Plant Gene and Trait 2026, Vol.17, No.3, 197-215
http://genbreedpublisher.com/index.php/pgt

Feature Review **Open Access**

Yield-Related Traits in Cucumber (*Cucumis sativus*) and Their Variation and Formation

Wenjing Xu [1], Mengting Luo [2]
1 Jiande Riyue Agricultural Development Co., Ltd., Jiande, 311616, Zhejiang, China
2 Institute of Life Sciences, Jiyang College of Zhejiang A&F University, Zhuji, 311800, Zhejiang, China
Corresponding email: mengting.luo@jicat.org

Plant Gene and Trait, 2026, Vol.17, No.3 doi: 10.5376/pgt.2026.17.0014
Received: 10 May, 2026
Accepted: 12 Jun., 2026
Published: 25 Jun., 2026

Preferred citation for this article:
Xu W.J., and Luo M.T., 2026, Yield-related traits in cucumber (*Cucumis sativus*) and their variation and formation, Plant Gene and Trait, 17(3): 197-215 (doi: 10.5376/pgt.2026.17.0014)

Abstract This study explored the yield-related traits of cucumber and their variation and formation mechanisms. The characteristics and interrelationships of major yield components, including vegetative growth traits, reproductive growth traits, population structure, and stress-resistance traits, were systematically analyzed. The effects of natural germplasm resources, artificial selection, and molecular-level genetic variation on the formation of cucumber yield traits were also discussed. Furthermore, the physiological mechanisms underlying yield formation, including photosynthesis and assimilate accumulation, hormonal regulation, and environmental factor regulation, were elucidated. Advances in functional genes related to fruit morphology, parthenocarpy, organ size, and stress resistance, as well as signal transduction networks and multi-omics studies, were summarized. In addition, the roles of cultivation technologies, such as greenhouse environmental regulation, water and fertilizer management, and cultivation pattern optimization, in cucumber yield formation were reviewed. Combined with recent advances in marker-assisted selection, genomic selection, CRISPR/Cas gene editing, high-throughput phenotyping, and artificial intelligence technologies, the current challenges and future breeding directions for high-yield cucumber research were further discussed. This review provides a theoretical reference for breeding new cucumber varieties with high yield, superior quality, stable production, and stress resistance, as well as for optimizing efficient cultivation techniques.

Keywords Cucumber; Yield traits; Genetic variation; Molecular regulation; High-yield breeding

1 Introduction

Cucumber (*Cucumis sativus* L.) is one of the most widely cultivated and economically important vegetable crops in the Cucurbitaceae family worldwide, particularly in Asia and Europe, and is also an important vegetable crop in both protected horticulture and open-field cultivation systems. Cucumber is characterized by a short growth cycle, strong adaptability, and high yield potential. Its fruits are crisp, juicy, and rich in nutrients, giving the crop high market demand and economic value. In recent years, with the rapid development of protected agriculture and the modern horticultural industry, cucumber has become one of the largest vegetable crops cultivated under protected conditions in China, and China accounts for a dominant proportion of global cucumber production. Meanwhile, consumers have placed higher demands on cucumber commodity quality, nutritional quality, and year-round stable supply, making high yield, superior quality, stress resistance, and adaptability to mechanized production important objectives in modern cucumber breeding (Dey et al., 2023). However, under the increasing pressures of global climate change and resource limitations, abiotic stresses such as drought, salinity, high temperature, and low temperature, as well as biotic stresses including downy mildew and viral diseases, significantly affect cucumber growth, development, and yield stability (Serhiienko et al., 2025). Therefore, in-depth studies on yield-related traits and their formation mechanisms are of great significance for improving cucumber productivity and promoting the sustainable development of protected horticulture.

Cucumber yield is a typical complex quantitative trait whose formation is jointly regulated by genetic background, physiological metabolism, environmental conditions, and cultivation management practices. In general, cucumber yield is mainly determined by fruit number per plant, single fruit weight, and effective plant number per unit area, while agronomic traits such as fruit length, fruit diameter, female flower number, branch number, and vine length are also closely associated with yield formation (Patidar et al., 2024). Correlation and path coefficient analyses have shown that fruit number, single fruit weight, and fruit size exert significant direct positive effects on yield per plant or yield per unit area, making them key factors influencing cucumber yield performance (Kaur et al., 2024; Lnu et al., 2025). In addition, the coordination between vegetative and reproductive growth directly affects yield formation. For example, plant height, leaf area, root activity, and photosynthetic capacity influence dry matter accumulation and assimilate transport, whereas female flower ratio, fruit set rate, and fruit enlargement rate determine yield formation capacity. Numerous studies have demonstrated that many cucumber yield-related traits possess high heritability and considerable genetic advance, indicating strong potential for genetic improvement and selection value (Negi et al., 2025).

However, cucumber yield-related traits also exhibit strong environmental sensitivity, with substantial differences observed among ecotypes, cultivation methods, and planting seasons (Lnu et al., 2025). Environmental factors such as temperature, light, water and fertilizer management, and cultivation conditions under protected or open-field systems can affect yield trait expression by regulating plant physiological and metabolic processes. Moreover, stresses such as high temperature, drought, salinity, and diseases interact complexly with genotypes, further influencing flowering, fruit set, and fruit development, thereby increasing the complexity of high-yield formation mechanisms in cucumber (Serhiienko et al., 2025). With the rapid development of molecular biology and omics technologies, studies on cucumber yield formation mechanisms have gradually expanded from traditional phenotypic observation and genetic analysis to genomics, transcriptomics, metabolomics, and epigenetic regulation. Studies have shown that cucumber yield formation is closely associated not only with physiological processes such as photosynthesis, hormonal regulation, carbon and nitrogen metabolism, and source-sink relationships, but also with the coordinated actions of multiple key genes and complex regulatory networks. For example, genes related to sex determination regulate female flower formation and fruit-setting ability, whereas fruit development-related genes directly affect fruit size, fruit shape, and single fruit weight (Dey et al., 2023). In recent years, technologies such as QTL mapping, candidate gene mining, genome-wide association studies (GWAS), genetic transformation, and CRISPR/Cas gene editing have been widely applied in studies of important agronomic traits in cucumber, providing new theoretical foundations and technical support for elucidating the genetic basis and molecular regulatory mechanisms of cucumber yield-related traits.

This study aims to explore cucumber yield-related traits and their variation and formation mechanisms by systematically reviewing research progress on genetic variation patterns, heritability, correlations, and gene effects of yield-related traits in different cucumber germplasm resources, landraces, breeding materials, and segregating populations. Due to differences in research materials, ecological environments, and evaluation criteria, systematic integration and unified understanding among different studies are still lacking. Considering the complexity of cucumber yield formation mechanisms and their importance in modern protected horticulture, this review focuses on summarizing the classification and characteristics of cucumber yield-related traits, patterns of genetic variation, physiological and molecular regulatory mechanisms, and the effects of cultivation techniques on yield formation. In addition, recent advances in multi-omics research and molecular breeding are discussed, and current research limitations and future development directions are analyzed and prospected. Through systematically summarizing relevant research achievements, this review aims to provide theoretical references for breeding new cucumber cultivars with high yield, superior quality, stable production, and stress resistance, as well as for optimizing efficient cultivation technologies, while also offering new insights into the genetic basis and regulatory mechanisms of complex quantitative traits in cucumber.

2 Yield-Related Traits in Cucumber

2.1 Vegetative growth traits

Vegetative growth traits in cucumber constitute an important foundation for determining plant vigor, canopy structure, and photosynthetic productivity. These traits mainly include vine length, internode length, branch number, leaf area, leaf number, root development, and photosynthetic capacity. Considerable phenotypic and genetic variation in these traits has been observed among different cucumber genotypes, landraces, and breeding materials, and some traits exhibit relatively high heritability, making them important indicators for high-yield breeding and ideal plant architecture selection in cucumber (Negi et al., 2025). Previous studies have shown that traits such as vine length, branching ability, and leaf area contribute substantially in principal component analysis and cluster analysis and are important agronomic indicators for distinguishing different cucumber germplasm resources.

The vegetative growth process essentially reflects the plant's capacity to establish source-sink relationships and directly influences assimilate accumulation, transport, and subsequent fruit formation. In general, plants with strong vegetative vigor usually possess larger functional leaf areas and higher photosynthetic efficiency, thereby providing sufficient assimilates for female flower differentiation, fruit set, and fruit enlargement. Correlation and path coefficient analyses have demonstrated that traits such as vine length, leaf area, branch number, and leaf number are significantly positively correlated with yield per plant and yield per unit area and may indirectly promote yield formation by increasing fruit number and single fruit weight (Patidar et al., 2024; Lnu et al., 2025; Negi et al., 2025). However, excessive vegetative growth may also lead to excessive vine elongation, canopy overcrowding, and imbalance between vegetative and reproductive growth, thereby reducing fruit set rate and yield stability during later developmental stages.

Leaves and roots are the two core organs affecting vegetative growth efficiency in cucumber. Leaves serve as the primary site of photosynthesis, and their size, chlorophyll content, and photosynthetic rate directly determine canopy light-use efficiency and dry matter accumulation capacity. Roots influence sustained plant growth and stress adaptability by regulating water and mineral nutrient uptake. Under protected cultivation conditions, root vigor is closely associated with continuous fruiting ability, and well-developed root systems enhance tolerance to stresses such as drought, salinity, and high temperature. Therefore, coordinating aboveground canopy development with belowground root growth and maintaining balanced source-sink relationships are important physiological foundations for achieving high and stable cucumber yields.

