo-Gen (DGWG) in rice, were responsible for this phenomenal achievement in the history of crop evolution. This gave an impetus to the breeding research in India and breeders geared up this momentum to deliver scores of improved cultivars in the ensuing decades in all the field crops.

1.4 Breeding Research on Field Crops

Until the beginning of the twentieth century, no organised breeding efforts had taken place in field crops, anywhere in the world. The breeding research in India also evolved simultaneously with similar efforts across the globe. Drawing parallel to the developments in the science of genetics, different breeding methods dominated the landscape of field crop improvement from time to time in India. In Fig. [1.1](#page-6-0), we have taken rice as the model crop to demonstrate the evolutionary pattern of breeding methods, because rice was not only genetically rich in India but also had undergone all the breeding methods developed so far. We would, therefore, be focussing our discussions in this chapter based on Indian experience on breeding methodologies during the past century and their evolution, establishment and impact made on improving different field crops. Also, elaborate details of individual crops will not be covered except for the key landmarks, keeping in mind that such details would be following in subsequent chapters dealing with different field crops.

In the early twentieth century, the indigenous cultivars in India were of genetically admixed populations. Admixed populations had extreme variability within, because of the significant proportion of wild alleles they carried. Since these populations did not undergo serious selection for yield, the wild alleles were more aligned to adaptation, rather than productivity. Because of these, the cultivars were

Fig. 1.1 Evolution of breeding methodologies in rice improvement. Unlike in rice, introduction of elite genetic materials had begun in other field crops much earlier (denoted by the dotted lines). Introduction in rice has been comparatively intermittent

tall, prone to lodging, hardy, less yielding, photosensitive and took longer time to yield. Although selections were carried out among these populations in the early years, only marginal yield improvement could be realised initially. However, beginning from the 1960s breeding research has started to become more organised, with the plans of pan India integration of varietal release systems and institutional research. This movement in research organisation paid off with the development and release of newer cultivars and invigorated research systems sowing the seeds of the green revolution in the coutry. A glance at the productivity spectrum of major field crops (Fig. [1.2](#page-7-0)) reveals that all the crops have experienced a yield gain of at least by a minimum of 107% as in red gram to 539% in maize in the next 70 years. The next highest yield increase was in wheat (516%), followed by cotton (513%), pearl millet (475%) and rice (405%).

1.4.1 Introduction

The initial part of the organisational plant breeding efforts in India was laden with scores of introductions of crop varieties from abroad. Owing to its rich indigenous diversity, introductions in rice were intermittent, but in other field crops such as wheat and maize, a considerable number of genotypes were introduced, particularly through international centres. Several direct introductions happened during the pre-green revolution period. The activity was so intense and programmed, a separate Division of Plant Introduction for coordinating the imports from abroad was started at IARI in 1961 (Pal [1962](#page-35-0)). The Division later became the current National Bureau of Plant Genetic Resources (NBPGR) in 1976. Among the most notable field crop introductions in IARI were Ridley from Australia; Lerma Rojo 64, Sonora 64 and PV18 from Mexico in wheat; LSB2 and Dolma from the USA; Clipper from

Fig. 1.2 Productivity of major field crops in India, between 1950 and 2020. Except for three crops, productivity increase was more than 200% during this period. *Crops such as sunflower, lentil and soybean were later introductions and their base data is of 1970. ¶ Sugarcane yield is given in quintals and not in kilograms. (Data source: GoI [2020](#page-34-0))

Australia in barley; IR8, IR20, IR36, IR50 and IR64 from the Philippines in rice; Peredovik and Aramvirikij from USSR in sunflower; Asiriya Mwitunde from Tanganyika (a territory in present Tanzania); Rehovot 33–1 from Israel; M13 from the USA in groundnut; Bragg and Lee, and Improved Pelican from the USA in soybean; and Improved Ghana from Ghana in pearl millet (Singh [1991\)](#page-36-0). Several of these introductions were directly absorbed into the breeding pipelines, while exceptional widely adapted genotypes were released as varieties. One of the most noted introductions was the first rice variety officially released worldwide by IRRI in 1966, IR 8 (Peng et al. [1999](#page-35-0)).

1.4.2 Pureline Selection

Besides the introduction, initial efforts were also focussed on selection in crops, with or without hybridisation. Before the green revolution in the mid-1960s, pureline selection was the common way of cultivar development in self-pollinated species like rice. Mostly involving local landraces and exotic introductions, there were hundreds of pureline rice varieties released across India. Among the success of pureline selection in India, GEB24 was a milestone rice cultivar. A selection from Konamani, also known as Athur Kichli Samba, a local landrace, GEB24 was considered as a spontaneous mutant. With its fine grain and high quality, GEB24 was officially released for cultivation in 1921 and is considered one of the first officially released crop varieties in India. GEB24 also served as one of the major parental lines in generating the initial breeding materials in IRRI, after its

establishment in 1960. By the end of 1965, there were 66 pureline selected rice varieties released in Tamil Nadu alone, out of 445 rice varieties released across India. Among these, outstanding releases were Dular, Latisail, Manoharsali, MTU 15 and Nagina 22, to name a few (Mishra [2002\)](#page-35-0). There were also noteworthy advancements in quality rice breeding, such as Type 3 (selection for Dehradooni Basmati), Basmati 370 and N105 (selection for Hansraj) and Type 9 (selection from Duniapat).

Unlike in rice, pureline selection in wheat did not sustain for a longer time in India, instead, hybridisation followed by pedigree selection was adopted as early as 1907 in Pusa (Howard [1909\)](#page-34-0). The first 20 years of Imperial Agricultural Research Institute witnessed the release of a few pureline selected wheat varieties such as NP4, NP6, NP12, Pb8, K13, K53, AO13, AO85, Motia, Bansi, Gulab, Arnej 206, etc. (Nagarajan and Singh [1997\)](#page-35-0). Although several of these lines were tested and grown in other countries, NP4 remained one of the most outstanding wheat varieties across the world for its grain quality. NP4 was selected from Mundia, an awnless landrace that had shown remarkable adaptability to varying environments in addition to its exceptional quality (Tomar et al. [2004](#page-36-0)). Within no time NP4 became the landmark contribution of IARI in its early history.

1.4.3 Recombination Breeding

Hybridisation and selection remained the most adopted breeding strategy among the field crops around the world. Among the early success of hybridisation in India, the most remarkable achievement was the 'nobilization of canes'. In sugarcane, interspecific hybridisation between Saccharum officinarum with S. spontaneum followed by backcrossing and selection could lead to the development of superior canes called 'noble canes' with high yield and sugar content (Barber [1915\)](#page-33-0). Subsequently, the improved canes coud revolutionize the sugar industry in India. In 1949, a most ambitious intersubspecific hybridisation programme was launched in rice under the aegis of the Food and Agricultural Organization (FAO), to combine the fertiliser responsiveness and hardiness of japonica with quality and adaptation of indica. Although the programme was not a great success, two popular varieties were evolved, namely, Mahsuri in Malaysia and ADT27 in India. Additionally, two more varieties, Malinja in Malaysia and Circna in Australia, were also released for cultivation under this programme.

The most important landmark in rice breeding came through the development of semi-dwarf varieties aided by the identification and introgression of sd1 gene. In 1961, Peter Jennings, a young agronomist from the USA was recruited to IRRI by the Rockefeller Foundation to investigate the dwarf rice. He came across a Taiwanese rice variety, Taichung Native 1 (TN1), that was widely grown. Semidwarf in nature, TN1 resembled its parent, Dee-geo-woo-gen (DGWG) for the plant height. Jennings made the first 38 crosses at IRRI, with 11 of them using DGWG or TN1 as one of the parents (Hargrove and Coffman [2006](#page-34-0)). The inheritance of semidwarfism was identified as single gene controlled. Later in 1963, Dr. Henry Beachell

made a selection of a line, IR8–288-3 from the F_4 generation of the Jennings' eighth cross, between Peta and DGWG. IR8–288-3, later became the 'miracle rice', IR 8. Introduced into India in the same year, IR8 was released for cultivation in the same name. IR8 could help boost the rice productivity by a whopping 150–200% in its first year of introduction, beginning to transform the face of agriculture itself from poverty-ridden to self-sufficiency.

The development of IR8 remains the most remarkable contribution of IRRI to the world. IR8 could cast the same magic spell worldwide, saving millions from poverty all across the major rice consuming countries like Bangladesh, Vietnam and India. Almost at the same time, a similar story was unfolding in wheat breeding too, wherein the dwarfing genes from a Japanese variety, Norin10 were utilised to develop semi-dwarf varieties. In the early 1960s, Dr. Norman E Borlaug in CIMMYT was striving to improve wheat yields in Mexico by using the semidwarfing trait. A series of crosses followed, and Dr. Borlaug could get exceptional success in his 8156th cross between Penjamo 62 and Gabo 55. Named as Ciete Cerros, 8156 was remarkably high yielding and could transform the wheat production scenario in Mexico by 1962. By the mid-1960s, Mexico became self-sufficient in wheat production. Introduced into Pakistan as Mexipak and Kalyan Sona in India, this variety scripted another chapter in the history of green revolution.

Although there were few hybridisation-based varieties released in rice before the 1960s, majority of the post-green revolution era varieties, both in India and elsewhere in the world were developed through hybridisation and selection. Among the nine hybridisation-based varieties released in Tamil Nadu before 1960, CO14 was the first variety released in 1940. As per the compiled information from the Directorate of Rice Development in India, there were 814 rice varieties released between 1969 to 2012, of which 89% came from pedigree breeding. Despite the huge number of varietal releases in India, only a handful went onto become 'mega varieties', having been grown in larger areas and for long time. The first mega variety released in India was Jaya, developed by crossing TN1 with Type 141.

Released in November 1968, Jaya soon replaced IR8 and TN1 that were ruling the rice production in the country. There was another variety, Padma (CR 28–25) released along with Jaya, and both became the torchbearers of the indigenously bred Indian rice under the AICRIP system (Hopper and Freeman [1969](#page-34-0)). Later on, other megavarieties were released, Swarna (MTU7029) in 1980, Savitri (CR1009) in 1983, Samba Mahsuri (BPT5204) and Pusa Basmati 1 in 1989 (Fig. [1.3a](#page-10-0)), Pusa 44 in 1994, Cotton Dora Sannalu (MTU1010) in 2000, Pusa Basmati 1121 (Fig. [1.3b](#page-10-0)) in 2005 and Pusa Basmati 1509 in 2013. The AICRIP system in India steadfastly increased the rice varietal output with an average upward trend (Fig. [1.4\)](#page-11-0). Although there were intermittent years with several releases such as 1978 and 2008, the average trend increased from 1–2 varieties per year during 1969 to 26 per year in 2012.

