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GENETIC IMPROVEMENT OF MUSKMELON (CUCUMIS MELO L.) FOR ENHANCED YIELD, FRUIT QUALITY AND RESILIENCE: CONVENTIONAL AND GENOMICS-ASSISTED STRATEGIES

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ABSTRACT

Muskmelon (Cucumis melo L.) is an economically important horticultural crop valued for its nutritional quality, flavour, and diverse fruit characteristics. Improving yield, fruit quality, and resilience to biotic and abiotic stresses remains a major breeding priority as climate changes and market demands increase. This review examines advances in conventional and genomics-assisted breeding strategies for improving muskmelons, emphasising genetic diversity, heterosis, quantitative trait loci (QTL) mapping, marker-assisted selection, genetic transformation, and genome editing. Conventional breeding approaches, including hybridization, selection, and backcrossing, remain essential for developing high-yielding and locally adapted cultivars. Advances in genome sequencing and molecular markers have facilitated the identification of genomic regions associated with fruit size, sweetness, pigmentation, ripening, shelf life, and disease resistance. Tissue culture and regeneration techniques provide important platforms for genetic transformation, while CRISPR/Cas9-mediated genome editing offers opportunities for functional gene validation and targeted trait improvement. However, challenges related to marker transferability, genotype-dependent regeneration, complex trait inheritance, and genotype × environment interactions continue to limit the practical application of these technologies. Integrating conventional breeding with molecular tools, validated markers, and multi-environment phenotypic evaluation is essential for translating genetic discoveries into measurable improvements in cultivar performance. Future breeding efforts should prioritize stable marketable yield, durable disease resistance, improved postharvest quality, and environmental adaptability to support sustainable muskmelon production.

KEYWORDS: Cucumis melo L.; genetic improvement; genetic diversity; heterosis; quantitative trait loci; marker-assisted selection; genome editing; fruit quality; stress tolerance.

INTRODUCTION

Muskmelon (Cucumis melo L.) is a member of the Cucurbitaceae and includes a variety of horticultural groups that are grown in various agroecological regions. Its fruits differ markedly in shape, mass, flesh and rind colour, soluble-solids concentration, aroma, texture and ripening behaviour. This diversity leads to cultivars for fresh consumption and transport, local markets and protected cultivation. However, muskmelon improvement must need to consider that the best appearance of the fruit or extended shelf life does not necessarily go together with the highest biological yield. Commercial performance is defined as the marketable yield, uniformity, eating quality and adaptability to production conditions (Nuñez-Palenius et al., 2008; Robinson and Decker-Walters, 1999).

Diseases, insect pests, fluctuations in irrigation-water quality, extremes of temperature, and nutrient deficiencies have an impact on the crop. Additionally, breeding objectives are different in different markets; for one market, weight and sweetness may be most important, for another market, firmness, colour and shipping qualities may be most important. Yield per plant, yield per unit area and marketable yield should be treated as separate outcomes, as larger fruits, more or fewer plants, and early maturity could all be used to achieve higher marketable yields without influencing each other. Useful improvement has been achieved by conventional selection and hybrid breeding, and genomic resources now offer means to describe the genetic architecture explaining the complexity of traits. (Garcia-Mas et al., 2012; Pereira et al., 2018).

Melon is a diploid species (2n = 2x = 24) that exhibits variable sex expression and divergent fruit phenotypes within the botanical as well as horticultural groups. A doubled haploid reference genome was used as a starting point to build a genomic reference for locating genes and sequence polymorphisms as well as for comparing and aligning marker data (Garcia-Mas et al., 2012). Having the chromosome-level resources changed the practical question for breeders: not only was there a question of whether a trait segregated, but there was also a question of whether diagnostic variation was sufficiently correlated with the causal locus to allow for rapid selection. However, the breeding values are still reported based on environment, not genome assembly.

Loss avoidance is also a factor in commercial yield. The number of fruit may be protected by resistance to vascular wilt or foliar pathogens; firmness may be maintained during transport and heat tolerance may help to maintain fruit set during

adverse flowering conditions. These mechanisms are very different from a direct increase in genetic yield potential. If a cultivar does not increase its biomass per fruit, it can also increase the number of fruits per plant to increase marketable yield, or reduce rejection, while retaining the same biomass per fruit. It is important to record a pathway that describes how the improvement is being brought about for comparison with conventional selection and biotechnology-assisted selection.

Breeding should be organized about the genetic basis of the desired phenotype and be aided by environmental testing. Highly heritable large-effect traits can be easily selected using well validated markers, while yield stability, fruit flavour and stress tolerance may involve replicated phenotyping and multiple favourable alleles. Tissue culture, transformation and genome editing are directly used for genetic discovery and experimental development, and their use for growers needs to be demonstrated with uniform and adapted cultivars with proven marketable yield.