2.2 Reproductive growth traits

Cucumber is a typical monoecious crop with separate male and female flowers, and its reproductive growth process is most directly associated with yield formation. Reproductive growth-related traits mainly include flowering time, node position of the first female flower, female-to-male flower ratio, number of female flowers, fruit set rate, fruit number, fruit length, fruit diameter, and single fruit weight. Among these traits, flowering time and first harvest time vary significantly among cucumber materials and exhibit moderate to high heritability in some studies, indicating considerable potential for improving early yield through selection for earliness (Negi et al., 2025). Studies have shown that total yield is negatively correlated with the periods from seedling emergence to flowering and from seedling emergence to fruiting, suggesting that earlier transition into the reproductive stage is beneficial for increasing cucumber yield (Serhiienko et al., 2025).

The capacity for female flower formation and fruit set are key determinants of cucumber fruiting potential. Generally, plants with a higher proportion of female flowers and lower node positions of the first female flower tend to exhibit stronger early fruiting ability. In modern cucumber breeding, gynoecious lines and parthenocarpic materials have been widely utilized in the development of high-yield hybrids. Gynoecious lines can significantly increase the number of female flowers, whereas parthenocarpic materials are capable of setting fruit without pollination, thereby improving yield stability under protected cultivation conditions (Dey et al., 2023; Kaur et al., 2024; Lnu et al., 2025). The genetic mechanisms underlying these traits are relatively complex, involving additive effects, dominant effects, and epistatic interactions among multiple genes. Therefore, integrated improvement strategies combining heterosis utilization and marker-assisted selection are generally required in breeding practice.

Fruit development traits constitute the core components of cucumber yield. Numerous studies have demonstrated that fruit number, fruit length, fruit diameter, and average single fruit weight are key determinants of yield per plant and yield per unit area (Patidar et al., 2024; Negi et al., 2025). These traits generally exhibit high phenotypic variation coefficients, heritability, and genetic advance, indicating substantial selection potential (Table 1) (Lnu et al., 2025). Meanwhile, plant hormones such as ethylene, auxin, and gibberellins play important regulatory roles in sex expression, fruit set, and fruit enlargement in cucumber. The elucidation of related functional genes and regulatory networks has also provided important molecular foundations for understanding the mechanisms underlying high-yield formation in cucumber (Dey et al., 2023).

Table 1 Coefficient of variation, heritability and genetic advance of yield and quality traits (Adopted from Lnu et al., 2025)

Trait	Mean	CV (%)	GCV (%)	PCV (%)	H2 (b.s.) (%)	G.A (%)	G.A (as % mean)
G.	16.08	5.75	13.58	14.77	84.66	4.14	25.76
Fruit diameter	3.57	6.04	15.99	17.1	87.53	1.1	30.84
Fruit weight	157.67	9.88	27.45	29.13	88.81	84.03	53.29
Pistil length	3.74	4.38	11.79	12.58	87.8	0.85	22.76
Internodal length	10.19	3.07	20.86	21.09	97.84	4.33	42.5
Vine length	328.52	4.13	25.65	25.98	97.45	171.33	52.15
Number of female flowers per node	1.21	7.24	26.44	27.43	92.89	0.63	52.49
Number of fruits set per node	0.15	14.95	34.36	37.41	84.38	0.09	65
Number of fruits per plant	14.81	4.98	35.43	35.77	98.12	10.71	72.29
Fruit setting percentage	13.34	19.28	2.36	39.83	0.35	0.04	0.29
Fruit yield per plant	2.14	14.62	24.61	27.64	79.35	0.97	45.18
TSS	2.66	9.3	12.76	15.82	65.06	0.56	21.21
Flesh to seed cavity ratio	1.94	14.94	12.47	19.56	40.67	0.32	16.38
Water content	97.51	0.78	0.17	0.79	4.68	0.08	0.08
Vitamin C	3.08	9.24	16.85	19.19	77	0.94	30.45

2.3 Population structure and stress-resistance-related traits

Population structure is an important factor affecting light energy utilization efficiency and yield per unit area in cucumber populations, mainly involving plant architecture, planting density, spatial leaf distribution, and canopy ventilation and light transmission capacity. A reasonable population structure can improve the uniformity of light interception within the canopy and enhance photosynthetic efficiency, thereby promoting dry matter accumulation and fruit formation. In contrast, excessively high planting density or overly luxuriant plant architecture can intensify competition among plants, leading to canopy closure, premature senescence of lower leaves, and increased disease incidence. Under protected cultivation and high-density planting conditions, optimizing population structure, improving the field microclimate, and enhancing the canopy light environment are important agronomic measures for increasing continuous fruiting ability and yield per unit area in cucumber.

Different cucumber germplasm resources exhibit significant differences in vegetative growth vigor, fruit characteristics, environmental adaptability, and yield potential, and they often form distinct groups in cluster analyses (Serhiienko et al., 2025). In evaluations of landraces and breeding materials, researchers have identified several groups showing superior performance in fruit number, fruit size, and overall yield. These materials can serve as important resources for selecting high-yield parental lines, genetic mapping, and heterosis utilization. Such rich genetic diversity is not only beneficial for the improvement of high-yield traits but also provides important material foundations for studying the genetic mechanisms underlying complex quantitative traits in cucumber (Kaur et al., 2024).

Stress-resistance-related traits are important guarantees for achieving high and stable cucumber yield. Cucumber is sensitive to low temperature, high temperature, drought, and salt stress, and adverse environmental conditions can lead to reduced photosynthesis, abnormal floral organ development, and decreased fruit-setting rate, thereby significantly affecting yield and fruit quality. In recent years, traits such as drought tolerance, salt tolerance, and resistance to viral diseases have gradually been incorporated into evaluation systems for high-yield cucumber breeding. Quantitative genetic studies have shown that some stress-related traits and disease indices possess certain levels of heritability and may be genetically associated with flowering habits and fruit development traits, indicating the potential for the synergistic improvement of stress resistance and high yield. With the development of marker-assisted selection, genomic selection, and gene-editing technologies, important genes and QTLs related to low-temperature tolerance, salt tolerance, disease resistance, and fruit development have gradually been identified, providing new technical support for breeding cucumber cultivars with high yield, multiple stress resistance, and adaptability to complex environmental conditions (Dey et al., 2023).

3 Genetic Variation of Cucumber Yield Traits

3.1 Variation in natural germplasm resources

Cucumber germplasm resources contain abundant genetic variation and constitute an important genetic foundation for breeding programs targeting high yield, superior quality, and stress resistance. Owing to long-term natural evolution, ecological adaptation, and geographical differentiation, cucumber materials from different regions and ecotypes have developed significant differences in plant architecture, flowering habits, fruit morphology, fruiting ability, and environmental adaptability. Extensive germplasm evaluations have demonstrated broad natural phenotypic diversity in yield-related traits such as fruit length, fruit diameter, fruit number per plant, single fruit weight, and yield per plant in cucumber (Tadkal et al., 2024). This rich natural variation not only reflects the long-term ecological adaptation and cultivation history of cucumber but also provides abundant allelic resources for the genetic improvement of high-yield traits.

Landraces are important sources of natural variation in cucumber and represent core germplasm types for maintaining genetic diversity. Previous studies have shown that different landraces exhibit high coefficients of variation and broad-sense heritability for traits such as yield per plant, fruit number per plant, single fruit weight, and vine-related characteristics, indicating strong selection potential and substantial genetic control over these traits (Tadkal et al., 2024). Compared with modern commercial cultivars, traditional landraces may possess certain limitations in terms of fruit uniformity and adaptability to protected cultivation systems; however, they still exhibit important breeding value in stress adaptability, continuous fruiting ability, and yield stability. Therefore, landrace germplasm resources are not only important components of cucumber genetic diversity but also valuable materials for mining superior yield-related genes.

With the establishment of global germplasm repositories and genomic databases, the population genetic structure of natural variation in cucumber has gradually been elucidated (Figure 1). The 1 234 cucumber accessions conserved in the U.S. National Plant Germplasm System can be classified into three major genetic subpopulations, which differ significantly in geographical origin and horticultural type. Further genome-wide SNP analyses and core germplasm construction have revealed abundant and structured genetic diversity within cucumber germplasm resources, particularly among East Asian materials, which exhibit distinct characteristics in fruit length and fruit shape index (Lin et al., 2024). The extensive genetic variation present in natural germplasm resources provides important genetic sources for breeding new cucumber cultivars with high yield, superior quality, and stress resistance and also establishes a material foundation for elucidating the genetic basis of complex quantitative traits.

3.2 Variation formed through artificial selection

Artificial selection has been an important driving force promoting the continuous optimization of cucumber yield traits and the differentiation of cultivation types. During long-term domestication, cultivation, and modern breeding processes, breeders have continuously selected materials with high yield, early maturity, high female flower ratio, strong continuous fruiting ability, and adaptability to protected cultivation, resulting in significant changes in plant architecture, flowering habits, fruit morphology, and yield components. Modern greenhouse cucumbers generally exhibit characteristics such as shorter internodes, higher degrees of femaleness, stable fruit set, and strong continuous fruiting ability, all of which are the result of long-term directional selection and genetic fixation. Artificial selection has not only altered the phenotypic range of yield-related traits in cucumber but also significantly affected the frequency distribution of related alleles and overall genome structure.

QTL mapping studies based on wild and cultivated cucumber populations have shown that multiple important loci associated with flowering time, fruit size, fruit number, and fruit weight per plant have undergone continuous selection during domestication. Some QTL regions exhibit clear signatures of domestication and breeding selection. Notably, certain alleles derived from wild or semi-wild materials still exert positive transgressive effects on fruit size and fruiting ability, indicating that wild germplasm resources retain abundant superior genetic variation that has not yet been fully utilized. Therefore, the genetic complementarity between wild germplasm and modern cultivated varieties provides new directions for high-yield cucumber breeding.

