Journal of Agricultural Sciences (Tarim Bilimleri Dergisi) 2025, 31 (4) : 873 – 891 DOI: 10.15832/ankutbd.1573413

Journal of Agricultural Sciences
(Tarim Bilimleri Dergisi)

J Agr Sci-Tarim Bili
e-ISSN: 2148-9297
jas.ankara.edu.tr

JAS

Decoding the Grain Aroma in Rice (*Oryza sativa* L.): Current Progress and Prospects for Improvement

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ARTICLE INFO
Review Article
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Received: 25 October 2024 / Revised: 20 April 2025 / Accepted: 19 May 2025 / Online: 30 September 2025

Cite this article
Rani M H, Hasibuzzaman A S M, Rahman M H S (2025). Decoding the Grain Aroma in Rice (*Oryza sativa* L.): Current Progress and Prospects for Improvement. *Journal of Agricultural Sciences (Tarim Bilimleri Dergisi),* 31(4):873-891. DOI: 10.15832/ankutbd.1573413

ABSTRACT

Aromatic rice is a distinct category of rice because of its pleasant fragrance. Basmati and Jasmine are the most popular types of aromatic rice in the global market. Short-grain aromatic rice cultivars of South and Southeast Asia are also popular but still need to be fully explored. Many researchers have attempted to explore the origin of aromatic rice, but it is still being clarified. Researchers depicted that evolutionarily aromatic rice demonstrates a close association with the *Japonica*-type gene pool and could be evolved in the Himalayan foothills through a natural hybridization between domesticated *Japonica* and wild rice. Genetics and environment intricately interact to control the formation and accumulation of aromatic compounds in rice grain. Although several candidate gene/QTLs for grain aroma have been identified, the *fgr* gene mapped on chromosome 8 as *BETAINE ALDEHYDE DEHYDROGENASE 2* (*BADH2*) encoding an oxidoreductase enzyme betaine aldehyde dehydrogenase, which oxidizes γ-aminobutyraldehyde (GAB-ald) and produces γ-aminobutyric acid (GABA), is considered as the major gene for grain aroma in rice. The loss of function of *BADH2* inhibits the GABA production and enhances the conversion of GAB-ald into 2-acetyl-1-pyrroline (2AP). 2AP is considered as one of the major fragrance components in rice grain. Being a volatile component, 2AP accumulation in rice grain is highly influenced by the environmental factors and crop management practices as well. Cool temperature and low humidity are good for the accumulation of volatile fragrance components in rice grain. Low yield, lodging and disease susceptibility are major constraints in commercial cultivation. Improving the agronomic performance and disease resistance are the major breeding objectives of aromatic rice breeding. Combining conventional, mutation, and molecular breeding methods could be a better solution to develop lodging-resistant and higher-yielding aromatic rice varieties. This review focused on the current progress in aromatic rice research and prospecting the future research programs.

Keywords: Aromatic rice; *BADH2,* γ-aminobutyraldehyde (GAB-ald), γ-aminobutyric acid (GABA), 2-acetyl-1-pyrroline (2AP)

1. Introduction

Rice (*Oryza sativa* L.) is one of the oldest domesticated crops that serve as the staple food for more than half of the world's population (Meyer & Purugganan 2013). The consumer demand for premium-quality rice is increasing globally. Good quality rice is ascertained by its physical appearance, cooking, sensory qualities, milling quality, and nutritional value of grains (Fitzgerald et al. 2009). Grain aroma is considered as the sensory property, and this trait gives the rice a distinct position among consumers. It was selected as the most attractive quality trait during domestication and maintained by specific cultures (Meyer and Purugganan 2013). The first evidence of aromatic rice can be found in 400 BC (Vemireddy et al. 2021), and since then, aromatic rice cultivars received ever-increasing attention. This particular sub-group of *Oryza sativa* is genetically related to the temperate Japonica and tropical Japonica-type rice varieties (Kovach et al. 2009). Fragrance, appearance, and unique taste make aromatic rice premium in the market. Basmati and jasmine-type aromatic rice varieties are most popular in the global markets, and these fetch high prices compared to the non-aromatic rice for their exclusive qualities. The demand for aromatic rice has increased dramatically in the last decades. In addition to Basmati and Jasmine types, many short-grain-type aromatic rice cultivars are being grown and consumed in South and Southeast Asia (Pachauri et al. 2010). The global market for aromatic rice continues to expand, driven by trade policies, consumer preferences, and breeding advancements. To ensure long-term market stability challenges such as export restrictions, climate variability, and evolving quality standards must be addressed.

Aromatic rice grains contain hundreds of chemical components, many of which are responsible for the most attractive and distinctive fragrance (Verma et al. 2018). 2AP, a heterocyclic derivative, is the potent volatile flavor component among these chemical components. Besides 2AP, some other amine heterocyclic components have recently been reported as potential contributors to the pleasant fragrance (Daygon et al. 2017). Genetically, 2AP accumulation in rice is controlled by a truncated allele of *BADH2* (Chen et al. 2008). Different environmental factors and management practices also affect flavor components' intensity. Temperature, humidity, and soil-water management practices impact on the strength of flavor components in aromatic rice (Monggoot et al. 2014).

Before the 21st century, scientists and farmers mainly focused on increasing the rice grain yield; therefore, complex questions like grain aroma and quality improvement should have been addressed. Still, there is enough enthusiasm among the farmers who nurtured and produced local aromatic rice cultivars. These local landraces are poor yielders and durable as well as susceptible to lodging and photo-sensitive in nature (Singh et al. 2000). In addition, all rice diseases, including the most common ones like bacterial leaf blight (BLB) and blast, can affect aromatic varieties severely (Raina et al. 2019). Hence, prior efforts mainly concentrated on developing semi-dwarf, photo-insensitive, high-yielding fragrant rice types without sacrificing their pleasing scent and grain quality.

The earlier attempts to introgress a semi-dwarf trait in aromatic rice cultivars met little success due to inter-group cross incompatibility, which resulted in hybrid sterility and reduced variants (Singh et al. 2000). Again, the lack of proper selection criteria and selection of multiple objectives for aromatic rice breeding programs led to lesser success in aromatic rice research (Kush & Juliano 1985). Nonetheless, researchers are better equipped to plan and implement effective attempts to improve aromatic rice now that they can access to more data regarding the genetic and biochemical basis of grain aroma and other grain quality attributes. This review aims to highlight the current progress in aromatic rice research focusing on the genetic and biochemical basis of grain aroma, expound the past breeding success, and define the future breeding strategies to improve aromatic rice further.

1.1. Genetic distinctness and evolutionary biology of aromatic rice

Historically rice cultivars are classified into two main sub-groups: *Indica* and *Japonica* sub-species (Ikehashi 2009). But there is a debate on the origin of these two sub-species. Two popular hypotheses divulge the origin of rice and way of differentiation into two ecotypes. The single origin model proposes that these two sub-species originated from the same source; the wild perennial *Oryza rufipogon* (Oka & Morishima 1982), and the multiple origin model suggests that *Indica* and *Japonica* sub-species evolved independently from two different sources. And these two ecotypes were hybridized naturally with each other in the way of their domestication (Sang & Ge 2007). Isozyme and whole genome sequencing data distinguished rice into several sub-groups such as *Indica*, *Tropical Japonica*, *Temperate Japonica*, *Aus,* and *Aromatic* (Glaszmann 1987; Li et al. 2014; Wang et al. 2014). Phylogeny analysis based on Single nucleotide polymorphism (SNP) uncovered that the aromatic sub-population is closely related to *Japonica* type varietal group. Several fragrant rice cultivars fall into *Indica* sub-population which includes the popular Jasmine rice of Thailand. This intricate relationship of the Aromatic group with the other sub-populations indicates its complex evolutionary history. The center of diversity of aromatic rice cultivars across the Himalayan foothills (Pachauri et al. 2010) associates it with the *Indica* type. However, it has distinct features which are closer to the *Japonica* type. Thus, it might be an in-between type of *Indica* and *Japonica* (Civáň et al.2019). Haplotype analysis of the aroma gene *BADH2* exposes that it originates from the *Japonica* type and later this trait was introgressed into the *Indica* type. When entirely domesticated *Japonica* arrived in the Indian sub-continent, it was naturally hybridized with a local wild relative of *Aus* rice and then aromatic rice was evolved (Pachauri et al. 2010; Civáň et al. 2019) and later it was spread to other parts of the world. Thereafter, the aroma gene was introgressed into the *Indica* type rice cultivars in the way of domestication. A hypothetical model for the evolution of aromatic rice has been illustrated in Figure 1. The model is theorized based on multiple origin of rice domestication hypothesis and it explicates the drift of the aroma gene from *Japonica* type rice cultivars to other types.

