



REVIEW ARTICLE

Maize leaf angle dynamics: Genetic architecture, hormonal regulation and phenomics approach

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Abstract

Maize (*Zea mays* L.), a key staple crop, supports human consumption, animal nutrition and diverse industrial uses. High-density planting (HDP) is an important strategy to improve crop yield per unit land area. Leaf angle (LA) is a key factor in determining maize plant architecture, photosynthetic efficiency and suitability for HDP. An urgent need exists to elucidate the genetic basis of these complex, polygenic traits, such as LA, to address the remaining information gaps in optimising canopy architecture. This review offers comprehensive insights into the molecular basis of regulatory networks involved in LA morphogenesis. It revisits advances in mutant and quantitative genetics research, identifying quantitative trait locus (QTL) across all 10 chromosomes and candidate genes through diverse studies employing genome-wide association studies (GWAS), genotyping by sequencing and linkage analysis. Leaf angle regulation is mediated by phytohormones and their crosstalk, as well as agronomic and environmental factors. Future progress depends on integrating advanced phenomics tools, such as 3D LiDAR, UAV-based hyperspectral imaging and deep learning, with CRISPR/Cas9-assisted breeding to precisely tune LA without undesirable pleiotropy. A standardised, ideotype-driven framework targeting upper-erect and lower-horizontal leaves will enable the development of climate-resilient, high-yielding maize varieties optimised for dense canopies.

Keywords: canopy structure; leaf angle; phenomics; plant signalling molecules; quantitative trait loci; *Zea mays*

Introduction

Maize (*Zea mays* L.) is a principal cereal crop worldwide, serving as both a staple food and an industrial resource vital to food security and the agricultural economy. In 2023, it accounted for 13 % of global crop output (1.2 billion tonnes), with the top three producers contributing 59–68 % of total production. Its expansion continues to shape global cereal supply, utilisation, stocks percentage and trade; projections for 2025 estimate 3023 million tonnes of production, 2938 million tonnes of utilisation, a 10 % increase in stocks, 2.2 % demand growth and 235.6 million tonnes in coarse grain trade (1). Under high-density planting (HDP), maize hybrids with upright leaves display compact architecture, minimising shading, improving light-driven photosynthesis and ultimately achieving higher grain yields than genotypes with flat leaves (2). The ideal plant architecture features narrow, upright leaves above the primary ear and broader angles above and below the ear, forming a tower-like canopy (3, 4). Leaf angle (LA) is a major factor in determining the ideal plant type and is a quantitative trait controlled by multiple genes with a complex genetic basis in maize. Leaf angle, defined as the angle between the vertical stem and the midrib of the leaf blade, is therefore a major breeding target for improving maize productivity,

as it directly determines canopy architecture and light interception. Over recent decades, identifying the optimal LA has remained a central objective of maize breeding programs aimed at maximising grain yield. This review synthesises current knowledge on the genetic regulation of maize LA, with an emphasis on mutant analyses, quantitative genetic studies and phytohormone-mediated regulatory networks. Recent advances in high-throughput imaging and machine learning now enable precise 3D phenotyping of LA in field-grown maize, offering new opportunities to dissect genotype × environment interactions. Integrating these phenotyping platforms with environmental and genetic insights will be crucial for developing climate-resilient maize ideotypes that sustain productivity and strengthen global food security.

Genetic architecture of maize leaf angle

Studies conducted in maize to dissect the genetic basis of LA have identified several quantitative trait locus (QTL) and genomic regions associated with LA across all 10 maize chromosomes. Identifying causal genes behind LA QTL and isolating mutants with changed LAs are the key steps to understanding how maize LA dynamics is genetically controlled.

Classical regulators and early quantitative trait locus mapping

Early linkage analysis using nested association mapping (NAM) populations identified key regulators, such as *liguleless2* on chromosome 3, as important determinants of LA. Subsequent genome-wide association studies (GWAS) further identified multiple significant single nucleotide polymorphism (SNPs), loci and candidate genes associated with variation in LA and leaf orientation across diverse maize germplasm panels (5–7). Quantitative trait Loci were detected using a maize F2:3 population derived from compact vs expanded inbred lines, evaluated across multiple environments; the regions were reported as linkage-based QTLs controlling LA and leaf orientation. In addition, two major genomic regions governing these traits were reported: qLA1 and q leaf orientation value (LOV)1 are linked to the marker umc2z226 on chromosome 1.02 and qLA5 and qLOV5 are located near bnlg1287 on chromosome 5 (8). Moreover, *ZmIBH1-1* was identified by map-based cloning in a near-isogenic background, followed by transgenic and expression analysis to confirm its role in plant architecture and leaf-angle regulation. It encodes a basic helix-loop-helix transcription factor that negatively regulates LA by modulating cell wall lignification and cell elongation (9). These early linkage studies and gene cloning laid the foundation for understanding the developmental regulation of LA.

Advanced linkage mapping, meta-quantitative trait locus analysis and validation of leaf angle loci

Following early QTL discovery efforts, more refined mapping approaches have been undertaken to validate genomic regions and identify stable hotspots associated with LA. These studies strengthened the reliability of key loci and facilitated their use in marker-assisted selection and breeding programs. Subsequently, 5 LA QTLs were mapped (chromosomes 1, 2, 3, 7, 8) in F2:3 families. Meta-analysis identified 21 QTLs and 17 mQTLs, including the qLA1-1/qLA2 hotspot. Key candidates: *DWARF4* (mQTL1-1), *liguleless1* (mQTL2-1; pleiotropic with LOV), *TAC1* (mQTL2-2), *liguleless2* (mQTL3-3). Markers: *AtDWARF4* (chr1), *OsLAZY* (chr4) (10). In a four-way cross, four QTLs (qLA2-1, qLA4-1, qLA4-2, qLA5-1) were validated in near-isogenic lines (NILs) with enhanced additive effects (11).

Moreover, four major QTLs (qLA1, qLA3, qLA7 and qLA8 QTLs), collectively explained 40.91 % of phenotypic variation, with *ArCYCD3; 2* in qLA7 regulating angle via retinoblastoma phosphorylation. Haplotype-based genetic analyses also support the polygenic nature of LA (12). The hapLA4.04 haplotype percentage explains up to 29 % of phenotypic variation and has stable SNP markers useful for breeding (13). In parallel, heterosis-related QTL mapping revealed seven stable QTLs for leaf length, width and angle across multiple testcross populations, identifying several candidate genes, including *Zm00001d022618* (SKP1-like, auxin signalling) and *Zm00001d008625* (ALBINO3, chloroplast function), which show leaf-specific expression and contribute to heterotic LA variation (14).

