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Restructuring plant architecture for maize breeding: current strategies and future directions

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Abstract

Plant architecture refers to the three- dimensional distribution of plant parts, which influences crop growth, yield and stress resistance. It plays a pivotal role in determining adaptability of maize cultivars under high-density planting by encompassing traits such as plant height, ear height, internode length, leaf angle and tassel density. These traits collectively contribute to yield by enhancing lodging resistance, photosynthesis efficiency, water and nutrient uptake efficiency. To meet the growing demand for increased food production and improved quality, various breeding methods aim to provide an adequate and nutrient-rich diet to populations. One effective strategy focuses on optimising plant architecture under high density planting, enabling more plants to grow within a unit area while maintaining productivity and resilience. This review explores key plant architecture traits and their contributions to yield, emphasizing the roles of phytohormones and their signaling pathways, quantitative trait loci (QTLs), genomic dynamics, and marker-assisted breeding. Additionally, we discuss multiomics approaches, advanced breeding strategies, and recent breakthroughs in maize research aimed at achieving sustainable production in the face of global challenges, such as climate change and resource limitations. The integration of these insights into practical breeding programs holds immense potential for developing high-yielding, resilient maize cultivars that cater to the needs of future food security.

Abbreviations

AS: Anthesis-silking interval
BRs: Brassinosteroids
CRISPR: Clustered regularly interspaced short palindromic repeats
DEGs: Differentially expressed genes
DHs: Double haploids
GA: Gibberellic acid
GID1: Gibberellin-insensitive dwarf1
GWAS: Genome wide association studies:
HDP: High density planting
HIR: Haploid induction rate
IAA: Indole acetic acid
ILE: Internode length above the primary ear
KASP: Kompetitive Allele-Specific PCR
PCR: Polymerase chain reaction
LAE: Leaf angle above the primary ear
LOV: Leaf orientation value
MAGIC: Multi-parent advanced generation inter-cross
Maize GDB: Maize genetics and genomics database
MAS: Marker assisted selection
MS: Mass spectrometry
NHEJ: Non-homologous end joining
NMR: Nuclear magnetic resonance
NSF: National science foundation
PIFs: Phytochrome interacting factors
PGR: Plant growth regulators
PPR: Pentatricopeptide repeat
RILs: Recombinant inbred lines
SAM: S-adenosyl-L-methionine
TALENs: Transcription activator-like effector nucleases
ZFN: Zinc finger nucleases

Introduction

Food and nutrient security are two major global challenges in the pursuit of sustainable agriculture, aiming to ensure that the population has access to sufficient and nutritious food with long-term sustainability. Maize holds significant economic importance globally as a staple food, sustaining millions of people worldwide and serving as a key ingredient in various food products. Its versatility extends beyond human consumption to include animal feed, biofuel production, and industrial applications. Additionally, maize cultivation generates income for farmers and supports various industries, contributing substantially to both local and global economies. The sustained importance of maize has driven ongoing research efforts to increase its yield, nutritional content, and overall resilience in the face of evolving agricultural challenges.

Plant architecture refers to the spatial organization of plant components, including size, shape, plant height, ear height, leaf angle and internode length, which collectively influence canopy structure, photosynthetic efficiency, and ultimately plant yield. Increasing plant density and shaping plant architecture are two effective measures for increasing maize yield (Geng *et al.*, 2022). The intricate interaction between genetic factors and environmental influences profoundly shapes maize plant architecture. Compact plant architecture can significantly boost yield under increased plant densities. For example, yield improves from low to medium densities (30,000 to 60,000 plants/ha) and further from medium to high densities (60,000 to 90,000 plants/ha) (Shi *et al.*, 2024). Understanding the genomic basis of key plant architecture traits that determine yield, such as plant height, leaf angle, ear height, internode number, and internode length, is vital for increasing crop productivity, adaptability, and resource utilization. Plant height directly influences light interception, nutrient acquisition, and overall crop performance. Unraveling the genetic determinants behind maize vertical stature can pave the way for targeted breeding strategies aimed at optimizing plant height for increased productivity. Similarly, investigating the genetics of leaf angle provides insight into the arrangement and orientation of leaves, influencing light penetration and photosynthetic efficiency. Ear height (EH), a critical agronomic trait strongly correlated with plant height, directly affects lodging resistance, nutrient utilization efficiency and maize yield. Achieving an optimal ear height is essential for improving plant density and maximizing the overall maize performance, including moisture and nutrients utilization as well as the inception of photosynthetically active radiation (Wang *et al.*, 2023). Plant height is determined by the number and length of internode in maize. Internode length varies from the bottom to the top of plant, but at high plant density, the internode length just below the ear increases due to the non photodestruction of auxin, which promotes internode elongation. Shorter internodes contribute to reduced plant height, increasing lodging resistance, enabling denser planting, and enhancing the harvest index.

In recent years, advancements in maize research have been remarkable across genetics, breeding strategies, agronomy, and technological application. These developments have not only deepened our understanding of the maize genome but have also paved the way for innovations aimed at addressing issues such as climate variability, pest pressures, and sustainable farming practices. This review provides a comprehensive exploration of the genomics underlying plant architecture traits in maize, highlighting molecular mechanism, quantitative trait loci (QTLs), and candidate genes governing these critical features it also examines recent breeding strategies employing multiomics approaches to increase maize yield by curbing various biotic and abiotic related stresses.

Historical perspective on maize breeding for plant architecture

Maize plant architecture is distinct among cereals, characterized by its single culm or pole-like structure, separate male and female inflorescence, and non- shattering nature. The unique plant architecture of maize has played pivotal role in its evolution and adaptability. In the early 20th century, the origin of maize became a topic of significant debate. Classical taxonomy suggested maize originated either form genus *Tripsacum* (gamagrass) or genus *Zea* (teosinte and maize). Archaeological and phylogenetic analyses later confirmed that maize was domesticated *Zea mays* ssp. parviglumis (Balsas teosinte) in the Balsas River Basin of South Mexico approximately 9,000 year ago (Matsuoka *et al.*, 2002). This domestication process involved a complete phenotypic transformation from its wild progenitor to modern maize. The transformation of maize from its wild ancestor was far more dramatic compared to the domestication of wheat, where wild and cultivated forms are morphological similar. Teosinte, the wild progenitor of maize, posed a significant challenge in identifying its relationship to maize due to its highly branched growth habit, multiple branched inflorescence, single spikelet, multiple ear, two-ranked capsule, enclosed fruitcase, shattering and deep dormancy (Figure 1). Several hypotheses were proposed to explain the origin of maize. Among these, the tripartite hypothesis (Mangelsdorf and Reeves, 1938) suggested that maize originated from an unknown plant with similar ear morphology, with teosinte being an offspring of maize and *Tripsacum*. The most widely accepted theory, however, is the teosinte hypothesis proposed by Beadle (1939). This hypothesis suggests that maize originated from teosinte through major mutation at few loci (Table 1). While teosinte and maize differ significantly in morphologically, DNA-level analysis revealed they share the same chromosome number and similar gene arrangement. Supporting the teosinte hypothesis, Doebley and stec (1991) conducted crosses between maize and *Zea mays ssp. mexicana* and *Zea mays ssp. parviglumis*. Their study identified five major chromosomal regions responsible for the morphological differences between maize and teosinte. Notably, the tb1 (*teosinte branched 1*) locus, when introgressed into teosinte, transformed its highly branched, tillering growth habit into the single-stalked structure characteristic of maize. Similarly, the *tga* (*teosinte glume architecture*) locus played a critical role in developing the naked kernel phenotype and affects peculiar outgrowth of floral stalk, and bracts. Other loci and genes have been identified as contributor to the architectural transformation that has resulted in modern maize. These wild relatives of maize serve as reservoirs of valuable genes and alleles for diverse climatic adaptations, resistance to biotic and abiotic stresses, and yield improvement. Characterizing and utilizing these wild species in breeding programs focused on plant architectural traits can lead to the development of maize varieties with enhanced yield potential, improved lodging resistance, and increased resilience against environmental stresses.