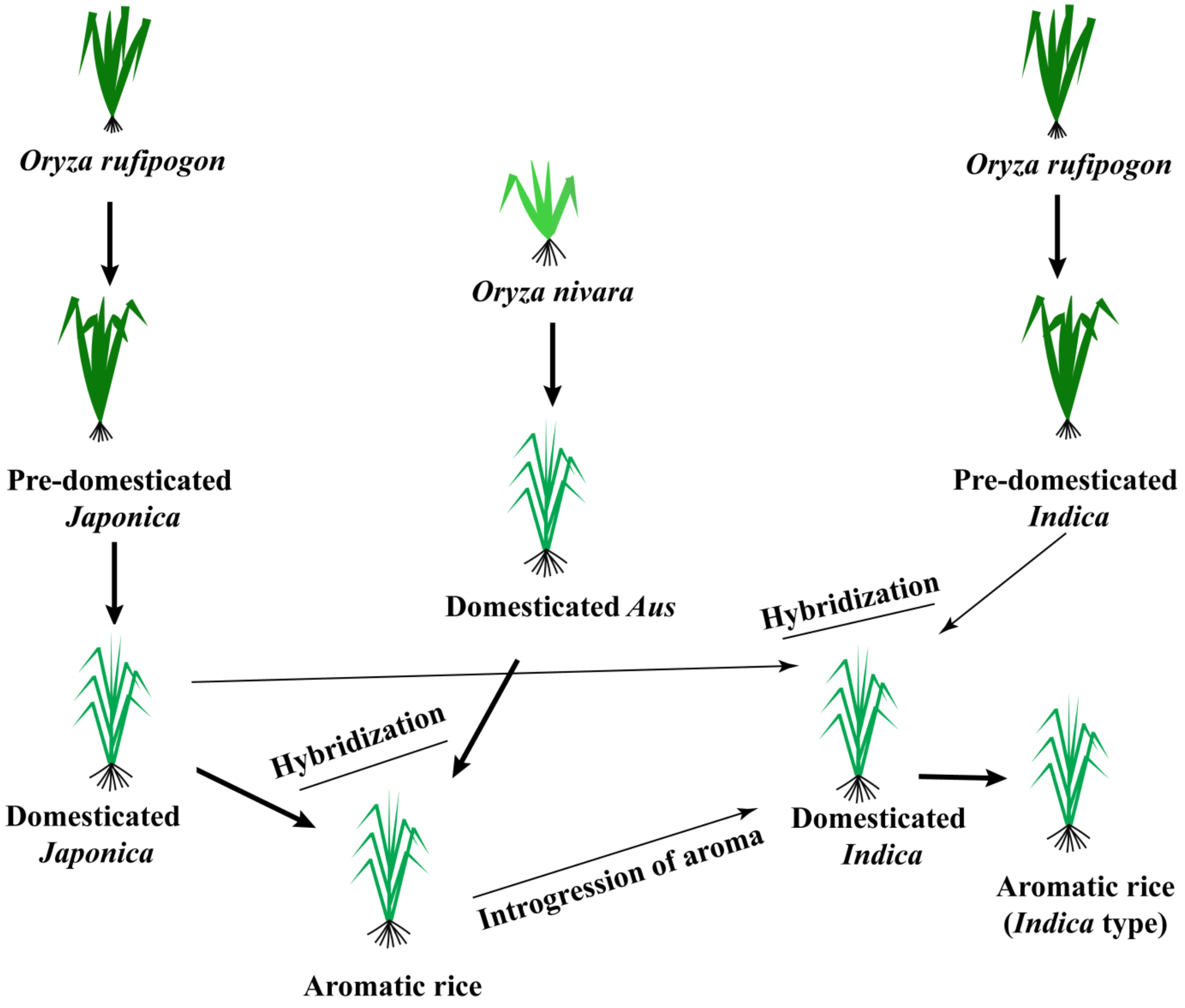

Figure 1- A hypothetical model illustrating the evolution of aromatic rice

1.2. The chemistry of rice grain aroma and its biosynthetic pathway

Hundreds of chemical components including alcohols, pyridines, aldehydes, esters, ketones, phenols, etc., have been detected in the aromatic rice grains (Verma & Srivastav 2018). Among these complicated compounds, the most prominent compound responsible for the characteristic aroma is 2AP. This heterocyclic compound is highly volatile with a very low threshold level. Non-aromatic rice cultivars also contain 2AP but at very low levels. It is found in all tissues with higher abundance in the young and healthy rice plant leaves except the root (Chen et al. 2010; Gay et al. 2010). The extracting method of 2AP requires heating (Bergman et al. 2000). Therefore, it could be assumed that 2AP may be the product of Millard reaction where a two-carbon sugar fragments acylates 1-pyrroline during heating (Fitzgerald et al.2008). But the case is that 2AP forms in the grains biochemically in the rice plant; even cooking or postharvest processing do not have any role. As an N-heterocyclic element, 2AP contains a ring structure of 1-pyrroline, making the combination vastly unstable. In this pyrroline ring, acetyl group replaces the hydrogen atom at position 2. In addition to 2AP, other volatile compounds such as pyrrole, 2-acetylpyrrole, hexanal, benzaldehyde, 1-pyrroline, 2- acetyl-L-pyrroline (E, E)- 2,4-decadienal, 4-vinylphenol, 2-amino acetophenone, decanal, octanal, 6-methyl-5-oxo-2,3,4,5-tetrahydropyridine (6M5OTP), 2-amino acetophenone, 4,5-epoxy-(E)-2-decenal, nonanal etc. have been identified in aromatic rice varieties as a contributor of flavor production (Jezussek et al. 2002; Daygon et al. 2017; Phitaktansakul et al. 2022). The compound 6M5OTP is a structural isomer of 2AP and contributes in developing pleasant aroma in rice. 2-acetylpyrrole gives sweet aroma in cooked rice. Hexanal gives grassy and fruity flavor and benzaldehyde provides almond-like sweet nutty flavor (Bergman et al. 2000). All these volatile compounds have increased level in aromatic rice compared to non-aromatic. Nevertheless, the metabolic pathways associated with these volatile compounds and their relationship with 2AP remain insufficiently elucidated.

The biosynthetic pathway of 2AP is still insufficiently deciphered, with key enzymatic steps and regulatory mechanisms yet to be fully elucidated. Moreover, involvement of other secondary metabolites may provide more insights into the mechanisms of developing aroma with varying intensities. Furthermore, 2AP in rice is synthesized through the polyamine degradation pathway (Yoshihashi et al. 2002; Chen et al. 2008). Polyamines such as proline, ornithine and arginine are catabolized to produce putrescine which is the substrate of the enzyme Diamino Oxidase (DAO) (Bradbury et al. 2008). DAO oxidizes putrescine and produce GAB-ald; the immediate precursor of GABA. Depending on the function of BADH2 enzyme, the fate of GAB-ald is ascertained into two possible ways (Fitzgerald et al. 2009; Prodhan & Qingyao 2020). Functional aldehyde dehydrogenase oxidizes GAB-ald into GABA. Contrarily, non-functionality enhances the accumulation of GAB-ald rather than oxidized into GABA in aromatic rice. GAB-ald cyclizes to Δ^1-pyrroline spontaneously. Then Δ^1-pyrroline is acetylated by acetyl CoA (Costello & Henschke 2002) or Methylglyoxal (MG) (Huang et al. 2008) to form 2AP. MG is generated during the process of glycolysis as a by-product (Shelp et al. 2012). It functions as a signalling molecule at low concentrations and becomes toxic to plant cells at high concentrations.