2. Breeding objectives and measurable genetic gain

First, improvement objectives need to be stated in biological and commercial terms and then a breeding technique chosen. The fruit yield depends on survival rates, reproductive success, fruit number, average weight of fruit and percentage of fruit achieving marketable quality. The quality characteristics that are sought are the soluble solids, sugar composition, aroma, flesh colour, firmness, eating quality and postharvest quality retention. Each of the targets has a relative weight depending on horticultural group, production time, transport distance, and the consumer preference. Selecting larger fruit size may increase the unit value in one market but decrease fruit number or ripening-associated aroma in other markets; breeding for firm fruit may be beneficial to handling, but impart a different desired ripening-associated aroma. A target product profile can be useful to rationalize such trade-offs (Nuñez-Palenius et al., 2008; Shahwar et al., 2023).

Phenotypes to be used in genetic gain evaluation should be appropriate to the breeding goal. A validated DNA marker is a documented inherited association, an experimental feasibility is a regeneration protocol. Automatically do not indicate increased commercial productivity. Significant progress is demonstrated by the ability of genetically defined progeny to exhibit target characteristics across independent populations and target environments, preferably using appropriate commercial checks as a comparison. Both total fruit mass and marketable output are reported for yield, and a measure of soluble solids is not a substitute for sensory, texture and shelf-life evaluation for quality. The breeding progress (Pereira et al., 2018; Esteras et al., 2026) is reinforced by the combination of these endpoints.

When a fruit's quality is being assessed for practical evaluation, fruit number per plant, average fruit weight and marketable yield/ha should be supplemented with harvest duration, total soluble solids, firmness and major defects. For disease studies, the pathogen identification should be reported, along with the inoculation conditions. For marker studies, the size of the segregating population and the material used for the validation study should be reported. These measures ensure that the results can be transferred across melon production areas, and that a large effect in one experimental condition will not be repeated in another.

3. Genetic Resources and the Architecture of Yield-Related Traits

Germplasm genetic variability is crucial in muskmelon breeding, especially in local and market-oriented germplasm. Abu Zaitoun et al. (2018) demonstrated the utility of SNP and DArTseq markers for characterizing Palestinian snake-melon populations. Similar approaches can support the identification of valuable genetic resources in Indian muskmelon and snapmelon. However, molecular diversity must be complemented by phenotypic evaluation to identify useful alleles for yield, quality and resistance.

3.1 Diversity, Germplasm and Parental Selection

Molecular characterization using SNPs and SSRs has revealed substantial genetic variation and population structure in melon germplasm, supporting parental selection and genetic improvement (Blanca et al., 2012; Saha et al., 2022; Tara et al., 2024). Genome-wide analysis of 1,175 accessions identified multiple domestication events and agronomically important genomic regions (Zhao et al., 2019). Phylogenetic studies further revealed relationships with Australian Cucumis taxa and divergent African and Asian lineages (Sebastian et al., 2010; Endl et al., 2018). Additionally, defence-related gene presence/absence variations provide opportunities for resistance breeding (González et al., 2013). Introgression-line populations facilitate identification of loci controlling fruit morphology, quality, ripening and resistance (Esteras et al., 2026). Nevertheless, successful selection of parents is dependent on a combination of factors including molecular diversity, crossing ability, disease resistance, and adaptation to the environment (Saha et al., 2022; Tara et al., 2024).

3.1.1 Population Structure, Domestication and Adaptation

PopGen analyses have revealed the intricate history of domestication in melon, as well as the value of genetic diversity within germplasm for plant breeding (Zhao et al., 2019). Distinct germplasm can carry desirable alleles, but at the same time can bring unwanted horticultural traits. Introgression lines are used to screen donor germplasm for beneficial regions in combination with an elite genetic background, even if some level of linkage drag remains that needs additional backcrossing (Esteras et al., 2026).

3.2 Quantitative Inheritance, Component Traits and Genotype × Environment Interactions

Muskmelon yield is a quantitative trait determined by the number of fruits per plant, fruit size, ripening, marketability, and environment. Quantitative inheritance and environmental influences on the yield-related traits were documented in genetic analysis (Sakulphrom et al., 2018). The selection of one trait may not always result in the improvement of the total marketable yield because of the possible trade-off between the traits. Genotype x Environment interactions also play a role in muskmelon productivity, resistance, and quality. Consequently, breeding programs should use multi-environment

trials with replication and selection indices including marketable yield, soluble solids, fruit uniformity, resistance and shelf life.

4. Conventional Breeding Strategies

Breeding techniques will always play an important role in the betterment of muskmelons, but marker-assisted selection increases efficiency. Monforte et al. (2004) used F_2 and doubled-haploid populations to detect QTLs for fruit quality and earliness, but Díaz et al. (2014) showed the introgression of fruit shape loci in commercial melons. The efficiency of the markers is based on genetic background and thus requires backcrossing. Sex expression is another important aspect affecting seed production. Boualem et al. (2022) pointed out CmACS7's involvement in floral sex and fruit shape formation, while Zhao et al. (2026) talked about sex determination.

