

Elite × Elite Breeding with Population Improvement

Bijendra Pal

Abstract Elite × elite breeding has long been central to hybrid maize development, shaping heterotic pools and driving genetic improvement. However, defining “elite” remains dynamic, influenced by evolving objectives and challenges. Breeding programs must balance immediate goals with long-term adaptability by maintaining genetic variability to sustain continuous gain. Selection intensity often risks losing traits deemed less relevant today, yet these may prove vital tomorrow—posing a key question: how can deselected traits be reintroduced if needed? This article explores strategies for contemporary elite-by-elite breeding while safeguarding future trait diversity. It advocates for adaptable breeding schemes that respond to shifting criteria and preserve resilience in genetic design. Drawing on historical techniques and modern insights, the proposed framework aims to sustain relevance and innovation in maize breeding over time.

Keyword: Breeding • Population • Heterosis • Inbred line
• DH and advance breeding tools

Introduction

Since the inception of scientific maize breeding in the early 20th century, we often observe that most of the breeders have practiced elite × elite breeding. In fact, maintenance of heterotic pools or population, the basis of hybrid maize breeding often adopts or practice elite × elite crosses while recycling of inbred lines, a process of development of new and improved inbred lines. The process represents an evolutionary process where the mean of the population is

altered in a desirable direction through selection of traits of interest. The underlying genetic mechanism responsible for altered mean is due to change in the frequency of alleles under selection. The term elite often dynamic depending on the contemporary requirements or the objectives of breeding programme of the country or company.

In breeding, defining “elite” is one of the most challenging tasks, and it is even more difficult to ensure that the characteristics of elite germplasm remain consistent throughout the breeding program’s duration and often influenced by several factors including new and emerging challenges which arises time to time. Development of breeding programme and its sustenance in long-run must consider maintenance of sufficient genetic variability to achieve continuous genetic gain. In this context, designing a breeding program and developing breeding schemes to meet the short, medium, and long-term goals of an organization or country is quite challenging. On the contrary, the selection process often involves a trade-off between traits of interest and those of lesser importance. Depending on the selection intensity applied while selection of traits of interest there are possibility to loose diversity in traits considered less important today. However, the same traits which are considered less important currently may become the criteria for classifying germplasm as elite in future. Thus, arises a critical question: what if the deselected traits become important in the future? How will we reintroduce these traits once they have been excluded from the breeding pool by design? With this understanding, it is decided to explore the concept of elite-by-elite breeding for today while maintaining sufficient variability for future use in case the criteria for elite traits change. The approach is devised to ensure adaptability of breeding programme to evolving requirements and remain relevant over time with sustained genetic gain in long-run. The present article

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touches one by one all the processes/concepts/techniques that have been tried and used over time and effort has been made to suggest a vital breeding scheme to address the issue of sustainable breeding program.

Population improvement

Population improvement forms the part of long-term plant breeding programs across different crops because of their significance in sustaining the genetic gain through maintaining genetic diversity and genetic base in the active breeding material (Syukur *et al.*, 2015; Huang *et al.*, 2015; Siswati *et al.*, 2015; Wulan *et al.*, 2017). While development and implementation of comprehensive population improvement program aligning with the long-term objective of the breeding program is very critical but it often regarded as thankless task and has taken backseat and more often being neglected in the recent past. However, it requires considerable time and resources to develop the desirable recombinants for line development or new cultivar creation. Sometimes, it is believed that population improvement programs are more relevant and effective in cross-pollinated crops as compared to self-pollinated crops though the genetic basis do not support it. However, population improvement programs form the fundamental support system for genetic diversity, genetic variability, and genetic resilience to all the mainstream breeding programs irrespective of the reproductive system of the crop (cross pollinated or self-pollinated). Further, even though plant breeders recognize the significance of discontinuous variability in population improvement program but investment of time resources to develop systemic population improvement plan is hardly being seen in the major breeding programs.

