



REVIEW ARTICLE

Analysis of various strategies for improvement of bitter gourd (*Momordica charantia* L.) crop: A review

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Abstract

Bitter gourd (*Momordica charantia* L.), belonging to the Cucurbitaceae family, is cultivated as both a vegetable and medicinal herb in Asia and Africa. Genetic diversity is crucial for agricultural growth and ecological adaptability, particularly as hybrid crops may threaten regional variations. Advanced breeding techniques offer significant advantages over traditional methods, enabling faster and more precise development of desirable traits, such as enhanced resistance and adaptability. Heterosis breeding improves bitter gourd quality by producing hybrids with uniform colour, fewer seeds, greater vigour and higher yields, thereby enhancing productivity and climate resilience. Introducing genetic variation through mutant breeding and inter-/intra-specific hybridisation facilitates the development of cultivars with disease resistance and stress tolerance. Biotechnological tools, such as tissue culture and genetic engineering, further enhance attributes like pest resistance and nutritional value. Marker-assisted selection (MAS) streamlines conventional breeding by incorporating single-gene traits into breeding lines. Recent advances in genomics, including high-throughput sequencing and the draft genome of the Japanese line OHB3-1, have provided deeper insights into the genetic structure of bitter gourd, enabling targeted crop improvement. Integrating these breeding techniques and technologies holds the potential to significantly enhance bitter gourd's productivity, resistance and adaptation across diverse agro-ecological conditions.

Keywords: agro-ecological adaptation; bitter gourd; genetic diversity; genetic engineering; heterosis breeding; marker-assisted selection (MAS)

Introduction

Cucurbits belong to the family Cucurbitaceae, which includes major crop groups such as gourds, melons, squashes and cucumbers. Cucurbits are consumed in various forms, including pickles (gherkins), salads (cucumber, gherkins, long melon), desserts (melons) and sweets (ash gourd, pointed gourd) (1). Cucurbit breeding programmes primarily aim to improve early yield, quality traits (colour, flavour and total soluble solids content), tolerance to biotic stresses (disease resistance), optimal plant type and overall yield (2). Within the family Cucurbitaceae, *Momordica* is one of the largest genera, comprising 59 species widely distributed across Asia and Africa (3). Of these, 34 species are dioecious, 22 are monoecious and the reproductive status of three species remains unclear (4). The genus includes four dioecious species; *Momordica dioica*, *Momordica sahyadrica*, *Momordica cochinchinensis* and *Momordica subangulata* and two monoecious species- *Momordica charantia* L. and *Momordica balsamina* L. (5).

Bitter gourd (*Momordica charantia* L.), also known as maiden apple, karela, cassilla, bitter cucumber, bitter melon and bitter squash,

is referred to by a variety of names across cultures (6). In Asia and Africa, *M. charantia* is cultivated both as a vegetable and a medicinal herb. The Indo-Burma region, particularly eastern India and southern China, is considered a potential centre of domestication of bitter gourd (*M. charantia* L.) (7). According to FAOSTAT (2024), India's gross production index for pumpkins, squash and gourds (including *M. charantia* L.) reached 223 (base: 2014–2016 = 100), reflecting a more than two-fold increase in production over the past decade (8). Bitter gourd is widely cultivated across India, Indonesia, Sri Lanka, Malaysia, the Philippines and tropical Africa and has been introduced and naturalised in parts of the Caribbean, Central and South America and southern North America (9). Bitter gourd is a monoecious member of the gourd family, bearing distinct yellow male and female unisexual flowers on the same plant and depends obligately on pollinators for successful fruit set (10). The fruit of bitter gourd is a pendulous, broadly ovoid, beaked berry that transitions from green at the immature stage to reddish-orange upon full ripening, at which point it splits open to expose seeds enclosed in a sticky red pulp (11). The crop's bitter taste is attributed to the cucurbitane-type triterpenoid glycosides, collectively referred to as momordicosides, which also underpins its

rich nutritional and medicinal value. In India, Kerala, Tamil Nadu, Maharashtra and Karnataka are among the major bitter gourd-producing states in India. Bitter gourd cultivation has increased due to growing awareness of its antidiabetic and nutritional benefits (12). In order to select better parents for hybrid production, recent crop development initiatives use combining ability studies and heterosis to improve yield and quality attributes. However, bitter gourd has a complex and cross-pollinated nature, coupled with challenges in accurate phenotyping and the potential for linkage drag. Linkage drag occurs when undesirable genes are inherited along with a target gene due to their close proximity on the chromosome, hence creating significant obstacles in conventional breeding programmes. Consequently, the application of advanced breeding techniques, such as marker-assisted selection (MAS), holds considerable promise for the improvement of this crop. Despite its agronomic potential, bitter gourd remains relatively underexplored in genomic research, with molecular marker development still in its early stages. This review aims to provide an overview of recent innovations in breeding strategies for bitter gourd, highlighting the potential of molecular tools to overcome current breeding limitations and enhance crop improvement efforts.