Canopy-level and environment-stable quantitative trait locus regulation of leaf angle

Beyond single-leaf measurements, recent studies have emphasised that maize plants dynamically regulate LA across different nodal positions throughout development, adjusting canopy geometry to maximise radiation use efficiency. These investigations supporting canopy-level regulation, uncovered 12 QTLs associated with lower

canopy LA and identified key genes, including *lg1*, *lg2*, *PhyC1*, *ZmTAC1*, and rice *TLD1* orthologs. Doubled haploids enabled the separation of leaf-specific and canopy-wide genetic effects (15).

Similarly, qLA5.1 controls LA across all eight consecutive leaves, while qLA3.1 and qLA9.1 regulate the upper and lower canopies, respectively. In addition, qLA4.1 and qLA6.1 were associated with desirable leaf positions within the canopy (16). Expanding this framework, a study mapped 59 QTLs at four canopy positions, including both stable and dynamic loci that may have been indirectly selected during breeding for high-density hybrids (17). Likewise, 12 QTLs mapped in doubled haploid lines, with qLA-5-2 and qLA-7-1 repeatedly observed across environments (18). These findings clearly demonstrate that maize LA is spatially regulated across canopy layers.

Genome-wide association studies, nested association mapping populations and functional genomic validation of leaf angle regulation

Advances in high-resolution genomic tools, GWAS and NAM have enabled the precise dissection of the genetic architecture of LA in populations. These approaches have facilitated the identification of major loci, allelic diversity and stable genomic hotspots that govern canopy architecture. Using these high-resolution platforms, 96 SNPs were reported to explain LA variation, grouped into 43 QTLs, with a major hotspot in bin 10.04 containing multiple consistent loci (19). Similarly, characterisation of 18 QTLs, among which 9 QTLs were associated with LA and LOV candidate genes, including those involved in auxin homeostasis, sulphur transport and transcriptional regulation (20). An advanced backcross NAM population identified 41 LA QTLs across subpopulations and detected 10 multi-trait QTL hotspots distributed across 9 chromosomes (21). Key maize LA genes include *ZmDWF1* (22), *lg1* (23), *te1* (24) and *lg2* (25).

Building upon these associations and NAM analyses, subsequent studies focused on dissecting gene action, functional mechanisms and breeding relevance. Mapped additive and dominant QTLs influencing LA variation, including clustered regions with three (qLAa1, qLAa3 and qLAPH5) in bin 3.06 and qLAd2 in bin 2.02 (26). An S-adenosylmethionine-dependent methyltransferase gene controlling ear leaf and upper LAs by enhancing vascular development and mechanical strength (27). Recurrent selection analysis revealed that regions on chromosome 7 were strongly associated with flag LA in doubled haploid lines (28). Further, 42 lateral angle QTLs were mapped and candidate genes such as *LG1*, *ZmYAB14* and *ZmDWF4* controlling ligule formation, leaf architecture and brassinosteroid (BR) biosynthesis were identified (29). Under high-density conditions, *lg1/lg2* mutants were shown to disrupt azimuthal re-orientation toward interrow light. This occurs due to impaired phot1-mediated phototropism and altered auxin signalling, resulting in negative phototropism, reduced interrow leaf number and decreased capture of photosynthetically active radiation (PAR) (30).

Recent K-mer-based GWAS analysis further refined upper canopy regulation by identifying *MADS69* as a major regulator of LA within a prominent chromosome 3 QTL shared across NAM populations (31). Co-expression in the turquoise module linked *MADS69* to hormone pathways, with its expression negatively correlating with upright angles across shoots of NAM founders. Ubiquitin-driven overexpression in transgenics consistently reduced

leaf uprightness and accelerated flowering, affirming pleiotropic control of architecture. Favourable k-mers in *MADS69* introns, shaped by transposon haplotypes, underwent positive selection in modern maize, enhancing canopy efficiency for dense planting. Recently, transcriptomics identified a stable QTL, qLA2-3 and candidate genes, including *Zm00001d006834* (32). Functional validation through CRISPR/Cas9 knockout of sorghum *LG1* (first reported) via particle bombardment yields monoallelic upright-leaf mutants and biallelic T1 progeny lacking ligules, which exhibit sharply erect LAs (33). Analogous targeting of *ZmLG1* in maize can yield transgene-free erectophile mutants, facilitating the rapid deployment of optimised canopy architectures suited to high-density cultivation regimes. These QTLs and genes provide reliable targets for MAS and CRISPR in erect-leaf-angle breeding.

Structural, epigenetic and signalling regulators underlying maize leaf angle

Researchers have identified structural, epigenetic and signalling regulators that converge on ligular and vascular development, thereby modulating maize LA and canopy architecture. *ZmTAC1* was cloned from the qLA2 region, showing that a “CCCC” to “CTCC” variation in the 5'-UTR modulates mRNA levels and LA, with expression positively correlated with LA size. The *ZmCLA4* gene, orthologous to *LAZY1* in rice and *Arabidopsis* and homologous to *ZmLA1* in maize, was cloned from the qLA4 QTL region and shown to regulate shoot gravitropism and LA in maize (34). Forward genetic approaches and functional mutant studies have clarified how these cloned genes influence leaf morphology at the cellular level (35). For example, the *drl1* maize mutant exhibits drooping leaves due to reduced midrib development and widened LAs caused by distal auricle extension at the blade-sheath boundary. These phenotypes become more pronounced when combined with the *drl2* enhancer allele, which resides within QTL regions controlling LA, leaf width and internode length (36). Similarly, a major QTL on chromosome 2 controlled by *ZmIL1*, a maize ortholog of rice *OsIL1* encoding a bHLH transcription factor, reinforces the role of bHLH-type regulators in shaping leaf architecture (37).

Beyond structural regulators, more recent work has highlighted epigenetic and hormone-mediated pathways that fine-tune LA. The histone methyltransferase SDG128 regulates LA formation, with SDG128 knockdown leading to wider LAs, reduced vascular bundles and interaction with the F-box protein ZmGID2. Both SDG128 and ZmGID2 knockdowns reduce expression of key cell wall genes (*ZmEXPA1*, *ZmEXPB2*, *GRMZM2G005887*), transcription factors (Lg1, *ZmTAC1*, *ZmCLA4*) and auxin-related genes (*ZmYUCCA7*, *ZmYUCCA8*, *ZmARF22*), highlighting coordinated transcriptional control of LA. Parallel transcriptomic and association mapping studies have further expanded the set of LA-related regulators (38). A study identified that ZmNF-YC13, a nuclear factor highly expressed in maize leaf bases, regulates plant architecture. Overexpression resulted in upright leaves and narrower angles, whereas knockouts produced wider angles. This gene functions in a transcriptional complex with ZmNF-YB9, ZmNF-YB10 and ZmNF-YA3 to repress *cytochrome P450* genes through ZmWRKY76 and ZmBT2 in the plastochron pathway (39). Another study reported 17 high-confidence SNPs associated with LA traits, including three novel loci and identified *DROOPING LEAF1* (*DRL1*) as a key regulator located on chromosome 1, underscoring the polygenic and modular nature of LA genetics (40).

