Chapter 5
Breeding Methods: Line Development

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Abstract In order to produce successful varieties, wheat breeding programs must develop several strategies that fall under one of the following topics: line development, population improvement, and selection methods. Part I of this chapter focuses on breeding activities related to line development, while Part II discusses population improvement and selection methods. Line development refers to the process of obtaining homozygous inbreds derived from crosses between parental lines. A wide variety of line development methods have been proposed in pursuit of greater efficiency and effectiveness. This chapter aims to provide basic knowledge on line development methods in relation to wheat breeding, describe how and why they came about, and synthesize the results of empirical studies that have evaluated them in order to foster critical thinking and innovation in breeding strategy design.

Keywords Breeding strategies · Line development · Pedigree breeding · Bulk breeding · Single seed descent · Doubled-haploids

5.1 Learning Objectives

- To provide background information on line development approaches in relation to wheat breeding.

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- To facilitate critical thinking around the role of line development in the design of wheat breeding programs.

5.2 Introduction

Wheat breeding programs that aim to develop varieties must first develop inbred breeding lines so that they can be reproduced for further testing and variety release. Pedigree, bulk, single seed descent, and doubled-haploids are the four main line development methods, while backcross breeding is generally considered to be a useful adjunct to these approaches. Regardless of the line development method being used, the first step is typically to make crosses between different parental plants in order to generate new genetic combinations. If the two parents used in crossing are themselves inbred, then the F_1 progeny will be identical. If one or both of the crossing parents are not inbred, then there will be genetic and phenotypic variability, referred to as 'segregation' in the F_1 progeny. As an alternative to crossing, a breeder can generate novel genetic variation by mutagenizing one or a few plants to induce genetic mutations. The next steps after F_1 seed or mutagenized plants are generated depends on the line development method employed. Following successive generations of line development, a breeder may choose to release one or more lines as varieties or to release a multiline variety composed of more than one selected inbred line.

5.3 Pedigree Breeding

The pedigree method of line development, developed in the 1840s by Vilmorin [1] and rediscovered by Hallett [2] and Nilsson-Ehle [3], allows selection among individual plants and whole families at every inbreeding generation. The process tends to emphasize visual selection among individual plants in the field over successive years as the plants approach homozygosity. To initiate the pedigree breeding process, F_1s from a single cross are space-planted to maximize seed production and to clearly identify individual plants. If there is segregation among the F_1 progeny, selection among F_1s may be imposed. The F_1 plants are harvested individually or bulk harvested, and the resulting F_2s are sown in rows according to the pedigree such that individual plants within families can be identified and harvested individually. Selection is imposed among the F_2 plants, and only the selected plants are carried forward. Each selected F_2 is given a unique identifier (ID) that is recorded along with its pedigree. F_2 plants are harvested individually for their F_3 seed. F_3s that originate from a single F_2 plant are referred to as F_2-derived F_3 families (F_2:F_3). The F_2:F_3 families are typically space planted in rows to enable selection of one or more single plants or single spikes from different plants within each family. The F_2:F_3 families may also be evaluated for yield or quality in order to more accurately select among

families. As in the previous generation, selected F_3 plants are given IDs which are recorded along with the ID of their F_2 plant of origin. F_4 seed is harvested from the selected F_3 plants and is planted as F_3:F_4 families in rows. Because most of the variability at this stage is among as opposed to within families, many whole families may be discarded either based on visual assessments of traits such as disease resistance or flowering time and/or quantitative data on traits such as grain yield. The best individual F_4 plants from within the best families are selected and given an ID. F_5 seed is harvested from the selected F_4 plants. The F_4:F_5s are now referred to as 'inbred lines' or 'fixed lines'. F_4:F_5s are expected to be 87.5% homozygous; therefore, they should be phenotypically uniform and stable across generations. The F_4:F_5s are planted as rows, and bulk harvests of each row produce F_4:F_6 seed, which is then used to establish multi-environment yield trials and disease nurseries. Because multiple generations of selection have already been imposed, the F_4-derived lines are expected to be better than the average of their F_1 parents for the traits selected during pedigree breeding, assuming selection during line development was effective. An advantage of the pedigree breeding method is that phenotypic information from related families can be considered during among-family selection to help improve selection accuracy.

