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Genetic Basis of Agronomic Traits in Cucumber: A Review of QTL Mapping Studies

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Abstract This study provides a comprehensive synthesis of the genetic basis underlying key agronomic traits in cucumber (*Cucumis sativus* L.), focusing on findings from quantitative trait loci (QTL) mapping studies. By analyzing over 300 QTLs across 42 traits, the review highlights the significant progress in identifying genetic markers associated with essential agronomic characteristics, including yield, fruit quality, disease resistance, and growth habits. Noteworthy discoveries include major QTLs such as Ef1.1, which influences early flowering, and FS5.2, a key regulator of fruit size and shape. These findings underscore the intricate genetic architecture governing cucumber traits and the potential for marker-assisted selection (MAS) to enhance breeding efficiency. The review also addresses challenges in the reproducibility and validation of QTLs across different genetic backgrounds and environments. Furthermore, the integration of next-generation sequencing technologies has bolstered QTL mapping precision, providing detailed genetic maps and facilitating candidate gene identification. Future directions involve leveraging gene-editing technologies like CRISPR/Cas9 and combining multi-omics approaches to further elucidate the regulatory networks underlying agronomic traits. The insights from QTL mapping not only advance cucumber breeding efforts but also set the foundation for developing resilient, high-yielding, and high-quality cucumber varieties to meet agricultural demands.

Keywords Cucumber (*Cucumis sativus* L.); Agronomic traits; QTL mapping; Genetic basis; Disease resistance; Fruit quality; Next-generation sequencing; CRISPR/Cas9; Cucumber breeding

1 Introduction

Cucumber (*Cucumis sativus* L.) is a globally significant vegetable crop, valued for its versatility and economic importance. It is cultivated extensively for both fresh consumption and processing purposes, contributing substantially to agricultural economies worldwide (Lee et al., 2020; Wang et al., 2020b). The crop's relatively short life cycle and self-compatible mating system make it an ideal candidate for genetic studies and breeding programs (Wang et al., 2020b).

Key agronomic traits in cucumber include yield, fruit quality, and disease resistance, all of which are critical for enhancing crop performance and meeting market demands. Yield-related traits such as fruit weight, length, and diameter are essential for maximizing production efficiency (Yuan et al., 2008; Zhu et al., 2016). Fruit quality traits, including flesh thickness and skin characteristics, are vital for consumer acceptance and marketability (Yuan et al., 2008; Miao et al., 2011). Disease resistance, particularly against pathogens like powdery mildew and downy mildew, is crucial for ensuring crop health and reducing losses (Lee et al., 2020; Wang et al., 2023). These traits are the primary focus of breeding programs aimed at improving cucumber varieties (Fazio et al., 2003; Bo et al., 2014).

Quantitative trait loci (QTL) mapping is a pivotal genetic tool used to identify loci associated with important agronomic traits. By linking phenotypic variation to specific genomic regions, QTL mapping facilitates the understanding of the genetic basis of complex traits (Yuan et al., 2008; Pan et al., 2017). This approach supports targeted breeding strategies, enabling the development of cucumber varieties with enhanced yield, quality, and disease resistance (Zhu et al., 2016; Wang et al., 2020b). The integration of high-density genetic linkage maps and next-generation sequencing technologies has further refined QTL mapping, making it a powerful method for genetic improvement in cucumbers (Zhu et al., 2016; Pan et al., 2022).

This study aims to review the current state of QTL (Quantitative Trait Loci) mapping research on key agronomic traits in cucumber, focusing on exploring the genetic basis of these traits. It summarizes the findings from various studies, highlights the significance of identified QTLs, and discusses their implications for cucumber breeding programs. The goal is to provide insights for future research and breeding strategies to enhance the improvement potential of this economically important crop.

2 Overview of Agronomic Traits in Cucumber

2.1 Description of key traits: yield, fruit quality, disease resistance, and growth habits

Cucumber (*Cucumis sativus* L.) is a globally significant vegetable crop, valued for its fresh and processed forms. The key agronomic traits in cucumber include yield, fruit quality, disease resistance, and growth habits. Yield in cucumber is influenced by several factors, including fruit size, fruit number, and flowering time. Quantitative trait loci (QTL) mapping has identified numerous QTLs associated with these traits. For instance, QTLs for fruit length and weight have been detected, with some explaining a significant portion of phenotypic variance (Wei et al., 2014; Zhu et al., 2016; Pan et al., 2022). Additionally, traits like fruit carpel number and sex expression also impact yield (Pan et al., 2020).

Fruit quality encompasses attributes such as fruit size, shape, flesh thickness, and skin characteristics. QTLs for fruit size and shape have been extensively studied, with major-effect QTLs identified on various chromosomes (Pan et al., 2017; Gao et al., 2020; Pan et al., 2022). For example, the QTL FS5.2 has been linked to fruit shape, influencing both longitudinal and radial growth (Pan et al., 2017). Other quality traits like fruit neck length are also controlled by specific QTLs, such as Fnl7.1, which encodes a late embryogenesis abundant protein (Xu et al., 2020).