Another possible pathway of 2AP biosynthesis encompasses the production of Δ^1-pyrroline-5-carboxylate (P5C) (Huang et al. 2007; Kaikavoosi et al. 2015; Li et al. 2017). P5C is an intermediate substrate for the biosynthesis as well as the catabolism of proline and it is produced through the glutamate and ornithine degradation pathways (Sánchez et al. 2002; Hayat et al. 2012). In glutamate degradation pathway, Δ^1-Pyrroline-5-Carboxylate Synthetase (P5CS) catalyzes glutamic acid and produce Glutamic γ-Semialdehyde (GSA) (Mezl & Knox 1976; Hien et al. 2003). After the formation, GSA automatically cyclizes into P5C (Chen et al. 2021). In ornithine pathway, ornithine is converted to P5C through the process of transamination where Ornithine Aminotransferase (OAT) acts as the catalyst (Anwar et al. 2018). In both pathways, P5C could be degraded to amino acid glutamate through the dehydrogenase activity of Δ^1-Pyrroline-5-Carboxylate Dehydrogenase (P5CDH) (Szabados & Savouré 2010) or it could be reduced by the catalyst Δ^1-Pyrroline-5-Carboxylate Reductase (P5CR) (Székely et al. 2008; Liu et al. 2018) and form proline. Once more, proline could be degraded and converted to P5C through the Proline Dehydrogenase (ProDH) enzyme activity (Guo et al. 2020; Luo et al. 2020). Perhaps, P5C is converted to 2AP through two potential ways. P5C could directly react with MG to produce 2AP or it could be degraded to Δ^1-pyrroline first which is further acetylated by acetyl CoA or MG and finally produce 2AP. Therefore, it is speculated easily that Δ^1-pyrroline, acetyl CoA or MG are the immediate precursor of 2AP. Contrarily, it could be hypothesized that 2AP functions as one of the detoxifying agents of MG. A schematic diagram represents the probable biosynthetic pathway of 2AP in rice has been described in Figure 2.

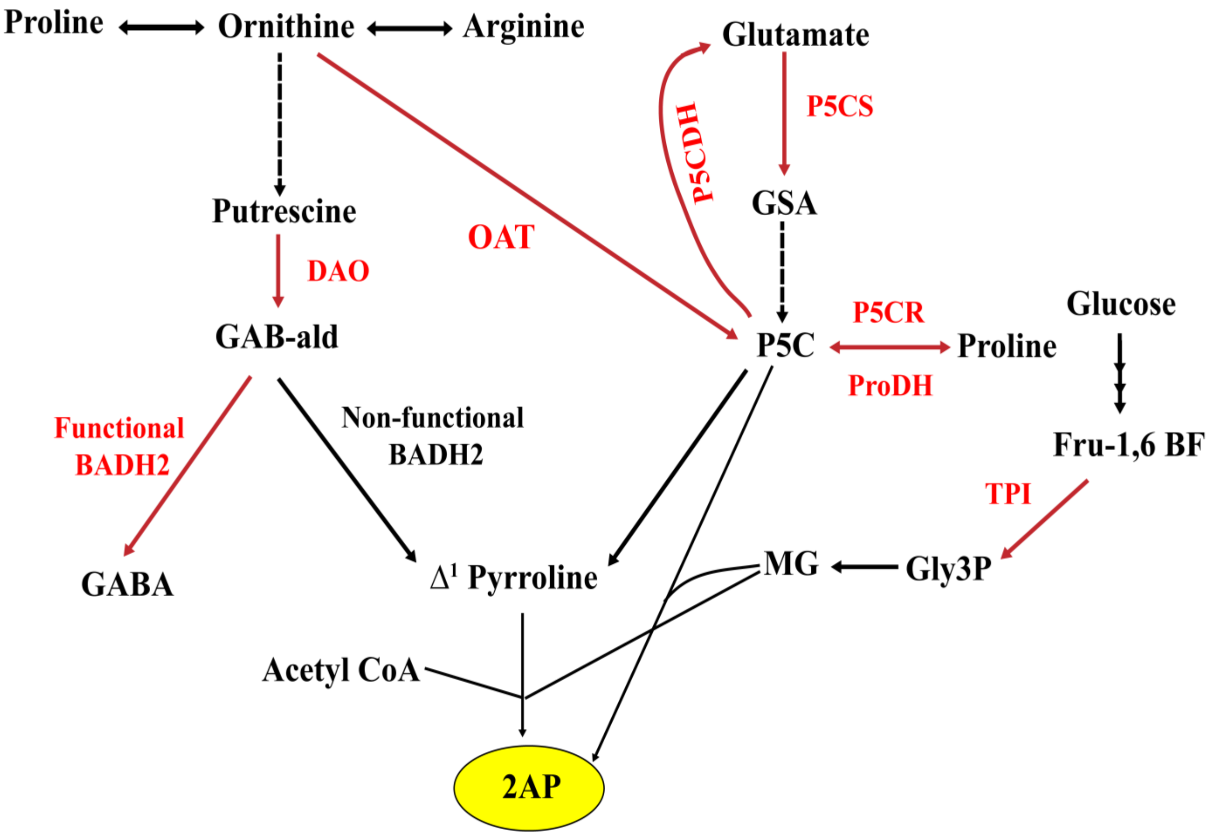

Figure 2- Schematic diagram of 2AP biosynthetic pathway

2AP, 2-acetyl-1-pyrroline; GABA, Gamma aminobutyric acid; GAB-ald, Gamma aminobutyraldehyde; P5C, Δ^1-pyrroline-5-carboxylate; P5CR, Δ^1 -pyrroline-5-carboxylate synthetase; BADH2, Betaine aldehyde dehydrogenase 2; DAO, Diamine oxidase; OAT, Ornithine aminotransferase; ProDH, Proline dehydrogenase; P5CS, Δ^1 -pyrroline-5-carboxylate synthetase; P5CDH, Pyrroline 5 Carboxylate Dehydrogenase; GSA, Gamma glutamyl semialdehyde; TPI, Triosephosphate isomerase; Gly3P, Glyceraldehyde-3-phosphate; MG, Methylglyoxal; Fru-1,6BP, Fructose-1,6-biphosphate

1.3. Genetic dissection for grain aroma in rice

Rice grain aroma is an intricate trait that is strictly controlled by genetic factors and highly influenced by environment as well. To clarify the genetic basis of grain aroma in rice, many investigations have been conducted so far. Due to the differences in methods of quantifying the aroma components the earlier reports were conflicting. Some researchers reported it as monogenic and controlled by a recessive or dominant gene while others assumed it as controlled by several recessive or dominant genes (Jodon 1944; Reddy & Reddy 1987; Tsuzuki & Shimokawa et al. 1990). The application of molecular techniques directed to the inference that a single recessive nuclear gene controls the grain aroma in rice. Application of Restriction Fragment Length Polymorphism (RFLP) molecular marker detected the fragrance (*fgr*) loci on chromosome 8 in a Near Isogenic Lines (NILs) population (Ahn et al. 1992). This result was more validated in a doubled haploid population by applying four types of molecular markers in combination with a standard phenotyping method (Lorieux et al. 1996). Genetic mapping in a transgressive segregant population constructed from a hybridization between scented and non-scented rice genotypes identified the candidate *fgr* gene as *BADH2* on the q- arm of chromosome 8 (Bradbury et al. 2005). The results were further validated in Recombinant Inbred Lines (RILs) developed through the hybridization between scented and non-scented rice varieties (Bourgis et al. 2008; Chen et al. 2008). The locus ID of *BADH2* is LOC_Os08g32870, with a genomic sequence length of 6268 nucleotides. It has 15 exons and 14 introns. The full-length *BADH2* has a 1512 bp coding sequence encoding 503 amino acid residuals (www.gramene.org; https://rice.uga.edu/). It has one domain *viz.* aldehyde dehydrogenase (PF00171; https://www.ebi.ac.uk/). The aldehyde dehydrogenase domain has two conserved sites *viz.* aldehyde dehydrogenases glutamic acid active site (PS00687) and aldehyde dehydrogenases cysteine active site (PS00070) (https://prosite.expasy.org/). In aromatic rice, this gene is mutated and produces a premature stop codon that results in a truncated protein.