Methods of crop improvement

Genetic diversity

Genetic diversity is essential for both plant survival in natural environments and agricultural progress. A lack of diversity can increase crop susceptibility to diseases and pests, negatively affecting food security and production (13). Plant breeders can leverage plant genetic resources (PGR) to develop improved cultivars with desired traits, such as larger seeds and higher yields. Additionally, they can enhance traits like disease resistance, photosensitivity and resilience to environmental changes and agricultural challenges (14). Green to dark green, medium-to-high bitter, spiny and short-fruited cultigens are predominantly reported from South Asia (15). The light green, smaller bitter gourd cultivars had the largest amounts of fibre and carbs, according to a study comparing their sizes and colours (16). In 2004, VNR Seeds (Raipur, India) introduced VNR 28, a high-yielding short-fruit bitter gourd cultivar. Using VNR 28 as a genetic base, other Indian seed firms have developed and marketed three hybrid cultivars: Parijat, Racer and US 390. Strong evidence of the close genetic relationship between these hybrid crops may be found in VNR 28. Due to breeding programmes' repeated cycling of a small number of genetically similar lines, this reflects the declining genetic diversity in commercial bitter gourd (15). The germplasm of bitter gourd from India, China, Myanmar and Bangladesh represents critical reservoirs of genetic diversity that require urgent conservation, as widespread adoption of elite hybrid cultivars poses a significant risk of genetic erosion. With 430 and 250 bitter gourd accessions respectively, the World Vegetable Centre in Taiwan and Kasetsart University in Thailand both have major collections. Additionally, there are roughly 1000 accessions in the national gene banks of India (15, 17). Recent studies emphasise the critical importance of conserving traditional cultivars and local varieties of bitter gourd to maintain genetic diversity and agricultural resilience, particularly as the rapid adoption of elite hybrid cultivars increasingly threatens the survival of indigenous regional types (18, 19).

The gene pool concept provides a framework for understanding crossability relationships among *Momordica* species.

The primary gene pool comprises *M. charantia* itself and its closest wild relative *M. balsamina*, which share the same basic chromosome number ($x = 11$), monoecious sex expression and cross-compatibility, allowing direct hybridisation and fertile progeny without special techniques (20). The secondary gene pool comprises species that are genetically related to *M. charantia* and can hybridise with it, although the resulting hybrids typically exhibit partial fertility. Species in this gene pool include *M. dioica*, *M. sahyadrica*, *M. subangulata* subsp. *renigera* and *M. cochinchinensis*. All possible combinations among these dioecious species demonstrated viable seed setting, except for two crosses: *M. dioica* $\times$ *M. cochinchinensis* and *M. cochinchinensis* $\times$ *M. sahyadrica*. The tertiary gene pool consists of species that are not closely related and cannot exchange genes without specific biotechnological techniques, such as genetic engineering, somatic hybridisation, embryo rescue or bridging crosses. *Momordica cymbalaria* belongs to this gene pool, as it failed to set seed when crossed with other *Momordica* species. Tetraploid *M. subangulata* subsp. *renigera* showed good fruit set when crossed with diploid *M. sahyadrica* and *M. dioica*, whereas the reciprocal crosses produced comparatively poor fruit setting (20, 21).

Heterosis breeding

Heterosis breeding can improve quality and yield of bitter gourd (*M. charantia*) by producing superior hybrids that are difficult to achieve through conventional breeding techniques alone. The superiority of hybrids over their mid-parent, better parent or standard check in terms of desired agricultural qualities is known as heterosis or hybrid vigour. The principal aim of heterosis breeding is to substantially enhance crop yield and quality (22). Recent research indicates that, heterotic hybrids may exhibit improved nutritional profiles, enhanced resistance to pests and diseases and greater environmental adaptability (23, 24). By developing cultivars that are more adaptable to diverse climates and farming systems, this breeding approach not only increases productivity but also supports sustainable agriculture practices.

Crosses between genetically divergent bitter gourd gene pools, such as those from Bangladesh and southern/eastern India, are expected to exploit heterosis for early maturity and high yield, given the substantial genetic variability documented among Asian accessions (15, 25). The number of nodes at which the first female and male flowers bloom, as well as the number of days it takes for them to appear, are important indicators of early maturity, a desirable attribute for achieving early economic returns (26). Furthermore, fruit weight, fruit length and fruit number per plant are key and closely related productivity traits. According to research, the average weight, length and girth of the fruits as well as the quantity of fruits produced have a substantial impact on fruit yield per plant. Positive heterosis is desirable for fruit weight, length, girth and number of fruits per plant, as higher values enhance total yield; conversely, negative heterosis is favourable for early maturity traits such as days to first flowering and node number at first female flower, where lower values indicate earlier crop maturity (27).