Disease resistance is a critical trait for maintaining cucumber yield and quality. Numerous QTLs have been identified for resistance to various pathogens. For instance, the legendary cucumber inbred line WI2757 possesses resistance against nine pathogens, with QTLs mapped for powdery mildew resistance and other diseases (Lee et al., 2020; Pan et al., 2020). The identification of these QTLs facilitates marker-assisted selection in breeding programs (Wang et al., 2020b).

Growth habits, including flowering time and plant architecture, are essential for optimizing cucumber cultivation. QTLs for flowering time have been mapped, with some playing significant roles in photoperiod-dependent flowering (Pan et al., 2017). Additionally, traits like fruit stalk length and plant height are influenced by specific QTLs, contributing to the overall growth habit of the plant (Yuan et al., 2008).

2.2 Agronomic importance and challenges associated with each trait

High yield is a primary goal in cucumber breeding. However, achieving consistent high yields can be challenging due to environmental variability and the complex genetic basis of yield-related traits. The identification of stable QTLs across different environments is crucial for developing high-yielding varieties (Wei et al., 2014; Zhu et al., 2016).

Fruit quality directly affects marketability and consumer preference. Breeding for desirable fruit quality traits, such as size, shape, and texture, is challenging due to the polygenic nature of these traits. Fine mapping and cloning of major QTLs, like FS5.2 and Fnl7.1, are essential for improving fruit quality through marker-assisted selection (Pan et al., 2017; Xu et al., 2020; Pan et al., 2022).

Disease resistance is vital for sustainable cucumber production. The narrow genetic base of cucumber poses a challenge for breeding disease-resistant varieties. The identification and utilization of QTLs for disease resistance, such as those found in WI2757, are critical for developing resilient cultivars (Lee et al., 2020; Pan et al., 2020).

Optimizing growth habits is important for efficient cultivation and harvesting. Traits like flowering time and plant architecture need to be finely tuned to suit different growing conditions. The genetic complexity of these traits requires comprehensive QTL mapping and the development of molecular markers for effective breeding (Yuan et al., 2008; Pan et al., 2017).

3 QTL Mapping: Methodology and Techniques

3.1 Principles of QTL mapping and its applications in cucumbers

Quantitative trait loci (QTL) mapping is a statistical method that links phenotypic data (traits) with genotypic data (genetic markers) to identify regions of the genome associated with specific traits. In cucumbers (*Cucumis sativus* L.), QTL mapping has been instrumental in understanding the genetic basis of various agronomic traits such as disease resistance, fruit size, and flowering time. The process involves creating a mapping population, phenotyping the population for traits of interest, genotyping the population with molecular markers, and then using statistical methods to identify associations between markers and traits (Wei et al., 2014; Pan et al., 2020; Wang et al., 2020b).

3.2 Advances in QTL mapping methodologies

Recent advancements in QTL mapping methodologies have significantly enhanced the resolution and accuracy of QTL detection. Traditional bi-parental mapping, which involves crossing two genetically distinct parents to produce a segregating population, has been widely used in cucumber research. This method has led to the identification of numerous QTLs for traits such as fruit length, fruit diameter, and disease resistance (Wei et al., 2014; Zhu et al., 2016; Pan et al., 2020).

Genome-wide association studies (GWAS) represent a more recent approach that leverages natural populations to identify QTLs. GWAS can provide higher resolution mapping compared to bi-parental mapping by utilizing the natural genetic diversity present in a population. This method has been successfully applied in various crops, including cucumbers, to identify QTLs associated with complex traits (Xu et al., 2017; Halladakeri et al., 2023).

3.3 Integration of molecular markers in QTL mapping

The integration of molecular markers, such as Single Nucleotide Polymorphisms (SNPs) and Specific Length Amplified Fragment (SLAF) markers, has revolutionized QTL mapping in cucumbers. The development of high-density genetic maps using these markers has facilitated the fine mapping of QTLs and the identification of candidate genes (Takagi et al., 2013; Wei et al., 2014; Zhu et al., 2016). For instance, SLAF sequencing has been used to construct high-density genetic maps, enabling the detection of QTLs for fruit-related traits with high precision (Wei et al., 2014; Zhu et al., 2016).

Moreover, the use of next-generation sequencing (NGS) technologies has allowed for the rapid identification and genotyping of molecular markers, making QTL mapping more efficient and cost-effective. Techniques such as QTL-seq, which combines bulked segregant analysis with whole-genome resequencing, have further streamlined the process, enabling the rapid identification of QTLs in cucumbers and other crops (Takagi et al., 2013).

4 QTL Mapping Studies for Major Agronomic Traits

4.1 Yield-related traits

Several QTL mapping studies have identified key loci associated with yield-related traits in cucumber. For instance, a high-density genetic map constructed using SLAF sequencing identified nine QTLs for fruit length and weight, with one QTL, fl3.2, explaining 44.60% of the phenotypic variance (Wei et al., 2014). Another study using recombinant inbred lines (RILs) detected multiple QTLs for fruit weight, length, and diameter, highlighting the genetic complexity of these traits (Yuan et al., 2008). Additionally, a study focusing on a narrow cross in cucumber identified QTLs for the number of fruit per plant and lateral branches, which are critical yield components (Fazio et al., 2003).

