



Genetic Architecture and Buffering Capacity of Multi-Parent and Double-cross Maize Hybrids for Forage Production: A Review.

Muhammad Shafique^{1*}, Rashad Rashid², Warda Ibrahim³, Ali Haider⁴

¹Department of Plant Breeding and Genetics, University of Agriculture, Faisalabad, Pakistan.

Corresponding Author: shafiqmahar25@gmail.com

Abstract

A major source of green fodder and silage for ruminant livestock in South Asia, maize (*Zea mays* L.) is a staple for livestock with chronic feed shortages, reduction in area of cultivation and rising climatic volatility limiting livestock productivity in the region. Single-cross hybrids that are selected for high yields in uniform high input systems are less suited for forage production because of high seed costs, uniformity, susceptibility to heat and drought stress, and selection criteria which are not based on vegetative yield and stover quality. The goal of this review is to synthesize what is known about the genetic makeup of multi-parent and double cross maize hybrids for forage and their buffering capacity. It examines the gene action (additive and non-additive) and general and specific combining ability of green fodder production, dry matter production, crude protein, fiber fractions (NDF, ADF and ADL) and invitro digestibility in relation to the utilization of the heterotic group. It also discusses the topics of population buffering, developmental homeostasis, genotype-by-environment interactions and stability analysis, as well as a few other miscellaneous topics. The biomass digestibility trade-off is discussed and explained by using a multivariate selection index (MGIDI and MTSI). Lastly, the use of marker-assisted selection, MAGIC and NAM populations, and genomic selection in combination with multi-parent breeding pipelines is discussed. These strategies can provide a feasible pathway towards creating dual purpose maize varieties that produce both grain and fodder, while simultaneously being able to withstand climate change, in South Asia.

Keywords: *Zea mays*, Forage Maize, Double-Cross Hybrids, Population Buffering, Biomass Digestibility Trade-off, Genomic Selection, Multi-Trait Selection Indic.

INTRODUCTION

Maize (*Zea mays* L.) is considered as one of the most important agricultural commodities in the world and is unique in its versatility as a staple food crop, as a backbone for the animal feed industry and as a raw material for various industrial bioproducts, (Erenstein et al., 2022). High yielding, stress adapted and nutrient dense cultivars are essential to ensure the long-term sustainability of agriculture and stability of global food production. Maize is cultivated in various Agro-ecological zones around the world in about 197 million hectares, yielding over 1,137 million tonnes of grain annually (Erenstein et al., 2022). The livestock production sector (Karnatam et al., 2023) is a critical component of global maize biomass utilisation. According to production allocation quantitative analysis, approximately 56 per cent of total global production is used as livestock feed (in the form of grain, forage or ensiled biomass), while only a small fraction of production (13 per cent) is used for human food and the remainder is processed into industry or bio-energy streams. The availability of milk, meat and animal products in general in the world depends on the genetic yield potential, biomass

accumulation rates and feeding value of green forage and silage maize varieties (Government of Pakistan, 2025).

Regional Fodder Dynamics, Livestock Sector and Deficits in South Asia

The agricultural economies of South Asia are predominantly based on livestock husbandry which provides dietary nutrition for rural households, a financial buffer and draft power for agriculture (Government of Pakistan, 2025). In Pakistan, the livestock sub-sector is becoming the biggest driving force for agricultural value addition as well as agricultural contribution with expansion rate of 4.72%, which is highest among all sectors, to the national Gross Domestic Product (GDP) at around 14.97% with contribution of 63.6% to agricultural value addition. More than eight million rural families are directly dependent on livestock operations, the country's livestock herd consists of 59.7 million cattle, 47.7 million buffaloes, 33.1 million sheep and 89.4 million goats, producing a gross volume of milk of 72.34 million tonnes (Government of Pakistan, 2025).

The lack of balanced silage (Ahmad et al., 2024; Hamed et al., 2022; Khan et al., 2024) and the acute shortage of green fodder throughout the year are limiting factors for the huge economic importance of ruminant livestock production in South Asia. The causes of fodder shortage in the regional production systems are related to several interacting agricultural issues, among which the competition for land use between fodder crops and main staple cereal crops and cash crops is high and area under special forage (Ahmad et al., 2024; Government of Pakistan, 2025) is high. The domestic economic statistics from recent years show that the cultivated area for maize has been reduced to 1.44 million hectares and this shrinking of the cultivated area coupled with adverse climatic conditions, led to a reduction in the total output of maize by 15.4% to 8.24 million tonnes of maize (Government of Pakistan, 2025). Excessive levels of unbalanced fertilizer inputs and inappropriate use of cultivars of grain crops for forage production results in low-quality biomass in terms of indigestible cell wall fiber (Ahmad et al. 2024; Hamed et al. 2022; Van Soest et al. 1991). The green fodder available in the extreme lean seasons (May-June and November-December) is very low and green fodder intake by lactating ruminants is also low, leading to great dietary deficiency (Ahmad et al., 2024; Hamed et al., 2022).

Areal expansion for arable land is difficult with limited land and the productivity of livestock can be improved by maximizing the production of green biomass per unit area while keeping the nutritional value, digestibility and crude protein content of green biomass constant (Ballard et al., 2001; Karnatam et al., 2023; Periyasamy et al., 2025). Fodder maize has a lot of good features that make it appropriate for this use, such as high yield potential of dry matter, good ensiling quality at 50% milk/dough stage (R3–R4), high palatability, rapid growth rate and the possibility of late harvest (Hamed et al., 2022; Horst et al., 2020; Khan et al., 2024; Nikolić et al., 2022).

The Single Cross Bottleneck in Fodder Production

The development of commercial maize hybrids over the last 60 years has been mainly based on using single-cross cultivars (F₁ crossings between two homozygous inbreds, A × B). Single Cross hybrids take maximum advantage of maximum heterotic expression and have uniform field phenotype, making them ideal for mechanized grain production under optimum agronomic conditions (Falconer & Mackay, 1996; Hosseini et al., 2025; Sorsa et al., 2023). However, if smallholder livestock producers use single-cross hybrids or single-cross hybrids are used for forage and silage production, then there are several genetic and economic bottlenecks: Prohibitive Seed Production Costs – Single-cross seed production involves the use of an inbred line as a maternal seed parent (A). Inbred parent

plants have reduced vigour, reduced seed productivity and increased stress sensitivity which leads to reduced commercial seed production per hectare (Sorsa et al., 2023). So, smallholders who harvest maize before grain harvest (Sorsa et al., 2023) will find the cost of single-cross hybrid seed prohibitive.

Single-cross hybrids are completely heterozygous and genetically uniform throughout the field population with good yield in favourable conditions, but genetically very vulnerable to climate shocks, drought spells and heat stress during pollination.

Ideotype Selection Disconnect: Single-cross breeding programs usually focus on grain harvest index, ear size, and rapid grain drying, rather than total vegetative biomass, plant height, broad leaves, digestibility of stover, low cell-wall lignification, and low crude protein content for grain (Karnatam et al., 2023; Periyasamy et al., 2025).

Multi Parent Advantage and Population Buffering Concepts

One way to overcome the economic and yield stability constraints of single-cross cultivars in forage production is the use of multi-parent hybrid systems, in particular double-cross $[A \times B] \times [C \times D]$ and three-way cross $[(A \times B) \times C]$ hybrids. A Double-Cross Hybrid is a cross between two single-cross F₁ hybrids, which is a combination of a four inbred parents, (Sorsa et al., 2023).

Forage production is enhanced by multi-parent genetic architectures, which offer important economic, physiological and genetic benefits **Maternal seed production Vigor:** A low yielding inbred line (Sorsa et al., 2023) is not used as the maternal parent in double-cross seed production; rather, a single-cross F₁ hybrid (A × B) is used. This maternal vigor significantly contributes to the commercial seed production per hectare, thus decreasing production costs and making hybrid seed available and affordable for fodder farmers (Sorsa et al., 2023).

