7 Rapid Generation Advancement and Fast-Track Breeding Approaches in Wheat Improvement

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Abstract

The development of homozygous pure lines in wheat requires more than 3 and 6 years with and without offseason facilities. The traditional way of generation advancement is time-consuming, laborious and high-cost task. In recent times, advances in understanding the plant physiology and response of plants to different photoperiod regimes have helped breeders to adopt rapid generation advancement (RGA) protocols. These protocols have enabled the rapid generation of homozygous lines with more number of crop generations per year while enhancing the rate of genetic gain. Breeding strategies such as marker-assisted backcross breeding (MABB) and genomic selection (GS) can be easily integrated with RGA technology to develop stress-resilient modern wheat varieties quickly and efficiently. Generally, standardized protocols of doubled haploid (DH) technology and speed breeding are available and can be employed to reduce the time required to achieve homozygosity and develop a cultivar in wheat. In this chapter, we discuss different RGA protocols, their adaptive costs and limitations for successfully applying these strategies for accelerated breeding and maximization of genetic gain through an increased number of generations per year.

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7.1 Introduction

According to the United Nations (UN) estimate, the global human population will be approximately 10.0 billion by 2050 (Yadav et al. 2018). The growing population and climate change have escalated global food security concerns. Additionally, land shrinkage for crop production due to environmental reasons and anthropogenic factors such as rapid urban and commercial development warrants the need to produce more crops per unit area. Besides fulfilling the food demand of the growing human population on planet earth, the science of plant breeding plays a pivotal role in adapting cropping systems under changing climate scenarios. The conventional breeding techniques demand colossal time and efforts to result in a successful and popular crop cultivar.

Wheat (*Triticum aestivum* L.) is one of the major food crops grown and consumed worldwide (Yadav et al. 2021). Conventional wheat breeding programmes globally have significantly delivered numbers of improved varieties with superior grain yield and resistance against various stresses in the past 100 years. However, in the present context, the progress achieved through conventional breeding looks slow, owing to lengthy breeding cycles, which often take approximately 10 years from cross to variety release. Despite increased wheat production due to bumper yields of the crop, which is achieved with fertilizer-responsive high-yielding wheat cultivars, the research community is far behind the target as far as wheat improvement is concerned. The current mean annual genetic gain in wheat has been around 1%, whereas the requirement is increasing by 1.7% annually. Therefore, 1.0 billion tonnes of wheat have to produce by 2050 to meet the target wheat requirement (Tadesse et al. 2019). At this juncture, rapid breeding cycles can play a crucial role in enhancing genetic gain by hastening the development and release of wheat cultivars with superior yield, stress resilience and quality traits.

Rapid generation advancement (RGA) techniques have been developed in many crops to quicken the breeding cycles and breeding advancement (Bhattarai et al. 2009; Depauw and Clarke 1976; Gaur et al. 2007; Ishigaki 2010; Rizal et al. 2014; Wang et al. 2011). The RGA technique was first proposed by Goulden (1939). Grafius (1965) suggested some modifications for the existing protocols, and subsequently, the most recent application of it in new form was proposed as 'speed breeding' (Watson et al. 2018). The time requisite in variety development depends on the number of cropping seasons required to create homozygous and stable genotypes followed by crossing two parents. In wheat, if only one crop generation is produced a year, it takes seven to nine cropping seasons or years to create

homozygous lines after hybridization. Therefore, production of doubled haploids (DH) and employment of rapid generation advance (RGA) methods are most common contemporary tools being practiced in reducing the number of years required to produce stable homozygous lines and to develop cultivars in a short period. Many crops have utilized these procedures to fast-track the breeding cycles and achieve genetic improvement in less time. RGA approaches also significantly reduce the harvest time of crops to speed up the agricultural research to ensure better food production to deal with the increasing population pressure. Application of new protocols called 'speed breeding' (Atlin et al. 2017), which has been designed to accomplish up to six wheat generations in a single year (Watson et al. 2018). Therefore, furnishing as an advantageous mechanism in minimizing the duration of breeding cycles (Alahmad et al. 2018). This technology involves the generation of complete plants by sowing immature seeds harvested at physiological maturity under controlled conditions. RGA methods enhance the genetic gain rate by reducing the time between the crop to crop and with accelerated selection cycles. In addition, the number of phenotyping methodologies was reshaped to the speed breeding system and has been expanded to permit the characterization and selection for crucial traits in wheat. For example, seminal root phenotyping for drought tolerance (Richard et al. 2015), grain dormancy for tolerance to pre-harvest sprouting and disease resistance traits like adult plant resistance (APR) to leaf rust (Hickey et al. 2011; Alahmad et al. 2018), stripe rust (Riaz et al. 2016), yellow spot (Dinglasan et al. 2016) and crown rot (Alahmad et al. 2018) in bread wheat. In comparison to pedigree/bulk breeding methods, RGA protocols are much easier and effective as they do not involve selection and maintenance at every generation. As most of the RGA protocols are designed to undertake under a controlled environment, thus the risk of local harsh weather conditions could be eliminated in achieving the target of generation advancements. RGA provides additional advantages in terms of space as we employ the single seed descent (SSD) method of generation advancement, which uses a single seed per plant and less time to generate the next immediate generation of seeds. In RGA, selections are not practiced in the early generations (F_2-F_4) of segregating populations, which saves time and avoids any risks of losing valuable genotypes, possessing unfavourable linkages. Here in RGA, the early generations are developed under controlled greenhouse conditions, which are very equipped with breeders. Subsequently, the advanced stable generations (F_5-F_6) are evaluated under field conditions for the agronomic and other physiological traits. The rapid breeding methods help in deploying crop improvement strategies with much more efficiency on a pilot basis at the regional research centres to fasten the breeding progress. Further, the integration of contemporary crop breeding techniques with RGA methods helps to overcome the limitations of varying photoperiods and adverse seasonal changes associated with field conditions with mere or no losses of breeding germplasm.

7.2 Importance of Rapid Breeding Cycles in Wheat

Wheat is affected by various biotic stresses comprising of diseases caused by fungi, bacteria, viruses, nematodes, etc. and insects pests. Among the biotic stresses, diseases caused by fungi are very critical to achieve the potential yield of newly bred wheat cultivars. These diseases pose hurdles in the realization of the maximum yield output. The major diseases are rusts, powdery mildew, foliar blights and upcoming blast disease, whose impact on wheat production is well established (Figueroa et al. 2018). Rust diseases constitute the highest economically important fungal diseases of wheat and have a wide distribution in wheat-growing regions across the globe Babu et al. (2020). Norman E. Borlaug famously and appropriately said, 'rust never sleeps', which means rust pathotypes continuously evolve. A constant vigil on their occurrence at the global level and continuous breeding efforts are needed to be one step ahead of these rust pathogens. These pathogens can transform themselves into new races, biotypes or variants, which can evolve in a short span of time. Therefore, the rapid breeding cycles support the wheat breeding against such type of ever-evolving rust pathogens through rapid generation advancement. Rapid screening under control conditions using speed breeding can be a possibility in a short time. The six generations of disease-resistant material can be achieved in a single year through screening against rust using rapid breeding cycles. Against leaf rust of wheat, 15 genotypes were tested at Wellington under field conditions and speed breeding. There were not many differences in the disease reaction patterns in susceptible and resistant cultivars under both conditions. But these accelerated breeding cycles with the technology of speed breeding hastened the screening process and can enable the development of resistant cultivars.

New biotic stresses in crops have appeared across the globe during the last few decades intimidating food safety and security. Till date, diseases and pathotypes of exotic origin such as the Ug99 race of wheat stem rust and blast of wheat are not reported from India, which can be noted as a remarkable success of our wheat researchers and policymakers working under the aegis of India's National Agricultural Research System. Apart from the Ug99 race of stem rust, the blast is another emerging disease in wheat caused by *Magnaporthe oryzae* pathotype *Triticum* (MoT). Since its first report in 1985 from the Parana state of Brazil, the wheat blast has spread to different countries and reached Bangladesh in Southeast Asia in 2016 (Mottaleb et al. 2018). Although the anticipatory breeding efforts are going on prior to the occurrence of wheat blast disease in the country. Nevertheless, speed breeding that enabled rapid breeding cycles may support the screening of potential genotypes against wheat blast disease under anticipatory breeding programmes at different sites in the countries where this disease exists. The ever-evolving pathogens like *Magnaporthe oryzae* pathotype *Triticum* (MOT) can push back by utilizing rapid breeding cycles, which allow six wheat generations in a single year and hasten the disease resistance breeding. However, handling of pathogenic inoculum, rapid inoculum multiplication, inoculations and latent period required for symptom expression under screening are to be tested on a wider scale for better adaptability of rapid breeding cycles in wheat resistance breeding programmes.