The aroma gene has several allelic variations derived through a variety of mutations occurring in the same gene (Kovach et al. 2009). Three bases substitutions and eight bases deletions in exon 7 and 7 bp deletion in the exon 2 were reported in the non-functional *badh2* (Bradbury et al. 2005; Shi et al. 2008). Haplotype analysis of *BADH2* allele from a mixed panel of *Oryza sativa* and *Oryza rufipogon* identified eight putatively mutated alleles of *BADH2* gene deletions, insertions, or substitution in exon 1, exon 10, exon 13, and exon 14. Another type of allelic variation was identified with a deletion in exon 12 (He & Park 2015). A discontinuous deletion on exon seven was identified in a RIL population derived through the hybridization between scented and non-scented Basmati rice varieties. But this deletion was insufficient to get a strong aroma as some of the RILs had mild or no aroma. Some Japanese aromatic rice varieties possess a SNP substitution between exon 1 and intron 1 of *BADH2* rather than the 8 bp deletion in exon 7 (Ootsuka et al. 2014). Sequence analysis in the aromatic rice variety ‘Zaimiaoxiangnuo’ identified a big deletion between exon 4 and 5 (Shao et al. 2011). This type of big deletion was also identified between the same exons during haplotype analysis of more than 500 aromatic rice accessions (Shao et al. 2013). Deletion, insertion, or substitution in the promoter and untranslated (UTR) region of *BADH2* can also enhance the production of fragrance components without any mutation in the coding region (Shi et al. 2014; Bindusree et al. 2017; Khandagale et al. 2020).

Although *badh2* is considered as a major gene controlling this quality trait in rice but the intensity of aroma in different aromatic rice varieties are not same which implies the existence of other genes/QTL or other epigenetic factors in rice which are also contributing to this quality trait (Fitzgerald et al. 2008). Haplotype analysis of Badh2 gene demonstrated a correlation between specific alleles and grain aroma. The Badh2-E7, linked to strong aroma, was present in a subset of elite aromatic rice varieties. The absence of this allele in other aromatic rice varieties indicate the presence of other factors in aroma development and 2AP is not the sole determinant of grain aroma (Chan-In et al. 2020). Transcriptomics, whole genome resequencing, genome wide association and bi-parental mapping results revealed the presence of minor effect aroma QTL along with *badh2* on the chromosome 1, 2, 3, 4, 8 and 12 (Lorieux et al. 1996; Amarawathi et al. 2008; Pachauri et al. 2014; Vemireddy et al. 2015; Daygon et al. 2017; Zinati & Delavari 2019; Kishor et al. 2020). Moreover, up-regulation or down-regulation of genes/transcription factors involved in the biosynthetic pathway of 2AP may impact on the intensity of fragrance in aromatic rice. For example, overexpression of *P5CS* and *DAO* increases the proline and GAB-ald accumulation, respectively and subsequently increases the intensity of fragrance (Huang et al. 2008; Kaikavoosi et al. 2015; Bao et al. 2021). Sashankar et al. 2024 proposed two additional genes from the amine metabolic pathway as the potential candidates for fragrance in Kon Joha rice. The contribution of these minor-effect QTL and genes to the biosynthesis of aroma volatile compounds in aromatic rice needs more clarification. Epigenetic modifications and environmental factors may also play a significant role in regulating aroma development.

1.4. Impacts of environmental factors and management practices on aroma formation in rice

Environmental factors and crop management practices highly influence aroma formation in rice grains. Temperature, soil moisture, growing area, and fertilizer management majorly influence the formation of volatile aroma compounds in rice grains (Figure 3).

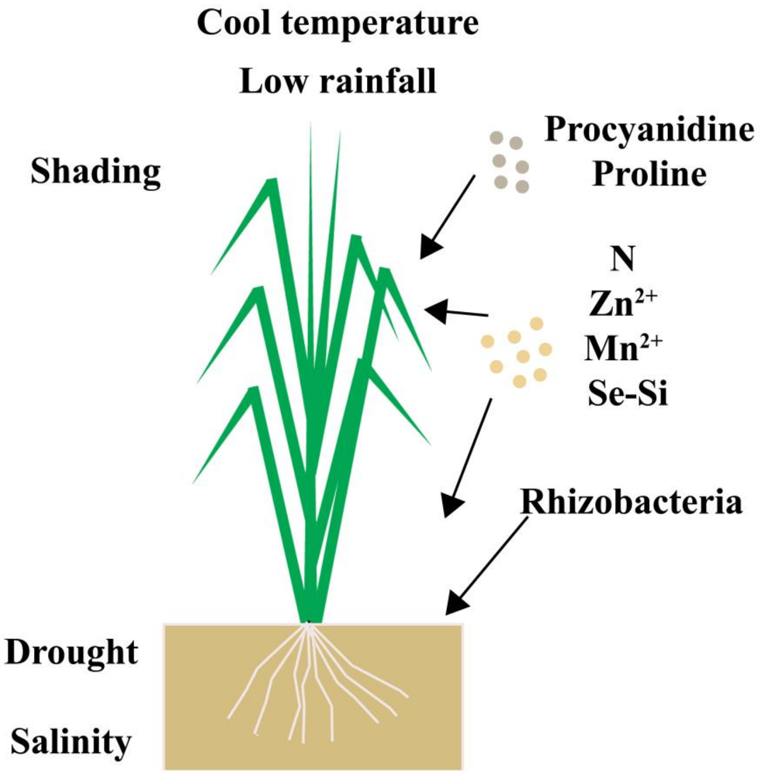

Figure 3- Environmental factors and management practices affecting aroma accumulation in aromatic rice

Temperature plays a vital role in the accumulation and retention of 2AP during grain formation as well as storage. High temperature causes rapid volatilization of 2AP. Moderately cool temperature (20-25 °C) during ripening can increase the 2AP content in the grain (Singh et al. 2000; Okpala et al. 2020). Prodhan et al. 2017 found more volatile compounds and maximum aroma score in rice genotypes grown at 25 °C. Cultivating at high altitude, low rainfall (Sansenya and Wechakorn, 2021) and harvesting earlier can increase the 2AP content in rice grain (Itani et al. 2004). Land at high altitude with less rainfall may often suffer from drought which increases the proline and 2AP production in plants. Similarly, air drying and low storage temperature can retain the 2AP in rice grain for a longer period (Yoshihashi et al. 2005). Storing for a long time also reduces the 2AP content. High temperature during storage causes fat rancidity which is negatively related to 2AP. Aromatic rice grown at high altitude upregulates the expressions of genes linked to fatty acid degradation and linoleic acid metabolism and downregulates the lipid biosynthesis genes leading to increased production of aromatic volatile compounds (Fayaz et al. 2024). If the 2AP forms before starch structure formation, it makes a complex with starch. During cooking this starch complex breaks down at high temperature and 2AP is released and then pleasant aroma comes from the rice (Yoshihashi et al. 2005). However, during storage the degradation process of volatile aroma compounds at molecular level is not fully elucidated.

Light intensity also impacts on the formation of volatile compounds in plants. It was observed that shading can modify the 2AP formation in rice grain (Mo et al. 2015; Shuochen et al. 2023). Shading in rice plant increases the abscisic acid (ABA) synthesis. The ABA regulates the enzymatic activity of P5CS and ProDH which results in the increased production of P5C and ultimately higher 2AP. Dense planting could create the shading environment in the rice field and increasing the 2AP in the grain. But at the same time shading decreases the photosynthetic activity of the leaf which results in decreased grain yield. GABA and Zn application combined with shading can increase the grain yield to some extent which balances the higher 2AP production with grain yield (Xie et al. 2021). Moreover, GABA can enhance different anti-oxidative activity by increasing the Mn^{2+} level in plant system.

2AP content in the rice grain increases if the crop is cultivated under drought or saline condition. Proline is believed to be an important precursor of 2AP formation which is reported to be increased during drought stress in the plant system (Luo et al. 2021; Gui et al. 2022). But it was observed that during drought proline is increased but the P5Cs and ProDH enzyme activity as well as *P5CS* and *ProDH* transcript level decreases. At the same time, it was reported that the enzyme activity of DAO and transcript level of *DAO4* were increased during drought. It could be assumed that under drought stress aromatic rice produces more 2AP from the oxidation of putrescine. When the drought stressed rice plants are recovered with irrigation water, the enzymatic activity of P5CS and ProDH are increased which enhances the production of more 2AP from the accumulated proline. Moderate drought could be recommended for the higher accumulation of 2AP as severe drought may cause complete crop losses (Luo et al. 2021). From this point of view, it could be concluded that alternate wetting and drying (AWD) method of irrigation might be a good suggestion for the higher accumulation of 2AP combined with higher grain yield (Ashraf et al. 2022).