In the tropics, both wild (*M. charantia* var. *muricata*) and cultivated bitter gourds are grown, with preferences for fruit characteristics such as colour, length, diameter, form, size and tubercles vary considerably from region to region (28). Long, smooth, cylindrical fruits that are light green are preferred by consumers in Vietnam, while similar tastes for long, smooth, light green fruits are prevalent in Thailand. Spindle-shaped, dark green

fruits with spiky exteriors that are tiny to medium in size are usually preferred by South Asian consumers. White fruit is a common ingredient in soups in Taiwan and India (15). Immature bitter gourd fruits are chopped for use in a variety of Asian recipes and their consistent green peel colour and excellent internal fruit quality are extremely valuable. Marketability is strongly influenced by fruit colour; in northern India, people choose long, dark green to glossy fruits, in southern India, white fruits and in eastern India, people prefer small, dark green fruits (18, 25).

There are notable differences between the bitter gourd's fruit and vegetative traits. The bitter gourd is an ideal crop for heterosis exploitation due to its high genetic diversity, monoecious nature, cross-pollination behaviour and prolific fruit set (29, 30). The traits: curved fruits, discontinuous ridges, tubercles and black seed coat colour are controlled by the dominant genes Cf, Cr, Tb and Bs, respectively (31, 32). Standard selection techniques can effectively improve bitter gourd traits governed by additive gene action, while traits exhibiting dominance gene effects are better exploited through heterosis breeding rather than conventional selection. Pedigree selection improves additive traits (27), while heterosis breeding and specialised selection improves non-additive traits. Techniques like reciprocal recurrent selection and diallel mating enhance both additive and non-additive traits (33, 34). Advances in genomic selection (GS) and molecular markers

provide more precise breeding tools (35). Significant variation in heterosis (%) over both mid-parent and better parent for yield and yield-related characters among bitter gourd genotypes was observed, as summarised in Table 1.

Mutation breeding

Mutation is a heritable change in an organism's genotype, occurring naturally or induced artificially. Mutation breeding is a highly promising approach for enhancing genetic diversity and accelerating crop improvement. Induced mutagenesis has enabled rapid genetic changes in targeted crops, facilitating the improvement of key commercial traits in food grain crops (41). This technique has been successfully applied to various crops, including okra (42), tomato (43) and cucumber (44). Furthermore, mutagenesis is increasingly recognised not only as a method for creating genetic variation but also as a valuable tool for understanding the genetic basis of traits, enhancing crop resilience and boosting productivity (45).

All mutagenic treatments exhibited an inhibitory effect on seed germination in the M1 generation. This could be due to interference with enzyme synthesis or accelerated degradation of preexisting enzymes (46). A dosage of 200–250 Gy γ radiation appears effective in producing useful and viable mutants for cultivating bitter gourds (47). Notably, exposure to 50–100Gy of

Table 1. Heterosis (%) over mid-parent and better parent values for yield and yield-related traits in bitter gourd

Sl. No.	Characters	Mid parent	Better parent	References
		-	-6.35-38.58	(36)
1	Vine length	-	-140.50-107.00	(37)
		-46.05-72.77	-57.82-48.47	(38)
		-28.65-17.35	-42.81-8.27	(39)
		-30.50-22.00	-45.00-15.00	(31)
2	Number of branches per plant	-13.85-26.82	-29.62-20.06	(39)
3	Number of male flowers per vine	-24.55-46.08	-42.55-40.62	(40)
		-48.29-1.47	-58.66-70.40	(40)
4	Node at first male flower appearance	-15.00-25.00	-30.00-20.00	(38)
		-20.00-30.00	-25.00-35.00	(30)
		-17.47-13.43	-4.19-31.14	(39)
5	Days to first male flower	-	-19.87-14.55	(37)
		-10.00-20.00	-15.00-25.00	(30)
		-12.00-15.00	-5.00-30.00	(38)
6	Number of female flowers per vine	-34.02-85.35	-53.42-72.73	(40)
7	Nodes at first female flower appearance	-53.47-4.14	-58.24-41.67	(40)
		-22.36-13.50	-19.87-29.77	(39)
8	Days to first female flower	-12.72-1.47	-20.17-15.22	(40)
		-15.00-25.00	-10.00-30.00	(30)
		-20.00-20.00	-5.00-35.00	(38)
9	Sex ratio (M/F)	-52.30-61.59	-73.39- -0.64	(40)
		-	2.51-48.75	(36)
		-12.30-19.74	-24.39-15.55	(38)
		-23.02-49.42	-38.24-10.58	(39)
10	Number of fruits per plant	-65.19-75.80	-78.30-68.89	(40)
		-20.00-30.00	-10.00-50.00	(38)
		-15.00-25.00	-5.00-40.00	(30)
		-20.77-131.16	-22.25-10.94	(38)
		-18.49-21.42	-9.66-36.25	(39)
		-	-25.35-4.02	(36)
		-	-35.87-31.73	(37)
		-	-57.14-62.50	(36)
		-12.42-172.71	-16.46-142.06	(38)
		1.77-52.73	1.63-36.13	(40)
		-0.29-51.96	-1.26-37.42	(39)
11	Fruit length	-	-16.90-79.58	(36)
		-	-58.27-73.51	(37)
		-13.33-137.06	-23.53-129.29	(39)
		-59.30-109.71	-64.32-68.89	(40)
		-29.98-58.77	-39.34-45.65	(38)
		-	-17.01-74.04	(36)
		2.44-29.48	-59.26-20.68	(40)
12	Yield per hectare	-52.33-48.30	-56.78-6.98	(40)

