The Original

IMPROVEMENT OF CUCURBITS: FROM CLASSICAL BREEDING TO MODERN BIOTECHNOLOGICAL APPROACHES - STRATEGIES AND LIMITATIONS

Suresh S[1], Malathi D[1], Shourov Dutta[2], Chiranjit Mazumder[3], D Vara Vinod[4], Pratyksh Pandey[5], Bhoirab Gogoi[6], Vignesh Manoharan[7*]

[1]Department of Plant Breeding and Genetics, MIT College of Agriculture and Technology, Musiri, Trichy, Tamil Nadu, India - 621 211.
[2]Subject Matter Specialist (Horticulture), Krishi Vigyan Kendra, Karbi Anglong, Assam, India.
[3]Scientist, ICAR-Indian Agricultural Research Institute, New Delhi, India.
[4]Department of Vegetable Science, College of Horticulture, Dr.YSR Horticultural University, Venkataramannagudem, Andhra Pradesh.
[5]Department of Agriculture, Mangalayatan University, Aligarh, Uttar Pradesh, India
[6] Subject Matter Specialist (Horticulture), Krishi Vigyan Kendra, Jorhat, Assam, India.
[7*] Department of Vegetable Science, Horticultural College and Research Institute, Tamil Nadu Agricultural University, Coimbatore, Tamil Nadu, India.

ABSTRACT

Cucurbits, including cucumber (*Cucumis sativus*), watermelon (*Citrullus lanatus*), melon (*Cucumis melo*), pumpkin, and squash (*Cucurbita* spp.), are among the most important horticultural crops worldwide due to their nutritional, economic, and industrial value. However, their productivity is severely constrained by numerous biotic and abiotic stresses, narrow genetic diversity resulting from domestication bottlenecks, and the complexity of breeding highly heterozygous and cross-pollinated species. This review examines the major strategies employed for cucurbit improvement, ranging from classical breeding approaches to advanced biotechnological interventions. The role of genetic resources, wild relatives, and traditional landraces in broadening the genetic base is discussed, along with the contributions of conventional breeding in developing improved cultivars with enhanced yield, quality, and disease resistance. The review further highlights the application of molecular marker-assisted selection for precise trait introgression, transgenic technologies for virus resistance, and genome editing tools such as CRISPR/Cas9 for targeted modification of agronomically important genes. In addition, the emerging potential of genomic selection for improving complex quantitative traits by utilizing genome-wide marker information is emphasized. Despite significant advances, several challenges, including limited transformation efficiency, regulatory constraints, rapid pathogen evolution, and climate change-related stresses, continue to restrict the full realization of these technologies in cucurbit breeding programs. Future improvement efforts will require the integration of genomic selection, genome editing, high-throughput phenotyping, artificial intelligence-assisted breeding, and the effective utilization of diverse genetic resources to accelerate the development of resilient, high-yielding, and climate-adapted cucurbit cultivars.

KEYWORDS: Cucurbits, plant breeding, genetic resources, marker-assisted selection, transgenic crops, CRISPR/Cas9, genome editing, genomic selection, climate-smart breeding.

INTRODUCTION

Cucurbits, belonging to the family *Cucurbitaceae*, comprise a diverse group of economically and nutritionally important crops such as cucumber (*Cucumis sativus*), watermelon (*Citrullus lanatus*), melon (*Cucumis melo*), and pumpkin and squash (*Cucurbita* spp.) (Prem 2007). These crops are cultivated worldwide across tropical, subtropical, and temperate regions and represent one of the largest and most widely consumed groups of vegetable crops. Their adaptability to varied agro-climatic conditions from arid regions to protected cultivation systems has made them indispensable in global agriculture and food systems (Dhillon et al. 2016). Cucurbits hold immense importance in human nutrition and food security. They are rich sources of vitamins (especially A and C), minerals, antioxidants, and dietary fibre, making them essential components of a balanced diet (Men et al. 2021). In addition to their nutritional value, cucurbits contribute to economic sustainability through their role in horticulture, processing industries, and seed production sectors. Some cucurbits also possess medicinal properties and industrial uses, while their seeds serve as sources of edible oil and protein. Furthermore, as horticultural crops, cucurbits play a critical role in diversifying diets and addressing micronutrient deficiencies globally (Rolnik and Olas 2020). Despite their significance, cucurbits are highly vulnerable to a wide range of biotic stresses. These include fungal diseases, bacterial infections, nematodes, and a large number of viral diseases. Notably, more than 70 viruses have been reported to infect cucurbit crops, many of which are transmitted by insect vectors, leading to severe yield losses and deterioration of fruit quality (Kumari et al. 2021). Insect pests themselves also directly damage plants and act as vectors, making crop protection even more challenging (Warsi et al. 2025). These stresses can affect plants at all growth stages, from seedling emergence to post-harvest storage, thereby reducing both productivity and market value.