Plant architecture traits: Key drivers of crop improvement

According to (Mock and Pearce, 1975), an ideal plant architecture includes the following traits: (1) narrow-leaf angle above the ear, (2) maximum photosynthetic

Table 1 - Domesticated genes/loci associated with morphological traits evolved from teosinte

Traits	Genes	Linkage group	Phenotype	
			Teosinte	Maize
Plant architecture	*tb1 (teosinte branched1)*	1	Highly branched plant with many inflorescence	Single stalk with single inflorescence
Glume hardness	*tga1 (teosinte glume architecture1)*	4	Covered fruitcase	Naked kernels
Rank capsule	*zfl2 (Zea floricaula leafy2)*	2	Distichous (two rank ear)	Polystichous (> 4 rank ear)
Spikelet	*ra1, ra2, ra3, ra4*	7 and 3	Single spikelet	Paired spikelet
Number of ears per plant	*gt1 (grassy tiller1)*		Multiple ear	Few ear
Shattering behavior	*ZmSh1-1*	1	Shattering	Non-shattering

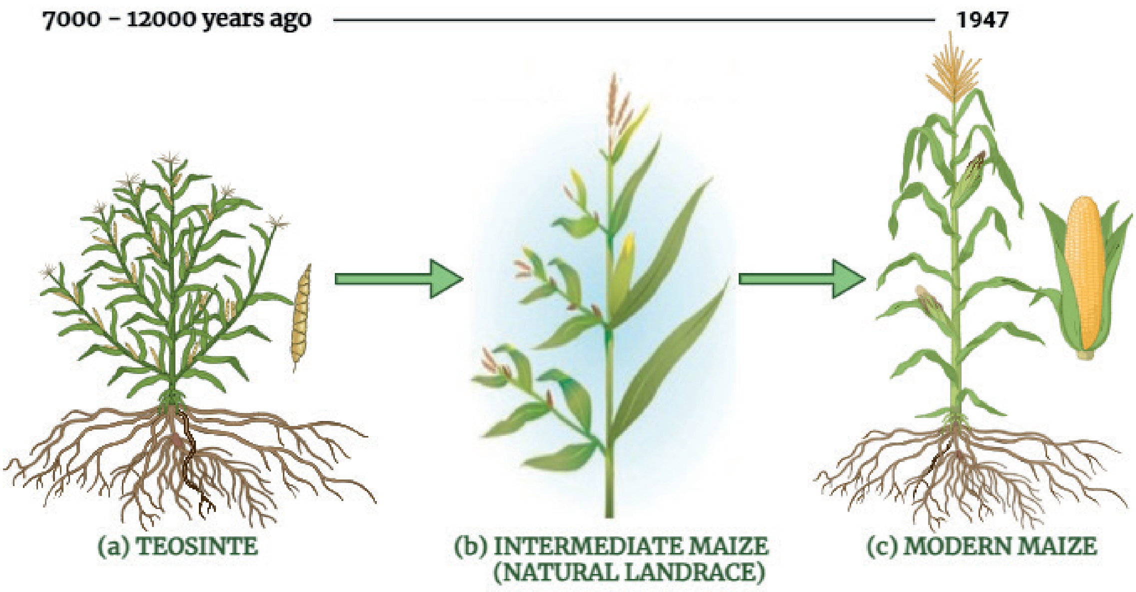

Fig. 1 - Illustration of domestication and evolutionary changes of maize from its wild ancestor teosinte.

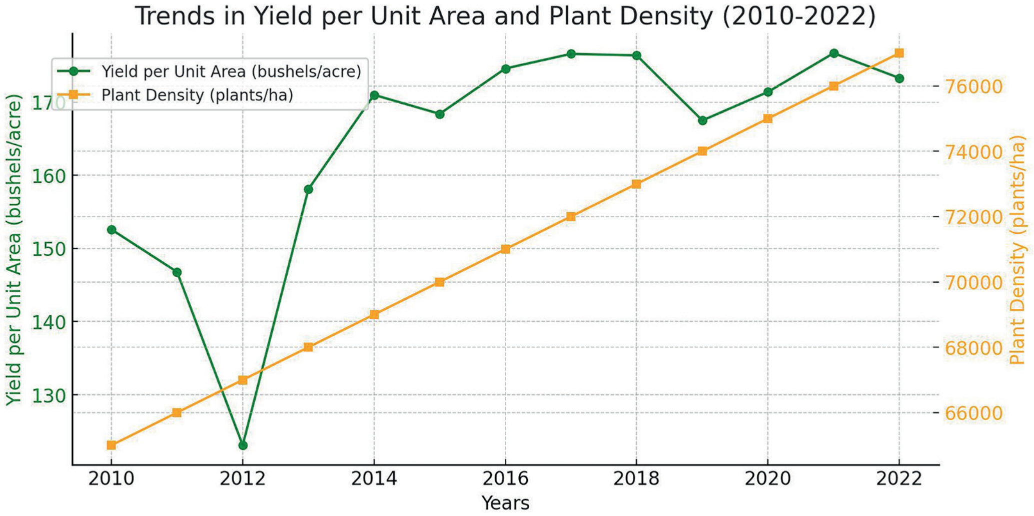

Fig. 2 - Crop yield response to plant density (i) The 2012 U.S. drought significantly reduced maize yields despite increasing planting rates; (ii)The significant drop in maize production in 2019 can be attributed to delayed plating in the U.S. Corn belt due to excessive rainfall and flooding; (iii) The yield drops in 2022 related to extreme drought condition (data from USDA-NAAS, 2022)

efficiency, (3) effective conversion of photosynthates to grain, (4) small tassel, (5) more than one ear (ear prolificacy), (6) shorter anthesis-silking interval, (7) insensitivity to photoperiod and (8) cold tolerance. In recent years, maize breeding for higher yields has required a combined approach with traits such as early maturity, high-density planting, resistance to biotic and abiotic stresses, and a high kernel ratio (Ci *et al.*, 2011). The plant characteristics that influences the quality and quantity of maize yield include plant height, days to 50% anthe-

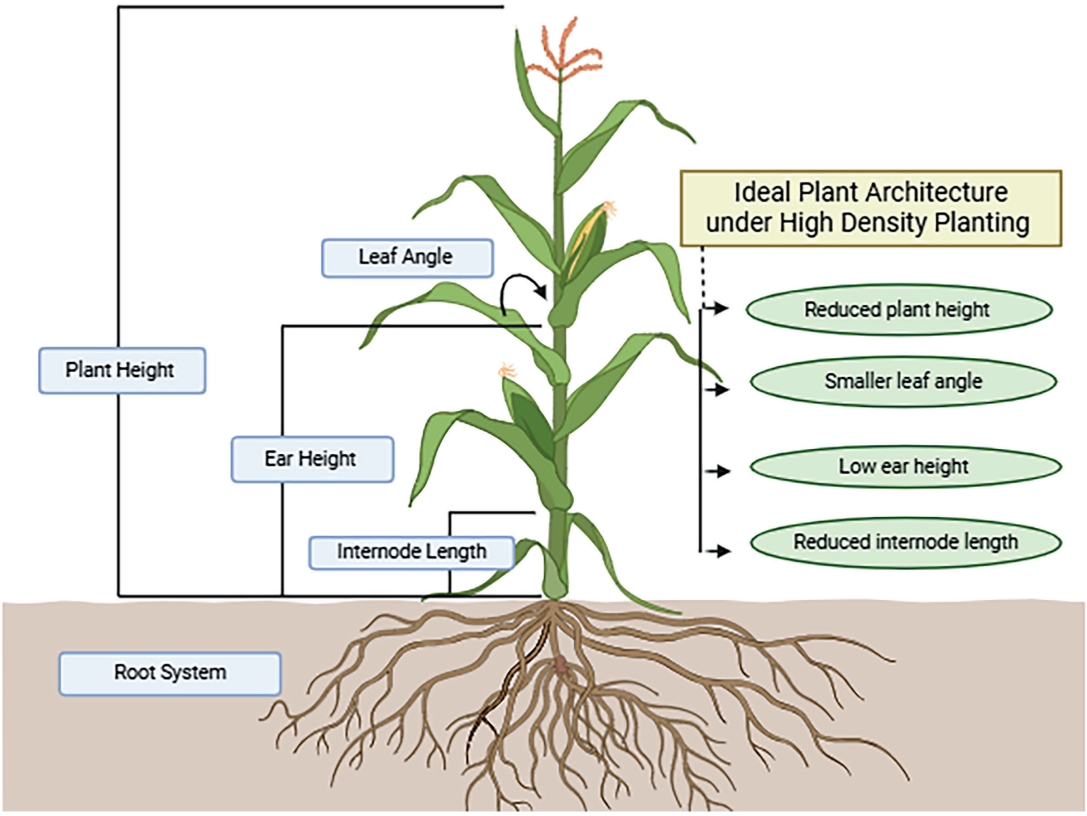

Fig. 3 - Key plant architecture traits of maize for enhancing productivity under high density planting (HDP).

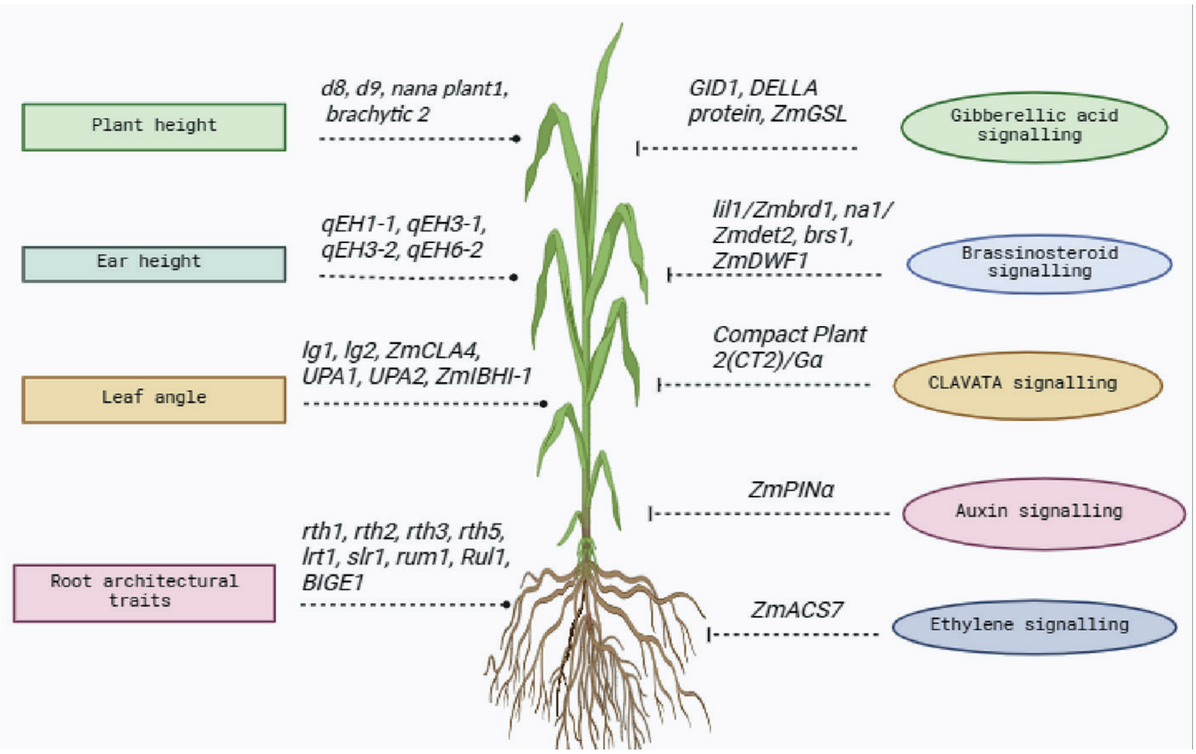

Fig. 4 - Genes/QTLs governing plant architecture traits and their biochemical signaling pathways

