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Review Article

In Vitro Culture and Biotechnological Advances in Mango (*Mangifera indica* L.): Progress, Challenges and Future Perspectives

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ABSTRACT

Mango (*Mangifera indica* L.) is one of the world's most economically important tropical fruit crops, yet its genetic improvement through conventional breeding is constrained by a long juvenile phase, high heterozygosity, irregular bearing and complex reproductive biology. Recent advances in plant biotechnology have provided alternative approaches to overcome these limitations, accelerate cultivar improvement, germplasm conservation and the development of superior planting materials. This review critically synthesises current progress in somatic embryogenesis, micropropagation, molecular marker-assisted technologies, genetic transformation and other emerging biotechnological tools for mango improvement. Particular emphasis is placed on explant selection and plant growth regulator combinations for efficient plant regeneration, the application of molecular markers for cultivar identification, genetic diversity assessment and the potential of genetic transformation to enhance disease resistance, postharvest quality and other economically important traits. The major biological factors limiting the large-scale application of these technologies, including genotype dependence, phenolic oxidation, microbial contamination, low regeneration efficiency and limited transformation success, are critically discussed. Finally, future research

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priorities are highlighted, focusing on integrating advanced biotechnological approaches with modern breeding strategies, genomics, genome editing and germplasm conservation to accelerate the development of climate-resilient and high-quality mango cultivars, thus supporting sustainable mango production worldwide.

Keywords: Mango, micropropagation, molecular markers, somatic embryogenesis, transgenic tools

INTRODUCTION

Mango (*Mangifera indica* L.) is one of the most popular tropical fruit crops in Asia and worldwide, having an ancient cultivation history dating back 4000 to 6000 years (Yadav et al., 2017). Mango germplasm has dispersed widely across tropical and subtropical regions for its extensive cultivation and domestication. Over the past two decades, global mango-growing regions have expanded significantly, and India is the largest mango producer, producing 26.2 million tons annually from a cultivation area of 2.69 million hectares (https://worldpopulationreview.com/country-rankings/mango-production-by-country) (Figure 1). Indonesia, Brazil, Pakistan, Bangladesh and China are mango-producing countries due to their warm climates with the least frost occurrence, which is ideal for tropical fruit production.

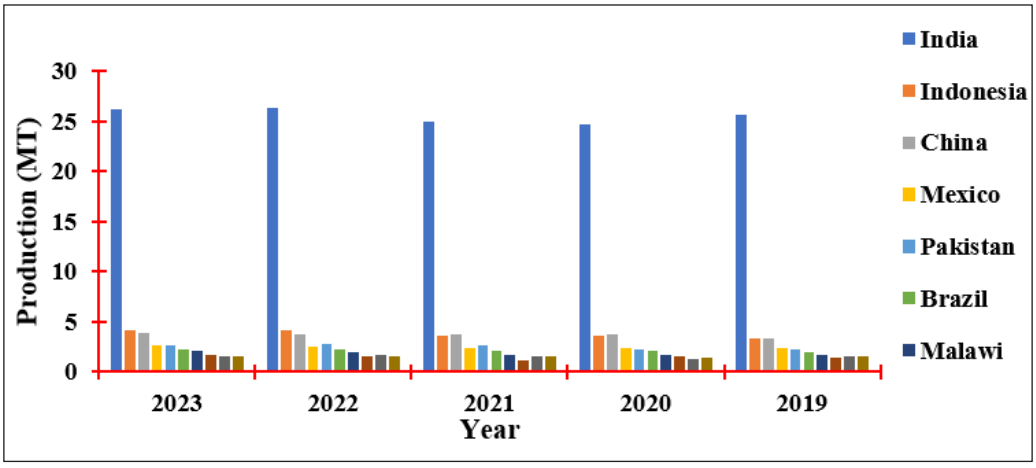

Figure 1. Global mango production report from 2019-2023
Source: WRP (Accessed on 11 April, 2026)

Despite its global importance, mango cultivation faces numerous biological constraints and production challenges like high heterozygosity, long juvenile phase, irregular bearing and inconsistent flowering behaviours. In the past, progress on large-scale commercial micropropagation through somatic embryogenesis has remained difficult due to recalcitrance, severe tissue browning and high genotype dependency (Krishna et al.,

2008). In addition, regeneration using *in vitro* derived explants like cotyledonary nodes is more responsive compared to regeneration protocols from mature elite plants (Conde et al., 2023). Although tropical climates allow year-round production to maintain a constant supply of quality fruits, it remains a challenge for growers and exporters due to natural and biological limitations. Hence, biotechnology offers promising opportunities to overcome some of these limitations. The identification and classification of mango germplasm have advanced significantly due to modern tools like genome sequencing and molecular markers (Faisal et al., 2025). Plant tissue culture techniques, particularly somatic embryogenesis, provide a powerful tool for the development of specific traits in floral biology, fruit quality and overall productivity. Selection and regeneration of elite mango genotypes using plant tissue culture techniques form the basis of breeding improvement programs.