mutagens resulted in increased fruit dimensions, weight and length. This may occur because, as observed in other crops, low concentrations of mutagens stimulate the activities of growth regulators and enzymes that enhance growth and yield component characteristics (42, 48). Additionally, chlorophyll, beta-carotene and ascorbic acid levels in immature fruit were not significantly affected by γ radiation in the M1 generation. The results indicated that fruit genotype was more sensitive to radiation, resulting in lower levels of beta-carotene and total chlorophyll, particularly in fruits with a chlorophyll deficit. Nevertheless, there was no significant relationship between radiation-induced reduction in beta-carotene and total chlorophyll content and the immature fruit's ascorbic acid content (49).

A study was conducted on mutation breeding in bitter gourd using four divergent inbred lines: BG 1346501, Meghna-2, Special Boulder and Selection-1. The effects of low to medium dosages of γ rays were examined, with Meghna-2 exhibiting the greatest radiosensitivity, while Special Boulder showed the highest radiation tolerance. In the M1 generation, γ radiation hindered seed germination across all genotypes, with significant variation in germination rates. Mutagenic treatments also inhibited vine growth and affected key traits, including germination, vine length and pollen viability in the M2 generation. However, BG-1346501 and Meghna-2 exhibited minimal reductions in pollen viability and seed germination (49, 50).

Interspecific hybridisation

Tracing the genomic link and enhancing crops through the transfer of specific traits like disease resistance, insect resistance and stress tolerance from wild relatives to cultivated varieties are made possible by inter- and intra-specific hybridisation. Inter-specific hybridisation in the genus *Momordica* has been thoroughly investigated in order to clarify evolutionary links and pinpoint advantageous characteristics (51). Recent studies indicate that hybrids exhibit intermediate characteristics in trichome distribution on stems and leaves, fruit shape and colour, seed number and ovary colour (52). Interspecific crosses among *Momordica* species were conducted to characterise plant morphology, pollen-pistil compatibility and crossability relationships; high pollen viability was observed in intraspecific crosses, while moderate viability was recorded in interspecific combinations, with incompatibility barriers limited to specific species combinations (53). Additional research demonstrated the potential of applying cutting-edge genomic approaches to enhance crop resilience and improve hybridisation outcomes (54). However, high crossability and pollen fertility have been reported in intervarietal crosses between *M. charantia* var. *charantia* and *M. charantia* var. *muricata*, while cytotaxonomic and crossability studies have also been conducted across dioecious *Momordica* species, including *M. dioica*, *M. cochinchinensis* and *M. subangulata* subsp. *renigera* (55). The importance of investigating bitter gourd hybridisation potential to improve desired traits is further supported by recent research (56). Moreover, effective hybridisation methods have been shown to overcome reproductive barriers in *Momordica*, enabling the transfer of advantageous traits from wild relatives to cultivated cultivars (57). This approach is increasingly recognised as a key strategy in crop improvement programmes.

There are relatively few crossability investigations in the *Momordica* species. However, some attempts have been made to cross *M. charantia* with *M. balsamina*, yielding varying degrees of

success. Five main crossover behaviour types have been documented in Indian *Momordica* species: (i) *M. charantia* $\times$ *M. charantia* var. *muricata* and *M. dioica* $\times$ *M. sahyadrica* exhibit cross-compatibility with viable pollen; (ii) *M. charantia* $\times$ *M. balsamina* shows partial compatibility with pollen fertility; (iii) *M. dioica* $\times$ *M. cochinchinensis* and *M. sahyadrica* $\times$ *M. cochinchinensis* demonstrate partial compatibility with pollen sterility; (iv) partial compatibility with pollen sterility (*M. dioica* $\times$ *M. cochinchinensis* and *M. sahyadrica* $\times$ *M. cochinchinensis*) and (v) cross-compatibility with pollen sterility occurs between diploid species (*M. dioica*, *M. sahyadrica* and *M. cochinchinensis*) and tetraploid species (*M. subangulata* subsp. *renigera*). Recent research further highlights the complexity and challenges of hybridisation within the *Momordica* genus, underscoring the necessity of advanced breeding methods to improve success rates (21, 26).

Breeding efforts aimed at identifying lines with desirable introgressed traits and advancing the development of novel cultivars require a thorough understanding of genome fragment insertion through extensive hybridisation. The hybridisation process between *M. balsamina* and *M. charantia* employed multiple *M. charantia* accessions as parental material to ensure adequate crossability assessment. The majority of cross combinations showed total incompatibility in both direct and reciprocal crosses. However, six cross combinations showed partial compatibility and successfully produced fruits with *M. charantia* as the female parent and *M. balsamina* as the pollen parent (DBGS-2, NEH-4, PDMGy-201, Pusa Aushadhi, DBGS-3 and NEH-3). Seeds obtained from these interspecific crosses were classified as non-viable based on the absence of a firm, papery seed coat, a standard morphological indicator of seed maturity and viability, with the exception of seeds derived from Pusa Aushadhi (*M. charantia*), which met the viability criterion. Similar challenges associated with interspecific hybridisation have also been reported in recent studies, emphasising the need for innovative strategies to enhance cross compatibility and seed viability in hybridisation programmes (58). The success rate of interspecific hybridisation, expressed as crossability (%), in *Momordica* spp. is presented in Table 2 and the crossing relationships among *Momordica* species are illustrated in Fig. 1.