Population Buffering & Environmental Stability: Multi-parent hybrids maintain high level of genetic diversity at the population-level whilst maintaining acceptable levels of agronomic uniformity. This larger pool of genetic variation gives developmental stability, allowing the population to withstand environmental variations, thermal peaks and moisture stress (Sorsa et al., 2023). Three and multi-parent crosses consistently yield better than single crosses in variable environments based on field testing (Sorsa et al., 2023). Green fodder yield, digestibility, crude protein, and fiber fractions (NDF, ADF, ADL) are all important components of forage value, and genetic variability can be used for simultaneous selection. Multi-parent genetic backgrounds offer an opportunity for higher additive variance components and increased recombination opportunities for selection for both high biomass yield and

digestibility of cell wall (Karnatam et al., 2023; Naharudin et al., 2021; Pawan et al., 2025; Periyasamy et al., 2025).

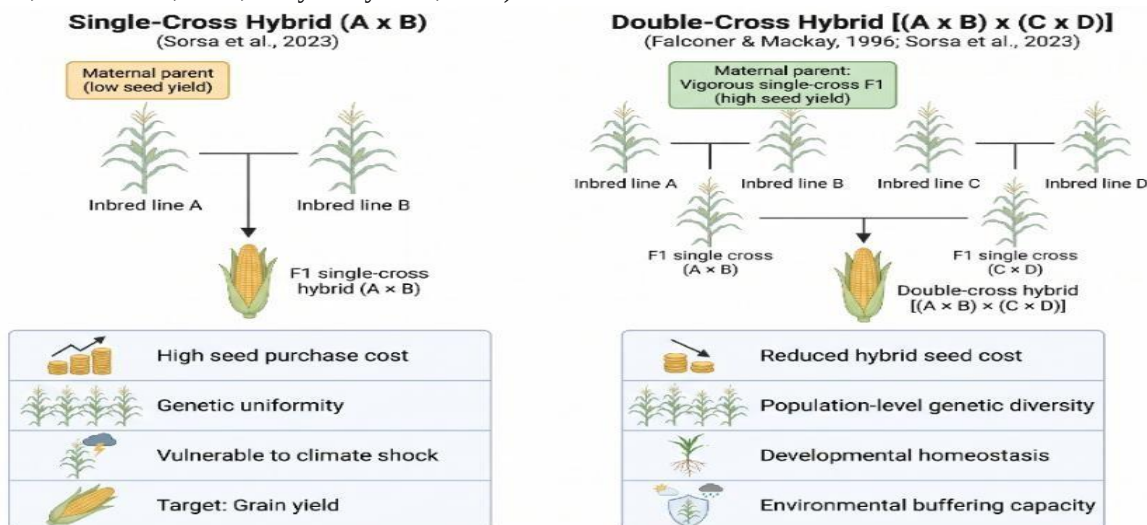


Figure 1. Schematic comparison of single-cross and double-cross hybrid breeding systems: genetic diversity, seed cost, and potential resilience to environmental stress.

Objectives and Structure of the Review

Knowledge about quantitative genetics, population buffering mechanisms, cell-wall digestibility trade-offs and multi-trait selection methods for double-cross maize hybrids under forage production conditions are still not consolidated (Karnatam et al., 2023; Periyasamy et al., 2025).

This review is aimed at synthesizing the multi-parent and double-cross maize system for green fodder and silage production (Karnatam et al., 2023; Periyasamy et al., 2025; Sorsa et al., 2023). Specifically, this paper; Analysed the genetic architecture and gene action (additive vs. non-additive effects, combining ability) of biomass yield and laboratory quality traits in multiline genetic backgrounds (Bertoia & Aulicino, 2014).

Understands physiological mechanisms of population buffering and developmental homeostasis in environmental stress (Falconer & Mackay, 1996; Sorsa et al., 2023). Combined morphological and quality parameters (CP, NDF, ADF, ADL, RFV) with genetic parameters (GCV, PCV, broad-sense heritability h_b^2 , genetic advance GA) (Burton & DeVane, 1953; Johnson et al., 1955; Kapoor & Batra, 2015; Naharudin et al., 2021; Pawan et al., 2025). Computes Bi-multivariate Selection Indices (e.g., MGIDI, MTSI) and other analyses based on trait correlation, path-coefficient direct and indirect effect to reduce negative correlation between biomass production and forage quality.

GENETIC ARCHITECTURE & QUANTITATIVE GENE ACTION IN MULTIPARENT AND DOUBLE-CROSS HYBRIDS

Additive versus Non-Additive Gene Action Governing Biomass Accumulation

Knowledge of the underlying genetic architecture of the biomass accumulation as well as the stover yield and forage quality parameters is essential to develop efficient breeding strategies in multi-parent and double-cross maize hybrids (Badu-Apraku et al., 2016). Multi-genic networks with both additive and non-additive gene actions control quantitative traits like green fodder yield and whole-plant dry matter yield and structural cellwall constituents Neutral Detergent Fiber [NDF] and Acid Detergent Fiber [ADF] (Ali et al., 2006; Hosseini et al., 2025; Melchinger & Gumber, 1998).

Biometric estimates based on diallel, line $\times$ tester and North Carolina mating designs agree in showing that vegetative biomass and green fodder yields are mainly under non-additive forms of gene action (dominance and epistatic deviations). By contrast, qualitative traits like crude protein content, early seedling vigor and mineral uptake efficiency often exhibit high values for additive genetic variance (Ali et al., 2006; Kapoor & Batra, 2015). In conventional singlecross hybrid production, the non-additive genetic variance is exploited in the F_1 generation but is not able to be fixed in subsequent generations due to Mendelian segregation (Falconer & Mackay, 1996). By contrast, multi-parent and double-cross designs formed by crossing two single crosses $[(A \times B) \times (C \times D)]$ allow for broader distribution and recombination of additive and non-additive gene complexes originating from four different inbred founders (Bernardo, 2020; Sorsa et al., 2023). This increased genetic configuration will diversify the overall genetic variance spectrum and provide an opportunity for plant breeders to select simultaneously for high stover yield, structural stalk integrity and enhanced cell-wall digestibility (Ertiro et al., 2013).

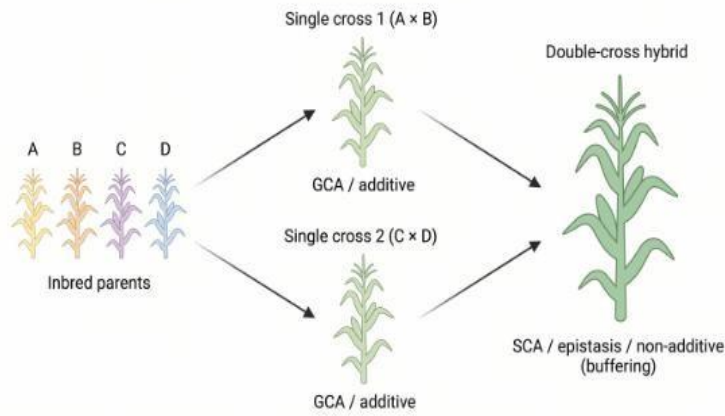


Figure 2. Genetic mechanisms underlying double-cross hybrid performance.

General Combining Ability (GCA) and Specific Combining Ability (SCA) Dynamics

Precise estimations of General Combining Ability (GCA) and Specific Combining Ability (SCA) are essential for successful exploitation and for systematic optimization of hybrid performance. GCA, the average performance of an inbred line in several hybrid crosses (Falconer & Mackay, 1996; Griffing, 1956), is largely additive and additive-by-additive epistasis. SCA, however, is the non-additive genetic variance, or the dominance and complex epistasis, that is expressed when particular parental lines are paired (Falconer & Mackay, 1996; Lynch & Walsh, 1998).