Mango productivity is heavily affected by high levels of cross-pollination. Furthermore, sexual reproduction does not ensure clonal fidelity because many commercially important cultivars are monoembryonic. It has been hypothesised that Florida mango hybrids originated from crosses between Southeast Asian (mostly polyembryonic) and Indian (monoembryonic) mango cultivars, as supported by molecular studies employing isozyme and RAPD markers (Olano et al., 2005). Polyembryonic mango cultivars have been reported to successfully produce somatic embryos (Litz, 2004; Sajana et al., 2022; Shukla et al., 2016). But frequent failure in culture due to the occurrence of contamination is another significant issue when utilising vegetative parts. *Colletotrichum gloeosporioides* isolates from diverse geographic regions are distinguished by their latency and pathogenicity on twigs, leaves, flowers, fruits and petioles of mango plants (Weir et al., 2012). Significant losses of mango yield in South America and Asia have been caused by severe infections with *Colletotrichum spp.* (Li et al., 2019b as cited in Dofuor et al., 2023; Tovar-Pedraza et al., 2020). Besides, *Alternaria alternata* and *Fusarium subglutinans* are among the latent fungal entities that have been documented in mango (Ploetz, 1994). The use of certain antibiotics against microbes to maintain sterile cultures of mango would be made possible by the identification and isolation of endophytic organisms. Most of the commercially grown mango cultivars do not fully satisfy the assertions of modern intensive horticultural systems, which demand dwarfism, early bearing, consistent production, resistance to pests and diseases and improved storage quality. Emerging trends in micropropagation and genetic marker-based technologies have promisingly accelerated mango breeding programs. A number of genes have been explored for genetic transformation in mango, which makes the transgenic mangoes technically more feasible (Pandey et al., 2022).

This review synthesises current *in vitro* methodologies and existing bottlenecks like recalcitrance and phenolic browning, guiding future optimisation of micropropagation protocols, evaluating the transition from juvenile to mature plants, and providing a clear roadmap for establishing reliable clonal regeneration systems in elite cultivars. Also

mapping out advancements in genetic transformation and molecular markers, the review establishes a foundation for integrating biotechnological tools into targeted mango breeding and crop improvement programs. Therefore, future research must focus on optimising explant selection and refining culture protocols along with molecular approaches to make micropropagation work across many different commercial cultivars for the successful application of biotechnological tools in mango improvement programs.

IN VITRO PROPAGATION

The process of developing plant and/or plantlets through a simulated medium under aseptic conditions is known as plant tissue culture. *In vitro* propagation demands cultivating explants such as roots, shoot tips, calli, reproductive organs (pollen, ovules), seeds, embryos or even a single cell from the mother plant on nutrients containing an aseptic medium (Kaya & Huyop, 2020; Vidyagina et al., 2021). Compared to *in vivo,* this technique has the potential to lower costs, while improved formulation and homogeneity result in superior clones and a rapid multiplication system. Mango varieties having positive mutations or gained diversity through somaclonal variation may be screened through *in vitro* selection. Various explants were investigated for *in vitro* regeneration of plantlets using Gamborg's (B5) as well as Murashige and Skoog (MS) media.

IN VITRO PROPAGATION OF MANGO

In vitro propagation is the art and science behind *in vitro* multiplication of plants. The procedure includes a number of steps, including stock maintenance, explant nomination, sterilisation, alteration of the proliferation media, adaptation and development into plantlets (Figure 2). Laboratory-raised seedlings reduce contamination for successful micropropagation of 'Irwin' mango using woody plant medium (WPM) in conjunction with a synergistic combination of zeatin and 6-benzyladenine (BAP) maximised both shoot growth and proliferation (Tetsumura et al., 2016). Numerous investigations have revealed a number of intrinsic concerns related to *in vitro* culture, including explant browning, phenol exudation, medium staining, *in vitro* tissue recalcitrance and extensive systemic contamination. Plantlet regeneration from different explants, such as nucellus tissues and branches, have become successful reported by Sajana et al. (2022) and Zhou et al. (2024), respectively. Despite some constraints, these techniques assure year-round explant availability in contrast to seeds that only offer propagating material at specific seasons of the year. Etiolated shoots exhibit a significant decrease in phenolic exudation and polyphenol oxidase (PPO) activity at earlier stages, as well as phenolic biochemical release at the post-culture phase when *in vitro* cultured. The contamination done by endogenous pathogens is another significant factor that hampers tissue culture of mango when utilising vegetative parts but can be mitigated by pretreatment of the mother plant