In the case of wheat, the initial focus of the erstwhile Imperial Agricultural Research Institute was to improve Indian varieties, which were of excellent grain quality. India majorly grows spring wheat and not winter wheat. One of the major problems with the local cultivars was the tall stature of the plants, which made them

Fig. 1.3 Some of the landmark varieties released from ICAR-IARI, New Delhi. (a) to (c): Pusa Basmati 1, the first semi-dwarf Basmati cultivar; Pusa Basmati 1121, a mega Basmati rice variety with maximum cultivation extent; Pusa RH 10, the first aromatic rice hybrid; (d) to (e): Two wheat mega varieties, HD2967 and HD3086 with remarkable scale of adoption; (f) Vivek QPM 9 Improved, the first QPM hybrid enriched with Pro-vitamin A; (g) Pusa 23, a pearl millet hybrid with A1 cytoplasm; (h) Pusa 10216, MAS-derived chickpea variety with drought tolerance

Fig. 1.4 Number of rice varieties released per year between 1969 and 2012 in India, mostly channelled through the AICRIP system. Dotted line indicates 10 years moving average. (Data source: Directorate of Rice Development, Patna)

prone to lodging. An additional problem was the rust disease. Therefore, the initial breeding emphasis was to improve rust resistance, and due to this, the grain yield of Indian wheat varieties relatively remained below 2.0 tons/ha until the beginning of the 1960s. Although the wheat hybridisation at Pusa had started as early as 1907, it did not make the expected success. Contrary to the expectations, an earlier attempt of direct introduction was also met a dead end. Pal and Ramanujam [\(1944](#page-35-0)) observed that during the first 40 years of IARI, the 40% increase in wheat area had come with a reduction in productivity. Until the import of semi-dwarf wheat from Mexico having Norin 10 lineage, the situation did not improve.

The inception of the All India Coordinated Wheat Improvement Project (AICWIP) in 1965 was a gamechanger in the wheat history of India. The first set of varietal introductions from CIMMYT included Sonora 63, Sonora 64, Mayo 64 and Lerma Rojo 64. Introduced into cultivation, these varieties helped to double the wheat production within two years, ending the 60 years' drought for highyielding varieties. It was so coincidental that the green revolution in the major staple crops, rice and wheat, happened at the same time, orchestrated by three genes, Sd1 in rice and Rht1 and Rht2 in wheat, all controlling the same trait, semi-dwarfism. Borlaug's 8156 became the first wheat megavariety in India, in the name of Kalyan Sona. Kalyan Sona had both the *Rht* genes. The post-green revolution era in wheat witnessed a cascade of new varieties as happened in rice, with IARI playing a flagship role. Starting from UP301 released in 1969, varieties were evolved continuously, all with Mexican lines as one of the parents. Cultivars such as Hira, Moti, Janak etc., followed, finding niches in the timely sown, high fertility conditions. As the years advanced, newer wheat varieties sharing complex pedigrees began to show up. Further, high yielding varieties such as HD2189, HD2204 etc. were also got **Example 19 Example 19 Example 19 Example 19 Example 19 Example 19 Example 11 Fig. 114** Number of rice varieties released per year between 1969 and 2012 in India, mostly source. Directions the AICRIP system.

with the latest editions of high yielding cultivars such as HD2967, HD3086, HD3226 and HD3249, wheat varieties have often helped to touch the surplus production marks in India. Released in 2014, HD2967 and HD3086 (Fig. [1.3d, e](#page-10-0)) together currently occupy more than 50% of the wheat area in India (Mishra et al. [2020\)](#page-35-0). The role of CIMMYT derived wheat lines in cultivar release in India is immense, and several high yielding varieties such as the recently released variety, DBW222 are direct introductions.

Introduced into India in the seventeenth century, maize was not the crop of choice of the Indian population as its staple cereal, unlike that of rice and wheat. At the beginning of the twentieth century, maize was in cultivation as a primitive cereal, in the north-eastern and sub-Himalayan India. Besides, there were other landraces too, but very limited in number and acreage. By the turn of the twenty-first century, however, there was a marked shift in the priority of maize in India's staple food spectrum, by becoming the third major food staple after rice and wheat (Yadav et al. [2014\)](#page-36-0).

Elsewhere in the world too, maize cultivation was not as advanced as today during the beginning of the last century. In the USA for instance, yield lingered around 1.5 tons/ha during the 1900s to around 2 tons/ha until 1950, with the world average touching 1.9 tones/ha by 1960 (Duvick [2005](#page-33-0)). Maize yield began to rise sharply since the 1950s, however, there was no single cause that can be attributed to the yield boom, as that in the case of rice and wheat. However, the availability of nitrogenous fertilisers and concerted efforts in hybrid breeding could be considered as the prominent reasons for improved maize yields. Introduced during the 1930s in the USA, inbred-based hybrids made a dramatic shift in maize production, with the yield levels climbing from 2 tons/ha to 4 tons/ha by 1945, while the hybrid area expanded from 1 to 99% by 1960. Yield continued to climb with the introduction of lines from other countries, deriving new combinations. Population improvement became a routine breeding practice this time around, having the name 'recurrent selection' introduced by George Frederick Sprague in 1952, to distinguish it from pedigree breeding (Hallauer [2000\)](#page-34-0).

In India, maize breeding got an impetus with the launch of the All India Co-ordinated Maize Improvement Project (AICMIP) in 1957, the first of its kind in the country. In the 1950s, average maize yield was around 600 kg/ha, predominated with tall flint type low yielding varieties and primitive lines. Realising the potential of maize as an alternate cereal with wide uses as food and feed, ICAR launched its first coordinated research programme in maize ahead of the staple cereals, rice and wheat. By the time AICMIP was launched, several introductions of exotic lines were facilitated by Rockefeller Foundation. AICMIP took the further initiative to bolster exotic genetic base subsequently with the help of CIMMYT, starting from the year of its inception in 1966. The initial launch of hybrids from AICMIP included Ganga 1, Ganga 101, Ranjit and Deccan by 1961 (Yadav et al. [2015\)](#page-37-0). Presently, all the high yielding maize cultivars in the country share the lineage with the introduced germplasm, which had both yield potential and adaptability in varying degrees under Indian conditions.

Population improvement played a significant role in maize improvement in India until the 1980s, beyond which hybrids have taken over the horizon. Currently, maize breeding has taken a major reorientation towards grain quality improvement and product diversification. With the introduction of quality protein maize (QPM) from CIMMYT, another milestone laid by Dr. Surinder K Vasal and Dr. Evangelina Villegas, India released its own QPM hybrid 'Sakthiman 1' in 1981. The role of IARI in recent maize improvement in India is noteworthy, with the release of several improved hybrids such as Pusa HQPM 5 Improved, Pusa HQPM 7 Improved, Pusa Vivek QPM 9 Improved (Fig. [1.3f](#page-10-0)) combining high pro-vitamin A together with increased lysine and tryptophan fractions. Pusa Vivek QPM 9 Improved is the world's first QPM hybrid combining pro-vitamin A.

Population improvement in other major cereals such as sorghum and pearl millet also drew parallels to the success in major cereals. Established in 1972, the International Crop Research Institute for Semi-Arid Tropics (ICRISAT) had a mission to reduce poverty, hunger, malnutrition and environmental degradation in the dryland tropics. All the five mandate crops of ICRISAT were field crops, two cereals—sorghum and pearl millet, and three legumes—chickpea, pigeon pea and groundnut, marked to provide a balanced nutrition of carbohydrates, protein and fat. Prior to this, ICAR launched a coordinated programme 'All India Coordinated Millet Improvement Project' in 1965 with IARI as its headquarters. Pearl millet was included in the project initially, and in 1969 sorghum was added. Later, with the substantial development, both the crops were separated into independent co-ordinating units, pearl millet in 1985 and sorghum in 1987.

With all the research systems in place, the breeding outturn in these crops was tremendous, with ICRISAT playing a major role in bringing in exotic germplasm. The results were commendable, pearl millet yields went up from 300 kg/ha to 1250 kg/ha under minimal input and harsh tropical conditions, within 70 years. Currently, there are about 175 hybrids released in pearl millet through the coordinated varietal evaluation system. Unlike that in maize, sorghum variability in India was tremendous, and the population improvement had begun as early as the 1930s. Sorghum improvement in India, as a whole, is not much celebrated in the later years of the twentieth century. Although yield potential improved, the area declined drastically since the 1990s, bringing down the total production along with.

1.4.4 Mutation Breeding

Another major method employed in the field crop breeding was induced mutagenesis, which became very popular after the 1960s. Established as a method for barley breeding (Freisleben and Lein [1942](#page-33-0)), mutation breeding soon became very popular in all the crops, particularly in field crops, due to the ease of mutation process. Although physical mutagens like X-rays were used in the early stages, chemical mutagenesis soon became the most popular choice. By the 1960s, use of gamma rays was introduced as a follow-up of peaceful use of ionising radiation after world war II (Micke et al. [1990\)](#page-35-0). A gamma garden was established in IARI in the year 1960, the

second in India, after the first one was established at the Bose Institute, Calcutta in 1959 (Pal [1962](#page-35-0)). By 1990, several mutant varieties were released around the world totalling 519 among the field crops such as rice, wheat, maize, sorghum, pearl millet, chickpea, pigeon pea, soybean, Brassica and cotton (Micke et al. [1990](#page-35-0)). Among these, 251 varieties (48.4%) were from rice, followed by 104 (20.0%) from wheat.

The early introductions of Mexican wheat such as Sonora 64 and Lerma Rojo 64A had red grains not preferred by Indian people. Mutation works on these varieties at IARI, resulted in the release of Sharbati Sonora and Pusa Lerma both with amber coloured grains. Although several mutants were developed in wheat through mutation breeding, only a few traits such as grain colour, disease resistance and plant height had notable improvement. Comparing to other methods of breeding, induced mutations were random and often produced relatively less success when compared to the number of mutagenic attempts. Further, the research accomplishments published on mutation breeding across crops were more academic and described similar mutagenic effects, camouflaging the actual success stories. Notwithstanding, the recent experience in identifying a novel herbicide-tolerant AHAS mutant of rice, 'Robin', reinforces the faith in mutation breeding (Shoba et al. [2017](#page-36-0)).