While once a popular approach, the pedigree breeding method in its original form is now seldom used in wheat breeding due to its inefficiency. With the pedigree breeding method, a large number of resources must be invested in selection among single plants in early generations. This requires evaluating the selection criteria, performing selection, maintaining seed purity of individual pedigrees, and keeping detailed records of each lineage. In return, a marginal amount of gain from selection is achieved. Although genotypic effects of early-generation families are theoretically predictive of their late-generation derivatives [4], early generation selection, as reviewed by Fischer and Rebetzke [5], is particularly ineffective for yield and other low-heritability traits with large genotype-by-environment (GxE) effects. In the case of yield, single plants or families in early generations experience low intragenotypic competition and high intergenotypic competition. Therefore, space planting of single plants or families is not representative of an actual production environments, and meaningful selections for yield performance cannot be made. This point has been demonstrated by empirical studies, which have found low or zero correlation between grain yield measured on single plants [6] or early-generation bulks [7] and grain yield measured in yield plots in later generations. In practice, yield is not typically measured on individual plants for selection during the pedigree breeding process. Instead, breeders often conduct visual selection of plants that appear to be higher yielding. While this visual selection approach is less costly than measuring yield, it is also largely ineffective. A selection experiment conducted by McKenzie and Lambert [8] found that, in barley (*Hordeum vulgare*), visual selection for overall appearance in the F_3 did not improve yield in the F_6, and it led to F_6 lines that were significantly taller and later maturing.

Even if selection in early generations could be conducted in a meaningful way, very little genetic gain would be realized for traits with large GxE effects unless families are evaluated across different locations and selection among families is

performed. A study which evaluated both early- and late-generation selection for grain yield or harvest index evaluated in a single environment showed that realized gains in grain yield were little better than random selection [9]. On the other hand, early-generation selection may be effective for traits of high heritability. A study examining the effectiveness of early-generation selection for yield and baking quality in wheat found that selection for protein content and thousand kernel weight in the F_3 generation was effective, but selection for other quality traits and yield was ineffective [10]. Because low-heritability traits like yield tend to be the primary targets of selection, the possible benefits of imposing selection in early generations often do not outweigh the costs. Today, many breeding programs are not conducting early-generation selection and instead employ line development schemes that aim to rapidly generate fixed lines that can be phenotyped accurately for yield and other traits of interest.

5.4 Bulk and Composite Breeding

In the early 1900s, Nilsson-Ehle developed the bulk breeding method [11] which greatly simplified the line development process and enabled breeders to generate lines from many different hybrid combinations with limited resources. In bulk methods of line development, early-generation families are planted and harvested as bulk populations. To begin the process, F_1 plants are harvested in bulk according to their pedigree. In the following season, the F_2 seed from each F_1 bulk is planted as a single row or small plot. Each selected F_2 family is harvested in bulk, producing F_3 seed. In the following season, each F_3 family is again planted as a plot, and selection among plots may be imposed. The process is repeated again until a desired level of uniformity and homozygosity is reached, at which point single spikes within the bulk plots are harvested in order to derive fixed lines. The fixed lines are given IDs and then planted as rows in the following season during which selection is often imposed among rows. Seed harvested from the selected rows is then used to evaluate yield and other traits. In the bulk breeding method employed by Nilsson-Ehle, mass selection (see Sect. 6.3 of Chap. 6) within bulk populations was considered to be an important feature. The idea was to 'assist nature in eliminating the delicate and in conserving the hardy' [11] by relying on abiotic and biotic stresses to aid the culling of poorly-adapted individuals within bulk populations over generations of inbreeding.

Several variations of the bulk breeding method have been suggested to further simplify or improve the process. Harlan and Martini [12] proposed to bulk progeny from multiple cross combinations, creating what is referred to as a 'composite cross population'. This approach enables the sampling of progeny from many diverse cross combinations and then allows natural selection to be imposed among the progeny. A bulk method which derives bulk families from selected F_2 plants and imposes selection among plants in bulk populations was described by Lupton and Whitehouse [13]. This approach was used extensively at CIMMYT, where it was referred to as a

'modified pedigree bulk' method [14]. The CIMMYT wheat program is currently using a 'selected bulk' [15] method in which selection within bulk populations is imposed, but selected plants within F_2 families are bulked rather than harvested individually.

