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Review Article

Genetic Diversity in Aromatic Rice Varieties and Molecular Insights into *BADH2* Gene Variability

Rakesh Kumar Bairwa[1*], Amarkant Kushwaha[2], Shiva Mohan[3], Sandeep Kumar[4], Arun Gupta[1], Umesh R Kamble[1] and Amit Kumar Sharma[1]

[1]*ICAR-Indian Institute of Wheat & Barley Research, Karnal, Haryana, India*
[2]*ICAR- Central Institute of Subtropical Horticulture, Lucknow, Uttar Pradesh, India*
[3]*Invertis University, Bareilly, Uttar Pradesh, India*
[4]*School of Agriculture, Uttaranchal University, Dehradun, Uttrakhand, India*

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****Corresponding author:***
E-mail: bhairwalrakesh90@gmail.com

Abstract

Aromatic rice is a very popular type of rice that is renowned for its distinctive aroma, exceptional cooking qualities, and nutritional attributes. Aromatic rice is native to the foothills of the Himalayas, which are also considered the center of diversity for this rice type. India boasts a diverse range of aromatic rice landraces, including the world-renowned Basmati rice. The fragrance of aromatic rice is an important quality trait, and it has been discovered that a compound called 2-acetyl-1-pyrroline (2AP) is responsible for it. The accumulation of 2AP is governed mainly by the *BADH2* gene in rice. The non-functional or recessive allele of the *BADH2* gene leads to the accumulation of the 2AP compound in rice. Since the discovery of the *BADH2* gene, researchers have identified several allelic variants across different germplasms from various countries. Several gene-specific and functional molecular markers have been developed to screen these allelic variants and select for aroma in the early stages of the breeding program. This review article presents an overview of the major aroma gene *BADH2*, highlighting its allelic variations and the development of functional markers used in breeding programs. The information presented here is essential for researchers and breeders working on aromatic rice breeding programs to develop new and improved varieties that can meet the increasing demand for aromatic rice worldwide.

Keywords: Rice, Basmati, aroma, *BADH2*, genetic diversity, functional marker

1. Introduction

Rice is vital for food security and the sustainability of the world's population. It is a staple food for more than half of the world's population (Brar and Khush, 2018). Rice is classified as fragrant or non-fragrant based on the presence of aroma (Singh *et al.*, 2000; Thada *et al.*, 2024; Bairwa *et al.*, 2024). Aromatic rices are a special group of rices that have fragrance and other exceptional cooking qualities. As a result of these qualities, they enjoy a higher market value and are more popular among consumers in Asia, the Middle East, Europe, and the United States of America (Singh *et al.*, 2000; Roy *et al.*, 2020). Aromatic rice contributes to 15–18% of the world's rice trade (Giraud *et al.*, 2013). There are more than a hundred volatile chemicals found in rice, but 2-acetyl-1-pyrroline (2AP) has been identified as the key compound responsible for a popcorn-like fragrance (Buttery *et al.*, 1983; Mathure *et al.*, 2014; Ramtekey *et al.*, 2021). Due to their taste, aromatic rices are widely preferred among consumers. These group of rice are also excellent in nutritional attributes; for example, Sitabhog and Remigeli