The identified QTLs play significant roles in yield improvement by influencing various yield components. For example, the QTL fl3.2 on chromosome 3 has a major effect on fruit length and weight, making it a prime target for marker-assisted selection (MAS) to enhance yield (Wei et al., 2014). Similarly, QTLs linked to fruit weight and length in RIL populations can be utilized to develop high-yielding cucumber varieties through MAS (Yuan et al., 2008). The loci associated with the number of lateral branches and fruit per plant also offer potential for breeding programs aimed at increasing overall yield (Fazio et al., 2003).

4.2 Fruit quality traits

Fruit quality traits such as size, shape, flavor, and color are governed by multiple QTLs. A major-effect QTL, FS5.2, was identified for fruit size and shape, influencing both longitudinal and radial growth (Pan et al., 2022). Another study mapped 21 QTLs for fruit shape traits, with consensus QTLs like FS1.1 and FS6.1 playing roles in fruit elongation and diameter, respectively (Zhang et al., 2019). Additionally, QTLs for fruit length and diameter were identified in a high-density genetic map, further elucidating the genetic basis of these traits (Zhu et al., 2016).

Understanding the genetic basis of fruit quality traits provides insights into consumer preferences. For instance, the QTL FS5.2, which affects fruit elongation and radial growth, can be targeted to breed cucumbers with desirable shapes (Pan et al., 2022). The identification of QTLs for fruit flavor and color, although less frequently reported, is crucial for developing varieties that meet market demands. The integration of these QTLs into breeding programs can lead to the production of cucumbers with improved taste and visual appeal, enhancing consumer satisfaction (Zhu et al., 2016; Zhang et al., 2019).

4.3 Disease resistance

Disease resistance in cucumber is a critical trait for sustainable production. A comprehensive review documented 109 QTLs for disease resistances against seven pathogens, highlighting the extensive genetic resources available for breeding disease-resistant varieties. Specific QTLs for resistance to powdery mildew, downy mildew, and other major diseases have been identified, providing valuable markers for breeding programs (Figure 1) (Wang et al., 2020b).

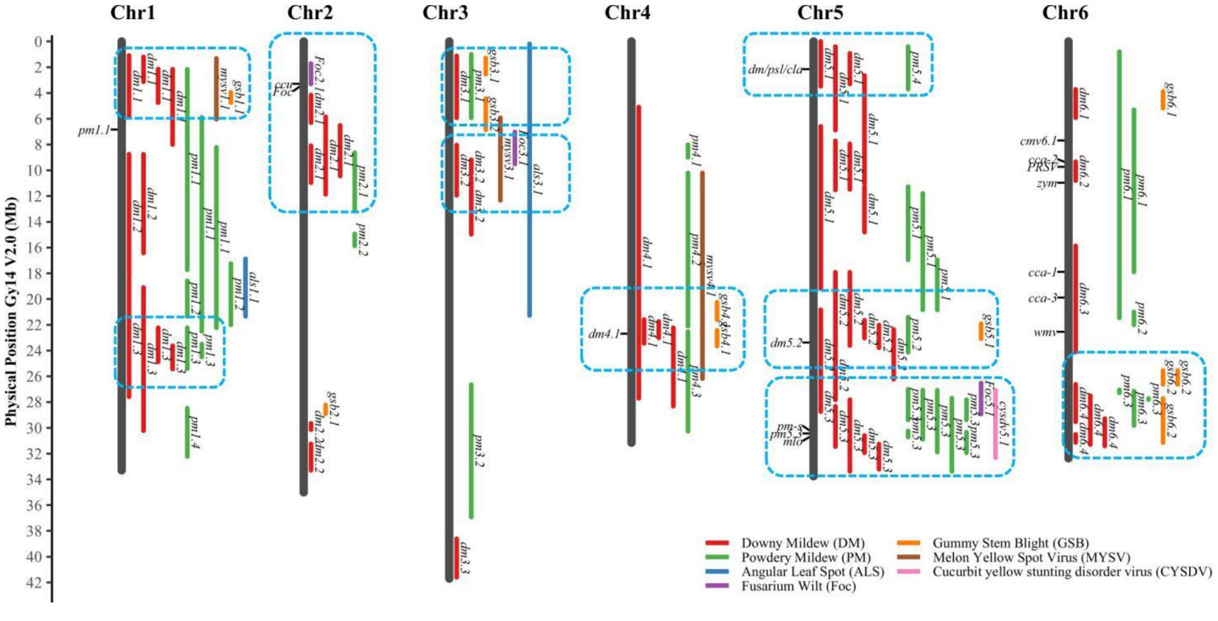

Figure 1 Ruler to the left indicates locations (in Mbp) in the Gy14 V2.0 draft genome assembly (drawn to scale). Vertical black lines are chromosomes. Cloned genes and QTL are aligned to the left and right of each chromosome, respectively. Vertical bar for each QTL represents 1.5 or 2.0 LOD confidence interval on the chromosome. Regions delimited by blue dashed rectangles indicate resistance gene/QTL hot spots or clusters (Adopted from Wang et al., 2020b)

The identification of QTLs associated with disease resistance has significant implications for breeding. By incorporating these QTLs into breeding programs, it is possible to develop cucumber varieties with enhanced resistance to multiple pathogens, reducing the reliance on chemical controls and improving crop sustainability. Marker-assisted selection using these QTLs can accelerate the development of resistant varieties, ensuring better yield stability and reduced losses due to diseases (Wang et al., 2020b).