The main advantage of bulk breeding methods is that they are simple and cost efficient because individual plants do not need to be harvested and documented individually. This cost savings can then be invested in the evaluation of fixed lines in multiple environments, which is much more effective for the improvement of low heritability traits like grain yield. At one time, natural selection within bulk populations was believed to be a useful feature of bulk breeding, but several experiments have demonstrated that natural selection within bulk populations often favors genotypes that do not perform well in realistic production environments [16]. The potential for natural selection to favor traits that may be advantageous in natural populations but undesirable in agronomical production systems is, in fact, the main disadvantage of bulk breeding methods.

5.5 Single Seed Descent

In light of the negative impacts of natural selection on bulk breeding populations, the single seed descent method (SSD) was proposed as a way to efficiently generate lines without allowing natural selection to take place [17]. This revolutionary idea enabled the use of off-season nurseries and controlled environments for generation advancement because selection for adaptation to these irrelevant environments could be avoided. In the SSD method, F_1 plants are assigned IDs and harvested for their F_2 seed. Many individual F_2 seeds from each F_1 are sown to generate F_2 plants. From each F_2, lines are derived by planting a single seed each generation. Specifically, one spike is harvested from each F_2 plant, and a single seed is planted to produce F_2:F_3 seed, which is then sown by family. One F_3 spike is harvested from each family, and a single seed is planted to produce F_3:F_4 seed. As in the previous generation, one spike is harvested from each F_4 plant and a single seed is planted. The process is repeated until the lines reach the desired level of homozygosity. For traits conferred by additive effects, the phenotypic distribution of the F_2 population will be the same as the phenotypic distribution of the F_2-derived inbred lines [18]. Thus, transgressive segregates will be preserved, although some anomalies, selection, or attrition is expected [19]. Concerns about missed opportunities for selecting during generation advancement are often raised. However, for yield improvement, the SSD and pedigree methods have been found to perform similarly [20], which is expected because selection for yield in early generations results in very little or no genetic gain [9].

The main advantage of the SSD method is that lines can be rapidly generated in a greenhouse or off-season nursery. Rapid generation advancement in greenhouses [21], also referred to as 'speed breeding', is a technique that is becoming increasingly popular for accelerating line development via SSD or bulk methods. These

accelerated breeding methods impose stresses that accelerate plant growth and development. Interestingly, with rapid generation advancement, breeders are reverting back to the random bulk method to simplify the process [21]. Tee and Qualset [22] suggested that under accelerated growth conditions, each plant produces only a few seeds and genetic differences in productivity are not apparent. If this is the case, then SSD is not necessary and bulking whole populations will not alter the genetic composition of the population. To test this hypothesis, Tee and Qualset [22] compared SSD and bulk methods in accelerated growth conditions in two populations. They found that in one population, taller genotypes were favored under bulk selection compared to SSD, while in the other population, there was no difference between bulk- and SSD-derived lines in terms of height, days to heading, and yield. The authors concluded that inadvertent selection in bulk populations was not enough of a concern to warrant using SSD. However, a simulation study by Muehlbauer et al. [19] found that when the standard deviation in the number of seeds produced per plant was greater than 25, progeny from 75% of the original F_2 plants were no longer represented in the population after four generations of bulk breeding. For any given breeding program, the relative merits of SSD and bulk breeding under rapid generation advancement will undoubtedly depend on the germplasm and the nature of the crosses being made. Intuitively, populations derived from parents that are phenotypically very different will experience greater intergenotypic competition effects and reduced between-line versus within-line variation in bulk breeding.

5.6   Doubled-Haploids

Doubled-haploids (DHs) allow breeders to develop homozygous genotypes from heterozygous genotypes in a single generation from the F_1 or in two generations from the F_2. For winter wheat, which can require eight or more weeks of vernalization, DH methods are often used for rapid line development. DHs in wheat can be produced using anther culture or via chromosome elimination, the latter of which is more reliable for wheat breeding. The chromosome elimination method of DH production in wheat begins by hybridizing F_1 wheat plants with maize (*Zea mays*) plants followed by embryo rescue and chromosome doubling using colchicine. For an extensive review of DH production methods in cereals, refer to Humphreys and Knox [23].