Another major limitation in cucurbit improvement is their narrow genetic base, resulting from domestication bottlenecks and limited interspecific hybridization. This restricts the availability of useful traits such as resistance to pests, diseases, and environmental stresses. Furthermore, the biological nature of cucurbits being insect-pollinated, highly heterozygous, and sprawling vines makes breeding and germplasm maintenance more complex (Tracy et al. 2019). Given these challenges, improving cucurbits has become a critical focus in modern agriculture. Traditional breeding approaches have contributed significantly over the past century; however, they are often time-consuming and limited by genetic constraints. In contrast, modern biotechnological tools offer new opportunities to enhance yield, quality, and stress resistance more efficiently. Therefore, this review will focus on the major problems affecting cucurbit crops and explore the strategies used for their improvement from classical breeding methods to advanced biotechnological approaches along with their associated limitations.

Genetic resources and diversity in Cucurbits

Cucurbits possess extensive genetic resources and diversity, making them one of the most variable groups of cultivated crops, with nearly 1000 species distributed across tropical, subtropical, and temperate regions (Yu et al. 2023b). Major cucurbit crops originated in different geographical regions, with Africa being the centre for watermelon, South and Southeast Asia for cucumber and several gourds, and Central and South America for pumpkin and squash. Following domestication, these crops spread to other parts of the world, where they underwent further diversification, leading to the formation of secondary centres of diversity in regions such as Asia, the Mediterranean, and parts of Africa (Grumet et al. 2021c). The genetic diversity in cucurbits is expressed at multiple levels, including morphological, molecular, and biochemical variation. There is wide variation in fruit size, shape, colour, and quality traits, along with significant differences at the DNA level revealed through modern genomic tools. Advances in genome sequencing have enabled the identification of genes controlling important agronomic traits such as yield, quality, and stress tolerance (Ma et al. 2022b). However, domestication and continuous selection for desirable traits have led to genetic bottlenecks in cultivated varieties, reducing their genetic base and limiting breeding potential (Aguirre-Dugua et al. 2023b). Despite this, wild populations and traditional landraces still retain high genetic variability shaped by environmental adaptation and evolutionary processes (Öztürk et al. 2022). Although cucurbits possess rich genetic resources, their effective utilization is constrained by several challenges. These include reproductive barriers that limit interspecific hybridization, genetic erosion due to loss of traditional varieties, and difficulties in germplasm maintenance caused by their cross-pollinated nature and vine growth habit (Grumet et al. 2021c). The major genetic resources, including landraces, wild relatives, and germplasm collections utilized in cucurbit improvement programs, are summarized in Table 1.

Methods to improve Cucurbits

Traditional breeding

Classical breeding has been the foundation of cucurbit improvement for a very long time and involves the selection and recombination of desirable traits from existing genetic variability. The process typically begins with collection and evaluation of germplasm, where diverse lines are screened for useful traits such as yield, fruit quality, or disease resistance. Selected parents with complementary traits are then crossed to produce an F_1 generation, followed by selfing or sib-mating to create segregating populations (F_2, F_3, etc.). In these generations, breeders perform phenotypic selection, choosing superior plants based on observable traits like fruit size, shape, sweetness, and resistance (Singh et al. 2023b). Methods such as pedigree selection, backcrossing, and recurrent selection are commonly used to stabilize and improve traits over successive generations (Behera et al. 2021). This approach relies heavily on careful field evaluation and repeated selection cycles to develop improved cultivars.

Classical breeding has been successfully used to improve several traits in cucurbits. For example, large-scale screening of germplasm has led to the identification of resistance to diseases such as Fusarium wilt, anthracnose, and nematodes, which are then incorporated into cultivated varieties through crossing (Ayala-Doñas et al. 2020). Similarly, traditional breeding has produced well-known disease-resistant cultivars such as *Poinsette* (cucumber), *Arka Manik* (watermelon), and *Punjab Chappan Kaddu-1* (squash) (Choudhary and Fageria 2002). Traits like high yield, early maturity, improved fruit quality, reduced bitterness, and enhanced nutritional traits have also been improved through continuous selection in segregating populations. Additionally, hybrid development exploiting heterosis has significantly enhanced yield and earliness in crops like cucumber, melon, and watermelon (Robinson 1999). These examples highlight how classical breeding has effectively utilized natural genetic variation to develop improved cucurbit varieties.

However, classical breeding has several limitations. It is time-consuming, often requiring many generations to stabilize desirable traits, especially for quantitative traits like yield. The process depends largely on phenotypic traits, making it difficult to select for complex or low-expression traits such as micronutrient content or stress tolerance (Behera et al. 2021). Moreover, the narrow genetic base of cultivated cucurbits restricts the availability of useful variation, while reproductive barriers limit the transfer of traits from wild species. Linkage drags and environmental influence on trait expression further complicate selection. As a result, although classical breeding has been highly successful, its efficiency is limited in addressing complex traits and rapidly evolving challenges such as climate change and emerging diseases. Representative cultivars developed through conventional breeding approaches and their key characteristics are summarized in Table 2.