4.4 Growth and development traits

Growth and development traits such as plant architecture, flowering time, and growth rate are influenced by various QTLs. For example, QTLs for flowering time and fruit size were identified in the semi-wild

Xishuangbanna cucumber, with FT6.2 and FS5.2 playing significant roles in photoperiod-dependent flowering time and round-fruit shape, respectively (Pan et al., 2017). Another study identified QTLs for plant architecture traits like lateral branching and main stem length, which are crucial for optimizing plant growth (Serquén et al., 1997).

The QTLs related to growth and development traits are essential for optimizing crop management and field adaptability. For instance, QTLs influencing flowering time can be used to develop varieties that are better suited to different growing seasons and climatic conditions (Pan et al., 2017). Similarly, QTLs affecting plant architecture can help in breeding compact plants with optimal branching patterns, improving field management and harvesting efficiency (Serquén et al., 1997). These genetic insights enable the development of cucumber varieties that are more adaptable to diverse agricultural environments, enhancing overall productivity and sustainability.

5 Comparative Analysis of QTL Studies

5.1 Consistency of QTLs across different studies and populations

The consistency of QTLs across different studies and populations is a critical aspect of QTL mapping in cucumbers. Several studies have identified overlapping QTLs for similar traits, suggesting a degree of consistency. For instance, the study by Wang et al. (2020b) documented 322 QTLs for 42 quantitative traits, including disease resistance, which were aligned on the latest cucumber draft genomes to infer consensus QTLs across multiple studies. Similarly, Gao et al. (2020) identified major QTLs for fruit size and shape, with some QTLs being consistent across different developmental stages and populations (Figure 2; Table 1). The identification of consensus regions on chromosomes, as seen in Gao et al. (2020), further supports the consistency of QTLs. Additionally, Zhang et al. (2019) found five consensus QTLs for fruit shape traits, indicating a level of reproducibility in different genetic backgrounds.

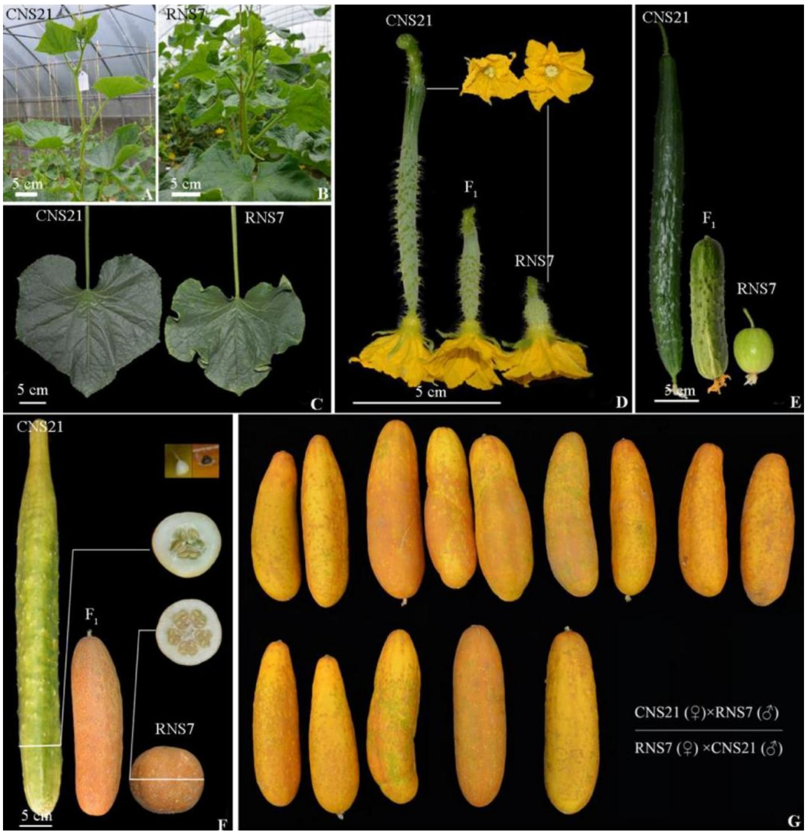

Figure 2 Phenotype of CNS21 and RNS7 (Adopted from Gao et al., 2020)

Image caption: A, B: Plant; C: Leaf; D: Ovary; E: The commercial fruit; F: The mature fruit, and the transverse cavities of CNS21 (high) and RNS7 (low), yellow mature skin and white spine of CNS21 and reddish brown mature skin and black spine of RNS7; G: F_1 of maternal inheritance (Adopted from Gao et al., 2020)

