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AROMATIC RICE: FROM AROMA GENETICS TO MODERN BREEDING STRATEGIES

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ABSTRACT

Aromatic rice (*Oryza sativa* L.) is a premium class of rice valued globally for its distinctive fragrance, superior grain quality, and high consumer preference, contributing significantly to food security and export economies, particularly in South and Southeast Asia. The characteristic aroma is primarily attributed to 2-acetyl-1-pyrroline (2-AP), whose biosynthesis is mainly regulated by the BADH2 (*fgr*) gene along with several associated quantitative trait loci and metabolic pathways. Despite their excellent sensory and cooking qualities, most traditional aromatic landraces are low yielding, tall, lodging-prone, and susceptible to biotic and abiotic stresses, limiting their large-scale cultivation. Conventional breeding approaches such as hybridization, convergent breeding, and mutation breeding have been widely employed to combine fragrance with improved yield, plant type, and adaptability. The exploitation of heterosis through cytoplasmic male sterility systems has further enabled the development of high-yielding aromatic hybrids. Recent advances in molecular breeding, particularly marker-assisted selection, gene pyramiding and genome-based approaches, have facilitated precise introgression of aroma and stress-resistance genes while preserving grain quality. Collectively, the integration of conventional and molecular strategies has accelerated the development of superior aromatic rice cultivars, offering significant prospects for sustainable production, enhanced farmer income, and meeting the growing global demand for premium rice.

Key words : Aromatic rice, 2-acetyl-1-pyrroline (2-AP), BADH2, Aroma biosynthesis, Molecular breeding, Marker-assisted selection, Genome editing.

Introduction

Rice (*Oryza sativa* L.) is one of the oldest domesticated crops and serves as the staple food for nearly half of the global population, playing a central role in food security and livelihoods, particularly in the Asia–Pacific region (Wakte *et al*., 2017; Meyer and Purugganan, 2013). Although aromatic rice accounts for only ~4% of global rice trade, it commands premium market value due to superior grain quality and strong consumer preference (Richaria *et al*., 1965; Prodhan *et al*., 2017). Historical records indicate the presence of aromatic rice as early as 400 BC (Vemireddy *et al*., 2021), and its cultivation has expanded steadily.

Rice grain quality is determined by physical appearance, milling recovery, cooking behavior, sensory traits and nutritional value (Fitzgerald *et al*., 2009). Among these, aroma is the most distinctive attribute and has been consciously selected during domestication. Aromatic rice represents a genetically distinct subgroup of *O. sativa*, closely related to temperate and tropical japonica types (Meyer and Purugganan, 2013; Vemireddy *et al*., 2021; Kovach *et al*., 2009). Basmati and Jasmine varieties dominate international markets owing to their characteristic fragrance, texture, and taste. India and Pakistan lead Basmati exports, while Thailand is the primary producer of Jasmine rice. In addition, numerous

short- and medium-grain aromatic landraces are traditionally cultivated in India and Southeast Asia to meet regional demand (Hinge *et al*., 2019; Singh *et al*., 2019; Ahuja *et al*., 1995; Pachauri *et al.*, 2010).

The characteristic fragrance of aromatic rice is mainly attributed to 2-acetyl-1-pyrroline (2-AP), a potent heterocyclic volatile compound (Buttery, 1982; Chakraborty *et al*., 2016; Luo *et al*., 2022). Other volatiles, including alcohols, aldehydes, esters, ketones, and amine heterocycles, also contribute to overall aroma perception (Verma *et al*., 2018; Daygon *et al*., 2017; Ashokkumar *et al*., 2020; Chen *et al*., 2022). The biosynthesis of 2-AP primarily involves polyamine degradation and amino acid metabolic pathways (Huang *et al*., 2008; Sakthivel *et al*., 2009).

Genetically, aroma is governed by a single recessive gene (*fgr*) located on chromosome 8, encoding betaine aldehyde dehydrogenase 2 (BADH2) (Bradbury *et al*., 2005; Hinge *et al*., 2016; Sasaki, 2005). Mutations or deletions in *OsBADH2* reduce enzyme activity, resulting in precursor accumulation and enhanced 2AP production (Chen *et al*., 2008; Shan *et al*., 2013; Chakraborty *et al*., 2016; van Quoc *et al*., 2023). Haplotype analyses indicated the japonica origin of the aromatic *badh2* allele, with the Himalayan foothills as the centre of origin (Vemireddy *et al*., 2021; Kovach *et al*., 2009; Pachauri *et al*., 2010). Additional genes, including *OsBADH1*, *OsGly* and *OsP5CS*, also influence aroma regulation (Prodhan and Shu, 2020; Lorieux *et al*., 1996; Amarawathi *et al*., 2008).

Besides genetic factors, environmental and agronomic conditions such as temperature, humidity, soil moisture, irrigation practices, and fertilizer management significantly affect volatile accumulation and aroma intensity (Monggoot *et al*., 2014). How-ever, most traditional aromatic landraces are low yielding, tall, lodging-prone, photo-sensitive, and susceptible to major diseases such as bacterial leaf blight and blast (Singh *et al*., 2000; Raina *et al*., 2019). Earlier yield-focused breeding often compromised aroma due to inter-group incompatibility and limited multi-trait selection (Kush & Juliano, 1985; Singh *et al*., 2000). Recent advances in genomics, molecular breeding, and precise aroma quantification have improved understanding of fragrance genetics and enabled the development of high-yielding aromatic cultivars without sacrificing grain quality.