Molecular Assisted Selection

Molecular breeding in cucurbits is an advanced approach that improves crop traits by selecting plants based on their genetic makeup rather than only visible characteristics. It primarily relies on tools such as molecular markers, genetic maps, and genome information to identify genes or genomic regions (QTLs) associated with desirable traits. The process begins with identification of target traits, followed by discovery of DNA markers linked to those traits using genetic mapping or sequencing. These markers are then validated in breeding populations, and plants carrying the desired marker alleles are selected through marker-assisted selection (MAS). This allows breeders to screen plants at early stages without waiting for trait expression, making the process faster and more precise compared to classical breeding. In cucurbits, commonly used markers include SSRs and SNPs, which help track genes controlling important agronomic traits (Ram et al. 2019b).

Molecular breeding has been successfully applied in cucurbits for improving disease resistance, yield, fruit quality, and stress tolerance. For example, in melon, several QTLs and molecular markers have been identified for resistance to fungal, bacterial, viral, and abiotic stresses, enabling targeted improvement of these traits (Shahwar et al. 2024). In cucumber, SNP-based markers have been developed to identify resistance to cucumber vein yellowing virus, allowing precise selection of resistant plants in breeding populations (Kahveci et al. 2021b). Similarly, in pumpkin, markers linked to resistance against viruses such as Tomato leaf curl New Delhi virus have been mapped and used to facilitate the transfer of resistance genes into elite cultivars (Schafleitner et al. 2024b). Molecular breeding is also used to improve fruit-related traits such as size, color, flavor, and nutritional quality. These examples demonstrate how molecular tools enhance the efficiency and accuracy of trait selection in cucurbit improvement programs.

Despite its advantages, molecular breeding also has certain limitations. The identification of reliable markers and their validation requires extensive genomic research, time, and cost, which may not be feasible in all breeding programs. The effectiveness of markers depends on their tight linkage with target genes; otherwise, selection may be inaccurate. Additionally, many important traits in cucurbits, such as yield and stress tolerance, are polygenic and influenced by environmental factors, making it difficult to fully capture them using markers alone. There is also a need for skilled expertise and infrastructure for genotyping and data analysis. Therefore, while molecular breeding significantly enhances precision and speed, it is most effective when integrated with conventional approaches and proper field evaluation (Collard and Mackill 2007; Xu and Crouch 2008). Important molecular markers, target traits, and associated genes/QTLs employed in cucurbit breeding are summarized in Table 3.

Transgenic method

Transgenic methods involve the introduction of a foreign gene into the plant genome to confer desirable traits that may not be available within the natural gene pool. This is typically done using techniques such as Agrobacterium-mediated transformation or direct gene transfer, where a gene of interest is inserted into plant cells, followed by regeneration of whole plants through tissue culture (Ziemienowicz 2014; Tzfira and Citovsky 2006). The introduced gene is then expressed in the plant, enabling it to perform new functions such as producing transgenic proteins. Unlike classical breeding, this method allows the transfer of genes across kingdom, making it possible to incorporate traits from unrelated organisms. Once transformed plants are developed, they are screened and evaluated under greenhouse and field conditions to confirm stable expression and effectiveness of the introduced trait.

Transgenic approaches have been particularly successful in cucurbits for developing virus-resistant varieties, which address one of the most serious constraints in these crops. A well-known example is transgenic squash engineered with coat protein genes from viruses such as cucumber mosaic virus (CMV), zucchini yellow mosaic virus (ZYMV), and watermelon mosaic virus (WMV). These plants showed high levels of resistance, with many lines remaining symptom-free and producing normal fruits even under heavy infection pressure (Tricoll et al. 1995). Some transgenic squash lines exhibited 40–95% resistance depending on the gene construct used, and multi-gene constructs provided broader resistance against multiple viruses simultaneously (Tricoll et al. 1995). Such varieties have even been commercialized and cultivated in countries like the United States, demonstrating their practical value in protecting yield and quality (Council and Plants 2002). Transgenic approaches have also been explored for improving traits such as pest resistance, stress tolerance, and shelf life, although virus resistance remains the most successful application in cucurbits.

Despite their advantages, transgenic methods face several limitations. The development process is technically complex, expensive, and time-consuming, requiring specialized infrastructure and regulatory approval before commercialization. There are also biosafety and environmental concerns, such as the potential transfer of transgenes to wild relatives through pollen flow, which has been observed in squash under field conditions (Fuchs et al. 2004b). Public acceptance of genetically modified crops remains a challenge in many regions, further limiting their widespread adoption. Additionally, transgenic approaches often focus on single traits, whereas many important characteristics like yield and stress tolerance are controlled by multiple genes. Therefore, while transgenic methods provide powerful tools for cucurbit improvement, their application is constrained by regulatory, ecological, and socio-economic factors (Qaim 2020; Mittler and Blumwald 2010). Major transgenic approaches applied in cucurbit crops and their breeding outcomes are summarized in Table 4.