The success of population improvement depends on several factors namely number of founder lines, selection intensity, initial genetic diversity among founder lines, etc. The genetic diversity or variability decreases with increased selection intensity. For example, selecting individual plants in the population reduces variability within the progenies obtained from the selected plants or early segregating inbred lines and increases the genetic as well as phenotypic uniformity. However, new variability can also be generated through intercrossing selected relatives or non-relatives irrespective of reproductive system of the crop plants. The continued extraction of inbred lines coupled with sustained genetic gain depends on the genetic

variability in the source population. Therefore, the sole objective of a population improvement program is to sustain genetic variability within the source population by maintaining the population equilibrium to support continuous extraction of inbred lines through new selections and also address the contemporary stakeholders' needs. In order to achieve this objective, breeders should continuously enhance the population mean for desirable traits while preserving adequate variability. Thus, population improvement programs should be considered continuous and ongoing processes. The process also ensures breeders that they can always return to the source population to make new selections when needed.

Population improvement programs, as pre-breeding activity, are crucial for the longevity and success of any breeding program. This allows new breeders to continue the existing breeding program from the same population, ensuring continuity. In this context, the current article discusses not only the importance of the population improvement programs but also delineates a systematic approach to design population improvement program using advanced tools in plant breeding to enhance new selection efficiency sustainably.

Designing the source population for population improvement

The fundamental step in designing base population is the selection of component genotypes which is crucial and requires high level of clarity. The genetic composition of source population determines the future outcome of the breeding program. Therefore, the process must include the clearly defined objectives of the population, the ecology in which the population will be utilized, the amount of breeding effort that can be allocated and any specific trait requirements for this population in the future. There can be two types of scenarios depending on the reproductive system (self- v/s cross-pollination) of the crop and/or the final product (variety/pure lines v/s hybrid) of the breeding program.

In cross-pollinated crops, hybrid is the final commercial product in most of the cases. In this scenario, the main objective of the population development is to extract improved inbred lines to support the hybrid breeding program. Würschum *et al.* (2023) emphasized that genetic distance between parental lines is a critical factor in hybrid breeding. Because, the commercially

successful hybrid requires minimum two heterotic inbred lines. Thus, population development to support hybrid breeding faces further challenge that at least two populations are required to extract inbred lines which are heterotic to each other. This has remained consistent since the inception of hybrid breeding programs. Further, to support the hybrid breeding program sustainably in long-run, the population *per se* needs improvement in relation to opposite and heterotic population. While maintaining the heterotic integrity of populations *per se*, the intra-population improvement support extraction of new and improved inbred lines. Population improvement strategies should incorporate genetic diversity as a core element to optimize hybrid performance.

In self-pollinated crops, the commercial product would be pure line or variety. In this scenario, the objective of the population is to create the desired variability for developing new and improved pure line or new variety/cultivar and it can be achieved through inter population crosses. In both scenarios, the process is to create new variability followed by its fixing. However, selection of base germplasm for hybrid development vis-à-vis variety or pure line is critical.

It is crucial to understand that the base population serves as a foundation for genetic improvement rather than immediate utilization. These populations are specifically designed to facilitate the development of novel recombinants, and their readiness is not instantaneous. Only after a sufficient number of recombinants have been generated can the population be effectively utilized for inbred line development. This contrasts with bi-parental or multi-parental populations, which are specifically created for direct application in inbred line development.

Population improvements for hybrid vis-à-vis pure line or variety development

The success of commercial product *viz.*, hybrid or pure line most often depends on ease with which the reproductive system of crop can be manipulated and also the availability of different tools and techniques required for controlled pollination and their economics. In general, the commercial product in different crops often associate with the reproductive system of the crop, for example, pure line to self-pollinated crops and hybrids to cross-pollinated crops. However, depending on the availability of controlled pollination tools and techniques, in several

self-pollinated crops, hybrids have the commercial value and vice versa. Therefore, the requirements in development of source population for heterosis breeding remain same for both self- or cross-pollinated crops. The balanced mix of different components or criteria while designing population is critical to achieve long-term sustainability of breeding program (Figure 1).