Recent research has advanced the characterisation of regulatory pathways. Paralogs *ZmIDD14* and *ZmIDD15*, which regulate auricle symmetry and LA formation through *LG1* expression control. Knockout lines (plants with *ZmIDD14* or *ZmIDD15* functionally inactivated) exhibited reduced adaxial sclerenchyma thickness and decreased LA, emphasising the importance of auricle symmetry and sclerenchyma development in LA regulation. In addition to genetic loci, recent signal integration and environmental response mechanisms have been elucidated (41). Under low-density planting conditions, ZmLG1 interacts with phyB-Pfr to suppress *ZmHBS3*, which regulates adaxial-abaxial axis development. This suppression alters the expression of *cyclin* and *expansin* genes, resulting in enlarged LAs that optimise light capture (42). Additionally, a two-stage developmental process within the ligular region is characterised by initial cell elongation followed by lignification of adaxial sclerenchyma cells. Single-nucleus RNA sequencing identified *bHLH30* and *bHLH155* as key regulators of cell expansion via *EXPA5* and of lignin biosynthesis via *PAL7*, thereby influencing LA determination. These regulators operate independently of rice LA pathways (e.g., *OsLCN2*) and species-specific regulatory mechanisms. Together, these findings establish maize LA as a systems-level trait shaped by coordinated developmental patterning, hormone signalling, chromatin modification and environmental response pathways acting at the auricle and ligular interface (43). The chronological discovery of major maize LA regulators and their associated hormone signalling pathways is summarised in Fig. 1.

Hormone signalling pathways

Hormone signalling pathways play a central role in regulating maize LA by integrating gibberellin (GA), BR, auxin, abscisic acid (ABA), ethylene and jasmonic acid (JA) signalling networks. Collectively, these hormonal pathways modulate cell elongation, division and ligule development, ultimately shaping plant architecture and canopy structure. Hormonal crosstalk coordinating maize leaf inclination is summarised in Fig. 2.

Brassinosteroid signalling pathway

Brassinosteroids are among the major hormonal regulators of maize LA. Mutations in BR biosynthesis genes such as *Brd1* and *nana plant2* disrupt normal BR levels and lead to pronounced morphological alterations, including dwarfism, altered leaf morphology and increased (more upright) LAs, thereby highlighting the crucial role of BRs in regulating plant architecture (44, 45). Extending this understanding, QTL-based studies have further clarified the genetic basis of BR-mediated. UPA1 and UPA2 QTLs conferring upright maize architecture suitable for HDP were identified. UPA2 involves a 2-bp promoter polymorphism located 9.5 kb upstream of *ZmRAVL1*, where DRL1 suppresses LG1-mediated activation of *ZmRAVL1*, reducing its expression and LA. Meanwhile, UPA1 encodes *BR C-6 oxidase1* (*brd1*) and ZmRAVL1-mediated regulation alters BR content to control leaf inclination. The beneficial UPA2 teosinte allele, lost during domestication, enhances yield when reintroduced into modern hybrids (46).

At the molecular level, BR signalling interacts extensively with auxin-associated developmental pathways through interconnected transcriptional regulators that coordinate cell expansion within the lamina joint. Regulatory components such as LG1, LG2 and ZmRAVL1 function as developmental hubs integrating BR-responsive signalling with organ-boundary formation (46, 47).

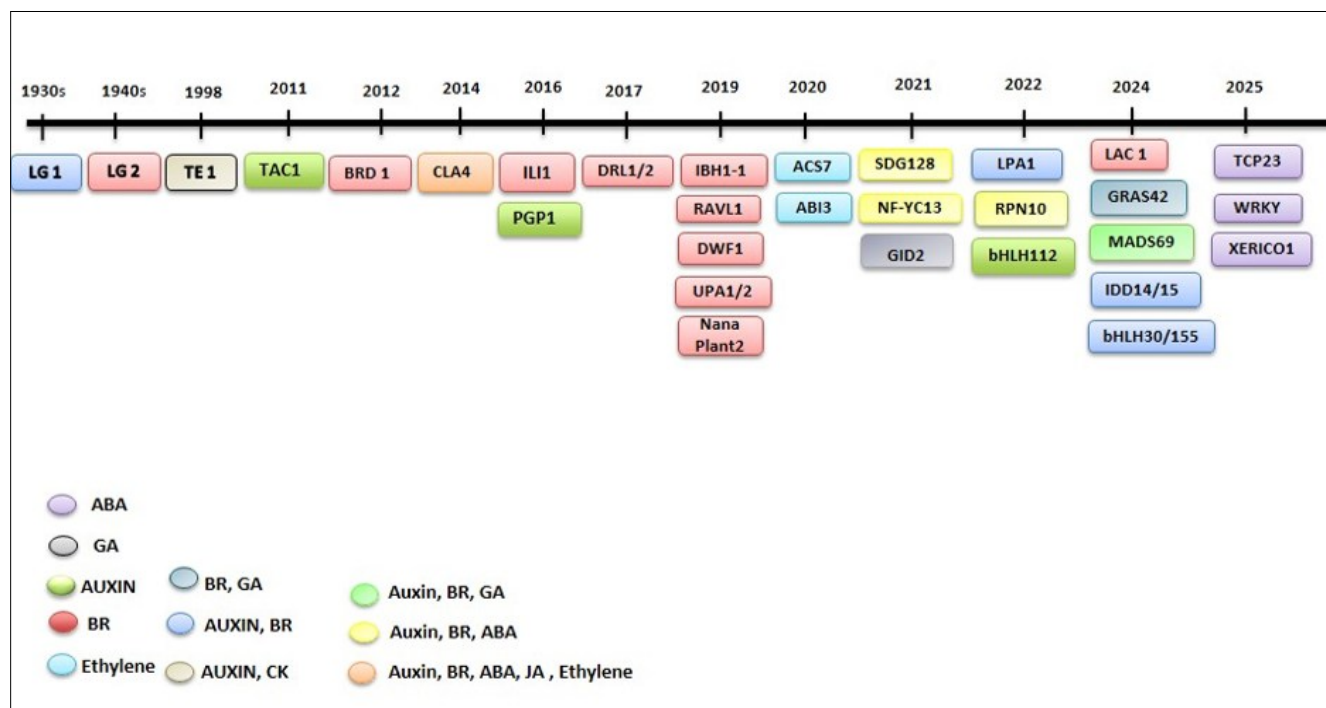


Fig. 1. Timeline of quantitative trait loci and hormone loci for maize leaf angle (1930–2025).