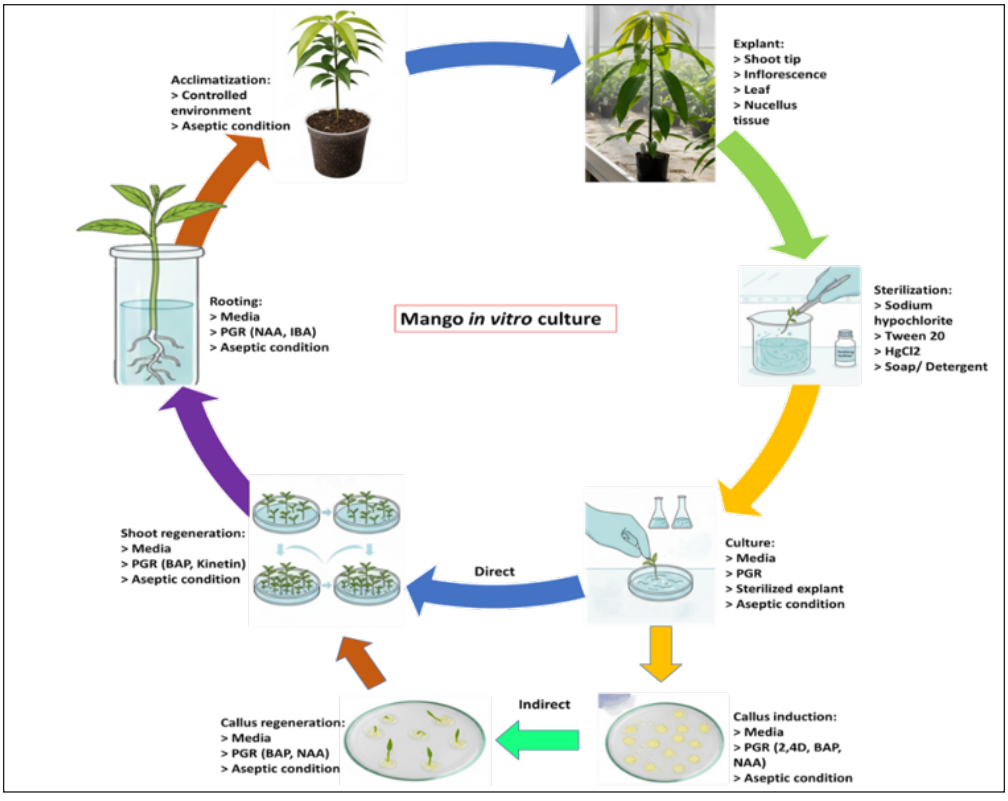

Figure 2. Primary steps of *in vitro* culture of mango

with azoxystrobin and following the preculture sterilisation protocol prescribed by Lee et al. (2025). Successful regeneration in mango tissue culture is also hindered by the physiology and inherent genetics of the donor plants, where nucellar embryos have become more successful compared to mature tissues (Thomas, 1999).

Recent advances in plant tissue culture emphasise that overcoming recalcitrance requires the precise optimisation of plant growth regulators (PGRs), particularly synergistic coalescence of cytokinin and auxins, including kinetin and 1-naphthaleneacetic acid (NAA), indole-3-butyric acid (IBA), and indole-3-acetic acid (IAA), respectively, to trigger organogenesis (Foo et al., 2018; Quiroz et al., 2025). Maintaining hormonal balance is vital for success, but the integration of antioxidants and adsorbents like polyvinylpyrrolidone (PVP) is equally critical to neutralise phenolic oxidation and prevent subsequent tissue necrosis (Hesami et al., 2025; Quiroz et al., 2025). Modern protocols increasingly combine these chemical additives with environmental controls such as dark incubation and cold pretreatment to manage the oxidative stress that frequently hinders the regeneration of complex genotypes (Hesami et al., 2025).

EMBRYOGENIC CULTURES

Embryogenic cultures are plant tissue cultures capable of developing into complete plants through the process of somatic embryogenesis, serving as a vital tool for plant regeneration, genetic transformation, and mass propagation. For instance, Khair et al. (2016) reported successful development of a somatic embryogenesis protocol from nucellar tissue of the 'Baramasi' mango variety by using specific hormone combinations, most notably 2,4-dichlorophenoxyacetic acid (2,4-D) for induction and a balanced mixture of gibberellic acid (GA_3), kinetin and IAA for successful plantlet germination. Somatic embryogenesis was found from nucellar tissue of the variety 'Ratnagiri' with the prescribed use of 2,4-D and thidiazuron (TDZ) reported by Malabadi et al. (2011). Sajana et al. (2022) stated that fruits collected 30 to 50 days after pollination are preferable for callus induction from the nucellar tissues of polyembryonic varieties 'Olour' and 'Vellaikolumban' with 2,4-D and GA_3. Nucellar tissues from younger fruits were employed as the initial explant by Flórez-Ramos et al. (2007) and the expected result was obtained with cv. 'Keitt', which had 48% embryogenic culture induction. MS media added with PGRs like N^6 (2-isopentenyl) adenine (2iP); 2,4-D was a successful inducer of embryogenic callus from nucellar tissue for the cultivar 'Chaunsa', reported by Solangi et al. (2023). According to Thomas (1999) pro and globular-shaped embryos were observed 14- 21 days after the formation of embryonic calli on the establishment medium and transferred to the expression medium. Growth regulators, such as cytokinin, can be used mostly to accelerate this process. According to Sajana et al. (2022), the application of abscisic acid (ABA) has a role in embryo maturation. Litz (2005) also recommended lowering the amount of sucrose in the maturation medium from 4-6% to provide good results. Moreover, a high sugar concentration has also been found to cause a delay in the somatic embryo elongation of mangoes at maturity. Ethylene may have an effect on regeneration systems, such as organogenesis and somatic embryogenesis, reported by Neves et al. (2021).