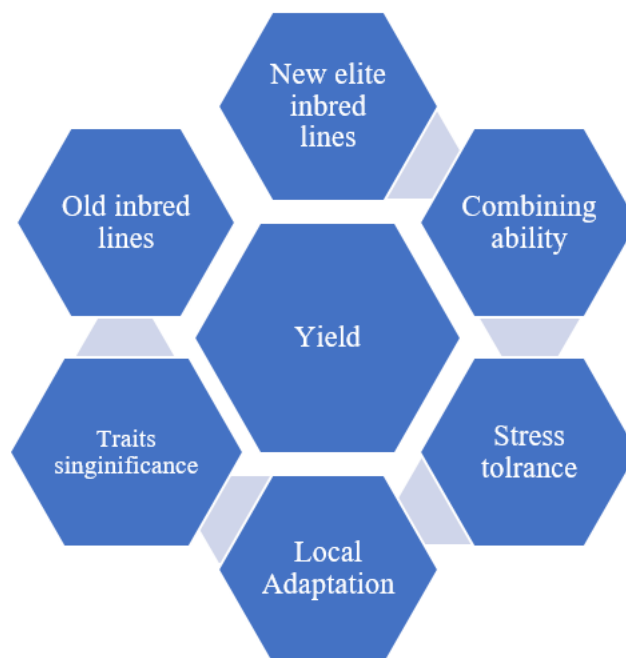


Figure 1. The critical components required for constitution of ideal base population

The critical traits namely amenability of plant type for mechanization (e.g. uniform ear placement, fast dry down), seed type (dent, flint, semi-dent/flint), trait uniformity (maturity, height etc.), shelf-life (seed germination and viability, seedling vigour etc.) forms the basis of selection of founder genotypes of population, key for successful plant breeding program, especially commercial plant breeding. The desirable traits of female vis-à-vis male parents often differs and consideration of such traits while developing heterotic female and male population is worth exploring.

Constitution of Cycle 0 –

The clearly defines objective brings clarity while selection of desirable founder genotypes. The founder genotypes should be as diverse as possible with each founder genotypes carrying one or two critical desirable traits. Develop F_1 crosses through inter-mating or chain crossing

among all founder genotypes in all possible combination, half diallel fashion to ensure high level of recombination/mixing at genomic level. All possible F_1 cross combinations (chain or diallel crosses) required to undergo at least two more cycles of inter-mating to achieve effective recombination. However, the number of inter-mating cycles again be determined by resource allocation, short-, medium-, long-term objectives. Nonetheless, most of the geneticists are in agreement that two rounds of inter-mating are considered sufficient to achieve the desired level of recombination. The key points which need consideration while developing/undertaking inter-mating are (i) optimized environmental conditions, (ii) equal seed contribution, (iii) comprehensive pollination opportunities.

Optimized environmental condition: The planting should be conducted in well-maintained environments to ensure optimal expression of genetic combinations

Equal seed contribution: The seed from each cross combinations should be mixed in equal quantity to maintain balance in genetic diversity, especially the allele frequency.

Comprehensive pollination opportunities: There is need to ensure adequate rounds of pollination to allow all plants (early to late flowering individuals) to participate in cross-pollination and to retain complete genetic variability.

Cycle 1 to Cycle n–

Population improvement through cycles is a critical process requiring clarity in objectives for each step undertaken by breeders, especially while making individual plant selection in the population. A single cycle of population improvement typically consists of one cycle of

selection followed by one cycle of recombination. Both steps are essential for enhancing the mean of targeted traits while maintaining genetic variability within the population.

Selection and selfing process

Initial selection: Approximately 400 ears from promising plants of Cycle 0 (last recombination) are individually shelled. From each ear, half of the seeds are planted in an ear-to-row fashion, forming 400 rows. The remaining seeds are bulked and stored as Cycle 0 seeds for the population. Based on all possible practical and theoretical considerations, approximately 400 ears are generally considered sufficient to retain or capture sufficient genetic diversity available in the population. Nonetheless, it is still can be debated based on the circumstances.