Successful DH production results in completely homozygous plants that then undergo seed increase and phenotypic evaluation. In theory, even in the absence of selection, means and variance of DH populations derived from F_1s may differ from those of equivalent SSD populations depending on the linkage phases and interaction effects of favorable loci [24]. The phenotypic distribution of DH populations can have greater kurtosis compared to SSD populations, which would make identifying individuals better than the population mean more difficult unless population sizes are increased [24]. However, empirical studies comparing DH and SSD populations have found little to no differences between them in terms of their phenotypic

distributions [25]. To allow greater opportunity for recombination and minimize differences between DH and SSD populations, producing DHs from F_2s or F_3s rather than from F_1s has been suggested [24].

While DHs are being used in some applied wheat breeding programs, their use has been limited by the cost of DH production and the difficulty of either establishing a specialized DH production laboratory in-house or finding a suitable DH service provider. The cost in 2020 of DH production charged by a popular DH service provider in the United States is between \$35 and \$50 USD per line depending on the details of the order (Heartland Plant Innovations, http://www.heartlandinnovations.com/). In the case of spring wheat breeding at CIMMYT, where two generations of line development can be conducted each year, using DH to develop fixed lines was not advantageous [26]. In winter wheat, off-season nurseries or rapid generation advancement in the greenhouse are alternatives to DH methods that could potentially deliver lines within the same timeframe and at lower cost. It is critical to remember that an established breeding program is producing new populations and lines every year, and accelerating line advancement is only advantageous when new lines are recycled as parents. As DH and generation advancement methods continue improving, breeders should continually reevaluate their options for rapid line development and select the most efficient method available.

5.7 Backcross Methods

Backcross breeding approaches can be employed to transfer a specific trait of interest from a parental donor into another breeding line referred to as the 'recurrent parent'. In this method, the parental donor line is repeatedly crossed to a recurrent parent with the goal of obtaining a line that is nearly genetically identical to the recurrent parent except for the addition of one or a few genes from the donor parent conferring the trait of interest. In practice, linkage drag can result in undesirable linked genes being transferred as well, especially in crosses in which exotic germplasm is the donor parent.

Backcrossing is sometimes referred to as a defensive or conservative breeding strategy because it involves the transfer up to three genes (limited by population size) conferring a simply-inherited trait of interest to correct a defect or otherwise improve a successful variety. It is therefore considered to be a useful adjunct to pedigree, bulk, SSD, and DH, which are typically employed to recover superior combinations of numerous alleles from both parents to improve quantitative traits such as yield. Self-fertilization and backcrossing produce parallel rates of inbreeding but very different genotypes (Table 5.1). An early example used backcrossing to develop 'Baart', a wheat cultivar resistant to common bunt (*Tilletia tritici*) [27]. The author noted that backcross-derived varieties should require less extensive testing prior to release and that the improved variety could then be used in future backcrossing programs rather than using the original exotic line.

Table 5.1 Approach to homozygosity and percent homozygosity at two loci of interest from self-fertilization or backcrossing

	Self-fertilized		Backcrossed	
Generations	% homozygous	% homozygous at 2 desired loci	% homozygous	% homozygous at 2 desired loci
1	25.00	6.25	25.00	25.00
2	56.25	14.06	56.25	56.25
3	76.56	19.14	76.56	76.56
4	87.79	21.97	87.89	87.89
5	93.84	23.46	93.84	93.84

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The general protocol for backcrossing depends on whether the trait being transferred follows dominant or recessive inheritance. If the trait is dominant, then the plants expressing the trait in each generation are heterozygous and are chosen for crossing to the recurrent parent. However, if the trait is recessive, it will not be obvious which plants carry the recessive allele. This can be remedied by making a test cross to the donor parent (or a self-pollination) at the same time the plant is crossed to the recurrent parent. The progeny of the test cross or self-pollination will segregate if the plant was heterozygous. The crosses made with the heterozygous plant are then advanced to the next backcross. With each backcross generation, the percentage of the recurrent parent genome recovered increases by half (Table 5.1). Population sizes required to have a certain probability of recovering individuals with the desired trait have been published in Sedcole [29]. However, in practice, it may be more efficient to process progeny in batches so that once the desired number of individuals carrying the trait is attained, the next round of backcrosses can be initiated and the entire population need not be evaluated.