SOMATIC EMBRYOGENESIS

The use of plant growth regulators (PGRs) is essential to guide nucellar tissue through the distinct morphological stages of somatic embryogenesis, with the combination of 2,4-D and GA_3 successfully inducing and proliferating globular embryos, while subsequent treatments with IAA, ABA and zeatin facilitated the transition through heart-shaped stages to final maturation and successful germination reported by Sajana et al. (2022) (Table 1). Jana et al. (1994) successfully leveraged the naturally disease-free properties of nucellar tissue from three mango varieties of India, 'Mundan', 'Alphonso' and 'Baneshan' to rapidly generate morphologically sound somatic embryos within a 75 to 80-day period. In other words, efficient somatic embryogenesis in monoembryonic cultivars allows the preservation of clonal genotypes and the elimination of pathogens, as well as being extensively researched

across polyembryonic varieties to mitigate disease and environmental stress (Pateña et al., 2002, as cited in Zuazo & Pleguezuelo, 2009). Culturing early embryos on a medium containing 5 mg/L kinetin for four weeks successfully produced plantlets *via* direct somatic embryogenesis with minimal tissue browning (Xiao et al., 2004). However, the effective recuperation of mango plantlets has also been hampered by issues with early germination and increasing necrosis. In general, there are some major stages to the protocols used: a) nucellus-induced embryogenic culture induction, b) embryogenic culture maintenance, c) the morphologically regular embryo maturation and development and d) the germination of somatic embryos into fully grown plantlets. DeWald et al. (1989) found that embryogenic cultures performed more effectively in suspension compared to solid media. Furthermore, compared to both MS and WPM, B5 basal modified medium was good for maintaining cultures as well as producing somatic embryos properly. Coconut water boosted somatic embryo development in 'Chaunsa' mango; biochemicals like casein hydrolysate and yeast extract were ineffective, and 'Anwar Rataul' failed to respond due to excessive phenolic interference (Usman et al., 2005).

ORGANOGENESIS

Organogenesis through *in vitro* culture is the developmental process where plant organs such as shoots, roots or flowers are regenerated from cultured cells, tissues or organs under controlled aseptic conditions. For instance, Zhou et al. (2024) successfully established a stable, genetically trustworthy regeneration protocol for cv. 'Keitt' using young shoots in WPM containing 1 mg/L 6-BA and 0.1 mg/L NAA for high-frequency shoot induction (73.63%) and Douglas-fir cotyledon revised medium (DCR) with 3 mg/L IBA for effective (66.13%) rooting (Table 1). Early investigations into mango organogenesis found that while kinetin and NAA could induce roots from cotyledon-derived callus, shoot growth remained elusive, with further studies noting that half-strength semi-solid MS media improved explant survival by reducing phenolic exudation (Rao et al., 1981; Singh et al., 1999). Conde et al. (2023) observed that axillary shoots were found from cotyledonary nodes using different mango varieties as explants. Precise application of zeatin (5 mg/L) plays a role in embryo germination, produces shoots and initiates root induction, as observed by Sajana et al. (2022). A promising protocol for embryogenic callus to organ formation, such as shoot, root and leaf formation reported by Khair et al. (2016) *via* somatic embryogenesis and the germination process using different media and PGRs. But every transitional phase requires different cultural conditions for promising output. As Mishra et al. (2010) reported, the culture conditions for somatic embryo germination and plantlet formation were 16h photoperiod with 40 mmol m^2s^{-1} quantum flux and 55% relative humidity at 25±2 °C.

PLANTLET DEVELOPMENT

The alteration of somatic embryos into viable plantlets is a complex process requiring specific media, environmental conditions and rooting treatments. Somatic embryos must be shifted to a liquid to semi-solid medium, typically half-strength B5 macro-salts with 1.0 mg/L GA_3 and maintained at 25 °C temperature under a 16 h photoperiod with soft white fluorescent light at 40-60 µmol $m^{-2}s^{-1}$ for successful transformation (Ara et al., 2000b; Litz, 2003). Alteration percentage can be further sped up by increasing the intensity of light to 160 µmol $m^{-2}s^{-1}$ in an environment facilitated with 2% CO_2 (Litz, 2003). The somatic embryos can be transferred to soil after full development into seedlings, though achieving high-quality rooting remains a challenge. While treatment with IBA in the dark can induce rooting in up to 90% of micro cuttings, it often results in stunted root elongation and poor overall growth even when utilising optimal potting media such as fine vermiculite (Tetsumura et al., 2016). A combination of 60% coconut fibre, 30% commercial substrate and 10% litonite provides the best output for adaptation of *in vitro* rooted mango shoots with the facility of a growth chamber having 16/8h light/dark cycle, 60% relative humidity, 45-50 µmol $m^{-2}s^{-1}$ light intensity, along with a temperature of 26±1 °C for plantlet rearing reported by Conde et al. (2023).

AUTHENTICATION OF CULTIVARS USING MOLECULAR TECHNIQUES

Cultivar identification can be accomplished by using molecular markers, including DNA and isozyme markers (Figure 3). Marker-assisted selection (MAS) is another tool to accelerate the breeding program. Genetic marker technologies, including Simple Sequence Repeat (SSR), Inter-Simple Sequence Repeat (ISSR), Random Amplified Polymorphic DNA (RAPD), Single Nucleotide Polymorphism (SNP), Restriction Fragment Length Polymorphism (RFLP), Amplified Fragment Length Polymorphism (AFLP), isozymes and DNA-based markers, have been extensively utilised to map mango progeny (Table 2). For identification of cultivars and to analyse the genetic diversity of genotypes, many researchers used different types of molecular marker-assisted biotechnological tools based on different monogenic and polygenic traits (Abdelsalam et al., 2018; Jena & Chand, 2021; Kalal et al., 2023; Sherman et al., 2015). Despite the efficiency of these molecular tools for studying traits, researchers frequently face challenges such as low polymorphism and the presence of PCR inhibitors like polysaccharides and phenolics (Ramírez, 2013). To overcome these limitations, specialised extraction protocols have been developed to isolate quality genomic DNA from complex mango tissues, including healthy and malformed floral structures (Gomathi et al., 2005; Ramírez, 2013).