sis, days to 50% silking, leaf angle, leaf attitude, tassel anthocyanin color, stem brace root color, glume color excluding base, anther color, spikelet density, tassel angle, tassel attitude, silk color, cob length, cob diameter, ear shape, grain color, type of grain, number of kernel rows, kernel row arrangement, and 100 kernel weights (Selvi *et al.*, 2013). Among these characteristics, a few are modified in certain ways to obtain an ideal plant architecture, which can be grown under high-density planting to achieve higher plant yields. Restructuring plant architecture is crucial for increasing yield per unit area by developing maize hybrids that adapt to relatively high plant densities (Figure 2). Understanding the regulatory mechanism of trait expression, genes and their action, and metabolic and biochemical pathways is essential for the modification of plant architecture traits or breeding for ideal plant architecture.

A compact plant architecture allows better and deeper penetration of light among plants towards the lowest canopy layers (Incognito *et al.*, 2020). The key plant architecture traits are plant height, ear height, leaf angle, and internode length (Zhao *et al.*, 2022). High-density planting is key to achieving yield breakthroughs in maize by developing ideal compact plants with shorter plant heights, narrow leaf angles, shorter ear heights, reduced internode lengths, and strong root systems (Figure 3). The introgression of genes in rice and wheat, which are responsible for reduced plant height, led to a green revolution. Similarly, in maize reduced plant height is desirable measure for the development of an ideal plant architecture. The leaf angle is an important factor in the architecture of plants. A greater number of plants with upright leaf orientation can grow under high-density planting resulting in increased kernel yield per unit area. The leaf angle is determined by the presence of a ligule and auricle at the junction of the sheath and blade. Brassinosteroids play predominant role in regulating lead angle through affecting cell elongation, cell division or auricle size in the ligular region. The auricle allows the blade to tilt back and capture more sunlight for photosynthesis. Reduced shade avoidance and increased photosynthesis efficiency are associated with the leaf angle (Ku *et al.*, 2011). Therefore, the selection of plants with small leaf angles is desirable in maize breeding for compact plant architecture. Ear position is another important trait considered for plant architecture. If the ear position is too high, the ear weight may bend the stalk or even break it whereas, a too low position ear is not ideal for harvesting (Wei *et al.*, 2018). Therefore, the optimum ear height is critical for improving population density and photosynthetically active radiation (X. Li *et al.*, 2016). In addition to other plant architecture traits internode length contributes to determining canopy structure, photosynthetic efficiency and lodging resistance. The desirable plant should have a smaller leaf angle above the primary ear

(LAE) and longer internode length above the primary ear (ILE), as the photosynthate used for grain filling mainly comes from leaves above the primary ear. Therefore, great photosynthetic potential is anticipated under dense planting conditions.

Phytohormones: Role and regulation of plant architecture traits

The regulation of plant architecture traits involves complex biochemical and metabolic processes. Plant architecture traits, mainly plant height and leaf angle are regulated primarily by phytohormones. In maize, an ideal plant architecture is intricately linked to specific biochemical processes and molecular mechanisms. Phytohormones such as gibberellins, auxins, cytokinin, and brassinosteroids influence plant growth (Figure 4). The application of PGR is considered an effective measure for improving plant architecture

Role of Gibberellin and its interaction with genetic regulators in plant growth

Gibberellic acid plays an important role in the plant life cycle ranging from germination to plant growth and development. Some studies have demonstrated that the exogenous application of gibberellic acid influences plant traits such as fruit setting in sweet cherries (Chen *et al.* , 2022), and citrus (Mesejo *et al.*, 2016), and increased yield in pepper (Tiwari *et al.*, 2012), reproductive development and stress response in fruits (Rachappanavar *et al.*, 2022). Likewise, plant architecture traits particularly plant height provide breeders with an alternative breeding strategy to enhance grain yield per unit area by growing more plants per unit area through high-density planting (HDP).

In maize, GA biosynthesis and signaling significantly influence plant height. The pathway involves the conversion of precursor molecules to bioactive GAs, promoting stem elongation and internode elongation. GA receptors, such as GID1 (GA-INSENSITIVE DWARF1), perceive bioactive GAs, initiating signaling cascades. This triggers the degradation of DELLA proteins, a key repressor of GA responses. The degradation of DELLA proteins unleashes the activity of transcription factors like PIFs (PHYTOCHROME INTERACTING FACTORS), promoting the expression of genes involved in cell elongation. Gibberellic acid also regulates root development. DELLA proteins are negative regulators of gibberellic acid biosynthesis (Takehara and Ueguchi-Tanaka, 2018) as these proteins release transcription factors that directly activate downstream genes and indirectly regulate GA biosynthesis genes (Xue *et al.* ,2022). 'DELLA' protein name defines the five conserved amino acid sequences (aspartic acid, glutamic acid, leucine, leucine, and alanine) present at the N-terminal region of protein (Phokas and Coates, 2021) which interact with gibberellic acid receptor GID1 (Gibberellin-insen-

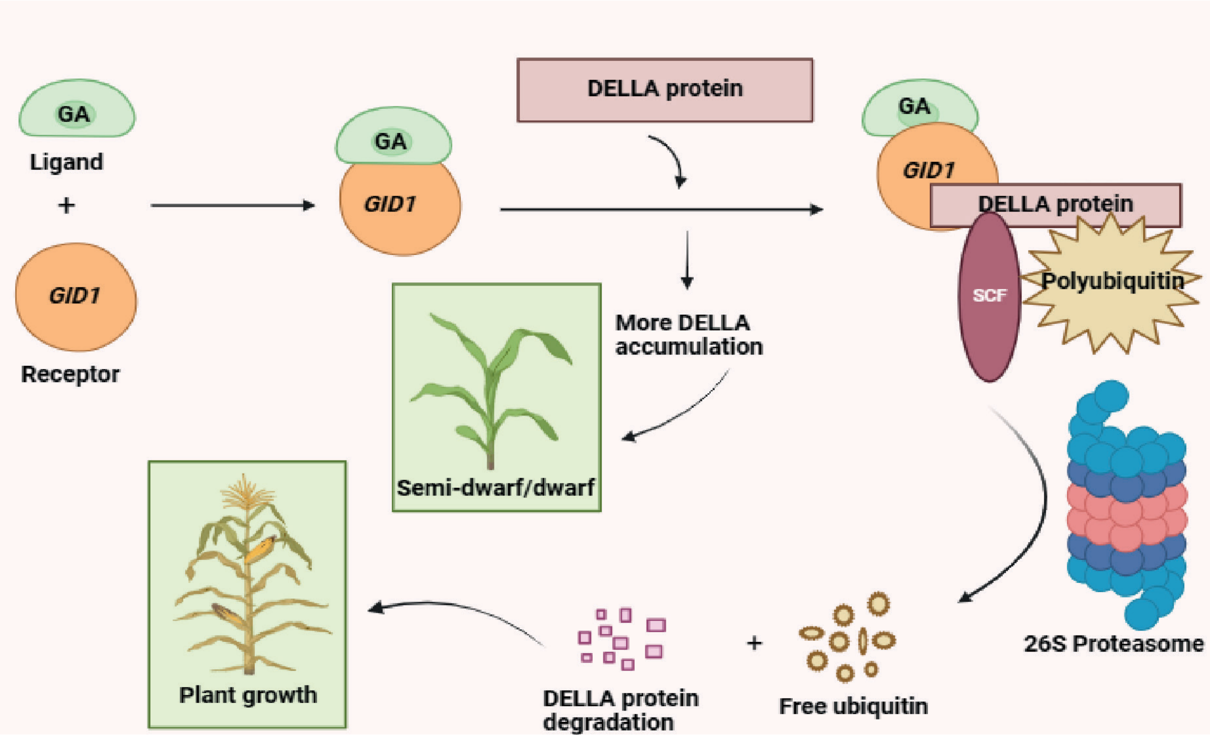

Fig. 5 - Plant growth in response to gibberellin signaling pathway

sitive dwarf1) and forms GID1-DELLA protein complex which de-repress the gibberellin signaling pathways (Figure 5) followed by polyubiquitylation of DELLA proteins by $SCF^{GID2/SLY}$ complex (Griffiths *et al.*, 2006). Maize contains two genetic loci *dwarf plant 8* (*d8*) and *dwarf plant 9* (*d9*) encoding DELLA protein (Lawit *et al.*, 2010), and these genes were reported to be similar to the *Reduced height* (*Rht1d*) gene from wheat (Peng *et al.*, 1999) which have been responsible for increase in food grain production of the 'Green revolution'. Another gene *ZmGSL* in maize which belongs to the *GAST-like* (*Gibberellic Acid Stimulated Transcript -like*) gene family plays a role in GA3-regulated lateral root development (Zimmermann *et al.*, 2010). Transcription factors are crucial in the expression of genes for growth and development. Recent studies highlight the involvement of WRKY TFs in Arabidopsis '*AtWRKY13*' (R. Li *et al.*, 2015) in the regulation of seed size and semi-dwarf phenotype), in rice '*OsWRKY36*' in the regulation of seed size and semi-dwarf phenotype (Lan *et al.*, 2020). Most of the '*wrky*' genes reported in maize are associated with abiotic stress while few researches have been conducted on their role in regulation of plant height. In maize, WRKY92 TF was found to interact with the promoter of ZmGA20ox7 and ZmGID1L2 to bring expression associated with GA synthesis which significantly affects plant height in maize (Fang *et al.*, 2024). Deciphering the genetic and molecular mechanism of GA in maize may offer new strategies for the genetic improvement of maize to high-density planting.