A potential drawback to backcross methods is that newer varieties developed using breeding methods such as pedigree, bulk, SSD, or DH may surpass the performance of a backcross-derived variety by the time it is released and available for commercial use. Also, unforeseen problems such as a new race of a pathogen can cause a long-time recurrent parent to become obsolete. In practice, it is recommended to introduce advanced lines into the backcrossing program as early as possible and to carry along several backcross families concurrently so that there can be selection among the families at the end of the program for traits other than the one(s) transferred.

5.8 Mutation Breeding

All genetic variation observed in living organisms has been generated by mutation, structural rearrangements, and recombination. Whereas the aforementioned breeding methods rely on recombination through crossing to develop new genetic

combinations and derive breeding lines, mutation breeding represents an alternative approach that does not require crossing and may be useful for improving traits that may lack natural genetic variation. Most natural mutations are deleterious, rare, and recessive. However, plant breeders have sought to generate potentially useful genetic variation by inducing mutations through various means. Because the mutagens are generally not selective, plant breeders are faced with the task of sorting out useful mutations from undesirable ones. Any individual mutagenized plant can have many hundreds or thousands of mutations, creating complications when a deleterious mutation obscures a useful one. Generating large segregating populations is therefore important for identifying useful genetic variants.

The first step in designing a mutation breeding program is to calibrate the dose of the chosen mutagen so that the frequency of mutations is maximized but lethality is limited. A dose/response calibration is required for each mutagen, species, and seed lot. The dose is adjusted by varying the intensity or time for radiation or by varying the concentration of a chemical mutagen. Radiation treatments can be applied to pollen, seeds, seedlings, buds, or whole plants, whereas chemical treatments are used for ungerminated seeds. Polyploids generally tolerate higher doses because of genetic redundancy, though that benefit may be offset by homeologous or duplicate genes masking the effects of recessive mutations. Following mutagenesis, the screening method for desirable mutations depends on the species and whether it is clonally propagated, outcrossing, or inbreeding. For an inbreeding, seed-propogated species such as wheat, mutations can be dominant or recessive with the latter being revealed through selfing. Mutations must be transmitted in the pollen or eggs in order to be transferred across generations.

Mutagenesis impacts the entire genome, producing a large number of undesirable mutants that require an efficient screening technique. Even if a desired variant is found, it is likely to be associated with undesirable mutations that will require elimination through outcrossing or backcrossing. Consequently, mutation breeding should only be considered for certain traits or applications. Examples of plant varieties developed using mutagenesis can be found in the Joint FAO/IAEA Mutant Varieties Database, which compiles information on more than 3200 officially released mutant varieties of over 200 plant species worldwide (https://mvd.iaea.org).

Oladosu [30] reviews multiple examples of mutation breeding for targeting a variety of traits. Assessment of the value of mutation breeding has to consider if the product has been proven to not be a result of outcrossing, recombination, or natural mutations. TILLING (targeting induced local lesions in genomes), which combines chemical mutagenesis and high-throughput screening for point mutations, has been used to create mutant populations for wheat [31]. In summary, mutation breeding can be a useful tool for improving certain traits that may lack natural genetic variation, but an efficient evaluation protocol is required such that large populations can be screened for desirable variants.

5.9   Multilines

Once inbred lines are produced through one or more of the aforementioned line development methods, the breeder may choose to create a multiline variety. It is important to distinguish multilines from blends or mixtures at the outset. Blends can be mixtures of existing varieties or species in various proportions and are sometimes referred to as 'multiblends' [32]. Varieties may be blended for many reasons such as to capture the performance of different varieties or to reduce seed inventory. In constrast to multiline varieties, the development of multiblends does not necessarily require research on the performance of different combinations of mixtures.