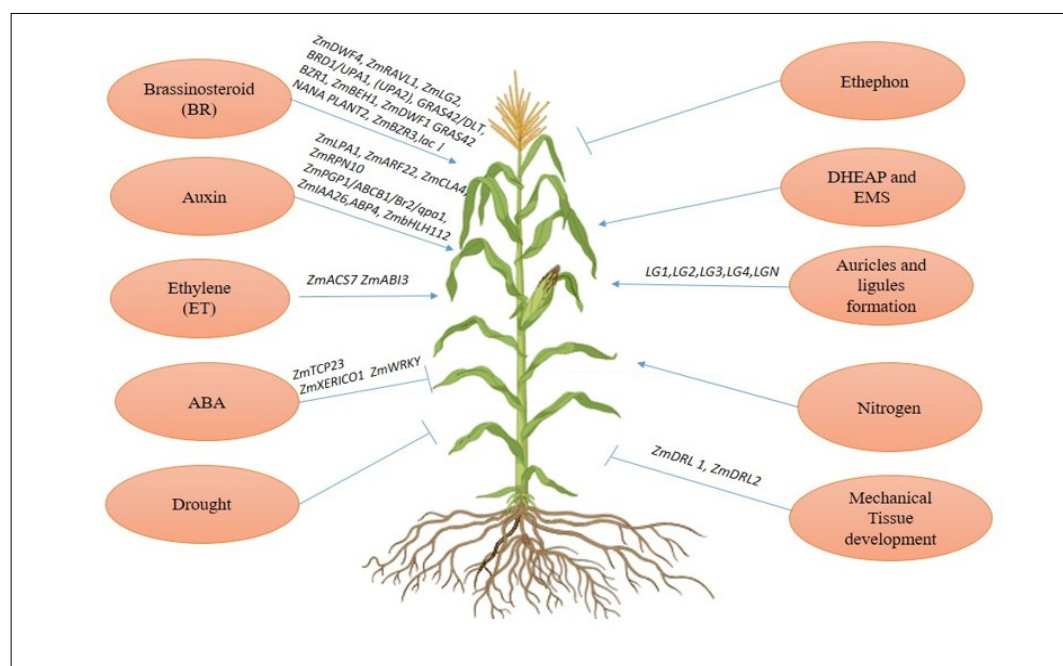


Fig. 2. Genes and hormones regulating leaf angle.

At the transcriptional level, ZmLG2 targets key transcription factors involved in BR signalling, including BZR1 and ZmBEH1, which further bind to the promoter of *GRAS42* (SCARECROW-LIKE 28 ortholog) to regulate LA. The maize *gras42* mutant exhibits upright leaves, indicating that *GRAS42* functions downstream of BR perception to promote lamina joint cell expansion (47). A semi-dwarf maize mutant carrying *gras42-mu1021149*, an ortholog of rice *DLT* and Arabidopsis *SCL28*. Loss of *gras42* results in short, dark green leaves, reduced tillering and an erect leaf phenotype. Although *GRAS42* acts as a positive regulator of BR-responsive gene expression, it suppresses GA-induced gene expression in a tissue-specific manner, indicating that BR signalling coordinates localised hormonal crosstalk between BR and GA pathways within developing lamina joint tissues rather than acting independently (48). This interaction likely prevents excessive elongation while maintaining optimal leaf erectness

during canopy development.

Temporal regulation further refines BR-mediated LA development. Brassinosteroid signalling is particularly active during early lamina joint differentiation, when rapid cell division and elongation establish the final degree of leaf inclination. Spatially restricted BR accumulation within the auricle and ligular tissues subsequently determines the bending angle between the blade and sheath. Supporting this localised mechanism, the *lac1* gene encoding a BR C-22 hydroxylase regulates BR metabolism specifically within upper-canopy lamina joints, thereby promoting erect canopy architecture without substantially altering whole-plant growth (49).

Auxin signalling pathway

Auxin acts as a central hormonal regulator of lamina joint development and leaf inclination. By modulating polar auxin

transport, signal perception and concentration-dependent responses, auxin precisely regulates cell elongation and cell division at the blade sheath boundary. Mutational analyses have provided direct evidence for auxin-mediated control of LA. In this regard, *abp1* and *abp4* mutants demonstrated that auxin-binding proteins regulate leaf inclination, where *abp1* mutants exhibit upright leaves, whereas *ABP4* and double mutants display wider LAs, indicating dominance of *ABP4* in auxin-light-mediated leaf declination (50). Auxin responses during LA formation are highly tissue-specific because auxin maxima are preferentially established within developing lamina joint and auricle tissues. Consistent with this transport-mediated mechanism, *ZmPGP1* (*ABCB1/br2*; *Brachytic2* or *qpa1*) encodes a P-glycoprotein regulating polar auxin transport and contributes to erect leaf (51, 52).

In addition, *ZmLPA1* regulates LA through auxin concentration-dependent responses, in which optimal indole-3-acetic acid (IAA) promotes lamina joint cell elongation and division, whereas excessive IAA inhibits these processes (53). Mechanistically, auxin signalling further converges with BR pathways through interconnected transcriptional networks. Transcriptomic and protein interaction studies revealed that *ZmRPN10* and *ZmBHLH112* participate in auxin signal transduction and influence BR-responsive growth-related genes. This coordinated regulation suggests that auxin and BR signalling jointly regulate lamina joint cell expansion through overlapping downstream transcriptional modules. Moreover, auxin signalling appears particularly important during the early stages of leaf primordia formation and lamina joint initiation, where coordinated auxin transport establishes developmental polarity necessary for proper leaf inclination. Mechanistically, auxin signalling further converges with BR pathways through interconnected transcriptional networks. Transcriptomic and protein interaction studies revealed that *ZmRPN10* and *ZmBHLH112* participate in auxin signal transduction and influence BR-responsive growth-related genes. This coordinated regulation suggests that auxin and BR signalling jointly regulate lamina joint cell expansion through overlapping downstream transcriptional modules. Moreover, auxin signalling appears particularly important during the early stages of leaf primordia formation and lamina joint initiation, where coordinated auxin transport establishes developmental polarity necessary for proper leaf inclination (54, 55).

Gibberellin signalling pathway

Gibberellins regulate maize LA. Through the regulation of cell elongation and interaction with other hormonal pathways, GA signalling coordinates plant height with leaf inclination responses. Genetic analyses have identified QTLs associated with GA-related pathways that influence LA variation. GA-associated QTLs were detected, showing that DELLA protein degradation promotes cell elongation and regulates LA in correlation with plant height. Thus, GA-mediated modulation of growth dynamics directly impacts canopy architecture. Furthermore, hormonal crosstalk refines this regulatory mechanism (56).