Soil salinity increases the enzymatic activity of P5CS and DAO, transcript level of *P5CS* and *DAO* and the level of proline, ornithine, and methylglyoxal in the aromatic rice (Gay et al. 2010; Poonlaphdecha et al. 2012; Renuka et al. 2022). Increased proline and ornithine levels enhance the synthesis of P5C which reacts with methylglyoxal and accumulates more 2AP.

Some rhizobacteria are known to be a synthesizer of 2AP in their system. This type of bacteria comprises *Pseudomonas*, *Enterobacter* and *Acinetobacter* and they can grow at the root zone of rice crop. These bacteria are reported to increase the 2AP content in rice grain (Deshmukh et al. 2016; Chinachanta et al. 2021). Among these rhizobacteria some bacteria such as *Enterobacter* are reported to have the capability to alleviate the salinity effect in the soil (Prittesh et al. 2020). This type of bacteria could be produced commercially and applied in the aromatic rice grown under saline soils.

Proper management of micro and macro nutrients may also intensify the 2AP formation in rice grain. Nitrogen (N) enhances the proline and pyrroline content in plants (Mo et al. 2019). It also increases the enzymatic activity in proline synthesis and degradation pathways. Therefore, higher application of N fertilizer during tillering stage has an impact on the increased synthesis of 2AP. The source of N fertilizer has also an impact on 2AP formation (Potcho et al. 2021). If NH_4^+ containing fertilizer such as urea is applied, it is readily absorbed by the plant system and assimilated into amino acids. However, N application in the form of NO_3^- may delay its assimilation into amino acids as it needs to convert into NH_4^+ first. In addition, K^+ improves the N absorption efficiency. Micronutrients such as Zn^{2+} and Mn^{2+} also increase the 2AP accumulation in rice grain by modulating the enzymatic activity in different 2AP biosynthetic pathways (Li et al. 2016; Shuochen et al. 2023). Other nutrients for instance, Selenium (Se) and Silicon (Si) can increase the 2AP content by modifying the enzymatic activity (Liu et al. 2020; Mo et al. 2017). Se might increases plant’s vulnerability towards lodging but Si could give stiffness to the plant. Furthermore, Si in the rice husk reduces the moisture losing rate at grain filling which also improves the 2AP content. Exogenous application of GABA (Xie et al. 2020, Xie et al. 2019), proline (Luo et al. 2020), and flavonoids like procyanidins (Luo et al. 2022) are reported to be an enhancing agent in increasing the 2AP content in rice grain. Finally, it might be concluded that dense planting, maintaining moderate drought condition in the field through AWD, timely and judicious application of N fertilizer as well as other micronutrient containing fertilizer and planting in cool environment could be suggested to increase the 2AP content and to balance the grain yield in the aromatic rice variety.

1.5. Approaches for aromatic rice breeding

Aromatic rice results from natural occurrences of non-functional *Badh2* mutations and farmers' careful selection and nurturing stretching back centuries (Prodhan & Qingyao 2020). Most traditional aromatic rice cultivars are low-yielder and subpar agronomically, extremely vulnerable to fluctuations in climate (Prodhan et al. 2017). Breeders have long struggled to find ways to increase both production and grain quality due to rice's susceptibility to climate fluctuations reducing the quality of the rice's aroma. Also, the success is hampered by low selection efficiency and the limited impact of individual QTLs. Notwithstanding the challenges, breeders have developed wide aromatic rice varieties that improve upon traditional cultivars in both yield and agronomic performance without compromising the original grains' distinctive aroma or qualities. An illustration representing different approaches to aromatic rice breeding is presented in Figure 4 and essential milestones in the history of breeding for fragrant rice are discussed in this section.

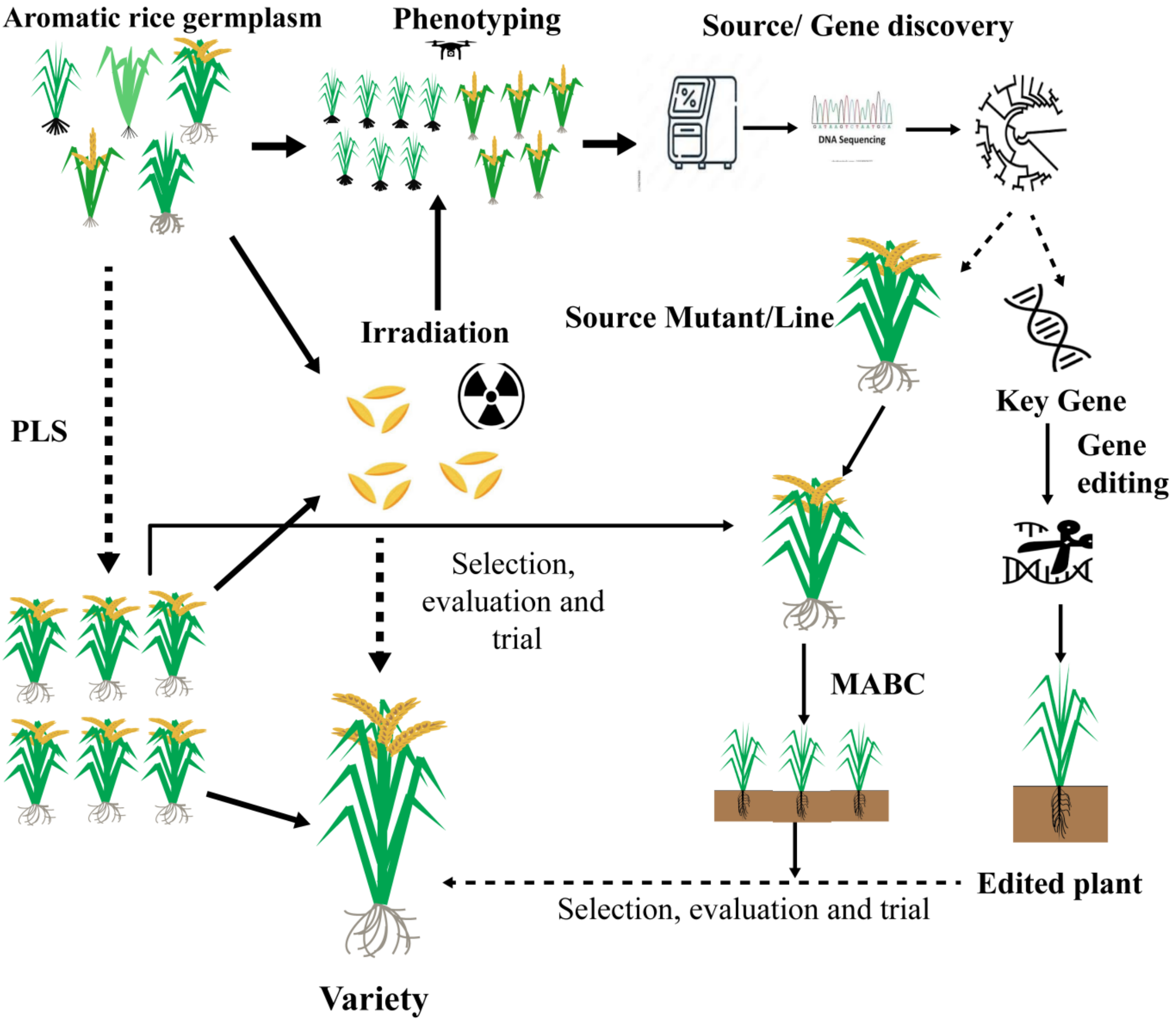

Figure 4- Approaches of aromatic rice breeding. PLS, Pure line selection; MABC, Marker assisted backcrossing

1.6. Pure line selection (PLS)

PLS is the oldest method applied by the breeders and farmers to purify and retain local landraces' aroma and grain quality attributes. The first effort was made in the early 1920s to cleanse the local Basmati cultivar, which resulted in the release of Basmati 370 in 1933 (Ahuja et al. 1995). Several generations of pure line selection developed several Basmati-type cultivars with increased productivity and improved grain quality (Table 1). Until the turn of the millennium, Basmati-217, Type-3, and Basmati 370 were the most popular Basmati type rice varieties grown in India (Sharma et al. 2021). Another well-known example of locally modified cultivar is Khao Dawk Mali 105 (KDML105) of Thailand. A farmer made the initial selection back in 1945. In 1959, the Kok Samrong Rice Research Station officially introduced the cultivar (Somrith 1996). Other countries' pure line selection programs have improved many additional native landraces (Ahuja et al. 1995, www.brri.gov.bd) that are presented in Table 1. However, successive breeding strategies for enhancing fragrant rice used Basmati 370 and KMDL105 as their foundation. However, pure line selection could lead to a narrow genetic base, which reduces adaptability to changing climates and makes it more vulnerable to biotic and abiotic stresses. Moreover, this approach is time-consuming due to the need for several generations of selfing.