Genome editing

Genome editing is a modern approach used in cucurbits to precisely modify specific genomic locations without introducing foreign DNA. The most widely used technique is CRISPR/Cas9, although earlier tools like ZFN and TALENs also exist (Doudna and Charpentier 2014). In this method, a guide RNA (gRNA) is designed to target a specific gene sequence, and the Cas9 enzyme creates a cut at that location in the genomic DNA. The natural repair system of the plants then modifies the gene, either by disrupting it or altering its function. The process involves selecting a target gene, designing gRNAs, constructing a CRISPR vector, and introducing it into plant cells, followed by regeneration of edited plants and confirmation of mutations (Hooghvorst and Nogués 2020). Compared to transgenic methods, genome editing is more precise and can create targeted changes without introducing genes from unrelated species. There is more advancement to CRISPR like base editors and prime editors which can increase the precision of genome editing.

Genome editing has shown promising applications in cucurbits for improving important traits such as yield, flowering behaviour, fruit quality, and shelf life. For example, in cucumber, editing of the CsWIP1 gene led to the development of gynoecious plants, which significantly improves hybrid seed production efficiency (Huang 2026). In melon, CRISPR/Cas9 has been used to modify genes related to fruit ripening, such as the CmACO1 gene, resulting in extended shelf life due to reduced ethylene production (Sasaki et al. 2025a). Similarly, editing of genes like phytoene desaturase (PDS) in melon and watermelon has demonstrated successful mutation induction and helped in studying gene function and improving crop traits (Wang et al. 2024b). These examples show that genome editing can directly target key genes controlling agronomic traits, making it a powerful tool for precise crop improvement.

Despite its potential, genome editing in cucurbits faces several limitations. One major challenge is the difficulty in plant transformation and regeneration, as cucurbits are often recalcitrant to tissue culture and genetic transformation (Hooghvorst and Nogués 2020). The efficiency of editing can also vary depending on the species, gene target, and delivery system, sometimes resulting in low mutation rates or chimeric plants. Additionally, many important traits such as yield and stress tolerance are controlled by multiple genes, making single-gene editing less effective for complex traits. There are also regulatory uncertainties in some countries regarding genome-edited crops, which may affect their adoption. Therefore, although genome editing offers high precision and speed, technical and biological constraints still limit its full-scale application in cucurbit improvement. Representative applications of genome editing in cucurbit crops and their resulting trait improvements are summarized in Table 5.

Genomic selection

Genomic selection (GS) is an advanced breeding approach that uses genome-wide markers to predict the overall breeding value of plants, thereby capturing the effects of both major and minor genes simultaneously. Unlike MAS, which focuses only on a few statistically significant QTLs, GS includes all genomic regions, even those with very small effects that are usually ignored because they do not meet statistical thresholds, thus addressing the problem of "missing heritability" in complex traits (Liu et al. 2024). This is particularly important for cucurbits, where key traits such as yield, fruit quality, and stress tolerance are controlled by many minor-effect loci influenced by environmental interactions, making MAS less efficient. Although the application of genomic selection in cucurbits is still limited, early studies in crops like squash have demonstrated that genome-wide prediction models can successfully improve complex traits such as fruit quality, even with moderate prediction accuracy (Hernandez et al. 2020b). Given the increasing availability of genomic resources and high-density markers in cucurbits, GS holds strong potential to accelerate improvement by enabling early and accurate selection, reducing dependence on extensive phenotyping, and increasing genetic gain. Therefore, genomic selection represents a promising strategy to overcome the limitations of traditional and marker-based approaches by effectively utilizing the cumulative contribution of numerous small-effect genes, which are otherwise neglected in conventional breeding systems.

CONCLUSION

Although considerable progress has been made in developing advanced breeding and biotechnological tools for crop improvement, their full potential remains largely unrealized in cucurbits improvement. Several promising solutions such as the use of wild relatives, climate-smart breeding, genomic prediction, AI-assisted selection, improved transformation platforms, and digital phenotyping have been proposed and demonstrated. However, their adoption in practical cucurbit breeding programs remains limited. Among these, genomic selection stands out as one of the most underexploited approaches despite its substantial advantages. By enabling early and accurate prediction of breeding performance using genome-wide marker information, genomic selection can accelerate breeding cycles, improve selection efficiency for quantitative traits, and increase overall genetic gain. Therefore, broader integration of genomic selection together with high-throughput phenotyping, advanced transformation systems, and genome editing technologies could significantly accelerate the development of resilient, productive, and climate-adapted cucurbit cultivars to meet future agricultural demands. Despite these advances, several biological, technical, and regulatory challenges continue to limit the efficient improvement of cucurbit crops. The major challenges and emerging opportunities for overcoming these constraints are summarized in Table 6.

Statements and Declarations

Funding

This work is not funded.

Consent for publication

All authors consent the publication of the current article.

Competing interests

The authors declare no competing interests.