are high in minerals, while Kataribhog and Kalanamak have low glycemic indexes, greater resistant starches, and antioxidants (Rajendran *et al.*, 2018; Nath *et al.*, 2022; Thada *et al.*, 2024). The Indian region is blessed with substantial genetic diversity in aromatic rice landraces and improved cultivars. Aromatic rices originated in the foothills of the Himalayas, particularly in the Indian states of Uttar Pradesh and Bihar and the Tarai region of Nepal. This region constitutes the center of diversity for aromatic rice landraces. Aromatic rice spread from these regions to other Indian states and adjacent nations in the northwest and northeast. At present, hundreds of locally adapted genotypes of fragrant rice exist in India that have evolved as a result of both natural and artificial selection (Khush, 2000; Bairwa *et al.*, 2023). The grain length of Indian fragrant rice varies significantly, from short to long grains. They also differ in fragrance, ranging from mild to strong (Singh *et al.*, 2000). Aromatic rice is further classified into Basmati and non-Basmati types. Basmati rice is mainly cultivated in the Indo-Gangetic region of northwestern India, which includes seven states, namely Punjab, Haryana, Himachal Pradesh, Uttarakhand, Jammu, and Kathua districts of Jammu and Kashmir, as well as 27 districts of western Uttar Pradesh. This specific region has been designated as the Geographical Indication (GI) for Basmati rice. In 2016, Basmati rice was granted GI status (GI No. 145 of the Geographical Indication Registry, Government of India, certificate No. 238 dated 15.02.2016). Non-Basmati types included several hundred aromatic rice landraces, which have been under cultivation in different states since ancient times due to their unique properties, such as the Kalanamak rice landrace, which is native to the Siddharthnagar district of Uttar Pradesh. Landraces are genetically heterogeneous, dynamic populations of cultivated plants that share common traits and are associated with many generations of farmer selection. Because of their strong potential to adapt to specific environmental conditions, landraces constitute a storehouse of important genes and are crucial for crop improvement programs (Azeez *et al.*, 2018). The importance of aroma led to research towards understanding the molecular and biochemical mechanisms of aroma and its improvement (Nadaf *et al.*, 2014; Gaur *et al.*, 2016; Huang *et al.*, 2024). Aromatic rice is distinguished from other rice varieties by the accumulation of the chemical 2-acetyl-1-pyrroline. The fragrance in rice is controlled genetically by the *BADH2* gene, which is located on chromosome 8. The recessive allele of *BADH2* leads to the accumulation of 2-acetyl-1-pyrroline, which is responsible for the fragrance. The fragrance is present in all parts of the rice plant except the roots (Yoshihashi, 2002). Although there are other aromatic rice varieties that have a strong aroma, they lack the mutant alleles of the *BADH2* gene, indicating that there may be other genes or alleles that are crucial for the aroma. All of the genes involved in fragrance have yet to be identified (Kaikavoosi *et al.*, 2015). Since the discovery of the *BADH2* gene in the 'Kyeema' cultivar, many allelic variants of the gene have been found across various genetic backgrounds (Bradbury *et al.*, 2005a; Kovach *et al.*, 2009; Shi *et al.*, 2008). Researchers have developed gene-specific and functional markers that can be used to detect these allelic variations in germplasm. These genetic markers are useful in breeding programmes as they allow for the early identification and selection of fragrant genotypes as well as the determination of the homozygous or heterozygous state of the fragrance locus. This paper provides a comprehensive review of the origin and diversity of aromatic rice in India, as well as the aroma gene and pathway involved in its development. Additionally, the allelic variants of the gene and the functional markers that have been developed in this area are discussed in detail.

2. Origin of aromatic rice

The centre of diversity for fragrant rice is located in the Himalayan foothills, which cover the regions of Uttar Pradesh and Bihar states in India and the Tarai region of Nepal (Khush, 2000). Over time, aromatic rices were introduced to the northwestern and north-eastern Indian states. As a result, there are currently many landraces of aromatic rice that have been tailored to the local environment. Aromatic rice also expanded from this region to neighbouring nations including Pakistan, Afghanistan, Iran, Iraq, Bangladesh, Myanmar, and Thailand. It is thought that aromatic rice cultivated in European nations like Italy and France was imported from Asia (Khush, 2000). According to Bourgis *et al.* (2008), the *badh2* mutation in Asian cultivated rice has a monophyletic origin. Based on a phylogeographic study, Civan *et al.* (2019) hypothesised that the *japonica* and *aus* types of rice hybridized to give rise to aromatic rice. They further proposed that the production of aromatic rice

resulted from a hybridization event between populations of *aus* wild rice from the southern Himalayas and populations of *japonica* rice (Civan *et al.*, 2015). According to Kovach *et al.* (2009), the fragrance allele emerged after the domestication of *Oryza sativa* and the subsequent divergence of this species into the two main subspecies: *indica* and *japonica*. The evidence presented in these studies supports the notion that aromatic rice originated in India and is closely linked to the *japonica* variety of rice.

3. Genetic structure of aromatic rice

The relationship of aromatic rice with other rice groups has been studied by various researchers. Glaszmann (1987) used Starch Gel Electrophoresis to study the enzymatic variability of 1688 traditional rice varieties from Asia and categorized rice varieties into 6 groups. Aromatic rices were placed into Group V, which is distributed geographically from Iran to Burma. Many of the varieties of rice in this group, including "Sadri" from Iran and "Basmati" from India, Pakistan, and Nepal, are renowned for their excellent quality, grain elongation, and aroma. Garris *et al.* (2005) inferred the population dynamics and evolutionary relationships of 234 rice accessions from Asia, the Americas, Africa, Europe, and Oceania using data of 169 nuclear loci and two chloroplast loci, and divided the rice accessions into five categories: *indica*, *aus*, *aromatic*, *temperate japonica*, and *tropical japonica*. Kovach *et al.* (2009) inferred a single origin of the allele with 8-bp deletion in a *japonica* like genetic background, and based on this study, aromatic rices were closely related to the *japonica group*. The Rice Genomes Project (The 3000 Rice Genomes Project, 2014) sequenced the whole genomes of 3010 rice accessions and analyzed 18.9 million SNPs. *Indica*, *japonica*, *aus/boro*, Basmati/Sadri, and intermediate kinds were among the 5 varietal categories that were reported. Based on this study, the Basmati group and the *japonica* group showed a close relationship. Phitaktansakul *et al.* (2022) reported that the *japonica* group and the aromatic group were found to have a close genetic relationship based on a population genetic structure study of a core set of 475 Korean rice accessions coupled with wild rice. Based on these studies, it is evident that the aromatic rice group is closely linked to the *japonica* group.