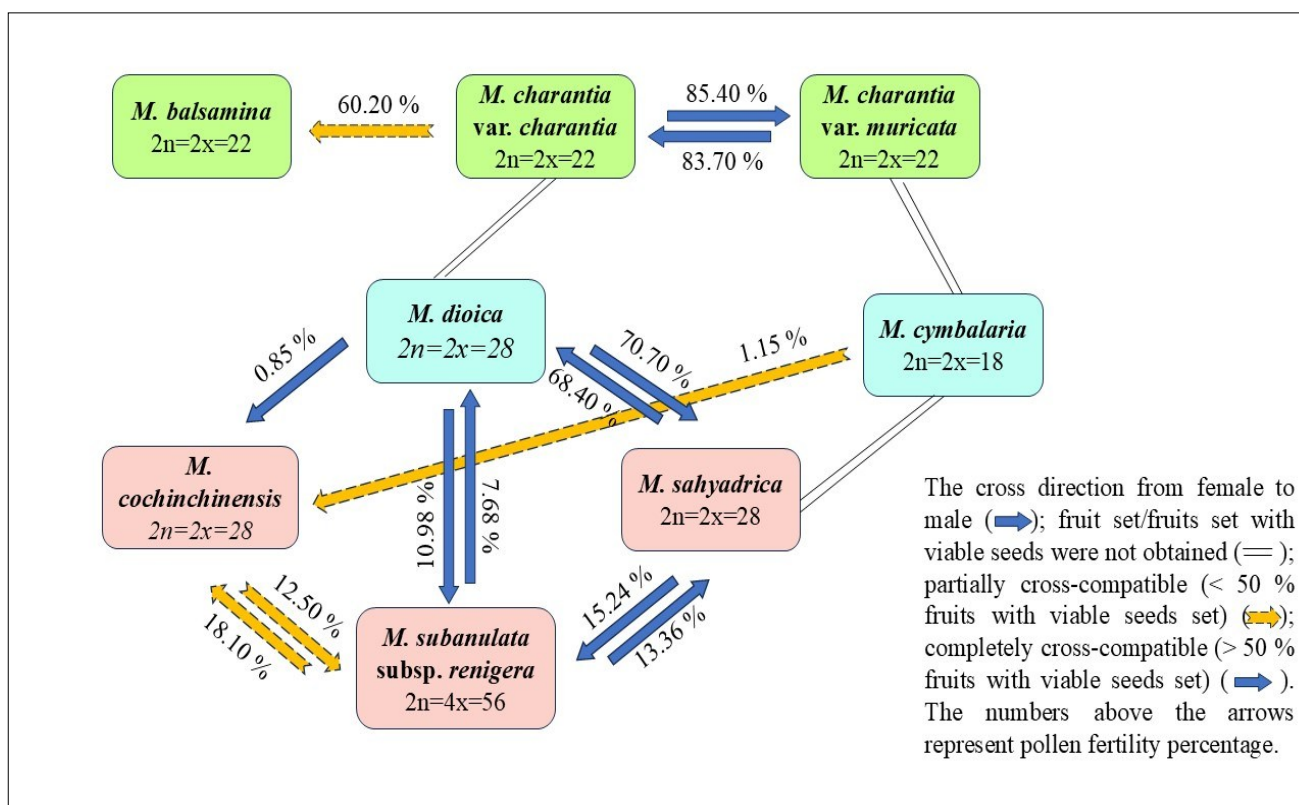
Biotechnology

Remarkable vegetable varieties have been developed by the application of traditional breeding methods. However, the limitations of these conventional techniques ultimately restrict the development of super cultivars in vegetable crops. Modern biotechnology now provides plant breeders with precise and innovative tools for crop improvement. These approaches include molecular genetics, cell and molecular biology, tissue culture and genetic engineering or gene manipulation (62). Genetic engineering, in particular, has enabled the introduction of traits such as enhanced nutritional value and insect resistance (63). Furthermore, advances in molecular genetics have facilitated MAS, allowing the rapid identification of desirable traits in breeding programmes (64). Collectively, these biotechnological advancements are redefining vegetable crop improvement and addressing the limitations associated with traditional breeding methods.

Enhancement of single gene-controlled characteristics, such as insect and herbicide resistance, was the main focus of biotechnology research over the past decade. Recently, however, attention has shifted toward multigenic agronomic traits, including

Table 2. Percentage of crossability in interspecific crosses of *Momordica* spp.