1.4.5 Hybrid Breeding

Hybrid vigour, or the superiority of progenies over their parents, has been observed by several naturalists much before Mendel, including him, but with marginal attention (Mather [1955](#page-34-0)). Darwin was convinced of the phenomenon and reported it in 1876 (Darwin [1876\)](#page-33-0). A century later, the phenomenon has become one of the most accomplished breeding methods in crop plants, ensuring food security to millions of humans and livestock. Hybrid development in each of the major field crops has a story to narrate, except in wheat which is still being explored to strike a convincing advantage for yield. The conviction that hybrid vigour can be used for crop improvement came much earlier, which saw the birth of the term 'heterosis' by G H Shull in 1914 (Shull [1914\)](#page-36-0) and after his extensive work on maize (Shull [1946\)](#page-36-0). But a major bottleneck remained – controlled pollination. Especially in crops like maize, every grain in a cob used to be a different hybrid due to open pollination. Shull could initially create several inbreds by inbreeding but could not control the deterioration in certain lines (Shull [1908](#page-36-0)).

Nevertheless, mechanical emasculation in maize was possible through detasselling, a laborious task, but hybrids could be produced. By the 1930s, commercial-scale maize hybrids were available in the USA. At this time around, the Texas Agricultural Experiment Station (TAES) at College Station was bustling with research activities on male sterility systems and hybrid vigour in crop plants. In the 1950s, came the phenomenal discovery of cytoplasmic genetic male sterility (CMS) in maize with the identification of Texas cytoplasm (cms -T). The cms -T was first described in the line 'Golden June' in 1952 (Rogers and Edwardson [1952](#page-35-0)) and became one of the most studied CMS systems in crop plants. Since cms-T was proved to be a perfect CMS system, soon several hybrids started appearing at commercial scale. It was strikingly popular that by 1970, 85% of the US maize hybrids possessed cms-T cytoplasm. Within the two years spanning 1969 and 1970, 15% of the hybrids were wiped out by the outbreak of southern corn leaf blight incited by *Bipolaris maydis* race T. The T toxin produced by the pathogen had a specific binding site on the T-urf13 protein produced by the *cms-T*. The devastation was so severe that by 1972, most of the hybrids with *cms-T* were withdrawn (Levings III [1990](#page-34-0)).

There were other cytoplasms available in maize (Beckett [1971\)](#page-33-0), that can be broadly grouped into C (Charrua) and S (USDA), that saved the hybrid maize industry (Weider et al. [2009](#page-36-0)). Use of these CMS systems has since been moved to other countries. In India, use of CMS systems for hybrid production is not commonly practised, because the process of detasselling is not as expensive as elsewhere. Further, the manual detasselling does not warrant any specific maintenance breeding as that in the case of male sterility systems. One of the major problems for CMS systems is the maintenance of parental lines. Maintenance breeding of three lines, A, B and R, particularly A-line is an arduous task with isolation distances and controlled pollination, which is expensive than detasselling. Moreover, contaminated A-lines are difficult to purify. Therefore, almost all of the commercial maize hybrids in India has normal cytoplasm. Nevertheless, most recently in IARI, a baby corn hybrid has been developed using cms-T which is currently in the advanced stages of variety release. Compared to other CMS, cms-T remains most stable in Indian conditions.

Although there were various reports of CMS discovery in rice, the breaking news of commercial hybrids came from China (Virmani and Edwards [1983\)](#page-36-0). In the autumn of 1970, Li Bi Hu of the Hunan Academy of Agricultural Sciences $(HAAS)$ identified a natural male sterile line among the weedy rice $Oryza sativa$ f. spontanea) populations in Hainan island. Named as 'wild abortive (WA)', Dr. Yuan Long Ping of HAAS made several crosses with this WA line to produce several MS lines. One of the first MS lines developed was Er-jiu-nan 1A, which was later used extensively in hybrid rice production (Lin and Yuan [1980](#page-34-0)). Er-jiu-nan 1A was developed from the early maturing variety 6044, by four backcrosses. Other male sterile lines were also developed subsequently such as Zhen Shan 97A, V20A and several others. The first set of WA-based hybrids was released soon, and by 1978, about five million ha was under hybrid rice in China. The first set of hybrids were named after their female parents. Those derived from Er-jiu-nan 1A were named as 'Nan-You', hybrids, those from Zhen Shan 97A were known as 'Shan-You' and those from V20A were named with the prefix 'Wei You'. In the initial years of development, there were two other male-sterile systems used in China, Boro and Hong-Lien, which showed practical prominence.

Boro cytoplasm was initially described by Shinjyo [\(1969](#page-36-0)) when the cross between Chinsurah Boro 2 was made with Taichung 65. However, efficient transfer of Boro type met with difficulties in indica rice, leaving WA as the only source of viable CMS in rice. The restorer genes, $Rf1$ and $Rf2$ were identified for Boro type, while Rf3 and Rf4 restored fertility in WA CMS system. Obtained from China through IRRI, WA cytoplasm and its derived lines spread throughout the world

with a new hope. By 1980, IRRI began full-fledged research of hybrid rice with WA cytoplasm as the pivot. Several, hybrids were developed, however, the resulting heterosis was not as prominent as reported in China. This slowed down the initial thrust a bit, but still, the works continued in several countries. In India, hybrid rice research had begun in 1980 with the collaboration of IRRI as the major knowledge and resource partner (Jachuck et al. [1986\)](#page-34-0).

By 1981, Er-jiu-nan 1A, Zhen Shan 97 A and V20A were introduced into India along with their maintainers. Initial hybrid development was done using the introduced lines directly, however, there was a significant issue of grain quality among the hybrids developed under Indian conditions. Moreover, they showed increased susceptibility to pests and diseases. Conversion of Indian lines into male sterile lines was felt indispensable. By 1989, a national programme on hybrid rice was launched. The efforts bore fruit, the first set of hybrid rice was released in India in 1994, comprising four of them, APRH1, APRH2, MGR1 and KRH1. At the initial stage, all the successful hybrids were developed using only one A-line, IR58025A. This line, IR58025A, was developed by Dr. Sant Singh Virmani, the hybrid rice breeder at IRRI in 1988. When the conversion of Indian lines took momentum, in IARI, the same was replicated using lines under Basmati lineage. Two lines were identified as maintainers of WA cytoplasm, Pusa 167–120–3–2 and Pusa 150–21– 1–1, both with exceptional grain quality, long slender grains and agronomic features. Among these, Pusa 167–12–3–2 was derived from the cross of Type 3/Ratna. IR48483A, a male sterile line developed at IRRI by crossing Zhen Shan 97A/ MR365, was backcrossed to Pusa 167–12–3–2, and after six backcrosses IR58025A was developed. As a result, this line possessed long slender grains with aroma. IR58025A was further crossed to Pusa 150–21–1–1 to develop Pusa 6A after six backcrosses. By 2001, Pusa 6A became the parent of the first superfine grain aromatic rice hybrid in the world, Pusa RH 10 (Fig. [1.3c](#page-10-0)). Before the development of indigenously derived male sterile lines with better combining ability and grain quality, IR58025A was the major A-line used in hybrid rice development in India. Among the 127 rice hybrids released as of today, at least 15% have been developed using IR58025A as female parent.

Besides the involvement in hybrid development, IR58025A stands as a major contributor to the male sterile line development in India. One of the major drawbacks of using IR58025A was the aroma it imparted in the hybrids, which was an undesired feature in the non-aromatic grain sector. However, this problem has now been overcome in the latest array of male-sterile lines. At the beginning of the 1990s, hybrid rice in India was restricted to the public sector institutions, as there were few private sector companies involoved. This sitiation soon changed, and during the 10 years between 2000 and 2009, 44% of the rice hybrids released were from the private sector. After 2010, the scenario completely changed with private sector hybrid contribution going up to 91%. Only seven public sector hybrids were released between 2010 to 2021.

In wheat, unlike in maize and rice, hybrid development has always been a dubious challenge. The existence of male sterility driven by cytoplasmic factors in wheat was known before that in rice, when Kihara ([1951\)](#page-34-0) reported it for the first

time. Ten years later, a usable version was identified when Triticum timopheevi cytoplasm was found to induce sterility by interaction with T. aestivum nucleus (Wilson and Ross [1962](#page-36-0)). By this time, several reports of male sterility manifestation were pouring out of laboratories worldwide. From India, Rana and Swaminathan (1968) (1968) reported T. *zhukovskyi* as a source of MS cytoplasm. But there was a common problem. The availability of restorer genes was scarce. For timopheevi cytoplasm, Rf genes were sourced from T. timpheevi itself. It was the only system that looked viable. The first male sterile line 'Bison' was developed (Wilson and Ross [1962\)](#page-36-0), and it could be successfully used to generate fertile hybrids (Schmidt et al. [1962\)](#page-36-0).

Other than the restorer gene scarcity, another major bottleneck existed in wheat for diversifying cytoplasm in the form of undesirable nuclear-cytoplasmic interactions. Here again, *timopheevi* cytoplasm showed an exception, as no such interaction was reported (Virmani and Edwards [1983](#page-36-0)). Additionally, hybrids based on male sterility systems often showed less yield heterosis than the hand-pollinated hybrids. In the meantime, some commercial hybrids were released, but with little impact. All over the world, enthusiasm for hybrid wheat was dying down, until in the 1990s the efforts took another turn with the advent of chemical hybridisation agents (CHA). CHAs are growth-regulating chemicals that can selectively interfere with pollen production (McRae [1985;](#page-35-0) Duvick [1999](#page-33-0)). With renewed hope, the global area under hybrid wheat has begun to rise, but at a slow pace. Altogether, in Europe and America more than 60 hybrids were released (Gupta et al. [2019](#page-34-0)). In India, no wheat hybrids are released for commercial cultivation, except for two CMS-based hybrids, Pratham 7070 and Pratham 7272. However, they could not compete with the high yielding pure line cultivars.