4. Biochemistry of fragrance

Based on current literature, two potential pathways have been proposed for the synthesis of the 2AP chemical in rice. The first pathway involves the conversion of amino acids such as proline, ornithine, and glutamate to produce a common metabolite called 1-pyrroline-5-carboxylic acid. This metabolite is then transformed into Δ^1-pyrroline, which is reacted chemically with methylglyoxal to produce 2AP (Yoshihashi *et al.*, 2002). The second pathway was suggested after the discovery of the putative aroma gene, known as the 'betaine aldehyde dehydrogenase 2 (*BADH2*) gene.' In this pathway, functional *BADH2* genes produce an enzyme called betaine aldehyde dehydrogenase, which converts γ-aminobutyraldehyde (GAB-ald) into γ-aminobutyric acid and inhibits 2AP accumulation in non-fragrant rice (Chen *et al.*, 2008). However, in the case of a non-functional or inactive *BADH2* gene, GAB-ald fails to convert into GABA, leading to GAB-ald

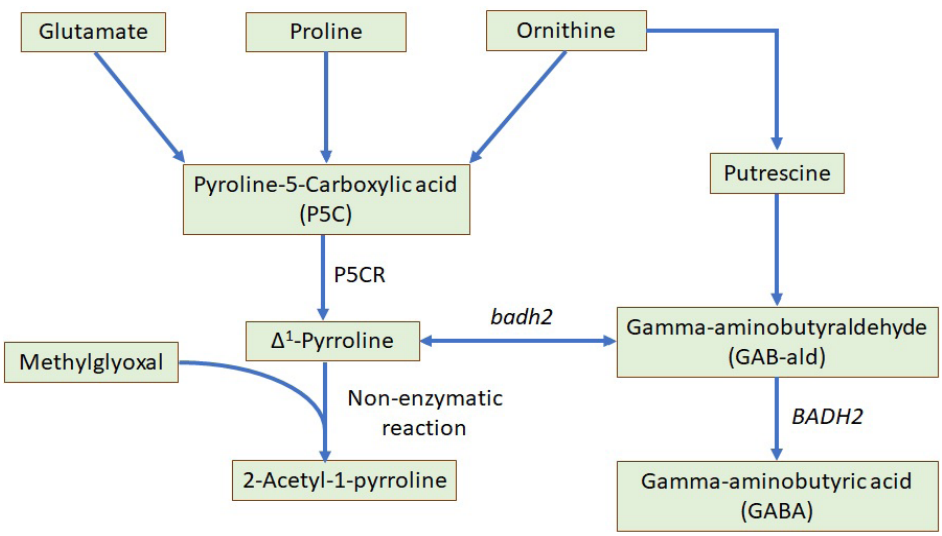

Fig. 1: The 2AP synthesis pathway in rice (modified from Imran *et al.*, 2023)

accumulation, which spontaneously undergoes cyclization to form 1-pyrroline and then produces 2AP. Gene expression analysis studies have shown that decreased levels of *BADH2* and glyceraldehyde-3-phosphate dehydrogenase (GAPDH) and increased levels of triose phosphate isomerase (TPI) and 1-pyrroline-5-carboxylic acid synthetase (P5CS) result in an increase in 2AP accumulation (Hinge *et al.*, 2016; Wakte *et al.*, 2017). The recessive form of the *BADH2* gene results in the accumulation of 2AP in rice grain. This gene is located on chromosome 8 and consists of 15 exons and 14 introns (Bradbury *et al.*, 2005a). Compared to non-fragrant rice, the 2AP content in fragrant rice is 15 times higher, with aromatic rice cultivars containing 0.14 ppm of 2AP, while non-aromatic types contain 0.9 ppm (Kim *et al.*, 1999). All these studies indicate that *BADH2* is the major gene responsible for the accumulation of 2AP in aromatic rice.

5. Diversity of aromatic rice landraces in India

Indian gene centre possesses relatively rich genetic wealth with respect to *indica* type rice. The list of various popular landraces and improved varieties of aromatic rice being cultivated in different states of the India is provided in Table 1. The landraces and varieties are classified based on grain size as short, medium, and long-grain aromatic rices. Some of the traditional aromatic rice landraces, like Kudrat, are suitable for organic farming (Supriya *et al.*, 2025).