Origin and Diversity of Aromatic rice

Origin of Aromatic rice

Historical, literary, and genetic evidence collectively suggest that aromatic rice originated in the Indian subcontinent. Ancient Hindu texts such as the *Charaka Samhita* (600 BC) provide early references to the cultivation of scented rice, indicating its antiquity in South Asia. Archaeobotanical and historical records further suggest that fragrant rice cultivation was prevalent not only in India but also extended to China and other South Asian regions at an early stage (Singh *et al*., 2019).

The Himalayan foothills, encompassing parts of Uttarakhand, Bihar, and the Tarai region of Nepal, are widely recognized as the primary centre of diversity of aromatic rice, where a large number of traditional scented rice varieties are still cultivated (Khush, 2000; Pachauri *et al*., 2010; Vemireddy *et al*., 2021). From this region, aromatic rice gradually spread to neighbouring and distant regions such as Afghanistan, Bangladesh, Iran, Iraq and Thailand, and spread to Europe, especially the countries like Italy and France, through trade and human migration (Khush, 2000; Roy *et al*., 2020; Vemireddy *et al*., 2021).

Evolution and Genetic Distinctness of Aromatic Rice

Traditionally cultivated rice (*Oryza sativa* L.) has been classified into two major subspecies, Indica and Japonica, although the evolutionary origin of these groups remains debated (Ikehashi, 2009). Two major hypotheses explain their divergence: the single-origin model, which proposes a common ancestor (*Oryza rufipogon*), and the multiple-origin model, which suggests independent domestication events followed by natural hybridization (Oka & Morishima, 1982; Sang & Ge, 2007).

Using isozyme markers, Glaszmann (1987) classified global rice germplasm into six groups, identifying Group V as aromatic rice, primarily comprising Basmati-type cultivars. Subsequent molecular studies using SSR, SNP and chloroplast markers consistently recognized aromatic rice as a distinct genetic subpopulation, alongside ‘indica’, ‘aus’, ‘tropical japonica’ and ‘temperate japonica’ groups (Garris *et al*., 2005; Li *et al*., 2014; Wang *et al*., 2014).

Phylogenetic analyses indicate that aromatic rice is genetically closer to ‘Japonica’, although several aromatic cultivars-such as ‘Thai Jasmine’ rice-are grouped within the Indica subpopulation, reflecting a complex evolutionary history (Garris *et al*., 2005; Hinge *et al*., 2019). This intermediate genetic position suggests that aromatic rice represents a bridge between ‘Indica’ and ‘Japonica’ types.

Haplotype analysis of the aroma gene (*BADH2*) revealed that the fragrance trait originated in Japonica rice and was later introgressed into ‘Indica’ and ‘Aus’ backgrounds through natural hybridization during domestication. It is proposed that fully domesticated ‘Japonica rice’ entered the Indian subcontinent and

hybridized with local wild or semi-domesticated 'Aus' relatives, giving rise to the present-day aromatic rice group, which later dispersed globally (Pachauri *et al*., 2010; Civáò *et al*., 2019).

Indigenous Germplasm and Landraces of Aromatic rice

Aromatic rice comprises a distinct group of indigenous varieties and landraces valued for their fragrance, grain quality, and premium market demand, which has increased steadily over recent decades (Verma *et al*., 2019). India represents the primary centre of diversity and trade for aromatic rice, particularly Basmati types cultivated in the Indo-Gangetic plains. Traditional Basmati landraces such as 'Taraori Basmati' and 'Basmati 370' are globally recognized and have received Geographical Indication status, strengthening their export value (Pachauri *et al*., 2010; Kishor *et al*., 2020; Roy *et al*., 2020). India remains the world's leading exporter of aromatic rice (Verma and Srivastav, 2017; Prasad *et al*., 2020).

Pakistan shares the Basmati gene pool and markets premium indigenous varieties such as Basmati 185 and Super Basmati (Singh *et al*., 2000). In Southeast Asia, Thailand is renowned for Jasmine rice, especially Khao Dawk Mali (Thai Hom Mali), which has international GI recognition, while related landraces are also grown in Cambodia and Laos (Verma *et al*., 2019; Roy *et al*., 2020; Vemireddy *et al*., 2021).

Iran conserves aromatic landraces including Sadri, Chamapa and Gerdeh, with Sadri types being highly preferred for their strong aroma and long slender grains (Nematzadeh *et al*., 2000; Roy *et al*., 2020). China maintains extensive traditional and improved scented rice germplasm, though consumer preference is largely for semi-aromatic types (Singh *et al*., 2000; Yang *et al*., 2012; Verma *et al*., 2019). Additional important aromatic landraces are found in Afghanistan (Bahra, Bala, Lawangi) and Bangladesh (Chinigura, Kataribhog, Badshabhog), where they hold strong cultural and market value (Singh *et al*., 2000; Anik and Talukder, 2002; Tama *et al*., 2015). Collectively, these indigenous aromatic rice landraces constitute a vital global germplasm resource supporting premium markets and future breeding programmes (Verma *et al*., 2019; Roy *et al*., 2020).