Table 1 Detected QTLs for fruit size and shape of F_2 and BC_1F_1 populations (Adopted from Gao et al., 2020)

Trait	Mapping pop	QTL detected	Chr.	LOD score	R^2/%	Add	DE	Left marker	Right marker
OL	2015F_2	*ol1.1*	1	7.47	3.58	2.03	0.69	MGA1	MGA4
	2016F_2	*ol1.1*	1	12.24	7.98	3.15	-1.89	MGA1	MGA4
	2016F_2	*ol1.2*	1	20.02	12.20	4.21	0.31	MGA10	MGA17
	2016BC_1F_1	*ol1.2*	1	17.05	28.15	4.94	-	MGA10	MGA18
	2015F_2	*ol1.2*	1	27.95	22.88	5.22	0.18	MGA12	MGA17
	2016BC_1F_1	*ol2.1*	2	28.30	46.80	6.46	-	MGB3	M2-5
	2015F_2	*ol2.1*	2	53.91	47.22	7.54	-0.33	M2-4	M2-6
	2016F_2	*ol2.1*	2	54.35	42.66	7.52	0.58	MGB3	M2-6
	2015F_2	*ol3.1*	3	8.92	4.05	2.09	0.13	M3-10	M3-12
	2016F_2	*ol3.1*	3	4.70	2.01	1.75	0.23	M3-10	M3-12
	2015F_2	*ol3.2*	3	4.28	1.87	1.47	0.55	M3-15	M3-16
	2016F_2	*ol5.1*	5	3.37	1.45	1.46	-0.19	M5-2	M5-4
	2015F_2	*ol6.1*	6	7.01	4.15	2.17	-0.19	M6-7	M6-10
OD	2016F_2	*od1.1*	1	19.78	10.30	-0.36	-0.28	MGA2	MGA6
	2016BC_1F_1	*od1.1*	1	12.62	20.49	-0.79	-	MGA5	MGA8
	2015F_2	*od1.1*	1	12.51	9.34	-0.42	-0.06	MGA6	MGA7
	2015F_2	*od1.2*	1	17.25	13.85	-0.45	-0.36	MGA10	MGA17
	2016F_2	*od1.2*	1	37.09	26.75	-0.62	-0.13	MGA10	MGA17
	2016F_2	*od2.1*	2	50.73	39.44	-0.74	0.01	MGB3	M2-4
	2016BC_1F_1	*od2.1*	2	18.60	33.69	-1.02	-	MGB3	M2-5
	2015F_2	*od2.1*	2	40.11	43.50	-0.90	-0.06	M2-4	M2-6
	2016F_2	*od4.1*	4	5.42	2.45	0.20	-0.06	M4-21	M4-32
OSI	2015F_2	*osi1.1*	1	18.25	9.40	0.72	-0.17	MGA2	MGA5
	2016F_2	*osi1.1*	1	11.79	8.14	0.67	-0.18	MGA2	MGA4
	2016BC_1F_1	*osi1.1*	1	6.06	5.90	0.41	-	MGA2	MGA6
	2016F_2	*osi1.2*	1	41.92	34.05	1.41	-0.01	MGA10	MGA17
	2015F_2	*osi1.2*	1	28.72	23.53	1.08	0	MGA12	MGA17
	2016BC_1F_1	*osi1.2*	1	18.44	22.27	0.79	-	MGA12	MGA18
	2016F_2	*osi2.1*	2	55.64	47.35	1.55	0.41	MGB3	M2-4
	2016BC_1F_1	*osi2.1*	2	27.63	31.99	0.96	-	MGB3	M2-5
	2015F_2	*osi2.1*	2	57.68	48.86	1.55	0.34	M2-4	M2-6
	2016F_2	*osi3.1*	3	3.14	1.44	0.24	0.22	M3-4	M3-7