Table 1: List of some popular aromatic rice landraces and improved cultivars

S. No.	State	Aromatic rice landraces/varieties	Reference
1.	Andhra Pradesh	Amritsari, Jeeragasambha, Kaki Rekhalu, Sukhdas, Sumati	Rani *et al.* (2006); Pachauri *et al.* (2010)
2.	Assam	Bengoli Joha, Bhabeli Joha, Bhugui, Boga Joha, Boga Tulsi, Bokul Joha, Borjoha, Borsal, Cheniguti, Chufon, Goalporia Joha, Joha Bora, Joha Cheniguti, Kaljeera, Kamini Joha, Ketaki Joha, Khorika Joha, Kola Joha, Kon Joha, Krishna Joha, Kunkuni, Kunkuni Joha, Malbhog, Manikimadhuri Joha, Prasad bhog, Ramphal Joha, Ranga Joha	Rani *et al.* (2006); Das *et al.* (2010)
3.	Bihar	Amod, Baikani, Bahami, Bhilahi, Bhuri Champaran, Brahmabhusi, Chenaur, Deobhog, Dewta Bhog, Gopal Bhog, Kali Champaran Basmati, Kamini, Kanakjeeri, Katami, Karia Kamod, Kasturi, Katarni, Kesar, Lal Basmati, Mircha, Mohan bhog, Ramjain, Ram Tulsi, Sataria, Shyam Jeera, Sona Lari, Sonachur, Tulsi Pasand	Singh *et al.* (2000); Rani *et al.* (2006); Pachauri *et al.* (2010)
4.	Chhattisgarh	Dubraj, Jawaphool, Maharaji, Tulasimanjari	Pachauri *et al.* (2010); Thada *et al.* (2024)
5.	Delhi	Pusa Basmati 1, Pusa Sugandh-2, Pusa Sugandh-3, Pusa Basmati 1121, Pusa Sugandh-5, PB1 (Improved) (PB 1460), PB 6 (Pusa 1401), PB 1509, Pusa RH10, PB1609, PB1637, PB1728, PB1847, PB1885, PB1886, PB1979, PB1985, Pusa Narendra Kalanamak 1638, Pusa Narendra Kalanamak 1652	Pachauri *et al.* (2010)
6.	Gujarat	Kamod 118, Kolhapur scented, Pankhali 203, Zeerasal, GR 101	Rani *et al.* (2006); Pachauri *et al.* (2010)
7.	Haryana	Basmati 370, CSR 30, CSR 36, Haryana Basmati 1, Haryana Basmati 2, Khalsa 7, Taraori Basmati	Pachauri *et al.* (2010)
8.	Himachal Pradesh	Achhu, Begmi, Baldhar Basmati, Chimbal Basmati, Hasan Sarai, Kasturi, Mushkan, Madhumalti, Panarsa local, Seond Basmati	Pachauri *et al.* (2010)
9.	Jammu & Kashmir	Kamad, Mushk Budji, Jammu Basmati 118, Jammu Basmati 123, Jammu Basmati 136, Ranbir Basmati, Saanwal Basmati, Shalimar Sugandh 1	Ashraf *et al.* (2016); Pachauri *et al.* (2010)

10.	Jharkhand	Birsamati	Pachauri *et al.* (2010)
11.	Karnataka	Chatri, Kagasali, Madhuri, Mugad Sugandha, Sindigi local Kagasali, Vishnu Parag	Rani *et al.* (2006); Pachauri *et al.* (2010)
12.	Kerala	Gandhkasala, Jeerakasala, Kagasali	Pachauri *et al.* (2010)
13.	Madhya Pradesh	Badshabhog, Baspatri, Chinni sagar, Chinni gauri, Chattri, Chinoor, Chinore, Dubraj, Jauphool, Kalu Mooch, Madhuri, Kali Kamod, Tulsi Manjari, Vishnubhog, Vishnu Parag Laloo	Rani *et al.* (2006); Pachauri *et al.* (2010)