In multi-parent and double-cross breeding schemes, parental crosses are first chosen because of their high GCA for biomass production and their good per se forage quality traits (BaduApraku et al., 2016; Sorsa et al., 2023). The intercrossing of two good single-cross hybrids ($A \times B$ and $C \times D$) to generate a double-cross hybrid uses maximal genetic complementation among four germplasm pools (Bernardo, 2020; Sorsa et al., 2023). A thorough analysis of the tropical and subtropical maize germplasm showed that the parental lines which produced a high GCA for plant height, stem diameter and leaf-to-stem ratio were the ones that were able to pass on these traits to the multi-parent progenies (Liu et al., 2018). In parallel, SCA effects control better accumulation of dry matter, lower lignification of the fiber and increased stability to environmental stress (Bertoia & Aulicino, 2014).

Quantitative Genetic Parameters: Heritability and Variance Components

Quantitative genetic parameters like the Phenotypic Coefficient of Variation (PCV), Genotypic Coefficient of Variation (GCV), broad-sense heritability (h^2) and expected Genetic Advance (GA) are essential diagnostic tools to measure the fidelity of the transfer of quantitative forage traits from parents to progeny (Ali et al., 2006; Burton & DeVane, 1953; Hallauer et al., 2010; Johnson et al., 1955).

The GCV and PCV values for both the green fodder and total dry matter yields obtained for segregating and multi-line maize populations showed moderate to high values and there was high broad-sense heritability and high genetic advance demonstrating that simple pedigree selection or recurrent selection can lead to rapid genetic gain (Ali et al., 2006; Kapoor & Batra, 2015; Pavithra et al., 2022). But there is often a significant genotype-by-environment ($G \times E$) interaction for quality parameters like Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), Acid Detergent Lignin (ADL) and In Vitro Dry Matter Digestibility (IVDMD) (Alvarado-Ramírez et al., 2023; Naharudin et al., 2021). These interactions can be quite misleading in reducing broad-sense heritability estimates if not assessed under carefully conducted multi-environment testing (Alvarado-Ramírez et al., 2023; Naharudin et al., 2021). To overcome this restriction, multi-parent populations can be used to reduce environmental variance by increasing genetic heterogeneity and, consequently, to stabilise heritability estimates for important nutritional components (Pawan et al., 2025; Periyasamy et al., 2025; Yu et al., 2008).

Trait / Parameter	Evidence & Genetic Mechanism	Breeding Relevance & Application Strategy	Key References
Green Fodder Yield	There are two types of gene actions affecting biomass yield: additive gene action (A) and non-additive gene action (SCA). Interaction between the genes and environment varies depending on the specific population background and trial environment.	Evaluate the performance of parents in multi-environment target conditions and test cross performance.	Ali et al. (2006); Hosseini et al. (2025)
Dry-Matter Yield	High G×E interaction results in large variations in quantitative expression among genotypes and environments.	Determine dry matter accumulation in replicated, multi-location tests to assure yield stability.	Melchinger & Gumber (1998); Bernardo (2020)
Crude Protein (CP)	The amount of total protein content is influenced mainly by the additive gene action but is associated with harvest maturity and biomass yield.	Determine protein content directly and choose at the same time to increase protein retention at dough stage (R ₃ -R ₄) with biomass yield.	Kapoor & Batra (2015); (Naharudin et al., 2021)
Cell-Wall Fiber Fractions (NDF & ADF)	Genotype, harvest maturity, and temperature stress have significant effects on fiber accumulation and cell-wall lignification	Establish uniform sampling procedures and laboratory methods (e.g., Van Soest analysis) for measuring fiber.	Van Soest et al. (1991); Hamed et al. (2022)
In Vitro Digestibility (IVDMD / IVDD)	Cell-wall composition (lignification), starch proportion and the plant maturity stage are the factors controlling digestibility.	Measure dry-matter digestibility directly and adjust for plant maturity differences when comparing genotypes.	Argillier et al. (2000); Periyasamy et al. (2025)

Table 1. Summary of Genetic Factors and Trait Dynamics in Forage-Maize Improvement.

Heterotic Group Utilization and Gene Pool Diversification

The success of multi-parent and double-cross hybrid depends on systematic diversification and utilization of different heterotic groups (Sorsa et al., 2023; Melchinger & Gumber, 1998). The typical single-cross breeding system relies on limited, highly recycled heterotic cross patterns (e.g., Lancaster Sure Crop × Stiff Stalk Synthetic) that are inherently genetically susceptible to new biotic stresses and climatic anomalies (Karnatam et al., 2023; Du Vick, 1999). In contrast, double-cross systems combine four different inbred lines from geographically and genetically diverse gene pools, thus increasing diversity and maximizing inter-population heterosis (Sorsa et al., 2023; Bernardo, 2020). These heterotic pools provide a range of advantages, including maximizing green biomass accumulation (via non-additive gene action) and the introduction of developmental homeostasis (stabilizing important forage quality traits under fluctuating environmental conditions).

POPULATION BUFFERING, ENVIRONMENTAL HOMEOMASIS and STABILITY MECHANISMS Developmental Homeostasis in Multi-Parent and Heterogeneous Populations

Under conditions of unpredictable climatic anomalies like terminal drought, erratic precipitation and extreme thermal fluctuations during flowering and grain filling, as seen in agricultural production environments, vegetative and forage yield stability are of major concern (Sorsa et al., 2023; Falconer & Mackay, 1996). Developmental homeostasis is the physiological and genetic ability of a plant population to withstand environmental fluctuations and to maintain stable phenotypic expression in various and/or stressful agro ecosystems (Allard & Bradshaw, 1964). Although conventional single-cross maize hybrids ($A \times B$) (Falconer & Mackay, 1996; Troyer & Larkins, 1985) are very productive under optimal and uniform input conditions, they have a high genetic uniformity of individuals within the field-population. In such monomorphic genetic architecture, there is less competition amongst individuals within a

population, however, the whole crop canopy is at risk from micro-environmental stresses because all plants have the same sensitivity thresholds (Duvick, 2005). By contrast, multi-parent and double cross maize hybrids ($[A \times B] \times [C \times D]$) combine the segregating genetic repertoire of four different inbred founder genetic stocks and provide a population with a balanced amount of population variability and field-level agronomic uniformity (Eckhardt & Bryan, 1940). This within-population diversity may buffer against environmental shocks by allowing physiological compensation between neighbouring plants so catastrophic harvest losses do not occur under abiotic stress (Creissen et al., 2013; Becker & Léon, 1988).

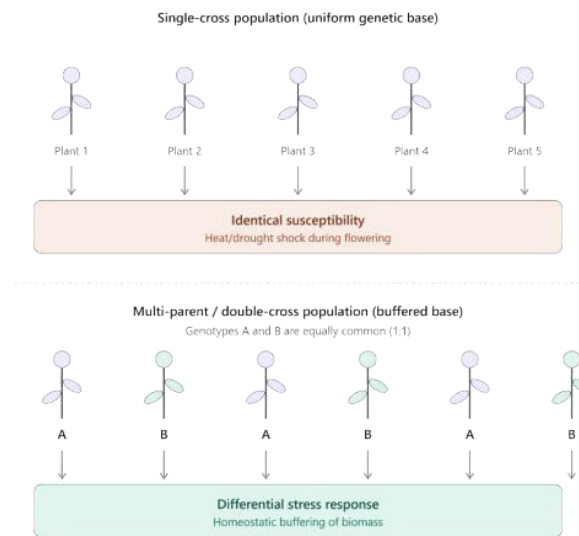


Figure 3. Differential Stress Responses in Wheat Genotypes Environmental Homeostasis and Genotype by Environment ($G \times E$) Interactions

The responsiveness of the cultivar to the environment for the phenotypic expression of forage yield and nutritional quality traits is influenced by the intrinsic genetic value of the cultivar as well as by complex Genotype-by-Environment ($G \times E$) interactions (Crossa, 1990; Nkurunziza et al., 2014). Production systems for forage maize are often faced with marginal soils, variable irrigation intensities and irregular heat waves in developing regions, causing greater $G \times E$ variance and lower predictability of traits (Karnatam et al., 2023; Badu-Apraku et al., 2016).