Table 1- Aromatic rice varieties developed through pure line selection

Variety	*Ancestor*	*Country*	*Characteristics*
Basmati 370	Local Basmati landrace	India and Pakistan (Punjab)	Strong aroma
N-10B	Hansraj	India (Uttar Pradesh)	Fine grain
N-12	Safeda	India (Uttar Pradesh)	Fine grain
Type 3	Basmati (Punjab)	India (Uttar Pradesh)	Fine grain
Type 9	Dimnepet	India (Uttar Pradesh)	Fine grain
Type 1	Ramjeevan	India (Uttar Pradesh)	Fine grain
Type 23	Kalasukhdas	India (Uttar Pradesh)	Fine grain
Taraori Basmati	Kamal local	India (Haryana)	Longer grain
Ranbir Basmati	Local landrace	India (Jammu and Kashmir)	Early maturing, rice gall midge resistant
Dehraduni Basmati	Type 3	India	
Khao Dawk Mali 105 (KDML105)	Local Jasmine	Thailand	High yielding, suitable for semi-deep ecosystem
3 distinct varieties	Jeerakasala	India (Kerala)	Higher yield potential
14 distinct varieties	Kalanamak	India (Uttar Pradesh)	Higher yield potential
C435	Jeerege Sanna	India (Karnataka)	Early maturing
K44-1	Kakasali	India (Karnataka)	Early maturing
DP33	Krishna Pasangi	India (Karnataka)	Early maturing
Madhuri selection 9A	Madhuri	India (Madhya pradesh)	Late sowing potential
Kadam phool	Local landrace (Chattishgarh)	India (Madhya pradesh)	Moderately drought tolerant
Della	Delitus	USA	Aroma
BR5	Badshabhog	Bangladesh	Short and bold grain
BRRI dhan34	Local landrace Khaskani	Bangladesh	Short grain

1.7. Selection followed by hybridization

Breeding and selection techniques, notably convergent and backcross strategies appear beneficial in breaking unwanted couplings and increasing the frequency of useful recombinants, but most traditional varieties are poor combiners. However, these attempts have limited success in aromatic rice breeding due to the cross-incompatibility between aromatic and other group of rice, which results in hybrid sterility. Dwarf Basmati-type breeding lines with high yield potentials and at least one or two quality features were generated and cross-bred using a stepwise convergent breeding technique. In addition, fragrant landraces are typically low-yielders and have an increased plant stature, making them vulnerable to lodging. Their photosensitivity is a further issue. As a result, various semi-dwarf, photo-insensitive, and high-yielding fragrant rice varieties like Kusuma, Kasturi, Haryana Basmati, Lateefy, BRRI dhan70, etc., have been released because of prior breeding programs aimed at overcoming these issues (Table 2).

Table 2- Aromatic rice varieties developed through selection followed by hybridization

Variety	*Parents*	*Method*	*Characteristics*	*References*
Pusa Basmati-1	Basmati 370/Karnal Local	Convergent breeding	Dwarf, photo-insensitive, and input responsive	Chandi & 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
BRRI dhan70	IR674423/IR65610	Pedigree	Fine grain, higher yield potential and strong aroma	www.brri.gov.bd
Kusuma	TN-1/Basmati 370	Pedigree	Long slender grain, aroma mild, higher yield potential	Hashemi 2015
PAU 29-295	Basmati 370/Hamsa	Pedigree	Fine grain, semi-dwarf, early maturing, higher yield potential and strong aroma	Saini & Kumar 1979
GR 101	IR8/Pankhali 203	Pedigree	Long (9.52 mm) slender grain, higher yield potential, mild aroma and resistant to neck blast	Desai et al. 1987
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 1985
Tainung Sen 20	Chianung Shi-pi 671178/ an F_4 line	Pedigree	Strong aroma, higher yield potential, resistant to blast and BPH	Yang 1988

In 1989, researchers made the first significant step towards creating higher-yielding Basmati rice by releasing Pusa Basmati 1. The Basmati rice hybrid between Pusa 150 and Karnal Local was the first variety to be semi-dwarf, photo insensitive, and produce higher yields. Many high-yielding non-aromatic rice varieties were utilized in a convergent breeding technique to develop the Pusa 150 breeding line; these included IR8, IR22, Taichung Native 1, and others; the classic Basmati 370 employed as a pollen parent for grain quality attributes. Rice variety Basmati 370 employed as a donor for quality attributes. The most sought-after variety among growers, exporters, and consumers was Pusa Basmati 1 due to its very-long slender, scented grains, quicker cooking time, and higher linear kernel elongation after cooking. It also had the potential to yield 5.0 t/ha of grain and had an intermediate duration of 135-140 days.

The Pusa Basmati 1121, introduced in 2003, marked the next significant advance in the breeding of Basmati rice. The average yield for semi-dwarf (110cm to 120cm) PB 1121 is 5.5 t/ha. The maturity period is between 140 and 145 days. Averaging a kernel length of 9.00 mm, a width of 1.90 mm, and an L/B ratio of 4.74, this variety stands out due to the extraordinarily long, slender grain with 2.70 kernel elongation ratio. In addition to being a superb cook, the panel test participants found that it had a strong fragrance (Singh et al. 2018). Thirteen different rice varieties and enhanced germplasm were employed to generate PB 1121. Traditional Basmati rice varieties, including Basmati 370 and Type 3, brought together the beneficial alleles at numerous loci for agronomic, grain, and cooking quality traits. PB 1121 was the foundation for developing several more enhanced Basmati rice varieties, including Pusa Basmati 6 and Pusa Basmati 1509 (Table 2) (Sing et al. 2014).

Likewise, Jasmine-type aromatic rice has been bred over time to improve its quality. Using IR77924-62-71-1-2 as the donor for two backcrosses to KDML and then pedigree selection, the first blast-tolerant variety with a Jasmine-like quality was initiated in 1999 (Supapoj et al. 2009). In 2006, a new aromatic rice variety, RD33, was introduced; it was a descendant of Jasmine rice bred to be resistant to blasts and not influenced by the length of the day. Marker-assisted breeding was crucial to further refinements in Jasmine rice (Vanavichit et al. 2018) and discussed in the following section.

1.8. Hybrid breeding

China succeeded 30 years ago in inventing and proving rice hybrid breeding technology with a new yield threshold to surpass the yield level rice varieties. Nonetheless, substantial research on fragrant hybrid rice has been conducted in India. Major problem in hybrid breeding of aromatic rice is the difficulty in finding compatible parental lines which could maintain both yield heterosis and other grain quality parameters. Moreover, crossing with non-aromatic parental lines leads to compromised grain aroma and reduced seed setting or complete sterility due to differences in the genetic background. This problem could be solved by introgressing desirable genes from non-aromatic rice cultivars and repeated backcrossing to maintain the grain quality traits. A diverse aromatic rice germplasm could be characterized to find parental lines that can meet both high yield and grain quality characters. Several attempts have been undertaken to achieve these goals. A perfect maintainer Pusa Basmati-1 was utilized as a pollen donor to create the Basmati-typical CMS line Pusa 3A, which is based on wild abortive cytoplasmic sterility (WA-CS) system. Several other cytoplasmic male sterile (CMS) lines were subsequently produced, including Pusa 5A, Pusa 6A, etc. Crossing Pusa Rice Restorer78 (PRR78) with the Pusa 6A CMS line resulted in the F_1 Pusa RH10, the world's first superfine grain aromatic rice hybrid (Basavaraj et al. 2009).