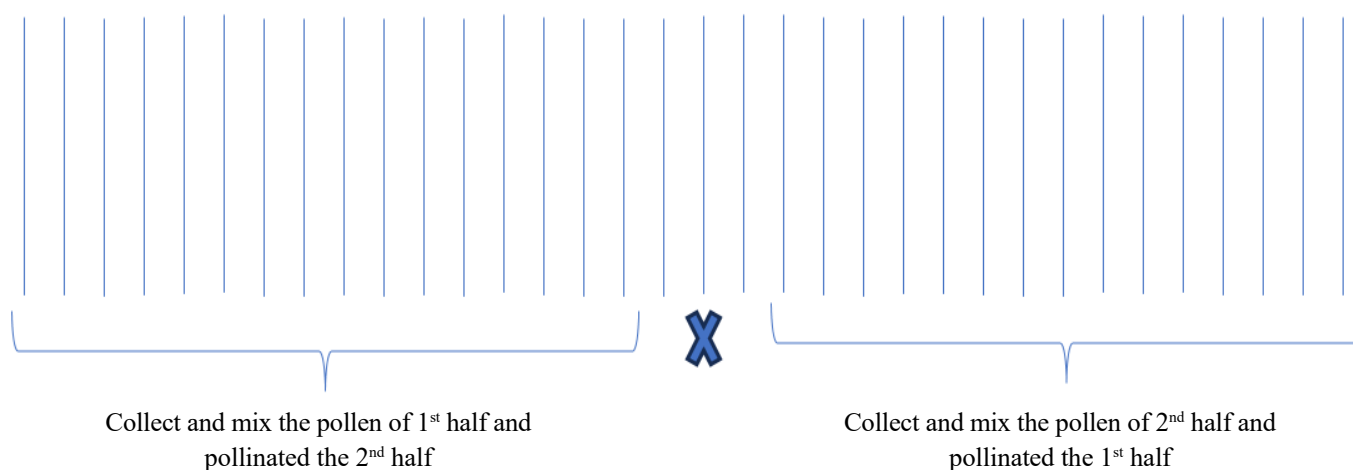
Grouping: The 400 rows can be divided into 80 groups, each containing 5 rows ($5 \times 80 = 400$ rows). The grouping step is to accommodate all possible unaccountable environmental variability or experimental error. Carry out selection of best two rows in each group, stratified selection before advancing to recombination step.

Self-pollination: Select at least five plants from each row and self-pollinate them. Harvest all five plants individually from the best row in each group, resulting in $80 \times 5 = 400$ selfed plants.

Recombination Process

Planting: The 400 selfed plants are grown in an ear-to-row fashion alongside available introduction.

Subset division and pollination: 400 rows are divided into two subsets with each subset containing 200 row each.



Pollen from the first subset and introductions (95% pollen from the population and 5% pollen from introductions) is collected, mixed, and used to pollinate the second subset. Similarly, pollen from the second subset and introductions is collected in similar proportion as in the first subset, mixed, and used to pollinate the first subset. To ensure broad participation, pollination is conducted over 2-3 rounds, allowing maximum plants to contribute to recombination.

Harvest: 200 ears are selected from each subset, resulting in $200 \times 2 = 400$ ears. Half of the seeds from each ear are used to initiate the next season's Cycle 2, while the remaining seeds are mixed and stored as Cycle 1 seeds.

Sustainable population improvement and line development program

A dedicated line development program can be initiated after completing the third cycle of population improvement. The inbred lines demonstrating high combining ability can be reintroduced into the population improvement program as introductions, contributing to enhanced genetic diversity and the refinement of targeted traits. Population improvement serves as pre-breeding work and must be conducted continuously. This process provides a consistent source of raw material for inbred line development. Advanced plant breeding and genomic tools can be employed to maintain the required allele frequencies for desirable traits in each cycle of selection. To align population improvement with evolving farming system requirements, there should be regular brainstorming sessions and reassessment of trait prioritization. Based on contemporary agricultural needs, a defined set of traits must be provided to the teams involved in population improvement. These traits will guide the direction of the population improvement program. Over 2-3 breeding cycles, the allele frequencies controlling newly prioritized traits can be increased effectively. This approach ensures the sustainability of any breeding program, preventing the need to restart from scratch. It promotes long-term success by continuously adapting to changing agricultural demands while maintaining genetic diversity. In the absence of new traits in the source population, the donor genotypes can be introduced carefully after thorough assessment of heterotic pattern of the donor genotype to maintain the integrity of the heterotic groups.