7.3 Maximizing Genetic Gain Through RGA

Genetic gain is an improvement in the mean trait value within a population over breeding cycles as a response to selection (Crespo-Herrera et al. 2017). The disparity in the realized genetic gain across the world could be due to germplasm nature, crop duration, agronomic practices, prevailing weather conditions, soil and many other factors. However, developing advanced crop cultivars through improving several agronomic traits has ever been the major reason to increase the genetic gain via grain yield productivity enhancements. Genetic gains have primarily been studied by systematic evaluation of historical varieties released over different points of time (Beche et al. 2014). In wheat, a shorter duration findings have estimated more than 1% genetic yield gain per year (Underdahl et al. 2008).

More interestingly, the generation cycle (L) is the single parameter in the denominator of the breeder's equation for estimating genetic gain. Thus, the exponential increase in genetic gain would be possible by manipulating the time factor compared to other factors such as additive variance, additive genetic variation within the population(σ_a), selection intensity(i) and selection accuracy (r) in the genetic gain equation. Eberhart (1970) later introduced the 'L' into the denominator as a way to evaluate efficiency by expressing the response to selection as change over time.

$$\text{Genetic gain } (\Delta G) = (\sigma_a)(i)(r)/L$$

This equation keeps its importance in any crop breeding programme. The quantum of improvements is measured in terms of few parameters that the breeder can manipulate to gain maximum in important economic traits. The application of RGA methods in breeding programmes is found to be very much essential in achieving genetic gains, very quickly and efficiently, by reducing the 'L'. Knowing the complexity of crop breeding programmes, in understanding genetic and phenotypic information to carry out selections, there is a need to incentivize the breeding teams for better exploitation of parameters deciding the genetic gains. Among the parameters in the breeder's equation, the generation cycle is the simplest to perceive, economical to deploy and the very potent parameter for enhancing the genetic gain. The generation cycle involves recycling of breeding materials from advanced segregating materials into the crossing block when the breeder determines that the genotype is over-performing than the average breeding value of the individuals in the population. The breeding values are usually estimated as genomic estimated breeding value (GEBV) using advanced estimates predicted from genomic selection models.

The most preferred way to increase the genetic gain is to reduce the generation cycle time without altering the growth and development of the crop plants. In wheat, it takes an average of 9–10 years to come out with a commercial wheat cultivar (Atlin et al. 2017). After the development of the variety, it takes a longer time in its commercialization and spread, which hinders in achieving the maximum genetic gains in any breeding programmes. The vernalization requirement of winter wheat to enter into flowering stage is very well-known phenomenon, and the same adds to the

prolonged cycle time of wheat (Davidson et al. 1985; Evans 1987). Many recent studies showed exciting findings that long exposure to cold temperatures has drastically reduced the cycling time in wheat (Watson et al. 2018). This strategy can be readily applied in wheat to reduce the cycle time and enhance the genetic gain as described in the breeder's equation.

As discussed earlier, though accelerating generation cycles will be the best approach to enhance the genetic gains, it has been very much underexploited by global breeding programmes across the world. The plant breeders emphasize the other three parameters of the breeders' equation, namely, heritable additive genetic variance, selection intensity and selection accuracy. Though these are very effective in the first few breeding cycles, they cause diminishing gains, leading to increased costs and decreased efficiency. A linear increase in heritability is an almost impossible task, and it does not increase the genetic gains linearly. The other two factors, selection accuracy and selection intensity, need a larger population size and come with higher cost investments in larger field trials and more replications to effectively reduce the amount of genetic gain achievable from the breeding materials. The impact of short breeding cycles in most breeding programmes is much greater than heritability or reduced selection proportion of breeding materials. Compared to the pedigree method, most RGA methods reduce the cultivar development time to 3–4 years, and there is still an opportunity to reduce the generation time to 1 or 1 0.5 years in many of the cereals and legumes. This can be achieved if the crop of interest is not very much sensitive to photoperiod and does not have specific photoperiod requirements. It is very common in many breeding programmes that the parents are selected only when they are completely stabilized and homozygous, which lengthen the breeding cycles. There are many approaches available wherein breeding values estimated on non-inbred individuals are considered and used as parents to maximize the genetic gains. Any typical breeding programme with an offseason facility would take two seasons a year and generate fixed lines in 3 years before taking up yield trials in the larger plots and multi-locations. Then the parents are selected among these better performing lines, and they would be cycled into the crossing blocks.

More typically, as well as understood phenomena, breeding cycles could be accelerated by carrying out selections in early generations of selfing, and the selected can be used as parents instead of waiting until later stages of fixation of lines. This will not only save time; it will also improve the breeding value of the population to develop better cultivars. As proposed by many workers, the recurrent selection is entirely based on crossing among individuals in the early generations of breeding and developing diverse lines instead of obtaining highly homozygous lines. In most recent times, invention of useful platforms like GS has greatly contributed in selecting parents based on the GEBVs, but still, experiments have to prove its effectiveness in estimating correct breeding values. Overall, recent advancements in achieving more generations in a year and fast-tracking the breeding programmes have shed a ray of hopes in maximizing genetic gains across the crops.

7.4 Accelerated Breeding Technologies in Wheat

7.4.1 Doubled Haploidy (DH)

With the availability of inadequate natural resources, land and water, and climate change-mediated stresses, the yield of staple food crops needs to be increased over time. Continued genetic gain in these major food crops requires innovative breeding technologies like doubled haploid (DH) technique which can significantly shorten the breeding cycles along with maintaining the genetic gain. Using DH strategy, the breeding process can be shortened to about 6–7 years, and rapid development of homozygous lines can be achieved instead of six to ten generations of inbreeding (Fig. 7.1; Prigge et al. 2012) which is a significant innovation to speed up varietal development (Dunwell 2010). Doubled haploids in wheat can be induced through anther culture and wide hybridization. However, it has commonly been experienced in recent years that the wheat x maize system of haploid induction is an effective and versatile tool among the available methods involving chromosome elimination.

Major wheat breeding programmes in the world like CIMMYT, ICARDA and PBI Sydney regularly utilize DH strategy in their wheat breeding programmes for genetic studies of economically important traits like rust resistance, nutritional quality, etc. Several countries, namely, China, Canada, France, Hungary and Romania have already released several wheat varieties developed through DH origin (Tadesse 2013). The wheat x maize DH production strategy is an integral part of the wheat breeding programme of Australia, which is dominated by two major companies, namely, Australian Grain Technology Pty. Ltd. (AGT) and Longreach Plant Breeder (Kuchel et al. 2005). Longreach came up with a wheat variety in 2016 named 'Longreach Reliant', developed through wheat × maize DH strategy. Public institutions in Australia like Plant Breeding Institute, University of Sydney, South Australian Research and Development Institute and Department of Agriculture and Food, Western Australia, have also employed this technique in their wheat breeding programmes for basic and applied research. In USA, wheat varieties 'Bond CL' and 'Gallagher' were developed in 2004 and 2012 by Colorado State University (Haley

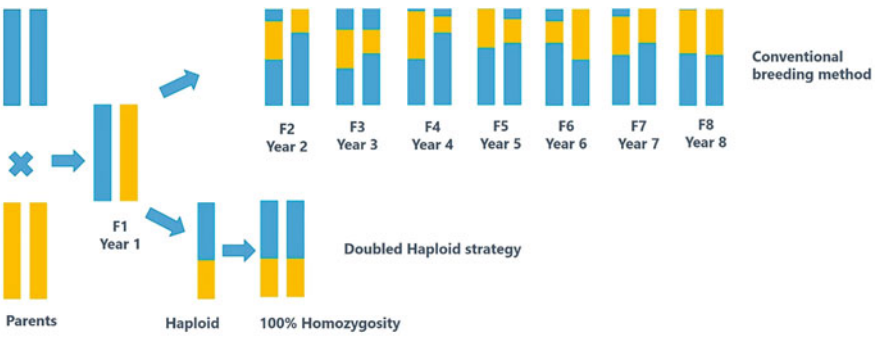

Fig. 7.1 Rapid development of homozygous wheat lines through DH strategy

et al. 2006) and Oklahoma State University using wheat × maize crosses. In Japan, the DH wheat cultivar 'Sanukioyume-2000' was developed through wheat × maize system (Yuichi et al. 2002).