A significant level of hybrid developments had happened in two other field crops, pearl millet and sorghum. Hybrid production in the early years of pearl millet improvement used the protogynous flowering behaviour as a mode of effecting cross-pollination. However, this method was not failproof, as any human error could result in reduced hybrid seed set. With the discovery of the CMS system 'Tift 23A' (Burton [1965a\)](#page-33-0), the hybrid production scenario was set for a change in pearl millet. Tift 23A was developed by Glenn W. Burton in 1965 at Tifton, Georgia, in the USA after several years of research on male sterility systems. Tift23A carried A1 cytoplasm, which was stable enough to promote hybrid seed production. Along with Tift23A, there was another line, Tift18A developed by Burton (Burton [1965b\)](#page-33-0). Introduced into India, two parallel programmes progressed, one for diversification and the other for hybrid development. IARI and Punjab Agricultural University (PAU) were the pioneers of pearl millet breeding in India (Srivastava et al. [2020\)](#page-36-0). The first hybrid, Hybrid Bajra 1 (HB1) was released by PAU in 1965. HB1 was developed from Tift23A by crossing to BilB3 (Athwal [1966](#page-33-0)). Subsequently, several other cytoplasms were reported, but A1 cytoplasm remained the major source of female lines for hybrid production in India (Kumar and Andrews [1984;](#page-34-0) Srivastava et al. [2020](#page-36-0)). One of the IARI developed hybrids, Pusa 23 using A1 cytoplasm, has become widely adopted in the northern plains (Fig. $1.3g$). The major issue with hybrid pearl millet was increased susceptibility to diseases, particularly downey mildew. Diversification of parental base hence has become a major strategy for

developing newer hybrids in pearl millet, an effort continuing in different institutions of India.

In the case of Sorghum too, hybrid breeding research before the pre-green revolution period was negligible. The preliminary report of the heterosis in sorghum came from the Lubbock substation of TAES in 1927 (Conner and Karper [1927\)](#page-33-0). Twenty-seven years later, Stephens and Holland ([1954\)](#page-36-0) reported a novel CMS cytoplasm 'Milo', from a cross between Double Dwarf Yellow sooner Milo and Texas Blackhull kafir at TAES. They identified the possibility of using the system for commercial hybrid production and developed Combine Kafir (CK) lines since kafir nuclear genes could restore the sterility induced by milo. Some of these lines were introduced to India, after the inception of AICMIP. Coordinated research efforts under the project on sorghum resulted in the release of the first hybrid, CSH1 or Coordinated Sorghum Hybrid 1 in 1964. Its parents were CK60A and IS84 (IS84-SA7529-55-1-1-1-1 from the Texas Durra Caudatum race) were both introduced from Texas. The second hybrid, CSH2 followed next year from the cross, CK60A/IS 3691. Initially, at least six hybrids were released with the directly introduced parents or from the lines selected within them. In the meantime, launch of ICRISAT has accelerated the hybrid breeding activities in sorghum, with an increasing number of conversions taking place using local germplasm. Starting with CSH1, as many as 26 Kharif sorghum hybrids have been released in India, until 2016.

Hybrid breeding in other field crops has not been much accomplished as that in cereals, particularly using male sterility systems. Notwithstanding, several commercial hybrids using conventional methods such as hand pollination has been released in sunflower, safflower, Brassica and groundnut claiming different levels of heterosis realisation. Notable exceptions are pigeon pea and Brassica, wherein extensive research on male sterility was done. First reported male sterility in pigeon pea was genetic male sterility (GMS) in 1978 (Reddy et al. [1978\)](#page-35-0). Although few other GMS systems were identified, maintenance of male sterility was the major bottleneck in the commercialisation of this technology. Search for alternate systems such as CMS was begun, with the particular objective of wide hybridisation. First report came in 1995, with Ariyanayagam et al. ([1995\)](#page-32-0) identifying Cajanun sericeus cytoplasm induced male sterility in C. cajan. The *sericeus* system was denoted as A_1 cytoplasm, followed by the discovery of A_2 cytoplasm from C. scarabaeoidus (Chauhan et al. [2004](#page-33-0)).

Dalvi et al. [\(2010](#page-33-0)) provided a comprehensive review on the male sterility systems in pigeon pea. So far, two hybrids are released, ICPH 3762 in 2010 and ICPH 2740 in 2015, but the breakthrough in yield and other desirable traits are yet to be realised. In Brassica also, the CMS systems such as *tour, trachy* and *mori* were used for hybrid development. The first CMS-based hybrid in India was released in Punjab, PGSH 51, based on tour cytoplasm. Later, CMS-based hybrids such as NRCHB 506, DMH 1 and Coral 432 (PAC 432) were released (Chauhan et al. [2011](#page-33-0)). Hybrid breeding in Brassica has another accomplishment. In 2008, a transgenic hybrid, DMH 11 was developed by Delhi University which became India's first transgenic hybrid (Jagannath et al. [2002](#page-34-0)). Recent developments in hybrid Brassica have attracted private sector researchers too (Yadava et al. [2012](#page-37-0)). There were also attempts to develop male sterility systems in chickpea and groundnut which remain unresolved at the commercial level.

1.4.6 Genomics-Assisted Breeding

By the end of the 1980s, genomics-based breeding began to take shape in field crops, pioneering from the development of DNA based markers in rice. Contemporarily, tissue culture techniques were also found extensive development, but the initial enthusiasm soon died as the expected returns eluded the researchers. The promise offered by genetic engineering for targeted crop improvement has faced hurdles in commercial deployment due to anti-genetically modified organisms (GMO) activism. Interest in this field was so enormous, several laboratories for agricultural biotechnology research have come up all over the world. Notwithstanding the setback in transgenic plants, techniques such as the development of linkage maps and mapping of loci, targeting both qualitative and quantitative traits, were invigorating the scientists with a ray of hope of success. During the 1990s, there was a quantum leap in molecular techniques, thanks to the Human Genome Project (HGP), a worldwide consortium. Began in 1990 and concluded in 2003 ([www.genome.](http://www.genome.gov) [gov\)](http://www.genome.gov), HGP provided several cutting-edge technologies that has parallelly been translated to crop genomes. The first attempt to sequence a cultivated crop genome began in 1998 with the inception of the International Rice Genome Sequencing Project (IRGSP) in the same mode as that of HGP.

The genome of the *japonica* cultivar, Nipponbare, was completely decoded by 2005 (IRGSP and Sasaki [2005](#page-34-0)). The availability of the genome information was soon made public. Parallelly, with the help of several bioinformatic tools supported by the modern computing platforms, the whole rice genome was annotated under a different project, Rice Genome Annotation Project (RGAP) beginning from 2004. Several databases have been created and made publically available. All these developments have completely reinvented the way trait-based breeding was done. Similar developments in other field crops had seen the unfolding of many crop genomes. Almost at the same period, the publications of the first linkage map of rice (McCouch [1990](#page-35-0); McCouch et al. [1988](#page-35-0)) based on restriction fragment length poly-morphism (RFLP) and microsatellite markers (Temnykh et al. [2001](#page-36-0); McCouch et al. [2002\)](#page-35-0) were made. Microsatellites, also known as simple sequence repeats (SSR) found abundantly in the genome particularly dispersed within the non-coding regions and widely distributed, could generate high density linkage maps due to their enormity in the rice genome.

All this was possible by the Nobel winning invention of Kary Banks Mullis, who described a lab-based method to amplify DNA in vitro using an enzymatic reaction (Mullis et al. [1986](#page-35-0)) known as polymerase chain reaction (PCR). This method was simple and very effective in the targeted amplification of DNA. PCR spurred a series of discoveries of different molecular markers, but none prevailed as that of SSRs. By the beginning of the twenty-first century, SSRs have been widely recruited as the molecular tool targeting various genetic studies such as diversity, linkage and quantitative trait locus (QTL) mapping. Most of the QTLs, mapped earlier using other marker systems such as RFLP were remapped using SSRs. Since SSR profiles were highly reproducible across genotypes, they found their way into the breeder's kit – as an indispensable selection tool.

To use any marker for selection, it must establish a close linkage with the gene of interest. Stronger the linkage more efficient the marker becomes in selection. Several QTLs have also been reported at the same time, flanked between two adjacent SSRs. The abundance of SSRs helped the researchers to narrow down to the gene by recruiting SSRs within the flanks. This way, most of the major QTLs have been fine mapped. Integrating the sequencing techniques of the amplified fragments, the target gene could be easily identified using an annotation database constructed from model species such as *Arabidopsis* and rice. Now gene-based/functional markers are also available for targeted selection.

1.4.7 Marker-Assisted Selection in Breeding

Marker assisted selection (MAS) denotes employing molecular markers in the selection process. Since they are based on the DNA itself, their usefulness becomes definitive in the selection process. Moreover, the whole process allows several progenies to be looked into, even when they are young, which adds to the throughputness of the MAS. Although MAS can be integrated into several breeding methods, it has been particularly successfull in backcross breeding for rectifying specific defects in already popular crop varieties. Currently, marker-assisted backcross breeding (MABB) is being widely used in field crops in India. MABB targets to augment the selection process to reduce the turnaround time for varietal development, most economically. After identifying the target gene/QTL, MABB allows them to be transferred to an elite/popular varietal background where specific traits need improvement. Additionally, integration of desired traits by pyramiding the target genes/QTLs can also be undertaken under MABB programmes.

During the last 10 years, MABB has undergone several refinements in the protocols targeting precision and economy. One of the major changes was the integration of a rigorous phenotypic selection along with foreground and background selection, particularly in the early generations (Singh et al. [2011\)](#page-36-0). This has not only helped recovery of the recurrent parent phenome to its near totality but also aided in accelerating the breeding process. Integration of phenotypic selection in MAB has been a crucial factor in Basmati breeding, because of the exclusive grain quality of this group of rice. Often when a non-Basmati source is used as the gene/ QTL donor, severe impairment of Basmati quality is experienced requiring further refinements (Babu et al. [2017\)](#page-33-0). In the preliminary protocols of MABB, only foreground and background selection were included (Liu et al. [2003](#page-34-0)) with the idea that recovery of maximum recurrent parent genome (RPG) would recover the phenome also. However, in practice, this does not seem to occur due to several undetected regions of the donor genome lying latently in the progenies. While this can be

attributed to the limited number of background markers, scaling them to a highdensity coverage can make the entire selection process expensive and timeconsuming (Ellur et al. [2016\)](#page-33-0), jeopardising the fundamental objective of accelerated breeding. However, the early generation phenotypic selection could address this issue effortlessly. Yet another improvement was the reductive screening in background selection, in which the completely recovered background markers were progressively eliminated from the selection process (Sagar et al. [2020](#page-36-0)). This could not only economise the selection by reducing the time but also could aid in conserving the resources.

