Available online at www.sciencedirect.com

ScienceDirect

Rice Science, 2023, 30(4): 294−305

Review

Germplasm Resources, Genes and Perspective for Aromatic Rice

Prafulla Kumar BEHERA, Debabrata PANDA

(*Department of Biodiversity and Conservation of Natural Resources, Central University of Odisha, Koraput 764 003, Odisha, India*)

Abstract: Aromatic rice is considered an important commodity in the global market because of its strong aroma and eating and cooking quality. Asian countries, such as India and Pakistan, are the leading traders of Basmati rice, whereas Thailand is the major supplier of Jasmine rice in the international market. The strong aroma of rice is associated with more than 300 volatile compounds, among which 2-acetyl-1-pyrroline (2-AP) is the principal component. 2-AP is a phenotypic expression of spontaneous mutations in the recessive gene *OsBadh2* or *Badh2*. The present review focuses on the origin, evolution and diversity of genetic resources of aromatic rice available worldwide. A brief discussion is presented on the genes responsible for quality traits along with details of their molecular genetics. This compilation and discussion will be useful for future breeding programs and the biofortification of quality traits of aromatic rice to ensure food security and nutritional need.

Key words: aromatic rice; 2-acetyl-1-pyrroline; polyamine degradation pathway; quality trait

Aromatic or fragrant rice is considered the best quality rice because it fulfills all desirable characteristics, and has a global identity (Hinge et al, 2019). In recent years, Basmati and short and medium-grain non-Basmati fragrant rice varieties are gaining popularity globally, not only in Asia but also among the consumers of Europe and America (Ashokkumar et al, 2020). India and Pakistan are the leading traders of Basmati rice, whereas Thailand is the major supplier of Jasmine rice in the international market (Singh et al, 2019). Along with Basmati rice, Indian traditional farmers cultivate many short and medium-grain non-Basmati scented rice varieties with high aroma and market value (Singh et al, 2019). 2-acetyl-1-pyrroline (2-AP) is identified as the principal volatile compound responsible for the aroma or fragrance of rice (Butterly, 1982; Chakraborty et al, 2016; Luo et al, 2022), and it is biosynthesized via the polyamine degradation pathway or other alternative pathways (Huang et al, 2008; Sakthivel et al, 2009). Notably, other volatile compounds, such as alcohol, aldehyde, ester and ketone, also contribute to aroma production in rice (Ashokkumar et al, 2020; Chen et al, 2022). The *fgr* gene (single recessive gene) on chromosome 8 controls the flavor and fragrance of rice (Bradbury et al, 2005; Peng et al, 2018), and it encodes betaine aldehyde dehydrogenase (BADH2). Inhibition, deletion or mutation in the *fgr* gene results in function loss of BADH2 enzyme, elevating levels of 2-AP precursors and accumulating 2-AP to generate aroma in aromatic rice (Shan et al, 2013; Chakraborty et al, 2016; van Quoc et al, 2023). Except for *Osbadh2* gene, a few other candidate genes have been identified by integration mapping and map-based cloning, such as *Osbadh1*, *OsGly* and *OsP5CS*. These genes are located on different loci and might be involved in producing high concentrations of 2-AP and hence aroma in rice (Prodhan and Shu, 2020).

Most of the studies in this field are mainly focused on studying Basmati, Jasmine and other popular rice

Received: 13 November 2022; **Accepted:** 2 March 2023

Corresponding author: Debabrata PANDA (dpanda80@gmail.com)

Peer review under responsibility of China National Rice Research Institute

http://dx.doi.org/10.1016/j.rsci.2023.03.011

from different countries. However, analysis of the quality of Indian non-Basmati aromatic short and medium-grain rice needs to be emphasized. Although a few of studies have performed initial characterization involving the determination of origin and biochemical and genetic pathways for aroma production (Nadaf et al, 2016; Wakte et al, 2017), a detailed understanding of several fronts is pending. These include determining allelic variants of aroma-related genes, the relationship between 2-AP and other volatile compounds for generating aroma, genes regulating aroma and quality traits, and future application of omics and gene editing technologies for improving different aromatic rice varieties. In this review, we summarized recent advances in availability of aromatic rice germplasm and understanding of genes responsible for quality traits, the association of the 2-AP pathway and volatile compounds for aroma, and molecular genetics of fragrance. These details will be useful for the future breeding program for the biofortification of quality traits of aromatic rice to ensure food security and nutritional need.