4.1 Selection, Controlled Crossing and Heterosis

Selection based on phenotype, selfing, pedigree breeding, backcrossing, and recurrent selection aid in the development of better parental lines and varieties (Robinson & Decker-Walters, 1999). Reproductive genetics plays an important role in hybridization success. Boualem et al. (2008, 2015) found ethylene-based genes responsible for sexual differentiation, whereas Martin et al. (2009) found that CmWIP1 is regulated epigenetically. Such results favor controlled pollinations and parental line selections. Hybrids are developed using heterosis for better earliness, quality, and productivity. Duradundi et al. (2018) found some promising heterotic combinations in muskmelons. Nevertheless, to develop good hybrids, it is necessary to study their combining ability and test in multiple environments.

4.2 Resistance Breeding and Adaptation

Muskmelon resistance breeding is necessary to safeguard against Fusarium wilt, powdery mildew, downy mildew and viral diseases. In the case of Sharma et al. (2026), they identified QTLs related to resistance to root-knot nematode, and Duan et al. 2024 fine-mapped powdery mildew resistance to a 63.5 kb interval. Wang et al. (2024) developed resistant near-isogenic lines via marker-assisted backcrossing. Likewise, Zhang et al. (2023) detected the DM9.1 downy mildew resistance locus, which accounted for 24.3–37.7% of phenotypic variation in the dataset. The results bolster resistance improvement but need to be tested in different pathogen populations and environments.

For productivity to be stable, abiotic-stress tolerance should also be important. Mendlinger and Fossen (1993) reported that cultivars differed in sensitivity to salinity in terms of growth, yield and fruit quality. Hence, it is essential to incorporate into breeding programmes physiological screening, flowering and fruit-set evaluation, marketable yield and multi-environment testing, to produce productive and stress-resilient muskmelon cultivars.

5. Tissue culture and regeneration as enabling technologies

Tissue culture offers opportunities for clonal propagation, selected cell line regeneration and the recovery of genetically modified plants. However, with melon, the recalcitrance of certain genotypes hinders the comparison of culture protocols. Cotyledon, hypocotyl and embryonic-axis explants are not synonymous because their organogenic competence is influenced by donor physiological age, response to wounds, auxin history, vessel conditions and cytokinin balance. Therefore, the highest regeneration percentage observed in one culture system should be replicated with the desired breeding genotype prior to introducing it into other culture systems. Stable plant regeneration and normal fertility in addition to early shoot formation is the requirements of an effective transformation pipeline.

Recent research provides examples of how protocol optimization can overcome these limitations. In the experimental background of melon, Li et al. (2025b), Cao, Liu et al. (2025) observed that prolonging the Agrobacterium co-culture without sucrose significantly boosted transformation efficiency and they also produced a tendril-less edited melon. The claimed fruit enhancement is not a direct increase in fruit yield, but rather a performance enhancement in the method. In addition, a melon hairy-root transformation system enabled the quick assessment of the effectiveness of the CRISPR targets and functional study of CmRHL1 in the development of root hairs (Li et al., 2025a). Confirmation of heritable edits and stable whole-plant phenotypes is necessary, and the hairy-root responses are merely used for selection of editing constructs. The differences are very critical when deciding whether a biotechnology protocol is ready to be adopted for varietal development.

5.1 Organogenesis and somatic embryogenesis

In vitro culture can be used to generate multiple plants, to regenerate plant after transformation, to carry out experimental mutagenesis and to rescue plants from tissues which are hard to maintain by conventional seed propagation. Organogenesis can occur directly from explants or indirectly after a callus phase; somatic embryogenesis can occur from somatic tissue to produce embryo-like structures that are able to form whole plants. Both methods can aid in plant recovery, but neither method in itself will improve fruit production. They are useful depending on explant response, genotype, stability of regenerants and their incorporation into a breeding pipeline (Nuñez-Palenius et al., 2008). The developmental pathway that is dominant in vitro is affected by explant identity, physiological age, genotype, basal media and carbohydrate-to-plant-growth-regulator ratios. Adventitious shoot production is usually tested in cytokinin-rich systems, while exposure to auxin and the adjustment of the auxin level may promote embryogenic competence. Callus-mediated regeneration methodology causes somaclonal changes, so when genetic fidelity is of importance, direct organogenesis is preferred. However, in situations requiring the rapid multiplication of experimental material, somatic embryogenesis or suspension-derived regeneration may be useful. The biological problem, and not just a maximised laboratory percentage, should dictate the selection of the regeneration route.

For the melon, Bairwa et al. (2010a) made an example-comparison of the embryonic-axis responses between four genotypes, and noted significant differences in the organogenesis and embryogenesis between the different culture media. Experiments illustrate a genotype dependence and the necessity of testing the regeneration systems with breeding material.

Embryogenic cell-suspension regeneration was later reported by Bairwa et al. (2012) which included the significance of hormone combinations and cultivar differences. These findings support the use of the tissue-culture system as a research tool to optimize the process of shoot regeneration, but it is not suggested that the shoot-regeneration rate be used directly as an indication of productivity in agricultural fields. Leaf tissue, hypothalli, and embryo axes have been tested as explants in melon, as has the embryo cotyledon. Previously, it was demonstrated that organogenesis and somatic embryogenesis can be influenced by the composition and concentrations of culture media, as well as the concentration of auxins and cytokinins (Oridate and Oosawa, 1986; Stipp et al., 2001). Changes in response in cultured embryonic axes and embryogenic suspension cultures demonstrated significant genotype differences in melons (Bairwa et al., 2010a, 2010b, 2012). Therefore, per cent regeneration from genotype or laboratories should not be termed a broadly optimized protocol without independent testing.