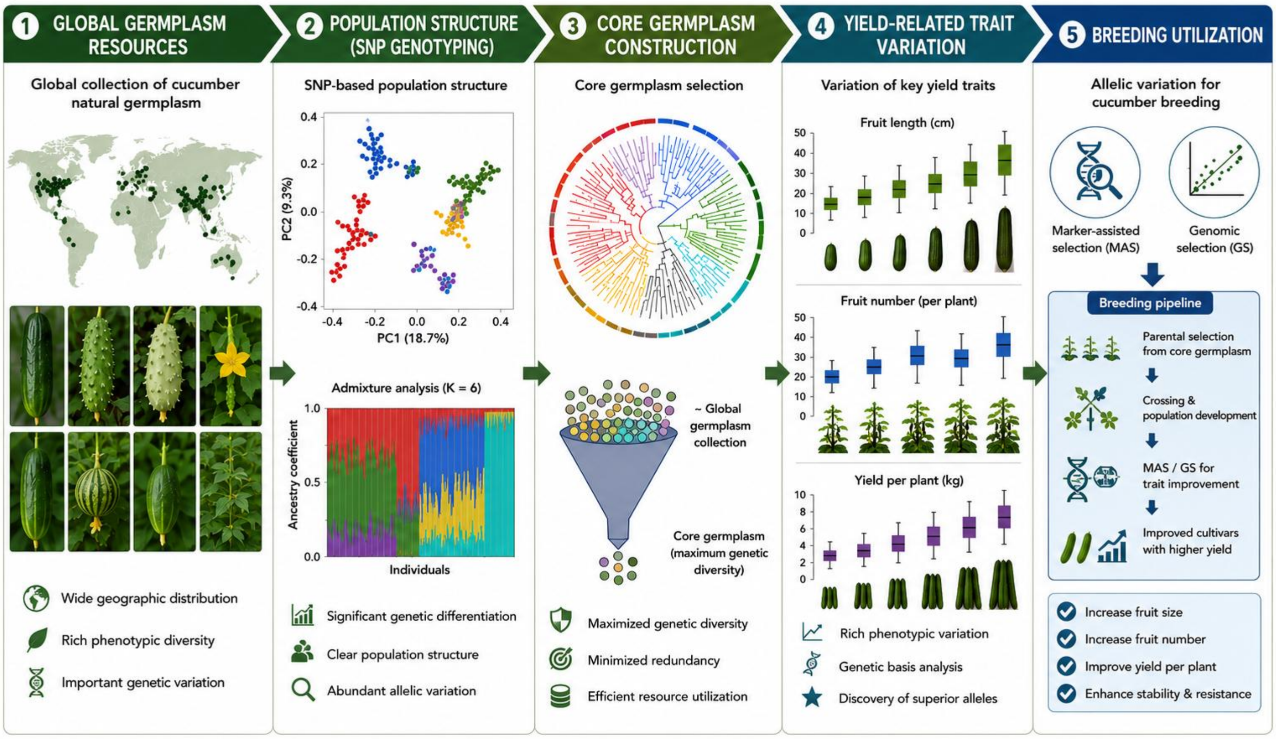

Figure 1 Genetic diversity and yield-related trait variation in cucumber natural germplasm resources

Clear signatures of artificial selection are also evident in modern breeding populations. Genome analyses of elite inbred lines from different breeding backgrounds have revealed significant differentiation in several important QTL regions associated with earliness, fruit size, and productivity, reflecting continuous reinforcement selection for high-yield-related traits during breeding processes. In addition, multi-environment evaluations and hybrid combination analyses have demonstrated substantial genetic variation among breeding materials, with some hybrid combinations exhibiting significantly higher total yield and fruit number than ordinary materials and even outperforming commercial control cultivars (El-Remaly and Shehata, 2023; Serhiienko et al., 2025). In recent years, the utilization of heterosis, marker-assisted selection, and pyramiding of complex traits have further improved the efficiency of cucumber yield improvement (Shukla et al., 2025). Artificial selection has not only shaped the genetic variation patterns of modern cucumber yield traits but has also driven the continuous evolution of cucumber from traditional landraces to protected-cultivation-adapted and high-yield, high-quality cultivars.

3.3 Molecular-level genetic variation

With the development of genomics and high-throughput sequencing technologies, studies on cucumber yield traits have gradually progressed from traditional phenotypic and quantitative genetic analyses to the molecular level. Molecular variations such as single nucleotide polymorphisms (SNPs), insertions/deletions (InDels), copy number variations, and structural variations constitute important genetic bases underlying differences among cucumber materials in fruit size, flowering time, female flower ratio, fruiting ability, and stress resistance. Numerous studies have demonstrated that cucumber yield traits are typical complex quantitative traits generally regulated by multiple loci with small or moderate effects and jointly influenced by environmental factors and gene interactions.

Based on genome-wide SNP data and high-density genetic maps, researchers have identified important QTLs and significant SNP loci associated with fruit length, fruit diameter, fruit shape, and fruit weight in multiple populations. Genome-wide association studies (GWAS) have shown that many significant loci related to fruit size and fruit shape are clustered within known QTL regions, suggesting that cucumber yield-related traits possess relatively stable genetic foundations (Lin et al., 2024). Meanwhile, high-density SNP genetic maps constructed using SLAF-seq technology have further improved QTL mapping resolution, and some major-effect loci can explain a relatively large proportion of phenotypic variation, thereby providing important foundations for candidate gene mining and marker-assisted selection. However, because of strong interactions among populations, environments, and cultivation conditions, some QTLs still exhibit environmental dependency and insufficient stability.

In addition to SNPs and InDels, structural variation and pan-genome studies have further revealed the deeper genetic basis underlying complex cucumber yield traits. Pan-genome analyses have identified large numbers of structural variations in cucumber, some of which are closely associated with important agronomic traits such as flowering time, fruit surface characteristics, and root development. Large chromosomal rearrangements and structural variations can directly influence the expression of key genes and may also regulate multiple yield components through linkage effects and pleiotropy. To date, numerous functional genes and QTLs related to fruit size, fruit number, and flowering time have been identified in cucumber, and molecular marker systems applicable to breeding are gradually being established. At the same time, advances in transcriptomics, metabolomics, and functional genomics, as well as the application of genetic transformation and CRISPR/Cas gene-editing technologies, have provided new technical approaches for elucidating the mechanisms underlying high-yield formation and for the targeted improvement of key yield traits in cucumber.

4 Physiological Mechanisms of Cucumber Yield Formation

4.1 Photosynthesis and assimilate accumulation

Cucumber yield formation is highly dependent on leaf photosynthetic carbon assimilation capacity and the efficiency of assimilate allocation to fruits. Through photosynthesis, leaves fix CO_2 and synthesize carbohydrates, thereby providing the material and energy sources required for vine growth, root development, female flower formation, and fruit enlargement. Therefore, photosynthesis constitutes the core physiological basis for dry matter accumulation and yield formation in cucumber. Studies have shown that increasing the activity of enzymes related to photosynthetic carbon metabolism can significantly enhance net photosynthetic rate and biomass accumulation in cucumber, indicating that improving photosynthetic biochemical capacity is an important approach for promoting greenhouse cucumber growth and increasing yield. In addition, cucumber fruit is a typical strong “sink” organ, and its continuous enlargement process is highly dependent on assimilate supply. Therefore, high-yield formation depends not only on the photosynthetic capacity of source organs but also on the competitive strength of sink organs and the coordination between source and sink.

The transport and distribution of assimilates in cucumber exhibit typical “source-sink-flow” regulatory characteristics. Functional leaves serve as the major “source” organs, fruits act as the primary “sink” organs, and phloem transport constitutes the pathway for assimilate translocation. Previous studies have demonstrated that cucumber fruit growth dynamics are closely related to assimilate supply capacity and sink activity, while temporary assimilate storage and redistribution can partially buffer imbalances between source and sink relationships. When vegetative and reproductive growth remain coordinated, assimilates are preferentially transported to fruits, thereby promoting fruit set and fruit enlargement. In contrast, excessive vegetative growth, premature leaf senescence, or reduced root vigor decreases assimilate transport efficiency, ultimately restricting fruit development and reducing yield. Therefore, maintaining balanced source-sink relationships is an important physiological basis for achieving high cucumber yield.

Environmental conditions can significantly influence photosynthesis and assimilate accumulation in cucumber. Increasing CO_2 concentration enhances carbon assimilation capacity, increases soluble sugar content, carbon-to-nitrogen ratio, and fruit dry matter accumulation, and promotes greater assimilate allocation to fruits, thereby improving fruit weight and yield. Root-zone temperature and nitrogen supply further affect photosynthetic acclimation and carbon-nitrogen balance. Increasing root-zone temperature and coordinating NO_3^- supply can alleviate photosynthetic inhibition under elevated CO_2 conditions and improve leaf nitrogen content and photosynthetic efficiency. In addition, canopy structure and light environment are important factors influencing canopy light-use efficiency. Under low-light conditions in winter, appropriate leaf area and supplemental lighting can improve canopy light interception and CO_2 assimilation efficiency, thereby increasing female flower number, fruit dry matter accumulation, and total yield (Koo et al., 2024).