Continuing Table

Trait	Mapping pop	QTL detected	Chr.	LOD score	R^2/%	Add	DE	Left marker	Right marker
	2015F_2	*osi3.2*	3	7.41	3.68	0.42	-0.09	M3-12	M3-15
	2015F_2	*osi6.1*	6	4.39	1.78	0.29	0.02	M6-5	M6-7
FL	2016F_2	*fl1.1*	1	7.01	4.40	14.95	-6.22	MGA1	MGA4
	2016BC_1F_1	*fl1.1*	1	3.75	4.59	11.19	-	MGA2	MGA6
	2016F_2	*fl1.2*	1	48.30	38.81	46.60	-0.20	MGA10	MGA17
	2016BC_1F_1	*fl1.2*	1	10.22	14.89	19.89	-	MGA10	MGA18
	2016F_2	*fl2.1*	2	55.16	49.89	49.61	12.61	MGB3	M2-4
	2016BC_1F_1	*fl2.1*	2	15.22	21.69	24.36	-	MGB3	M2-5
	2016F_2	*fl3.1*	3	2.70	1.16	8.08	3.28	M3-15	M3-16
FD	2016F_2	*fd1.1*	1	3.46	3.30	-1.22	-0.53	MGA2	MGA4
	2016BC_1F_1	*fd1.2*	1	5.82	12.16	-4.77	-	MGA10	MGA18
	2016F_2	*fd1.2*	1	26.48	27.06	-3.39	-1.00	MGA10	MGA17
	2016F_2	*fd2.1*	2	38.42	40.83	-4.16	0.06	MGB3	M2-4
	2016BC_1F_1	*fd2.1*	2	14.21	33.14	-8.00	-	MGB3	M2-5
	2016F_2	*fd5.1*	5	2.92	1.99	-0.94	0.33	M5-5	M5-8
FSI	2016F_2	*fsi1.1*	1	14.46	9.06	0.77	-0.17	MGA2	MGA4
	2016BC_1F_1	*fsi1.1*	1	7.01	6.64	0.50	-	MGA2	MGA6
	2016F_2	*fsi1.2*	1	48.63	34.47	1.53	0.09	MGA10	MGA17
	2016BC_1F_1	*fsi1.2*	1	15.61	18.58	0.82	-	MGA10	MGA18
	2016F_2	*fsi2.1*	2	63.42	50.94	1.72	0.49	MGB3	M2-4
	2016BC_1F_1	*fsi2.1*	2	27.04	31.06	1.08	-	MGB3	M2-5
	2016F_2	*fsi3.1*	3	2.72	1.10	0.18	0.28	M3-4	M3-7

Note: OL: Ovary length; OD: Ovary diameter; OSI: Ovary index (OL/OD); FL: commercial fruit length; FD: Commercial fruit diameter; FSI: Fruit shape index (FL/FD); Add: Additive effect; DE: Dominance effect (Adopted from Gao et al., 2020)

5.2 Environment and genotype interactions

The interaction between environment and genotype plays a significant role in the expression of QTLs. Studies have shown that QTLs can exhibit varying effects depending on environmental conditions. For example, Yağcioğlu et al. (2019) conducted QTL analysis for low temperature germination ability across five different environments and found that three QTLs were consistently detected, explaining a significant portion of the phenotypic variance.

This highlights the importance of multi-environment trials in QTL mapping. Similarly, Pan et al. (2020) reported that the performance of the cucumber inbred line WI2757 varied under different field conditions, affecting the expression of QTLs for traits like flowering time and fruit number. These findings underscore the necessity of considering environmental factors when validating QTLs.

5.3 Challenges in reproducibility and validation of QTLs

Reproducibility and validation of QTLs remain challenging due to several factors. One major issue is the genetic background of the populations used in different studies. For instance, Lee et al. (2020) utilized a diverse germplasm collection to conduct a genome-wide association study, which may lead to the identification of QTLs that are not easily reproducible in other populations. Additionally, the presence of minor-effect QTLs, as discussed in Wang et al. (2020a), complicates the validation process since these QTLs may not consistently express in different genetic backgrounds or environmental conditions. Another challenge is the fine mapping and cloning of QTLs, which is often required for validation.

As noted by Pan et al. (2022), fine mapping of the major-effect QTL FS5.2 involved developing near-isogenic lines and detailed genetic analysis, which is resource-intensive and time-consuming. Despite these challenges, efforts to standardize QTL nomenclature and collaborative research, as recommended by Wang et al. (2020b), can improve the reproducibility and validation of QTLs in cucumber research.

6 Integration of QTL Mapping with Genomic Selection

6.1 Opportunities for combining QTL mapping with genomic selection for trait prediction

The integration of Quantitative Trait Loci (QTL) mapping with genomic selection (GS) presents a promising approach for enhancing trait prediction in cucumber breeding programs. QTL mapping identifies specific genomic regions associated with phenotypic traits, while GS uses genome-wide markers to predict the genetic value of individuals. Combining these methods can leverage the strengths of both, improving the accuracy and efficiency of breeding programs.

QTL mapping has been extensively used to identify loci associated with important agronomic traits in cucumber, such as fruit size, shape, and disease resistance (Gao et al., 2020; Pan et al., 2020; Wang et al., 2020b). These identified QTLs can serve as valuable markers in GS models, enhancing the prediction accuracy for complex traits. For instance, the integration of QTL information into GS models can help in the selection of individuals with desirable traits, even in the absence of phenotypic data (Liu et al., 2021). This is particularly useful for traits with low heritability or those that are difficult to measure.

Moreover, the use of high-density genetic maps and advanced genotyping techniques, such as genotyping-by-sequencing (GBS), has facilitated the identification of numerous QTLs across the cucumber genome (Yang et al., 2019; Lee et al., 2020). These advancements provide a rich source of genetic markers that can be incorporated into GS models, thereby improving the prediction of genetic merit and accelerating the breeding cycle.

6.2 Case studies and examples in cucumber breeding programs

Several cucumber breeding programs have successfully integrated QTL mapping with genomic selection to enhance trait prediction and selection efficiency. For example, a study on the cucumber inbred line WI2757 identified multiple QTLs for traits such as flowering time, fruit length, and disease resistance (Pan et al., 2020). By incorporating these QTLs into GS models, breeders can more accurately predict the performance of new hybrids, thereby improving the selection process.