In Canada, 12 years after the release of the first wheat DH variety, 27 wheat varieties were released that were developed through wheat x maize crosses approach at wheat breeding centres of Universities of Saskatchewan, Agriculture and Agri-food Canada and Manitoba (DePauw et al. 2011). Another widely used high protein variety, 'Lillian' having the gene *Gpc-B1*/*Yr36*, was also a product of DH technology (DePauw et al. 2011). In India, during the year 2015–2016, two DH lines PBW751 and PBW755 developed by Punjab Agricultural University, Ludhiana, were tested under National Initial Varietal Trials in a coordinated programme (Srivastava and Bains 2018). India's first wheat DH cultivar, 'Him Pratham', was bred at Himachal Pradesh Agricultural University, Palampur, through wheat × *Imperata cylindrica* crosses (Chaudhary et al. 2014), and was released in 2013. Integration of the DH technology combined with marker-assisted breeding can also effectively expedite wheat improvement programmes. In conclusion, wheat × maize DH production strategy offers an opportunity for rapid development of homozygous lines through accelerated breeding and therefore is reflected in the release of so many wheat varieties from major wheat breeding programmes across the globe.

7.4.2 Shuttle Breeding

Shuttle breeding refers to raising two or more crop generations in contrasting environments to shorten the breeding cycle and advance the generations. Shuttle breeding was initially employed at the International Maize and Wheat Improvement Centre (CIMMYT) by Norman E. Borlaug (Borlaug 1968). CIMMYT had identified two sites for shuttling their breeding material, namely, the Toluca station (19^0N latitude, 3660 m ASL), which is in the state of Mexico, and Ciudad Obregon station (27.5^0N latitude, 40.8 m ASL) in the state of Sonora, in Mexico. These Toluca and Obregon stations have diverse climatic conditions with respect to rainfall, temperature and photoperiods. These differences in climatic conditions allow various diseases to infect wheat and help in an efficient screening of breeding material against them. This shuttle breeding not only helps in reducing the breeding cycle time by half but also aids in developing climate-resilient, widely adapted wheat germplasm in a limited time. Researchers at CIMMYT routinely use shuttle breeding to identify disease-resistant, water and resource use efficient, heat-tolerant, high-yielding and better end-use quality lines to be supplied to international partners in the form of nurseries. With regard to shuttle breeding programme of CIMMYT in Mexico, segregating populations are grown in two environmentally contrasting sites. The Ciudad Obregon site is fertile and sunny suitable for identifying high-yielding lines grown under irrigated conditions. At this site, lines are also tested for water use efficiency, heat tolerance, leaf and stem rust infection and end use quality traits. The Toluca station has a cooler and high land environment with high humidity. These climatic conditions favour efficient screening of breeding material against

stripe rust, *Septoria tritici* blotch (STB) and fusarium. At Cd. Obregon, planting of wheat is done in the month of November, and harvesting is carried out in the month of April or May. On the other hand, at the Toluca site, planting is done in May/June, and the produce is harvested in the month of October. The segregating material is routinely shuffled between these two sites, making it a useful approach for selecting the lines and studying the inheritance of simplex or complex traits at a relatively low cost. The CIMMYT wheat breeding programme has also extended its shuttle breeding facility at the Njoro station in Kenya to screen wheat germplasm for resistance against Ug99 and other variants of stem rust. Every year thousands of wheat breeding lines from many countries are screened at this site against the deadly Ug 99 stem rust race.

The wheat genetic enhancement programme at International Centre for Agricultural Research in the Dry Areas (ICARDA) also utilizes a shuttle breeding programme for developing wheat germplasm lines suitable for rainfed and irrigated ecologies throughout the world. For spring bread wheat, a shuttle breeding approach involving the winter-summer cycle at Terbol station (34° N; 36° E, 900 m ASL) in Lebanon, winter cycle at Merchouch station (33.6° N; 6.7° W, 430 m ASL) in Morocco, the Sids station (29° N; 31° E, 32.2 m.a.s.l.) in Egypt and the summer cycle at the Kulumsa station (08° N; 39° E, 2220 m.a.s.l) in Ethiopia is being followed (Tadesse et al. 2019). ICARDA has established germplasm phenotyping facilities in partnership with national programmes of the above-mentioned countries. In this context, Merchouch station is utilized for screening against stripe rust, *Septoria*, Hessian fly resistance and drought tolerance. The Sidi Alydi stations in Morocco are being used for terminal drought stress; Sids station in Egypt for yield potential; Izmir station in Turkey for SRT and APR screening against rust; Wadmedani station in Sudan for heat tolerance; and Kulumsa station for stem and stripe rust, Septoria blotch and Fusarium blight (Tadesse et al. 2019).

The Indian wheat breeding programme was initiated around 1905. However, till 1962 the pace in developing improved varieties was slow. The varieties developed during these 60 years were tall with weak stems and were unsuitable for intensive agriculture (Smale et al. 2008). After the onset of the 'Green revolution', semi-dwarf, lodging tolerant, disease-resistant, fertilizer-responsive genotypes were developed. During this period, the regional station of ICAR-Indian Agricultural Research Institute, at Wellington, was effectively utilized for shuttle breeding purpose. The seeds of imported Mexican varieties (Sonora 64, Lerma Roho) were multiplied at IARI-Wellington during 1964–1965 (SMS Tomar personal communication). After this, this station was regularly utilized for generation advancement and screening breeding material against leaf and stem rust. After the harvest of wheat in the month of April/May (winter season), the sowing is immediately taken (May/-June, off-season) at IARI- Wellington station, and the breeding material with one generation advanced is made available in the month of October for planting at main season again. This station is now providing space for many major wheat breeding centres for screening their breeding material against rusts, powdery mildew, fusarium head blight and generation advancement (Fig. 7.2).