4.2 Hormonal regulatory mechanisms

Plant hormones are important endogenous signals regulating cucumber yield formation. By coordinating vegetative growth, reproductive development, and fruit formation processes, hormones directly influence cucumber fruiting ability and yield level. Cucumber is a typical monoecious crop with separate male and female flowers, and its female flower formation, fruit set stability, and fruit enlargement processes are highly dependent on hormonal balance. Hormones such as auxin, gibberellins (GA), ethylene, cytokinins, and abscisic acid (ABA) not only participate in sex differentiation and floral organ development but also influence fruit formation by regulating cell division, cell expansion, and assimilate transport (Baral et al., 2025). Therefore, hormonal regulation essentially constitutes an important physiological basis for “sink formation” and yield establishment in cucumber.

Ethylene is an important regulator of sex expression in cucumber and generally promotes female flower formation and increases the proportion of female flowers. Materials with stronger ethylene synthesis capacity often exhibit lower node positions of the first female flower and higher fruit-setting ability, thereby showing stronger early fruiting potential. Meanwhile, auxin and GA play key roles during fruit development. Auxin mainly participates in ovary development, cell division, and cell expansion, whereas GA regulates vine elongation, floral organ formation, and early fruit growth. Studies have shown that hormone signaling pathways mediated by Aux/IAA, ARF, and GA signaling components regulate cell proliferation and expansion during the early stages of fruit development, whereas ABA and ethylene levels gradually increase during fruit maturation (Baral et al., 2025). Dynamic changes in these hormonal signals collectively determine fruit formation efficiency and final yield performance.

Studies on cucumber parthenocarpy further demonstrate the important role of hormonal balance in maintaining stable fruit set and continuous fruiting. Materials with strong parthenocarpic ability generally exhibit higher cytokinin and GA levels but relatively lower ABA levels. Exogenous application of cytokinins, auxin, or GA_{4+7} can induce parthenocarpic fruit formation in weakly parthenocarpic materials. These processes are accompanied by enhanced expression of cytokinin synthesis and response genes and reduced expression of ABA signaling receptors, indicating that higher levels of promotive hormones are beneficial for maintaining stable fruit set. In addition, hormones such as brassinosteroids, melatonin, and ethylene also participate in fruit formation regulation, while synergistic and antagonistic interactions among different hormonal pathways further increase the complexity of cucumber yield formation mechanisms.

4.3 Environmental regulatory mechanisms

Cucumber yield formation is highly sensitive to environmental conditions. Factors such as temperature, light, CO_2 concentration, water availability, and root-zone environment can regulate yield formation by influencing photosynthesis, hormone metabolism, and reproductive development. Environmental factors not only determine plant assimilate production capacity but also affect female flower differentiation, fruit set, and fruit enlargement by regulating hormonal signaling pathways involving ethylene, auxin, GA, and ABA (Aparna et al., 2023). Under the background of climate change, stresses such as high temperature, drought, low light, and waterlogging often lead to reduced photosynthetic efficiency, imbalance between source and sink relationships, and restricted fruit development, thereby decreasing cucumber yield stability.

Temperature and light are key environmental factors affecting cucumber yield formation. Low-temperature conditions inhibit photosynthesis and root absorption capacity, impair floral organ development, and cause flower and fruit abortion, whereas high temperatures increase transpiration, reduce photosynthetic efficiency, and negatively affect gamete viability and fruit set rate (Aparna et al., 2023). Meanwhile, prolonged low-light conditions easily induce excessive elongation growth, reduce leaf functional capacity, and inhibit female flower differentiation, thereby restricting yield formation in greenhouse cucumber production. Supplemental lighting combined with CO_2 fertilization can effectively enhance photosynthetic source strength and increase female flower number, fruit dry matter accumulation, and total yield (Koo et al., 2024). Furthermore, optimization of greenhouse light environments based on cucumber light response characteristics can further improve canopy light-use efficiency and greenhouse production efficiency.

Water availability and root-zone environment also significantly affect cucumber yield formation. Cucumber possesses a relatively shallow root system and is highly sensitive to changes in soil moisture. Water deficit inhibits photosynthesis and cell turgor, thereby restricting fruit enlargement, whereas excessive water accumulation can cause root hypoxia and disease occurrence, reducing CO_2 assimilation efficiency and PSII photochemical activity. Under protected cultivation conditions, coordinated management of CO_2 concentration, temperature, light, water, and fertilizer can effectively improve dry matter accumulation and fruit quality. Studies have shown that the combination of elevated CO_2 and appropriate temperature not only promotes the accumulation of sugars, organic acids, and amino acids but also enhances fruit heat tolerance under high-temperature conditions while maintaining yield stability (Du et al., 2024). Therefore, under climate change scenarios, combining precise environmental regulation in protected cultivation systems with the breeding of stress-resistant genotypes is an important strategy for improving cucumber yield stability and resource-use efficiency.

5 Molecular Mechanisms of Cucumber Yield Formation

5.1 Yield-related functional genes

Cucumber yield formation is a complex process jointly determined by multiple genes, loci, and regulatory pathways, involving vegetative growth, sex differentiation, floral organ formation, fruit set, fruit enlargement, organ size regulation, and stress responses. With the continuous advancement of cucumber genomics, fine QTL mapping, and functional genomics studies, an increasing number of functional genes and major-effect QTLs closely associated with yield component traits have been identified, providing an important foundation for elucidating the mechanisms underlying high-yield formation and for conducting molecular design breeding in cucumber. Yield-related functional genes in cucumber mainly affect final yield through the regulation of fruit morphology, organ size, source-sink relationships, and stress adaptability.

Fruit length, fruit diameter, fruit shape index, and single fruit weight are core traits constituting cucumber yield and are also the major focus of current functional gene studies. The major fruit shape QTL FS5.2 has been finely mapped to a 95.5-kb interval, and its candidate gene, CsCRC, encodes a YABBY transcription factor that influences fruit morphology by regulating cell length and cell layer number, resulting in the short and thick fruit phenotype of Xishuangbanna cucumber. CsTRM5, a homolog of tomato TRM5, controls the round-fruit locus FS2.1, and loss of its function alters the direction of cell division and weakens cell expansion, thereby producing spherical fruits (Xie et al., 2023). In addition, CsSUN, located at the FS1.2 locus, is a homolog of the SUN gene and contains a 161-bp deletion in round-fruit types, significantly affecting the fruit length-to-diameter ratio. These studies indicate that cell division orientation, cell layer number, and cell expansion processes are important cytological bases determining cucumber fruit morphology and single fruit weight.

In addition to fruit morphology-related genes, some functional genes can influence yield by regulating leaf size, photosynthetic source strength, organ development, and continuous fruiting ability. The R2R3-MYB transcription factor CsRAXs suppresses leaf size and continuous fruiting ability by promoting auxin glycosylation. Its triple mutants exhibit larger leaves, higher fruit number per plant, and higher yield, whereas overexpression lines display reduced leaf area and fruit number (Chen et al., 2024). The littleleaf (LL) gene encodes a WD40 protein that restricts cucumber organ size and is closely associated with the expression of organ size regulators and hormone-related genes (Xu et al., 2023). SF1 encodes a RING-type E3 ubiquitin ligase that regulates fruit elongation through ethylene-dependent cell division processes (Xie et al., 2023). To date, 81 simply inherited genes or major-effect QTLs and 322 QTLs associated with 42 quantitative traits have been systematically identified in cucumber, many of which are related to fruit size, fruit shape, fruit number, and other yield component traits, and diagnostic markers applicable to breeding have been developed. In addition, heat shock proteins, antioxidant enzymes, hormone signaling factors, and members of transcription factor families such as

MYB, NAC, WRKY, bHLH, and ERF/AP2 can maintain fruit-setting ability and yield stability by regulating photosynthetic stability, hormonal balance, and stress responses.

5.2 Signal transduction and regulatory networks

Cucumber yield formation depends not only on the effects of individual functional genes but also on the coordinated regulation of complex signal transduction and transcriptional regulatory networks. Plant hormone signaling serves as an important bridge linking functional genes, cellular development, and yield phenotypes. Hormones such as ethylene, auxin, gibberellins, cytokinins, and abscisic acid participate in sex differentiation, floral organ formation, parthenocarpy, fruit elongation, and organ size regulation through synergistic or antagonistic interactions. The dynamic balance among different hormonal pathways determines fruit set stability, fruit development efficiency, and final yield level in cucumber. Therefore, shifting from single-gene effects to integrated regulatory networks is an important direction for understanding the molecular mechanisms of cucumber yield formation.

Within the fruit morphology regulatory network, CsCRC acts as an important hub connecting transcriptional regulation, hormone signaling, and cellular development. FS5.2/CsCRC regulates auxin content and the expression of auxin-responsive genes, linking YABBY-mediated transcriptional regulation with auxin-regulated cell division and cell expansion processes. Meanwhile, gibberellin signaling also participates in CsCRC-dependent fruit elongation regulation. Further studies have shown that CsPIF1 can directly activate CsCRC transcription, whereas the YABBY protein CsINO and the bHLH protein CsSPT1 physically interact with CsCRC, thereby integrating light signaling, reproductive development, and auxin regulation into the fruit elongation process (Xie et al., 2023). Transcriptome analyses of near-isogenic lines with long and short fruits further revealed significant activation of microtubule-, cell cycle-, and hormone-related genes, while multiple transcription factor families, including MYB, bHLH, NAC, and ERF/AP2, were involved in fruit length regulation (Che et al., 2023; Xing et al., 2023).