The media combinations from representative regeneration approaches are combined in Table 1, without repeating the combinations from the studies to which they belong, if the combinations are not directly comparable. Care must be taken in differentiating the number of responsive explants, shoots per responsive explant and the frequency of complete plant recovery when comparing such. Future protocols should include genotype, age of explant, basal medium, concentration of regulator used, culture period, and the denominator used to calculate each percentage.

Table 1. Selected melon regeneration approaches and their experimentally supported roles.

Regeneration Approach	Plant Material / System	Demonstrated Contribution	Interpretation for Breeding	Reference
Suspension-callus regeneration	Melon cell cultures	Plant regeneration through somatic embryogenesis	Establishes an effective regeneration pathway, without demonstrating yield improvement	Oridate and Oosawa (1986)
In vitro morphogenesis	Cucumis melo var. inodorus explants	Organogenic and embryogenic responses under different culture conditions	Regeneration efficiency depends on genotype and culture protocol	Stipp et al. (2001)
Embryonic-axis regeneration	Embryonic axes of four melon genotypes	Successful organogenesis and somatic embryogenesis with genotype-dependent responses	Provides a potential regeneration system for muskmelon breeding	Bairwa et al. (2010a)
Embryogenic suspension culture	Cotyledon- and hypocotyl-derived embryogenic callus	Establishment of embryogenic cell suspensions and regeneration of plantlets	Supports regeneration, tissue-culture research and experimental applications	Bairwa et al. (2012)
Transformation-assisted regeneration	Cotyledon explants from different melon genotypes	Improved transformation and plant regeneration using developmental regulatory genes	Facilitates functional genomics and genome-editing applications	Wan et al. (2023)

5.2 Cell suspensions, somaclonal variation and polyploidization

Cell suspension cultures typically consist of isolated cells or cell clusters from growing calluses, cultured in a liquid medium. Unlike isolated microspore cultures, male gametophytic cells are cultured for androgenic or haploid development. Bairwa et al., (2012) reported the production of embryogenic suspensions from muskmelon tissues and found that they were influenced by genotype and exogenous regulators. These systems provide opportunities for cell recovery following selection or transformation, but practical issues like somaclonal instability, culture length and keeping regeneration competency are present.

During tissue culture, unexpected changes in the phenotype or genome that are termed somaclonal variation may occur. Certain variants may be useful in the discovery of traits, but random changes can result in loss of genetic fidelity in elite lines or parental stocks. Likewise, polyploidy induction, or spontaneous induction, is a scientific curiosity not necessarily with increased commercial benefits. Ploidy changes could impact fertility, fruit development and stability. Before any promising regenerated line can be regarded as an improved cultivar it must be confirmed as being ploidic, molecularly characterized if applicable and retested in the field.

Somaclonal variation is a challenge and potential source of novelty. The number of chromosomes, DNA sequence or epigenetic state may change in tissue culture; the frequency and effects are genotype-dependent and will depend on the duration of tissue culture. Plants generated for uniform clonal material should be screened for ploidy, genetic stability, and phenotypic fidelity. If variation is intentionally pursued it is necessary for candidate somaclones to be sexually propagated and tested against suitable controls before they can be used in cultivar development. No callus diversity is proof of useful stress tolerance; it is heritable.

5.3 Embryo rescue, haploid production and doubled haploids

Embryo rescue is the technique of culturing immature or poor-quality embryos to recover plants which may not have been possible to obtain. Success is dependent on the crossing combination used and the stage of embryo excision and

reproductive barriers can remain even after in vitro culture. Haploid and doubled haploid (DH) production can speed the development of homozygous lines, but the efficiency of the methods is strongly dependent on the biological system. Microspore culture should be considered separately from somatic suspensions. The culture conditions described by Nguyen (2023) eliminated from isolated melon microspores should not be applied to all melon germplasm, nor should it be considered a field-yield improvement technique.

DH methods can be useful for fixing useful alleles quickly and ease the process of combining ability testing when stable fertile lines are generated. However, recyclable haploid embryos, genotype responsiveness and plant fertility are still factors limiting the use of this technique. The watermelon and other cucurbit reports suggest some possible technical pathways but are not a direct validation of the routine production of doubled-haploid muskmelons. Breeders should evaluate the time and costs of DH pipelines against traditional inbreeding before they are widely used.

Haploid and double haploid methods may be helpful in creating a homozygous line to complement predictable hybrid development. But it is important to remember that while successful, there are differences between species of cucurbit and between genotypes of melon, and that microspore culture, ovary culture and irradiated-pollen all represent different ways of doing it, and cannot be considered interchangeable. A documented haploid plant is just a stepping stone. The material becomes a stable parental resource only after having been confirmed for chromosome number, chromosome doubling, fertility and true genetic homozygosity and after having been evaluated for agronomic performance.