Absciscic acid signalling pathway

Unlike growth-promoting hormones that primarily enhance cell elongation, ABA functions as a modulator, adjusting developmental growth in response to internal and environmental cues. Emerging evidence indicates that ABA influences LA by regulating cell proliferation and hormone balance within the lamina joint and auricle tissues. In support of this role, *Zm00001d008651*, located in bin 8.02,

encodes a pyruvate decarboxylase containing ABA-responsive promoter elements, which was identified and functionally characterised. Functional analysis revealed that this gene regulates leaf architecture predominantly through ABA-mediated pathways rather than BR signalling. Mutant lines exhibited increased ear LA traits, confirming ABA-dependent regulation of leaf inclination (57).

ZmTCP23 was shown to directly activate *LG1* expression, thereby suppressing *ZmXERICO1*, an ABA catabolism gene. This regulatory module modulates ABA accumulation, enhances cell proliferation in tassel pulvini and leaf auricles and ultimately enlarges LA and tassel branch angle. In agreement with this observation, *Zmtcp23* mutants reduce cell division and alter ABA sensitivity, while ABA biosynthesis inhibition restores the normal LA phenotype (58).

Ethylene and jasmonic acid signalling pathway

Beyond classical growth regulators, certain phytohormones influence LA by modifying localised tissue differentiation and simultaneously coordinating stress responses. In this context, ethylene and JA play distinct yet interconnected roles in shaping maize canopy architecture. Ethylene influences LA by regulating auricle cell expansion. A mutation in *ZmACS7* elevates ethylene levels, promoting auricle cell expansion and resulting in enlarged LAs in the *Sdw3* maize mutant (59). Therefore, increased ethylene biosynthesis contributes to a wider leaf inclination through targeted cellular enlargement at the lamina joint.

Conversely, JA signalling links plant defence with architecture. Loss-of-function of *LG1* promotes erect leaves while simultaneously enhancing resistance to corn leaf aphids through stabilised *ZIM1* and increased JA signalling. This reveals a pleiotropic relationship between leaf architecture and pest defence, underscoring the adaptive coordination between plant form and biotic stress tolerance (60).

Multihormonal crosstalk and regulatory hub networks governing leaf angle

Leaf inclination in maize emerges from a finely balanced regulatory circuitry in which multiple hormonal pathways converge at the lamina joint. Rather than functioning independently, these pathways interact through shared transcriptional regulators that synchronise developmental and physiological responses. In this regard, transcriptomic analysis revealed that ligule-mediated LA regulation is governed by integrated organ-boundary developmental networks involving auxin, BR and GA pathways, with ZHD/GRAS transcription factors promoting erect architecture and compact canopy formation (61).

At the molecular level, BR and auxin signalling exhibit particularly strong convergence through shared transcriptional modules that regulate elongation of lamina joint cells. BR-responsive regulators such as *BZR1*, *ZmBEH1* and *ZmRAVL1* collectively coordinate with auxin-associated factors, including *ZmARF22* and *ZmIAA26*, through interconnected regulatory networks controlling lamina joint development (47, 48, 62). This hormonal crosstalk enables synchronised regulation of cell proliferation, elongation and tissue differentiation required for precise leaf inclination ABA.

Hormonal regulation of LA is also highly tissue-specific and temporally dynamic. Early developmental stages are dominated by auxin-mediated establishment of developmental polarity and lamina joint initiation, whereas BR and GA signalling become

increasingly important during subsequent cell elongation and bending processes. Absciscic acid, ethylene and JA pathways subsequently modulate these developmental responses in response to environmental and stress-related cues, thereby integrating canopy architecture with adaptive physiological responses.

Furthermore, at the systems level, ZmCLA4 operates as a central regulatory hub that interlinks diverse hormone signalling modules. It integrates ZmARF22 and ZmIAA26 associated with auxin transport, ZmBZR3 involved in BR signalling, ZmWRKYs associated with ABA metabolism, ZmCYP75B1 and ZmCYP93D1 related to JA metabolism and ZmABI3 linked to ethylene signalling by directly binding to the promoters of multiple hormone-responsive genes. Consequently, this multilayered crosstalk ensures precise modulation of maize LA and supports architectural optimisation under HDP systems (62). Table 1 provides an overview of the key genes and hormonal responses associated with maize LA regulation.

Understanding these molecular and hormonal pathways advances the prospects for targeted genetic improvement of LA traits, enabling precise manipulation of maize canopy architecture without undesirable pleiotropic effects. Future research that dissects downstream signalling cascades and cross-regulatory hubs will provide deeper insights essential for engineering maize ideotypes optimised for light capture and HDP adaptations.

Exogenous hormonal manipulation and chemical modulators of leaf angle and canopy architecture

Exogenous application of phytohormones and plant-growth-regulating chemicals offers a rapid, flexible strategy to fine-tune leaf inclination and canopy configuration without altering the underlying genome. Such manipulations have been used to promote more erect architecture under high-density planting, improve light distribution and alleviate stress-induced architectural penalties, thereby complementing breeding-based optimisation of maize plant type. Exogenous BR application plays a key role in modulating lamina joint growth and leaf inclination. Exogenous BR treatment at low concentrations promotes more upright (reduced) LAs in maize by enhancing cell elongation in the leaf cushion (lamina joint) region, where optimal doses induce vertical flag-leaf formation through a transition from cell division to cell expansion (63).

Conversely, BR treatment at higher concentrations increases LA in certain leaves or developmental stages while improving photosynthetic efficiency, indicating a context- and dose-dependent physiological response (64). Supporting BR responsiveness, exogenous BR treatment increases LAs in both wild-type maize and the ZmLPA1 mutant, though the mutant shows reduced sensitivity and an earlier peak response. The ZmLPA1 mutation impairs brassinolactone biosynthesis and BRI1 receptor function, enlarging

angles primarily via pulvinus cell elongation rather than division (65). These BR-dependent responses are summarised in Fig. 3. Transcriptome analysis reveals upregulated auxin, cytokinin and BR pathways with downregulated ABA responses, while Weighted Gene Co-expression Network Analysis (WGCNA) identifies key gene modules linked to BR-mediated LA regulation.

Chemical canopy regulators also modify spatial leaf arrangement and light distribution. N, N-diethyl-2-hexanoyl oxygen radical ethyl amine phosphoric acid salt (DHEAP) alters maize canopy architecture by inhibiting internode elongation, reducing leaf area and increasing upper-canopy LAs, while reducing middle/lower-stratum angles to enhance light penetration and radiation use efficiency during grain filling. Multiple linear regression analysis revealed that LA predominantly influences upper canopy strata, whereas leaf auricle size has a stronger effect on middle and lower strata (66).