Parthenocarpy is an important mechanism enabling greenhouse cucumber to maintain stable yield under insufficient pollination, low-light conditions, or environmental stresses, and its formation also depends on precise hormonal network regulation. Materials with strong parthenocarpic ability generally exhibit higher cytokinin and gibberellin levels and lower ABA levels, accompanied by upregulated expression of cytokinin biosynthesis and response genes as well as auxin signaling components. Exogenous application of cytokinins, auxin, or GA_{4+7} can induce parthenocarpic fruit formation in weakly parthenocarpic materials. The GA biosynthesis gene CsGA20OX1 is considered a positive regulator of parthenocarpy, and both its expression level and related hormone contents are significantly increased in induced parthenocarpic fruits (Meng et al., 2026). In addition, LL-mediated organ size regulation is associated with auxin and cytokinin pathways, whereas CsTRM5-mediated fruit shape variation involves ABA accumulation and changes in the expression of genes related to cell wall formation and ABA signaling. Exogenous ABA can reduce fruit elongation by inhibiting cell expansion (Figure 2) (Xie et al., 2023; Xu et al., 2023). These findings indicate that cucumber yield formation results from the combined action of multi-level regulatory networks involving hormone signaling, transcriptional regulation, cell division, and cell expansion.

5.3 Multi-omics studies and molecular breeding

The development of multi-omics technologies has provided important tools for systematically elucidating the mechanisms underlying cucumber yield formation. Genomics can reveal genetic variation, structural variation, and candidate genomic regions among different materials; transcriptomics can analyze dynamic gene expression under different developmental stages and environmental conditions; and proteomics and metabolomics help clarify the relationships between yield formation and processes such as signal transduction, hormone metabolism, cell wall formation, sugar metabolism, and amino acid metabolism. Through integrated multi-omics analyses, researchers can construct molecular regulatory networks underlying high-yield formation in cucumber at multiple levels, including “gene-transcript-protein-metabolite-phenotype”.

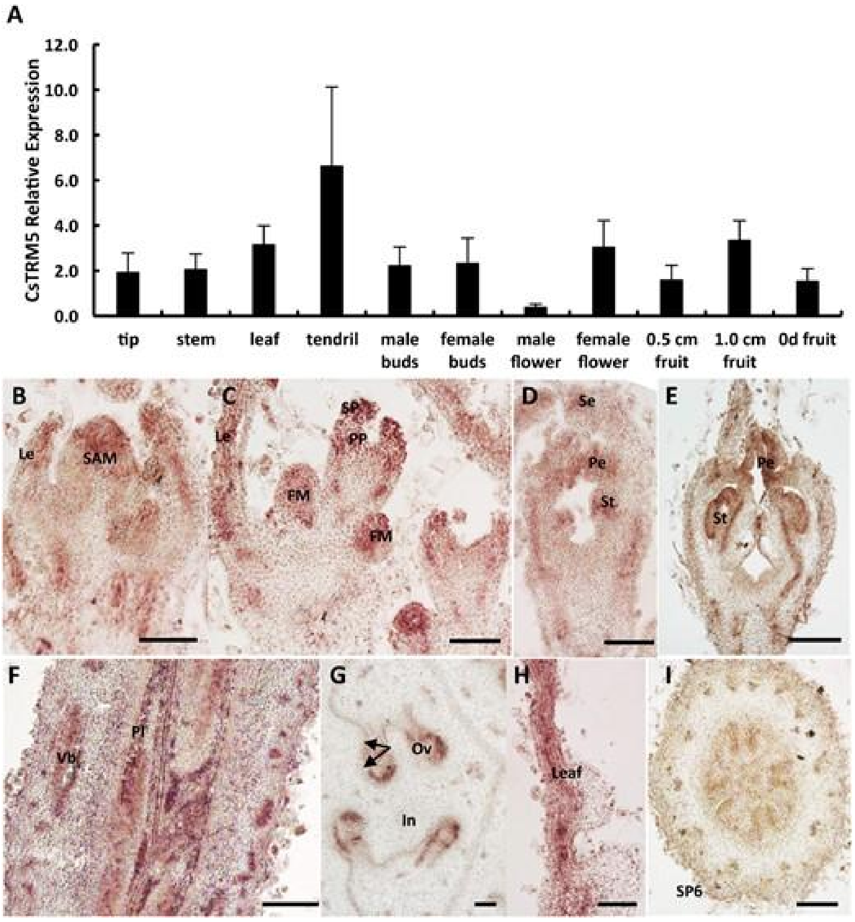

Figure 2 Expression pattern analysis of CsTRM5 in cucumber (Adopted from Xie et al., 2023)

Image caption: A Expression levels of CsTRM5 in different organs of 32X line detected by qRT-PCR. B-HIn situ hybridization of CsTRM5 in cucumber shoot tip (B), leaf (H), and floral organs (C-G). I, Negative control of CsTRM5 sense probe in fruit cross-section. Le, leaf; SAM, shoot apical meristem; FM, floral meristem; SP, sepal primordium; PP, petal primordium; Se, sepal; Pe, petal; St, stamen; Vb, vascular bundle; Pl, placenta; Ov, ovule; In, integument. Scale bars: 100 µm (Adopted from Xie et al., 2023)

In studies of fruit size and fruit shape, multi-omics approaches have demonstrated significant advantages. RNA-seq analysis of FS5.2 near-isogenic lines identified hundreds of differentially expressed genes mainly enriched in auxin biosynthesis and signaling, cell cycle regulation, and cell wall formation, thereby establishing the CsCRC-mediated regulatory network controlling fruit size and shape. Comparative transcriptome analyses of early fruits from materials with different fruit lengths identified 3,955 differentially expressed genes, including numerous microtubule-related genes, cell cycle genes, and members of various transcription factor families, providing genome-wide evidence for fruit length regulation. In addition, combined analyses using QTL-seq, bin-map resequencing, and RNA-seq identified multiple major-effect fruit length QTLs and differentially expressed genes related to auxin efflux carriers and hormone signaling, thereby providing important evidence for candidate gene mining (Che et al., 2023; Xing et al., 2023). In studies of parthenocarpy and stable fruit set, integrated transcriptomic and metabolomic analyses linked the GA biosynthesis gene CsGA20OX1 and hormone pathways with GA-mediated parthenocarpic fruit development, indicating that multi-omics integration can effectively identify key regulators controlling stable fruit set and yield formation (Meng et al., 2026). Moreover, continuous omics studies in cucumber have identified numerous candidate genes associated with fruit length, locule formation, parthenocarpy, and fruit quality traits, thereby providing theoretical support for marker-assisted selection, genomic selection, and molecular design breeding.

The development of molecular breeding technologies is promoting the transition of cucumber yield improvement from empirical selection to precision breeding. Marker-assisted selection (MAS) can rapidly identify superior materials using markers tightly linked to target traits; genomic selection (GS) can predict breeding values of complex quantitative traits based on genome-wide markers; and CRISPR/Cas gene-editing technology enables precise modification of key functional genes. Currently, systematic gene and QTL databases, developed diagnostic markers, and continuously expanding functional gene studies are building molecular tool systems for pyramiding superior alleles associated with fruit size, organ size, parthenocarpy, continuous fruiting ability, and stress resistance. In the future, integrated “pan-omics” platforms combining genomics, transcriptomics, proteomics, metabolomics, phenomics, machine learning, and gene editing will become an important direction for accelerating high-yield and stable-yield cucumber breeding (Roychowdhury et al., 2023).

6 Effects of Cultivation Techniques on Yield Formation

6.1 Environmental regulation in protected cultivation

Protected cultivation is an important production system for achieving high and stable cucumber yield. Its core advantage lies in the artificial regulation of key environmental factors, including temperature, light, humidity, CO_2 concentration, and root-zone conditions, thereby creating relatively suitable ecological conditions for vegetative growth, reproductive development, and fruit enlargement. Cucumber is a thermophilic crop; low temperatures inhibit root vigor, nutrient uptake, and photosynthetic metabolism, whereas high temperatures can reduce pollen viability, decrease fruit set rate, hinder fruit development, and accelerate plant senescence. Therefore, in protected cultivation systems, maintaining appropriate day and night temperatures through ventilation, shading, covering, heating, cooling, and misting is an important basis for sustaining continuous fruiting and high yield formation. Comparative studies of commercial greenhouses have shown that optimized heating, cooling, and semi-hydroponic systems can significantly increase winter cucumber yield per plant and improve chlorophyll fluorescence parameters, indicating that low-stress and near-optimal environments are beneficial for maintaining high photosynthetic activity and productivity. Microclimate monitoring in polyethylene greenhouses has also demonstrated that appropriate natural ventilation and mist cooling can effectively reduce greenhouse temperature and maintain cucumber growth within a more suitable temperature range.

Light conditions are another key limiting factor affecting yield formation in protected cucumber cultivation. During winter and spring greenhouse production, insufficient natural light often leads to excessive stem elongation, reduced leaf functionality, inadequate female flower differentiation, and slow fruit enlargement. Therefore, optimizing canopy structure, implementing proper pruning practices, supplementary lighting, and spectral regulation are important measures for improving light energy utilization efficiency in protected cucumber populations. Different covering materials and light-conversion films can influence photosynthesis and yield performance by altering greenhouse spectral composition, temperature, and vapor pressure deficit (VPD). Near-infrared reflective plastic films can reduce greenhouse temperature and VPD, enhance photosynthetic rate and transpiration, and improve fruit characteristics and yield. Red-orange light-enhancing films (RPO) can increase photosynthetically active radiation, promote cucumber yield and nutritional quality, and simultaneously affect auxin content and related gene expression in the fruit pedicel (Li et al., 2024). These studies indicate that greenhouse covering materials and light-environment regulation not only affect source strength formation but also further influence fruit set and fruit development processes.