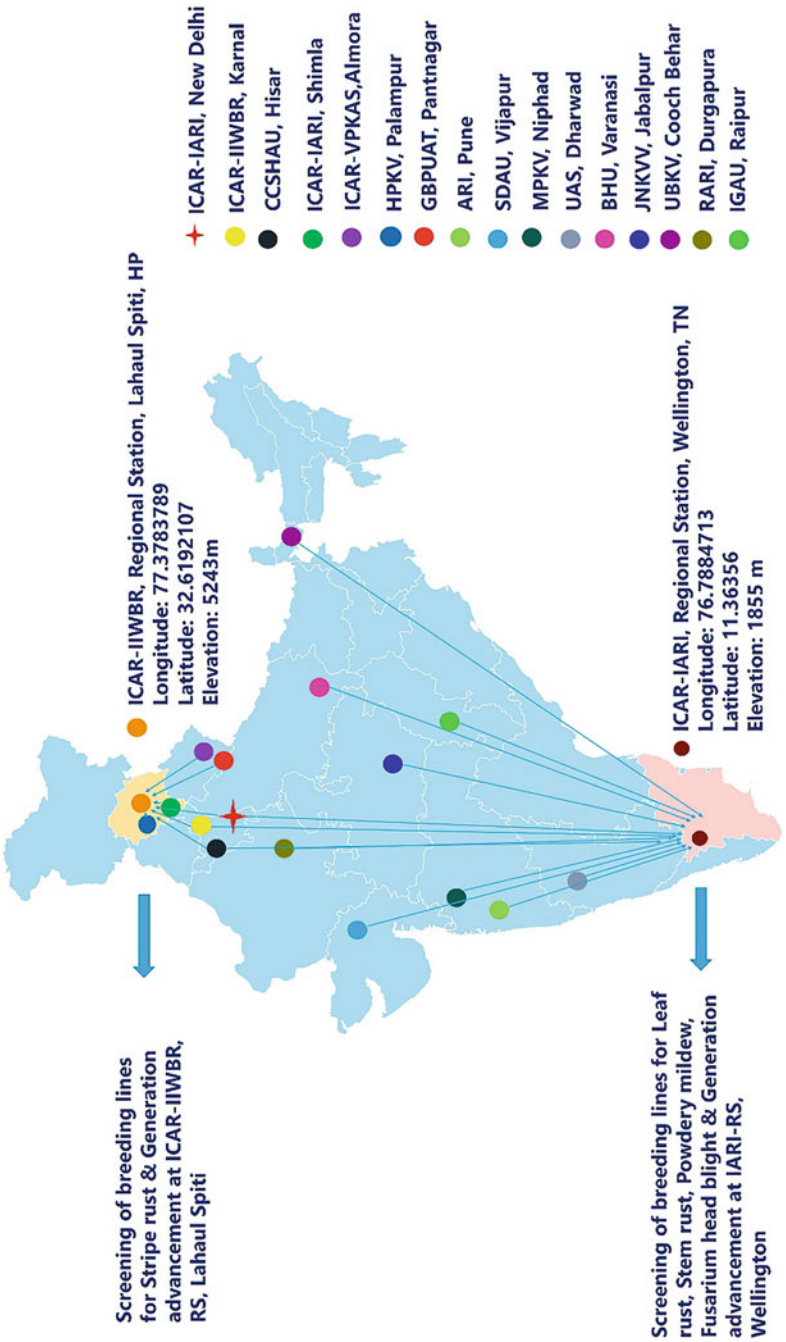

Fig. 7.2 Shuttle breeding programme of wheat operated at ICAR-IIWBR, RS Lahaul Spiti and ICAR-IARI, Wellington

Another important shuttle breeding facility is provided by the regional station of ICAR-Indian Institute of Wheat and Barley Research at Dalang Maidan, Lahaul Spiti, Himachal Pradesh. This station is regularly utilized for screening the breeding material against stripe rust, generation advancement and making corrective crosses. Major institutes working on wheat improvement programmes in North India like ICAR-IARI New Delhi, ICAR-IIWBR Karnal, CCSHAU Hisar, ICAR-IARI Shimal, HPKV Palampur, GBPUAT Pantnagar, etc. are utilizing this station as an off-season nursery (Fig. 7.2). These two stations working with major wheat breeding centres are playing an important role in assisting the breeding of improved wheat varieties with resistance to many biotic stresses.

7.4.3 Speed Breeding

The development of cultivars with conventional generation advancement procedures requires several years after the crossing of selected parental lines. The four to six generations of inbreeding are typically required to have the advanced stable lines for evaluation of grain yield and agronomic traits (Watson et al. 2018). This is even time-consuming for wheat having the off-season generation advancement through shuttle breeding with two generations per year. Globally, shuttle breeding in wheat improvement has been effectively utilized over the past decades, and the pace of yield gain has remained at par with the rising wheat demand. However, by 2050, crop production including wheat needs to double to fulfil the projected good grain requirement resulting from population growth, diet shifts and increasing biofuel consumption (Ray et al. 2013). Globally, the grain yield of wheat was increased by 0.9% per year, non-compounding rates, which is less than the required growth rate, i.e. 2.4% per year to double production by 2050 (Ray et al. 2013). Further, the presence of the narrow genetic base of breeding stocks is also a tremendous challenge to achieve the required growth rate of 2.4% per year. At the current growth rate of wheat production, global production would increase by only 38%, which would fall very short to meet projected demand. Therefore, the accelerated genetic gain of grain yield is the utmost requirement to meet the projected demand and save millions of people from hunger and starvation. The breeders' equation clearly shows that genetic gain can be enhanced by increasing the selection intensity, accuracy and additive genetic variance and shortening the breeding cycle. Tweaking selection accuracy and intensity can lead to minor improvements in genetic gain; however, shortening the breeding cycles per year would be very useful to boost the rate of genetic gain substantially (Li et al. 2018). From the equation, it is well evident that genetic gain can be double if the breeding cycle is reduced to half while maintaining the other factors like selection intensity, heritability and additive genetic variance as such. The shortening of breeding cycles per year can be accomplished by shuttle breeding and speed breeding under controlled artificial conditions.

In speed breeding, environmental conditions for crop growth are artificially manipulated under fully enclosed, controlled environment growth chambers aiming to accelerate flowering and seed set to advance to the next breeding generation as

quickly as possible. The research and findings related to speed breeding are not of recent time; the systematic findings had been reported back to the year 1880. Siemens (1880) reported the effects of continuous light on the growth of quick-growing crops such as mustard, carrot, beans, cucumber and melons. Since then, research work on deciphering the effect of artificial environment on plant growth and development and improvement in LED technologies have been carried out (Pfeiffer 1926; Arthur et al. 1930; Bula et al. 1991; Darko et al. 2014; Stutte 2015). The first dwarf wheat variety, 'USU-Apogee' suited for rapid cycling under controlled conditions, was developed by NASA and Utah State University (Bugbee and Koerner 1997). However, the term 'speed breeding' was coined by researchers at the University of Queensland after getting inspiration from NASA in 2003. The systematic and very efficient protocol of speed breeding in wheat was designed by the researchers of the same organization (Watson et al. 2018; Ghosh et al. 2018). This technique requires the crop-specific optimal quality light, light intensity, day length and controlled temperature to speed up photosynthesis and flowering, which is coupled with early harvest of seed to shorten the generation time (Hickey et al. 2019). It is appropriate for variable germplasm and does not necessitate specialized laboratory facilities for in vitro culturing (Hickey et al. 2019). Speed breeding is a highly adaptable platform to achieve rapid generation advancement, where up to six generations per year can be achieved in bread wheat and durum wheat (Watson et al. 2018). The basic purpose of speed breeding is to develop the panel of homozygous lines with sufficient diversity retention after crossing parental lines as early as possible. Therefore, it would be very useful in accelerating the wheat improvement programme through faster generation of populations and adult plant phenotyping for specific traits (Watson et al. 2018) and identification of genomic regions associated with traits of interest. This technique would be very useful in harnessing the diversity present in gene banks by an integrated approach using a combination of speed breeding and genomic selection that could accelerate gene bank mining (Li et al. 2018). Speed breeding can be effectively integrated with novel breeding strategies like genomic selection to enhance the genetic gain per unit of time and multiplex genome editing with CRISPR-Cas9 tool for large-scale genome re-writing (Li et al. 2018) to understand the complex biochemical pathways and/or improvement of trait of interest. In Australia, the first spring wheat variety, i.e. DS Faraday, was released in 2017 after discovering new sources of resistance and genomic regions linked with DNA markers in the Vavilov wheat collection (Riaz et al. 2017).