Recently, postponing the entire background selection to a later generation was also attempted, relying initially on phenotypic selection along with foreground selection. The results were dramatic, as the final selections could accumulate as much RPG recovery as possible along with the phenome recovery, ultimately saving a lot of time and money, along with aiding the initial screening of a large number of progenies (Oo et al. [2021\)](#page-35-0). Cultivar releases using MAS in India has taken off in 2007, with the release of Improved Pusa Basamti 1 and immediately followed by Improved Samba Mashsuri. Since then, several improved varieties have been released for commercial cultivation (Table [1.2](#page-22-0)). Among the institutions, IARI has the maximum share of 36% among the releases, covering three crops, rice, maize and chickpea. All of the rice cultivars released using MABB, targets bacterial blight and/or blast resistance, while in maize hybrids focus was on developing QPM hybrids, with or without pro-vitamin A enrichment. In chickpea, two MAS derived cultivars were released, Super Annigeri 1 and Pusa Chickpea 10,216 (Fig. [1.3g](#page-10-0)) having fusarium wilt resistance and drought tolerance, respectively. There are four Indian rice cultivars improved by IRRI, directly released for cultivation in India such as Swarna Sub1, Samba Sub1, CR1009 Sub1 and IR64 Drt1 (DRR Dhan 42).

1.4.8 Genomic Selection (GS)

GS is the contemporary buzzword in genomic assisted breeding. If MAS is used for individualistic improvement, especially targeting elite cultivars, GS envisions population improvement even for self-pollinated crops. Similar to MAS, GS also weighs on the availability of desired alleles and amasses them into a set of individuals through a series of breeding steps. However, there are fundamental differences in the approaches that are followed. MAS requires mapping of the target alleles before their use in the introgression or pyramiding programmes, whereas GS does not require mapping individual target alleles. While MAS requires donor and recipient (recurrent) parents, GS typically needs training and testing (breeding) populations. Fundamentally, GS operates on a closed breeding system, which means it starts with a set of diverse founders that are known to harbour different allelic combinations of target loci. Thus, founders in the GS programme are elite genotypes with high breeding values, that are interbred to develop a large number of biparental populations. Bred to near homozygosity, the progenies of these crosses are divided into two, a training set and a testing set. Training set undergoes a low- or mid-density SNP genotyping

IARI ICAR-Indian Agricultural Research Institute, New Delhi, ICRISAT International Crops Research Institute for Semi-Arid Tropics, Patancheru, IIRR ICAR-Indian Institute of Rice Research, Hyderabad, IISR ICAR-Indian Institute of Soybean Research, Indore, IRRI International Rice Research Institute, Los Banos, NRRI ICAR-National Rice Research Institute, Cuttack, PAU Punjab Agricultural University, Ludhiana, TNAU Tamil Nadu Agricultural University, IARI ICAR-Indian Agricultural Research Institute, New Delhi, ICRISAT International Crops Research Institute for Semi-Arid Tropics, Patancheru, IIRR ICAR-Indian Institute of Rice Research, Hyderabad, IISR ICAR-Indian Institute of Soybean Research, Indore, IRRI International Rice Research Institute, Los Banos, NRRI ICAR-National Rice Research Institute, Cuttack, PAU Punjab Agricultural University, Ludhiana, TNAU Tamil Nadu Agricultural University, Coimbatore, VPKAS ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora Coimbatore, VPKAS ICAR-Vivekananda Parvatiya Krishi Anusandhan Sansthan, Almora covering the whole genome, as well as a multi-location evaluation within the target population of environment (TPE). The data is used for generating a valid model that connects genotypic and phenotypic data. This model is then used for predicting the genomic estimated breeding values (GEBVs) of the testing panel. Since the training data involves multi-location data, the element of genotype-by-environment interaction is inbuilt in the GS model.

A minimum of three locations is required, and not more than two replications to improve heritability. There are several statistical approaches to modelling, however, two methods, genomic best linear unbiased predictor (gBLUP) and ridge regression BLUP (rrBLUP) are adjudged to be the best methods in model building (Meuwissen et al. [2001\)](#page-35-0). Further, a large population is desirable because the GS models attempt to capture total additive genetic variance for predicting GEBVs. A larger population requires robust experimental designs such as augmented, spatial, partially replicated (p-rep) or sparse testing. The selected lines based on the GEBVs form the Stage 1 cohort, which can either be recycled for the next breeding cycle or be advanced for varietal development. Selection intensity needs to be high to capture maximum number of allelic combinations. Further, accelerated breeding cycle improves the effectiveness of GS in crop breeding programmes.

1.5 An Overview of Breeding Research in the Last Decade

In the decades past 1960s, the green revolution has cast its magical spell to a significant extent on the field crops. All the crops experienced an emulated version of the yield increase as that happened in the three prime cereals. Strong scientific intervention on varietal development, along with improved cultural practices and calculated fertilisation, has all contributed to increased productivity. In the last 10 years, two remarkable shifts have occurred; for the first time, use of markerassisted breeding has resulted in the release of 46 cultivars, and a quantum increase in the release of cultivars bred by the private sector. In rice alone, 29 cultivars were released by marker-assisted breeding, with notable improvement in disease resistance targeting both bacterial blight and blast, either singly or in combination (Table [1.2\)](#page-22-0). In rice, about 90% (68 out of 75) of the hybrids released during the last decade has come from the private sector (Fig. [1.5](#page-26-0)). This is a welcome change, as several private producers are coming forward in seed production and marketing, making the seed availability to farmers unlimited. Furthermore, private-sector research organisations are looking for higher yield and grain quality besides stress resilience as the major breeding targets to sustain competition among themselves as well as with the public sector institutions. This major shift towards commercial agriculture is not for rice alone. Currently, the hybrid sector in field crops is dominated by private organisations and are giving stiff competition to public sector organisations. The exception is wheat, wherein private seed suppliers produce and market high yielding pure line varieties to a considerable extent.

Another noteworthy development in the breeding research in India comes from the varietal turnover, particularly from the non-hybrid sector. So far, this sector

Fig. 1.5 Pattern of release of rice hybrids in India between 1994 and 2021. There is a marked shift in private sector hybrids during the last ten years. The dotted lines indicate three year moving average. *Data for 2021 is incomplete

remains the mainstay for the public sector institutions. The varietal release system in India takes two routes, national varietal release and provincial varietal release. National release follows rigorous nationwide testing and widely adapted cultivars are only passed through this system, ultimately released and notified by the Central Sub-committee on Crop Standards, Notification and Release of Varieties for Agricultural Crops (CVRC). Most of the specifically adapted cultivars are approved through provincial bodies such as State Varietal Release Committees (SVRCs). Examining the varietal release during the last 10 years, in 14 field crops, which included both hybrid and non-hybrid cultivars, one could see a marked difference in the pattern of release. The most striking feature is the number of releases, 743 under SVRC, a 34% increase over the CVRC releases totalling 554 cultivars (Fig. [1.6\)](#page-27-0). However, CVRC releases looked relatively more balanced than the SVRC releases. Although rice dominated the number of releases, an equally good number of varietal releases happened in maize, wheat and cotton under CVRC, while a predominance of rice cultivar release was seen under SVRC.

In rice, SVRC release was three times more than that in CVRC. This pattern raises more concerns than comfort because indiscriminate release of varieties that are specifically adapted would render them less adopted, leaving the varieties mostly to the breeder than the ultimate stakeholder, the farmer. This also would slow down the dissemination of widely adapted cultivars, which need to find its adoption against the flash flood of narrowly adapted varieties. Another dimension to this problem is the performance evaluation system of the breeder's service under public funded organisations. Often, the number of cultivars released than the number adopted is the

Fig. 1.6 Varietal release pattern among 14 field crops between 2011 and 2021. The CVRC releases were relatively more balanced among the major crops, while SVRC releases were mostly dominated by rice cultivars

criteria followed for assessing a breeder. This leads to unhealthy practices and competitions, thwarting the very basic objective of crop improvement.

Notwithstanding, the breeding efforts during the first two decades of the twentyfirst century has been eventful. Several high yielding varieties have seen remarkable adoption within a short period of time from release. Varieties such as HD2967 and HD3086 in wheat, Pusa Basmati 1121 and Pusa Basmati 1509 in rice, etc. have grown into megavarietal proportions. Another important dimension is the focus shift towards grain quality, as well as climate resilience. With the technological advancements, breeding efforts in India is yet to venture into genomics assisted breeding. Modern tools such as genomic selection and gene editing have not been used in improving field crops in India. Although the research in this direction is progressing, the looming threat of anti-GMO campaigns shadows the future of geneedited breeding lines, although all of them do not fall under the category of GMOs. Recently, efforts are also underway to integrate technologies to translate breeding success into genetic gain.

1.6 Towards Improving Genetic Gain

Genetic gain, the advantage accrued every generation within a unit of time, by genetic improvement of crops has been a pivot of discussion for a long time. Hazel and Lush [\(1942](#page-34-0)) defined genetic gain as the average improvement in genotypic/ phenotypic value within a population as a consequence of selection. In the practical sense, this means a perpetual increase in productivity, described more comprehensively as an 'evergreen revolution' by Prof. M. S. Swaminathan (Swaminathan [1996\)](#page-36-0). The dimensions of the evergreen revolution are multifaceted and subsume ecological, economical and sustainable components (Swaminathan [2006\)](#page-36-0). Genetic gain is an ultimate translation of trait advantage as a result of the accrual of beneficial alleles. Therefore, the gain can happen in any trait individually or in combination resulting in an overall advantage to the selected population. The combining of multiple traits for selection can be realised through the use of appropriate selection indices. One of the primary requirements to achieve gain is heritability. We know that heritability increases in several ways, the most common route is through the accumulation of favourable alleles which cumulatively improves the trait expressivity. Breeding interventions such as selecting a large set of genotypes increases the probability of accumulating more variants, and more variants provide the opportunity of generating several allelic combinations. Several allelic combinations allow the steady accumulation of them, a perpetual increase leading to the evergreen revolution.

Encapsulating all these components into a mathematical expression, Jay Laurence Lush ([1937\)](#page-34-0) made the famous breeder's equation, which would help to predict the expected genetic gain in generations under selection. Breeder's equation primarily has three components, the selection intensity (*i*), heritability (h^2) and additive variance (σ_A^2) , the product of which will help us to predict the gain. As discussed above, i allows drawing the maximum number possible from a spectrum of alleles (σ_A^2) , with h^2 translating the effect into the gain. Later a fourth component was added as a denominator to the equation, the cycle time (L), which is the average time per generation (Eberhart [1970](#page-33-0)), which has more relevance today than during the time of Lush. Probably, Lush could not have imagined having this component added as the original equation was framed for animal breeding, and it was not relevant to animal breeding as reducing the gestation period in animals was impractical. Having several generations squeezed within a time frame allows more opportunities for accrual of alleles, therefore lower the cycle time increases the gain phenomenally. For instance, keeping all the genetic factors constant, but having two generations a year than the regular one, alone can double the gain. But directly applying the equation to the public sector plant breeding has a catch. Mostly, the public sector plant breeding has been random, which means parents are selected at random and progenies are also selected at random which leads to the breeding success also becoming random. Breeder's equation does not work with this randomness but requires a closed system rather than an open one. A closed system means the founders of the population should breed and the progenies must interbreed, recycled through the selection process, accumulating the gain. The conundrum of random breeding therefore cannot provide an actual assessment of genetic gain in the true sense. However, assuming the whole breeding population within a species as the breeding population, we can make a rough estimate of gain through era trials.