Another notable example is the use of genomic prediction in the breeding of cucumber plants, where 81 inbred lines were genotyped, and 16 662 markers were identified to represent the genetic background of cucumber (Liu et al., 2021). The study demonstrated that the predictive ability for 12 commercial traits ranged from 0.38 to 0.95 under cross-validation strategies, highlighting the potential of integrating QTL mapping with GS for trait prediction. Additionally, the development of near-isogenic lines (NILs) for major-effect QTLs, such as FS5.2 for fruit size and shape, has provided valuable insights into the genetic control of these traits (Figure 3) (Pan et al., 2022). By fine-mapping these QTLs and incorporating the associated markers into GS models, breeders can achieve more precise selection for desired fruit characteristics.

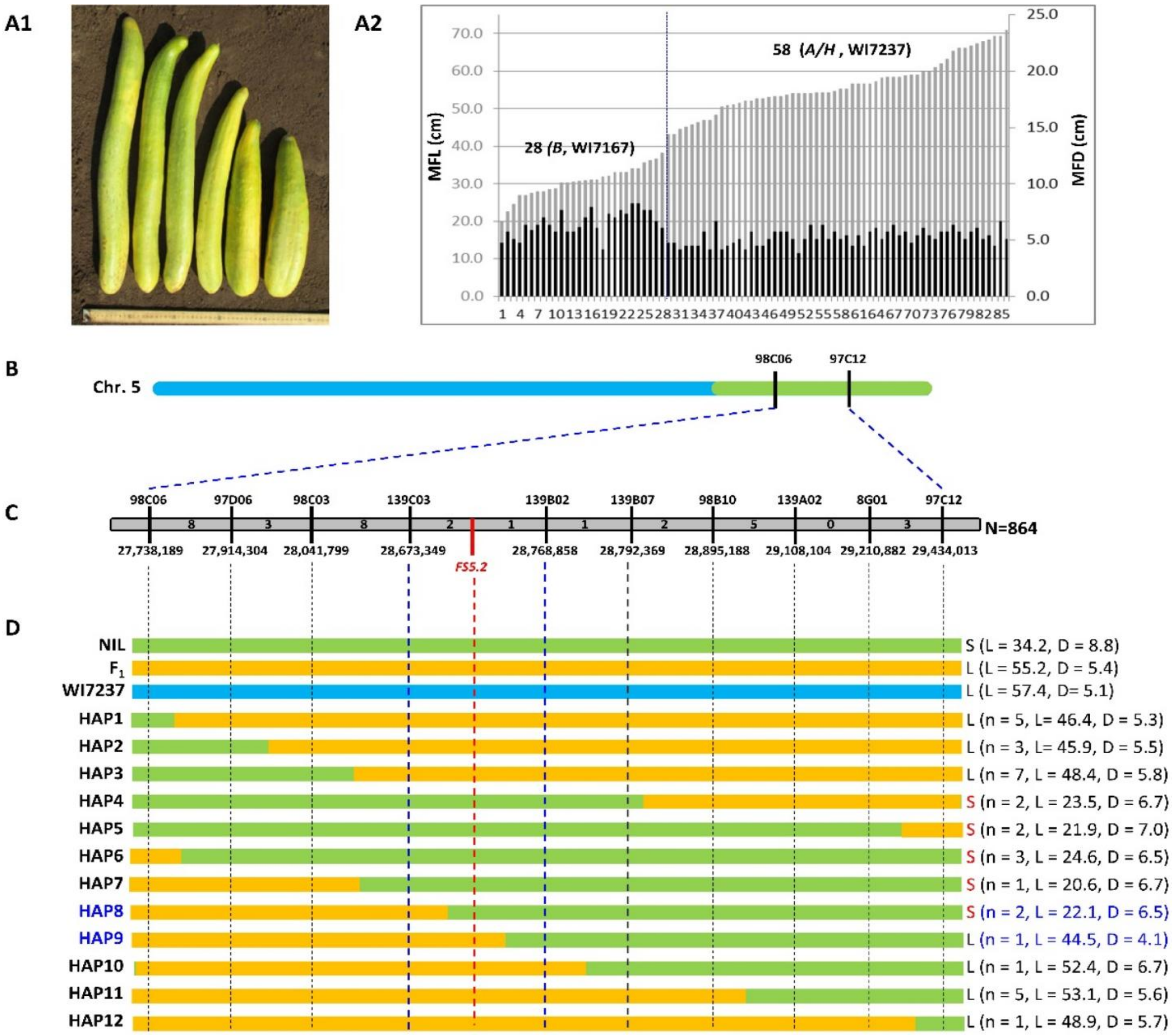

Figure 3 Fine mapping of FS5.2 major-effect QTL (Adopted from Pan et al., 2022)