14.	Maharashtra	Ambemohar, Ambemohar-102, Ambemohar-157, Ambemohar-159, Ambica, Bagavati, Chinore Ambemohor-152, Indrayani, Kagasali, Pawana, Prabhavati, Sakoli-7	Rani *et al.* (2006); Pachauri *et al.* (2010)
15.	Manipur	Agasali, Angangbi (pink/red scented rice), Buhman, Chahao Amubi (black scented rice), Chahao Prabhavati, Ching Chakhao Amubi, Chakhao, Chakhao Angenba, Chakhao Poiretol, Kabo Chakhao, Chakhao Phor, Chinore, Maklei, Prabhavati, Sakoli-7	Singh *et al.* (2000); Pachauri *et al.* (2010);
16.	Orissa	Acharmati, Baiganamanji, Baluchi, Barangomati, Bastabhoga, Baukunja, Basanapuri, Basubhoga, Bhatagundi, CR Sugandh Dhan-907, CR Sugandh Dhan-908, CR Sugandh Dhan-909, CR Sugandh Dhan-910, Deulabhoga, Dubraj, Dudhamani, Durgabhog, Gangabali, Geetanjali, Jaiphool, Kalajeera, Karpurkali, Ketaki Joha, Krisna bhog, Kuyerkuling, Laktimachi, Muktabali, Navakaljeera, Navapipri badhshah, Nadiarasa, Nua Dhusara, Nua Chinikamini, Poornabhog, Prasadbhog, Rambana Basmati, Sapuri, Sagartara, Shantibhog, Tikichudi, Tulasi	Rani *et al.* (2006); Roy *et al.* (2016); Bhuvaneswari *et al.* (2020); Panda *et al.* (2022); Sarkar *et al.* (2022); Behera *et al.* (2023)
17.	Punjab	Basmati 217, Basmati 370, Basmati 385, Basmati 386, Punjab Basmati 1, Punjab Basmati 2, Punjab Basmati 3, Punjab Basmati 4, Punjab Basmati 5, Ranbir Basmati, Super Basmati	Pachauri *et al.* (2010)
18.	Rajasthan	BK-79, Khushboo, Mahisugandha	Pachauri *et al.* (2010)
19.	Tamil Nadu	Jeeragasamba, JJ 92	Rani *et al.* (2006); Pachauri *et al.* (2010)
20.	Uttar Pradesh	Adamchini, Badshapasand, Bhanta Phool, Bindli, Chhoti, Chinnawar, Dhania, Dubraj, Duniapat, Hansraj, Jeerabattis, Kalanamak, Kala Sukhdas, Karmuhi, Kesar, Laungchoor, Lalmati, Moongphali, Motachinaeum, Nagina 12, Parsam, Rambhog, Ramjawain, Safeda, Sakkarchini, Tapovan Basmati, Thakurbhog, Tilak Chandan, Tinsukhia, Vishnuparag, Yuvraj	Singh *et al.* (2000); Rani *et al.* (2006); Pachauri *et al.* (2010)
20.	Uttarakhand	Pant Basmati 1, Pant Basmati 2, Type 3, Pant Sugandh Dhan 15, Pant Sugandh Dhan 17, Pant Sugandh Dhan 21, Pant Sugandh Dhan 25, Vallabh Basmati 21, Vallabh Basmati 22, Vallabh Basmati 23, Vallabh Basmati 24	Pachauri *et al.* (2010)
21.	West Bengal	Badshabhog, Badshah Pasand, Chinisakkar, Danaguri, Gandheshwari, Kalo Nunia, Kanakchur, Katanbhog, Kataribhog, Radhunipagal, Sitabhog, Tulai Panji, Tulsibhog	Singh *et al.* (2000); Rani *et al.* (2006); Pachauri *et al.* (2010)