REFERENCES

1. Aguirre-Dugua X, Barrera-Redondo J, Gasca-Pineda J, Vázquez-Lobo A, López-Camacho A, Sánchez-de la Vega G, Castellanos-Morales G, Scheinvar E, Aguirre-Planter E, Lira-Saade R, Eguiarte LE (2023b) Population Genomics of Domesticated Cucurbita ficifolia Reveals a Recent Bottleneck and Low Gene Flow with Wild Relatives. Plants 12 (23):3989
2. Ayala-Doñas A, Cara-García Md, Talavera-Rubia M, Verdejo-Lucas S (2020) Management of Soil-Borne Fungi and Root-Knot Nematodes in Cucurbits through Breeding for Resistance and Grafting. Agronomy 10 (11):1641
3. Behera T, Jat G, Lata S, Kumar S (2021) Classical Genetics and Traditional Breeding in Cucumber (*Cucumis sativus*) L. In: Wang H (ed) Cucumber Economic Values and Its Cultivation and Breeding. IntechOpen, London. doi:10.5772/intechopen.97593
4. Cavatorta J, Moriarty G, Henning M, Glos M, Kreitinger M, Munger HM, Jahn M (2007) 'Marketmore 97': a monoecious slicing cucumber inbred with multiple disease and insect resistances. HortScience 42 (3):707-709
5. Chandrasekaran J, Brumin M, Wolf D, Leibman D, Klap C, Pearlsman M, Sherman A, Arazi T, Gal-On A (2016) Development of broad virus resistance in non-transgenic cucumber using CRISPR/Cas9 technology. Molecular plant pathology 17 (7):1140-1153
6. Choudhary B, Fageria M (2002) Breeding for multiple disease resistance in cucurbits (water melon, musk melon, cucumber and squash)-a review. AGRICULTURAL REVIEWS-AGRICULTURAL RESEARCH COMMUNICATIONS CENTRE INDIA 23 (4):300-304
7. Collard BCY, Mackill DJ (2007) Marker-assisted selection: an approach for precision plant breeding in the twenty-first century. Philosophical Transactions of the Royal Society B: Biological Sciences 363 (1491):557-572.
8. Council NR, Plants CoEIAwCoT (2002) Case Studies of APHIS Assessments. In: Environmental Effects of Transgenic Plants: The Scope and Adequacy of Regulation. National Academies Press (US),
9. Dhillon NP, Sanguansil S, Singh SP, Masud MAT, Kumar P, Bharathi LK, Yetişir H, Huang R, Canh DX, McCreight JD (2016) Gourds: bitter, bottle, wax, snake, sponge and ridge. Genetics and genomics of cucurbitaceae:155-172
10. Doudna JA, Charpentier E (2014) The new frontier of genome engineering with CRISPR-Cas9. Science 346 (6213):1258096.
11. Fuchs M, Chirco EM, Gonsalves D (2004b) Movement of coat protein genes from a commercial virus-resistant transgenic squash into a wild relative. Environ Biosafety Res 3 (1):5-16.
12. Grumet R, McCreight JD, McGregor C, Weng Y, Mazourek M, Reitsma K, Labate J, Davis A, Fei Z (2021c) Genetic Resources and Vulnerabilities of Major Cucurbit Crops. Genes (Basel) 12 (8).
13. Hernandez CO, Wyatt LE, Mazourek MR (2020a) Genomic prediction and selection for fruit traits in winter squash. G3: Genes, Genomes, Genetics 10 (10):3601-3610
14. Hooghvorst I, Nogués S (2020) Opportunities and challenges in doubled haploids and haploid inducer-mediated genome-editing systems in cucurbits. Agronomy 10 (9):1441
15. Huang C (2026) AI assisted optimization of CRISPR Cas systems and functional gene screening in cucurbit crops. Discover Plants 3 (1):84
16. Kahveci E, Devran Z, Özkaynak E, Hong Y, Studholme DJ, Tör M (2021a) Genomic-assisted marker development suitable for Cscvy-1 selection in cucumber breeding. Frontiers in plant science 12:691576
17. Kumari S, Krishnan N, Dubey V, Das B, Pandey KK, Singh J (2021) Investigations on annual spreading of viruses infecting cucurbit crops in Uttar Pradesh State, India. Sci Rep 11 (1):17883.
18. Liu C, Du S, Wei A, Cheng Z, Meng H, Han Y (2024) Hybrid prediction in horticulture crop breeding: progress and challenges. Plants 13 (19):2790
19. Ma L, Wang Q, Zheng Y, Guo J, Yuan S, Fu A, Bai C, Zhao X, Zheng S, Wen C, Guo S, Gao L, Grierson D, Zuo J, Xu Y (2022b) Cucurbitaceae genome evolution, gene function, and molecular breeding. Horticulture Research 9.
20. Martín-Hernández AM, Picó B (2020) Natural resistances to viruses in cucurbits. Agronomy 11 (1):23
21. Men X, Choi SI, Han X, Kwon HY, Jang GW, Choi YE, Park SM, Lee OH (2021) Physicochemical, nutritional and functional properties of Cucurbita moschata. Food Sci Biotechnol 30 (2):171-183.
22. Mittler R, Blumwald E (2010) Genetic Engineering for Modern Agriculture: Challenges and Perspectives. Annual Review of Plant Biology 61 (Volume 61, 2010):443-462. doi:https://doi.org/10.1146/annurev-arplant-042809-112116