Table 1
Embryogenic and organogenic accomplishments of some mango cultivars

	Genotype	Explant	Media with PGRs	Culture Conditions	Corresponding Effects	References
1.	Keitt	Shoot tips	WPM (1 mg/L 6-BA, 0.1 mg/L NAA)	At 25±2 ºC temperature with 16h photoperiod and 33.6 $molm^{-2}s^{-1}$ light intensity	Adventitious shoot induction	Zhou et al., 2024
2.	Irwin, Keitt (monoembryonic), Ataulfo, Sabre and Gomera-4 (polyembryonic)	Mature seeds (4 months after full bloom)	Half strength of MS, 0.5 mg/L GA_3, 100 mg/L cysteine, 3% sucrose, 0.7% agar)	Cultured in the dark at 25±1 °C for three weeks	Good germination rate	Conde et al., 2023
3.	Keitt	Cotyledonary nodes from *in vitro* germinated seeds	Germination medium (GM); 0, 0.5 and 1 mg/L GA followed by MI2 medium, 3.0 mg/L kinetin and 1.0 mg/L IAA. MI2 medium, 3.0 mg/L kinetin or 1.0, 2.0 and 3.0 mg/L TDZ	Cool-white fluorescent bulbs with 16h photoperiod at 45 µmol m^{-2} s^{-1} light intensity (wavelength 400-700 nm) and incubated at 25±1 °C temperature	Shoot development and regeneration	Conde et al., 2023
4.	Saroli, Langra and Chaunsa	Nucellus tissue	Modified MS and B5 (9.83 µM 2iP and 4.52 µM 2,4-D)	Incubated in complete darkness at 24° C temperature	Callogenesis	Solangi et al., 2023
5.	Vellaikolumban and Olour	Nucellus tissue	Rugini olive medium (RO), 5 mg/L 2,4-D and GA_3, 6% sucrose	Usually maintained at 25±2° C in the dark during the initial callus induction stage, followed by a 16h light with an intensity of 40-45 µmol $m^{-2}s^{-1}$	Embryogenic calli development	Sajana et al., 2022
6.	Anwar Rataul	Shoot tips	MS, 1 mg/L BAP MS media with 3 mg/L NAA, 1 mg/L IAA	At a room temperature of 25±2 °C with a 16/8h of photoperiod	Shoot induction Root induction	Qureshi et al., 2021
7.	Sabre and 13-1	Nucellus	B5 or MS media, 0.5 mg/L 2, 4-D, 1.0 mg/L thiamine HCl, 400 mg/L L-glutamine, 150 mg/L ascorbic acid, 100 mg/L myo-inositol, 6% sucrose, 100 mg/L citric acid, 1.5 g/L activated charcoal	8 weeks in a growth chamber at 27±2 ºC with a photoperiod of 1500 cdm^{-2} from soft fluorescent lamps for 16/8 h per day	Somatic embryogenesis	Shehata, 2021

Table 1 *(Continued)*

	Genotype	Explant	Media with PGRs	Culture Conditions	Corresponding Effects	References
8.	Ubá and Carlota	Immature embryo	Half strength of MS with 0.5 mg/L GA_3, 100 mg/L cysteine and 30 g/L sucrose with 2.2 g/L phytagel	30 µmol $m^{-2}s^{-1}$ photon flux density at 27±1 °C and 16h of photoperiod (for embryo development) 22 µmol µmol $m^{-2}s^{-1}$ photon flux density at 22±1 °C temperature and 12h of photoperiod (for plantlet)	Somatic embryogenesis and plantlet development	Souza et al., 2020
9.	Alphonso, Carabao and Turpentine	Nucellus	Modified MS and B5 media (1 mg/L 2, 4-D alone or in combination with 0.25 mg/L BAP)	Incubated at 25±2 °C, maintaining 60% relative humidity in dark conditions	Somatic embryogenesis	Shukla et al., 2016
10.	Ratnagiri	Nucellus tissue	MS, 2.27 µM TDZ and 4.52 µM 2,4-D	At 55-60% relative humidity and 25±3 °C temperature under soft white fluorescent (100 µmol $m^{-2}s^{-1}$)	Embryogenic callus induction	Malabadi et al., 2011
11.	Irwin	Young shoots	Different strengths of MS, Gamborg (B5) and WPM (10 µM zeatin)	At 28 °C temperature under 16h of photoperiod	Shoot proliferation	Sakota et al., 2010
12.	Ambalavi	Nucellus tissue	Modified basal medium containing (0.25 mg/L BAP, 0.5 mg/L 2iP and 1 mg/L NAA)	At 70±5% relative humidity and 27±1 ºC temperature with a 15h of photoperiod having a quantum flux of 25 µmol $m^{-2}s^{-1}$	Plantlet regeneration through somatic embryogenesis	Chaturvedi et al., 2004
13.	Amrapali	Nucellus tissue	Modified MS medium (half macro, full micro salts and organics) with 6% sucrose, 0.57 mM ascorbic acid, 2.74 mM L-glutamine, 4.5 mM 2,4-D and 0.8% agar	In darkness at 25±2 ºC temperature	Plantlet regeneration through somatic embryogenesis	Ara et al., 2000a