The quantitative geneticists introduced stability parameters like Eberhart and Russell's regression coefficient (b_i) and deviation from regression (S_{di}^2) to quantify the stability and homeostatic capacity of different field trials across various locations (Eberhart & Russell, 1966). Multi-line and multi-parent composite cultivars have been tested and shown to greatly minimize unpredictable interactions, causing the deviation from regression values ($S_{di}^2 \approx 0$) to be nearly zero

and regression coefficients to be close to unity ($b_i = 1.0$). The multi-parent double-cross hybrids presented this kind of statistical behavior, which shows that they are suitable for sustainable fodder production in South Asian countries under varying soil fertility and water availability levels (Sorsa et al., 2023; Hadebe et al., 2017).

$G \times E$ Physiological Mechanisms Conferring Stability under Abiotic Stress

The physiological mechanisms for population buffering in multi-parent maize hybrids include coordinated mechanisms to maintain photosynthetic capacity, osmotic balance and structural integrity of the cell wall under stress (Farooq et al., 2009; Cakir, 2004). Single-cross hybrids can have poor stover digestibility due to rapid leaf senescence, quick stem lodging and early lignification under water deficit or high temperature stress at the vegetative and pre-flowering stages, leading to impacts in crude protein fractions (Bänziger et al., 2000; Assefa et al., 2018).

These negative physiological changes are reduced by multi-parent and double-cross architectures in a number of complementary ways like Root System Architecture and Plasticity: Four different inbred genomes combine to provide better deep-soil penetration and root angle diversity for better water and deep-soil nutrient acquisition in dry periods (Trachsel et al., 2013; Lynch, 2013). Osmo protectant Accumulation and Membrane Stability: Several genetic backgrounds show different levels of accumulation of soluble sugars, proline and antioxidant enzymes (superoxide dismutase, peroxidase) that allow cellular membranes to remain stable in the presence of reactive oxygen species (ROS) generated during drought stress.

Stay-Green Trait Expression: Multi-parent populations provide inter-genotypic variation for delayed photosynthetic activity and chlorophyll retention in leaves and upper stalks (stay-green phenotype) and this will directly result in a more sustained dry matter accumulation and a lack of abrupt decreases in in vitro digestibility of dry matter (IVDMD) (Thomas & Howarth, 2000; Christopher et al., 2008).

Agronomic Implications for Fodder and Silage Resilience

Population buffering and environmental homeostasis are key considerations in maize breeding and directly linked to the structural feed shortages that livestock farmers in South Asia encounter (Karnatam et al., 2023; Government of Pakistan, 2025). Forage maize grown as a dual purpose or dedicated green chop crop is more important to the farmer for yield consistency from year to year than for maximum absolute production under more idealized experimental Station (Erenstein et al., 2022; Hamed et al., 2022).

The buffering of a double-cross and multi-parent genetic design ensures that agriculture systems can maintain green fodder yieldst ha^{-1} and dry matter outputs regardless of

failure of seasonal monsoons or high ambient temperatures in summer crop window (Sorsa et al., 2023; Khan et al., 2024). Thus, multi-parent breeding can be an effective approach to connect the dots between agronomic stability and maintenance of nutritional quality in climate-vulnerable agricultural landscapes (Periyasamy et al., 2025; Pawan et al., 2025).

QUANTITATIVE GENETIC PARAMETERS, HERITABILITY and SELECTION INDICES FOR FORAGE TRAITS

Partitioning Phenotypic and Genotypic Variability (PCV and GCV)

Systematic improvement of the maize (*Zea mays* L.) specifically adapted for high yielding green fodder and quality silage production requires basic knowledge of the available genetic variability and its nature and distribution within the breeding population (Ali et al., 2006; Burton & DeVane, 1953). Single-cross hybrid breeding programs in traditional varieties often have limited and narrow genetic bases that greatly limit long-term genetic improvement for more complex agronomic and nutritional traits (Duvick, 1999; Bernardo, 2020). Conversely, multi-parent and double-cross composite designs are effective at capturing genetic diversity from four genetically diverse inbred founder lines and purposefully increasing the range of genetic diversity for selection (Sorsa et al., 2023; Karnatam et al., 2023).

Quantitative geneticists use variabilities to measure and partition the variability effectively for deployment in breeding, that are known as Phenotypic Coefficient of Variation (PCV) and Genotypic Coefficient of Variation (GCV). Extensive studies under a wide range of tropical and subtropical conditions have invariably shown high values for PCV and moderate to high values for GCV of green fodder yield ($t\ ha^{-1}$) and total whole-plant dry matter yield respectively, indicating a high genetic variability (Kapoor & Batra, 2015; Pavithra et al., 2022). But vegetatively and biomass traits are notoriously sensitive to microenvironment (e.g. differences in soil fertility gradients, moisture and micro-climatic changes, etc.), values of phenotypic variance are often larger than genotypic variance, thereby increasing the difference between the estimates of PCV and GCV (Ali et al., 2006; Naharudin et al., 2021). Multi-parent populations counteract this environmental noise by spreading genetic variation throughout the crop canopy, allowing true genotypic variation to be observed and maintained in multi-location evaluation trials (Pawan et al., 2025; Periyasamy et al., 2025).

Broad Sense and Narrow Sense Heritability (h^2)

Heritability is an extremely useful diagnostic tool for plant breeders, as it identifies the proportion of total phenotypic variance that is caused by genetic factors and, therefore,

determines the range of response to selection. Heritability estimates are widely different between different morphological yield components and between complex biochemical nutritional traits (Ali et al., 2006; Naharudin et al., 2021) in forage and silage maize.

All qualitative nutritional traits (e.g., crude protein content (CP) and specific mineral accumulation efficiencies) generally show high broad-sense and narrow-sense heritability ($h^2 > 0.60$) (Naharudin et al., 2021), and this heritability is mainly driven by additive gene action. Because this trait is highly heritable, plant breeders will quickly be able to eliminate undesirable alleles at early segregating generations, using intensive progeny selection. In contrast, estimates of heritability for the complex physiological and structural components of cell-wall, such as Neutral Detergent Fiber (NDF), Acid Detergent Fiber (ADF), Acid Detergent Lignin (ADL) and In Vitro Dry Matter Digestibility (IVDMD) are often low to moderate (Naharudin et al., 2021). These deflated heritability values are the result of a large Genotype by Environment ($G \times E$) interactive effect and non-additive dominance effects which obscure the true genetic value (Naharudin et al., 2021). These heritability values are stabilized with double-cross and multi-parent mating designs, which capture more complex epistatic effects across a wide range of genetic backgrounds, and improve selection for highly digestible stover (Pawan et al., 2025; Periyasamy et al., 2025).

Expected Genetic Advance and Selection Response Dynamics

Heritability values alone can sometimes be confusing and must therefore always be interpreted in the context of the expected percentage (Genetic Advance (GA)) of the population mean (Johnson et al., 1955; Burton & DeVane, 1953). If high broad-sense heritability is accompanied by high expected genetic advance, then additive gene action is in full effect, meaning direct selection for phenotype will provide the quick and sure genetic gain (Ali et al., 2006; Johnson et al., 1955).

In segregating multi-parent and double-cross populations, green fodder yield, plant height and stem diameter routinely show high heritability and a high genetic advance, indicating that additive gene control occurs alongside high complementary non-additive variance (Sorsa et al., 2023; Pawan et al., 2025). Conversely, if the heritability of a trait is high and the genetic advance is very low, then non-additive gene action (dominance and complex epistasis) will be dominant and hybrid strategies that exploit this heterosis will be required, as opposed to simple pedigree selection. With structured multi-parent mating schemes, the breeders are able to make simultaneous, balanced genetic progress in both

biomass accumulation and nutritional quality parameters (Karnatam et al., 2023; Periyasamy et al., 2025).