Sl. No.	Inter-specific combinations of <i>Momordica</i> spp.	Crossability percentage	References
1	<i>M. charantia</i> var. <i>muricata</i> × <i>M. balsamina</i>	6 %	(59)
2	<i>M. charantia</i> var. <i>charantia</i> × <i>M. charantia</i> var. <i>muricata</i>	97 %	(20)
3	<i>M. charantia</i> var. <i>muricata</i> × <i>M. charantia</i> var. <i>charantia</i>	85 %	(59)
4	<i>M. subangulata</i> subsp. <i>renigera</i> × <i>M. dioica</i>	65 %	(59)
5	<i>M. subangulata</i> subsp. <i>renigera</i> × <i>M. cochinchinensis</i>	2 %	(59)
6	<i>M. subangulata</i> subsp. <i>renigera</i> × <i>M. sahyadrica</i>	84 %	(59)
7	<i>M. dioica</i> × <i>M. subangulata</i> subsp. <i>renigera</i>	53 %	(59)
8	<i>M. dioica</i> × <i>M. cochinchinensis</i>	60 %	(59)
9	<i>M. dioica</i> × <i>M. sahyadrica</i>	6 %	(59)
10	<i>M. cochinchinensis</i> × <i>M. subangulata</i> subsp. <i>renigera</i>	5 %	(59)
11	<i>M. sahyadrica</i> × <i>M. dioica</i>	81 %	(59)
12	<i>M. sahyadrica</i> × <i>M. cochinchinensis</i>	65 %	(59)
13	<i>M. sahyadrica</i> × <i>M. subangulata</i> subsp. <i>renigera</i>	50 %	(59)
14	<i>M. charantia</i> var. <i>muricata</i> × <i>M. charantia</i> var. <i>charantia</i>	88.89 %	(59)
15	<i>M. charantia</i> var. <i>charantia</i> × <i>M. charantia</i> var. <i>muricata</i>	100 %	(60)
16	<i>M. charantia</i> var. <i>charantia</i> × <i>M. charantia</i> var. <i>muricata</i>	90.98 %	(61)
17	<i>M. charantia</i> var. <i>muricata</i> × <i>M. charantia</i> var. <i>charantia</i>	84.43 %	(59)

**Fig. 1.** Interspecific hybridisation showing the crossing relationships among *Momordica* species (65).

increased yield and improved product quality. Strategies to enhance photosynthetic efficiency and overall plant performance include modifying genes and enzymes involved in photosynthesis, regulating plastid number, optimising chlorophyll content and chlorophyll a/b binding proteins and managing senescence-related processes (65). Plant tissue culture is widely used in commercial production, plant breeding and basic biological research, providing an efficient means for the rapid propagation of superior cultivars (66). Since bitter gourd is gaining increasing importance, improving its cultivation and developing new types is necessary. Recent biotechnological approaches can facilitate this. Plant regeneration and callus induction are also affected by factors such as the type of explants used, media composition, growth conditions, genotype and the physiological status of the explants. Notably, leaf explants produced the highest percentage of callus compared to stem and cotyledon explants (67). Moreover, recent research has indicated that supplementing specific growth regulators enhances callus induction and regeneration rates in bitter gourd (33).

Gynoecium in bitter gourd

Monoecious bitter gourds (*M. charantia*) are the most common sexual form, although gynoecious varieties have been reported in regions including China, Japan and India (68). Gynoecious × monoecious hybrids mature earlier and demonstrate higher yield potential, while gynoecious lines exhibit superior general combining ability (GCA) for earliness and yield traits (69). Gynoecious lines simplify hybrid seed production by eliminating the need for mechanical emasculation and pollination.

The gynoecious trait is controlled by a single recessive gene, *gy1* (58, 70). However, bitter gourds can display partial dominance in gynoecious sex expression (71). Three gynoecious collections-Gy23, Gy63 and Gy263B-have been identified as exhibiting fully gynoecious flowering behaviour, meaning the plants bear exclusively pistillate flowers (72). Since then, several populations have emerged with noticeably higher percentages of pistillate flowers (over 90 %). DBGy-201 and DBGy-202 are two gynoecious lines isolated from wild populations of *M. charantia* var. *muricata* and maintained through

sib-mating and have since been utilised for gynoeious hybrid development in bitter gourd breeding programmes (68).

Three monoecious lines (Preethi, Priyanka and MC133) and the gynoeious line KAUMCGy-101 were used to evaluate heterosis in *M. charantia*. The yield and earliness traits of the monoecious and gynoeious parents differed significantly in hybrids produced through both direct and reciprocal crosses. Many of these traits exhibited significant heterosis. All hybrids displayed heterosis in the desired negative direction for key earliness traits, including the number of days to the first female flower and the node at which it appeared (73).

Pollination is necessary to promote earlier fruit set in the gynoeious inbred line used as the seed parent for the early, high-yielding bitter gourd hybrid known as Kumaken BP1 in Japan (74). OHB61-5, a prominent gynoeious line discovered in Okinawa, is thought to have developed as a result of a spontaneous mutation. Analysis of F2 progenies from a cross between this line and the monoecious line OHB95-1A confirmed that the gynoeious trait is controlled by a single recessive gene (75). The potential for improved gynoeious expression through selective breeding was highlighted by selecting the cultivar NBGH-167 for transgressive segregants.