Moreover, modulation of hormonal pathways through genetic and chemical interactions has also been documented. Knotted-1 (KN1) regulates leaf growth through hormone signalling pathways. Ethyl methanesulfonate (EMS)-induced *kn1* mutants treated with optimal phytohormones (10 μ M ABA and 100 μ M IAA) exhibited significantly reduced LA and plant height. Differential gene expression analysis revealed that KN1 regulates IAA, BR and GA signalling pathways, as well as flavonoid biosynthesis and PG/XTH-mediated cell wall remodelling, suggesting that LA variation in *kn1* mutants occurs through hormone-mediated cell wall modification (67).

Ethylene-releasing compounds such as ethephon are widely used to reduce LA and regulate canopy compactness. Increased planting density reduces maize leaf angles and ethephon had no effect at low density but significantly decreased upper LAs at high density. In addition, pollen density was positively correlated with upper leaf area and angle (68). Higher ethephon doses of 0, 300, 600 and 900 g a.i. ha⁻¹ applied at V8 stage progressively decreased maize ear LA by 12–28°, with 900 g ha⁻¹ achieving maximum reduction ($r = -0.82$ correlation with lodging index, particularly at the ear leaf, by releasing ethylene that disrupts hormonal balance, restricts cell elongation and leaf expansion and enhances light capture at the ear region, thereby improving lodging resistance with a significant negative correlation between LA and lodging index (69). Table 2 provides an overview of key exogenous compounds and their effects on maize LA.

Combined ethephon diaminodihydroxy acid (EDAH) spraying and slow-release fertilisation significantly reduced maize stem-LAs across upper-ear, ear and under-ear leaves while increasing leaf orientation values. Collectively, these findings highlight that exogenous hormonal treatments and chemical regulators are effective tools for fine-tuning maize LA and canopy

Table 1. Hormonal regulation of leaf angle in maize

Sl. No.	Hormones	Key genes	Effect on leaf angle	References
1	Brassinosteroid	<i>ZmDWF4</i> , <i>ZmRAVL1</i> , <i>ZmLG2</i> , <i>BRD1/UPA1</i> , (<i>UPA2</i>), <i>GRAS42/DLT</i> , <i>BZR1</i> , <i>ZmBEH1</i> , <i>ZmDWF1</i> , <i>GRAS42</i> NANA <i>PLANT2</i> , <i>ZmBZR3</i> , <i>lac 1</i>	Increases LA	(29, 44, 45, 46, 47, 49)
2	Auxin	<i>ABP4</i> , <i>ZmPGP1/ABCB1/Br2/qp1</i> , <i>ZmLPA1</i> , <i>ZmIAA26</i> , <i>ZmCLA4</i> , <i>ZmRPN10</i> , <i>ZmbHLH112</i> , <i>ZmARF22</i>	Increases LA	(50, 51, 52, 53, 54, 55, 62)
3	Gibberellin	<i>ZmGID2</i> , <i>DELLA</i> via <i>GRAS42</i>	Modifies LA	(38, 56)
4	Absciscic acid	<i>ZmTCP23</i> , <i>ZmXERIC01</i> , <i>ZmWRKY</i>	Decreases LA	(58, 62)
5	Ethylene	<i>ZmACS7</i> <i>ZmABI3</i>	Increases LA	(59, 62)
6	Jasmonic acid	<i>ZIM1</i> , <i>ZmCLA4</i> targets, <i>ZmCYP75B1</i> , <i>ZmCYP93D1</i>	Decreases LA	(60, 62)

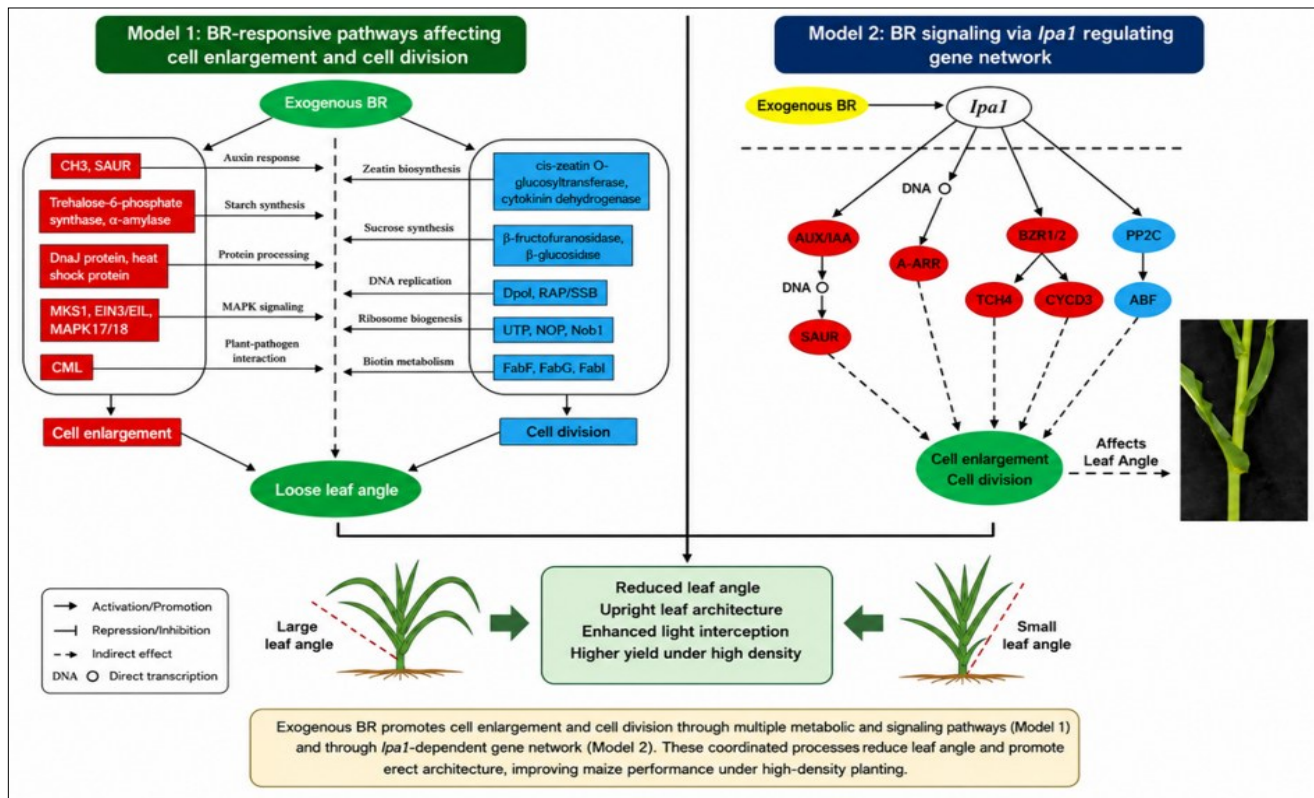


Fig. 3. Integrated molecular model exogenous BR regulates maize leaf angle (63, 65).