23. Öztürk Hİ, Dönderalp V, Bulut H, Korkut R (2022) Morphological and molecular characterization of some pumpkin (Cucurbita pepo L.) genotypes collected from Erzincan province of Turkey. Scientific Reports 12 (1):6814
24. Prem N CUCURBITS - EVERYONE'S CROP. In, 2007. International Society for Horticultural Science (ISHS), Leuven, Belgium, pp 485-492.
25. Qaim M (2020) Role of new plant breeding technologies for food security and sustainable agricultural development. Applied Economic Perspectives and Policy 42 (2):129-150
26. Ram C, Berwal MK, Gora JS, Kumar R, Haldhar SM, Gurjar K, Singh D (2019b) Genomic and biotechnological interventions for crop improvement in cucurbitaceous crops: A review. Journal of Agriculture and Ecology 7 (7):1-15
27. Robinson R i Decker-Walters DS, 1997. Cucurbits CAB International, New York
28. Robinson RW (1999) Rationale and Methods for Producing Hybrid Cucurbit Seed. Journal of New Seeds 1 (3-4):1-47.
29. Rolnik A, Olas B (2020) Vegetables from the Cucurbitaceae family and their products: Positive effect on human health. Nutrition 78:110788.
30. Sasaki K, Urano K, Mimida N, Nonaka S, Ezura H, Imai R (2025a) A long shelf-life melon created via CRISPR/Cas9 RNP-based in planta genome editing. Front Genome Ed 7:1623097.
31. Schafleitner R, Chen-yu L, Laenoi S, Shu-mei H, Srimat S, Gi-An L, Chatchawankanphanich O, Dhillon NPS (2024b) Molecular markers associated with resistance to squash leaf curl China virus and tomato leaf curl New Delhi virus in tropical pumpkin (Cucurbita moschata Duchesne ex Poir.) breeding line AVPU1426. Scientific Reports 14 (1):6793.
32. Shahwar D, Khan Z, Park Y (2024) Molecular markers for marker-assisted breeding for biotic and abiotic stress in melon (Cucumis melo L.): A review. International Journal of Molecular Sciences 25 (12):6307
33. Singh D, Upadhyay M Breeding potential of indigenous germplasm of cucurbits. In: I International Conference on Indigenous Vegetables and Legumes. Prospectus for Fighting Poverty, Hunger and Malnutrition 752, 2006. pp 209-212
34. Singh H, Sekhon BS, Kumar P, Dhall RK, Devi R, Dhillon TS, Sharma S, Khar A, Yadav RK, Tomar BS, Ntanasi T, Sabatino L, Ntatsi G (2023b) Genetic Mechanisms for Hybrid Breeding in Vegetable Crops. Plants 12 (12):2294
35. Tracy WF, Shuler SL, Dodson-Swenson H (2019) The Use of Endosperm Genes for Sweet Corn Improvement. In: Plant Breeding Reviews. pp 215-241.
36. Tricoll DM, Carney KJ, Russell PF, McMaster JR, Groff DW, Hadden KC, Himmel PT, Hubbard JP, Boeshore ML, Quemada HD (1995) Field Evaluation of Transgenic Squash Containing Single or Multiple Virus Coat Protein Gene Constructs for Resistance to Cucumber Mosaic Virus, Watermelon Mosaic Virus 2, and Zucchini Yellow Mosaic Virus. Bio/Technology 13 (12):1458-1465.
37. Tzfira T, Citovsky V (2006) Agrobacterium-mediated genetic transformation of plants: biology and biotechnology. Current Opinion in Biotechnology 17 (2):147-154.
38. Wang C-S, Lin S-Y, Huang J-H, Chang H-Y, Lew D-K, Wang Y-H, Hwu K-K, Huang Y-F (2024a) Identification of powdery mildew resistance quantitative trait loci in melon and development of resistant near-isogenic lines through marker-assisted backcrossing. Botanical Studies 65 (1):31
39. Wang Z, Wan L, Ren J, Zhang N, Zeng H, Wei J, Tang M (2024b) Improving the Genome Editing Efficiency of CRISPR/Cas9 in Melon and Watermelon. Cells 13 (21).
40. Warsi S, Li Y, Mbata GN, Simmons AM (2025) Insect Abundance and Richness in Squash Agroecosystems of Georgia, United States: The Role of Cultivar Selection and Weather Conditions. Agronomy 15 (6):1411
41. Xu Y, Crouch JH (2008) Marker-Assisted Selection in Plant Breeding: From Publications to Practice. Crop Science 48 (2):391-407.
42. Yu J, Wu S, Sun H, Wang X, Tang X, Guo S, Zhang Z, Huang S, Xu Y, Weng Y, Mazourek M, McGregor C, Renner SS, Branham S, Kousik C, Wechter WP, Levi A, Grumet R, Zheng Y, Fei Z (2023b) CuGenDBv2: an updated database for cucurbit genomics. Nucleic Acids Res 51 (D1):D1457-d1464.
43. Ziemienowicz A (2014) Agrobacterium-mediated plant transformation: Factors, applications and recent advances. Biocatalysis and Agricultural Biotechnology 3 (4):95-102.