With the development of intelligent protected agriculture, environmental regulation technologies based on sensors, crop models, and machine learning have gradually been applied in cucumber production. Yield prediction and greenhouse microclimate modeling studies have shown that total radiation and air temperature are important environmental factors determining weekly greenhouse cucumber yield (Hong et al., 2024). Integrating light intensity, temperature, and CO_2 concentration with photosynthetic response models can dynamically optimize light saturation points, photosynthetic rates, and environmental control strategies, thereby improving production stability under different climatic and radiation conditions (Bello et al., 2023). Therefore, environmental regulation in protected cucumber cultivation is transitioning from experience-based management to model-driven and intelligent decision-making systems, with the goal not merely of optimizing individual environmental factors but of achieving coordinated optimization of temperature, light, gas exchange, water, and nutrient conditions.

6.2 Water and fertilizer management techniques

Water and nutrient supply constitute the important material basis for high cucumber yield formation. Cucumber has a relatively shallow root system and is sensitive to root-zone moisture and aeration conditions. Appropriate irrigation promotes root growth, nutrient uptake, photosynthesis, and fruit enlargement, whereas prolonged water deficit causes leaf wilting, reduced photosynthetic rate, flower and fruit abortion, and restricted fruit development. Excessive irrigation, however, can lead to root-zone hypoxia, nutrient leaching, and increased disease incidence. Nitrogen, phosphorus, and potassium are the primary nutrients required for cucumber growth and yield formation. Nitrogen affects leaf growth and photosynthetic capacity, phosphorus promotes root development and floral bud differentiation, and potassium participates in assimilate transport, fruit enlargement, and fruit quality formation. Micronutrients such as calcium, magnesium, and boron are also closely associated with cell wall stability, enzyme activity regulation, and fruit quality. Studies on multi-nutrient optimization have demonstrated that irrigation and nitrogen fertilizer significantly promote cucumber yield, whereas magnesium can improve reducing sugar and amino acid contents and alleviate nitrogen deficiency effects through interactions with nitrogen, thereby reducing nitrate accumulation (Li et al., 2023).

Integrated water and fertilizer management technologies can simultaneously deliver water and nutrients to the root zone through drip irrigation systems, enabling precise supply, improving water and fertilizer use efficiency, and reducing resource waste and environmental risks. Under arid climatic conditions, experiments combining different irrigation levels and nitrogen fertilizer rates have shown that moderate deficit drip irrigation combined with appropriate nitrogen application can achieve relatively high yield while improving fruit size and SPAD values, indicating that moderate water-saving practices do not necessarily reduce cucumber yield (Bello et al., 2023). Greenhouse soil cultivation studies have also shown that moderate irrigation combined with suitable nitrogen fertilizer application can achieve near-maximum yield, high water-use efficiency, and desirable fruit quality, whereas excessive nitrogen application may slightly increase yield but reduce nitrogen-use efficiency. Therefore, the key to cucumber water and fertilizer management lies not in simply increasing inputs but in achieving coordinated water and nitrogen supply according to plant demand, cultivation substrate, and environmental conditions.

In substrate cultivation, solar greenhouse systems, and high-input protected cultivation systems, the interaction between water and fertilizer exerts even greater influence on cucumber yield and resource-use efficiency. Studies on substrate bag cultivation have shown that high irrigation levels combined with standard nutrient solution application can achieve the highest yield, whereas appropriately reducing fertilizer application improves nitrogen-use efficiency. Meanwhile, water-use efficiency tends to decrease with increasing irrigation levels. Studies conducted in solar greenhouses on the North China Plain further demonstrated that sufficient water and fertilizer supply can maximize leaf area index, dry matter accumulation, and yield, whereas moderate reductions in water and fertilizer input have relatively small effects on yield but significantly improve water- and nitrogen-use efficiency and may even enhance fruit quality under certain conditions (Wang et al., 2025). In addition, aerated irrigation can alleviate root-zone hypoxia under high water and fertilizer conditions, thereby increasing cucumber yield and nitrogen-use efficiency. These findings indicate that efficient water and fertilizer management in cucumber production should shift from the concept of “high input for high yield” toward the coordinated improvement of yield, quality, and resource-use efficiency.

6.3 Optimization of cultivation patterns

Optimization of cultivation patterns is an important strategy for improving canopy light-use efficiency, source-sink coordination, and yield per unit area in cucumber. It mainly includes planting density, row spacing configuration, pruning method, vine training method, pruning timing, and spatial arrangement. Traditional high-density planting systems can increase plant number per unit area, but excessive density often causes canopy overcrowding, poor ventilation and light penetration, premature senescence of lower leaves, and increased disease incidence, thereby restricting fruit set and fruit enlargement. Modern greenhouse cucumber production places greater emphasis on optimizing population structure by adjusting planting density, stem number, and spatial leaf distribution to achieve balance among yield per unit area, productivity per plant, and fruit quality. Greenhouse experiments have shown that under natural light conditions, moderately reducing planting density does not reduce weekly or total yield per unit area but instead increases yield per plant, dry matter allocation to fruits, and nutritional quality while reducing nitrite content. However, in recirculating hydroponic systems with sufficient water and nutrient supply, higher planting density combined with double-stem pruning significantly increases total and marketable yield, indicating that the optimal density is not fixed but depends on greenhouse environment, cultivar type, and resource availability (Babatunde et al., 2023).

Pruning and vine training are important techniques for regulating canopy structure and assimilate allocation in protected cucumber cultivation. Appropriate pruning reduces the consumption of nonproductive branches and leaves, improves ventilation and light penetration, and promotes assimilate allocation to fruits. Greenhouse studies comparing different planting densities and pruning methods have shown that higher density and double-stem pruning increase total and marketable yield but reduce fruit diameter, reflecting the trade-off between fruit number and fruit size. Comparative studies of single-stem pruning and natural growth in different cucumber cultivars have also demonstrated that both cultivar type and pruning method significantly influence plant height, leaf area, biomass allocation, and production performance. Single-stem pruning promotes biomass allocation to reproductive organs and alters root-to-shoot ratio and tissue water content (Cheng et al., 2025). Therefore, pruning strategies should be optimized according to cultivar vigor, target yield, fruit size requirements, and cultivation environment rather than simply maximizing branch number or fruit number.

Row spacing configuration and spatial arrangement also affect cucumber canopy light environment, water and fertilizer supply efficiency, and convenience of field management. In solar greenhouses, wide-narrow row configurations combined with drip irrigation lines arranged in narrow rows while wide rows serve as operation channels can improve ventilation and light conditions in the middle and lower canopy while simultaneously accommodating efficient water and fertilizer supply and field management requirements (Wang et al., 2025). In addition, emerging cultivation systems such as substrate cultivation, soilless cultivation, vertical cultivation, and recirculating hydroponics can improve root-zone conditions and enhance land-use and resource-use efficiency, representing important directions for green and efficient cucumber production in protected cultivation systems. Overall, the core objective of cultivation pattern optimization is not to identify a single optimal parameter but to establish integrated cultivation schemes based on cultivar characteristics, greenhouse type, light and temperature conditions, water and fertilizer supply, and market demand in order to achieve coordinated improvement of high yield, superior quality, stable production, and efficient resource utilization.

7 Existing Problems and Future Development Trends

7.1 Current problems in research

Although significant progress has been made in recent years regarding cucumber yield-related traits and their formation mechanisms, the dissection of complex quantitative traits still faces considerable challenges. Cucumber yield is jointly influenced by multiple genes, regulatory networks, environmental factors, and genotype-by-environment interactions, exhibiting characteristics of polygenic control, small genetic effects, and strong environmental sensitivity. Numerous QTLs and functional genes have been reported, including 81 simply inherited genes or major-effect QTLs and 322 QTLs associated with 42 traits; however, these data remain fragmented, and QTL nomenclature systems, cross-population comparisons, and integration standards have not yet been unified. Only a limited number of loci have been successfully cloned, functionally validated, and widely applied in breeding practice. In addition, many identified QTLs explain only a small proportion of phenotypic variation, and insufficient attention has been paid to QTL-by-environment interactions, limiting the application of stable high-yield traits across different ecological regions and cultivation systems.

Insufficient exploitation and utilization of cucumber germplasm resources also represent important constraints on yield improvement. Although large numbers of landraces, wild relatives, and breeding materials are conserved worldwide, practical breeding still faces problems such as inadequate mining of superior alleles, narrow genetic backgrounds of parental lines, and repeated use of core germplasm. Long-term directional selection has promoted improvements in fruit quality, maturity, and adaptation to protected cultivation, but it may also reduce genetic diversity in certain market types, thereby limiting further genetic gain in yield. For example, the yield improvement of processing cucumbers in the United States has shown little progress over the past 15 years despite long-term selection, suggesting that reliance solely on conventional selection may be insufficient to overcome yield plateaus.

The application of molecular breeding technologies to the improvement of complex yield traits still faces several bottlenecks. Because yield is generally controlled by multiple loci with small effects, the efficiency of marker-assisted selection (MAS) for complex yield traits remains limited, and the transferability of markers across different market types and genetic backgrounds is often inadequate. For example, background-selection SNP markers developed for Korean Baekdadagi-type cucumber exhibit reduced polymorphism in other materials, requiring the establishment of specialized marker systems. Even for major-effect traits, the lack of tightly linked and breeding-applicable markers can limit their practical use. Breeding for cucumber vein yellowing virus resistance was greatly constrained before the fine mapping of the CsCvy-1 gene and the development of KASP markers. Furthermore, candidate genes, QTLs, and regulatory mechanisms identified under laboratory or single-environment conditions still require validation across multiple locations, seasons, and cultivation systems to assess their stability and breeding value. This is particularly important under protected cultivation conditions, where temperature, light, CO_2 concentration, water and fertilizer supply, diseases, pests, and management practices interact strongly. Therefore, the translation of fundamental research findings into practical production systems remains a major challenge.