6. Genomics-Assisted Breeding and Marker Development

Advances in melon genome sequencing have improved the identification and mapping of yield- and quality-related traits. The reference genome established a foundation for molecular breeding (Garcia-Mas et al., 2012), while improved genome assemblies and high-density bin maps enhanced QTL resolution and candidate-gene identification (Ruggieri et al., 2018; Lian et al., 2021). Monforte et al. (2014) identified associations between fruit-weight QTLs and candidate genes from the CNR/FW2.2 and KLUH/FW3.2 families, along with OVATE-family genes related to fruit shape. Similarly, Zhao et al. (2023) mapped loci associated with soluble solids, rind firmness and flesh firmness. However, QTL effects vary across populations and environments, requiring independent validation before breeding applications.

6.1 Genome Resources, Molecular Markers and QTL Mapping

Molecular markers, including SNPs, SSRs and insertion/deletion markers, facilitate genetic characterization, linkage mapping and marker-assisted selection. Pereira et al. (2018) employed high-density genotyping-by-sequencing to identify fruit-quality QTLs in a recombinant inbred population derived from Védrantais and Piel de Sapo. Amin et al. (2025) identified the fruit-size QTL Cmfs on chromosome 9, with phenotypic variance explained differing between experimental years as shown in Figure 1. Genome-wide resequencing has further revealed domestication-related diversity and structural variation in melon germplasm (Zhao et al., 2019). Additionally, Xu et al. (2025) developed a telomere-to-telomere genome assembly and functional genomic resources for C. melo ssp. agrestis, strengthening candidate-gene discovery. QTL intervals may however harbor more than one gene, which makes fine mapping, validation, and evaluation across several environments necessary for the proper use of QTLs.

6.2 Fruit Morphology and Nutritional Pigmentation

Fruit shape, size and color can affect the marketability and preference of muskmelons. Two genes, CmFSI8/CmOFP13 that are related to fruit shape (Ma et al., 2022) and a chromosome 9 QTL related to fruit diameter and length (Amin et al., 2025), have been identified. Marker-assisted selection (MAS) is a tool to transfer desirable alleles and to recover elite genetic backgrounds. Fan et al. (2025) bred peel colour improvement with the CmAPRR2 linked markers and marker-assisted backcrossing. Likewise, Tzuri et al. (2015) linked CmOr to carotenoid accumulation and orange flesh, and Oren et al. (2019) showed the involvement of APRR2 in fruit pigmentation. The results will aid in targeted improvement of fruit morphology and quality, though validation of the markers is required in other genetic background.

6.2.1 Genetic Regulation of Ripening and Shelf Life

Melon ripening is the result of a complicated system of interactions of ethylene signalling, transcription factors, and fruit quality. According to Ríos et al. (2017), one of the NAC-domain regulators of climacteric ripening was identified. Liu et al. (2022) have shown the importance of CmNAC-NOR by genome editing, whereas Giordano et al. (2022) have studied CTR1-like and ROS1, and Santo Domingo et al. (2024) - ERF024. Additionally, Mayobre et al. (2021) mapped aroma-related loci, while Dos-Santos et al. (2023) associated ETHQB3.5 with ripening physiology and volatile composition. These findings support genetic improvement of shelf life while maintaining desirable flavour, texture and consumer acceptability.

6.3 Resistance Loci, Gene Pyramiding and Genomic Prediction

Molecular breeding has advanced the identification of resistance loci against major muskmelon pathogens. For Fusarium wilt, Fom-2 was investigated through resistance-gene mapping and cloning (Wang et al., 2002; Joobeur et al., 2004). Patel et al. (2021) evaluated Indian melon accessions using Fom-associated markers, while Muthusamy et al. (2026) provided functional evidence supporting Fom-1 through CRISPR-mediated gene disruption. However, resistance effectiveness varies among pathogen races and genetic backgrounds. Various sources of resistance and genomic regions have been identified in powdery mildew studies (Wang et al., 2016; Cui et al., 2022). KASP markers linked to a chromosome 12 resistance locus were developed by Cao et al. (2021) and resistance from PI 164637 was fine-mapped by Duan et al. (2024). Wang et al. (2024) also bred resistant near-isogenic lines using marker-assisted backcrossing. Zhang et al. (2023) found that DM9.1 is the major QTL for downy mildew. Hassan et al. (2018) and Hu et al. (2018) also identified markers and candidate genes for resistance to gummy stem blight. Adams and McGregor (2022) mapped resistance to Stagonosporopsis citrulli in Citrullus amarus, and this was done as a comparison only, and not for muskmelon.

Pyramiding involves stacking multiple resistance loci to attain resistance breadth and durability, which also needs confirmation of target alleles and multiple rounds of disease screening. Root-knot nematode resistance QTLs were mapped using the GBS approach by Sharma et al. (2026). Karnatam et al. (2026) used genome-wide association analysis (GWAA) and genomic prediction (GP) to address resistance to powdery mildew and cucurbit yellow stunting disorder virus (CYSDV) in 341 melon accessions. Use of disease scoring from a single non-replicated field environment, however, indicates the need for independent validation. Thus, the use of validated molecular markers, gene pyramiding, genomic prediction and multi-environment screening are indispensable for the development of resistant and productive muskmelon cultivars.