Advanced Multi-Trait Selection Indices (MGIDI and MTSI)

One of the biggest and recurring problems in the breeding of dedicated forage maize is the negative phenotypic correlation between high biomass accumulation and better nutritional quality, which is commonly referred to as the biomass-digestibility trade-off (Karnatam et al., 2023; Periyasamy et al., 2025). When trying to breed exclusively for high massive green fodder weight, there is often an unintended consequence of coarse, highly lignified stalks with greatly reduced In Vitro Dry Matter Digestibility (IVDMD) reducing animal intake and milk production (Debnath et al., 2024; Palaniyappan et al., 2025).

In order to overcome this physiological constraint and to perform simultaneous multi-criteria selection without any loss of feed quality, modern quantitative breeding programs use advanced multi-variable selection indices, particularly the Multi-Trait Genotype-Ideotype Distance Index (MGIDI) and the Multi-Trait Stability Index (MTSI) (Debnath et al., 2024; Palaniyappan et al., 2025). These advanced statistical indices enable breeders to establish an ideal plant ideotype with high green fodder yield, improved crude protein, optimum fibre fractions and improved digestibility at the same time (Debnath et al., 2024). The combination of MGIDI and MTSI into multi-parent and double-cross breeding pipelines allows the researchers to efficiently screen large segregating populations, thereby avoiding unwanted biological compromises, and obtain climate-smart and dual-purpose maize cultivars specifically for sustainable animal husbandry in South Asia (Olivoto et al., 2021).

The correlation between traits and the path-coefficient analysis of forage yield and quality parameters were presented.

Phenotypic and Genotypic Inter-Relationships Among Forage Traits

The analysis of correlation structure between morpho-physiological traits plays an important role in quantitative assessment of fodder maize (*Zea mays* L.) since in any breeding program biomass yield is never inherited as a single unit (Ali et al., 2006; Dewey & Lu, 1959). Green fodder yield and whole-plant dry matter are complex traits affected by secondary traits like plant height, stem diameter, leaf-to-stem ratio and green leaf duration (Brar et al., 2010). Evaluation of different maize populations reveals that there is a strong positive phenotypic and genotypic correlation between plant height, stalk thickness (Ali et al., 2006; Pavithra et al., 2022) and green fodder yield.

But breeders are confronted with a biological challenge: that high biomass yield may also be associated with sub-optimal

nutritional quality parameters, such as crude protein and In Vitro Dry Matter Digestibility (IVDMD) (Ballard et al., 2001; Barriere et al., 2003). High vegetative bulk creates high amounts of Neutral Detergent Fiber (NDF) and Acid Detergent Fiber (ADF) which dilutes protein and reduces digestibility (Naharudin et al., 2021; Singh et al., 2023). Multi-parent and double-cross crosses can overcome these linkage blocks, and breeders can recover lines with high yields and low-lignin profiles.

Direct and Indirect Effects via Path-Coefficient Analysis

Correlation coefficient are measures of mutual association but may not be decomposed into direct and indirect causal paths (Dewey & Lu, 1959; Falconer & Mackay, 1996). Path coefficient analysis overcomes this by partitioning the correlation into direct and indirect effects through other traits (Jakhar et al., 2017).

Research has proven that the direct positive effect of plant height and stem diameter on the green fodder yield is the highest, followed by leaf area index (Ali et al., 2006; Kapoor & Batra, 2015). On the other hand, the structural fibers, such as NDF and ADF, have negative direct paths to animal intake, suggesting that structural traits should be selected for morphology while reducing cell-wall recalcitrance (Barriere et al., 2003; Nikolić et al., 2022). Net genetic gain (Widiayani et al., 2025) is maximized using a multi-parent nursery through path analysis, which identifies selection criteria.

Implications of Trait Inter-Relationships for Multi-Parent Breeding Strategies

The correlation structures show the boundary of single trait selection in forage maize (Dewey & Lu, 1959; Ali et al., 2006). Since there are overlapping genetic networks between yield and nutritive value it is difficult to achieve improvement in both traits without using multivariate methods (Karnatam et al., 2023; Periyasamy et al., 2025).

The multi-parent systems can handle these compromises through high intrapopulation recombination (Sorsa et al., 2023). Selection for biomass and silage quality are coupled with simultaneous selection for path-coefficient drivers, such as stem diameter, and stay-green duration, to ensure that neither biomass nor silage quality are compromised. Incorporating these into breeding pipelines contribute to the development of cultivars resistant to climate change to overcome fodder shortages in the South Asian region.

MOLECULAR MARKER-ASSISTED BREEDING AND GENOMIC SELECTION IN MULTI-PARENT MAIZE POPULATIONS

Integrating High-Throughput Genomic Tools into Forage Maize Breeding Programs

The use of conventional phenotypic selection methods for boosting the green fodder yield and improving the whole-plant architecture, ensiling suitability and stover quality

parameters of maize (*Zea mays* L.) are often limited by high environmental variation, large genotypic and environmental interactions (Ali et al., 2006; Bernardo, 2020) and long, labor-intensive selection cycles. To overcome these biological and operational limitations, the improvement of crops is increasingly using high-throughput genotyping platforms, molecular marker techniques, and advanced biometrical pipelines to dissect and map quantitative trait loci (QTLs) that control complex biomass accumulation and cell-wall digestibility pathways (Yu et al., 2008).

In multi-parent composite breeding, like Advanced Generation Inter-Cross (MAGIC) populations, multi-parent inter-cross pools and nested association mapping (NAM) panels, extensive and repeated recombination events successfully remove undesirable linkage drag and allow for an unusually high level of resolution mapping for complex quantitative traits (Yu et al., 2008). Marker-assisted selection (MAS) allows the breeders to accurately follow major effect alleles involved in important physiological and morphological mechanisms, irrespective of the influence of micro-environmental fluctuations (Barriere et al., 2003; Thomas & Howarth, 2000). These target mechanisms include stay-green leaf senescence retention, root system architecture plasticity and enzymatic pathways involved in lignin biosynthesis, ferulic acid cross-linking and polysaccharide architecture within the stalk cell walls (Trachsel et al., 2013; Periyasamy et al., 2025). In addition, marker-assisted tracking at the early nursery stages means that breeding programs can also remove undesirable segregants prior to spending land, water and money on large-scale multi-location field testing, maximizing the genetic gain in unit of time and operational cost (Karnatam et al., 2023).

Dissecting Linkage Disequilibrium and Recombination Dynamics in MAGIC and NAM Populations

The resolution of quantitative trait loci (QTL) affecting complex forage traits and their structures is directly related to the linkage disequilibrium (LD) and frequency of historical recombination events in the mapping population (Yu et al., 2008). Traditional bi-parental mapping populations have limited recombination cycles, which leads to large confidence intervals for the location of QTLs, and limited use of markers on different genetic backgrounds (Bernardo, 2020). By contrast, multi-parent advanced generation inter-cross (MAGIC) populations and nested association mapping (NAM) designs involve crossing several successive generations of multiple elite inbred founders before selfing or DHs are produced (Cavanagh et al., 2008). For each chromosome, this multi way crossing method creates an exponential number of crossings over breakpoints, effectively fragmenting large blocks of linkage disequilibrium and enabling breeders to map the loci down to

sub-centimorgan resolution. High resolution MAGIC populations separate undesirable genetic correlations between tall biomass and high lignification for traits of particular interest such as Neutral Deterrent Fiber (NDF) degradability and stalk shear strength. Thus, functional, diagnostic markers that are associated with Minor effect QTLs can be identified by quantitative geneticists and used to introgress digestible cell wall alleles into elite multi-parent synthetic pools without yield penalties (Sorsa et al., 2023).