6. Molecular basis of aroma in rice

Earlier researchers have observed that the fragrance attribute is controlled by diverse genetic mechanisms, including monogenic, digenic, and polygenic inheritance patterns with complementary, dominant, recessive, and duplicate gene responses (Berner and Hoff, 1986; Lorieux *et al.*, 1996). Bradbury *et al.* (2005a) established that one major gene, *BADH2*, is responsible for aroma in rice. Understanding the inheritance of fragrance is

particularly challenging because it is regulated by one major gene, *BADH2*, and a few other genes that have yet to be identified; it is also influenced by weather conditions. Since the *BADH2* gene was discovered and cloned, more than a dozen mutation locations have been identified and several molecular markers have been developed for these loci. Bradbury *et al.* (2005a) sequenced 14 fragrant rice cultivars and 64 non-fragrant rice cultivars of various origins and established that the aroma of fragrant rice 'Kyeema' (a tall fragrant indica cultivar) is caused by a non-functional allele (*badh2*) of the *BADH2* gene. The *BADH2* gene is rendered inactive by an 8-bp deletion (5'-GATTATGG-3') and three single nucleotide polymorphisms (SNPs) in exon 7. Accumulation of 2-AP in fragrant rice will occur as a result of loss of function. The removal of *BADH2* functionality has little impact on rice plant development. This gene serves as the ideal illustration of how a recessive characteristic was chosen during domestication. The gene consists of 14 introns and 15 exons (Bradbury *et al.*, 2005a). The 8-bp deletion in exon 7 was first identified in the *japonica* aromatic rice cultivar 'Azucena' by Bourgis *et al.* (2008). In another study, three genes, namely *Badh2*, *Cah*, and *Mccc2*, from the non-aromatic rice cultivar "Nanjing 11" were used to alter the aromatic rice cultivar "Wuxianging." In transgenic lines carrying the *Badh2 gene*, a decreased amount of 2AP was found (Chen *et al.*, 2008). Shi *et al.* (2008) discovered another novel allele by comparing the sequences of 24 aromatic and 10 non-aromatic rice cultivars from China. A 7-bp deletion (5'-CGGGCGC-3') in exon 2 of chromosome 8 (Shi *et al.*, 2008) is rendered the *BADH2* gene non-functional in this case. In another study, Amrawathi *et al.* (2008) mapped three putative QTLs, designated as *aro3-1*, *aro4-1*, and *aro8-1,* located on chromosomes 3, 4, and 8, respectively, by using the mapping populations of recombinant inbred lines (RILs) from Pusa 1121 and Pusa 1342. They also discovered a discontinuous deletion of 8-bp instead of the previously identified common 8-bp deletion in Pusa 1121. Kovach *et al.* (2009) discovered eight allelic variants of the *BADH2* gene by sequencing wild and cultivated rice accessions representing 38 countries in Asia. These alleles evolved during the course of evolution across various geographic locations and populations. They also confirmed the absence of the 8-bp deletion allele in wild rice (*O. rufipogon* and *O. nivara*). These variants include a 2-bp deletion in exon 1 (*tropical japonica*), a 1-bp insertion in 10th exon (*tropical japonica*), a 1-bp deletion in 10th exon (*indica*), a G/T SNP in the 10th exon (*aus*), 3-bp insertion in the 13th exon (group V), C/T SNP in the 13th exon (*tropical japonica*), 1-bp insertion in the 14th exon (*aus*) and G/T SNP in the 14th exon (*tropical japonica*). Another novel allelic variant having a deletion of 803-bp between exons 4 and 5 of the *BADH2* allele was discovered by Shao *et al.* (2011) in the "Zaimiaoxiangnuo" rice variety. They also discovered a unique allelic variant having portions of exons 4-5 and an 806-bp deletion in intron 4 by sequencing 549 rice accessions from 15 counties, including 516 fragrant and 33 non-fragrant varieties (Shao *et al.*, 2013). In their study, Myint *et al.* (2012) performed a sequencing analysis of aromatic rice landraces from Myanmar. They discovered a 3-base pair insertion (TAT) in exon 13 of the Pathein Nyunt and Yangon Saba varieties. In the fragrant rice cultivar "Nankai 138", a new variant was found that had an 8-bp insertion in the promoter as well as a 3-bp deletion in the 5' UTR (untranslated region). Additionally, 8-bp insertion was also found in the promoter region of exon 7 (Shi *et al.*, 2014). A study conducted by Ootsuka *et al.* (2014) involved screening various Japanese fragrant landraces for potential mutations in the *BADH2* gene. During the study, a previously unknown allele with a G to T substitution at the exon 1-intron 1 junction was discovered in the 'Nioi-mochi 2' landrace. Using PCR-based sequencing, 30 rice accessions (25 scented and 5 unscented) were sequenced. Exon 12 of the *BADH2* gene has a 3-bp deletion in a novel allelic variation of this gene (He and Park, 2015). Using a searchable SNP-Seek database with SNPs and InDels, allelic variations for the *BADH2* gene (including the -1326 bp upstream area) were examined in 76 aromatic rice cultivars from the 3000 rice genome project. From this group, 39 rice types have either badh2-E7 (8-bp deletion on exon 7) or badh2-p (8-bp insertion in the promoter region). A short grain rice cultivar called "Seeragasamba" had its entire genome sequenced. It was found that the promoter region of "Seeragasamba" contains an 8-bp insertion (Bindushree *et al.*, 2015). Witnana *et al.* (2020) identified a SNP mutation in the 9th exon of the Thai rice cultivar known as 'E Pluak'. The specific mutation was a deletion of the nucleotide T. The sequence analysis of the promoter region of aromatic Kagesali and Kalakrishna revealed a 250-bp deletion (Chandanshive *et al.*, 2024), which is distinct from the 8-bp insertion of Shi *et al.* (2014).