Table 2. Effects of exogenous treatment on leaf angle

Sl. No.	Hormones	Key genes	Effect on leaf angle	References
1	Brassinosteroids	<i>ZmLPA1</i>	Increased	(65)
2	N, N-diethyl-2-hexanoyl oxygen radical ethyl amine phosphoric acid salt	-	Increased	(66)
3	Ethyl methanesulfonate	-	Decreased	(67)
4	Ethephon	-	Decreased	(69)

configuration to enhance productivity under intensive cultivation systems (70).

Leaf angle dynamics under high-density planting and their agronomic implications

Agronomic practices such as optimised planting density, nitrogen management and plant growth regulator application interact synergistically with genetic LA traits to enhance canopy efficiency and yield stability. Studies have shown that different hybrid types of exhibit contrasting LA patterns under HDP. Three-way crosses (TWC) were reported to have taller plants, higher ears, longer anthesis-silking intervals (ASI), higher chlorophyll content index (CCI) and wider LAs, whereas single crosses (SC) exhibited narrower LAs under a high-density system. These observations highlight the variability of LA among genetic backgrounds and its impact on plant architecture (71). Correspondingly, superior hybrids were found to exhibit smaller LAs above the ear, longer upper internodes and improved light transmission, thereby contributing to higher leaf area index (LAI), crop growth rate (CGR), net assimilation rate (NAR) and radiation use efficiency (RUE) (72). Similarly, erect leaves above the ear position increase PAR in the mid-lower canopy, while horizontal leaves below the ear enhance interception in basal layers. These results highlight the importance of vertical stratification of LAs for efficient light distribution (73).

In addition to genetic effects, nitrogen-responsive regulation has been described through *ZmZIP27*. Leaf angle serves as a visible marker for early nitrogen deficiency symptoms in maize seedlings, showing significant changes with N supply (74). Mechanistically,

ZmZIP27 represses *Zm-miR528* to promote ligule lignification and erect leaves under sufficient nitrogen, while mutants show wider angles regardless of nitrogen supply (75). Higher planting densities were found to narrow upper LAs, whereas nitrogen application increases them, producing an upper < lower < middle pattern that optimises light distribution (76, 77). Consistently, high density has been shown to increase the insertion angles of the upper ear and primary ear leaves, promoting a more erect architecture (78).

Optimal canopy architecture features upright upper leaves, moderately erect middle leaves and flatter basal leaves for maximum light interception (79, 80). High-yield maize shows smaller LAs above/below ears vs. low-yield types, with erect upper leaves enhancing density tolerance (81). Density-nutrient interactions reduce light extinction (K) while increasing biomass/ precipitation use efficiency PUE (82). Narrower upper LAs mitigate border effects, boosting overall yield (83). Under drought, 25–30° LAs correlate with higher grain yield (84). Table 3 provides an overview of effects of external factors on leaf angle; *lg1* additionally confers northern leaf blight resistance (85). The erect upper leaves thus serve as reliable indicators of density tolerance.

Advanced phenomics, three-dimensional imaging and artificial intelligence-based leaf angle quantification

The phenotypic complexity of maize LA necessitates advanced measurement technologies to enable rapid, accurate and large-scale data collection, which is essential for modern breeding programs. Traditional manual phenotyping is labour-intensive, time-consuming and prone to observer bias, limiting its utility for

Table 3. Effects of external factors on leaf angle

Sl. No.	External factors	Effect on leaf angle	References
1	High plant density	Decreased	(76, 77)
2	Nitrogen application	Increased	(76, 77)
3	Border effect	Increased	(83)
4	Drought	Decreased	(84)

large populations. Early research established the conceptual and methodological foundation for maize LA phenotyping through stereovision-based structural measurements. Stereovision models were pioneered to estimate leaf height and orientation angles within maize canopies, providing one of the first quantitative frameworks for measuring leaf inclination in three dimensions (86). This work laid the groundwork for modern 3D plant phenotyping systems by demonstrating that canopy geometry, including leaf orientation, can be accurately derived from image-based reconstruction.

Subsequent advances introduced high-throughput phenotyping and machine-learning-assisted trait analysis to quantify structural traits, such as LA, at scale. A LiDAR-based 3D phenotyping instrument capable of capturing maize morphological architecture with high precision, enabling rapid measurement of plant structural traits, including leaf orientation (87). In parallel, a machine learning-based high-throughput phenotyping approach to dissect the genetic architecture of bulliform cell patterning in maize leaves, a microscopic trait functionally linked to leaf rolling and drought tolerance. The researchers collected 60780 epidermal leaf impression images from a genetically diverse panel of maize inbred lines and developed convolutional neural networks (CNNs) to automatically quantify bulliform cell column counts and cell widths, thereby replacing labour-intensive manual measurements. Using CNN-extracted phenotypes, they performed a GWAS integrated with RNA-seq transcriptomics data from the bulliform cell ontogenic zone to prioritise candidate genes. The study identified significant QTLs and candidate genes regulating bulliform cell patterning, with functional annotation revealing roles in cell division and DNA methylation pathways (88). This work represented the first application of natural genetic variation to investigate bulliform cell patterning and demonstrated how machine learning can overcome phenotyping bottlenecks for microscopic leaf traits, enabling

large-scale genetic analyses that were previously infeasible with traditional microscopic methods. Extending the framework, the LA extractor, an image-processing and machine learning framework specifically designed for automated and scalable LA measurement in maize and sorghum, marks a major step toward standardised LA phenotyping pipelines (89).

Recent technological developments have further improved the precision and scalability of LA estimation by integrating hyperspectral sensing with 3D structural data. Combining hyperspectral imagery with 3D point cloud models enables the removal of leaf-angle-induced spectral distortions, thereby improving the accuracy of spectral trait estimation and explicitly accounting for canopy angular structure. This work highlighted the necessity of incorporating leaf-angle information into remote sensing-based crop-monitoring frameworks (90).

From 2023 onwards, deep learning, robotic vision and UAV-based sensing have emerged as dominant approaches for field-scale LA phenotyping. Stereo vision integrated with deep CNNs achieved high accuracy for automated field-based LA detection, demonstrating feasibility for large breeding populations (91). As shown in Fig. 4, manual field measurement and 3D point cloud analysis differ in precision, throughput and suitability for large-scale phenotyping.