Era trials, evaluation of representative cultivars of different breeding eras, can help us in indirectly estimating the realised genetic gain approximately (Rutkoski [2019a](#page-35-0), [b](#page-35-0)). Era trials have been used to estimate the genetic gain in maize hybrids (Meghji et al. [1984\)](#page-35-0), which was later extended to later eras as well (Duvick [2005\)](#page-33-0). There are other cautions too, era trials cannot compare the effect of breeding

Fig. 1.7 A hypothetical relationship between realised yield and genetic gain in a crop for 100 years. The yield differential is calculated with respect to the base value at the beginning of the breeding. Progressive genetic gain is calculated per year. Once the yield plateaus gain starts to decay significantly

programmes, such as genetic gains by hybrids vs pure line varieties, because the breeding itself is an outcome of a random set of parents and the pattern of yield increase is not linear between eras. Further, the random representative(s) of each era may not be truly representative. However, era trials can depict an overall picture of where the breeding system stands currently. Another factor that decays the genetic gain is the yield plateauing. In a hypothetical system as given in Fig. 1.7, the yield plateauing can result in decay in genetic gain significantly if no breeding intervention is made to uplift the yield levels, a situation currently being faced by several field crops.

Realised genetic gains in field crops in India, show varying trends. It is not surprising because, the quantum genetic gain for the evergreen revolution in different crops should differ, based on their importance in the food chain as well as on the base yield potential. It is proposed that a genetic gain of 1.3% per annum is required to sustain food production in wheat (Rosegrant and Agcaoili [2010\)](#page-35-0). Currently, data are being generated to quantify realised genetic gains through era trials in major field crops. In a recent exploration of yield and related traits in wheat, Yadav et al. [\(2020](#page-37-0)) examined wheat yield from 1905 to 2016 by mining the historical data and found that average genetic gain ranged from 0.54% per year to 0.82% per year (over the first released variety, NP4). This estimate comes closer to the estimates made by Lopes et al. ([2012\)](#page-34-0) using CIMMYT lines within a window of 30 years, in which a gain of 0.9% among high yielding, 0.7% among intermediate and 0.5% among low yielding cultivars have been reported. However, considering the wide window used by Yadav et al. ([2020\)](#page-37-0), (no methods were found to explain how the estimates were made) the yield gain in India could have been much larger, if we consider the decay in genetic gain over the periods of intermittent yield stagnation.

Throwing light into this assumption, the preliminary trend from the era trials in wheat indicates improved gain (unpublished data). The wheat yield improvement in India could be attributed to parallel genetic gain in biomass, grain number per spike and reduced duration. Examining the genetic gain in rice, with a specific focus on rainfed environments, Kumar et al. ([2021\)](#page-34-0) report rather a short-term genetic gain in rice, for a 10-year window between 2005 and 2014. They found an annual genetic gain of 0.68% among irrigated checks, which increased to 0.87% under moderate reproductive stage drought stress, while 1.9% gain could be achieved under severe drought conditions. Although these figures cannot be scaled to rice breeding in general, but indicates that trait targeted breeding still offers opportunities to improve gain in crops like rice. In another such study in pearl millet, Yadav et al. [\(2021](#page-37-0)) report achievement of 4% genetic gain per year during the last 30 years, primarily attributable to hybrids. There was a marked gain in ear length and ear diameter, and they are rated as the major components of yield gain. In chickpea too, the preliminary reports from era trials indicate significant genetic gain for the last 60 years (unpublished data). Presently, efforts are underway to accelerate genetic gain in crop breeding systems involving field crops.

One of the global movements towards accelerating the genetic gain is to employ GS in a strict sense that oversees all the components of genetic gain. In India, recently a pilot programme has been launched with selected field crops and involving several national and international institutions to start GS-based crop improvement with the help of organisations such as Bill and Melinda Gates Foundation (BMGF), Excellence in Breeding (EiB) and Breeding programme assessment tool (BPAT). The major objective of this project is to generate crop product profiles for TPEs, breeding programme optimisation, implementing GS and data digitalisation through breeding management system (BMS).

1.7 Threats and Opportunities

In this section, we concisely present the prospects of crop breeding in India. This is not particular to field crops alone. For several parts of the last 120 years, owing to various factors, crop breeding in India has progressed through leaps and bounds. Except for few milestones, public sector plant breeding has not been much eventful before the 1950s. Restructuring of breeding research was the main highlight of the pre-green revolution phase, which could successfully prepare the grounds for green revolution. Yadav et al. [\(2019\)](#page-37-0), while examining the production and productivity pattern of major cereals, reveal that the phase immediately following the green revolution was more productive than the green revolution itself. Although the threat of yield stagnation is lingering, as seen occurring in wheat yield in Europe (Brisson et al. [2010\)](#page-33-0), the current situation in India shows a more comfortable scenario. However, with unpredictable phenomena such as climate change on the horizon, time is ripe to have another reorientation of breeding research in India to sustain an evergreen revolution. With the caveats of climate change around, it is estimated that as many as 30% of the world population would be at risk of hunger by 2050.

Events related to climate change are currently being reported around the world, and in India, a tropical country, the threat is more formidable. Major challenges are drought, flood, soil salinisation, submergence, temperature fluctuations, low nutrients besides biological threats from pests, diseases and weeds. Besides, physiological disorders can also emerge under shifting environments. Therefore, future breeding should reorient towards precision agriculture with added resilience in crops to face unexpected adverse events. This means the future belongs to widely adapted cultivars than specifically adapted ones. It is time to recycle specifically adapted cultivars through breeding to evolve wide adapted ones.

Agriculture is the largest industry in the world with the lowest capital input. This is particularly relevant to countries like India, where crop breeding happens unorganised. Comparing to other nations, Indian agriculture has a long way to go in harnessing crop productivity in key crops. The most single reason for this is the lack of adequate support. Despite having human and genetic resources, crop breeding development in India has been heavily dependent on international inputs. Several genes that are being used today are discovered in Indian landraces but the discoveries have been made abroad. Unless increased focus is given with sufficient institutional and financial support, future of plant breeding in India will be challenging. The reorientation of agricultural research that happened in the post-1950s came with futuristic investments such as AICRP and research institutions. Since its inception, the AICRP system has not undergone serious restructuring, and still follows outdated protocols. A total reorientation of breeding with product profile and TPE oriented system attached with state of the art infrastructure, standard operating protocols, a modernised AICRP system and a renewed futuristic plan is the need of the hour from the policy intervention front.

The technologic front in crop breeding has been transformative in the last three decades. Particularly, developments in genome biology have changed the landscape of trait-based breeding. With accurate interventions such as MABB, now we have the capability to transfer a target allele to an elite background, where a particular allele is lacking. Besides, techniques for large scale mining of alleles are also available. With the high-end computational capabilities and high throughput genotyping and phenotyping platforms breeding time is set to reduce considerably in the future. Accurate predictions are taking over phenology-based selections. Besides, accelerated generation turnover technologies such as doubled haploids, rapid generation advancement and speed breeding are going to augment genomics assisted breeding for better realisation of genetic gain. Additionally, genome editing techniques are also getting ready for manipulation of individual genes to generate novel traits that are hitherto lacking. In the twenty-first century, technological options are unlimited for breeding modernisation. However, rational use of these techniques is warranted for which appropriate human resource development is essential.

The natural reserves of enormous genetic diversity and the availability of the best human resources in the world are the primary opportunities we are bestowed with.

Compared to the global scenario, several genetic resources in India remain underutilised. Currently, a megaproject is in operation to characterise and utilise 15,000 Indian rice landraces that are conserved in the National Gene Bank, for allele mining, gene and trait discovery targeting several biotic and abiotic stress tolerance, physiological and quality parameters. This project is expected to offer various novel solutions hitherto not utilised in rice breeding. One of the major problems concerning human resources has been the insufficient number of highly trained personnel in research. Brain drain in agriculture research needs to be plugged, particularly in crop improvement, for which strategic integration of genetic resources, institutions, infrastructure, human resources, technology and market is to be made.

We need to build a globally competitive research and education system in India. Further, the research should be strictly oriented to meet the challenge of future food needs for our growing population. With his futuristic vision, Prof. Swaminathan wrote while introducing the concept of the evergreen revolution, 'Countries like India, China, and Bangladesh have to produce more and more food and other farm commodities from diminishing per capita arable land and irrigation water resources. Therefore, productivity enhancement is the only pathway available to us to produce more to feed the growing population. This is why an Evergreen Revolution approach is exceedingly important. An Evergreen Revolution needs the integration of frontier technologies like biotechnology and information communication technology with traditional ecological prudence' (Swaminathan [2006\)](#page-36-0).

1.8 Conclusion

In the present chapter, we have chronicled the breeding research in India, particularly keeping field crops in focus, while introspecting the achievements made. More discussions happened around the major field crops, but without critical details as there are specific chapters to follow for those crops. However, we have tried to narrate the milestones in the history of breeding wherever appropriate, while keeping the future course in mind. No specific dealing of stress tolerance and quality improvement has been made in this chapter, as that would be redundant. From the modest beginning with the inception of IARI to commence the organised research in agriculture, then through ICAR, modern breeding has transformed India from a 'ship to mouth' economy to a self-reliant economy. We have also discussed the opportunities of utilising modern technologies in fast-forwarding breeding and thereby genetic gain.