Influence of CLAVATA signaling on plant architecture

Plant shoot architecture is primarily determined by meristem whose function is associated with organ initiation. CLAVATA/WUSHEL feedback regulation pathway plays an important role in controlling PH/EH in maize, meristematic cell maintenance in root and shoot and is also involved in biotic and abiotic stress responses in plants (Basu and Parida, 2023). CLAVATA3 (CLV3) a secretive peptide, cell surface leucine-rich repeat (LRR) receptors, such as the CLV1 receptor kinase 3 and the LRR receptor-like protein CLV2 is involved in CLAVATA signaling. In maize, THICK TASSEL DWARF 1 (TD1) mutant encodes a protein homologous to the Arabidopsis leucine-rich repeat receptor-like kinase CLV1, which regulates maize inflorescence enlargement and reduced plant height (Bommert *et al.*, 2005). Another mutant, COMPACT PLANT2 (CT2) encodes predicted α-subunit of heteromeric GTP binding protein which helps in CLAVATA signal transmission, affecting apical meristem development and reducing plant height (Bommert *et al.*, 2013).

Auxin significantly regulates plant architecture

Auxin concentration in plant parts also determines root morphology and development (Overvoorde *et al.*, 2010) as well as cellular differentiation during embryogenesis and endosperm development (Forestan *et al.*, 2010). In the past years, investigations into the polar

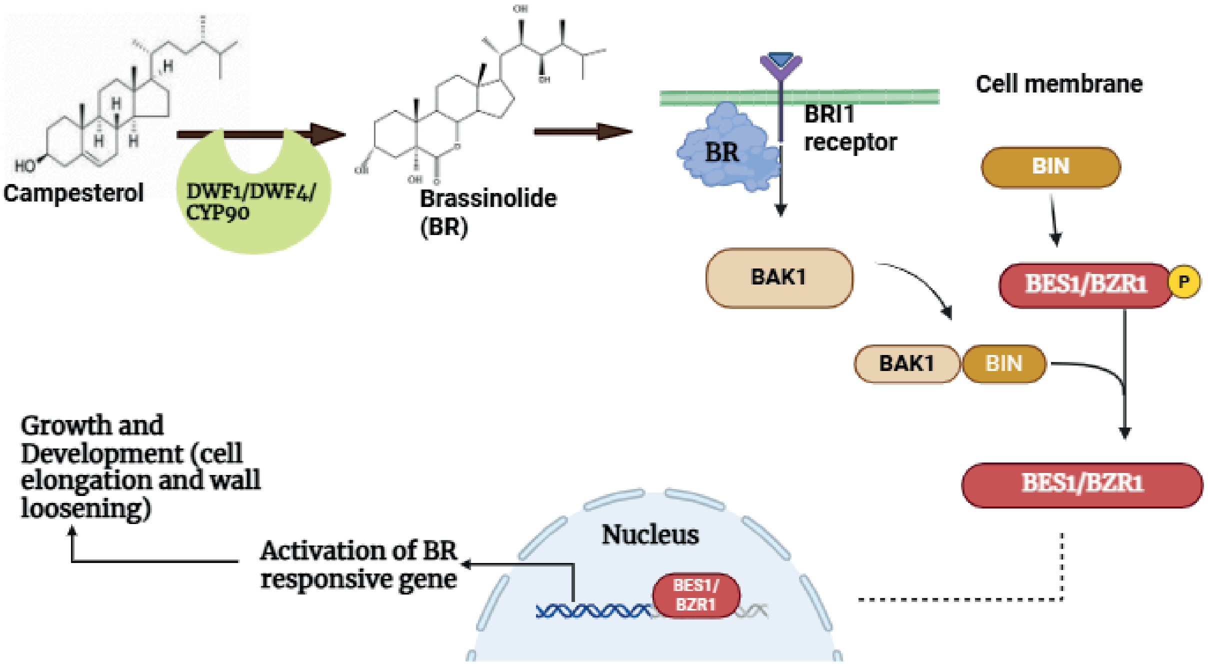

Fig. 6 - Brassinosteroid signaling pathways

Table 2 - Domesticated genes/loci associated with morphological traits evolved from teosinte

Traits	Genes/QTLs	Functions	Reference
Plant height	*brachytic2*	Height reduction due to loss of P-glycoprotein that regulates auxin transport	(Multani *et al.*, 2003)
	ZmDWF1	Involved in brassinosteroids synthesis	(Tao *et al.*, 2004)
	dwarf 8 and dwarf 9	Encoding DELLA proteins and found to produce dwarfing phenotype	(Lawit *et al.*, 2010)
	nana plant1	Dwarf mutant accumulates (24R)-24-methylcholest-4en-3-one which negatively affect downstream brassinosteroids metabolites	(Hartwig *et al.*, 2011)
	ZmGA3ox2	Encodes GA3 β-hydroxylase which is associated with plant height	(Teng *et al.*, 2013)
	qPH10	Regulates plant height	(Zhou *et al.*, 2016)
Ear height	*qEH1-1, qEH3-1, qEH3-2, qEH6-2*	Encodes urea transmembrane transporter for efficient use of nitrogen by plants	(X. Li *et al.*, 2016)
Leaf angle	*lg1 (liguleless1)*	Encodes nuclear-localized protein SBP (SQUAMOSA PROMOTER BINDING PROTEIN) which regulates ligule and auricle induction during leaf organogenesis	(Moreno *et al.*, 1997)
	lg2 (liguleless2)	Encodes a basic leucine zipper protein required for initiating leaf blade-sheath boundary	(Walsh *et al.*, 1998)
	ZmTAC1	Significant expression in leaf blade, leaf sheath, leaf pulvinus thus regulating leaf angle	(Ku *et al.*, 2011)
	ZmCLA4	Homolog to LAZY1 in rice and Arabidopsis which negatively regulate polar auxin transport (PAT)	(Zhang *et al.*, 2014)
	ZmIBHI-1	Leaf angle is regulated by differential cell wall lignification and cell elongation in ligular region	(Cao *et al.*, 2020)
	UPA1 and UPA2	Conferring upright plant architecture	(Tian *et al.*, 2019)
	SDG128 and ZmGID2	SDG128 interacts with F-box protein ZmGID2. Knockdown of both proteins resulted in larger leaf inclination	(S. Wang *et al.*, 2021)
Leaf associated traits (Leaf length, Leaf width, Leaf area)	*Warty1*	Affects maize leaf expansion and division without altering leaf shapes	(Reynolds *et al.*, 1998)
	ZmPIN1b	Expression pattern associated with the differentiating vascular tissues	(Carraro *et al.*, 2006)
	yabby9	Transcriptional regulator on adaxial side of incipient and developing leaf primordia during maize leaf development	(Juarez *et al.*, 2004)
	KNOTTED-1 (KN1)	High expression of KN1 lack apical dominance and are extremely dwarf in height and leaf size	(Sinha *et al.*, 1993)

Table 2 - Domesticated genes/loci associated with morphological traits evolved from teosinte

Traits	Genes/QTLs	Functions	Reference
Root architecrural traits (Root length, Root surface area, Root volume, Root number, Root angle	*rth1*	Root hair mutant encode a sec3 homolog associated with exocytotic process in plant development and affect root hair elongation	(Wen *et al.*, 2005)
	rth2	Abnormal root hair morphologies	(Wen and Schnable, 1994)
	rth3	Encodes a COBRA-like protein that are involved in various types of cell expansion and cell wall biosynthesis	(Hochholdinger *et al.*, 2008)
	rth5	Encodes monocot-specific NADPH oxidase and mutant displays defect in root hair initiation and elongation	(Nestler *et al.*, 2014)
	rth6	Encodes CSLD5 a cellulose synthase and regulates transition from bulge formation to tip growth	(L. Li *et al.*, 2016)
	lrt1	*Mutant deficient in initiation of lateral roots at primary and seminal lateral roots*	(Hochholdinger and Feix, 1998)
	slr1	Lateral root specific cell elongation	(Hochholdinger *et al.*, 2001)
	rum1	*Encodes monocot-specific Aux/IAA protein required for initiation of embryonic seminal and post-embryonic lateral root initiation in primary roots*	(von Behrens *et al.*, 2011) *(Woll et al., 2005)*
	Rtcl	Encodes LOB domain protein that regulates post-embryonic shoot borne root initiation	(Taramino *et al.*, 2007)
	Rul1	Exhibit 95% similarity with rum1 and a key regulator of lateral and seminal root formation	(Zhang *et al.*, 2016)
	Lrp1	Encodes a transcriptional activator that is regulated by RUM1	(Zhang *et al.*, 2015)
	BIGE1	Causes accelerated leaf and root initiation and enlargement of embryo scutellum	(Suzuki *et al.*, 2015)

auxin transport mutant of Arabidopsis have revealed the significance of local auxin concentration and polar auxin transport in influencing root morphology and development (Habets and Offringa, 2014). An ideal plant architecture for improved yield under high-density planting (HDP) should have a modified phenotype, a well-developed root system, and reduced plant height which helps plants to stand against lodging and drought resistance. (Li *et al.*, 2018) proved experimentally that the overexpression of *ZmPIN1a* in maize has improved auxin (IAA) transportation from shoot to root, as a result number of lateral roots increased and simultaneously reduced in plant height, ear height, and internode length. Increased auxin transportation to roots enables plants to accumulate more carbohydrates in roots and provides resistance to environmental stresses and enhanced root growth.