Biochemical Basis of Aroma in rice

Volatile Compounds contributing to Aroma

Volatile compounds contributing to rice aroma include hydrocarbons such as alcohols, aldehydes and ketones, which play a major role in aroma development in aromatic rice (Ashokkumar *et al*., 2020; Yang *et al*., 2008). Hexanal, a linoleic acid–derived aldehyde, contributes green, fruity and grassy notes to rice aroma (Bergman *et al*., 2000). Important heterocyclic aroma-active compounds identified in rice include 2-pentylfuran, 2-ethyl-3,5-dimethylpyrazine, and 2-methylfuran, with 2-pentylfuran being particularly associated with nutty aroma in aromatic rice (Wakte *et al*., 2017; Grimm *et al*., 2011; Hinge *et al*., 2016). Phenol and several alcohols such as 1-hexanol, 1-nonanol, and 1-octen-3-ol also contribute significantly to rice flavour, with higher levels of 1-hexanol and 1-octen-3-ol reported in Basmati rice varieties (Mathure *et al*., 2014). Additionally, benzyl alcohol has been reported in higher concentrations in aromatic and Basmati rice and is associated with a sweet aroma note (Sansenya *et al*., 2018).

Structure and Chemistry of 2-Acetyl-1-Pyrroline (2-Ap)

Among the volatile aroma compounds, 2-acetyl-1-pyrroline (2-AP) is recognized as the principal molecule responsible for the characteristic popcorn-like fragrance of aromatic rice, owing to its extremely low odour threshold (Buttery, 1982; Wakte *et al*., 2017; Hu *et al*., 2020). Chemically, 2-AP is an N-heterocyclic compound containing a 1-pyrroline ring, in which the hydrogen at the second position is substituted by an acetyl group bearing a methyl ketone functionality, a feature that contributes to its high reactivity and instability (Hu *et al*., 2020). Aromatic rice varieties typically contain 2-AP in the range of 0.04–0.09 ppm, whereas non-aromatic rice exhibits nearly ten-fold lower concentrations, often below detectable sensory levels (<0.006–0.008 ppm) (Prodhan and Shu, 2020). Due to the instability of the pyrroline ring, even trace amounts of 2-AP are sufficient to be perceived by the human olfactory system, making it a critical determinant of rice aroma (Buttery, 1982; Hu *et al*., 2020).

The methyl ketone group of 2-AP reacts with 2,4-dinitrophenyl hydrazine to form a coloured hydrazone derivative, a reaction that has been exploited for qualitative detection of aroma in scented rice (Kumari *et al*., 2019). Studies reported the presence of 2-AP in most aerial parts of aromatic rice plants, while it is largely absent or present at negligible levels in roots and in non-aromatic genotypes (Maraval *et al*., 2010; Prodhan and Shu, 2020). However, the site and timing of 2-AP formation remain debated, with some reports suggesting its generation during cooking via Maillard reactions (Hofmann and Schieberle, 1998), while others indicate in-planta synthesis during the growth period, particularly peaking around five weeks after heading and declining

thereafter during grain maturation (Yoshihashi, 2002; Hu *et al*., 2020). Quantitative analyses indicated a substantial variation in 2-AP content among aromatic rice cultivars, with reported levels of 76.2 µg/L in Della, 156.1 µg/L in Jasmine and 87.4 µg/L in Basmati 370.

Biosynthesis Pathway of 2AP

The biosynthesis of 2-acetyl-1-pyrroline (2-AP) in rice is primarily associated with the polyamine degradation pathway, although the complete pathway and its regulation are not yet fully resolved (Yoshihashi *et al*., 2002; Chen *et al*., 2008; Prodhan and Shu, 2020). In this pathway, polyamines such as arginine, ornithine, proline, and putrescine serve as key nitrogen sources and are catabolized to form γ-aminobutyraldehyde (GAB-ald), mainly through the action of diamine oxidase on putrescine (Bradbury *et al*., 2008). GAB-ald represents a critical metabolic branch point, as its fate is determined by the functionality of the BADH2 enzyme.

In non-aromatic rice, functional BADH2 (encoded by *OsBADH2*) oxidizes GAB-ald into ã-aminobutyric acid (GABA), thereby suppressing 2-AP formation, whereas in aromatic rice, the non-functional BADH2 (encoded by *osbadh2*) leads to the accumulation of GAB-ald (Bradbury *et al*., 2008; Fitzgerald *et al*., 2009; Prodhan and Shu, 2020). The accumulated GAB-ald spontaneously cyclizes to Δ^1-pyrroline, which is a direct precursor of 2-AP and plays a central role in aroma formation (Chen *et al*., 2008). Δ^1-pyrroline is subsequently acetylated either by acetyl-CoA or by methylglyoxal, a glycolytic by-product, resulting in the formation of 2-AP (Costello and Henschke, 2002; Huang *et al*., 2008; Shelp *et al*., 2012). Thus, both enzymatic and non-enzymatic reactions involving polyamine degradation, glycolysis-derived methylglyoxal and BADH2 activity collectively contribute to 2-AP biosynthesis, although additional metabolites and regulatory steps are likely involved in determining aroma intensity in aromatic rice (Yoshihashi *et al*., 2002; Chen *et al*., 2008; Prodhan and Shu, 2020).