6.3.1 Marker validation and environment-dependent disease QTLs

To demonstrate field relevance of any associations found between markers and traits in a mapping population, these associations should be tested in different disease pressures and in different genetic backgrounds. The research carried out by Sharma et al. (2026) on root-knot nematode resistance reveals the necessity to cautiously interpret QTLs showing genotype and environment-specific effects. Even though the resistant donor is useful for introgressing resistance into new lines, a QTL found in one cross is only a hypothesis for breeding purposes until its validation. Disease-resistance breeding programs can be improved by selecting not only markers but also plants' health, yield, and lifespan under stress.

7. Genetic Transformation and Genome Editing

7.1 Transgenic Research: Feasibility and Target Traits

Transformation allows for the introduction of certain genes to muskmelons by either the Agrobacterium method or particle gun bombardment technique. Fang and Grumet (1990) successfully transformed and regenerated cotyledons of muskmelon. Further research has been done on virus resistance through coat protein gene expression (Fuchs et al., 1997), delaying ripening by the expression of antisense ACC oxidase (Silva et al., 2004), and carbohydrate metabolism involving acid invertase and sucrose phosphate synthase manipulation (Yu et al., 2008; Tian et al., 2010). Despite this research having made significant genetic and physiological manipulations, no improved commercial productivity has been realized. Nuñez-Palenius et al. (2008) highlighted advances in transgenic melon research while noting the absence of commercially released transgenic cultivars at that time. Therefore, commercial applications require verified trait performance, biosafety evaluation and regulatory approval.

7.2 Transformation Efficiency and Gene Editing

Genome Editing, especially the CRISPR/Cas9 system, provides possibilities for functional validation of genes and targeted improvement of muskmelon. Wan et al. (2023) optimized transformation efficiency by applying developmental regulators AtGRF5 and AtPLT5, and successfully edited CmPDS. Giordano et al. (2022) studied the functions of CTR1-like and ROS1 in ethylene biosynthesis and climacteric ripening. Likewise, Ríos et al. (2017) showed that CmNAC-NOR is involved in ripening process and Liu et al. (2022) showed its functional relevance by using CRISPR/Cas9 editing. Santo Domingo et al. (2024) also showed that ERF024 is a regulator of climacteric ripening. The results point to the multiple genetic control of ripening, via ethylene signaling and transcription factors (TFs) (Pujol & Garcia-Mas, 2023). The efficiency of the genome editing, the stability of the edited genome, potential off-target effects, and the fruit quality parameters, however, need to be assessed to ensure successful genome editing. A higher transformation efficiency or later ripening does not necessarily lead to higher yield or commercial suitability; field performance, shelf life, flavour and consumer acceptance should also be evaluated. Table 2 shows Evidence-supported examples of molecular breeding, transformation and editing in melon.

Table 2. Evidence-supported examples of molecular breeding, transformation and editing in melon

Technique and target	Reported result	Not established result	References
Agrobacterium transformation; nptII marker	Regeneration of transformed melon plants	Resistance to fungi or superior field yield	Fang & Grumet (1990)
Viral coat-protein transgenes	Field resistance evaluated against CMV, ZYMV and WMV-2	General protection against all diseases	Fuchs et al. (1997)
GBS-based QTL mapping	Genomic intervals for fruit-quality traits	Universal markers across melon groups	Pereira et al. (2018)
CRISPR knockout of CTR1-like and ROS1	Changed climacteric ripening/ethylene profiles	Increased harvest tonnage	Giordano et al. (2022)
Agrobacterium + AtGRF5/AtPLT5; CmPDS editing	Higher transformation/regeneration and edited plants	Agronomic superiority of edited lines	Wan et al. (2023)
BSA-seq and fruit-size QTL mapping	Chromosome 9 Cmfs interval for fruit size	Commercial yield effect in unrelated backgrounds	Amin et al. (2025)
CmAPRR2 marker development and backcrossing	Yellow-peel breeding germplasm	Yield improvement without yield trials	Fan et al. (2025)

GWAS and genomic prediction	Candidate loci and prediction for two diseases	Multi-environment validation of performance	Karnatam et al. (2026)

8. Relationship between breeding and production management

Yield improvement under suboptimal conditions depends on genetic adaptation and crop management. Functional analysis identified the salt-responsive CmSOS2-family candidate MELO3C010334, associated with improved ion homeostasis (Yang et al., 2026), while CmADF1 was implicated in cold-stress responses (Lv et al., 2024). However, these findings require field validation through assessments of flowering, fruit set, marketable yield and quality under realistic stress conditions. Grafting provides a complementary approach to improving melon productivity. Flores-León et al. (2021) demonstrated that rootstock selection influences agronomic performance, pathogen responses and sensory characteristics in snake melon. In the same way, Guan et al. (2014) assessed the resistance to RKN and yield and fruit quality of Cucumis metulifer rootstocks. The grafting effectiveness, however, is dependent on rootstock–scion compatibility, disease pressure and environmental conditions. While genetic potential is determined by breeding, these factors contribute to the expression of genetic potential: irrigation, nutrition, plant density and root-zone management. Wang et al. (2020) assessed the effects of drip irrigation and mulching on photosynthesis and biomass allocation and Preciado-Rangel et al. (2018) reported potassium-dependent effects in fruit yield and quality. The results underlined the need for standard management in the process of varietal evaluation. So, genetic improvement and agronomic measures should be evaluated individually and as interaction to attain sustainable productivity of muskmelon.