The International Rice Research Institute (IRRI) further progressed the aromatic hybrid rice research by developing a few CMS lines and restorers from fragrant rice like IR67684 A, IR68280 A, IR68281 A, IR69617 A, and IR70372A. Several promising Basmati-type genotypes, *viz.*, Pusa 1280-1-2-1, BTCE 10-98, l ET 15391, and UPRI 93-63-2, were identified as effective maintainers against CMS lines. These can be used to develop new CMS lines through recurrent backcrossing. Besides, the effective restorers, namely lET 15392, RP 3644-36-15-8-4, TM 970267, RP 3644-41-9-5-5, and RP 3644-41-9-5-5 against Pusa 3A background while RP 3135-17-12-88, Pusa 2512-97-83-98-4 and Taraori Basmati against IR 58025A may be utilized in Basmati hybrid breeding program (Pradhan et al. 2006).

1.9. Mutation breeding

Increasing the genetic diversity of crops has been a goal of mutation breeding program for nearly a century. Over the past 60 years, various crops have been improved by using mutation breeding in conjunction with other breeding methods to identify gene functions (Ma et al. 2021). In the case of aromatic rice, this method introduced dwarf stature in typically tall Basmati rice or to correct flaws like disease and pest susceptibility (Singh et al. 2000). Initially, induced mutation through gamma ray irradiation produced two significant offsprings: waxy type Jasmine rice mutant RD6, and short duration rice mutant RD15 which were introduced in 1977 and 1978, respectively (Vanavichit et al. 2018). The mutant aromatic rice varieties RD15 and RD6, as well as their parent KMDL 105, have been widely cultivated in Thailand's 70% rice-growing region, which consists of a stressed mega-ecosystem (Jongdee et al. 2006). It has moderate drought, salinity, and acid sulphate soil tolerance. In addition, these two mutant types can generate an acceptable yield in areas moderately affected by salt (2-6 dS/m) (Vanavichit et al. 2018).

Aromatic rice mutants in India bred from Basmati types have met with mixed success. Kalimoonch-6, Bindli, Kamal Local, Type-9, NP-49, T412, Kalanamak, Gobindbhog, Badshapasand, and Basmati 370 are just a few of the genotypes for which mutant lines have been created. To exploit them in future breeding programs, favorable mutants (such as those with dwarfism, lodging resistance, or early maturation) are preserved (Sharma et al. 2021).

The University of Florida and the University of Arkansas used gamma radiation to introduce two essential Jasmine-type characteristics successfully. Other notable features include being semi-dwarf, advantageous for combined harvesting, and non-photoperiod sensitive, broadening the planting season. In 2010, farmers could access Jasmine rice because of this scheme (Napasintuwong 2012). In 2013, a mutant aromatic rice variety named Binadhan-13 was released in Bangladesh after being produced using gamma irradiation (www.bina.gov.bd).

1.10. Marker assisted selection

Backcrossing, mutation breeding, or traditional cross-breeding on existing aromatic genotypes can improve aromatic rice grain quality. Developing new varieties takes a lot of effort and time (Shan et al. 2015). Marker aided molecular selection has become increasingly common in the study and improvement of fragrant rice due to the introduction of genetic markers, exceptionally functional markers of the *BADH2*. With this method, numerous new fragrant rice types have been bred and authorized for widespread usage in production, drastically shortening the time it takes to bring this variety of rice to market (Peng et al. 2018). Meanwhile, marker-assisted backcrossing has been extensively used to correct flaws of aromatic rice, especially abiotic and biotic stress susceptibility. Many aromatic rice varieties were developed through this method addressing the major stresses (Table 3).

Table 3- Aromatic rice varieties derived through marker-assisted breeding with improved traits

Parents/ Variety	***Traits***	***Gene***	***Reference(s)***
Pusa Basmati-1	BLB resistance	*xa13*, *Xa21*	Joseph et al. 2004
Pusa 6B	BLB resistance Blast resistance Sheath blight resistance	*xa13*, *Xa21* *Pi54* *qSBR11-1*, *qSBR11-2 and qSBR7-1* (QTLs)	Basavaraj et al. 2009; Sing et al. 2015
Pusa Rice Restorer78	BLB resistance, Blast resistance	*xa13*, *Xa21* *Pi1*, *Piz-5*	Basavaraj et al. 2010; Gouda et al. 2013
Pusa 1121	BLB, Blast, BPH	*xa13*, *Xa21* *Pi54*, *Piz-5* *Bph-3*, *Bph-18*	Singh et al. 2011
Pusa Basmati 6	BLB, Blast, BPH	*xa13*, *Xa21* *Pi54*, *Piz-5* *Bph-3*, *Bph-18*	Singh et al. 2011
Kalanamak	Semi dwarf plant height	*Sd1*	Srivastava et al. 2019
Mushk Budji	Blast resistance	*Pi54*, *Pi1*, *Pita*	Khan et al. 2018
HM80	Flash flooding tolerance	*Sub1*	Siangliw et al. 2003
HM83	Flash flooding, BLB and BPH	*Sub1*, *Xa21*, *Bph (Q12)*,	Vanavichit et al. 2018
HM84	Flash flooding, BLB, Blast and BPH	*Sub1*, *xa5*, *Xa21*, *Q1*, *Q11*, *Q12*, *Bph-3*, *Bph32*	Vanavichit et al. 2018

1.11. Genetic engineering

Transgenic technology is used to develop new aromatic rice varieties by inserting a copy of the *Badh2* gene into rice plants. This was made possible by designing linked *Badh2* primers (Jin et al. 2003), which in turn led to the designing of a series of *Badh2* functional markers (Bradbury et al. 2005; He & Park 2015). Already, work has begun to insert desirable genes into well-known aromatic rice cultivars to assist the farmers to overcome the limitations of current cultivars.

Tarom molaii+cry1ab was the first transgenic aromatic rice line with insect resistance developed by the Agricultural Biotech Research Center of Iran in 2005 through genetic engineering (https://www.isaaa.org/gmapprovaldatabase).

1.12. Genome editing

Breeding aromatic rice varieties with higher grain yield along with aroma is often a challenge. The mechanisms behind the association between poor agronomic characters and fragrance gene is not well understood. This problem could be solved by editing *BADH2* gene in a high yielding non-aromatic rice variety. Non-aromatic rice varieties with wider adaptability and stress tolerance could be converted into aromatic by the targeted mutation of *BADH2* (Bradbury et al. 2005; Shi et al. 2008; Kovach et al. 2009). As a result, *Badh2* gene dysfunction can boost 2AP synthesis and accumulation, and mutations that lead to *Badh2* gene dysfunction may also develop novel aroma alleles.

1.13. RNA interference (RNAi)

Silencing or downregulation of *BADH2* could be achieved through RNAi or incorporation of miRNA to change non-aromatic rice cultivars into aromatic ones (Chen et al. 2012; Khandagale et al. 2020). The inability of the RNAi approach to completely suppress the expression of the *Badh2* gene necessitates screening many transgenic progenies. This method is subjected to strict monitoring and a risk evaluation late transgenics. Furthermore, the certification process for the new transgenic rice modified with RNAi is also being examined. (Peng et al. 2018).

1.14. Transcription Activator-like effector nucleases (TALEN)

Non-aromatic rice variety can be turned into an aromatic one using TALEN technology. This technology could create genetically homozygous mutant of aromatic rice plants. Knocking out the *Badh2* gene through TALEN enhanced the 2-AP level to 0.35–0.75 mgkg^{-1} (Shan et al. 2015).

1.15. Clustered regularly interspaced short palindromic repeats (CRISPR) and CRISPR-Associated Protein 9 (CRISPR/Cas9)

New possibilities for swiftly enhancing rice grain quality by targeted mutagenesis have emerged with gene editing technologies like CRISPR/Cas9 system. A non-aromatic rice variety (Zhonghua 11) was successfully transformed into an aromatic rice variety using the CRISPR/Cas9 technology (Shao et al. 2017). As a result, breeders can more easily change critical genes in the genomes of major crops by decorating the CRISPR/Cas9 tool with all genome editing capabilities (such as knock-in, knock-out, and knock-down) which has enormous untapped potential. Pathway-level research can be aided by multiplexed genome-editing methods, allowing for the engineering of complex multigenic grain quality traits like rice aroma. Research is rapidly moving towards using the CRISPR/Cas9 system for targeted mutagenesis, which has promise as a means of overcoming obstacles in breeding rice with enhanced scent (Fiaz et al. 2019). New variants of the rice *BADH2* fragrance gene have been developed using CRISPR/Cas9-mediated gene editing, as reported by (Ashokkumar et al. 2020).