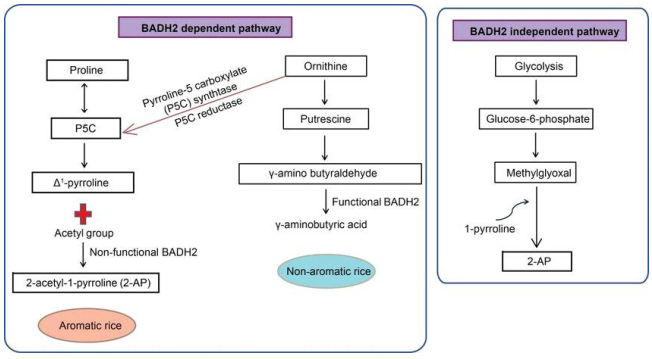


Fig. 1 : 2-Acetyl-1-pyrroline (2-AP) biosynthetic pathway (BADH2-dependent and BADH2-independent) for aroma production in aromatic rice (Behera *et al*., 2023).

Genetic control of aroma

Genetic regulation of aroma in scented rice: BADH2 gene and associated QTLs

Aroma in scented rice is primarily controlled by the BADH2 (OsBADH2) gene on chromosome 8, which regulates the biosynthesis of 2-acetyl-1-pyrroline (2-AP). The genetic basis of fragrance was first identified through the recessive *fgr* locus, later confirmed to encode BADH2 (Ahn *et al*., 1992; Bradbury *et al*., 2005). BADH2 consists of 15 exons and 14 introns and encodes a 503-amino-acid betaine aldehyde dehydrogenase. Fragrance results mainly from loss-of-function mutations, particularly an 8-bp deletion with three SNPs in exon 7 that introduces a premature stop codon and produces a truncated, non-functional enzyme (Bradbury *et al*., 2005; Bradbury *et al*., 2008; Chen *et al*., 2008).

Extensive allelic variation has been reported at BADH2 locus, including deletions in exon 2, large deletions between exons 4 and 5 and mutations in promoter, intronic, splice-site and 5′ -UTR regions, indicating substantial genetic diversity for aroma among fragrant rice germplasm (Shao *et al*., 2011; Shi *et al*., 2014; Ootsuka *et al*., 2014; Ghosh and Roychoudhury, 2020). Functional validation further showed that introduction of the dominant non-fragrant BADH2 allele suppresses aroma, confirming *badh2* as the principal determinant of fragrance (Bourgis *et al*., 2008; Chen *et al*., 2008; shi *et al*., 2008).

Besides BADH2, aroma intensity is quantitatively influenced by additional QTLs. Early mapping identified loci on chromosomes 4 and 12 (Lorieux *et al*., 1996), while studies in Basmati rice detected major QTLs on chromosomes 3 (aro3-1), 4 (aro4-1) and 8 (BADH2), suggesting oligogenic control (Amarawathi *et al*., 2008; Peng *et al*., 2018). The 'aro4-1' region contains OsBADH1, a BADH2 homolog with similar function but lower polymorphism and additional association with salinity tolerance, possibly representing a gene cluster affecting aroma expression (He *et al*., 2015; Peng *et al*., 2018; Prodhan and Shu, 2020). The *aro3-1* locus contributes minor complementary effects, and further loci on chromosomes 5 and 12, including OsGlyI, link methylglyoxal metabolism to fragrance formation (Amarawathi *et al*., 2008; Talukdar *et al*., 2017).

Several candidate genes participate in aroma biosynthesis pathways, notably OsBADH2, OsBADH1, glyoxalase genes and Δ^1-pyrroline-5-carboxylate synthetase (P5CS), which function in polyamine, proline and methylglyoxal metabolism (Huang *et al*., 2008; Pachauri *et al*., 2014; Kaikavoosi *et al*., 2015).

Transcriptomic analyses further indicated transcriptional regulation, with more than 26 transcription factor families-including WRKY, MYB, NAC, bHLH, bZIP, GATA and AP2-modulating aroma-related genes. Consistent expression of P5CS2, DAO5 and BADH2 with 2-AP accumulation highlights their roles as key nodes in the regulatory network (Imran *et al*., 2022; Bao *et al*., 2021).

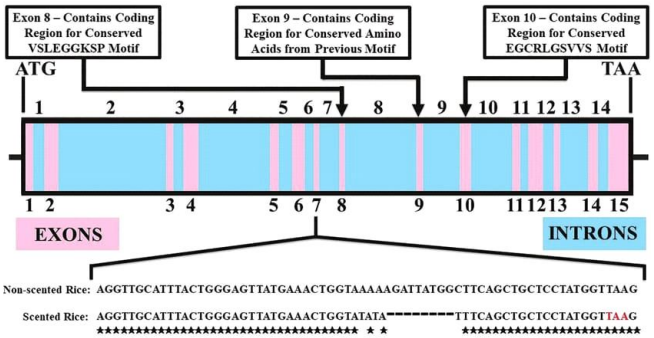


Fig. 2 : Structure of the *fgr* gene showing ATG, initiation codon, exons (15), introns (14) and the termination site (TAA) (Varatharajan *et al*., 2021).