Table 1. Genetic Resources and Diversity in Major Cucurbit Crops

Crop	**Important Genetic Resources**	**Valuable Traits Identified**	**Breeding Importance**	**Major Constraints**	**Reference**
Cucumber (*Cucumis sativus*)	Poona Kheera, PI 183967, PI 197087, wild relative *Cucumis hardwickii*	Disease resistance, abiotic stress tolerance, fruit quality traits	Used for hybrid breeding and resistance introgression	Narrow genetic base due to domestication bottlenecks	(Grumet et al. 2021b; Ma et al. 2022a)

Watermelon (*Citrullus lanatus*)	African Egusi landraces, Kordofan melon accessions, *C. amarus* and *C. mucosospermus* accessions, PI 296341, PI 560023	Drought tolerance, disease resistance, fruit quality variation	Important for stress-resilient cultivar development	Limited interspecific compatibility	(Grumet et al. 2021b)
Melon (*Cucumis melo*)	Horticultural groups Dudaim, Flexuosus, Momordica, Cantalupensis, Inodorus, traditional Asian and Mediterranean landraces	Fruit aroma, sweetness, shelf life, disease resistance	Valuable for fruit quality and stress breeding	Genetic erosion of traditional cultivars	(Ma et al. 2022a; Yu et al. 2023a)
Pumpkin (*Cucurbita moschata*)	Turkish local pumpkin genotypes from Erzincan Province, indigenous Anatolian landraces	Nutritional quality, adaptability, disease resistance	Useful for climate resilience breeding	Cross-pollinated nature complicates maintenance	(Öztürk et al. 2022; Grumet et al. 2021b)
Squash (*Cucurbita pepo*)	*C. pepo* subsp. texana, scallop squash and ornamental squash landraces, wild *C. pepo* accessions	Virus resistance and environmental adaptability	Source of resistance genes for breeding programs	Linkage drag during introgression	(Grumet et al. 2021b)
Figleaf gourd (*Cucurbita ficifolia*)	Mexican traditional populations, Andean landraces, farmer-maintained accessions from Central and South America	Adaptation to environmental stress and disease tolerance	Potential donor for broad genetic diversity	Low gene flow with wild relatives	(Aguirre-Dugua et al. 2023a)

Table 2. Traditional Breeding Approaches Used for Improvement of Cucurbits

Cucurbit Crop	**Variety / Line Developed**	**Trait Improved**	**Classical Breeding Method Used**	**Major Result / Outcome**	**Reference**
Cucumber (*Cucumis sativus*)	Poinsett 76	Resistance to downy mildew, powdery mildew, anthracnose, CMV	Hybridization + backcross selection	Developed a stable multi-disease-resistant cucumber cultivar extensively used in breeding	(Choudhary and Fageria 2002)
Cucumber	Marketmore 97	Multiple disease and insect resistance	Recurrent selection and pedigree breeding	Broad resistance to several diseases and insects with good fruit quality	(Cavatorta et al. 2007)
Cucumber	Palmetto	Downy mildew resistance	Germplasm introduction and selection	Improved adaptability and disease resistance under humid environments	(Robinson)
Watermelon (*Citrullus lanatus*)	Arka Manik	High yield + resistance to anthracnose, powdery mildew, downy mildew	Hybridization + backcross breeding	High-yielding cultivar with combined disease resistance	(Choudhary and Fageria 2002)
Watermelon	Pusa Bedana	Seedlessness	Polyploid breeding	Successful development of seedless watermelon	(Singh et al. 2023a)

			(triploid breeding)	with improved consumer preference	
Muskmelon (*Cucumis melo*)	Hara Madhu	High TSS and fruit quality	Pure line selection	Improved sweetness and market quality	(Grumet et al. 2021a)
Muskmelon	Punjab Hybrid	Earliness and yield	Hybridization and selection	Early maturing, high-yielding muskmelon hybrid	(Singh and Upadhyay 2006)
Summer squash (*Cucurbita pepo*)	Punjab Chappan Kaddu-I	Early maturity and disease tolerance	Selection from segregating populations	High yield with tolerance to major diseases	(Choudhary and Fageria 2002)
Summer squash	Zucchini resistant lines	Resistance to ZYMV and WMV	Conventional hybridization and selection	Improved tolerance to viral diseases	(Martín-Hernández and Picó 2020)
Pointed gourd (*Trichosanthes dioica*)	IIVR Seedless Clones	Seedlessness and uniformity	Clonal selection	Development of uniform seedless lines	(Singh and Upadhyay 2006)