The concept of a multiline variety was proposed by Jensen [33] and defined as a combination of pure lines chosen from a breeding program for uniformity of appearance, especially for height and maturity, but also for other characteristics important for a desirable agronomic type. The purpose is to combine different genotypes that have desirable attributes but do not reduce the phenotypic uniformity. Performance data on the components are necessary so that only compatible lines are blended. The individual component lines are maintained separately so that the original blend can be recreated by mixing the seed stocks in the correct proportions, and the breeder has the option of adding or removing individual lines over time. Theoretically, a multiline variety could have a longer life because of enhanced yield stability, broader adaptation, and resistance to diseases. The component lines could have resistance to different races of the pathogen, thus avoiding a potentially devasting disease outbreak that could occur if they were released individually. In summary, the advantages of multiline cultivars include (1) they provide a method to quickly develop a well-buffered, disease-resistant cultivar that can employ several resistance genes; (2) the useful life of a disease resistance gene is extended while a conventional breeding program is ongoing; (3) reduced losses due to disease should stabilize the cultivars deployed; and (4) an individual breeding program can distribute cultivars over a wide area without risk of homogenizing the pathogen population. Disadvantages include (1) the utility of multilines is limited to high-risk regions for disease outbreaks; (2) usually there is no genetic improvement for yield or agronomic traits; (3) substantial labor is required to produce and maintain the component lines; and (4) release of an improved recurrent variety is delayed until the components are produced.

To quantify the performance of multilines, Jensen and Federer [34] applied the concepts and computation of combining ability to competitive ability in wheat. In this application, general combining ability (GCA) refers to the average performance of a line in combinations, and specific combining ability (SCA) refers to the deviations in the expected average performance of combinations. Jensen [32] outlined four different examples for forming a multiline: (1) using a single backcross to generate lines for use in the multiline; (2) crossing unrelated lines; (3) crossing to different selected recurrent parents; and (4) making double crosses where each single cross has a common parent.

Marshall and Brown [35] used statistical models to determine the effect of intra-populational genetic diversity on the stability of performance of mixtures as estimated by their variance in yield across environments. Their models suggested that, in the absence of intergenotypic interactions, the yield of a multiline will vary less than the least variant component when the component lines perform differently in different environments. Conversely, when there are intergenotypic interactions, the stability of a mixture will be more stable than the best line only when each component responds differently to different environments. They also predicted that, when mixtures are compared to their pure line components, it is expected that improved stability is more easily attained than improved yield because improvements in yield require net positive intergenotypic interactions whereas stability does not.

In addition to stability, the use of multilines has the potential to improve resistance to disease. Borlaug and Gibler [36] developed wheat lines for multiline cultivars at CIMMYT using 'donor parents' selected from the International Wheat Rust Nursery and backcrossed to recurrent parents. A number of studies have examined possible mechanisms for the observed enhancements in disease resistance within multilines, and generally agree that the reduced inoculum load results from both a lower frequency of initial infection when a spore lands on a resistant component of the multiline and a lower rate of increase in inoculum. A review of multilines for disease control was published by Mundt [37].

Given the changing climate and the need for greater protection of natural ecosystems and sustainable agricultural practices, multilines and multiblends will likely play an important role in the future agricultural production systems. Further research is warranted on durability of resistance in multilines, experimental design, and design of mixtures.

5.10 Key Concepts

Pedigree, bulk, single seed descent, and doubled-haploids are the four main line development methods. Backcross, mutation and multiline breeding methods are useful supplements to line development. Pedigree breeding is rarely used in wheat breeding because a large number of resources must be invested in selection. Bulk breeding methods are simple and cost efficient. The main advantage of the SSD method is that lines can be rapidly generated in a greenhouse or off-season nursery. Doubled-haploids allow breeders to develop homozygous genotypes from heterozygous genotypes in a single generation but are limited by the high cost. The choice of line development method(s) depends on resources available and selection methods chosen.

5.11   Conclusion

Given the array of options for developing inbred lines, the main challenge is to determine how to build a coherent and efficient breeding strategy given a fixed budget and other resources. It is common for wheat breeding programs to implement multiple line development methods at different stages of the breeding pipeline. Breeders must also consider how to strategically combine line development approaches with population improvement and selection methods, which are described in Chap. 6, in order to produce superior varieties.

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