7.4.4 Marker-Assisted Backcrossing

In marker-assisted backcross breeding (MABB), initially genomic regions associated with a trait of interest are identified with the QTL mapping approach utilizing the mapping population developed either from bi-parental crossing or natural population having sufficient variability for a trait of interest (Gaikwad et al. 2020). MABB is quite effective in transferring traits controlled by few genes and having a large effect on the phenotypic appearance of the target trait. In

conventional backcross breeding, at least six to eight backcrosses are required to completely recover the recurrent parent genome (Collard et al. 2005). This typical formula, i.e. $(2^{n+1}-1)/2^{n+1}$, gives the theoretical percentage of the recurrent parent genome after n generations of backcrossing under no genetic drift (Collard et al. 2005). The recurrent parent genome recovery would be 75% in BC1; 87.5% in BC2; and 93.8% in BC3; likewise, four to six generations are needed for almost recovery of recurrent parent genome. However, recurrent parent genome recovery is average recovery over all individuals of the entire population. Some of the individuals might be carrying a more percentage of recurrent parent genome than average genome recovery. For rapid generation advancement and fixation of homozygosity, the selection of these individuals having high parent genome recovery is crucial. In this regard, molecular markers are very useful, by which researchers can select the individuals having the high proportion of recurrent parent genome. As a result, maximum recurrent parent genome recovery within two to three backcrosses and the target trait of interest is possible, making rapid generation advancement feasible. In MABB, tightly linked flanking markers to QTLs or gene(s) of interest and evenly distributed genome-wide markers from other genomic regions of the recurrent parent are employed for selection, the introgression of target QTLs and retrieval of recurrent parental genome (Collard et al. 2005). Although recurrent parent genome recovery in MABB largely depends on the number of markers, population size in each backcross generation and selection strategies (Rai et al. 2018). Frisch et al. (1999) did the computer simulation study to compare selection strategies with respect to proportion of the recurrent parent genome recovery, number of marker data points and population size in each generation for effective introgression. He observed that increasing population sizes from generation BC_1 to BC_3 reduced the required marker data points by 50% without disturbing the proportion of the recurrent parent genome recovery. In BC_1 and BC_2, two-stage selection (1. select individuals carrying the target allele and 2. select one individual which is homozygous for the recurrent parent allele at the maximum number of all markers across the genome) is superior to three- and four-stage selection because it reaches a larger recurrent parent genome proportion with given population size. However, suppose the removal of linkage drag is on high priority. In that case, three-stage (in addition to two-stage, 'Select individuals homozygous for the recurrent parent allele at most flanking markers') and four-stage (in addition to three-stage, 'Select individuals homozygous for the recurrent parent allele at all additional markers on the carrier chromosome') selection should be applied. A four-stage selection approach reduced the required number of marker data points by as much as 75% compared to all markers across the genome. The shortening of backcross generations, i.e. from six to three, with the requirement of moderate population sizes and the number of marker data points, is viable and efficient method to accelerate the breeding program. MABB can also be very effectively integrated with speed breeding for getting the maximum output per unit of time in the wheat improvement program.

7.4.5 Genomic Selection

To enhance wheat productivity, breeders need to use novel breeding strategies which can boost larger genetic gains in shorter times. The capacity of RGS methods to ensure the logistical and cost benefits has its own substantial advantages in crop breeding. The possibility of choosing parents from early generations of breeding cycles (first or second stage of selfing after hybridization) has largely proved their benefits in achieving maximum genetic gains. Though an effective combination of various contemporary approaches in practical crop improvement programmes remains challenging and requires substantial validation. A recent breeding strategy termed 'genomic selection' (Meuwissen et al. 2001) in crop plants has been studied carefully by many workers, and the primary advantage it offers is through reduced cycle time but not the increased accuracy. In its comparison, RGA with much lower cost involvement has the same capacities as genomic selection allows for more quickly realized genetic gains with the reduction in generation cycles. These two tools (GS and RGA) affect important steps in the breeding cycle, including choosing better candidates through selection and the production of seeds for the next generation and reducing the length of the breeding cycle with increased genetic gain per unit of time. Reductions in cycle time due to these methods are useful due to the more accurate selections and evaluation of homozygous, stable lines in replicated yield trials, which is not easier in pedigree and bulk methods without a proper selection and advancement among segregation generations of breeding cycles.

The only major point to be noted when anyone thinks to integrate GS in breeding programmes is the genotyping of fixed lines, which makes it non-economical. It could be employed to enhance the number of selection and individual genotypes with a standard budget provided genotyping is cheap as compared to field phenotyping. The GS has become an integral part of most wheat breeding programmes and has proved its effectiveness in accurately predicting yield, quality and disease resistance traits. Many parametric and nonparametric genomic prediction models with high accuracy have been proposed on specific experimental designs and data sets. Compared to phenotypic selection, GS contributes to higher genetic gain with slightly reduced selection accuracy, which is compensated by lowering breeding cycles (Heffner et al. 2010). Further, in winter wheat, Heffner et al. (2010) employed and trained GS model in the material developed from F_5 lines, which are generated through rapid generation advance (RGA) scheme. The accuracy of genomic predictions relies mainly on the training population, and it needs a larger size of the population with due consideration to the genetic relatedness of the population from which individuals are selected. Moreover, higher epistasis in the total genetic variance would need nonparametric models, and the additive genetic variance can be easily predicted using parametric models.

The higher genetic gains in any breeding programmes are more profound when breeding approaches bring rapid changes in the factors affecting genetic gains. It can be achieved through exploring methods which allow an increase in selection intensity, reduced generation cycles and higher heritability of important traits. The approaches like RGA and GS could enhance the genetic gains achieved per unit

area with a positive impact on these factors. GS is very phenomenal in improving the '*i*' component (selection intensity), and RGA shortens the generation time (*L*). In addition to the higher selection intensity and the reduced generation time, these approaches in combination are more effective in reducing the costs of breeding programmes. The GS approach would reduce the large-scale field evaluations of individual lines and allows a larger number of different populations to be tested (Endelman et al. 2014). Therefore, GS increases the genetic gains per unit time with lesser costs in the development of new cultivars. Because of phenotyping of only selected individuals with minimal replication, increase both the accuracy and intensity of selection. Lorenz (2013) and Riedelsheimer and Melchinge (2013) in their simulation studies confirm that the use of genomic prediction usually led to an increased response to selection. Before advanced yield testing, selective screening of genotypes in an early stage of selection with markers linked to few economically important traits like disease resistance would be advantageous in increasing the selection intensity (*i*). But, due to undesirable linkages or correlations between some of the characteristics evaluated under early generations, it may not be feasible to select lines based on the early generation testing compared to more advanced generation testing for traits like yield and quality. The intense selection in early generations can result in reduced response to selection in addition to selection intensity and genetic gain. Hence, parallel testing should be done to study the impact of early generation selection prior to testing of advanced generations on overall genetic gain for important economic traits.

In conclusion, as genomic selection can be carried out on immature seedlings, it could reduce the breeding cycle time to a year or even less, and a new generation cycle can be initiated as soon as the selected candidates reach maturity through rapid generation advancement. Optimization of resources is also possible as GS reduces the size from F_3 generation onwards. It provides a significant advantage compared to traditional breeding through increasing the genetic improvement rate by tenfold. The only prerequisite in the successful integration of RGA and GS is to have an optimized breeding programme and strategies to reduce breeding cycle time in a cost-effective way.

7.5 Procedures and Protocols of Rapid Generation Advancement

7.5.1 Doubled Haploidy (DH)

In wheat, the fixation of target marker loci to stabilize crop yield, stress resilience and other agronomic traits using traditional breeding techniques would take several years for continuous inbreeding and selection. Doubled haploid production in wheat would be the best alternative to facilitate the wheat breeders to achieve line fixation in a single year and deliver lines with cent per cent homozygosity in a very short period. There are several strategies to produce DHs in wheat, including interspecific hybridization, microspore culture and wheat x maize-based crossing system. Among