Taxonomy, historical evidence, and evolution of aromatic rice

Several studies have been conducted on the origin and differentiation of aromatic rice in many countries globally. Ancient records suggested that the origin of scented rice is in the Indian subcontinent, and several pieces of evidence mentioned that fragrant rice is cultivated in China and other South Asian countries (Singh et al, 2019). Ancient Hindu religious books, such as *Charaka Samhita* (600 BC), have mentioned aromatic rice cultivation (Singh et al, 2019). Glaszmann (1987) conducted a popular study using 1 688 rice cultivars collected from various countries (China, Iran, Pakistan, Thailand, Vietnam, Cambodia, India, Myanmar, Bangladesh, Afghanistan and Indonesia), and revealed the differentiation of 95% rice cultivars into six groups (Group I to Group VI), whereas Group V represents *aromatic* rice. The *aromatic* rice includes rice germplasms from Afghanistan, Bangladesh, China, India, Iran, Myanmar and Pakistan. The grouping of rice illustrated by Glaszmann (1987) was further supported by analysis of diverse germplasms using different molecular markers (Roy et al, 2020). Garris et al (2005) analyzed 234 rice (*Oryza sativa*) varieties by applying 169 simple sequence repeat (SSR) markers and 2 chloroplast loci, and divided the studied rice germplasms into 5 genetic groups: *aus*, *aromatic*, *indica*, *tropical japonica*, and *temperate japonica*. Caicedo et al (2007), employing single nucleotide polymorphism (SNP) markers, also classified rice into five genetically distinct subpopulations, the same as Garris et al (2005). Based on the phylogenetic analysis, the *indica* and *aus* groups belong to *O. sativa* L. spp *indica*, whereas *aromatic*, *temperate japonica* and *tropical japonica* groups are the members of *O. sativa* L. spp *japonica* (Hinge et al, 2019). The diversity center of aromatic rice is the foothills of the Himalayan region, Uttarakhand, Bihar and Tarai region of Nepal, where scented rice varieties are being cultivated in large numbers, and over the period, aromatic rice has been spreaded to other countries such as Afghanistan, Bangladesh, Iran, Iraq and Thailand (Khush, 2000; Vemireddy et al, 2021). It is also believed that aromatic rice in European countries, such as Italy and France, is introduced from Asian countries (Roy et al, 2020).

Germplasm resources and worldwide distribution of aroma rice

For the past half-century, the demand for aromatic rice has been continuously increasing in the local and international markets because of its strong aroma (Verma et al, 2019). The strong aroma and high grain quality of Basmati rice are crucial characteristics that have placed it in a unique varietal group in international trade and among consumers (Kishor et al, 2020). Furthermore, several countries, such as India, Afghanistan, Vietnam, China, the Philippines, and the USA, are involved in producing special aromatic rice cultivars (Table 1). The name 'Basmati' means 'the fragrant one' in Hindi literature, and it is frequently referred to as the 'King of rice' (Pachauri et al, 2010). The Basmati rice of Indian states in the Indo-Gangetic plains on the Himalaya foothill regions, such as Delhi, Jammu & Kashmir, Haryana, Punjab, Uttarakhand, and some regions of Uttar Pradesh and Himachal Pradesh, has achieved geographical indication product tag since February 2016 (Roy et al, 2020).

India is one of the most important rice exporters in the international market for exporting quality nutritious rice (Verma and Srivastav, 2017; Roy et al, 2020). Between April 2018 and March 2019, India exported 4.4 million tons of Basmati rice to global market valued at 4 722 million USD and 7.6 million tons of non-Basmati rice valued at 3 048 million USD (Prasad et al, 2020). The popular Basmati rice varieties are Taraori Basmati and Basmati 370

Table 1. Genetic resources of popular aromatic rice varieties distributed throughout the world.