Recent developments in genomic technologies have further enhanced our understanding of the genetic basis of bitter gourd gynoeicy. More thorough investigations have identified additional SNP markers and putative QTLs associated with gynoeicy, improving the precision of MAS in breeding initiatives (76). Next-generation sequencing (NGS) techniques have also facilitated the identification of new markers linked to gynoeious traits, potentially simplifying hybrid seed production in the future (77). These developments will greatly support breeding initiatives to increase hybrid bitter gourd vigour and productivity.

Molecular breeding

Recent advances in molecular biology have significantly transformed crop breeding methods, shifting the focus from phenotypic traits to gene-based selection. MAS, which employs DNA markers, enhances traditional backcrossing by enabling the rapid and precise insertion of genes from diverse genetic resources into breeding materials. This approach allows breeders to select for desired traits early in development, enhancing the efficiency and success of breeding programmes and accelerating the process of improving desirable crop traits. Selecting phenotypes for quantitative traits is challenging and influenced by environmental factors. Molecular markers, being non-destructive and independent of environmental changes, offer an effective solution for improving disease resistance (78).

The importance of molecular markers in enhancing crop attributes has been further demonstrated by recent developments in molecular breeding techniques. High-throughput genotyping techniques, for example, enable rapid marker identification, greatly reducing the time and cost associated with conventional phenotyping (64). Additionally, the integration of GS into breeding programmes has improved the effectiveness of selecting desired traits by enabling more precise predictions of phenotypic performance.

The first molecular diversity analysis of *M. charantia* evaluated 38 Indian genotypes, including commercially released cultivars, using 116 RAPD primers, of which 29 were polymorphic and informative; notably, clustering patterns based on molecular

markers and yield-related traits were not consistent with geographical distribution, suggesting complex multigenic control of quantitative traits (79). Recently, Simple Sequence Repeats (SSRs) have become the preferred genetic markers due to their high polymorphism and relevance to plant breeding (80). Simple Sequence Repeats provide a reliable method for genetic diversity evaluation and MAS (64).

Amplified fragment length polymorphism (AFLP) markers offer greater distinguishing ability compared to inter-simple sequence repeat (ISSR) and random amplified polymorphic DNA (RAPD) markers, due to their high polymorphism, broad genomic coverage and high multiplex ratio (81). A recent study has confirmed the efficiency of AFLP markers in assessing genetic diversity and linkages in crops, including bitter gourd (82). Additionally, SSR and SNP markers were used to assess genetic diversity in bitter gourd, emphasising the importance of combining multiple molecular techniques (83). Building on these approaches, next-generation sequencing (NGS) technologies have further advanced marker discovery, enabling more comprehensive assessment of genetic diversity in bitter gourd breeding programmes.

Recent research highlights the role of molecular markers in assessing bitter gourd genetic diversity and purity. For instance, the use of combined SSR and SNP markers has enabled the identification of markers linked to desirable traits (84). Genomic selection has also been emphasised for enhancing breeding accuracy and efficiency (35). Additionally, advancements in high-throughput sequencing techniques have provided deeper insights into bitter gourd's genetic makeup, enabling the identification of polymorphic markers related to key agronomic traits (85). These innovations significantly contribute to bitter gourd improvement.

Practical breeding pipeline: molecular tools integration

Practical breeding pipeline combines molecular tools to increase crop improvement efficiency. The process begins with the collection of diverse genotypes, followed by detailed phenotypic evaluation, which accurately assess characters to recognize valuable genetic resources (86). Thereafter, molecular markers are developed for specific characters, assisting the detection of genetic variations related with favourable characteristics (87). These markers enable the selection of genotypes expressing favourable characters, simplifying the breeding process. MAS is implemented to select the genotypes with desired characters at initial stages, accelerating the breeding cycle and improving efficiency (88). Hybridisation and cross-breeding are carried out using selected genotypes, resulting in novel hybrids with superior traits, hence enhancing crop performance (89). Genomic selection uses genomic data to estimate breeding values, facilitating the selection of individuals with high genetic potential for desired traits (90). Developed hybrids are subjected to multi-locational trials to estimate their adaptability and stability across different environments, confirming its consistent performance (91). Finally, verified hybrids are released and commercialised, offering farmers with improved varieties that fulfil consumer demand and contribute to enhance productivity (92). Details of bitter gourd varieties developed through different breeding approaches along with their key traits are summarised in Table 3.

This practical breeding pipeline effectively confronts key challenges in crop improvement (Fig. 2). Collection of diverse genotypes broadens the genetic base and elevates variability. The utilisation of MAS and GS assists in reducing linkage drag and

accelerates the breeding cycles. High-throughput phenotyping ensures accurate trait evaluation, whereas multi-location trials analyse hybrid adaptability, minimising environmental sensitivity. Overall, this integrated approach bridges the critical gaps and enhance the productivity and precision of modern breeding programmes.