7.2 Future directions driven by emerging technologies

With the rapid development of modern biotechnology, information technology, and intelligent agriculture, research on cucumber yield formation mechanisms is shifting from single-gene and single-trait analyses toward multi-omics, multi-environment, and data-driven systematic investigations. High-quality reference genomes, saturated SNP genetic maps, and genotyping platforms based on SLAF-seq, GBS, and resequencing technologies have provided important tools for high-density QTL mapping of fruit size, branching, flowering traits, parthenocarpy, and other yield-related traits. Some identified loci can explain a substantial proportion of phenotypic variation and provide important foundations for fine mapping and gene cloning (Wang et al., 2024). In the future, greater emphasis should be placed on comparisons among different genetic backgrounds, cultivation environments, and market types to improve the stability and breeding applicability of key loci.

Multi-omics technologies will further enhance the dissection of complex yield traits in cucumber. Next-generation sequencing, transcriptomics, metabolomics, and proteomics can generate large amounts of molecular marker, expression, and metabolic regulatory data, thereby supporting genome-wide association studies (GWAS), haplotype mapping, candidate gene mining, and stress adaptation research. Future studies should strengthen the integration of genomic, transcriptomic, proteomic, metabolomic, phenomic, and environmental data to construct association models linking “genes-regulatory networks-physiological processes-yield phenotypes-cultivation environments.” Such approaches will promote the transition from single candidate-gene analysis to comprehensive dissection of complex regulatory networks.

Gene editing, high-throughput phenotyping, and artificial intelligence technologies will become major driving forces in high-yield cucumber breeding. CRISPR/Cas systems enable precise modification of key functional genes. For example, targeted knockout of the cucumber eIF4E gene has produced non-transgenic materials with broad-spectrum resistance to multiple RNA viruses without causing significant negative effects on yield, demonstrating that precise gene editing can rapidly achieve durable disease resistance and indirectly stabilize yield. In the future, gene editing should be integrated with MAS, genomic selection (GS), and multi-omics-based candidate gene mining to pyramid superior alleles related to high yield, superior quality, disease resistance, stress tolerance, and adaptation to protected cultivation systems (Bhat et al., 2023; Kumar et al., 2024). Meanwhile, intelligent phenotyping systems based on image recognition, automated sensors, three-dimensional reconstruction, unmanned platforms, and machine learning can continuously monitor plant architecture, leaf area, flowering dynamics, fruit development, and stress responses, thereby providing important support for predicting gene-trait relationships, optimizing hybrid combinations, and designing ideal plant architectures (Bhat et al., 2023; Farooq et al., 2024; Zhu et al., 2024).

7.3 Prospects for high-yield cucumber breeding

Future high-yield cucumber breeding will increasingly rely on the deep integration of conventional breeding, molecular breeding, intelligent phenotyping, and digital decision-making technologies. Existing gene and QTL databases, together with gradually standardized nomenclature systems, provide important foundations for constructing genome-wide resource libraries of yield-related loci, plant architecture loci, sex expression loci, and disease-resistance QTLs, thereby facilitating the pyramiding of superior genes through MAS and marker-assisted backcrossing (Dhall et al., 2023). Studies on multi-pistillate flowering QTLs, the parthenocarpy locus Parth2.1, sex expression, and fruit diameter indicate that multiple genetic factors affecting fruit number and fruit size can be effectively pyramided through molecular breeding approaches, enabling the development of ideal high-yield plant architectures adapted to different market types and production systems (Wang et al., 2024).

Future breeding objectives will shift from the simple pursuit of high yield toward the coordinated improvement of high yield, superior quality, stable production, stress resistance, and resource-use efficiency. As consumer demands for fruit quality, nutritional value, and food safety continue to increase, new cucumber cultivars should not only possess high yield potential but also exhibit excellent marketability, enhanced nutritional quality, strong disease and stress resistance, and adaptability to water-saving, fertilizer-saving, low-pesticide-input, and intelligent greenhouse management systems. Particularly under the background of climate change, breeding cultivars resistant to low temperature, low light, high temperature, salinity, and multiple diseases will become an important strategy for ensuring stable vegetable supply in protected horticulture systems (Mirzwa-Mróz et al., 2024).

Accelerated breeding technologies will substantially shorten the breeding cycle of new cucumber cultivars and improve selection efficiency for complex yield traits. Doubled haploid (DH) technology, rapid generation advancement, speed breeding in greenhouses, high-throughput phenotyping, and artificial intelligence-assisted selection can be integrated with GS and molecular design breeding to improve prediction accuracy and breeding efficiency for complex traits (Bhat et al., 2023). At the same time, multi-omics studies will further elucidate the regulatory networks underlying yield formation and stress adaptation and guide precise gene editing and molecular marker design (Mirzwa-Mróz et al., 2024). It can be anticipated that with the integrated development of genomics, phenomics, artificial intelligence, gene editing, and intelligent protected agriculture, high-yield cucumber breeding will gradually enter a new stage characterized by precision, intelligence, and sustainability.

8 Concluding Remarks

Cucumber is one of the most important vegetable crops worldwide, with an annual global production reaching tens of millions of tons. It has extremely high market demand in major producing countries such as China; therefore, improving and stabilizing cucumber yield is of great economic and food-supply significance. Cucumber yield is determined by multiple interacting traits, including earliness, sex expression, fruit number and size, and resistance to biotic and abiotic stresses. The genetic basis of these traits is being progressively elucidated through QTL mapping, mutant analysis, and molecular characterization. Owing to its relatively small genome, diploid structure, short life cycle, and abundant natural and artificial genetic variation, cucumber has become an ideal model crop for dissecting yield-related traits and rapidly applying research findings to breeding practice.

To date, systematic studies have identified at least 81 simply inherited genes or major-effect QTLs, as well as 322 QTLs associated with 42 quantitative traits, many of which are directly or indirectly related to cucumber yield, fruit size and shape, flowering time, sex expression, and stress resistance. Wild ancestral species and diverse landraces provide rich allelic resources for flowering traits, fruit size, and yield components. Some QTLs exhibit clear signatures of domestication and improvement selection; however, positive transgressive segregation can still occur when favorable wild alleles are introgressed into elite cultivated backgrounds. Fine mapping and cloning studies of major fruit-size QTLs, such as FS5.2/CsCRC, and parthenocarpy QTLs, such as Parth2.1, have demonstrated that their regulatory mechanisms mainly involve auxin, gibberellin, and cytokinin signaling pathways, as well as the regulation of cell division and expansion, thereby revealing how genetic variation is translated into different yield architectures. Meanwhile, studies on sex expression, multi-pistillate flowering, and parthenocarpy have identified multiple key loci and marker-trait associations, further clarifying the genetic networks underlying increased female flower production and enhanced fruit set and their contributions to yield formation.

Future breeding for high-yield cucumber cultivars will increasingly rely on the integrated application of genomic resources, multi-omics data, and advanced selection technologies. Comprehensive gene/QTL databases, high-density SNP molecular markers, and background-selection marker systems provide powerful tools for the precise pyramiding of favorable alleles related to yield, quality, and stress resistance. Genomic selection (GS), genome-wide association studies (GWAS), and gene-editing technologies, combined with rapid generation advancement and efficient phenotyping approaches, are expected to accelerate the development of ideal cucumber plant types possessing desirable fruit size, high female flower ratio, multi-pistillate flowering ability, stable parthenocarpy, and broad stress resistance. At the same time, continuous exploration of wild resources and underutilized germplasm, as well as further dissection of domestication-related QTLs and heterosis-associated loci, will broaden the allelic resource pool for high-yield and stable-yield cucumber breeding. Overall, the integration of conventional breeding approaches with genomics and molecular biology technologies has made cucumber an important crop in which high and stable yield can be achieved through the rational design and targeted pyramiding of yield-related traits.

Conflict of Interest Disclosure

The authors affirm that this research was conducted without any commercial or financial relationships that could be construed as a potential conflict of interest.