Genomic Selection (GS) and Prediction Accuracy in Complex Populations

Marker-assisted selection has proven to be very efficient for traits with few genes of major effect that are controlled by qualitative loci, however, complex agronomic traits like total dry matter yield (t ha^{-1}) and In Vitro Dry Matter Digestibility (IVDMD) are polygenetic, meaning that they are controlled by hundreds or thousands of genes of minor effect spread throughout the entire maize genome (Falconer & Mackay, 1996; Hosseini et al., 2025). It is statistically impractical and cost prohibitive to try to tag every individual minor locus by traditional MAS. Genomic Selection (GS) is the use of genome-wide marker profiles (such as DArTseq, genotyping-by-sequencing, or high-density SNP arrays) to estimate the cumulative effects of all these loci simultaneously and determine a Genomic Estimated Breeding Value (GEBV) for phenotypic candidate lines (Bernardo, 2020; Yu et al., 2008). Genomic selection in multi-parent double-cross and multi-line composite breeding architecture significantly shortens breeding cycle by allowing segregating progenies to be selected at an early stage prior to field testing (Karnatam et al., 2023; Taşkın et al., 2025). The accuracy of the prediction from the GS models is essentially influenced by the size of the training population, the density of markers, the heritability of the trait and by the genetic relatedness of the training population with the selection candidates (Bernardo, 2020; Meuwissen et al., 2001). A multi-parent population can provide a huge amount of allelic diversity and richness and thus is a good training population for a genomic prediction model (Sorsa et al., 2023). Thus, GS can be incorporated into multi-parent breeding pipelines to enable quantitative geneticists to gain higher prediction accuracy for complex nutritional and stover traits, enabling fast identification of high-yielding and high-digesting forage hybrids for intensive livestock production systems (Periyasamy et al., 2025; Vinayan et al., 2021).

Synergizing Conventional Multi-Parent Crosses with Modern Genomic Frameworks

To achieve successful advanced breeding in forage maize, a smooth integration of multi-parent population building and state-of-the-art genomic selection and high throughput phenotyping techniques is essential (Sorsa et al., 2023).

Evaluation of all segregating families at several drought or heat stress testing environments is physically and cost prohibitive in traditional multi-parent breeding designs. Genomic prediction models trained from well characterized subset of multi-parent lines, can be used to screen thousands of candidates per season with minimal field expenditure (Bernardo, 2020; Taşkın et al., 2025). This strong integration

allows fully harnessing the physiological homeostasis and developmental buffering effects of double-cross and multi-parent systems with modern molecular speed, allowing a scientifically sound and sustainable solution to address chronic livestock fodder security in South Asian farming systems.

Tool or approach	Main purpose	Strengths	Limitations	Recommended use in multiparent forage breeding
Diallel and line $\times$ tester analysis	Estimate general and specific combining ability	Identifies superior parents and useful cross combinations	Requires controlled mating designs and adequate replication	Use to select parents for double-cross or multi-parent hybrids
MAGIC and NAM populations	Increase recombination and improve mapping resolution	Capture broad allelic diversity and reduce linkage disequilibrium	Development and maintenance are resourceintensive	Use for mapping biomass, fibre, digestibility, and stressresilience traits
Marker-assisted selection	Track major alleles or genomic regions	Useful for traits with major- effect loci	Less effective for highly polygenic traits	Apply to validated loci for stay-green, root traits, disease resistance, or lignin-related traits
Genomic selection	Predict genomic estimated breeding values using genome-wide markers	Suitable for complex, polygenic traits such as biomass and digestibility	Requires training population, dense markers, and reliable phenotypes	Use to select early-generation lines before costly multi- location testing
High-throughput phenotyping	Measure canopy, root, water status, and biomass traits efficiently	Enables repeated, nondestructive or large-scale measurements	Requires calibration with agronomic and quality traits	Combine UAV, thermal, multispectral, and root phenotyping with field trials
Multi-trait selection indices	Balance yield, quality, and stability	Helps manage biomass– digestibility trade-offs	Requires clearly defined selection objectives and trait weights	Use MGIDI and MTSI to identify genotypes with high performance and stability
Multi-environment trials	Quantify genotype $\times$ environment interaction	Essential for identifying stable forage hybrids	Costly and timeconsuming	Conduct across representative rainfall, temperature, soil, and management environments

Table 2. Breeding and genomic tools for improving yield, quality, and stability in multi-parent forage maize

CONCLUDING REMARKS, STRATEGICROADMAP and FUTURE OUTLOOK

The Paradigm Shift: Moving Beyond Narrow-Base Single-Cross Limitations

The ongoing and increasing shortages of livestock feed and silage in South Asian cropping and farming systems are a structural problem which cannot be addressed with conventional, restricted base breeding approaches (Erenstein

et al., 2022; Karnatam et al., 2023). Commercial maize development has focused for decades on elite single-cross hybrids adapted to high input, uniform environment for grain production. But when grown under intensifying climate volatility (high fluctuations of monsoonal rainfall, terminal heat stress and extended dry spells), these narrow-base single-cross cultivars show pronounced physiological instability with high genotype by environment ($G \times E$)

interaction variance and steep reduction in yield (Sorsa et al., 2023; Bänziger et al., 2000).

To ensure long term agricultural sustainability and animal protein security, quantitative breeders need to undergo an urgent paradigm shift to multi-parent composite breeding systems such as Advanced Generation Inter-Cross (MAGIC) populations, multi-parent diallel and double-cross synthetic systems ($[A \times B] \times [C \times D]$) (Huang et al., 2015). The high intrapopulation recombination frequencies and multi-allelic buffering capacity have been successfully utilized with these advanced genetic designs for stable green biomass and dry matter accumulation in the various agro-ecological zones which are prone to stress.

Resolving the Biomass-Digestibility Antagonism Through Next-Generation Integration

One of the most important physiological constraints that have limited breeding for dedicated forage maize has been the universal biological antagonism between high green biomass production and high nutritional value for ruminants, commonly referred to as the biomass digestibility trade-off (Ballard et al., 2001; Barriere et al., 2003). When choosing for high stover tonnage ha⁻¹ only, coarse, highly lignified stem is invariably selected, which is directly reflected in low In Vitro Dry Matter Digestibility (IVDMD), low voluntary dry matter intake and low net milk production efficiency in dairy ruminants (Naharudin et al., 2021; Singh et al., 2023). Breaking this trade-off will require discarding old univariate approaches to selection and adopting multivariate ideotype breeding frameworks (Debnath et al., 2024). Combining the advanced selection indices (Multi-Trait Genotype-Ideotype Distance Index (MGIDI) and Multi-Trait Stability Index (MTSI)) with the high-density genomic selection (GS) model will enable breeders to assess and predict breeding values for multi-genic stover traits (Palaniyappan et al., 2025). This synergy enables quantitative geneticists to simultaneously optimize for biomass accumulation, reduction of cell-wall

recalcitrance, crude protein retention, and persistence of stay-green leaf senescence to shorten breeding cycles and accelerate release of elite dual-purpose cultivars (Periyasamy et al., 2025; Taşkın et al., 2025).

Concluding Recommendations and Future Outlook

In summary, the future of cereal forage improvement in South Asia depends on the aggressive use of multivariate ideotype selection and high throughput genomic prediction (Periyasamy et al., 2025; Vinayan et al., 2021), path-coefficient trait dissection and high-resolution multiparent mapping along with the application of quantitative genetic theory. To do this full scale framework working effectively, agricultural research institutions and national breeding programmes need to focus on the following strategic priorities; Establish Regional Multiparent Nurseries: Create public sector special breeding pools or MAGIC populations for tropical/southern forage adaptation and inject new variation on an ongoing basis (Sorsa et al., 2023).

Routine application of multivariate selection indices (MGIDI, MTSI) in multi-location testing to co-select high stover yield and optimal ruminal digestibility; make it a habit to use multivariate selection indices ((Palaniyappan et al., 2025)). Deploy Genomic Selection Pipelines: Develop genomic prediction models based on core multi-parent training sets, high density SNP genotypes and use to cull in early generations and recycle superior parental lines.

Combine genomic tools, UAV based multispectral canopy sensing and automated root architectural profiling methods to quantify physiological stress resilience under real field conditions (Integrate High-Throughput Phenomics). Through the implementation of this integrated roadmap, agricultural scientists and livestock sectors will be able to develop climateresilient maize cultivars with high nutritional value and productivity, revolutionize forage production, and ensure a sustainable supply of animal protein in South Asia in the future.