Aromatic Rice in India

Aromatic rice in India comprises nearly 300 indigenous collections and is broadly classified into Basmati and non-Basmati types based on kernel dimensions such as kernel length, breadth and length/ breadth ratio before and after cooking (Table 1). Based on grain length, Indian aromatic rice types range from small (≤5.51 mm), medium (5.51–6.60 mm), long (6.61–7.51 mm), to very long (>7.51 mm), where long grains being characteristic mainly of Basmati types. Non-Basmati aromatic rice, which includes small to long-grained types, indicated its centre of diversity in the Himalayan foothills, eastern Indo-Gangetic plains and adjoining regions (Uttar Pradesh, Bihar and the Tarai region of Nepal) and includes well-known varieties such as Gobindbhog (West Bengal), Kalanamak (Uttar Pradesh), Joha (Assam), Ambemohar (Maharashtra), Jeerakasala and Gandhakasala (Kerala), many of which possess GI tags (Pachauri *et al*., 2010; Singh *et al*., 2000].

Basmati rice, indigenous to the Himalayan foothills, is characterized by long to very long slender grains, strong aroma, high kernel elongation after cooking, intermediate amylose content, distinct physio-chemical properties, and is taxonomically considered an intermediate group between indica and japonica (Ahuja *et al*., 2008). Importantly, while all Basmati rice is aromatic, not all aromatic rice qualifies as Basmati; a variety must satisfy the minimum quality standards prescribed under the Seeds Act, 1966 and the Export of Basmati Rice (Quality Control and Inspection) Rules, 2003. Based on these regulations, Basmati rice is classified into Traditional Basmati, consisting of six pure-line selections such as *Basmati-370*, *Type-3*, *Taraori Basmati*, *Ranbir Basmati* and Evolved Basmati, which includes improved varieties developed through hybridization using traditional Basmati parents, such as *Pusa Basmati-1*, *Pusa Basmati-1121*, *Pusa Basmati-1509*, *CSR-30* and *Punjab Basmati-3* (Sharma *et al*., 2021). Owing to its premium quality and export value, Basmati received GI registration in 2016, confined to seven Indian states-Jammu & Kashmir, Himachal Pradesh, Punjab, Haryana, Delhi, Uttarakhand and Uttar Pradesh-with APEDA and the Basmati Export Development Foundation playing key roles in quality regulation, seed certification, and export promotion.

Table 1 : Differentiation of Basmati and non-Basmati types.

Kernel dimension	Basmati type	Non-Basmati type
Kernel length	6.4-7.6 mm	5.2-5.4 mm
Kernel length/breadth ratio before cooking	3.5-5.6	3.3-3.5
Kernel length/breadth ratio after cooking	4.9-5.6	2.95-3.8
Elongation ratio of kernel length	1.7-1.83	1.4-1.57
Elongation ratio of kernel breadth	1.26-1.33	1.31-1.61

Table 2 : Minimum standard of Basmati rice quality traits.

Traits	Value
Average pre-cooked milled rice length	>6.61 mm
Average pre-cooked milled rice breadth	<2 mm
Average length/breadth ratio of pre-cooked milled rice	>3.5
Average cooked rice length	>12 mm
Average pre-cooked rice length/pre-cooked rice length (elongation ratio)	>1.7
Average volume expansion ratio	>3.5
Amylose content range	20-25%
Alkali spreading value range	4-7
Minimum brown rice recovery	76%
Minimum milled rice recovery	65%
Minimum head rice recovery	45%
Aroma	Present
Texture of cooked grain (without surface bursting of cooked rice kernel), non-stickiness, tenderness, good taste and mouth feel	Present

Conventional Breeding approaches

Pureline selection

Pure line selection (PLS) is the earliest and most widely used method for the improvement and purification of aromatic rice landraces. This approach was primarily adopted to stabilize aroma, grain quality and local adaptation by selecting superior individual plants from heterogeneous traditional cultivars and advancing them through repeated selfing. One of the earliest and most successful applications of PLS was in Indian Basmati rice, where systematic purification of traditional Basmati types during the early twentieth century led to the release of Basmati 370 in 1933, which subsequently became the genetic foundation for several aromatic rice breeding programmes in South Asia (Ahuja *et al*., 1995; Mann, 1987).

In India and Pakistan, pure line selection resulted in the development of several region-specific aromatic rice varieties such as Type-3, Basmati-217 and Kala Shah Kaku Basmati, which were valued for superior eating quality, strong aroma and export preference despite their relatively low yield potential (Sharma *et al*., 2021). Similar efforts were also successful in other Asian countries. In Thailand, farmer-led selection from the local landrace Khao Dawk Mali culminated in the release of Khao Dawk Mali 105 (KDML105), a premium-quality jasmine rice known for its soft texture and stable aroma (Somrith, 1996). In Bangladesh and Vietnam, pure line selection from indigenous aromatic landraces led to the development of varieties adapted to short duration and local agro-ecological conditions (Thinh *et al*., 1995).

Although, PLS has been highly effective in conserving and enhancing aroma and grain quality, its major limitation lies in the narrowing of the genetic base, which restricts adaptability and increases susceptibility to biotic and abiotic stresses. Additionally, the method is inherently time-consuming due to the requirement of several generations of selfing and evaluation before varietal stabilization (Ahuja *et al*., 1995).