Country	Popular variety	Reference
Afghanistan	Bahra, Lawangi, Sela Takhar, Bala, Lawangin, Pashadi, Germa Bala, Sarda Bala, Luke Qasan, Torishi, Sela Doshi, Surkha-Bala, Pashadi Konar	Singh, 2000; Itani, 2002
Bangladesh	Kataribhog, Bau-pagal, Badshabhog, Kala Namak, Dadkhani, Kalazira, Banshful, Kataribagh, Tulshimala, BR36, BR6, BR26, Dolhabhog (BR5), Chinigura, BRRI dhan 70, Binadhan 13, BRRI dhan 38	Anik and Talukder, 2002; Vemireddy et al, 2021
Cambodia	Somali, Phka Rumduol, Phka Rumdeng, Phka Roment	Pachauri et al, 2010; Roy et al, 2020
China	Xianggeng 3, Xiangyou 63, Zhe 9248, Ganwanxian 22, SR5041, Dechangxiangmi, Beijingkoutou, Shuangzhuzhan, Xiangnuo 4, Tainung Sen 20, Yongshunxingdao, Qingbuxiangjingmi, Congjiangxixiangmi, Jingxixiangdao, Huanglongxiangmi, Jingcixiangdao, Jiangyongxiangdao, Qufuxiangmi	Yang et al, 2012; Verma et al, 2019
India	Basmati 370, Haryana Basmati 1, Kalanamak, Ranbir Basmati, Taraori Basmati, Basmati 386, Type 3, Pusa Basmati 1, Pusa Basmati 1121, Punjab Basmati 1, CSR30, Pusa 33, Amritsari Basmati	Nagaraju et al, 2002; Kiani et al, 2012; Singh et al, 2018; Verma et al, 2019
Indonesia	Rojo Lele, Bengwan Solo, Pare Kembang, Batang Gadis, Mentik Wangi, Sukanandi, Sinyanur, Pulu Mandoti, Pandanawangi, Gunung Perak	Kamath et al, 2008; Pachauri et al, 2010; Verma et al, 2019
Iran	Tarom Mahalli, Anbar-boo, Mirza, Fajr, Champa, Mir tarom, Hassani, Shiroudi, Nemat, Mehr, Mosa Tarom, Poya, Domsiah, Hasan, Sadri, Hashemi	Fukuoka et al, 2006; Kiani et al, 2012; Vemireddy et al, 2021
Iraq	Anbarboo	Pachauri et al, 2010
Japan	Miyakaori, Iwaga, Sari Queen, Kouikuka 37, Hieri, Jakou, Kabashiko, Oitakoutou	Hien et al, 2007; Ootsuka et al, 2014
Malaysia	MRQ74	Vemireddy et al, 2021
Myanmar	Boke Hmwe, Balugyun, Taungpyan Hmwe, Nyakywe, Nama Tha Lay, Pawsan Hmwe	Pachauri et al, 2010
Nepal	Basamati Pahade, Basmati Gola, Brahmaphool, Jetho Budho, Rato Basmati, Kalo, Basmati Uzarka, Basmati Dhan, Lamo, Basmati Red	Pachauri et al, 2010; Kishor et al, 2020
Pakistan	Basmati Pak, Basmati 385, Super Basmati, PK50005-3, Basmati 185, Basmati 50021-1, Basmati 377, Sathi Basmati	Khush, 2000; Kishor et al, 2020
Thailand	Buer Neo Moo, Hawm Klong Luang, Buer Ner Moo Pho Phi, Hawn Mali, RD15, Baow Hawm 62, Buer Ner Moo Phardo, Jao Mali, KDML105, Siamati, Hawm, Som Hung, Hawm Baow, RD6, Hawm Supanburi, Pla Sew, Nahng Nuan, Khao Dawk Mali, Thung Kula Rang-Hai Tahi Hom Mali	Itani et al, 2004; Pachauri et al, 2010; Verma et al, 2019; Roy et al, 2020
the Philippines	Azucena, Milagrosa, Binicol, Mangareez, Milfore 6(2)	Pachauri et al, 2010; Ootsuka et al, 2014
the USA	Texamati, Della, Carolina, A201, Dellamont, Kasmati, Jasmine 85, Sierra, Delrose, Delmont, Jazzman, JES	Khush, 2000; Verma et al, 2019
Vietnam	Di Huang, Tam Xuan Hai Hau, VD 20, Nang Thom, Nep Hoa Vang, Tam On, Nang Huong Ran, Nang Thom Muong, Tam Canh, Lam Thao, Hai Hau, Nep Bac, Tam Xoan, Can Duoc, Nep Rong, Lua Tam, Nam Dinh	Hien et al, 2007; Pachauri et al, 2010; Verma et al, 2019