Note. CW = coconut water, CH= casein hydrolysate

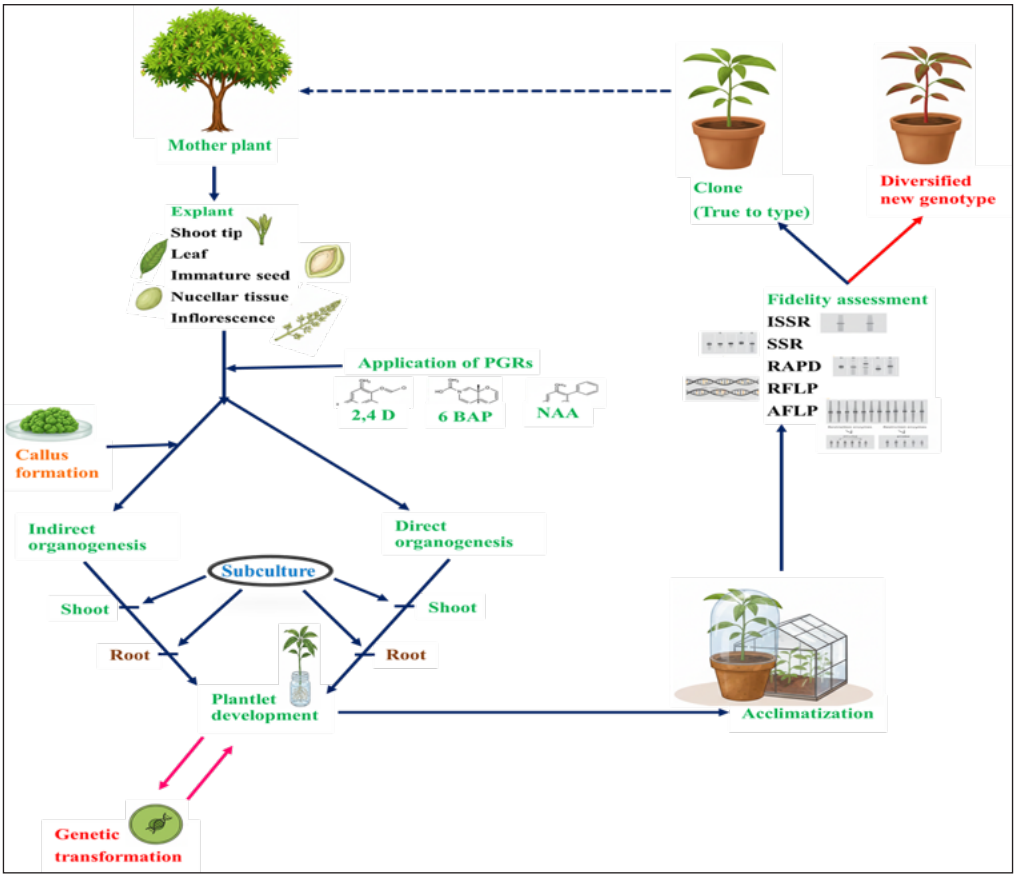

Figure 3. Advancement of *in vitro* culture and fidelity assessment by molecular markers

Table 2
A summary of key molecular tools in in vitro culture and mango breeding purposes

	Molecular Tools	Key Findings	References
1.	ISSR	Identification as well as genetic diversity in mango	Zhou et al., 2024
2.	SSR, RAPD	Identifying genetic diversity in mango population and efficiency comparison	Hussein et al., 2023
3.	SSR (Including MiIIHR23, MiIIHR17, and LMMA12)	Differentiation of nucellar and zygotic embryos of polyembryonic Olour and Vellaikulamban	Kalal et al., 2023
4.	SSR	Each locus has an average of 3.0 alleles and 2-5 alleles. Each locus had a total of 21 alleles that were identified by 7 polymorphic primers	Arogundade et al., 2022
5.	SCoT, RAPD, CBDP, ISSR, SSR and DAMD	SSRs detected the highest genetic variability	Jena & Chand, 2021

Table 2 *(Continued)*

	Molecular Tools	Key Findings	References
6.	SCoT	244 (72.4%) of the 337 fragments produced by 45 primers expressed polymorphism and 89% of genetic variation was found within populations in 2 clusters, compared to 11% between groups	Zhou et al., 2020
7.	RAPD and ISSR	High polymorphism levels were found using 10 RAPD and ISSR markers; RAPD (91.9%) and ISSR (98.1%) produced 162 and 145 loci, respectively	Ho & Tu, 2019
8.	SSR	10 sets of 3 SSR markers separated 83 genotypes using 46 polymorphic SSR markers. Southeast Asian and Indian types can be distinguished genetically by 3 clusters with Floridian varieties being more similar to the Indian variety	Yamanaka et al., 2019
9.	SSR and EST-SSR	Both morphological characteristics and genetic polymorphism exhibited notable variance, between 0.71% to 100%	Abdelsalam et al., 2018
10.	SSR	The accessions displayed similarity coefficients between (75 to 100) %	Nazish et al., 2017
11.	SSR	387 mango accessions from all over India were reported and classified them into 2 subpopulations (south/west and north/east)	Ravishankar et al., 2015
12.	Subset of 239 SNP	74 Israeli mango accessions were genotyped and surveying its structure and diversity (GWAS preliminary step)	Sherman et al., 2015
13.	SSR	Analysis of the variety of the Australian collection revealed that trinucleotide motifs were more common than dinucleotide motifs and that is consistent with the current findings	Dillon et al., 2014
14.	SSR	Diversification in local germplasm collections	Tsai et al., 2013
15.	RAPD	UPGMA proposed 5 genotypic groups and found 55 polymorphic loci	Souza et al., 2011
16.	RAPD	9 clusters with 75% similarity were constructed and RAPD indicated a (2-31) % range of genetic diversity	Fitmawati et al., 2010
17.	AFLP	Evaluating the genetic relationships and species diversity of mangos	Yamanaka et al., 2006
18.	RFLP	Genetic kinship estimation between poly and monoembryonic cultivars	Ravishankar et al., 2004
19.	Molecular and isozyme markers	Identification of hybridized mangoes	Jintanawongse & Changtragoon, 2000