Role of Ethylene in determining plant architecture

Ethylene is a gaseous plant hormone that plays a crucial role in various aspects of plant growth and development including seed germination, fruit ripening, leaf and flower senescence, root development, abiotic/biotic stress responses (Mattoo and Suttle, 1991). Ethylene biosynthesis begins with amino acid methionine serves as a precursor and converts to SAM (S-Adenosyl-L-Methionine) an intermediate that subsequently converts into ACC (1-aminocyclopropane-1-carboxylic acid) and finally ACC into ethylene through the action of enzyme ACC oxidase (ACO; (Yang and Hoffman, 1984). ZmACS7 gene encodes 1-aminocyclopropane-1-carboxylic acid (ACC) synthase 7 in maize mutant *Semidwarf 3 (Sdw3)* which exhibits shorter plant height and wider leaf angle. Candidate gene ZmACS7 spontaneously mutated by transposon insertion which alters the C-terminus of ZmACS7 as a result ACC and ethylene content dramatically increased in Sdw3 mutant, leading to reduced plant height and large leaf angle. In addition, ZmACS7 also controls root development, flowering time, and leaf number in maize (H. Li *et al.*, 2020). PGR Ethephon and diethyl aminoethyl hexanoate (EDAH) improve maize density tolerance by reducing plant height, and ear height, increasing the number of vascular bundles, and enhancing structural compound in basal internode when mixed with 27% ethephon and 3% DH (Zhang *et al.*, 2017). In China, 2011 patented PGR named N, N-diethyl-2-hexanoyl oxygen radical-ethyl anime phosphonic acid releases ethylene when absorbed by plants shapes canopy structure, and increases the leaf orientation value (LOV) of upper leaves, better interception of light in the middle canopy, enhanced yield and radiation use efficiency under high-density planting (Huang *et al.*, 2024). Orchestrating expression of genes affects ethylene biosynthesis may help maize adaptation to higher plant density.

Genes and QTL associated with plant architecture traits in Maize

The conventional breeding approach of crop improvement relies on phenotypic variability existing in the population. Breeding methods and practices use the variability either existing in the population or by creating through hybridization, for the development of varieties. Most of the economic traits are governed by several genes and have a huge influence on the environment on the phenotypic traits therefore it is necessary to opt for those practices that can minimize environmental effects or else QTL mapping of traits. QTL (quantitative trait loci) is defined as any genomic region associated with the quantitative traits. Mapping of QTL requires a highly dense genetic map that represents the location and the order of markers with genetic distance in terms of recombination frequency. Results obtained from QTL mapping analysis can be used in Marker-assisted selection (MAS) for the varietal development. The conventional method of QTL mapping utilizes biparental mapping populations such as the F2 population (Sibov *et al.*, 2003), Double haploids (DHs) (J. Ren *et al.*, 2020), Recombinant inbred lines (RILs) (Fei *et al.*, 2022), F2 derived F3 population (Chen, 2016), Advanced Backcross population (Trachsel *et al.*, 2016), Near Isogenic lines (Szalma *et al.*, 2007), and Immortalized F2 population (Tang *et al.*, 2010) for linkage map construction in which two genetically diverse inbred lines are crossed to produce genetically segregating progeny. Mapping populations developed from bi-parental crosses exhibit inadequate diversity and a shortage of recombination events. GWAS (Genome-Wide Association Studies) provides abundant diversity for QTL identification with high-resolution mapping (Weng *et al.*, 2011). However, some limitations reduce the statistical power of GWAS (Xiao *et al.*, 2017). Several advanced populations have been introduced to GWAS such as the MAGIC (Multi-parent advanced generation inter-cross) population (Dell'Acqua *et al.*, 2015), and NAM (Nested Association Mapping) (Fei *et al.*, 2022). In this section of the review, we highlighted different plant and root architectural traits in maize and their QTL information. Combined GWAS, linkage mapping, and transcriptome studies found the QTLs associated with plant architecture-related traits such as plant height, ear height, and leaf number (Lu *et al.*, 2024). Several genes have been identified such as *Anther ear 1 (An1), An2, dwarf1, D3, D5, D8, D9, br2, Brevis plant 1 (BV1), Brachytic2, ZmPIN1α* which assist in synthesis and transport of gibberellic acid and auxins that regulates plant height (Avila *et al.*, 2016; Y. Chen *et al.*, 2014; Gallavotti *et al.*, 2008; Harris *et al.*, 2005; Hedden and Phinney, 1979; Lawit *et al.*, 2010; Multani *et al.*, 2003) and most of the genes for leaf angle in maize are associated with brassinosteroids (BRs), e.g. *BRD1 (brassinosteroid C-6 oxidase1) and BRI1 (brassinosteroid in-sensitive 1)* (Wang *et al.*, 2022). Genes *lg1* (*liguleless1*) and *lg2* (*liguleless2*) are important for the orientation of leaf in maize (Moreno *et al.*, 1997; Walsh *et al.*, 1998). In the absence of *lg1* leaf orientation is upright. An erect leaf trait can contribute to maize grain yield by enhancing photosynthetic efficiency and allowing for increased planting density. For instance, the mutant *Lgn-R* displays narrower and shorter leaves with defective ligules and auricles (Moon *et al.*, 2013). A small kernel mutant *ZmSMK9* encodes PPR protein involved in RNA splicing in intron1 and intron4 of mitochondrial NADH dehydrogenase5 which delays embryo and endosperm development and develops into the plant with upright leaf architecture (Pan *et al.*, 2019). In a recent study (Li *et al.*, 2024) *ZmNTL2*, a semi-dominant allele effectively reduces multiple organs in maize, particularly alteration in leaf size, stem diameter, internode length, ear size, and root size. Many genes related to the phytohormone brassinosteroids (BRs) have been found to regulate leaf angle in maize (Cao *et al.*, 2022; Ku *et al.*, 2011; Z. Ren *et al.*, 2020; Zhang *et al.*, 2014) Examples of these genes are BRD1 (*brassinosteroid C-6 oxidase1*) and BRI1 (*brassinosteroid insensitive 1*). To increase the leaf angle by enlarging the auricle and reducing the number of sclerenchyma cells on the adaxial side, BRD1, which encodes brassinosteroid C-6 oxidase1, was overexpressed. Similarly, BRI1, which encodes a Leu-rich repeat receptor kinase that is responsible for BR binding to start BR signal transduction (Figure 6), was knocked out, leading to upright leaves with decreased auricle formation (Makarevitch *et al.*, 2012). Breeding of maize varieties with ideal architecture is an important strategy for the further improvement of grain yield. Here, some information regarding different traits in maize their gene effects, and the number, and strength of QTLs is mentioned in the following table character-wise (Table 2)

Genetic diversity for Maize Plant Architecture traits

Genetic diversity is a pre-requisite requirement for initiation of any plant breeding program. It is mainly concerned with the total amount of genetic variation present in the population that is utilized for the development of superior genotypes which add to its commercial value. One of the prime objectives of plant breeding is to reduce the gap between demand and supply by increasing production. Yield is governed by many genes therefore for the improvement of single quantitative traits breeders must target major yield-contributing traits. Maize exhibits extensive genetic variability, crucial for its adaptability and resilience. This variability is evident in diverse traits such as yield, resistance to pests and diseases, and tolerance to environmental stresses like drought or extreme temperature. The genetic variability in maize extends to plant architecture traits, influencing factors like plant height, leaf structure, leaf angle, and internode length as well as root architecture traits such as root length, root number, root surface area, root angle, and root width (Guo *et al.*, 2022). This variability allows breeders to select and develop varieties with desired characteristics such as improved yield, resistance to environmental stresses, and optimal adaptation to different growing conditions.