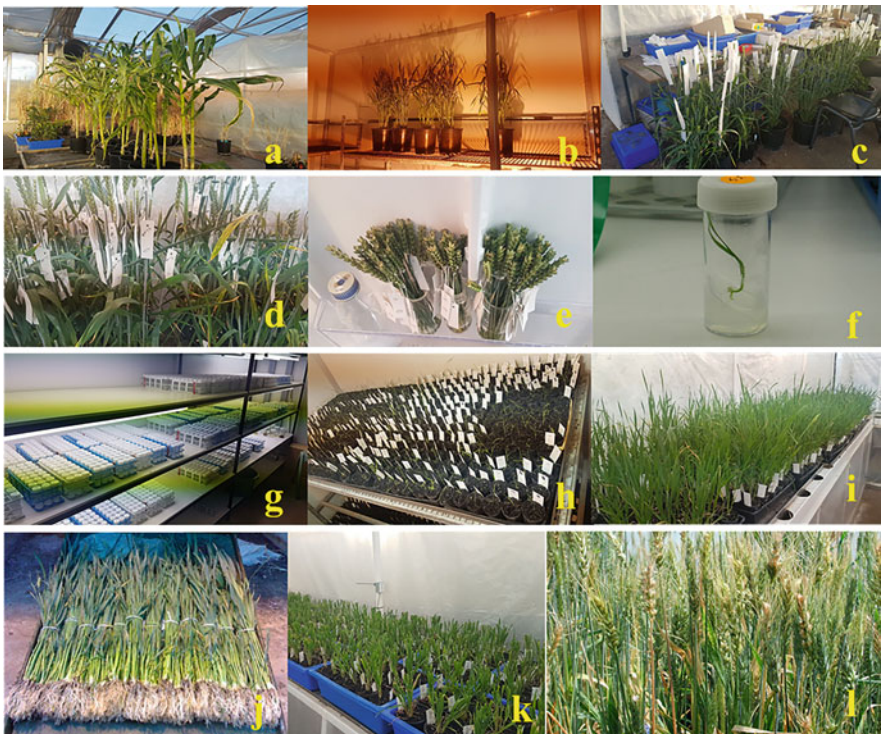

Fig. 7.3 Production of DH in wheat: (**a**) growing maize as a pollen source, (**b**) wheat in controlled conditions from synchronization, (**c**) the emasculated wheat plants, (**d**) 2,4-D treated ears of wheat, (**e**) the ears with caryopses harvested, (**f**) growing haloid plants under tissue culture, (g) culturing haploid plants under tissue culture facility, (**h**) hardening haploid plants under controlled conditions, (**i**) tillering in haploid plants, (**j**) colchicine-treated haploid plants, (**k**) planting and hardening colchicine-treated plants and (**l**) the production of DH seed on colchicine-treated plants

these, wheat × maize-based system is the easiest and feasible method, which works on the principle that the chromosomes of maize are eliminated on crossing with maize which is followed by an embryo rescue technique and doubling of wheat haploid chromosomes using colchicine (Sadasivaiah et al. 1999; Ushiyama et al. 2007). In wheat doubled haploids were successfully employed in gene/QTL mapping and GWAS, including several genetic studies (Collard et al. 2005; Czembor et al. 2003; Trkulja et al. 2012) (Fig. 7.3; Table 7.1).

7.5.2 Speed Breeding

Speed breeding or accelerated plant breeding is a fast-accepting strategy among plant research groups worldwide to achieve plant generations more rapidly and

Table 7.1 A simple protocol for DH production in wheat is provided below

Steps	Stages	Detailed procedure
Emasculation of wheat spikes	Stage I	Desired ear of the wheat should be medium hard, and anther colour must be light green to green. Central florets of the spikelets are cut off, leaving the primary and secondary florets on the left and right side for better emasculation and seed set
	Stage II	Five to eight spikelets from the central portion of wheat ear must be used for the emasculation and hybridization. Later the emasculated spike is closed with crossing bags to avoid any further pollen contamination
Pollination	Stage I	After 2–3 days of emasculation, a pool of fresh maize pollen is dusted on to the spikelets for pollination. For good fertilization, it may be done two times between 8.30 am to 12 noon and 2.00 pm to 3.30 pm
	Stage II	After the pollination, cover the spike again with a crossing paper bag
Application of 2, 4-D	Stage I	Twenty-four hours after pollination, a drop of 150 ppm 2, 4-D needs to be applied using a plastic pasture pipette at the central portion of two florets.
	Stage II	The spikes should not be covered with crossing bag after 2, 4-D spraying to avoid any fungal growth
Collection of caryopses	Stage I	Wheat ears are cut off from the wheat plants 20–21 days after pollination and are placed in a flask with sterilized water. Later caryopses are scooped out of florets carefully using forceps, sterilized and cultured on to the medium on the same day
	Stage II	Full-strength Milton antibacterial soln. 0.95% w/w sodium hypochlorite equivalent to 1.00% w/w available chlorine is used for sterilization followed by rinsing three times with distilled water
Culturing caryopses	Stage I	The caryopses are cultured on B5 medium in a 30-ml tissue culture vial
	Stage II	Then keep the tubes in a refrigerator for 2 days at 4 °C, followed by shifting to a growth chamber maintained at 20–22 °C with 16 h of light for 3 weeks
Growing haploid plants	Stage I	After 20 days, carefully transfer the haploid plants from tissue culture tubes into small pots containing hardening soil media without fertilizer
	Stage II	After 4–5 days, the plants are shifted to a net house for tillering and establishment
Colchicine treatment	Stage I	The roots of haploid plants are thoroughly washed and treated in 0.15% colchicine solution for 3 h. roots are dipped in the solution up to the crown root level
	Stage II	After 3–4 h, plantlets will be removed from colchicine solution and are washed thoroughly under running tap water
	Stage III	The plants will then be transplanted in larger pots filled with soil
Production of doubled haploids	Stage I	After 2 weeks, plants are transferred to a net house and grown at 22–30 °C for production of seeds

develop varieties at a quicker pace. The procedures followed in undertaking the speed breeding involve simpler protocols and are easily adopted by research groups with minimal facilities with congenial environments. Under speed breeding, plants are grown under controlled greenhouse conditions using optimal light intensity and required day length and temperature. The conditions provided under these controlled conditions can accelerate several physiological activities in plants, particularly photosynthesis and flowering, consequently reducing the generation time. Additionally, speed breeding also allows to accomplish four to six generations per year instead of two to three generations which can be achieved where offseason facilities are available or under the controlled conditions. The speed breeding protocols are well established in some important staple crops and can be referred to Watson et al. (2018).

7.5.3 Marker-Assisted Backcross Breeding

Plant breeders widely use marker-assisted backcross breeding to transfer gene(s) of interest into superior agronomic lines. Commonly, those crops with less than two generations that can be taken in a year would need at least 4 years to develop gene introgressed lines (NILs). The integration of RGA with the MABB method can enable the quick genetic fixation of lines through modifying plant's growth conditions such that early flowering and seed set is achieved as compared to normal field conditions. The major benefits of RGA strategies compared to conventional approaches are speed, technical simplicity, the requirement of fewer resources and reduced costs. A schematic representation of integrating the RGA and MABB for simultaneous characterization and introgression of genes is given in Fig. 7.4.

7.6 Conclusion

The rapid breeding cycles are very important in wheat (*Triticum* spp.), which can be utilized to achieve superior wheat cultivars with better yield, disease resistance and nutritional status within the shortest time required from hybridization to release of varieties. Moreover, these rapid breeding cycles can be employed to get more yield per unit area from better performing wheat cultivars in the near future, which will be pertinent due to unfold urbanization and the development of commercial buildings on agricultural land.

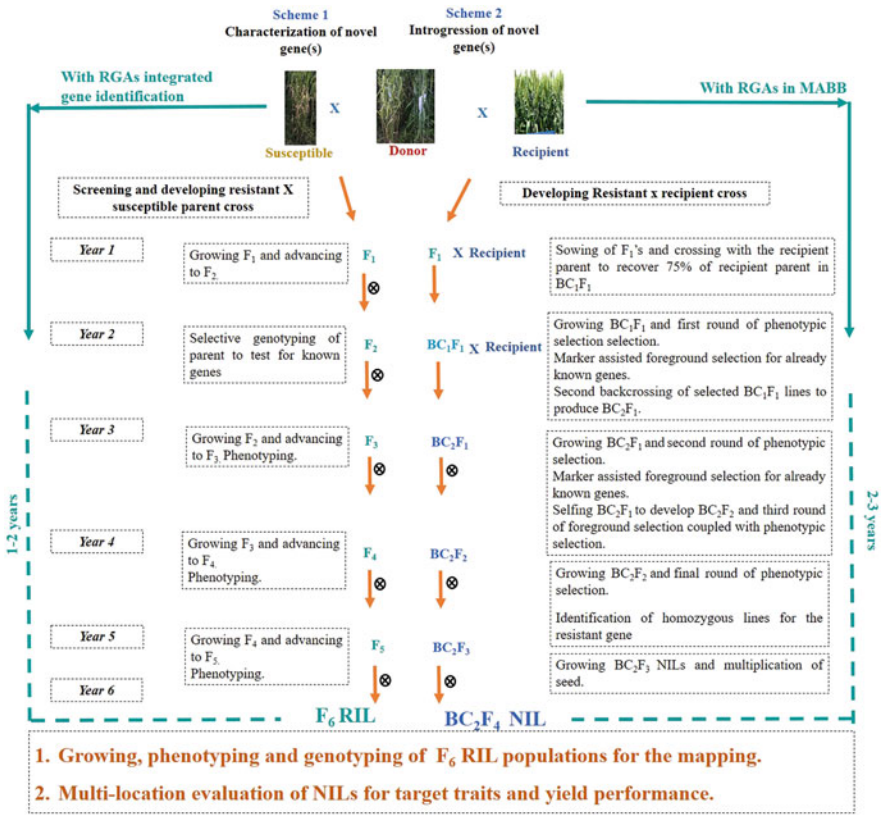

Fig. 7.4 A schematic representation showing the integration of RGA and MABB for simultaneous characterization and introgression of genes for various stress-resilient and agronomic traits