References

Ariyanayagam RP, Rao NA, Zaveri PP (1995) Cytoplasmic genic male sterility in interspecific matings of Cajanus. Crop Sci 35:981–985. [https://doi.org/10.2135/cropsci1995.](https://doi.org/10.2135/cropsci1995.0011183X003500040008x) [0011183X003500040008x](https://doi.org/10.2135/cropsci1995.0011183X003500040008x)

- Athwal DS (1966) Current plant breeding research with special reference to Pennisetum. Indian J Genet Plant Breed 26A:73–85
- Babu NN, Krishnan SG, Vinod KK et al (2017) Marker aided incorporation of Saltol, a major QTL associated with seedling stage salt tolerance, into Oryza sativa cv. 'Pusa basmati 1121'. Front Plant Sci 8:41. <https://doi.org/10.3389/fpls.2017.00041>
- Barber CA (1915) Some difficulties in the improvement of Indian sugarcanes. Ann Appl Biol 1:211. <https://doi.org/10.1111/j.1744-7348.1915.tb07993.x>
- Beckett JB (1971) Classification of male-sterile cytoplasms in maize (Zea mays L.). Crop Sci 11: 724–727. <https://doi.org/10.2135/cropsci1971.0011183X001100050037xa>
- Brisson N, Gate P, Gouache D et al (2010) Why are wheat yields stagnating in Europe? A comprehensive data analysis for France. Field Crop Res 119:201–202. [https://doi.org/10.](https://doi.org/10.1016/j.fcr.2010.07.012) [1016/j.fcr.2010.07.012](https://doi.org/10.1016/j.fcr.2010.07.012)
- Burton GW (1965a) Pearl millet Tift 23A released. Crops Soils 17:19
- Burton GW (1965b) Cytoplasmic male-sterile pearl millet Tift 18A released. Crops Soils 18:19
- ARIC (1909) Report of the Agricultural Research Institute and College, Pusa 1907–1909. Superintendent of Government Printing, Calcutta
- CGIAR (2020) Growing resilience for a better future. Annual Performance Report 2020. CGIAR system organization, Montpellier
- Chauhan RM, Parmar LD, Patel PT, Tikka SBS (2004) Fertility restoration in cytoplasmic genic male sterile lines of Pigeonpea (Cajanus cajan (L.) Millsp.) derived from Cajanus scarbaeoides. Ind J Genet Plant Breed 64:112–114
- Chauhan JS, Singh KH, Singh VV et al (2011) Hundred years of rapeseed-mustard breeding in India: accomplishments and future strategies. Indian J Agric Sci 81:1093–1109
- Cheek M, Lughadha EN, Kirk P, Lindon H, Carretero J, Looney B, Douglas B, Haelewaters D, Gaya E, Llewellyn T, Ainsworth AM, Gafforov Y, Hyde K, Crous P, Hughes M, Walker BE, Campostrini R, Khoon F, Wong M, Niskanen T (2020) New scientific discoveries: plants and fungi. Plant People Planet 2:371–388. <https://doi.org/10.1002/ppp3.10148>
- Conner AB, Karper RE (1927) Hybrid vigour in sorghum. Bull Texas Agric Exp Stat 359:5–23
- Dalvi VA, Saxena KB, Luo RH et al (2010) An overview of male-sterility systems in pigeonpea [Cajanus cajan (L.) Millsp.]. Euphytica 173:397–407. [https://doi.org/10.1007/s10681-010-](https://doi.org/10.1007/s10681-010-0140-0) [0140-0](https://doi.org/10.1007/s10681-010-0140-0)
- Darwin CR (1876) The effects of cross- and self-fertilisation in the vegetable kingdom. John Murray, London
- Duvick DN (1999) Commercial strategies for exploitation of heterosis. In: Coors JG, Pandey S (eds) Genetics and exploitation of Heterosis in crops. American Society of Agronomy, Inc, Crop Science Society of America, Inc, Soil Science Society of America, Inc, Madison, pp 295–304
- Duvick DN (2005) The contribution of breeding to yield advances in maize (Zea mays L.). Adv Agron 86:83–145. [https://doi.org/10.1016/S0065-2113\(05\)86002-X](https://doi.org/10.1016/S0065-2113(05)86002-X)
- Eberhart SA (1970) Factors affecting efficiencies of breeding methods. Afr Soils 15:655–680
- Eckardt NA (2010) Evolution of domesticated bread wheat. Plant Cell 22:993. [https://doi.org/10.](https://doi.org/10.1105/tpc.110.220410) [1105/tpc.110.220410](https://doi.org/10.1105/tpc.110.220410)
- Ellur RK, Khanna A, Krishnan GS et al (2016) Marker-aided incorporation of Xa38, a novel bacterial blight resistance gene, in PB1121 and comparison of its resistance spectrum with $xal3$ + Xa21. Sci Rep 6:29188. <https://doi.org/10.1038/srep29188>
- FAO (1996) Food for all. In: Proceedings of the world food summit 1996. Food and Agriculture Organization of the United Nations, Rome
- Freisleben R, Lein A (1942) Uber die Auffindung einer mehltauresistenten Mutante nach Rontgenbestrahlung einer anfalligen reinen Linie von Sommergerste. Naturwissenschaften 30: 608
- Ghose RLM, Ghatge MB, Subramanian V (1960) Rice in India. Indian Council of Agricultural Research, New Delhi
- GoI (1928) Report of the royal commission on agriculture. Government of India Press, Bombay
- GoI (2020) Agricultural statistics at a glance. Directorate of Economics and Statistics. Department of Agriculture, Cooperation & Farmers Welfare, Ministry of Agriculture & Farmers Welfare, Government of India
- Gupta PK, Balyan HS, Gahlaut V, Saripalli G, Pal P, Basnet BR, Joshi AK (2019) Hybrid wheat: past present and future. Theor Appl Genet 132:2463–2483. [https://doi.org/10.1007/s00122-019-](https://doi.org/10.1007/s00122-019-03397-y) [03397-y](https://doi.org/10.1007/s00122-019-03397-y)
- Hallauer AR (2000) George Frederick Sprague 1902–1998. In: Biographical memoirs 78. National Academy Press, Washington
- Hargrove T, Coffman WR (2006) Breeding history. Rice Today 5:34–38
- Hazel LN, Lush JL (1942) The efficiency of three methods of selection. J Hered 33:393–399. <https://doi.org/10.1093/oxfordjournals.jhered.a105102>
- Hopper WD, Freeman WH (1969) From unsteady infancy to vigorous adolescence rice development. Econ Polit Wkly 4:A17–A21
- Howard A (1909) Report of the imperial economic botanist. In: Report of the agricultural research institute and college, Pusa 1907–09. Superintendent Government Printing, Calcutta, pp 31–37
- Howard H, Howard GLC (1929) The development of Indian agriculture. Oxford University Press, Bombay
- IRGSP, Sasaki T (2005) The map-based sequence of the rice genome. Nature 436:793–800. [https://](https://doi.org/10.1038/nature03895) doi.org/10.1038/nature03895
- Jachuck PJ, Mahadevappa M, Sidhu GS (1986) Hybrid rice in India. In: Hybrid rice. International Rice Research Institute, Manila, pp 287–288
- Jagannath A, Arumugam N, Gupta V et al (2002) Development of transgenic barstar lines and identification of a male sterile (barnase)/restorer (barstar) combination for heterosis breeding in Indian oilseed mustard (Brassica juncea). Curr Sci 82:46–51
- Kihara H (1951) Substitution of nucleus and its effects on genome manifestation. Cytologia 16: 177–193. <https://doi.org/10.1508/cytologia.16.177>
- Kumar SS (2011) Land accounting in India: issues and concerns. presented in the expert meeting on ecosystem accounts. United Nations Statistics Division, London. 5–7 December 2011, Published online at Accessed on 04 August 2021 [https://unstats.un.org/unsd/envaccounting/](https://unstats.un.org/unsd/envaccounting/seeales/egm/lod.htm) [seeales/egm/lod.htm](https://unstats.un.org/unsd/envaccounting/seeales/egm/lod.htm)
- Kumar KA, Andrews DJ (1984) Cytoplasmic male sterility in pearl millet [*Pennisetum americanum* (L.) Leeke]. Adv Appl Biol 10:113–143
- Kumar A, Raman A, Yadav S, Verulkar SB, Mandal NP, Singh ON, Swain P, RamT BJ, Dwivedi JL, Das SP, Singh SK, Singh SP, Kumar S, Jain A, Chandrababu R, Robin S, Shashidhar HE, Hittalmani S, Satyanarayana P, Venkateshwarlu C, Ramayya J, Naik S, Nayak S, Dar MH, Hossain SM, Henry A, Piepho HP (2021) Genetic gain for rice yield in rainfed environments in India. Field Crop Res 260:107977. <https://doi.org/10.1016/j.fcr.2020.107977>
- Levings CS III (1990) The Texas cytoplasm of maize: cytoplasmic male sterility and disease susceptibility. Science 250:942–947. <https://doi.org/10.1126/science.250.4983.942>
- Lin SC, Yuan LP (1980) Hybrid rice breeding in China. In: Innovative approaches to rice breeding. International Rice Research Institute, Manila, pp 35–51
- Liu SP, Li X, Wang CY et al (2003) Improvement of resistance to rice blast in Zhenshan 97 by molecular marker-aided selection. Acta Bot Sin 45:1346–1350
- Loftas T (1995) Dimensions of need—an atlas of food and agriculture. Food and Agriculture Organization of the United Nations, Rome
- Lopes MS, Reynolds MP, Manes Y et al (2012) Genetic yield gains and changes in associated traits of CIMMYT spring bread wheat in a "historic" set representing 30 years of breeding. Crop Sci 52:1123. <https://doi.org/10.2135/cropsci2011.09.0467>
- Lush JL (1937) Animal breeding plans. Iowa State College Press, Ames
- Mather K (1955) The genetical basis of heterosis. Proc R Soc B Biol Sci 144:143–150. [https://doi.](https://doi.org/10.1098/rspb.1955.0040) [org/10.1098/rspb.1955.0040](https://doi.org/10.1098/rspb.1955.0040)
- McCouch SR (1990) Construction and applications of a molecular linkage map of rice based on restriction fragment length polymorphism (RFLP). PhD Thesis. Cornell University, New York, p 177
- McCouch SR, Kochert G, Yu ZH et al (1988) Molecular mapping of rice chromosomes. Theor Appl Genet 76:815–829. <https://doi.org/10.1007/BF00273666>
- McCouch SR, Teytelman L, Xu Y et al (2002) Development and mapping of 2240 new SSR markers for rice (Oryza sativa L.). DNA Res 9:199-207. <https://doi.org/10.1093/dnares/9.6.199>
- McRae DH (1985) Advances in chemical hybridization. Plant Breed Rev 3:169–191. [https://doi.](https://doi.org/10.1002/9781118061008.ch3) [org/10.1002/9781118061008.ch3](https://doi.org/10.1002/9781118061008.ch3)