8.1 Grafting, salinity and resource-use interactions

Grafting can affect performance by modifying rootstock water extraction, root-zone disease interactions and/or vigour without altering the nuclear genome of the commercial scion. Rootstock studies to develop integrated management strategies for specialty melon grafted on Cucumis metulifer were evaluated by Guan et al. (2014) under nematode related challenges. Such experiments can be used to determine if an apparent advantage comes from the scion genotype, rootstock, or the combination of scion and rootstock. Similarly, the salinity tolerance must be understood in relation to the composition of the irrigation water and the stage of growth and fruit quality requirements (Mendlinger & Fossen, 1993). There may be a cultivar that works well in one management situation that does not work well in another.

9. Integrating methods into a practical breeding pipeline

A successful muskmelon breeding program combines molecular markers, conventional crossing and testing in the field. The marketable yield, fruit size, sweetness, texture, maturity, shelf life, disease resistance and environmental adaptation should be defined in a target product profile. Parental lines are chosen for complementarity of characters, followed by limited hybridization to choose parents for the next generation, progeny selection, and validation by marker-assisted screening. Early generation selection is aimed at selecting for major traits and disease resistance; advanced lines are subjected to replicated multi-environment testing to evaluate yield, fruit quality and stability.

An example of the importance of combining the molecular and phenotypic selection is the sweetness of melon. Argyris et al. (2017) found sugar related loci in several populations and Tzuri et al. (2025) emphasized the quantitative inheritance of soluble solids and sucrose accumulation. They conclude that opportunities for simultaneously improving fruit size and sweetness exist, and the genetic effects are likely to be environmental dependent. Hence, the quality of fruit should be evaluated at the same maturity level by measuring soluble solids and by sensory evaluation. Table 3 presents a proposed decision framework linking major muskmelon breeding challenges with suitable improvement approaches and their critical validation criteria.

A stage-wise breeding strategy should include parental characterization, creation of segregating populations, validated marker assisted selection (MAS) and multi-environment evaluation (MEE) against commercial checks. Major effect markers can be useful for early selection, while complex traits must be evaluated through multiple phenotypic assessments. Local pathogen resistance, seed purity, postharvest performance, marketability and economic competitiveness should be taken into account in final cultivar advancement. Genomic prediction, tissue culture and genetic transformation should be used where it is clear that they offer breeding benefits and backed up by the necessary molecular and field validation. Table 4 summarizes representative genetic advances, their experimentally demonstrated contributions, and their implications for practical muskmelon breeding.

9.1 Data quality, population design and translational barriers

Map and genome editing projects should provide information on the population identity, quality of markers used, size of the population, segregating generation architecture, and scoring procedures for the traits. With regard to polygenic yield, a bigger mapping population with poor phenotyping may have less utility than a small and well-defined population with repeat phenotyping and strict fruit selection criteria. In addition, it is important that the threshold for QTL identification and estimation of explained variation is considered against the background of the population size and conditions under which the experiments were done.

Table 3. Proposed decision framework for selecting a muskmelon improvement method

Breeding problem	Primary approach	Critical validation criterion
Limited parental diversity	Germplasm screening + SSR/SNP characterization	Trait phenotype and combining ability

High-yield, market-specific F1 cultivar	Inbred-line development + testcrosses	Replicated marketable yield and fruit quality
Single major-effect colour/resistance locus	QTL validation + MAS/backcrossing	Marker transferability and linked negative traits
Polygenic resilience	Multi-environment trials + genomic prediction	Independent prediction accuracy and stability
Regeneration-dependent gene study	Explant-specific tissue culture and transformation	Fertile, genetically characterized regenerants
Candidate ripening-regulator function	Editing/transformation plus controlled phenotyping	Stable phenotype, quality and field outcomes
Saline or disease-prone production area	Genotype × management/rootstock trials	Marketable yield under target stress

Table 4. Representative, genetic advances and their implications for muskmelon breeding.