References

Aparna A., Skarzyńska A., Pląder W., and Pawełkowicz M.E., 2023, Impact of climate change on regulation of genes involved in sex determination and fruit production in cucumber, Plants, 12(14): 2651.
https://doi.org/10.3390/plants12142651

Babatunde A., Deborah R., Gan M., and Simon T., 2023, Effects of plant density and stem pruning on plant biomass yield and economic benefits in a low-cost gravel bed aquaponic system, Journal of Applied Aquaculture, 35(4): 837-863.
https://doi.org/10.1080/10454438.2022.2033664

Baral R., Vainer A., Melzer S., Hause B., and Panda S., 2025, “Bud to fruit”-hormonal interactions governing early fruit development, Journal of Experimental Botany, 76(22): 6657-6673.
https://doi.org/10.1093/jxb/eraf363

Bello A.S., Huda S., Chen Z., Khalid M.A., Alsafran M., and Ahmed T., 2023, Evaluation of nitrogen and water management strategies to optimize yield in open field cucumber (*Cucumis sativus* L.) production, Horticulturae, 9(12): 1336.
https://doi.org/10.3390/horticulturae9121336

Bhat J.A., Feng X., Mir Z.A., Raina A., and Siddique K.H.M., 2023, Recent advances in artificial intelligence, mechanistic models and speed breeding offer exciting opportunities for precise and accelerated genomics-assisted breeding, Physiologia Plantarum, 175(5): e13969.
https://doi.org/10.1111/ppl.13969

Che G., Song W., and Zhang X., 2023, Gene network associates with CsCRC regulating fruit elongation in cucumber, Vegetable Research, 3: 7.
https://doi.org/10.48130/vr-2023-0007

Chen J.C., Liu L., Chen G.X., Wang S.Y., Liu Y.Q., Zhang Z.Y., Li H.F., Wang L.M., Zhou Z.Y., Zhao J.Y., and Zhang X.L., 2024, CsRAXs negatively regulate leaf size and fruiting ability through auxin glycosylation in cucumber, Journal of Integrative Plant Biology, 66(5): 1024-1037.
https://doi.org/10.1111/jipb.13655

Cheng C., Dong C.Y., Wu L., Wu Y., Wang J.L., Gong Z.H., Feng L.P., Li Z.F., Yang F.Y., and Zheng S.H., 2025, Interaction effects of cucumber varieties and pruning methods across different growth stages, Horticulturae, 11(5): 464.
https://doi.org/10.3390/horticulturae11050464

Dey S.S., Sagar V., Kujur S.N., Priyanka N., Munshi A.D., Pandey S., and Behera T.K., 2023, Cucumber: breeding and genomics, Vegetable Science, 50(Special): 208-220.
https://doi.org/10.61180/vegsci.2023.v50.spl.07

Dhall R.K., Kaur H., Manchanda P., and Kaur E., 2023, Genetics and marker-assisted breeding for sex expression in cucumber, Frontiers in Genetics, 14: 1180083.
https://doi.org/10.3389/fgene.2023.1180083

Du X., Song Y., Pan L., and Cui S., 2025, Optimizing cucumber (*Cucumis sativus* L.) fruit metabolomics under elevated CO_2 and high-temperature stress in the greenhouse, Horticulturae, 11(1): 10.
https://doi.org/10.3390/horticulturae11010010

El-Remaly E.A., and Shehata A.I., 2023, Egyptian cucumber germplasm genetic diversity as an approach for developing novel hybrids under heat stress conditions, Journal of Plant Production, 14(1): 1-11.
https://doi.org/10.21608/jpp.2022.179569.1199

Farooq M., Gao S., Hassan M.A., Huang Z., Rasheed A., Hearne S., Prasanna B.M., Li X., and Li H., 2024, Artificial intelligence in plant breeding, Trends in Genetics, 40(10): 891-908.
https://doi.org/10.1016/j.tig.2024.07.001

Hong I., Yu J., Hwang S., and Kwack Y., 2024, Estimation of cucumber fruit yield cultivated under different light conditions in greenhouses, Horticulturae, 10(10): 1117.
https://doi.org/10.3390/horticulturae10101117

Kaur T., Dhall R.K., Manchanda P., and Kumari P., 2024, Utilizing gynoecious cucumber (*Cucumis sativus* L.) inbreds to investigate inheritance of gynoecium, fruit yield and its contrasting traits, Genetika, 56(2): 255-269.
https://doi.org/10.2298/gensr2402255k

Koo J., Hwang H., Hwang J., Park E., Yu J., Yun J., Hwang S., Choi H., and Hwang S., 2025, Supplemental lighting and CO_2 enrichment on the growth, fruit quality, and yield of cucumber, Horticulture, Environment, and Biotechnology, 66: 77-85.
https://doi.org/10.1007/s13580-024-00638-y

Kumar R.R., Das S., Choudhury B.U., Kumar A., Prakash N., Verma R., Chakraborti M., Devi A.G., Bhattacharjee B., Das R., Das B., Devi H.L., Das B., Rawat S., and Mishra V.K., 2024, Advances in genomic tools for plant breeding: harnessing DNA molecular markers, genomic selection, and genome editing, Biological Research, 57: 80.
https://doi.org/10.1186/s40659-024-00562-6

Li J., Yang X., Zhang M., Li D., Jiang Y., Yao W., and Zhang Z., 2023, Yield, quality, and water and fertilizer partial productivity of cucumber as influenced by the interaction of water, nitrogen, and magnesium, Agronomy, 13(3): 772.
https://doi.org/10.3390/agronomy13030772

Li R., Gao Y., Cai B., Li G., Xue Z., Wang X., and Li Q., 2024, RPO film effectively promotes fruit quality and yield of cucumber through adjusting greenhouse environment and hormone contents, BMC Plant Biology, 24(1): 1250.
https://doi.org/10.1186/s12870-024-05946-0

Lin Y., Weng Y., Fei Z., and Grumet R., 2025, Mining the cucumber core collection: phenotypic and genetic characterization of morphological diversity for fruit quality characteristics, Horticulture Research, 12(3): uhae340.
https://doi.org/10.1093/hr/uhae340

Lnu R., Dhall R.K., Manchanda P., Kumari P., and Singathiya P., 2025, Study on characters associations and path coefficient analysis for yield and quality traits of parthenocarpic cucumber genotypes in poly-net house conditions, Discover Plants, 2: 15.
https://doi.org/10.1007/s44372-025-00103-9

Meng S., Wang K., Han Q., Xie Y., Li X., Song X., Jia J., Wang C., Yan L., Guo P., Zhang J., and Zhang J., 2026, Multi-omics analysis reveals the regulatory role of CsGA20OX1 in GA-mediated parthenocarpy of cucumber, Molecular Breeding, 46: 23.
https://doi.org/10.1007/s11032-026-01635-y

Mirzwa-Mróz E., Zieniuk B., Yin Z., and Pawełkowicz M.E., 2024, Genetic insights and molecular breeding approaches for downy mildew resistance in cucumber (*Cucumis sativus* L.): current progress and future prospects, International Journal of Molecular Sciences, 25(23): 12726.
https://doi.org/10.3390/ijms252312726

Negi C., Shah K.N., and Rana D.K., 2025, Evaluation of variability components and trait association in cucumber germplasm for yield contributing characters in Garhwal region of Uttarakhand, India, Ecology, Environment and Conservation, 31(Suppl. 2): S389-S394.
https://doi.org/10.53550/eec.2025.v31i02s.067

Patidar P., Kumar P., and Sharma C., 2024, Study on correlation and path coefficient analysis for certain quantitative traits in cucumber (*Cucumis sativus* L.), International Journal of Advanced Biochemistry Research, 8(9): 361-364.
https://doi.org/10.33545/26174693.2024.v8.i9e.2172

Roychowdhury R., Das S.P., Gupta A., Parihar P., Chandrasekhar K., Sarker U., Kumar A., Ramrao D.P., and Sudhakar C., 2023, Multi-omics pipeline and omics-integration approach to decipher plant's abiotic stress tolerance responses, Genes, 14(6): 1281.
https://doi.org/10.3390/genes14061281

Serhiienko O., Solodovnyk L., Harbovska T., Nemchenko S., Radchenko L., and Alsina I., 2025, Factors influencing the variability of the traits "yield," "earliness," and their components in breeding genotypes of cucumber in open field conditions, Vegetable and Melon Growing, (76): 6-13.
https://doi.org/10.32717/0131-0062-2024-76-6-13

Shukla H., Upadhyay D.K., Jha A., Paswan S.K., Singh A.K., and Yadav R.K., 2025, Genetic evaluation for variability, heritability and genetic advance in cucumber (*Cucumis sativus* L.) genotypes, Journal of Advances in Biology and Biotechnology, 28(6): 2500.
https://doi.org/10.9734/jabb/2025/v28i62500

Tadkal R., Rajasree V., Swarnapriya R., Senthil N., and Raveendran M., 2024, Exploring genetic variability, heritability, and genetic advance in growth and yield characteristics of cucumber (*Cucumis sativus*), International Journal of Advanced Biochemistry Research, 8(7): 1595.
https://doi.org/10.33545/26174693.2024.v8.i7sh.1595

Wang C., Qiang X., Wang K., Li H., Zhang X., Liu S., and Gong X., 2025, Optimization of water and nitrogen application rates for synergistic improvement of yield and quality in solar greenhouse cucumber production on the North China Plain, Plants, 14(9): 1285.
https://doi.org/10.3390/plants14091285

Wang W., Xu Z., Qian L., Hang S., Niu Y., Shen C., Wei Y., and Liu B., 2024, Genetic mapping and validation of QTL controlling fruit diameter in cucumber, BMC Plant Biology, 24(1): 1271.
https://doi.org/10.1186/s12870-024-06000-9

Xie Y., Liu X., Sun C., Song X., Li X., Cui H., Guo J., Liu L., Ying A., Zhang Z., Zhu X., Yan L., and Zhang X., 2023, CsTRM5 regulates fruit shape via mediating cell division direction and cell expansion in cucumber, Horticulture Research, 10: uhad007.
https://doi.org/10.1093/hr/uhad007

Xing Y., Cao Y., Yang Y., Wang F., Xin S., and Zhu W., 2023, QTL mapping and transcriptomic analysis of fruit length in cucumber, Frontiers in Plant Science, 14: 1208675.
https://doi.org/10.3389/fpls.2023.1208675

Xu N., Fang X., Xie K., Cheng S., Wang Y., Yang S., Zhu H., Sun S., Weng Y., and Yang L., 2023, Transcriptional and phytohormone regulatory network involved in LITTLELEAF-mediated organ size development in cucumber (*Cucumis sativus*), Scientia Horticulturae, 321: 112294.
https://doi.org/10.1016/j.scienta.2023.112294

Zhu W., Li W., Zhang H., and Li L., 2025, Big data and artificial intelligence-aided crop breeding: progress and prospects, Journal of Integrative Plant Biology, 67: 722-739.
https://doi.org/10.1111/jipb.13791