Table 3 - List of Plant architecture traits in Maize for which variability is reported in the literature

Traits	Gene action	References
Plant height	Additive gene action	(Nzuve et al., 2014)
Ear height	Additive gene action	(Nzuve et al., 2014), (Kharel et al., 2017)
	Non-additive gene action	(Raut et al., 2017)
Ear length	Additive gene action	(Sharma et al., 2014)
	Non-additive gene action	(Raut et al., 2017)
Leaf angle	Non-additive gene action	(Kharel et al., 2017)
Number of leaves	Additive gene action	(Ogunniyan and Olakojo, 2014), (Rathod et al., 2021)
	Non-additive gene action	(Sharma et al., 2014), (Kharel et al., 2017)
Leaf length	Additive gene action	(Rathod et al., 2021)
	Non-additive gene action	(Magar et al., 2021)
Leaf width	Additive gene action	(Rathod et al., 2021)
	Non-additive gene action	(Magar et al., 2021)
Leaf area	Additive gene action	(Ogunniyan and Olakojo, 2014)
Grain yield per plant	Additive gene action	(Magar et al., 2021)
	Non-additive gene action	(Nzuve et al., 2014)

Maize genome sequencing and Marker developed

The maize genome was fully sequenced in 2009. In September 2002, the National Science Foundation (NSF) announced the launch of the Maize Genome Sequencing Project (Chandler and Brendel, 2002). It consists of approximately 2.3 billion base pairs distributed across ten chromosomes and over 32,000 genes (Schnable *et al.*, 2009). Key features of the maize genome include a high level of repetitive DNA (Haberer *et al.*, 2005), which comprises about 85% of the genome (Schnable *et al.*, 2009) and these repetitive elements make assembly and annotation difficult. The B73 maize inbred line has been widely used as the maize reference genome which was published in 2009 by a consortium of researchers, marking a significant milestone in maize genomics. Since the initial release of the B73 reference genome, several efforts have been made to improve its quality and accuracy which includes refining the assembly, gene annotation, and identifying genome structural variation and other genomic features. Duplication and polyploidization, DNA transposition and retro transposition, recombination, and gene conversion, and single base mutation are the main mechanisms of maize genome evolution and diversity (Rafalski and Ananiev, 2009). The genome also harbors genes responsible for various traits like grain quality, resistance to biotic and abiotic stresses, adaptation to different environments, and most importantly grain yield.

Several databases, such as MaizeGDB (Maize Genetics and Genomics Database), provide comprehensive information on the maize genome, including gene annotations, QTLs (Quantitative Trait Loci), genetic maps, and tools for data analysis. (Haberer *et al.*, 2005) analyzed 0.6% of the maize genome by randomly selecting 100 BACs to define gene content and repetitive sequences to characterize the structure and architecture of the maize genome. The results revealed that 66% of the maize genome consists of repetitive sequences and among the transposons DNA transposons are less frequent than retrotransposons. While in rice the contrary is true. Therefore, the larger size of retrotransposons in maize explains significant differences in the genomes of maize and rice. Maize genome sequencing provides a way to explore the genetic makeup and evolutionary history of this vital crop species in the context of modern plant genetics and breeding.

The discovery of molecular markers has revolutionized agricultural crop production by aiding breeding for desirable traits and understanding genetic diversity and evolutionary relationships. Common types of molecular markers in maize including RFLP, RAPD, AFLP, SSR, and InDels have been successfully utilized to accelerate breeding programs and enhance maize productivity and resilience. Molecular markers are abundantly distributed throughout the genome with high polymorphism. Advancements in sequencing technology have made it easy to scan the whole genome and identify variations for single nucleotide (Single Nucleotide Polymorphism; SNP) which is the most abundant source of genetic variation in the genome (Rafalski, 2002). The discovery of new markers in maize depends on the advances in genomic technology and understanding the genetic basis of agriculturally important traits. Two CAPS (Cleaved Amplified Polymorphic Sequence) markers dhnC397 and rspC1090 reflected a strong association with drought resistance in maize (S. Liu *et al.*, 2015). In recent times, KASP (Kompetitive allele-specific PCR) SNP genotyping has become a cost-effective, simple gel-free fluorescent PCR assay and widely used in maize studies on QTL mapping, fine gene mapping, Marker-assisted selection, Marker-assisted backcrossing, and genetic diversity (Semagn *et al.*, 2014). For instance, 71,311 KASP SNP markers were identified by combining RNA sequencing data and bioinformatics methods and the accuracy ratio of KASP SNP markers was 92.00% which suggests that the developed markers are accurate and polymorphic (Chen *et al.*, 2021). Development of biofortified maize hybrid enriched with vitamin-E along with amino acid lysine, tryptophan, and ProA by stacking favorable alleles using marker-assisted backcross breeding where 81-103 SSR markers were used for 95.45%recovery of desired parent genome (Das *et al.*, 2021). Similarly, to increase beta-carotene concentration in maize through MABC one gene-specific primer (crtRB13'TE) for foreground selection and 214 SSR markers for background selection were used and hybrids with 7.3 folds increase in beta-carotene were obtained (Natesan *et al.*, 2020). The marker's role in crop development is pivotal, offering precise tools for selection, breeding, and genetic improvement, ultimately enhancing crop productivity, resilience, and quality.

Advanced breeding strategies for enhancing crop performance

Breeding strategies have transformed with a focus on developing productive genotypes expressing high heterosis that exhibit increased resilience and productivity. Marker-assisted selection and genomics tools play pivotal roles in identifying and incorporating desirable traits, contributing to the creation of maize varieties that meet the demands of a changing agricultural landscape. In recent years, genomic studies have accelerated our understanding of maize genetics, unlocking opportunities for targeted improvement in traits such as yield, resistance to pests and diseases, and adaptation

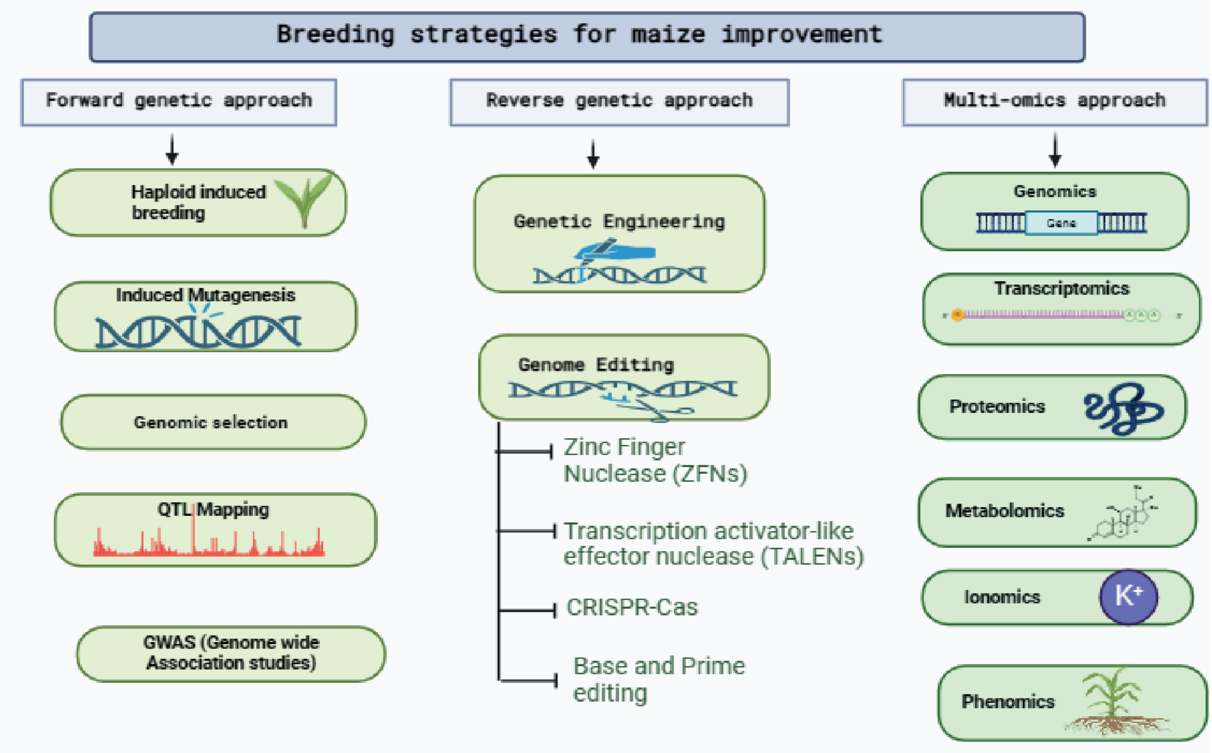

Fig. 7 - Different breeding strategies for maize crop improvement including forward genetics, reverse genetics, and multi-omics approaches

to environmental stresses (Figure 7). The utilization of advanced technology like CRISPR-Cas9 has initiated a new area of precision breeding, allowing researchers to make specific modification to the maize genome with unprecedented accuracy.

Haploidization

Haploidization in maize is a specialized breeding technique that involves the production of haploid plants containing a single set of chromosomes. The process is valuable in maize breeding programs for creating double haploid lines, which are genetically pure and homozygous. Haploidization expedites the development of stable inbred lines, enhancing the efficiency of maize breeding. Several methods are employed for haploidization in maize, with one of the most common being the generation of haploids through the induction of spontaneous chromosome doubling. This involves the creation of haploid embryos through wide crosses or tissue culture techniques. Chemical treatments such as colchicine, are often utilized to induce chromosome doubling, resulting in the formation of homozygous double haploid lines. Advanced molecular techniques, including anther culture and microspore culture, have also been developed for efficient haploidization.