Image caption: (A1) Representative fruits from NIL-derived F_2 plants showing segregation of fruit size/shape in this population. (A2) Distribution of mature fruit length (MFL) and diameter (MFD) among 82 F_2 plants based on field data. Genotype of each plant at the fs5.2 locus was also shown. (B-D) From 864 F_2 plants, 33 recombinants were identified with flanking markers 98C06 and 97C12, which were phenotyped and genotyped with eight additional markers (C). Twelve haplotypes (HAP) could be recognized, which allowed mapping of FS5.2 into a 95.5 kb region with 15 predicted genes (D). In (D), S=short fruit, L=long fruit, and n=# recombinants with the specific haplotype. The light-green, light-blue, and orange bars indicate the genotypes of NIL, WI7237, and F_1, respectively. L and D are mean fruit length and diameter, respectively, of the haplotype (in cm) (Adopted from Pan et al., 2022)

7 Future Directions in QTL Mapping for Cucumber

7.1 Potential of next-generation sequencing in enhancing QTL resolution

Next-generation sequencing (NGS) technologies have revolutionized genetic research by providing high-resolution data that can significantly enhance QTL mapping. The application of NGS allows for the generation of dense genome-wide markers, which improves the accuracy and resolution of QTL identification. For instance, the use of genotyping-by-sequencing (GBS) has enabled the construction of high-density haplotype maps, facilitating the identification of significant SNPs and candidate genes for various traits in cucumber (Lee et al., 2020). Additionally, NGS-based bulked segregant analysis (BSA) has been employed to identify QTLs with greater precision, as demonstrated in the mapping of fruit neck length in cucumber (Xu et al., 2020). The integration of NGS with traditional QTL mapping approaches can thus provide a more detailed understanding of the genetic architecture of agronomic traits in cucumber (Nguyen et al., 2019).

7.2 Functional validation of QTLs through gene editing technologies (e.g., CRISPR)

The functional validation of QTLs is crucial for confirming their roles in trait expression and for potential application in breeding programs. Gene editing technologies, such as CRISPR/Cas9, offer powerful tools for this purpose. By precisely targeting and modifying specific genes within QTL regions, researchers can validate the effects of these genes on phenotypic traits. For example, the identification of candidate genes for fruit shape and size QTLs in cucumber can be followed by CRISPR-mediated knockout or overexpression studies to confirm their functional roles (Gao et al., 2020; Pan et al., 2022). This approach not only validates the QTLs but also provides insights into the underlying molecular mechanisms, paving the way for the development of improved cucumber varieties with desirable traits.

7.3 Integrating QTL data with transcriptomic and proteomic studies for comprehensive trait analysis

To achieve a comprehensive understanding of the genetic basis of agronomic traits, it is essential to integrate QTL mapping data with transcriptomic and proteomic analyses. This integrative approach can reveal the regulatory networks and pathways involved in trait expression. For instance, transcriptome profiling of near-isogenic lines (NILs) has been used to identify differentially expressed genes associated with fruit size and shape QTLs in cucumber, highlighting the role of auxin-mediated cell division and expansion (Pan et al., 2022). Similarly, combining QTL mapping with RNA-seq data has led to the identification of key genes and transcription factors involved in fruit length regulation (Xing et al., 2023). By incorporating proteomic data, researchers can further elucidate the protein interactions and modifications that contribute to trait development, providing a holistic view of the genetic and molecular basis of agronomic traits in cucumber.

8 Conclusion

The genetic basis of agronomic traits in cucumber has been widely investigated through QTL mapping and genome-wide association studies (GWAS), leading to substantial advancements in identifying and characterizing genes and QTLs linked to key phenotypic traits. A notable review documented 81 simply inherited trait genes or major-effect QTLs that have been cloned or fine-mapped, alongside 322 QTLs for 42 quantitative traits, such as disease resistance to seven pathogens. For parthenocarpy- a critical trait in cucumber production—six loci have been identified via GWAS, showing its polygenic nature. Genetic studies on cucumber populations reveal high heritability for most agronomic traits, underscoring their strong genetic basis. Additionally, research using microsatellite markers and SNPs has provided valuable insights into cucumber germplasm’s genetic diversity and structure, which are essential for effective breeding programs. Key discoveries, such as the NS gene for fruit spine density and the Ef1.1 QTL for early flowering, further underscore the progress in understanding the genetic regulation of important agronomic traits in cucumber.

These findings have profound implications for future cucumber breeding and crop enhancement efforts. Identifying specific genes and QTLs offers valuable markers for marker-assisted selection (MAS), allowing breeders to target desirable traits like disease resistance, parthenocarpy, and early flowering more efficiently. High heritability of major traits suggests that genetic improvements through selective breeding could yield substantial gains in crop performance.The genetic diversity found within cucumber germplasm collections provides a rich resource for developing new varieties with improved traits, enhancing both crop resilience and productivity. Furthermore, knowledge of genetic pathways controlling traits like leaf morphology, fruit development, and plant architecture can guide breeding strategies for better crop management. The use of molecular techniques, such as CRISPR/Cas9 for precise gene editing, offers potential for targeted trait modifications, expediting the creation of superior cucumber varieties. These advances in genetic research lay a strong foundation for ongoing improvement in cucumber breeding, equipping agriculture to tackle present and future challenges.

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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.

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