Note. SCoT = Start Codon Targeted, CBDP = CAAT Box-Derived Polymorphism, DAMD = Directed Amplification of Minisatellite-region DNA

Application of Different Molecular Markers

ISSR amplification is regarded as a rapid, relatively low cost as well as highly repeatable tool for assessing genetic diversity and identifying closely related fruit tree cultivars. Zhou et al. (2024) ensured the genetic fidelity of *in vitro* cultured 'Keitt' mangoes by demonstrating a complete lack of somaclonal variation compared to the mother plant. Beyond stability testing, ISSR primers have proven effective in detecting polymorphisms for variety identification and offer significant potential for enhancing mango breeding through rootstock characterisation and parentage confirmation (Zhou et al., 2024).

The advantages of SSRs, often referred to as microsatellite DNA markers, compared to other markers include their high polymorphism, abundance, co-dominance in inheritance, ease of analysis and transferability. Using SSR markers, Kalal et al. (2023) successfully differentiated zygotic from nucellar embryos in polyembryonic mango genotypes 'Olour'. Characterisation using SSR markers revealed that Indian mango cultivars cluster into two genetically distinct populations that align with their specific geographical origins (Sherman et al., 2015). Genetic diversity and phylogenetic relationships among mango cultivars have also been extensively analysed using RAPDs, RFLPs and microsatellites based biotechnological tools to verify parentage and map genetic structures. Through a comparative analysis of 17 mango cultivars, the cultivar 'Zebda' was identified as the most diverse, with SSR markers demonstrating greater efficiency than RAPD markers in assessing genetic variability and determining cultivar identities (Hussein et al., 2023). High polymorphism levels were found using ten RAPD markers (91.9%) reported by Ho and Tu (2019). Mango cultivars are identified using AFLP data, which is also used to get genetic linkage maps and investigate the genetic relationships between rootstocks and cultivars. Yamanaka et al. (2006) evaluated the genetic relationships and species diversity of mangos by using AFLP markers. Furthermore, the genetic kinship of polyembryonic and monoembryonic cultivars along the Indian coast was examined *via* genomic and chloroplast DNA RFLP analysis, revealing close relationships among certain hybrids despite morphological differences (Ravishankar et al., 2004).

Other Techniques

Polymorphic mango and *Citrus sinensis* may have close kinship according to published genomes, and the sweet orange genome project reported 1.06×10^6 SNPs in the entire genome, with one-third in genic regions (Malik et al., 2012, as cited in Sherman et al., 2015; Xu et al., 2013). DNA fingerprint patterns of specific mango genotypes were examined by Adato et al. (1995) using minisatellite multi-locus probes to analyse variable number tandem repeats (VNTRs), which consist of short nucleotide sequences clustered in tandem across various chromosomes.

GENETIC TRANSFORMATION

Mango improvement initiatives are significantly expedited by biotechnology, which supplements traditional breeding limitations such as long juvenile phases and high heterozygosity (Song et al., 2023). Researchers have primarily relied on *Agrobacterium*-mediated systems and embryogenic cultures to introduce genes associated with delayed fruit ripening, disease resistance, and stress tolerance (Table 3). However, widespread application remains challenging due to strong genotype-dependency and difficulties in regenerating fully developed transgenic plants from targeted tissues. Pandey et al. (2022) reported the amenability of an apical meristem-targeted and tissue culture-independent *planta* transformation strategy to bypass recalcitrant *in vitro* regeneration barriers. A resistance mechanism of red mango skin to abiotic and biotic stresses through transcriptomic analysis was described by Sudheeran et al. (2021).

LIMITATIONS

The *in vitro* propagation of mango (*Mangifera indica* L.) remains a formidable challenge and a highly recalcitrant process plagued by a cascade of physiological and technical barriers. The major constraint is strong phenolic exudation caused by excision, which rapidly browns the culture medium, resulting in tissue necrosis; this problem is especially apparent when using explants from mature plants, which have less morphogenic potential than juvenile tissues (Krishna & Singh, 2007; Petri et al., 2021). Oxidative stress is a persistent issue in microbial contamination, particularly internal pathogens that can survive after surface sterilisation, which has been identified as a major roadblock for specific varieties such as the Harumanis mango (Lee et al., 2025). Furthermore, the success of these cultures is highly sensitive to the initial explant state, as seen in the high oxidation rates (up to 60% within 72 hours) observed in immature embryos (Souza et al., 2020) and the critical dependence on explant age and specific genotype (Krishna & Singh, 2007). A prolonged juvenile phase is another barrier for mango cultivation. Ultimately, these factors culminate in a notoriously slow growth response and low rates of somatic embryo conversion, often resulting in significant attrition during the final acclimatisation phase. Specific protocol development for economically important varieties may solve many of the above-mentioned problems, and biotechnological tools will also play a role in maintaining homogeneity. Sometimes, a coupling approach can also mitigate the constraints of long juvenility, latent pathogenicity and stress tolerance of the variety. Tissue culture techniques, along with the gamma irradiation approach, can reduce the endo-pathogenic problem, provide stress tolerance and balance hormonal effects to shorten the lifespan.