References

Alahmad S, Dinglasan E, Leung KM, Riaz A, Derbal N, Voss-Fels KP, Able JA, Bassi FM, Christopher J, Hickey LT (2018) Speed breeding for multiple quantitative traits in durum wheat. Plant Methods 14:36. https://doi.org/10.1186/s13007-018-0302-y

Arthur JM, Guthrie JD, Newell JM (1930) Some effects of artificial climates on the growth and chemical composition of plants. Am J Bot 17:416–482

Atlin GN, Cairns JE, Das B (2017) Rapid breeding and varietal replacement are critical to adaptation of cropping systems in the developing world to climate change. Glob Food Sec 12: 31–37. https://doi.org/10.1016/j.gfs.2017.01.008

Babu P, Baranwal DK, Harikrishna PD, Bharti H, Joshi P, Thiyagarajan B, Gaikwad KB, Bhardwaj SC, Singh GP, Singh A (2020) Application of genomics tools in wheat breeding to attain durable rust resistance. Front Plant Sci 11:567147. https://doi.org/10.3389/fpls.2020.567147

Beche E, Benin G, da Silva CL, Munaro LB, Marchese JA (2014) Genetic gain in yield and changes associated with physiological traits in Brazilian wheat during the 20th century. Eur J Agron 61:49–59

Bhattarai SP, La PenaRC D, Midmore DJ, Palchamy K (2009) In vitro culture of immature seed for rapid generation advancement in tomato. Euphytica 167:23–30. https://doi.org/10.1007/s10681-008-9855-6

Borlaug NE (1968) Wheat breeding and its impact on world food supply. In: Finlay EW, Sheperd KW (eds) 3rd International Wheat Genet Symp. Australian Academy of Science, Canberra, pp 5–15

Bugbee B, Koerner G (1997) Yield comparisons and unique characteristics of the dwarf wheat cultivar 'USU-apogee'. Adv Space Res 20:1891–1894

Bula RJ, Morrow RC, Tibbitts TW, Barta DJ, Ignatius RW, Martin TS (1991) Light-emitting diodes as a radiation source for plants. Hort Sci 26(2):203–205

Chaudhary HK, Kaila V, Rather SA, Tayeng T (2014) Distant hybridisation and doubled-haploidy breeding. In: Alien gene transfer in crop plants, vol 1. Springer, New York, NY, pp 143–164. https://doi.org/10.1007/978-1-4614-8585-8_6

Collard BC, Jahufer MZ, Brouwer JB, Pang EC (2005) An introduction to markers, quantitative trait loci (QTL) mapping and marker-assisted selection for crop improvement: the basic concepts. Euphytica 142(1):169–196. https://doi.org/10.1007/s10681-005-1681-5

Crespo-Herrera LA, Crossa J, Huerta-Espino J, Autrique E, Mondal S, Velu G, Vargas M, Braun HJ, Singh RP (2017) Genetic yield gains in CIMMYT's international elite spring wheat yield trials by modeling the genotype× environment interaction. Crop Sci 57(2):789–801. https://doi.org/10.2135/cropsci2016.06.0553

Czembor PC, Arseniuk E, Czaplicki A, Song QJ, Cregan PB, Ueng PP (2003) QTL mapping of partial resistance in winter wheat to Stagonospora nodorum blotch. Genome 46:546–554

Darko E, Heydarizadeh P, Schoefs B, Sabzalian MR (2014) Photosynthesis under artificial light: the shift in primary and secondary metabolism. Philos Trans R Soc B Biol Sci 369(1640):20130243

Davidson JL, Christian KR, Jones DB, Bremner PM (1985) Responses of wheat to vernalization and photoperiod. Aus J Agri Res 36(3):347–359

Depauw RM, Clarke JM (1976) Acceleration of generation advancement in spring wheat. Euphytica 25:415–418. https://doi.org/10.1007/BF00041574

DePauw RM, Knox RE, Humphreys DG, Thomas JB, Fox SL, Brown PD, Singh AK, Pozniak C, Randhawa HS, Fowler DB, Graf RJ (2011) New breeding tools impact Canadian commercial farmer fields. Czech J Genet Plant Breed 47(Special Issue):New-breeding. https://doi.org/10.17221/3250-CJGPB

Dinglasan E, Godwin ID, Mortlock MY, Hickey LT (2016) Resistance to yellow spot in wheat grown under accelerated growth conditions. Euphytica 209:693–707. https://doi.org/10.1007/s10681-016-1660-z

Dunwell JM (2010) Haploids in flowering plants: origins and exploitation. Plant Biotechnol J 8(4):377–424. https://doi.org/10.1111/j.1467-7652.2009.00498.x

Eberhart SA (1970) Factors effecting efficiencies of breeding methods. African Soils 15(1/3):655–680

Endelman JB, Atlin GN, Beyene Y, Semagn K, Zhang X, Sorrells ME, Jannink JL (2014) Optimal design of preliminary yield trials with genome-wide markers. Crop Sci 54(1):48–59

Evans L (1987) Short day induction of inflorescence initiation in some winter wheat varieties. Funct Plant Biol 14:277–286. https://doi.org/10.1071/PP9870277

Figueroa M, Hammond-Kosack KE, Solomon PS (2018) A review of wheat diseases—a field perspective. Mol Plant Pathol 19(6):1523–1536. https://doi.org/10.1111/mpp.12618

Frisch M, Bohn M, Melchinger AE (1999) Minimum sample size and optimal positioning of flanking markers in marker-assisted backcrossing for transfer of a target gene. Crop Sci 39:967–975. https://doi.org/10.2135/cropsci1999.0011183X003900040003x

Gaikwad KB, Rani S, Kumar M, Gupta V, Babu PH, Bainsla NK, Yadav R (2020) Enhancing the nutritional quality of major food crops through conventional and genomics-assisted breeding. Front Nutrit 7:533453. https://doi.org/10.3389/fnut.2020.533453

Gaur PM, Samineni S, Gowda CL, Rao BV (2007) Rapid generation advancement in chickpea. J SAT Agric Res 3(1)

Ghosh S, Watson A, Gonzalez-Navarro OE, Ramirez-Gonzalez RH, Yanes L, Mendoza-Suárez M, Simmonds J, Wells R, Rayner T, Green P, Hafeez A (2018) Speed breeding in growth chambers and glasshouses for crop breeding and model plant research. Nat Protoc 13(12):2944–2963. https://doi.org/10.1038/s41596-018-0072-z

Goulden CH (1939) Problems in plant selection. In: Burnett RC (ed) Proceeding of the seventh genetics congress. Cambridge University Press, Edinburgh, pp 132–133

Grafius JE (1965) Shortcuts in plant breeding. Crop Sci 5:377

Haley SD, Johnson JJ, Peairs FB, Quick JS, Westra PH, Stromberger JA, Clayshulte SR, Clifford BL, Rudolph JB, Giura A (2006) Registration of 'Bond CL' wheat. 46(2):993. https://doi.org/10.2135/cropsci2005.0031

Heffner EL, Lorenz AJ, Jannink JL, Sorrells ME (2010) Plant breeding with genomic selection: gain per unit time and cost. Crop Sci 50:1681. https://doi.org/10.2135/cropsci2009.11.0662

Hickey LT, Lawson W, Platz GJ, Dieters M, Arief VN, German S, Fletcher S, Park RF, Singh D, Pereyra S, Franckowiak J (2011) Mapping Rph20: a gene conferring adult plant resistance to *Puccinia hordei* in barley. Theor Appl Genet 123:55–68. https://doi.org/10.1007/s00122-011-1566-z