A multi-angular UAV reflectance framework with Extra Trees classifiers achieved f1-scores of 0.79–0.89 for maize canopy structural trait classification (including leaf orientation), significantly outperforming the standard orthomosaic approach (f1-score 0.70). The method extracted 890–2593 multispectral spectra per plot from nadir and oblique flights (VZA 0–50 °), with optimal performance at ground sampling distance (GSD) 100 cm using specific VZA/VAA combinations (back/forward scattering). Peak accuracies reached 89 % for LAI/GLAI and 84 % for biochemical traits under clear-sky

**Fig. 4.** Manual field measurement vs. 3D Point cloud analysis (91).

conditions, demonstrating that multi-angular data provide 50–200 × more informative spectra than orthomosaic blending for precision phenotyping of maize canopy architecture (92). Multispectral UAV-derived point cloud models were also developed to analyse the anisotropic reflectance properties of maize leaves, reinforcing the importance of integrating spectral and structural information for accurate characterisation of canopy angular traits (93).

Parallel advances in 3D morphological modelling have strengthened structural quantification of maize leaves and canopies. 3D point cloud reconstruction from RGB images of 478 maize inbred lines at the grain-filling stage, enabling automated extraction of 13 leaf morphological descriptors, including leaf inclination angle, 3D leaf area, blade self-twisting angle and margin amplitude. Using geometric algorithms on high-density point clouds, they quantified significant genetic variation across leaf surfaces, with 84.62 % of traits showing heritability > 0.3. The approach generated the first comprehensive 3D phenotypic dataset revealing complex environmental influences on maize leaf morphology for genetic studies (94). Computational intelligence-based 3D canopy modelling treating maize phytomers as intelligent agents that iteratively optimise azimuth angles to maximise sunlit leaf area ratio, incorporating collision detection via mesh deformation. Validated across 2 varieties (JNK728, JK968) at 3 planting densities ($3\text{--}9 \times 10^4$ plants ha⁻¹), the method achieved $R^2 = 0.71$ for the leaf azimuth angle distribution between adjacent leaves and a canopy coverage error of 7–17 %. The models successfully captured density-dependent LA adjustments, with leaves perpendicular to rows increasing beyond 9×10^4 plants/ha to optimise light interception. The most recent generation of phenotyping models integrates radiative transfer theory with deep learning to directly estimate LA from hyperspectral UAV observations (95). PROSAIL-Net, a dual-stream transfer learning neural network capable of simultaneously estimating leaf chlorophyll and LA from UAV hyperspectral data, significantly outperforms traditional inversion methods and represents a major advance toward real-time, non-destructive field phenotyping (96). Dense 3D point-cloud reconstruction has demonstrated high-precision measurement of maize leaf phenotypic parameters, including LA, confirming the reliability of point-cloud approaches for detailed structural phenotyping (97). Machine learning validation showed that erect upper-canopy leaves (< 25 °) and moderate upright curvature significantly enhance light interception and photosynthetic efficiency (random forest, $R^2 = 0.69$; SVM, $R^2 = 0.62$), outperforming linear regression in predicting canopy-yield relationships (98).

Despite the significant progress achieved in advanced phenotyping technologies, several constraints still limit their widespread application in routine maize breeding programs. The high acquisition and operational costs associated with LiDAR systems, UAV platforms, hyperspectral sensors and high-performance computational infrastructure remain major limitations, particularly for breeding programs in developing countries with limited technical and financial resources (88, 93, 97). In addition, field-based phenotyping is strongly influenced by environmental variability, including wind-induced leaf movement, fluctuating illumination, canopy overlap and changing atmospheric conditions, which can reduce image quality and affect the throughput, consistency and reproducibility of automated measurements (90–93).

Another important challenge is the transferability of machine learning and deep learning models across genetically diverse germplasm. Many currently available models are developed using relatively restricted datasets representing specific genotypes, developmental stages or environmental conditions, which may limit their predictive robustness when applied across diverse maize populations and multi-environment breeding trials (88, 89, 91, 96). Therefore, broader validation across diverse germplasm pools and agroecological conditions is essential for developing universally applicable phenotyping frameworks. Furthermore, although automated phenotyping systems greatly improve throughput and reduce observer bias, calibration and standardisation are still necessary to ensure measurement accuracy and biological reliability across platforms. Manual measurements, therefore, continue to serve as important reference standards for validating automated approaches, particularly under complex canopy architectures and partially occluded leaf conditions (86, 89, 97).

Overall, the integration of LiDAR, UAV-based imaging, hyperspectral sensing, three-dimensional reconstruction and artificial intelligence has transformed maize LA phenotyping from labour-intensive manual assessment into automated, high-throughput and data-driven precision systems. These technologies substantially improve the efficiency of identifying optimal canopy architectures and accelerate the development of breeding strategies to enhance light interception, photosynthetic efficiency and grain yield in maize.

Conclusion

Optimising maize plant architecture, particularly leaf angle (LA), is critical for maximising light interception and photosynthetic efficiency under high density planting (HDP) conditions and enhancing resilience to environmental stress. Recent molecular studies have shed light on the hormone-mediated networks and genetic regulators that control LA, including SQUAMOSA promoter-binding protein-like (SPL) family genes, gibberellin (GA) biosynthesis pathways and dwarf mutants, thereby providing concrete targets for developing compact maize varieties capable of sustaining yields at increased planting densities. The integration of multi-omics approaches spanning genomics and transcriptomics provides a comprehensive understanding of the intricate networks governing canopy traits. These systems-level insights allow breeders to simultaneously select for multiple complementary traits, overcoming the limitations of conventional single-trait approaches and accelerating genetic gain. Complementing these advances, gene-editing tools such as CRISPR/Cas9 enable precise modification of target genes, facilitating the rapid introduction of favourable alleles into elite germplasm without the generational lag inherent to traditional breeding. Incorporating genotype-by-environment interactions and exploiting phenotypic plasticity are essential to ensure stable yields across diverse and changing environments. Advanced phenotyping platforms, including 3D modelling technologies, allow precise measurement and simulation of canopy architecture, expediting ideotype design. The ultimate aim is to create “smart canopies” in which LAs are dynamically modulated across canopy layers to optimise light interception and maximise photosynthetic efficiency. Future efforts should focus on functional validation of key regulators, leveraging phenotypic plasticity for resilience and integrating AI-driven phenotyping with predictive crop

modelling. Collectively, these strategies promise to accelerate the development of maize ideotypes that can sustain high yields under dense planting systems while meeting the growing global demand for food amid climate variability.

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Authors' contributions

RJ and KRVSS have conceptualized the draft. RJ reviewed the literature and drafted manuscript. TS, RR and VBRP verified the contents. All authors read and approved the final manuscript.

Compliance with ethical standards

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