Double haploid lines obtained through this process are genetically stable, allowing for the rapid development of true-breeding varieties. Haploidization accelerates the fixation of desirable traits and simplifies the breeding process by eliminating the need for multiple generations of self-pollination. This efficiency is crucial for the development of new maize varieties with improved traits such as yield, disease resistance, and stress tolerance. While haploidization in maize breeding is a powerful tool, challenges exist (Comai and Tan, 2019). The efficiency of Haploidization methods can vary, and the regeneration of plants from haploid embryos may encounter obstacles. Advancements in molecular biology and genomics may provide new insight into the manipulation of specific genes related to Haploidization, further enhancing the precision and success of maize breeding programs. Two methods in-vivo and in-vitro used for haploid production however, the in-vitro method of haploid production is not reliable for large-scale DH line production therefore not currently being used (Liu *et al.*, 2016). In contrast, the in-vivo method has paved the way for the production of a large number of DH lines in the maize breeding program. 'Haploid inducers' are lines that increase the frequency of haploid production compared to normal ones. Haploid inducers are paternal or maternal inducers based on the desired genetic constitution of haploids. Paternal inducers are the female lines that induce haploid production of the corresponding male parent in progeny. Mutation in *igl* (*indeterminate gametophyte*) of paternal haploids (Evans, 2007) but it has not been used commercially due to low (1-2%) success rate (Kermicle, 1994). The maternal inducer is used as the male parent and the resulting haploid holds the genetic constitution of the female parent. The first inducer, "Stock 6" maternal haploid inducer, which had the highest haploid induction rate, and many inducer lines have been developed in the past two decades using Stock 6. CIMMYT and the University of Hohennein developed first-generation TAILs (Tropically Adapted Inducer Lines) having high haploid induction rate (HIR) and superior agronomic performance (Chaikam *et al.*, 2016). The most important and challenging step in DH line production is the identification of haploid lines. Anthocyanin-based phenotypic markers are mostly used for differentiating haploid and diploid seeds as anthocyanin production requires three genes (*Whp1, A1*, and *A2*), and homozygous recessive genotype for any of these genes do not synthesize anthocyanin (Coe and Sarkar, 1964). The traditional method of haploid production is based on an inbred called Stock 6 that induces haploid production when crossed as male (Coe Jr, 1959). In this process, the haploid inducer line is intra-crossed with a line of interest and uniparental progeny produced lack the genome of the haploid inducer line. Several QTLs studies have been reported which govern haploid induction such as *qhir2-qhir8* (C. Liu *et al.*, 2015), *qmhir1* and *qmhir2* having maternal genetic effect of haploid induction (Wu *et al.*, 2014) and *qhmf1-qhmf4* for haploid male fertility (Ren *et al.*, 2017). Haploid can also be obtained from the progeny of interspecific hybridization. Wheat haploids are produced by the wheat x maize system but maize chromosomes are soon eliminated to form wheat embryos (Laurie and Bennett, 1986). Maize is a popular pollen donor for the induction of haploids in other cereals like triticale, oats, and rye (Kapoor and Singh 2017; Marcińska *et al.*, 2018; Wędzony, 2003). A gene called Matrilineal (*MATL*) is expressed primarily in pollen (Gilles *et al.*, 2017) and mutation in this gene has resulted in the induction of haploids in crops like rice and wheat (Yao *et al.*, 2018). (Kelliher *et al.*, 2017) have established through gene editing and fine mapping that haploid induction in maize was triggered by 4bp insertion in the carboxy terminus of the *MATL* (*MATRILINEAL*) gene encoding pollen-specific phospholipase. An alternative method of haploid production (Ravi and Chan, 2010) was developed by crossing Arabidopsis lines which are structurally different for centromere histone H3 (CENH3) protein. CENH3, a variant of histone H3 critical factor for determining the position of the kinetochore on each chromosome and essential for the segregation of chromosomes. Haploid inducer-derived centromere with defective CENH3 would be eliminated, producing haploids (C. Wang *et al.*, 2019) and leaving only chromosomes from the line of interest. The major advantage associated with cenh3 approach is that the method can be used for creating either maternal or paternal haploids (N. Wang *et al.*, 2021).

Marker-assisted selection (MAS)

Marker-assisted selection is an indirect selection process of agriculturally important traits for crop improvement using morphological, biochemical, and DNA marker (Ashraf *et al.*, 2012). Indirect selection is based on marker association at high frequency with QTLs/genes of interest due to genetic linkage. Marker-assisted selection (MAS) in maize involves the use of molecular markers to identify and select plants with specific traits of interest. For example, maize rough dwarf disease resistance is improved by a combination of MAS and conventional breeding strategies where SSR markers are used for recovery of recurrent parent genome (background selection) and IDRQ2 and IDRQ20 marker interval (foreground selection) for selection of *qmrdd8* QTL having resistant to rough dwarf disease (Xu *et al.*, 2020). MAS has been a powerful tool for various traits such as resistance to head smut and enhancing yield-related traits by exploiting the *ZmWAK* gene at *qHSR1* (Zuo *et al.*, 2015), *ZmCCT* and *ZmAuxRP1* for stalk rot resistance (Wang *et al.*, 2017; Ye *et al.*, 2019), *Scmv1* and *Scmv2* for resistance against SCMV (Xing *et al.*, 2006). MAS with phenotypic selection is low-cost and highly efficient in enhancing breeding programs for disease resistance in maize.

Nutritional quality improvement is the most important aspect of maize breeding. To increase proA content in germplasm lines marker-assisted breeding was employed using an InDel marker specific to *CrtRB1* encodes for beta-carotene hydroxylase (Duo *et al.*, 2021). Quality protein maize (QPM) that has enhanced levels of essential amino acids (lysine and tryptophan), more biological value (80%), and protein intake utilization (74%) than normal maize has revolutionized the nutritional value of maize (Mertz *et al.*, 1964). *The opaque2 (o2)* gene which is located on chromosome 7 has led to the development of QPM lines that are crossed in original combination to produce hybrids (Kaur *et al.*, 2020). Recessive o2 mutant does not fulfill the daily required intake of humans therefore, a novel recessive gene, *Opaque-16* (o16) located on chromosome 8 was found to enhance lysine by 30-40% and tryptophan by 50-60% along with *o2* gene (Sarika *et al.*, 2018). The nutritional value of the white maize hybrid is enhanced through MABC by introgression of recessive o2 and o16 genes in popular hybrids HM5 and HM12 at IARI, New Delhi (Chand *et al.*, 2022). Maize with enhanced levels of micronutrients especially Zn (Andersson *et al.*, 2017) have also been improved by MABC. Breeding efforts at CIMMYT and IITA to meet the target level of Zn-kernel 33ppm (Bouis *et al.*, 2011) as the founder line in pedigree-based breeding. Generally, marker-assisted selection in maize combines genetic information with traditional breeding methods, offering a more efficient and targeted approach to developing maize varieties with improved traits.

Genome editing

Genome editing enables site-specific modification of target sequence through genome engineering techniques such as Mega nuclease, Zinc finger nucleases (ZFN), Transcription activator-like effector nucleases (TALENs), Clustered regularly interspaced short palindromic repeats (CRISPR) Cas system, Base editing, and Prime editing. Genome editing in maize has been actively researched with CRISPR-Cas9. CRISPR-Cas system widely used genome editing technique of crop improvement for traits like yield-related traits, quality traits, disease resistance, haploid induction, male sterility, and plant architectural traits in maize due to its precise genome editing and less unintended cleavage at untargeted genomic sites (Table 4). It's a microbial adaptive immune system that uses RNA-guided nuclease to cleave foreign particles/attack. This technology is based on gene knockout which is carried out by two components of the CRISPR-Cas system *i.e. SgRNA* (Single guide RNA) and Cas9 nucleases. Guide RNA is designed complementary to the target sequence which is the DNA binding domain while Cas9 has nuclease activity which induces a double-strand break on the target site. Double strand break on the target site is repaired either through a non-homologous end joining (NHEJ) pathway or a Homologous directed repair (HDR) mechanism. In plants, the NHEJ pathway is majorly utilized for repairing HDR. (Zhang *et al.*, 2019) demonstrated the successful use of CRISPR-Cas9 in maize and introduced a modified tRNA-adaptor system to enhance the efficiency of genome editing. CRISPR-Cas-based reverse genetic approach utilized in various crops for determining the function of genes. For example, candidate gene *ZmGA20ox3* function is determined by a loss-of-function mutation in maize using CRISPR based system and results conclusively depict a decrease in inter-node length by reducing bioactive GAs content and also suggest upregulation of various transcription fac-

Table 4 - List of different genes and modified functions using genome editing technologies in maize

Genome editing tools	Target gene	Functions	Reference
Zinc finger nuclease (ZFN)	*IPK1*	Phytate reduction	(Shukla *et al.* 2009)
TALENs	*glossy2 (gl2)*	Glossy phenotype	(Char *et al.*, 2015)
CRISPR-Cas	*zb7*	Albino phenotype	(Feng *et al.*, 2018)
	ALS1 & ALS2	Herbicide resistance	(Svitashev *et al.*, 2015)
	ZmGA20ox3	Semi-dwarf phenotype	(Liu *et al.*, 2024)
	MATRILINEAL	Haploid induction	(Kelliher *et al.*, 2017)
	ZmPLA1	Haploid induction	(Liu *et al.*, 2017)
	ZmDMP	Haploid induction	(Zhong *et al.*, 2019)
	ZmPLD3	Haploid induction	(Li *et al.*, 2021)
	ZmLG1	Reduced leaf angle	(Baobao Wang *et al.*, 2019)
	ZmABCG26	Male sterility	(Jiang *et al.*, 2021)
	ZmPHD11	Male sterility	(Jiang *et al.*, 2021)
	ZmMS8	Male sterility	(Chen *et al.*, 2018)
	ZmTGA9-1/2/3	Male sterility	(Jiang *et al.*, 2021)
	ZmWAXY1	Waxy maize	(Gao *et al.*, 2020)
	ZmPHYC1	Early flowering	(Q. Li *et al.*, 2020)
	ZmPHYC2	Early flowering	(Q. Li *et al.*, 2020)
	Psy1	Seed color	(Zhu *et al.*, 2016)
	CLE	Yield improvement	(Liu *et al.*, 2021)
	ARG058	Yield improvement under drought stress	(Shi *et al.*, 2017)
	ZmEPSPS	Herbicide resistance	(Kaul *et al.*, 2024)
Base and prime editing	*ZmALS1*	Herbicide tolerance	(Y. Li *et al.*, 2020)
	ZmALS2		

tors involved in the biosynthesis of ABA and JA which provide tolerance against the water deficit stress (Liu *et al.*, 2024). Genome editing have been utilized in several plant species and large number of agronomic traits have been improved using CRISPR/Cas9 system.