Table 3
Genetic transformation in mango to develop elite traits using transgenic tools

	Variety	Gene/Tool	Goal	Response Activity	Reference
1.	Amrapali	*GFP* and *Hptll* in binary vector *pCAMBIA1302*	Demonstrate the amenability of a tissue culture-independent, apical meristem-targeted *in planta* transformation strategy to bypass recalcitrant *in vitro* regeneration barriers	Preliminary screening identified 65% of the seedlings displaying GFP expression and molecular characterization (PCR, sqRT-PCR) confirmed transgene integration	Pandey et al., 2022
2.	Amrapali	*GUS* (beta-glucuronidase with a catalase intron) and *nptII* (kanamycin resistance) in binary vector *pCAMBIA2301*	Demonstrate the amenability of a tissue culture-independent, apical meristem-targeted *in planta* transformation strategy	Preliminary histochemical assay identified 57.14% of the plants showing GUS expression at the pricked regions; PCR and sqRT-PCR verified transcript accumulation	Pandey et al., 2022
3.	Shelly	Transcriptomic analysis: *WRKY, DREB*	Resistance mechanism of red skin for abiotic and biotic stresses	Induce defense response and resistance of red mango skin against anthracnose (*C. gloeosporioides*)	Sudheeran et al., 2021
4.	Siji	*MieIF* genes	To identify and characterise the eIF gene family	Role in abiotic stress tolerance	Li et al., 2019a
5.	-	*CPLL*, Immunoproteomics	Investigate a protein against a certain allergen	Proteins made cause of allergic reactions	Cardona et al., 2018
6.	Kent	ACC (*ACO*) oxidase and ACC (ACS) synthase	Genes are used in experiments to prolong shelf life and prevent ethylene generation.	Investigating the role of particular hydrolytic enzymes to prolong shelf life.	Dautt-Castro et al., 2015
7.	Zill	Illumina *RNA*-seq technology	Explore the transcriptome sequence	Investigations into protein identification and gene expression of ripening	Wu et al., 2014
8.	-	*CPLL*	Examine peptidome content	Assess the entity of allergens and peptides bestowed with biological activities	Fasoli & Righetti, 2013
9.	Keitt	Proteomic investigation	Reduction of the biosynthesis of the hormone during ripening	Recurrence of biological phenomena related to ripening	Andrade et al., 2012
10.	Vellaikolumban	*β-glucuronidase (GUS)* reporter gene	Viability of gene transfer demonstrated in embryogenic callus.	To identify transgenic plants, the reporter transgene's expression was verified using the *GUS* assay	Samanta et al., 2007

Note. GFP = Green Fluorescent Protein, *hptII* = Hygromycin Phosphotransferase, *CPLL* s= Combinatorial peptide ligand libraries, *DREB* = Dehydration-Responsive Element-Binding protein, *MieIF* = *Mangifera indica* Eukaryotic Initiation Factor, ACC = 1-aminocyclopropane-1-carboxylate, *NptII* = neomycin phosphotransferase II

CONCLUSION AND FUTURE EXPECTATIONS

Significant economic value is attributed to the mango fruit, particularly in tropical regions where productivity is frequently jeopardised by numerous diseases and stresses. The micropropagation of mango is significantly impeded by phenolic browning and contamination during the establishment of aseptic cultures from mature explants. However, the mango-oriented economy could be transformed by biotechnology through the use of precise genetic manipulation to develop desirable varieties. Goals like resistance against endophytic and exophytic pathogens, short juvenile periods, less phenolic exudation and exceptional fruit quality, which have not been accomplished by conventional breeding, may be achieved through these biotechnological approaches. Homogeneous lines can be raised *via* tissue-culture techniques, and the production of stable offspring for various traits is being progressively investigated. Though mango has been successfully transformed using recurrent somatic embryogenesis, a low incidence of effective genotype regeneration into normal plantlets is still observed. In the future, it is expected that research will be focused on increasing the frequency of *in vitro* developed plantlets. Significant genetic loss within the *Mangifera* genus will be mitigated by the essential creation of *ex situ* and *in situ* germplasm collections. Future resistance to anthracnose, stem end rot and powdery mildew is expected to be sourced from other *Mangifera* species to bolster crop security. The challenges posed by both biotic and abiotic stressors will likely be addressed through continued biotechnological advancements. It is anticipated that the role of mango as a significant global crop will be strengthened by these emerging scientific innovations. New protocols for regenerating plants from shoot or nodal segments are expected to be refined to overcome current propagation limits. A more resilient mango industry will be established as genetic transformation techniques are set for commercial use. The preservation of natural biodiversity will be prioritised to ensure that rare genetic traits are not lost. Ultimately, the global contribution of the mango will be expanded as biotechnology is integrated more deeply into agricultural practices.

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CONFLICTS OF INTEREST

The authors declare no conflict of interest.

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