Hybridization

Hybridization has been widely used to improve aromatic rice by combining the superior grain quality and aroma of traditional landraces with the high yield, semi-dwarf stature and improved plant architecture of non-aromatic varieties through pedigree selection, backcrossing and convergent breeding (Siddiq *et al*., 2012). Early progress was limited by poor combining ability, hybrid sterility and partial cross-incompatibility between aromatic and non-aromatic types, which were addressed through stepwise backcross and recombination strategies.

A major breakthrough came with the release of Pusa Basmati 1 in 1989, the first semi-dwarf, photo-insensitive, high-yielding Basmati developed from IR8, IR22, Taichung Native 1 and Basmati 370, yield potential of 5.0 t/ha. Subsequent hybridization produced Pusa Basmati 1121, characterized by higher yield, exceptional grain length, kernel elongation, strong aroma and later serving

Table 3 : Aromatic rice varieties developed through pure line selection.

Variety name	Ancestor / source population	Country	Key characteristics
Basmati 370	Traditional Basmati landrace	India	Strong aroma, long slender grains, excellent cooking quality, late maturity
Type-3 (Dehradun Basmati)	Selection from Basmati landraces	India	Superior grain quality, export preference, photoperiod sensitive
Basmati-217	Traditional Basmati population	India	Fine grain, stable aroma, moderate yield
Kala Shah Kaku Basmati	Local Kala Shah Kaku landrace	Pakistan	Exceptional eating quality, limited area cultivation
Khao Dawk Mali 105 (KDML105)	Khao Dawk Mali landrace	Thailand	Jasmine aroma, soft texture, premium export quality
Nang Huong	Local aromatic landrace	Vietnam	Stable aroma, good grain quality, local adaptability
BRRI dhan34	Local landrace Khaskani	Bangladesh	Short grain
Type 23	Kalasukhdas	India	Fine grain, good quality and high yielding
C435	Jeerega Sanna	India	Early maturing
3 distinct varieties	Jeerakasala	India	Higher yield potential
14 distinct varieties	Kalanamak	India	High yield potential
Type-9	Dimnepet	India	Better quality and high yielding

Table 4 : Aromatic rice varieties developed through hybridization.

Variety	Parents	Methods	Characteristics	References
Pusa Basmati-1	Basmati 370/Karnal Local	Convergent breeding	Dwarf, photo-insensitive and input responsive	Chandi and Sogi (2008)
Pusa Basmati 1121	Sister line of Pusa Basmati-1	Convergent breeding	Extra-long slender grains (9.00 mm), pleasant aroma, an exceptionally high cooked kernel elongation ratio of 2.5 (22.0 mm)	Singh *et al.* (2018)
Pusa Basmati-6	Pusa Basmati-1/ Pusa 1121	Pedigree	Semi-dwarf, high yielding	Singh *et al.* (2018)
Super Basmati	Basmati320/IR661	Pedigree	Long slender grain	Siddiq *et al.* (2012)
Kusuma Hashemi 2015	TN-1/Basmati 370	Pedigree	Long slender grain, aroma mild, higher yield potential	Hashemi (2015)
Haryana Basmati-1	Sona/Basmati 370	Pedigree	Long slender grain, resistant to neck blast, stem rot and WBPH	Singh *et al.* (2000)
Kasturi	Basmati 370/Karnal Local	Pedigree	Semi-dwarf, blast resistance	Arumugachamy *et al.* (1992)
Lateefy	IR 760-A1-22-2-3/ Basmati 370	Pedigree	Semi-dwarf, early maturing, higher yield potential, stemborer resistance	Bhatti and Soomro (1985)
Tainung Sen 20	Chianung Shi-pi 671178/ an F4 line	Pedigree	Strong aroma, higher yield potential, resistant to blast and BPH	Yang (1988)

as the genetic base for Pusa Basmati 6 and 1509 (Singh *et al*., 2014; Singh *et al*., 2018). Parallel efforts in Pakistan released semi-dwarf aromatic cultivars such as Lateefy (Bhatti and Soomro, 1985), while Thailand developed blast-tolerant Jasmine-type varieties like RD33 through backcross breeding (Supapoj *et al*., 2009).

Mutation breeding

Mutation breeding has long been employed to enhance genetic variability in crops, particularly when conventional breeding is limited by a narrow genetic base. Over the past six decades, induced mutagenesis using physical or chemical mutagens has been integrated with conventional methods to modify specific traits while maintaining the original genetic background (Ma *et al*., 2021). In aromatic rice, the strategy is especially useful as many traditional varieties possess superior aroma and grain quality but suffer from tall plant stature, lodging susceptibility, late maturity and poor tolerance to biotic and abiotic stresses (Singh *et al*., 2000; Sharma *et al*., 2021).

A well-known example is from Thailand, where gamma irradiation of the elite Jasmine cultivar Khao Dawk Mali 105 (KDML105) produced the useful mutants RD6 (waxy aromatic) and RD15 (early-maturing), released in 1977 and 1978, respectively (Vanavichit *et al*., 2018; Vemireddy *et al*., 2021). Together with KDML105, these varieties occupy nearly 70% of Thailand's rainfed and stress-prone areas and show stable yields under drought, salinity and acid sulfate soils, with tolerance to salinity levels of 2-6 dS m^{-1} (Jongdee *et al*., 2006; Vanavichit *et al*., 2018).