1.16. Omics based research

Although *badh2* is a major gene responsible for aroma development in rice, the intensity of 2AP accumulation indicates the presence of other fragrance alleles in rice (Fitzgerald et al. 2008). Multi-omics-based technologies like transcriptomics, proteomics and metabolomics could be applied in identifying all possible genes and metabolic pathways responsible rice grain aroma. Researchers can easily pinpoint this genetic variation and manipulate it for enhancing the development of fragrance in rice grain.

1.17. Prospects of aromatic rice research

The improvement of aromatic rice cultivars commenced in the 1920s and continues today. Although breeding priorities shifted over time, work to develop fragrant rice proceeded persistently. However, Basmati and Jasmine type aromatic rice have been the primary targets of previous breeding initiatives. The wild and local short-grained fragrant landraces were left behind during these breeding initiatives in favor of developing long, slender grains with scent. As a result, there are plenty of opportunities for improving the locally grown short-grain scented rice cultivars. Across Asia, short-grain fragrant rice germplasm exists abundantly, and it has not yet been fully utilized. Recent advances in rice functional genomics, along with current molecular and biotechnological techniques, have made it possible to gain insight into the mechanism and genetics, together with the function and control, of fragrance genes in rice, making them more amenable to commercial use. The aromatic rice breeding program may be completely revamped if more attention were paid to the use of wild and local germplasm. Such efforts have the potential to reveal new genes for aroma in rice which can revolutionize the future improvement of aromatic rice.

In addition, both wild and cultivated varieties with desirable agronomic characteristics can be benefitted from the development of novel alleles for scent using cutting-edge genome editing techniques. In particular, the recent trend in targeted mutagenesis using CRISPR/Cas9 system can be a viable technique for overcoming hindrances in breeding for enhancing fragrance as well as the quality traits in rice.

Considering all the obstacles and scope in aromatic rice improvement program, here, in this paper, we propose a model aromatic plant (Figure 5) for future having some specific traits regarding the aroma, grain quality, and panicle structure and plant architecture. As the principal volatile component responsible for grain aroma is 2-AP (Haowen et al. 2022), the grains should have aroma to a certain level that is preferred by the consumer. In this case, regulation of node genes like *BADH2*, *P5CS*, and *DAO* in the 2-AP biosynthetic pathway (Bao et al. 2021) and key transcription factors like WRKY, MYB, NAC, bHLH, bZIP (Imran et al. 2022) can be considered. Molecular breeding and/or genome editing for genes regulating grain shape [*GS3* (Wang et al. 2012); *GS9* (Zhao et al. 2018); *GW8* (Wang et al. 2012); *DEP1* (Huang et al. 2009); *GW2* (Song ET AL. 2007), *GW5*, *GS5* (Wan et al. 2006)], amylose [*Wx* (Ni et al. 2011), *SBEI*, *SBEIIb* (Tian et al. 2009)], starch [*FLO2*, *FLO5/ALK* (Wu et al. 2015), *PHO1* (Fiaz et al. 2019)] content and chalkiness (*chalk5* (Li et al. 2014), *WCR1a* (Wu et al. 2022)] can positively contribute to the grain eating and cooking quality. Yield has always remained as one of the major concerns for aromatic as they cannot compete with the modern high yielding varieties. Thus, panicle as well as the plant architecture must be optimized to assure considerable higher yield. To achieve a longer panicle with dense seed, the key target genes could be *Gn1a*, *IPA1*, *GS3*, *DEP1* (Li et al. 2016), *Pin1a* (Liu et al. 2021), *Pin5b* (Zeng et al. 2020), *GW2*, *GW5*, *GW6* (Xu et al. 2016), *Cytochrome P450* (Usman et al. 2020), *EP3* (Shen et al. 2017), *PYL1*, *PYL4* and *PYL6* (Miao et al. 2018). In addition, ideal plant with semi-dwarfness, dense and erect tiller can be achieved through regulating *SD1* (Hu et al. 2019), *GA20ox2* (Han et al. 2019), *FWL4* (Gao et al. 2020), *Se5* (Andrés et al. 2009), *HD1*, *HD2* (Gao et al. 2014), *LPA1* (Liu et al. 2016) and *HTD1* (Zou et al. 2006) genes. However, breeding a variety incorporating all the above-mentioned traits may not be achievable. Thus, breeding program must focus on the specific preference of the consumers, socio-economic conditions, and target environments.

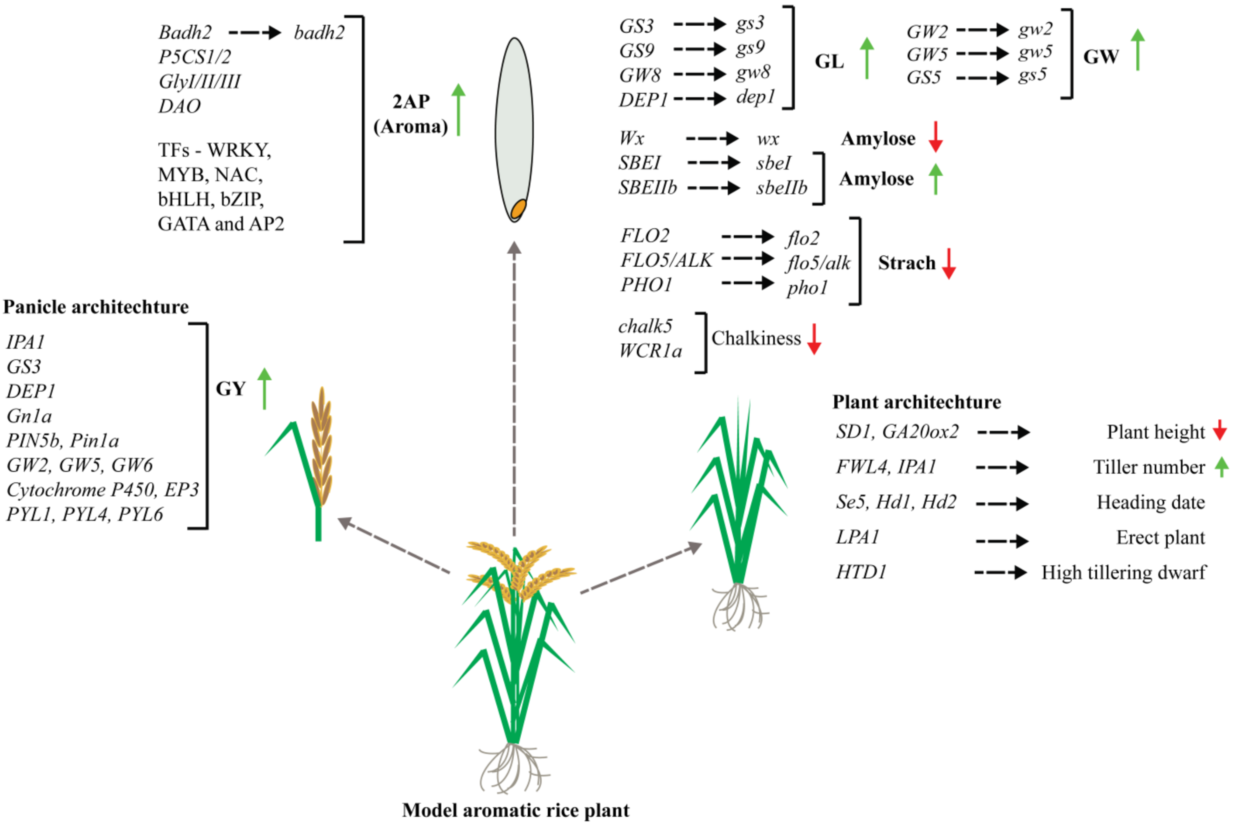

Figure 5- Model aromatic rice plant

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