(traditional Basmati variety), and other improved Basmati genotypes include Pusa Basmati 1 (PB1) and Pusa Basmati 1121 (PB1121) (Table 1). In general, the traditional aromatic cultivars have undesirable characteristics, such as low yield, photoperiod sensitivity, long growth period, and lodging susceptibility, and this aromatic rice is cultivated in an area of 600 000 hm^2 in Indian states, such as Assam, West Bengal, Chhattisgarh, Maharashtra, Odisha, Madhya Pradesh and Bihar for domestic consumption (Prasad et al, 2020). Non-Basmati aromatic rice is far superior to Basmati rice in terms of various quality-related characteristics, including superb scent, grain length/width (L/W) ratio, grain elongation after cooking, texture, appearance and taste, and hence Non-Basmati aromatic rice is high in demand (Dela Cruz and Khush, 2000; Verma et al, 2012, 2013, 2015; Nadaf et al, 2016). Singh (2000) reported that milled Basmati rice has high-quality attributes such as grain length > 6.6 mm, grain width < 2.0 mm, L/W ratio > 3.0, creamy white, translucent, and long slender grain type, high rice recovery (> 40%), optimal amylose content (20%–22%), elongation ratio (> 1.80), sweet taste, and strong aroma. Undesirable characteristics (such as low yield, temperature sensitivity, and tall stature) of traditional Basmati rice prompt the development and release of many elite Basmati cultivars by different stakeholders of the Government of India, such as Basmati 370 (the release year 1933 to the 1980s) (Ramaiah and Rao, 1953), PB1 (the release year 1989), Taraori Basmati (the release year 1996) (Singh and Singh, 2010), and PB1121 (the release year 2003) (Singh V P et al, 2018; Roy et al, 2020).

Except for India, several other countries, including Pakistan (Basmati rice), Thailand (Jasmine rice), Cambodia, Iran (Sadri rice), the USA, China, Indonesia, Malaysia, Japan, Vietnam, Afghanistan and Bangladesh, also produce valuable aromatic rice with a high market value in the international market (Table 1) (Pachauri et al, 2010; Verma et al, 2019; Vemireddy et al, 2021). Pakistan is one of the major traders of Basmati rice globally and produces improved Basmati varieties, such as Basmati 185 and Super Basmati. Notably, Super Basmati is considered the most popular and premium variety (Singh et al, 2000). Thailand produces Jasmine rice, which contains novel aroma components and is the most famous rice in this country. Khao Hawm (known as the Thai fragrant rice) is a national pride of Thailand, and every household cultivates it for personal consumption only. However, Khao Dawk Mali, which has a higher cooking quality, is considered to have a high market value (Singh et al, 2000; Verma et al, 2019; Roy et al, 2020). Jasmine rice Thung Kula Rang-Hai Tahi Hom Mali from Thailand is the first Asian rice product to be registered with geographical indication in the European Union (Vemireddy et al, 2021). Further, Hong Kong of China and Singapore are the largest market of Jasmine rice (Verma et al, 2019; Roy et al, 2020). Cambodia and Laos also cultivate Jasmine rice, such as Phka Rumduol and Phka Rumdeng (Roy et al, 2020). In Iran, rice is the second staple food after wheat (Kiani et al, 2012). The rice produced in Iran can be classified into three categories: Sadri, Chamapa and Gerdeh (Nematzadeh et al, 2000). Sadri rice is considered the most acceptable category in the Iranian market because of its strong aroma and extra-long slender grain type, fetching high premium prices (Roy et al, 2020) (Table 1). In the USA, three major types of aromatic rice are Basmati type, long grain type, and Jasmine type. The long grain type aromatic rice varieties in the USA include Della, Sierra, Delrose, A201 and Delmont. Further, Jasmine 85, Jazzman and JES (private company varieties) are examples of Jasmine type, whereas Calmati 201 and Calmati 202 are examples of Basmati type (Verma et al, 2019; Vemmireddy et al, 2021). China is a massive rice producer, and the major popular traditional scented rice varieties in China include Yongshunxiangdao, Qingbuxiangjingmi, Congjiangxixiangmi, Jingxixiangdao, Huanglongxiangmi, Jingcixiangdao, Jiangyongxiangdao and Qufuxiangmi (Yang et al, 2012; Verma et al, 2019). In China, semi-aromatic rice is preferred (Singh et al, 2000), and the improved scented rice varieties include Tainung Sen 20, Ganwanxian 22, Shuangzhuzhan, and Zhe 9248 (Verma et al, 2019). Bahra is the prominent aromatic rice variety of Afghanistan (Singh et al, 2000), and other popular varieties of Afghanistan are Bala, Lawangi and Pashadi (Table 1). In Bangladesh, aromatic rice varieties have a major market potential and are cultivated organically without using fertilizers (Anik and Talukder, 2002; Tama et al, 2015). Some of the principal cultivars of scented rice grown in several locations of Bangladesh include Badshabhog, Tulshimala, Chinigura, Kataribhog, Banshful and Dadkhani (Table 1).