In India, mutation breeding generated useful mutants from traditional genotypes such as Kalimoonch-6, Bindli, Kamal Local, Type-9, NP-49, T-412, Kalanamak, Gobindbhog, Badshapasand and Basmati 370, with several lines showing dwarf stature, lodging resistance and early maturity (Singh *et al*., 2000; Sharma *et al*., 2021). The ICAR-NRRI maintains over 100 aromatic mutants, including released varieties, Geetanjali and ADT 41 derived from Basmati 370, while outside South Asia, the U.S. variety A-201 was developed from a Basmati-derived mutant, highlighting the broad applicability of induced mutagenesis (Ma *et al*., 2021; Sharma *et al*., 2021). Overall, the success of RD6, RD15 and Basmati-derived mutants demonstrates that mutation breeding effectively complements conventional aromatic rice improvement (Singh *et al*., 2000; Vanavichit *et al*., 2018; Ma *et al*., 2021).

Hybrid Breeding

Hybrid rice breeding became a major breakthrough after China demonstrated commercial heterosis in rice, achieving yields higher than conventional varieties. Although, initial research focused on non-aromatic types, efforts soon extended to fragrant and Basmati rice despite challenges related to aroma retention, grain quality, fertility restoration and reproductive compatibility (Virmani *et al*., 1998; Singh *et al*., 2000). In aromatic rice, limited availability of suitable parental lines, partial cross-incompatibility, and aroma dilution from non-fragrant backgrounds often resulted in poor seed set or sterility, necessitating careful parental selection and backcross-based introgression strategies (Virmani *et al*., 1998; Pradhan *et al*., 2006). In India, systematic breeding advanced with the development of Basmati-based cytoplasmic male sterile (CMS) lines using the wild abortive (WA-CS) system, where Pusa Basmati-1 was identified as a maintainer, enabling the development of CMS lines such as Pusa 3A, Pusa 5A and Pusa 6A (Pradhan *et al*., 2006; Basavaraj *et al*., 2009).

These CMS lines facilitated effective heterosis exploitation within the Basmati gene pool, leading to the successful cross of Pusa 6A with Pusa Rice Restorer 78 (PRR78) and the release of Pusa RH10, the world's first super-fine grain aromatic hybrid combining semi-dwarf stature, high yield, and acceptable Basmati grain quality (Basavaraj *et al*., 2009; Vemireddy *et al*., 2021). Concurrently, international programs, particularly at IRRI, developed CMS and restorer lines from fragrant backgrounds such as IR67684A, IR68280A, IR68281A, IR69617A, IR70372A and identified Basmati-type maintainers and restorers to strengthen recurrent backcross breeding and broaden the genetic base (Pradhan *et al*., 2006; Virmani *et al*., 1998). Collectively, these efforts advanced aromatic hybrid breeding from exploratory crosses to stable CMS–restorer systems and commercial Basmati-type hybrids while balancing heterosis, aroma expression and grain quality (Virmani *et al*., 1998; Basavaraj *et al*., 2009; Vemireddy *et al*., 2021).

Marker Assisted breeding

Marker-assisted breeding (MAB) has become a powerful strategy for improving aromatic rice by enabling precise introgression of target genes while preserving grain quality and aroma. Compared with conventional backcrossing, molecular marker–based selection shortens breeding duration and enhances efficiency, particularly for complex or difficult-to-phenotype traits such as aroma, disease resistance and abiotic stress tolerance (Shan *et al*., 2015; Peng *et al*., 2018). The availability of functional markers for the BADH2 gene has further accelerated the development of improved fragrant cultivars suited for large-scale cultivation.

Marker-assisted backcrossing has been widely used to overcome major biotic stress constraints in Basmati rice. In India, Pusa 1460 was developed from Pusa Basmati 1 through introgression of *Xa13* and *Xa21* for bacterial blight resistance (Gopalakrishnan *et al*., 2008), followed by Pusa Basmati 1718 with pyramided resistance (Singh *et al*., 2018). Additional bacterial blight–resistant aromatic lines such as IC-R28, IC-R32, IC-R42 and IC-R68 were also developed using similar marker-assisted strategies (Baliyan *et al*., 2018).

Gene pyramiding has enabled simultaneous improvement of multiple resistance traits. Varieties including Pusa 6B, Pusa Rice Restorer 78, Pusa 1121 and Pusa Basmati 6 were enhanced by incorporating combinations of *Xa13*, *Xa21*, *Pi54*, *Pi1*, *Pi5*, *Bph-3* and *Bph-18*, conferring resistance to bacterial blight, blast and brown planthopper (Basavaraj *et al*., 2009; Singh *et al*., 2011; Basavaraj *et al*., 2010; Gouda *et al*., 2013). Similarly, blast resistance in Mushk Budji was improved through introgression of *Pi54*, *Pi1*, and *Pita* genes (Khan *et al*., 2018).