Key Term	Full form	Description
Green fodder yield	—	Fresh weight of maize biomass harvested per unit area for feeding livestock
Dry-matter yield	—	Weight of maize biomass after water removal; important for silage quality and feed value
Silage	—	Fermented and preserved maize forage used as livestock feed
Single-cross hybrid	F1 hybrid from two inbred lines	A genetically uniform hybrid made by crossing two inbred parents; high yield but high seed cost
Double-cross hybrid	Hybrid from four inbred parents	A hybrid made by crossing two single-cross hybrids; may provide greater buffering and lower seed cost

GCA	General combining ability	Average ability of a parent to transmit desirable performance to its crosses
SCA	Specific combining ability	Superior or inferior performance of a particular cross due to non-additive gene action
Genotype × environment interaction	G × E interaction	Change in genotype performance across different environments, seasons, or management conditions
Population buffering	—	Ability of a genetically diverse population to maintain stable performance under stress or environmental variation
Genomic selection	GS	Use of genome-wide DNA markers to predict the breeding value of plants and speed up selection

Table 3. Key Terms description.

References

- Ahmad, H., Ahmed, U., Ullah, I., & Masud, H. (2024). Comparing fodder production of maize varieties under varied nitrogen levels.
- Allard, R. W., & Bradshaw, A. D. (1964). Implications of genotype-environmental interactions in applied plant breeding.
- Alvarado-Ramírez, E. R., Ballesteros-Rodea, G., Salem, A. Z. M., Reyes-Hernández, J., Herrera-Corredor, C. A., Hernández-Meléndez, J., ... & Rivas-Jacobo, M. A. (2023). The impact of genotype on chemical composition, feeding value and in vitro rumen degradability of fresh and ensiled forage of native maize (*Zea mays* L.) from Mexico. *Agriculture*, 13(11), 2161.
- Argillier, O., Méchin, V., & Barrière, Y. (2000). Inbred line evaluation and breeding for digestibility-related traits in forage maize. *Crop Science*, 40(6), 1596–1600.
- Assefa, Y., Vara Prasad, P. V., Carter, P., Hinds, M., Bhalla, G., Schon, R., ... & Ciampitti, I. A. (2016). Yield responses to planting density for US modern corn hybrids: A synthesis-analysis. *Crop Science*, 56(5), 2802–2817.
- Badu-Apraku, B., Fakorede, M. A. B., Talabi, A. O., Oyekunle, M., Akaogu, I. C., Akinwale, R. O., Annor, B., Melaku, G., Fasanmade, Y., & Aderounmu, M. (2016). Gene action and heterotic groups of early white quality protein maize inbreds under multiple stress environments. *Crop Science*, 56(1), 183–199.
- Ballard, C. S., Thomas, E. D., Tsang, D. S., Mandebvu, P., Sniffen, C. J., Endres, M. I., & Carter, M. P. (2001). Effect of corn silage hybrid on dry matter yield, nutrient composition, in vitro digestion, intake by dairy heifers, and milk production by dairy cows. *Journal of dairy science*, 84(2), 442–452.
- Bänzinger, M. (2000). *Breeding for drought and nitrogen stress tolerance in maize: from theory to practice*. Cimmyt.
- Barrière, Y., Guillet, C., Goffner, D., & Pichon, M. (2003). Genetic variation and breeding strategies for improved cell wall digestibility in annual forage crops: A review. *Animal Research*, 52(3), 193–228.
- Becker, H., & Léon, J. (1988). Stability analysis in plant breeding. *Plant Breeding*, 101(1), 1–23.
- Bernardo, R. (2020). *Breeding for quantitative traits in plants* (3rd ed.). Stemma Press.
- Bertoia, L. M., & Aulicino, M. B. (2014). Maize forage aptitude: Combining ability of inbred lines and stability of hybrids. *The Crop Journal*, 2(6), 407–418.
- Brar, S. P. S., Sukhchain, & Kumar, M. (2010). Inter-relationships among different morphological traits over different environments in fodder maize (*Zea mays* L.). *Crop Improvement*, 37(2), 133–135.
- Burton, G. W., & De Vane, D. E. (1953). Estimating heritability in tall fescue (*Festuca arundinacea*) from replicated clonal material.
- Cakir, R. (2004). Effect of water stress at different development stages on vegetative and reproductive growth of corn. *Field Crops Research*, 89(1), 1–16.
- Cavanagh, C., Morell, M., Mackay, I., & Powell, W. (2008). From mutations to MAGIC:
- Christopher, J. T., Manschadi, A. M., Hammer, G. L., & Borrell, A. K. (2008). Developmental and physiological traits associated with high yield and stay-green phenotype in wheat. *Australian Journal of Agricultural Research*, 59(4), 354–364.
- Creissen, H. E., Jorgensen, T. H., & Brown, J. K. (2013). Stabilization of yield in plant genotype mixtures through compensation rather than complementation. *Annals of botany*, 112(7), 1439–1447.
- Crossa, J. (1990). Statistical analyses of multilocation trials. *Advances in Agronomy*, 44, 55–85.
- Debnath, P., Chakma, K., Bhuiyan, M. S. U., Thapa, R., Pan, R., & Akhter, D. (2024). A novel multi trait genotype ideotype distance index (MGIDI) for genotype selection in plant breeding: Application, prospects, and limitations. *Crop Design*, 3(4), 100074.
- Dewey, D. R., & Lu, K. (1959). A correlation and path-coefficient analysis of components of crested wheatgrass seed production 1. *Agronomy journal*, 51(9), 515–518.
- Duvick, D. N. (1999). Heterosis: Feeding people and protecting natural resources. In J. G. Coors & S. Pandey