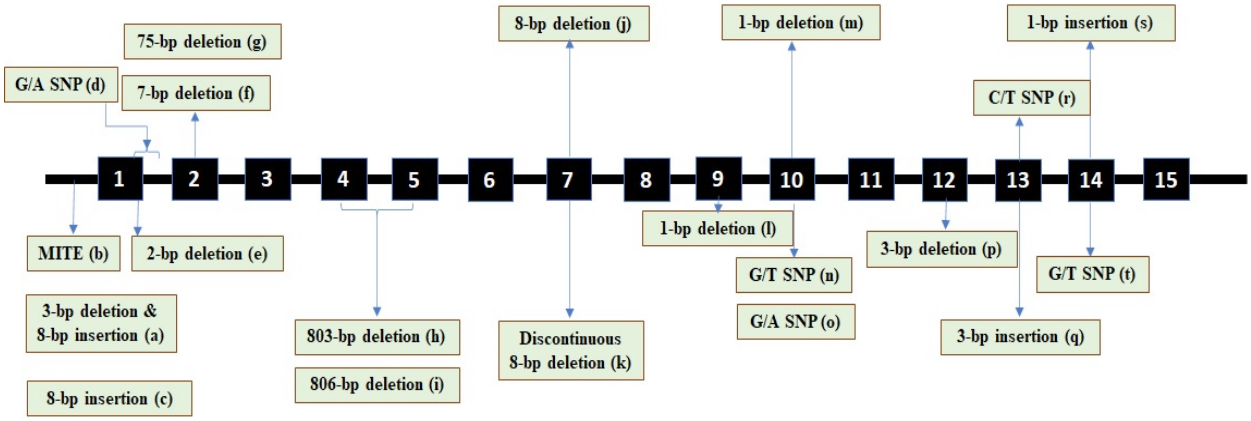

Fig. 2: Allelic variants of *BADH2* gene of aromatic rice (a) A 3-bp deletion in the 5′ UTR and an 8-bp insertion in the promoter (Shi *et al.*, 2014) (b) A miniature interspersed transposable element (MITE) insertion in promoter region (Bourgis *et al.*, 2008) (c) 8-bp insertion in the promoter (Bindusree *et al.*, 2015) (d) G/A SNP at the junction of exon 1 and intron 1 (Ootsuka *et al.* (2014) (e) 2-bp deletion in the 1st exon (Kovach *et al.*, 2009) (f) 7-bp deletion in the 2nd exon (Shi *e t al.*, 2008) (g) 75-bp deletion in the 2nd exon (Shao *et al.*, 2013) (h) 803-bp deletion between the exons 4 and 5 (Shao *et al.*, 2011) (i) 806-bp deletion in intron 4 and parts of exons 4-5 (Shao *et al.*, 2013) (j) 8-bp deletion in the 7th exon (Bradbury *et al.* 2005a) (k) 8-bp discontinuous deletion in the 7th exon (Amarawathi *et al.*, 2008) (l) 1-bp deletion in the 9th exon (Withana *et al.*, 2020) (m) 1-bp deletion in the10th exon (Kovach *et al.*, 2009) (n) G/T SNP in the 10th exon (Kovach *et al.*, 2009) (o) G/A SNP in the 10th exon (Shao *et al.*, 2013) (p) 3-bp deletion in the 12th exon (He and Park, 2015) (q) 3-bp insertion in the 13th exon (Myint *et al.*, 2012) (r) C/T SNP in the 13th exon (Kovach *et al.*, 2009) (s) 1-bp insertion in the 14th exon (Kovach *et al.*, 2009) (t) G/T SNP in the 14th exon (Kovach *et al.*, 2009).

In addition to *BADH2*, another gene, *BADH1*, located on chromosome 4, has been identified as potentially involved in the regulation of aroma in rice. *BADH1* shares a similar function with *BADH2*. Singh *et al.* (2010) reported a significant association between *BADH1* protein haplotypes and aroma score in 80 rice genotypes. But He *et al.* (2015) and Phitaktansakul *et al.* (2022) found no correlation between aroma and *BADH1* haplotypes. This may be due to the different genotypes and fragrance analysis stage. Also, *BADH1* has lower affinity for gamma-aminobutyraldehyde and higher affinity for other aldehyde substrates (Wongpanya *et al.*, 2011). The RNAi-mediated *BADH1* lines showed an absence of aroma, which suggests a physiologically discrete role of this gene (Tang *et al.*, 2014). Moreover, minor quantitative trait loci (QTLs) associated with fragrance have been detected on chromosomes 3 and 5 (Amarawathi *et al.*, 2008; Pachauri *et al.*, 2014; Talukdar *et al.*, 2017). Among these, *BADH2* remains the primary gene known to control aroma in rice, as confirmed by numerous studies (Chen *et al.*, 2008; Ashokkumar *et al.*, 2020). Multiple allelic mutations–including insertions, deletions, and single nucleotide polymorphisms–have been discovered in the *BADH2* gene. Variations that disrupt BADH2 function result in the accumulation of 2AP, the key compound responsible for the fragrance in rice. This inactivation has been linked to several specific mutations: an 8-base pair deletion and three SNPs in exon 7 (Bradbury *et al.*, 2005a); a 7-base pair deletion in exon 2 on chromosome 8 (Shi *et al.*, 2008); and an 803-base pair deletion between exons 4 and 5 (Shao *et al.*, 2011). There is also potential to investigate the biochemical and functional impacts of other allelic variants further.

7. Molecular mapping and aroma specific functional markers

During the 1980s, researchers devised physical methods for determining aroma by chewing the vegetative parts, heating the vegetative parts in water (Nagaraju *et al.*, 1975), or using the alkali method (Sood and Siddiq, 1978). First Ahn *et al.* (1992) identified a RFLP marker, namely RG28 on chromosome 8, which is closely linked (4.5 cM) to the aroma gene by studying near isogenic lines of Lemont and Aromatic Lemont. It can be used for early selection of fragrant genotypes and for revealing the homozygous or heterozygous condition of the aroma locus. Pinson (1994) observed the recessive nature of the fragrance gene and reported one gene in four rice varieties, i.e., A-301, Della-X2, PI 457917, and Jasmine 85, and two genes in four rice varieties, i.e., Amber and Dragon Eyeball 100. Lorieux *et al.* (1996) identified one major gene for aroma on chromosome no. 8 and two QTL on chromosome no. 4 and chromosome no. 12 by studying the double haploid population of IR 64 × Azucena. SSR based codominant markers were developed for selection of fragrant type