Table 3. Molecular Markers and Target Traits in Cucurbit Crops

Crop	**Marker Type**	**Target Trait**	**Gene/QTL Identified**	**Application**	**Reference**
Cucumber (*Cucumis sativus*)	SNP markers	Resistance to cucumber vein yellowing virus	*CsCvy-1* locus	Marker-assisted selection for virus resistance	(Kahveci et al. 2021a)
Melon (*Cucumis melo*)	SSR and SNP markers	Biotic and abiotic stress tolerance	Pm-x, qPx1.1, qPx5.1, Fom-1, Fom-2, Fom-4	Stress-resilient cultivar development	(Shahwar et al. 2024)
Pumpkin (*Cucurbita moschata*)	Molecular markers	Resistance to ToLCNDV and SLCuV	AX-177354082 (ToLCNDV resistance), AX-177360734 (SLCuV resistance)	Introgression of resistance into elite lines	(Schafleitner et al. 2024a)
Watermelon (*Citrullus lanatus*)	SNP markers	Fruit quality and yield traits	ClFC4.1, SSC2.1, QBRX2-1, FS1.1	Fruit quality improvement breeding	(Ram et al. 2019a)
Melon (*Cucumis melo*)	QTL mapping	Fruit sweetness and aroma	SSC6.1, SSC11.1, SUCQSC5.1	Improvement of fruit quality traits	(Ma et al. 2022a)

Table 4. Transgenic Approaches Applied in Cucurbit Crops

Crop	**Introduced Gene**	**Target Trait**	**Transformation Method**	**Major Outcome**	**Reference**
C. pepo – line CZW-3 (Guan-Lei)	Virus resistance (ZYMV, WMV2, CMV)	Resistance to cucumber mosaic virus	Agrobacterium-mediated transformation	No systemic infection; ~64% only local lesions; 50× increase in marketable yield vs. non-transgenic	(Tricoll et al. 1995)
C. pepo – line ZW-20 (Whitaker)	ZYMV coat protein gene	Resistance to zucchini yellow mosaic virus	Genetic transformation	78% remained virus-free (22% CMV infected); 40× yield increase vs. control	(Tricoll et al. 1995)
C. pepo – line Z-33 (Whitaker)	WMV coat protein gene	Broad-spectrum viral resistance	Transgenic expression system	Fully resistant to ZYMV; susceptible to CMV/WMV; nonetheless ~20× yield vs. control	(Tricoll et al. 1995)
Squash (*Cucurbita pepo*)	Multiple viral coat protein genes	Multi-virus resistance	Agrobacterium-mediated transformation	Stable field resistance against CMV, WMV, and ZYMV	(Fuchs et al. 2004a)

Table 5. Genome Editing Applications in Cucurbit Crops

Crop	Target Gene	Trait Improved	Major Outcome	Reference
Cucumber (*Cucumis sativus*)	*CsWIP1*	Gynoecious flowering habit	Improved efficiency of hybrid seed production	(Huang 2026)
Melon (*Cucumis melo*)	*CmACO1*	Shelf-life extension	Reduced ethylene production and delayed ripening	(Sasaki et al. 2025b)
Melon (*Cucumis melo*)	*PDS*	Functional genomics validation	Successful mutation induction and albino phenotype generation	(Wang et al. 2024a)
Watermelon (*Citrullus lanatus*)	*PDS*	Functional genomics validation	Demonstrated efficient genome editing system	(Wang et al. 2024a)
C. sativus	*eif4E*	Broad virus resistance	Homozygous mutants immune to Cucumber vein yellowing virus and resistant to ZYMV and PRSV-W	(Chandrasekaran et al. 2016)

Table 6. Future Challenges and Emerging Opportunities in Cucurbit Improvement

Challenge	Major Limitation	Emerging Solution	Potential Future Impact	Reference
Narrow genetic base	Reduced variability in cultivated germplasm	Utilization of wild relatives and pre-breeding strategies	Enhanced stress resilience and broader trait diversity	(Aguirre-Dugua et al. 2023a; Grumet et al. 2021b)
Climate change	Heat, drought, and unpredictable environmental stress	Climate-smart breeding and genomic selection	Development of stress-resilient cultivars	(Liu et al. 2024)
Complex polygenic traits	Difficult phenotypic selection for yield and quality traits	Genomic prediction and AI-assisted breeding	Faster genetic gain and breeding efficiency	(Hernandez et al. 2020a; Huang 2026)
Poor transformation efficiency	Low regeneration capacity in cucurbits	Improved tissue culture and transformation systems	Increased success of genome editing programs	(Hooghvorst and Nogués 2020)
Regulatory and biosafety concerns	Delayed commercialization of biotech crops	Harmonized biosafety regulations	Wider adoption of genome-edited cultivars	(Qaim 2020)
Rapid pathogen evolution	Breakdown of resistance genes	Durable and multi-gene resistance breeding	Sustainable disease management	(Shahwar et al. 2024)
Limited phenotyping efficiency	Slow and labour-intensive trait evaluation	High-throughput phenotyping and digital agriculture	Accelerated breeding pipelines	(Liu et al. 2024)