Omics approaches to elucidating the genetic network governing maize plant architecture

Omics studies in maize involve analyzing various biological components on a large scale. Genomics explores the maize genome, transcriptomics studies gene expression, proteomics examines proteins, metabolomics looks at metabolites, and epigenomics investigates epigenetic modification. These approaches provide comprehensive insights into maize biology, aiding crop improvement, and understanding responses to environmental factors, and play a crucial role in understanding the molecular basis of plant architecture traits. Multiple genes typically govern complex properties in plants, and it has always been challenging to analyze complex traits genetically. By studying the genes, their expression patterns, and the corresponding proteins involved in traits like plant height, branching, and leaf morphology, researchers gain insights into the regulatory network shaping plant architecture.

Transcriptomics for Crop Improvement

It is commonly observed that when an individual plant of the same inbred line is grown in the same microenvironment, it can exhibit a distinct phenotype and this variation may account for the variation in mRNA and protein expression. With the advent of next-generation sequencing platforms, transcriptomics has become easy to construct gene expression profiles of plant species. Transcriptomics deals with transcriptome which includes mRNA, tRNA, rRNA, non-coding RNAs, snRNAs, snoRNAs, etc. The transcriptomic profile of an individual is initiated from total RNA isolation or mRNA (for gene expression) as primary material followed by synthesis of cDNA, library preparation, sequencing, and data analysis. Several QTLs governing different traits have also been identified by transcriptome in association with other breeding strategies. Combined GWAS and transcriptome analysis identified major genes involved in seed germination (Ma *et al.*, 2022), fusarium ear rot resistance, and seminal root length in maize (Guo *et al.*, 2020; Yao *et al.*, 2020). While only transcriptomic-based gene identification governs root branching in maize (Jansen *et al.*, 2013). One study was conducted (Cruz *et al.*, 2020) in which ear leaf transcriptome and ear leaf metabolome of individual plants of the same inbred line were used to predict gene function and to predict individual plant phenotype. Transcriptomics studies have played a significant role in detecting tissue-specific expression under different developmental stages, and physiological or pathological conditions. Under drought conditions, ABA-dependent and NAC-mediate stresses and protein folding acclimation are major organ-specific response networks in maize (Baomei Wang *et al.*, 2019). Differentially expressed genes (DEGs) were observed under different drought, salinity, heat, and cold stresses and functional annotation of these genes suggests the involvement of hormone metabolism and signaling, very long chain fatty acid biosynthesis and lipid signaling, transcription factors in response to abiotic stresses (Li *et al.*, 2017) which gives an understanding of the molecular mechanism of maize in response to stresses. Maize pollen is highly sensitive to heat and drought stresses therefore combined metabolomics and transcriptomics analysis show structural and physiological characteristics and identify mechanisms in the biosynthesis of UDP-glucose which reduces the activity of sucrose synthase SH-1that suppresses sucrose transfer to UDP-glucose resulting in exhaustion in pollen viability (Li *et al.*, 2022). Transcriptomic profiling of plants at the seedling stage under cold stress provides valuable insight into pathways such as carotenoids, lipid metabolism, transcription factor, peroxisome and amino acid metabolism, ABA transporter, MAPK signaling, and role of long non-coding RNAs (lncRNAs) in understanding the molecular mechanism underlying maize response to cold stress (Waititu *et al.*, 2021). Transcriptomics study provides an understanding of the plant-pathogen interaction and plant response to it. Maize stalk rot is caused by *Fusarium proliferatum* and the molecular mechanism responsible for providing resistance against disease and involvement of TF families including MYB, bHLH, NAC, and WRKY, and certain enzymes phenylalanine ammonia-lyase (PAL), peroxidase (POD), polyphenol oxidase (PPO) which catalyzes lignin biosynthesis, as lignin provides structural barrier in plant-pathogen interaction while other enzymes Chalcone synthase (CHS) and chalcone isomerase (CHI) form series of flavonoids which induces crystal structure formation and callose and tylose synthesis thereby reducing pathogen spread in growing parts by blocking down vascular tissues (Sun *et al.*, 2024). Transcriptomics has also been employed in the developmental dynamics of maize leaf (Li *et al.*, 2010), functional differences in floral development (Yang *et al.*, 2022), and gene co-expression networks between species (Chang *et al.*, 2019).

Metabolomics for crop improvement

Metabolomics has been developed into a powerful tool for evaluating phenotypic variance within broad genetic populations. In an attempt to connect the gap between genomes and end-phenotypes, the analysis of differences in metabolite abundance has also proved to be an efficient strategy (Obata *et al.*, 2015). Mass spectrometry (MS) and nuclear magnetic resonance (NMR) are two major approaches essentially used for metabolome analysis (Obata and Fernie, 2012). Metabolomics platforms are being exploited to understand complex biological pathways and explain hidden regulatory networks regulating plant growth and development. The performance of plants under different environmental conditions is highly influenced by the synthesis of a large number of metabolites. Among various functions of metabolomics include the interaction of plants with the environment, abiotic and biotic stress tolerance, biochemical or metabolic pathways and permit genotype-metabolic-phenotypic level of understanding (Razzaq *et al.*, 2019). Several studies have been on maize metabolic traits and a considerable number of QTLs have been identified (Yan *et al.*, 2011). QTL mapping in association with variation in the level of metabolites helps in comparing metabolic profiles in different tissues of plants for examining tissue-specific expression of genes. Metabolome in association with GWAS has been utilized to dissect the genetic basis of metabolic diversity in maize kernels and identified major candidate genes involved in metabolic traits (Wen *et al.*, 2014). Metabolomics studies have been utilized for studying plant evolutionary processes between rice and maize, and key metabolites contribute to maize and rice domestication (Deng *et al.*, 2020). Metabolic responses of maize under drought and salinity conditions were reported in some studies and suggest accumulation of amino acid, sugar, and certain metabolites which act as Osmo protectants to help maintain osmotic balance (Sun *et al.*, 2015). Under high salinity conditions, shoots were more metabolically affected than roots (Gavaghan *et al.*, 2011). Salinity stress study also suggests differential metabolic pathways and determines maize adaptation to salinity by the metabolism of an amino acid (alanine, aspartic acid, glutamic acid), purine, pyrimidine, synthesis of aminoacyl t-RNA and subsequent degradation of purine, pyrimidine, amino acid, and fatty acid (Yue *et al.*, 2020). Combined transcriptome and metabolome study shows the expression pattern of auxin-related genes at different stages of growth and biosynthetic pathways (Jiang *et al.*, 2022). The omics study on maize has provided a comprehensive understanding of complex molecular mechanisms governing various aspects of plant biology.

Conclusion and Perspectives

The future of genetic improvement in maize plant architecture lies in adopting multidisciplinary and technology-driven approach. As climate patterns continue to shift, the development of maize genotypes with adaptive and optimized plant architecture becomes increasingly critical for ensuring sustainable production. Identifying and characterizing genetic factors, such as QTLs and regulatory genes, that contribute to resilience and adaptability under diverse environmental conditions will be pivotal for future breeding efforts. Advances in functional genomics, including transcriptomics, proteomics, and metabolomics, will deepen our understanding of the molecular mechanisms and regulatory pathways that govern plant architecture traits. The integration of these insights with high-throughput phenotyping technologies and large-scale genomic datasets will enable precise and efficient selection of favorable traits. Combining genomic tools such as genome-wide association studies (GWAS) and marker-assisted selection with advanced bioinformatics will accelerate the identification of complex genetic interactions and streamline the breeding process. High-throughput phenotyping, in particular offers a powerful avenue for rapid and accurate trait measurement, complementing genomic data to validate genes associated with plant architecture. The integration of phenomics and genomics not only addresses current gaps but also enhances our capacity to reengineer plant traits for high-density planting systems.

By embracing a holistic framework that incorporates cutting-edge technologies, collaborative research efforts, and multiomics approaches, the breeding community can achieve transformative improvements in maize productivity. These efforts will not only contribute to higher yields and better resource-use efficiency but also address global challenges such as food security, climate resilience, and sustainable agriculture.

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