Hickey LT, Hafeez AN, Robinson H, Jackson SA, Leal-Bertioli SC, Tester M, Gao C, Godwin ID, Hayes BJ, Wulff BB (2019) Breeding crops to feed 10 billion. Nat Biotechnol 37(7):744–754. https://doi.org/10.1038/s41587-019-0152-9

Ishigaki Y (2010) Establishment of cultivation technique with rapid generation advancement of *Cyclamen persicum* by sowing seeds right after picking seeds. Bull Gifu Pref Res Inst Agr Sci in Hill Mount Are 6:7–12

Kuchel H, Ye G, Fox R, Jefferies S (2005) Genetic and economic analysis of a targeted marker-assisted wheat breeding strategy. Mol Breed 16(1):67–78. https://doi.org/10.1007/s11032-005-4785-7

Li H, Rasheed A, Hickey LT, He Z (2018) Fast-forwarding genetic gain. Trends Plant Sci 23(3): 184–186. https://doi.org/10.1016/j.tplants.2018.01.007

Meuwissen TH, Hayes BJ, Goddard ME (2001) Prediction of total genetic value using genome-wide dense marker maps. Genetics 157(4):1819–1829. https://doi.org/10.1093/genetics/157.4.1819

Mottaleb KA, Singh PK, Sonder K, Kruseman G, Tiwari TP, Barma NC, Malaker PK, Braun HJ, Erenstein O (2018) Threat of wheat blast to South Asia's food security: an ex-ante analysis. PLoS One 13(5):e0197555. https://doi.org/10.1371/journal.pone.0197555

Pfeiffer NE (1926) Microchemical and morphological studies of effect of light on plants. Bot Gaz 81(2):173–195

Prigge V, Xu X, Li L, Babu R, Chen S, Atlin GN, Melchinger AE (2012) New insights into the genetics of in vivo induction of maternal haploids, the backbone of doubled haploid technology in maize. Genetics 190(2):781–793. https://doi.org/10.1534/genetics.111.133066

Rai N, Bellundagi A, Kumar PK, Kalasapura Thimmappa R, Rani S, Sinha N, Krishna H, Jain N, Singh GP, Singh PK, Chand S (2018) Marker-assisted backcross breeding for improvement of drought tolerance in bread wheat (Triticum aestivum L. em Thell). Plant Breed 137(4):514–526. https://doi.org/10.1111/pbr.12605

Ray DK, Mueller ND, West PC, Foley JA (2013) Yield trends are insufficient to double global crop production by 2050. PLoS One 8(6):e66428. https://doi.org/10.1371/journal.pone.0066428

Riaz A, Periyannan S, Aitken E, Hickey L (2016) A rapid phenotyping method for adult plant resistance to leaf rust in wheat. Plant Methods 12(1):1–10

Riaz A, Athiyannan N, Periyannan S, Afanasenko O, Mitrofanova O, Aitken EA, Lagudah E, Hickey LT (2017) Mining Vavilov's treasure chest of wheat diversity for adult plant resistance to Puccinia triticina. Plant Dis 101(2):317–323. https://doi.org/10.1094/PDIS-05-16-0614-RE

Richard CA, Hickey LT, Fletcher S, Jennings R, Chenu K, Christopher JT (2015) High-throughput phenotyping of seminal root traits in wheat. Plant Methods 11(1):1–1. https://doi.org/10.1186/s13007-015-0055-9

Riedelsheimer C, Melchinge AE (2013) Optimizing the allocation of resources for genomic selection in one breeding cycle. Theor Appl Genet 126(11):835–2848

Rizal G, Karki S, Alcasid M, Montecillo F, Acebron K, Larazo N, Garcia R, Slamet-Loedin IH, Quick WP (2014) Shortening the breeding cycle of sorghum, a model crop for research. Crop Sci 54(2):520–529. https://doi.org/10.2135/cropsci2013.07.0471

Sadasivaiah RS, Orshinsky BR, Kozub GC (1999) Production of wheat haploids using anther culture and wheat x maize hybridization techniques. Cereal Res Commun 27(1):33–40

Siemens CW III (1880) On the influence of electric light upon vegetation, and on certain physical principles involved. Proc R Soc London 30(200–205):210–219. https://doi.org/10.1098/rspl.1879.0108

Smale M, Singh J, Di Falco S, Zambrano P (2008) Wheat breeding, productivity and slow variety change: evidence from the Punjab of India after the green revolution. Aust J Agric Resour Econ 52(4):419–432. https://doi.org/10.1111/j.1467-8489.2008.00435.x

Srivastava P, Bains NS (2018) Accelerated wheat breeding: doubled haploids and rapid generation advance. In: Biotechnologies of crop improvement, vol 1. Springer, Cham, pp 437–461. https://doi.org/10.1007/978-3-319-78283-6_13

Stutte GW (2015) Commercial transition to LEDs: a pathway to high-value products. Hort Sci 50(9):1297–1300. https://doi.org/10.21273/HORTSCI.50.9.1297

Tadesse W (2013) Methods and applications of doubled haploid technology in wheat breeding-A technical manual https://hdl.handle.net/20.500.11766/7530

Tadesse W, Sanchez-Garcia M, Assefa SG, Amri A, Bishaw Z, Ogbonnaya FC, Baum M (2019) Genetic gains in wheat breeding and its role in feeding the world. Crop Breed Genet Genom 1: e190005

Trkulja D, Kondić-Špika A, Brbaklić L, Kobiljski B, Hristov N (2012) Marker-trait associations for spike-related characters in a doubled haploid population of wheat. Rom Agric Res 29:9–16

Underdahl JL, Mergoum M, Ransom JK, Schatz BG (2008) Agronomic traits improvement and associations in hard red spring wheat cultivars released in North Dakota from 1968 to 2006. Crop Sci 48(1):158–166. https://doi.org/10.2135/cropsci2007.01.0018

Ushiyama T, Kuwabara T, Yoshida T (2007) Effects of various phytohormones on haploid wheat production in wheat x maize crosses. Plant Prod Sci 10(1):36–41

Wang X, Wang Y, Zhang G, Ma Z (2011) An integrated breeding technology for accelerating generation advancement and trait introgression in cotton. Plant Breed 130(5):569–573. https://doi.org/10.1111/j.1439-0523.2011.01868.x

Watson A, Ghosh S, Williams MJ, Cuddy WS, Simmonds J, Rey MD, Md Hatta MA, Hinchcliffe A, Steed A, Reynolds D, Adamski NM, Breakspear A, Korolev A, Rayner T, Dixon LE, Riaz A, Martin W, Ryan M, Edwards D, Batley J, Raman H, Carter J, Rogers C, Domoney C, Moore G, Harwood W, Nicholson P, Dieters MJ, DeLacy IH, Zhou J, Uauy C, Boden SA, Park RF, Wulff BBH, Hickey LT (2018) Speed breeding is a powerful tool to accelerate crop research and breeding. Nat Plants 4(1):23–29. https://doi.org/10.1038/s41477-017-0083-8

Yadav R, Gaikwad K, Bhattacharyya R, Bainsla NK, Kumar M, Yadav SS (2018) Breeding new generation genotypes for conservation agriculture in maize-wheat cropping systems under climate change. In: Yadav SS, Redden RJ, Hatfield JL, Ebert AW, Hunter D (eds) Food security and climate change, pp 189–228. https://doi.org/10.1002/9781119180661.ch10

Yadav R, Gupta S, Gaikwad KB, Bainsla NK, Kumar M, Babu P, Ansari R, Dhar N, Dharmateja P, Prasad R (2021) Genetic gain in yield and associated changes in agronomic traits in wheat cultivars developed between 1900 and 2016 for irrigated ecosystems of Northwestern Plain Zone of India. Front Plant Sci 12:719394. https://doi.org/10.3389/fpls.2021.719394

Yuichi H, Takashi O, Tetsuhiro M, Shinji T (2002) Breeding of new wheat cultivar 'Sanukinoyume 2000'. Bull 55:1–8