rice (Garland *et al.*, 2000; Cordeiro *et al.*, 2002). Jin *et al.* (2003) reported a single nucleotide polymorphism marker, 'RSP04, linked with the fgr gene. Madhav *et al.* (2010) developed a tightly linked SSR based marker 'ARSSR-3', which is 97 kb away from the *BADH2* gene for selection of aroma trait in marker assisted breeding programme. While the initial markers were random, subsequent research has focused on development of genic markers located within genes, for more precise selection of the aroma trait in rice breeding. A single-tube allele-specific amplification (ASA) assay targeting an 8-bp deletion in exon 7 was developed by Bradbury *et al.* (2005b) to distinguish between rice genotypes with and without fragrance. Later, Shi *et al.* (2008) developed two pairs of functional primers specific to the 7-bp deletion in exon 2 and the 8-bp deletion in exon 7. Amarawathi *et al.* (2008) developed another set of functional primers (nksbad2F and nksbad2R) targeting an 8-bp deletion in exon 7 of the *badh2* gene. In another study, Sakthivel *et al.* (2009) reported six functional primer pairs to detect the 8-bp deletion in exon-7 of rice chromosome 8. Another functional primer (FMbadh2-E4-5) specific to the 803-bp deletion between exon 4 and exon was designed by Shao *et al.* (2011). To check the presence of 3-bp insertion in exon 13 of BADH2 gene a PCR based marker 3In2AP was developed (Myint *et al.*, 2012). Functional markers targeting base substitution in the intron of exon 2, exon 7, and the p-5'UTR region of the *badh2* allele were developed to detect aroma (Shi *et al.*, 2014). A CAPS-based novel marker, Bad2.7CAPS, was developed to identify varieties possessing a nucleotide insertion 'G' in the 14th exon of *BADH2* gene (Dissanayaka *et al.*, 2014). He and Park (2015) developed six pairs of functional markers (FMU1-2, FME2-7, FME7, FME12-3, FME13-3, and FME14I) specific to a 5-bp deletion in the 5' UTR, a 7-bp deletion in exon 2, an 8-bp deletion in exon 7, a 3-bp deletion in exon 12, a 3-bp insertion in exon 13, and a 1-bp insertion in exon 14 of the *badh2* gene. Sheng *et al.* (2019) designed a new InDel marker 'Badh2-1' specific to 8-bp deletion located in the 7th exon of Badh2. A Kompetitive allele specific PCR assay was developed to characterize the 8-bp functional deletion in the *BADH2* gene (Addision *et al.*, 2020). A very recent technique, Kompetitive Allele Specific PCR (KASP), was used to develop two primer pairs (SNP badh2-E2 and SNP badh2-E7) that are specific to the 7-bp deletion in exon 2 and the 8-bp deletion in exon 7 (Li *et al.*, 2020). Zeng *et al.* (2022) developed and validated two real-time PCR SNP molecular markers specific to 806 bp deletion between exon4-5. A novel KASP marker was designed and validated to detect 1-bp insertion in exon 14 of *badh2* gene (Pingyong *et al.*, 2023). In the field of crop improvement, genetic markers have proven to be a valuable tool for identifying desirable traits and selecting individuals with those traits. The discovery of the *BADH2* gene and its various allelic variants has opened up a new avenue for researchers to improve crop yields and quality. To better understand the implications of these allelic variants, researchers have developed specific markers for these variants. These markers can be used to screen germplasm during crop improvement programs, allowing researchers to selectively breed plants with desired traits.

Future scope

The distinct aroma of rice is primarily regulated by the *BADH2* gene, although there are numerous other genes that contribute to this characteristic. The vast array of germplasm resources available in India provides an opportunity to explore the genetic basis of rice aroma and identify other genes and quantitative trait loci (QTLs) responsible for this trait. In addition to studying the genetic diversity of rice germplasm, researchers can also investigate the allelic variants of the *BADH2* gene present in these lines. By doing so, they can gain a deeper understanding of the mechanisms behind rice aroma and identify potential targets for breeding programs aimed at developing rice varieties with desirable aromatic properties. Overall, the diversity of aromatic rice germplasm in India presents a valuable resource for researchers seeking to understand the genetic basis of rice aroma and develop improved rice varieties with enhanced flavour and fragrance.

Conclusion

Rice is a staple food for more than half of the world's population, and aromatic rice, a special group of rice with a distinct fragrance and grain quality, originated in the foothills of the Himalayas. Aromatic rice displays tremendous diversity in the form of landraces and improved cultivars. The aroma of rice is a complex trait that is influenced by various factors, such as soil and temperature. The *BADH2* gene, located on chromosome number 8, primarily governs the aroma in rice. The non-functional allele of aroma is responsible for the accumulation of 2-acetyl-pyrroline in rice, which is

the main compound responsible for its aroma. More than twenty allelic variants have been identified in the *BADH2* gene, some of which directly affect the fragrance trait. These allelic variants have been discovered across germplasm from different countries. The most common allele found is the 8-bp deletion in the 7th exon of the *BADH2* gene. Molecular markers have been developed to select desirable aromatic types during breeding programmes, making them very useful for breeders when planning breeding programmes. This review provides insight into the diversity of aromatic rice in India, the allelic variants identified, and the molecular markers developed, which can aid breeders in their breeding programmes for aroma.

Authors' Contributions

All authors contributed equally for preparing the final version of the manuscript.

Conflict of Interest

Authors declare no conflict of interest.

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