Determining the number and structure of populations in the breeding programs

As mentioned in the beginning, population development is resource demanding, time consuming, laborious, and many times it is a thankless task with little or no credit. Based on the resources available at the disposal of the breeder, many population improvement programs can be designed. However, the question on how many population improvement programs are optimum for sustainable breeding program is quite challenging mainly due to the absence of definitive research or established methodologies. Nonetheless, it can be safely being considered that for crops with well-defined heterotic patterns, the number of population improvement programs can be aligned with the number of heterotic groups utilized in the breeding program. However, the new and emerging challenges have forced breeders to develop different number of population improvement programs. For example, the resource constrained breeding programs hardly concentrate or take up any population breeding programs, whereas some breeders keep population improvement programs simple by making selection less intensive like simple male and female populations; while others opt for development of more sophisticated trait-based populations, such as those for abiotic stress tolerant (drought and/or waterlogging and/or heat), biotic stress tolerant etc. depending on the requirement of the breeding program.

Trait-based populations are particularly advantageous for crops where pure line or variety has commercial value. For hybrid programs, it is essential to partition genetic variability effectively so that heterosis can be systematically exploited for all the essential or desirable traits. Maintaining populations based on heterotic groups is generally more desirable, as this strategy increases the likelihood of maximizing heterosis consistently over time. Simultaneous improvement can be achieved in both populations that are heterotic to each other, ensuring ongoing progress within the breeding program.

The structure of the population is critically important in contemporary breeding programs. Leveraging advancements in genomics and implementing them to enhance precision can significantly improve the genetic merit of the population. Melchinger and Frisch (2023) proposed the integration of genomic predictions into recurrent selection methodologies. This approach not only

increases the accuracy of allelic frequency improvement for traits of interest but also enhances the efficiency of developing elite inbred lines.

Conclusions

Inbred line development is a critical activity in hybrid breeding programs, as the quality of inbred lines largely determines the success of the hybrid breeding program. Additionally, 'speed to market' has become a key focus for breeders, as there is an increasing need to develop hybrids more rapidly than was traditionally possible. To address this demand, the use of bi-parental populations and multi-parent populations has become common. These approaches are often described as 'discard-oriented,' as they enable breeders to effectively eliminate traits or alleles that do not align with the desired objectives. However, the approach often compromises with the genetic diversity/resilience and also questions the long-term sustainability and genetic gain.

Another technology gaining attention among both small- and large-scale breeding programs is application of double haploid (DH) technology for rapid development of inbred lines. This is also a discard-oriented approach, where undesired alleles or traits are systematically removed to streamline the process of developing elite lines. In contemporary breeding, this selective process aligns with the evolving definition of what constitutes 'elite' germplasm. However, impact of long-term application or use of DH technology on maintaining sufficient genetic diversity and also maintaining sufficient number of recombinants in the population remains to be known as this technology is of recent one.

The discard-oriented approaches offer significant efficiency in addressing the immediate requirements of

today. However, it is equally critical to recognize the importance of maintaining genetic variability for the future as well, especially to address unforeseeable challenges. Population improvement programs play an essential role in achieving this balance by continuously enhancing the genetic base and introducing novel genetic material into base populations. Plant breeders can ensure the sustainability and adaptability of breeding programs through designing and maintaining appropriate parallel population improvement programs. It is often realized that every breeding program, regardless of its size or focus, should prioritize population improvement as a core strategy to meet both current and future demands effectively.

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