- (Eds.), The genetics and exploitation of heterosis in crops (pp. 19–29). American Society of Agronomy, Crop Science Society of America, and Soil Science Society of America.
- Duvick, D. N. (2005). The contribution of breeding to yield advances in maize (*Zea mays* L.). *Advances in Agronomy*, 86, 83–145.
- Eberhart, S. A., & Russell, W. A. (1966). Stability parameters for comparing varieties. *Crop Science*, 6(1), 36–40.
- Eckhardt, R. C., & Bryan, A. A. (1940). Effect of the method of combining the four inbred lines of a double cross of maize upon the yield and variability of the resulting hybrid.
- Erenstein, O., Jaleta, M., Sonder, K., Mottaleb, K., & Prasanna, B. M. (2022). Global maize production, consumption and trade: trends and R&D implications: Erenstein, Jaleta, Sonder, Mottaleb and Prasanna. *Food security*, 14(5), 1295–1319.
- Ertiro, B. T., Twumasi-Afriyie, S., Blümmel, M., Friesen, D., Negera, D., Worku, M., ... & Kitege, K. (2013). Genetic variability of maize stover quality and the potential for genetic improvement of fodder value. *Field Crops Research*, 153, 79–85.
- Falconer, D. S., & Mackay, T. F. C. (1996). Introduction to quantitative genetics (4th ed.). Longman.
- Farooq, M., Wahid, A., Kobayashi, N. S. M. A., Fujita, D. B. S. M. A., & Basra, S. M. (2009). Plant drought stress: effects, mechanisms and management. *Agronomy for sustainable development*, 29(1), 185–212. *Frontiers in plant science*, 9, 1117.
- Government of Pakistan. (2025). Pakistan Economic Survey 2024-25, Chapter 2: Agriculture. Finance Division, Economic Adviser's Wing, Islamabad, Pakistan.
- Griffing, B. (1956). Concept of general and specific combining ability in relation to diallel crossing systems. *Australian Journal of Biological Sciences*, 9(4), 463–493.
- Hadebe, S. T., Modi, A. T., & Mabhaudhi, T. (2017). Calibration and testing of AquaCrop for selected sorghum genotypes. *Water SA*, 43(2), 209–221.
- Hallauer, A. R., Carena, M. J., & Miranda Filho, J. D. (2010). *Quantitative genetics in maize breeding*. Springer Science & Business Media.
- Hamed, A., Zamir, M. S. I., Tanveer, A., & Yaseen, M. (2022). Comparison of maize hybrids for production of quality fodder and silage in Faisalabad, Punjab, Pakistan. *Journal of Bioresource Management*, 9(4), 6.
- Horst, E. H., López, S., Neumann, M., Giraldez, F. J., & Bumbieris Junior, V. H. (2020). Effects of hybrid and grain maturity stage on the ruminal degradation and the nutritive value of maize forage for silage. *Agriculture*, 10(7), 251.
- Hosseini, S. M. S., Shiri, M., Mostafavi, K., Mohammadi, A., & Miri, S. M. (2025). Genetic analysis and association detection of agronomic traits in maize genotypes. *Scientific Reports*, 15(1), 399.
- Huang, B. E., Verbyla, K. L., Verbyla, A. P., Raghavan, C., Singh, V. K., Gaur, P., ... & Cavanagh, C. R. (2015). MAGIC populations in crops: current status and future prospects. *Theoretical and Applied Genetics*, 128(6), 999–1017.
- Jakhar, D. S., Singh, R., & Kumar, A. (2017). Studies on path coefficient analysis in maize (*Zea mays* L.) for grain yield and its attributes. *International Journal of Current Microbiology and Applied Sciences*, 6(4), 2851–2856.
- Johnson, H. W., Robinson, H. F., & Comstock, R. E. (1955). Estimates of genetic and environmental variability in soybeans. *Agronomy Journal*, 47(7), 314–318.
- Kapoor, R., & Batra, C. (2015). Genetic variability and association studies in maize (*Zea mays* L.) for green fodder yield and quality traits. *Electronic Journal of plant breeding*, 6(1), 233–240.
- Karnatam, K. S., Mythri, B., Un Nisa, W., Sharma, H., Meena, T. K., Rana, P., ... & Sandhu, S. (2023). Silage maize as a potent candidate for sustainable animal husbandry development—perspectives and strategies for genetic enhancement. *Frontiers in Genetics*, 14, 1150132.
- Khan, N., Shah, T. A., Akhtar, H. M. S., Salamatullah, A. M., Bourhia, M., Mekonnen, A. B., ... & Khan, N. A. (2024). Influence of maize genotypes and harvest stages on in-silo fermentation quality and nutritional value of corn silage during hot summer condition of the tropics. *BMC Plant Biology*, 24(1), 490.
- Lynch, J. P. (2013). Steep, deep and cheap: an allele selection strategy for root phenotypes optimizing nitrogen and water acquisition in maize. *Annals of Botany*, 112(2), 347–357. <https://doi.org/10.1093/aob/mct112>
- Lynch, M., & Walsh, B. (1998). Genetics and analysis of quantitative traits. Sinauer Associates.
- Melchinger, A. E., & Gumber, R. K. (1998). Overview of heterosis and heterotic groups in agronomic crops. *Concepts and breeding of heterosis in crop plants*, 25, 29–44.
- Meuwissen, T. H., Hayes, B. J., & Goddard, M. (2001). Prediction of total genetic value using genome-wide dense marker maps. *genetics*, 157(4), 1819–1829.
- Naharudin, N. S., Sin, M. A., & Saleh, G. (2021). Genetic variance and correlation of forage yield and quality traits in tropically adapted maize. *Sains Malaysiana*, 50(1), 45–52.
- Nikolić, V., Simić, M., Žilić, S., Kravić, N., Babić, V., Filipović, M., & Srdić, J. (2022). Quality parameters of maize hybrids intended for silage production. *Acta agriculturae serbica*, 27(54), 157–163.
- Nkurunziza, L., Kornher, A., Hetta, M., Halling, M., Weih, M., & Eckersten, H. (2014). Crop genotype-environment modelling to evaluate forage maize cultivars under climate

variability. *Acta Agriculturae Scandinavica, Section B-Soil & Plant Science*, 64(1), 56-70.

Olivoto, T., Nardino, M., Meira, D., Meier, C., Follmann, D. N., de Souza, V. Q., ... & Baretta, D. (2021). Multi-trait selection for mean performance and stability in maize. *Agronomy Journal*, 113(5), 3968-3974.

Palaniyappan, S., Ganesan, K. N., & Manivannan, N. (2025). Selection of superior fodder maize (*Zea mays*) parental inbreds using multi trait genotype ideotype distance index (MGIDI) and multi trait stability index (MTSI).

Pavithra, A., Ganesan, K. N., Meenakumari, B., & Sivakumar, S. D. (2022). Genetic studies on green fodder yield and quality traits in fodder maize (*Zea mays* L.). *Electronic Journal of Plant Breeding*, 13(2), 432-439.

Pawan, K. D., Ganesan, K. N., Manivannan, N., Vellai, K. S., Senthil, N., & Pravukalyan, M. (2025). Magnitude and impact of genetic heterogeneity on nutritional and fodder quality traits in segregating population of fodder maize (*Zea mays* L.). *Plant Science Today*, 12.

Periyasamy, A., Ramamoorthy, P., Rajasekaran, R., Natesan, S., Alagarsamy, S., Doraiswamy, U., ... & Thailappan, E. (2025). Genetic approaches to enhance fodder traits in maize: progress and prospects. *The Nucleus*, 1-20. resources for gene discovery, validation and delivery in crop plants. *Current opinion in plant biology*, 11(2), 215-221.

Sardar Ali, S. A., Hidayat-ur-Rahman, H. U. R., Raziuddin, R., Shah, S. S., & Hassan, G. (2006). Estimates of variability, heritability and genetic advance for fodder traits in two maize populations.

Singh, D., Kumar, B., Kumar, P., & Rakshit, S. (2023). Evaluation of maize hybrids and composites for fodder yield and ensiling quality. *Range Management and Agroforestry*, 44(2), 344-352.

Sorsa, Z., Mohammed, W., Wegary, D., & Tarkegne, A. (2023). Performances of three-way cross hybrids over their

respective single crosses and related heterosis of maize (*Zea mays* L.) hybrids evaluated in Ethiopia. *Heliyon*, 9(5).

Taşkın, S. Z., Duman, A., & Bilgili, U. (2025). Accelerating silage maize breeding: forage yield and nutritive quality of doubled haploid-derived hybrids. *PeerJ*, 13, e20197.

Thomas, H., & Howarth, C. J. (2000). Five ways to stay green. *Journal of experimental botany*, 51(suppl_1), 329-337.

Trachsel, S., Kaeppler, S. M., Brown, K. M., & Lynch, J. P. (2011). Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant and soil*, 341(1), 75-87.

Troyer, A. F., & Larkins, J. R. (1985). Selection for early flowering in corn: 10 late synthetics. *Crop Science*, 25(4), 695-697.

Van Soest, P. V., Robertson, J. B., & Lewis, B. A. (1991). Methods for dietary fiber, neutral detergent fiber, and nonstarch polysaccharides in relation to animal nutrition. *Journal of dairy science*, 74(10), 3583-3597.

Vinayan, M. T., Seetharam, K., Babu, R., Zaidi, P. H., Blummel, M., & Nair, S. K. (2021). Genome wide association study and genomic prediction for stover quality traits in tropical maize (*Zea mays* L.). *Scientific Reports*, 11(1), 686.

Widiayani, N., Anshori, M. F., Nasaruddin, N., Farid, M., Ridwan, I., Bahrin, A. H., ... & Seleiman, M. F. (2025). A new approach for evaluating maize transgressive segregants and their three-way cross potential in the S4 convergent breeding population. *BMC Plant Biology*, 25(1), 122.

Yu, J., Holland, J. B., McMullen, M. D., & Buckler, E. S. (2008). Genetic design and statistical power of nested association mapping in maize. *Genetics*, 178(1), 539-551.

Zhou, Z., Zhang, C., Lu, X., Wang, L., Hao, Z., Li, M., ... & Li, X. (2018). Dissecting the genetic basis underlying combining ability of plant height related traits in maize.