- Meghji MR, Dudley JW, Lambert RJ et al (1984) Inbreeding depression, inbred and hybrid grain yields, and other traits of maize genotypes representing three eras. Crop Sci 24:545–549. [https://](https://doi.org/10.2135/cropsci1984.0011183X002400030028x) doi.org/10.2135/cropsci1984.0011183X002400030028x
- Mercader J (2009) Mozambican grass seed consumption during the middle stone age. Science 326:1680–1683. <https://doi.org/10.1126/science.1173966>
- Meuwissen THE, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genomewide dense marker maps. Genetics 157:1819–1829
- Micke A, Donini B, Maluszynski M (1990) Induced mutations for crop improvement. Mutat Breed Rev 7:1–44
- Mishra B (2002) Varietal improvement for rice production in India. In: Nguyen VN (ed) Genetic diversity in rice production, case studies from Brazil, India and Nigeria. Food and Agricultural Organization of United Nations (FAO), Rome, pp 37–91
- Mishra CN, Tiwari V, Khan H et al (2020) DBW222 (Karan Narendra): a new high-yielding, lodging-tolerant wheat variety for North Western plains of India. Crop Breed Appl Biotechnol 20(3):e32902037. <https://doi.org/10.1590/1984-70332020v20n3c41>
- Mullis K, Faloona F, Scharf S et al (1986) Specific enzymatic amplification of DNA in vitro: the polymerase chain reaction. Cold Spring Harb Symp Quant Biol 51:263–273. [https://doi.org/10.](https://doi.org/10.1101/Sqb.1986.051.01.032) [1101/Sqb.1986.051.01.032](https://doi.org/10.1101/Sqb.1986.051.01.032)
- Nagarajan S, Singh B (1997) Wheat: India and international collaboration. In: Braun et al (eds) Wheat: prospects for global improvement. Kluwer Academic Publishers, Dordrecht, pp 539–545
- Oo KS, Krishnan SG, Vinod KK et al (2021) Molecular breeding for improving productivity of Oryza sativa L. cv. Pusa 44 under reproductive stage drought stress through introgression of a major QTL, $qDTY12.1$. Genes 12:967. <https://doi.org/10.3390/genes12070967>
- Pal BP (1962) Some contributions of botany to human welfare. J Ind Bot Soc 41:161–172
- Pal BP, Ramanujam S (1944) Plant breeding and genetics at the Imperial agricultural research institute New Delhi. Ind J Genet Plant Breed 4:43–53
- Peng S, Cassman KG, Virmani SS et al (1999) Yield potential trends of tropical rice since the release of IR8 and the challenge of increasing rice yield potential. Crop Sci 39:1552–1559. <https://doi.org/10.2135/cropsci1999.3961552x>
- Rana RS, Swaminathan MS (1968) Triticum zhukovskyi as a source of male sterile cytoplasm and fertility restorer genes. What Inf Serv 27:1–2
- Reddy BVS, Green JM, Bisen SS (1978) Genetic male-sterility in pigeonpea. Crop Sci 18:362–364. <https://doi.org/10.2135/cropsci1978.0011183X001800030002x>
- Rogers JS, Edwardson JR (1952) The utilization of cytoplasmic male-sterile inbreds in the production of corn hybrids. Agron J 44:8–13. [https://doi.org/10.2134/agronj1952.](https://doi.org/10.2134/agronj1952.00021962004400010004x) [00021962004400010004x](https://doi.org/10.2134/agronj1952.00021962004400010004x)
- Rosegrant MW, Agcaoili M (2010) Global food demand, supply, and price prospects to 2010. Food Policy Research Institute, Washington
- Rutkoski JE (2019a) A practical guide to genetic gain. Adv Agron 157:217–249. [https://doi.org/10.](https://doi.org/10.1016/bs.agron.2019.05.001) [1016/bs.agron.2019.05.001](https://doi.org/10.1016/bs.agron.2019.05.001)
- Rutkoski JE (2019b) Estimation of realized rates of genetic gain and indicators for breeding program assessment. Crop Sci 59:981–993. <https://doi.org/10.2135/cropsci2018.09.0537>
- Sagar V, Dhawan G, Krishnan SG et al (2020) Marker assisted introgression of genes governing resistance to bacterial blight and blast diseases into an elite basmati rice variety, 'Pusa basmati 1509'. Euphytica 216:16. <https://doi.org/10.1007/s10681-019-2549-4>
- Schmidt JW, Johnson VA, Mann SS (1962) Hybrid wheat. Nebr Exp Sta Qtrly 9:9
- Shinjyo C (1969) Cytoplasmic genetic male sterility in cultivated rice, *Oryza sativa* L. II. The inheritance of male sterility. Japan J Genet 44:149–156
- Shoba D, Raveendran M, Manonmani S et al (2017) Development and genetic characterization of a novel herbicide (Imazethapyr) tolerant mutant in rice (Oryza sativa L.). Rice 10:10. [https://doi.](https://doi.org/10.1186/s12284-017-0151-8) [org/10.1186/s12284-017-0151-8](https://doi.org/10.1186/s12284-017-0151-8)
- Shull GH (1908) The composition of a field of maize. Am Breed Assoc 4:296–301
- Shull GH (1914) Duplicate genes for capsule form in *Bursa bursa pastoris*. Z Indukt Abstamm Vererbungs 12:97–149
- Shull GH (1946) Hybrid seed corn. Science 103:547–550. [https://doi.org/10.1126/science.103.](https://doi.org/10.1126/science.103.2679.547) [2679.547](https://doi.org/10.1126/science.103.2679.547)
- Singh BP (1991) Plant introduction and exchange. In: Paroda RS, Arora RK (eds) Plant genetic resources conservation and management concepts and approaches. International Board for Plant Genetic Resources, New Delhi
- Singh AK, Gopalakrishnan S, Singh VP et al (2011) Marker assisted selection: a paradigm shift in basmati breeding. Indian J Genet Plant Breed 71(2):120–128
- Srivastava RK, Bollam S, Pujarula V et al (2020) Exploitation of heterosis in pearl millet: a review. Plan Theory 9:807. <https://doi.org/10.3390/plants9070807>
- Stephens JC, Holland PF (1954) Cytoplasmic male sterility for hybrid sorghum seed production. Agron J 46:20–23. <https://doi.org/10.2134/agronj1954.00021962004600010006x>
- Swaminathan MS (1996) Sustainable agriculture: towards an evergreen revolution. Konark Publication, New Delhi
- Swaminathan MS (2006) An evergreen revolution. Crop Sci 46:2293–2303. [https://doi.org/10.](https://doi.org/10.2135/cropsci2006.9999) [2135/cropsci2006.9999](https://doi.org/10.2135/cropsci2006.9999)
- Swaminathan MS (2009) Norman E. Borlaug (1914–2009): Plant scientist who transformed global food production. Nature 461:894. <https://doi.org/10.1038/461894a>
- Temnykh S, DeClerck G, Lukashova A, Lipovich L, Cartinhour S, McCouch S (2001) Computational and experimental analysis of microsatellites in rice $(Oryza sativa L)$: frequency, length variation, transposon associations, and genetic marker potential. Genome Res 11:1441–1452. <https://doi.org/10.1101/gr.184001>
- Tomar SMS, Vinod, Singh B (2004) Distant hybridisation in wheat. Indian Agricultural Research Institute, New Delhi, p 160
- van Dijk M, Morley T, Rau ML et al (2021) A meta-analysis of projected global food demand and population at risk of hunger for the period 2010–2050. Nat Food 2:494–501. [https://doi.org/10.](https://doi.org/10.1038/s43016-021-00322-9) [1038/s43016-021-00322-9](https://doi.org/10.1038/s43016-021-00322-9)
- Virmani SS, Edwards IB (1983) Current status and future prospects for breeding hybrid rice and wheat. Adv Agron 36:145–214. [https://doi.org/10.1016/s0065-2113\(08\)60354-5](https://doi.org/10.1016/s0065-2113(08)60354-5)
- WCVP (2020) World checklist of vascular plants, version 2.0. Royal Botanic Gardens, Kew
- Weider C, Stamp P, Christov N et al (2009) Stability of cytoplasmic male sterility in maize under different environmental conditions. Crop Sci 49:77. [https://doi.org/10.2135/cropsci2007.12.](https://doi.org/10.2135/cropsci2007.12.0694) [0694](https://doi.org/10.2135/cropsci2007.12.0694)
- Willcox G, Buxo R, Herveux L (2009) Late Pleistocene and early Holocene climate and the beginnings of cultivation in northern Syria. Holocene 19:151-158. [https://doi.org/10.1177/](https://doi.org/10.1177/0959683608098961) [0959683608098961](https://doi.org/10.1177/0959683608098961)
- Wilson JA, Ross WM (1962) Male sterility interaction of the *Triticum aestivum* nucleus and Triticum timopheevi cytoplasm. Wheat Inf Serv (Kyoto) 14:29
- Yadav OP, Karjagi CG, Jat SL et al (2014) Overview of maize improvement in India. Indian Farming 64:5–11
- Yadav OP, Hossain F, Karjagi CG, Kumar B, Zaidi PH, Jat SL, Chawla JS, Kaul J, Hooda KS, Kumar P, Yadava P, Dhillon BS (2015) Genetic improvement of maize in India: retrospect and prospects. Agribiol Res 4:325–338. <https://doi.org/10.1007/s40003-015-0180-8>
- Yadav OP, Singh DV, Dhillon BS et al (2019) India's evergreen revolution in cereals. Curr Sci 116: 1805–1808. <https://doi.org/10.18520/cs/v116/i11/1805-1808>
- Yadav R, Gupta S, Gaikwad K et al (2020) Genetic gain and traits plasticity in wheat cultivars developed for irrigated ecosystems of NWPZ of India from 1900 to 2016. [https://doi.org/10.](https://doi.org/10.21203/rs.3.rs-107131/v1) [21203/rs.3.rs-107131/v1](https://doi.org/10.21203/rs.3.rs-107131/v1)
- Yadav OP, Gupta SK, Govindaraj M et al (2021) Genetic gains in pearl millet in India: insights into historic breeding strategies and future perspective. Front Plant Sci 12:645038. [https://doi.org/](https://doi.org/10.3389/fpls.2021.645038) [10.3389/fpls.2021.645038](https://doi.org/10.3389/fpls.2021.645038)
- Yadava DK, Vasudev S, Singh S et al (2012) Breeding major oil crops: present status and future research needs. In: Gupta SK (ed) Technological innovations in major world oil crops, volume 1: breeding, pp 17–51. https://doi.org/10.1007/978-1-4614-0356-2_2
- Zuo X, Lu H, Jiang L et al (2017) Dating rice remains through phytolith carbon-14 study reveals domestication at the beginning of the Holocene. Proc Natl Acad Sci U S A 114:6486–6491. <https://doi.org/10.1073/pnas.1704304114>