Focus	Reported experimental contribution	Breeding interpretation	References
Diversity / domestication	Resequencing of 1,175 accessions; 208 associations across 16 agronomic traits	Resource for donor selection; associations need validation	Zhao et al. (2019)
Fruit quality mapping	High-density GBS linkage mapping of fruit-related QTLs	Map intervals and verify effects in new genetic backgrounds	Pereira et al. (2018)
Flesh pigmentation	CmOr variant associated with orange-flesh carotenoid accumulation	Potential functional marker for flesh colour	Tzuri et al. (2015)
Fruit morphology	CmFSI8/CmOFP13 implicated in fruit shape	Track shape allele alongside weight and market acceptance	Ma et al. (2022)
Peel colour / backcrossing	CmAPRR2-related foreground markers and backcross-derived yellow-peel germplasm	Demonstrated marker-assisted germplasm improvement	Fan et al. (2025)
Fruit dimensions	Chromosome 9 fruit-size QTL detected across two years	Year-specific effects require cautious prediction	Amin et al. (2025)
Root-knot nematodes	GBS-based mapping identified resistance QTLs in segregating melon families	Validate loci for resistance deployment	Sharma et al. (2026)
Foliar disease resistance	GWAS and genomic prediction using 341 melon accessions	Prospective independent-population testing needed	Karnatam et al. (2026)
Fruit ripening	CmNAC-NOR mapping and gene-editing functional evidence	Balance shelf-life targeting with sensory quality	Ríos et al. (2017); Liu et al. (2022)
Transformation	Improved transformation/regeneration through protocol changes and regulators	Enables functional assays; not direct yield evidence	Wan et al. (2023)
Powdery mildew fine mapping	Chromosome 6 locus reduced to a 63.5 kb candidate interval	Promising linked InDel marker, subject to validation	Duan et al. (2024)
Marker-assisted backcrossing	Powdery mildew QTLs transferred into resistant near-isogenic lines	Evidence of applied marker-assisted breeding	Wang et al. (2024)
Downy mildew genetics	DM9.1 major QTL mapped and refined using QTL-seq and linkage mapping	Stage- and background-dependent resistance validation needed	Zhang et al. (2023)

10. Research Gaps and Emerging Priorities

Marker portability and genetic architecture are still great hurdles in muskmelon improvement. QTLs for fruit quality found in certain mapping populations must be validated across the groups of melons grown commercially and in different genetic backgrounds (Monforte et al., 2004; Díaz et al., 2014). Further, the total soluble solids is a complex trait indicating that a

single marker is not sufficient to predict sweetness (Tzuri et al., 2025). Multi-parent, multi-environment studies should be the focus of future research that include fruit number, fruit size, sweetness, firmness, aroma, and disease resistance. These types of studies could enhance the accuracy of genomic prediction and also help to estimate the realized genetic gains.

Targeted improvement of fruit quality and shelf life via genome editing holds great promise. Nonaka et al. (2023) engineered CmACO1 for increased shelf life, and Sasaki et al. (2025) showed that an RNA-mediated editing reaction of the ribonucleoprotein complex occurred in planta and was correlated with delayed ripening. However, genetic stability, inheritance, off-target effects, fruit quality and field performance will need to be confirmed for commercial application. The characteristic flavour, aroma and consumer acceptability (including appropriate assessment by regulatory authorities) also must be maintained in order to improve the shelf life of the product.

The translation of biotechnology into productive gains is met with several restrictions. There are numerous studies that assess regeneration efficiency or marker associations in narrow genetic and/or large population size, and limited field validation to date. The resistance to the disease is affected by pathogen races and fruit quality is influenced by the maturity at harvest and storage conditions. Furthermore, the performance under heat, salinity and variable soil conditions is affected by genotype × environment interactions. Future studies should, therefore, incorporate functional validation, independent marker testing, and repeated field tests along with economic feasibility and consumer preference.

Increased germplasm diversity, especially introgression lines and underutilized regional landraces, may aid in identifying adaptive alleles for stress resistance, disease resistance and fruit quality. The use of pangenome analysis, multi-omics, better transformation and genome editing will make the identification of candidate genes and the functional characterization slightly quicker. The molecular associations, however, should be backed up with biological evidence and reliable phenotypic measurements. It is still important to breed independently validated resistance and quality alleles, with a minimum of linkage drag.

In commercial breeding, improvements in marketable yield, fruit quality and adaptation as measured by the discoveries of the genome are required. Trials should be performed in various environments, including proper commercial checks and sufficient sample numbers, and include uncertainty estimates and standardized phenotyping. For genomic prediction, independent testing is needed and for resistance durability, testing against different pathogen populations. Plants grown from tissue culture should be tested for genetic fidelity, ploidy stability and reproductive performance, as well. When combined with breeding knowledge of economics, cultivation of productive and climate-tolerant cultivars will be further reinforced by integration of these approaches with seed production and acceptance by consumers.

11. CONCLUSION

Muskmelon improvement should be considered as a breeding process in which molecular and tissue culture technologies are integrated, rather than a series of interchangeable high technology interventions. The development of desirable yield, quality and resistance properties in adapted breeding populations relies on selection, hybridization and introgression. Genome resources and QTL work and functional markers enhance the accuracy of selection, while recent work on fruit size, peel colour and resistance represents real progress in establishing a relationship between genetic variation and valuable breeding objectives. The use of somatic regeneration, haploid technologies, transgenic research and genome editing opens up new possibilities for experiments but necessitates careful distinction between methodological success, genetic validation and agronomic benefit.

The most likely pathway to the desired long-term gains is to combine genetically diverse and localized resources with systematic phenotyping and well-established genomic resources and multi-environment trials that assess marketable yield and consumer-relevant product quality. This evidence-based approach can lead to the development of cultivars of muskmelon with more consistent production success in altered production environments but without unsupported extrapolation from successful performance in the laboratory or from muskmelon relatives.

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