In Thailand, molecular breeding improved Jasmine rice backgrounds such as KDML105 by incorporating tolerance to multiple stresses, resulting in varieties like HM80 (Sub1 for submergence tolerance), HM812 (*Xa21*, *xa5*, *xa33(t)*, *xa34(t)*, *qBB11* for bacterial blight resistance) and HM84, which combines *Sub1*, *Xa21*, *xa5*, *BphQ12*, *Bph32*, *Bph3* and *BLQ* for tolerance to drought, salinity, brown planthopper, bacterial blight and blast (Siangliw *et al*., 2003; Korinsak *et al*., 2009; Vanavichit *et al*., 2018; Vemireddy *et al*., 2021). Marker-assisted approaches also improved plant architecture and abiotic stress tolerance through introgression of *Sd1* in Kalanamak, *Pi9 + sd1* in Pusa Basmati 1637 × Ranbir Basmati recombinants and the Saltol QTL in Pusa Basmati 1 for salinity tolerance (Srivastava *et al*., 2019; Singh *et al*., 2018).

RNA Interference (RNAi)

RNA interference has been explored as a genetic engineering approach to induce aroma in rice by silencing or downregulating the BADH2 (OsBADH2) gene, which plays a central role in regulating the accumulation of 2-acetyl-1-pyrroline (2-AP), the key compound responsible for rice aroma. By suppressing BADH2 expression through RNAi constructs or microRNA (miRNA) incorporation, non-aromatic rice cultivars can be

converted into aromatic types with elevated 2-AP levels (Chen *et al*., 2012; Khandagale *et al*., 2020).

Experimental studies demonstrated that RNAi-mediated suppression of OsBADH2 can substantially enhance aroma expression; for example, a nearly 20-fold increase in 2-AP content was reported in the japonica rice cultivar *Nipponbare* using RNAi technology (Ashokkumar *et al*., 2020). However, complete silencing of the BADH2 gene is often not achieved, requiring the screening of large numbers of transgenic progenies to identify lines with stable and strong aroma expression (Peng *et al*., 2018). In addition, the application of RNAi-based aromatic rice is subject to stringent biosafety regulations, risk assessment protocols and extended certification procedures for transgenic crops, which currently limits its practical deployment in commercial breeding programs compared with conventional and marker-assisted approaches (Peng *et al*., 2018).

CRISPR/Cas9

The CRISPR/Cas9 genome-editing system has enabled rapid and precise improvement of rice grain quality through targeted mutagenesis, offering a powerful alternative to conventional and transgenic breeding approaches. Using this technology, the non-aromatic rice cultivar Zhonghua 11 was successfully converted into an aromatic type by targeted editing of the fragrance-related BADH2 gene, demonstrating the feasibility of directly inducing aroma in elite backgrounds (Shao *et al*., 2017). The flexibility of CRISPR/Cas9 to generate knock-out, knock-in and knock-down mutations, along with multiplex genome-editing capability, allows the manipulation of complex, multigenic pathways underlying grain quality traits such as aroma (Fiaz *et al*., 2019). Recent studies have further reported the development of novel BADH2 allelic variants using CRISPR/Cas9, leading to enhanced aroma expression without the introduction of foreign DNA, thereby highlighting its potential for efficient aromatic rice improvement (Ashokkumar *et al*., 2020).

Economic importance of Aromatic rice in India

India's aromatic rice, particularly Basmati, plays a significant role in the country's agricultural export economy. In the recent fiscal year, 2024–25 (April–March), India exported around 60.65 lakh tonnes of Basmati rice valued at about ` 50,312 crore (nearly $5.87 billion), marking growth in both volume and value compared to the previous year, and reaching over 154 export destinations worldwide. Saudi Arabia, Iraq and Iran have consistently been the largest buyers by quantity, with other important markets including the UAE, Yemen, USA, UK, Kuwait, Oman and Qatar. This strong demand underscores India's dominance in premium aromatic rice trade and helps sustain higher foreign exchange earnings for the country's rice sector.

India's position as a leading aromatic rice exporter has also strengthened amid broader global rice trade expansion. Recent statistics indicated record or near-record export volumes of basmati rice-exceeding 6 million tonnes in 2024 with a trade value above $6 billion and exports growing to more than 150 countries, highlighting the rice's global acceptance and the economic benefit it provides to farmers, millers and exporters. Middle Eastern countries remain core markets, but significant purchases also come from Western markets like the USA and UK. Continued diversification of export destinations and sustained quality improvements are likely to further enhance India's aromatic rice earnings in coming years.

Future Prospects

The future of aromatic rice breeding centres on combining premium grain quality with high yield, stability, and resilience. Although, aromatic rice fetches a high market price due to its aroma, cooking quality, grain elongation, and taste, most traditional fragrant varieties—particularly short- and medium-grain types-remain low yielding and stress sensitive. Earlier breeding programs largely focused on Basmati and Jasmine types, leading to the neglect of vast indigenous and wild aromatic germplasm. Renewed emphasis on locally adapted landraces and wild relatives offers strong potential to widen the genetic base, discover new aroma-related alleles and improve resistance to biotic and abiotic stresses while preserving region-specific quality traits.

Recent advances in functional genomics, metabolomics and molecular breeding have improved understanding of aroma biology, showing that 2-acetyl-1-pyrroline (2-AP) interacts with multiple volatile compounds and grain quality genes. Marker-assisted selection, genomic selection, and genome editing tools such as CRISPR/Cas9 enable precise improvement of fragrance and quality traits directly in high-yielding backgrounds, reducing breeding time and minimizing linkage drag. These approaches allow the development of aromatic rice varieties that combine high yield, superior quality and adaptability, ensuring sustainable production, farmer profitability and expanded domestic and global markets.

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