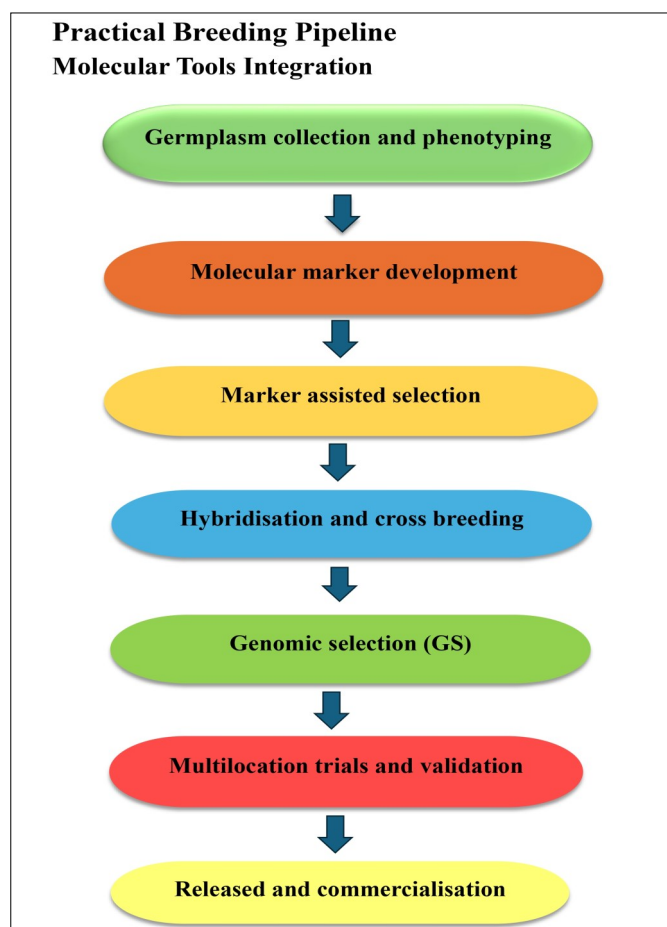


Fig. 2. Integrated molecular breeding pipeline.

Conclusion and future prospects

Despite significant breeding challenges, including a narrow genetic base, interspecific hybridisation barriers and limited exploitation of wild germplasm, *Momordica charantia* L. holds considerable untapped potential for crop improvement through heterosis breeding, advanced genomic and molecular breeding tools and systematic utilisation of underexplored wild genetic diversity. Traditional breeding methods have been hindered by its complex nature, cross-pollination and issues like inaccurate phenotyping and linkage drag. However, recent advances in molecular breeding techniques, particularly MAS, offer promising solutions to address these obstacles and enhance the efficiency of breeding

programmes. Despite the crop's potential for agronomic improvement, genomic research on bitter melon remains limited, with molecular marker development still in its early stages.

However, several translational challenges still remain before these advances can be effectively applied in large-scale breeding programmes. The manifestation of heterosis often represents environmental sensitivity, the available genetic base is narrow and the scope for germplasm exchange remains limited. Recent findings from whole-genome sequencing of various genotypes highlight the value of tapping into global germplasm resources, especially those from South and Southeast Asia, to broaden genetic diversity. At the same time, recent findings need to test promising hybrids across multiple locations to ensure yield stability and adaptability to different environments. By integrating advanced molecular tools with insights from global research collaborations, bitter melon improvement can evolve beyond theoretical advances towards practical outcomes that contribute to global betterment, benefiting both farmers and consumers.

Future research should focus on expanding the genomic resources available for bitter melon, including developing a comprehensive set of molecular markers for traits of interest. Additionally, the integration of advanced genomic techniques like genome-wide association studies (GWAS) and Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)-based gene editing could further revolutionise breeding strategies. It is also essential to explore the genetic diversity within wild and cultivated bitter melon populations to better understand the genetic basis of key traits such as disease resistance, fruit quality and yield. As molecular breeding tools continue to evolve, there is great promise for improving the productivity, sustainability and resilience of bitter melon. The future of bitter melon breeding lies in the application of these cutting-edge technologies, which can accelerate the development of superior cultivars tailored to meet both consumer demands and environmental challenges.

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Table 3. Bitter melon varieties developed by various breeding approaches with key traits

Variety/Line	Breeding method	Key traits	References
CO2	Mutation breeding	Early maturing	(85)
		Fruit length: 34-40 cm	
MDU 1	Mutation breeding (gamma irradiation of MC-103)	Thick fruits	(85)
		Average yield: 30 t/ha	
		Female: male ratio: 1:20	
		Average fruit weight: 410 g	
		Average fruit length: 40.34 cm	
		Yield potential: 30-32.5 t/ha	
		Tolerant to fruit fly, pumpkin beetle and leaf spot disease	

Authors' contributions

VK and VP conceptualised the study, conducted the systematic literature review and prepared the initial manuscript draft. AK, UP and DS contributed to the graphical representations. AS and RB critically revised the manuscript. K and DS were involved in manuscript editing and coordination. SKM, AS and UP also contributed to manuscript editing and sample analysis. All authors read and approved the final manuscript.

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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