Rice flavor chemistry and volatile compounds reported in aroma rice

Approximately 300 volatile compounds have been found in rice according to Wakte et al (2017). Hydrocarbon volatile compounds, such as alcohol, aldehyde and ketone, also enhance aroma production in aromatic rice (Ashokkumar et al, 2020). Hexanal is a linoleic acid derivative and an important volatile compound in rice that contributes to the green, fruity, and grass flavor of lower odor (Hu et al, 2020). The hexanal content in scented rice from the USA and Thailand is 543–2 541 ng/g (Bergman et al, 2000). Furthermore, important heterocyclic compounds responsible for aroma in rice include 2-pentylfuran, 2-ethyl-3,5-dimethylpyrazine and 2-methyl furan. A high content of 2-pentylfuran (the most important alkylfuran) is reported in aromatic rice with a nutty odor (Grimm et al, 2011; Hinge et al, 2016). Phenol and other alcohols (1-hexanol and 1-nonanol) have been shown to contribute to rice flavor (Hu et al, 2020). Yang et al (2008) reported that, in cooked white rice, alcohol and aldehyde constitute approximately 20.3% and 60.9%, respectively, of the total volatile compounds. Mathure et al (2014) reported that the contents of hexanol and 1-octen-3-ol are significantly higher in Basmati varieties than in non-Basmati rice. In addition, Sansenya et al (2018) revealed that benzyl alcohol is to be high amounts in aromatic and Basmati rice in comparison to non-aromatic and non-Basmati rice, respectively, and hence provides a sweet flavor.

2-AP is principal fragrant compound

2-AP is the principal and key aromatic compound responsible for the aroma of rice (Wakte et al, 2017; Hu et al, 2020). Buttery (1982) first identified 2-AP as the most predominant volatile compound that provides rice with a popcorn-like aroma and low odor threshold. The 2-AP molecule is extremely unstable due to the presence of a pyrroline ring, and hence is one of the key aroma and flavor molecules in fragrant rice, and it produces a popcorn scent. Therefore, very low quantities of 2-AP can be sensed by the human nose (Hu et al, 2020). The methyl ketone group of 2-AP can react with 2,4-dinitrophenyl hydrazine (ketone detecting reagent) to form 2-acetyl phenyl hydrazone, an orange-red colored derivative compound, which is utilized to detect 2-AP in scented rice (Kumari et al, 2019). 2-AP levels can be found in different parts of aromatic rice plants except for roots (Maraval et al, 2010), but in the case of non-aromatic rice, the concentration of 2-AP is too low to be easily recognized (Prodhan and Shu, 2020). There is controversy regarding the 2-AP formation in aromatic rice. Some researchers have demonstrated that 2-AP is produced while cooking aromatic rice as a result of the Maillard reaction among different carbohydrates and amino acids (Hofmann and Schieberle, 1998). In contrast, Yoshihashi (2002) suggested that 2-AP is produced in aerial parts of rice plants during the growing season. The highest 2-AP content is detected at five weeks after heading and decrease to 20% of the maximum content after 7 weeks of the heading stage in brown rice (Hu et al, 2020). Tanchotikul and Hsieh (1991) estimated the levels of 2-AP in several scented rice, such as Della (76.2 μg/L), Jasmine (156.1 μg/L), and Basmati 370 (87.4 μg/L). Bounphanousay et al (2008) suggested that brown rice contains 50% more 2-AP than milled rice, and showed that 2-AP concentration in scented rice is greatly affected by the environmental and growth conditions of rice plants. For instance, early harvesting and low planting density enhance the aroma of scented rice. Furthermore, 70%–80% humidity during grain filling stage and temperature of about 20 ℃–32 ℃ during day time increases 2-AP concentration and aroma in fragrant rice (Vemireddy et al, 2021). Hence, to distinguish aromatic and non-aromatic rice varieties, in addition to 2-AP availability and concentrations, understanding of other associated attributes is required.

Biosynthesis pathway of 2-AP

The polyamine degradation pathway is considered the main pathway of 2-AP biosynthesis (Prodhan and Shu, 2020). Polyamine is an organic compound consisting of more than two amino groups. Vanavichit et al (2005) first proposed that 2-AP is synthesized through the polyamine pathway. In the polyamine degradation pathway, the polyamine (consisting of arginine, putrescine, ornithine and others) is converted to γ-amino butyraldehyde (GABald), which is a precursor of γ-aminobutyric acid (GABA). The GABald spontaneously cyclizes to Δ^1-pyrroline, which is the precursor of 2-AP and is considered an important factor in regulating 2-AP biosynthesis (Chen et al, 2008). In non-aromatic rice (Fig. 1), GABA is formed from GABald by regulating the functional BADH2 enzyme (encoded by *OsBadh2* gene) that inhibits 2-AP biosynthesis. In aromatic rice (Fig. 1), the non-functional BADH2 enzyme (encoded by *osbadh2*) does not convert GABald to GABA, causing accumulation of GABald and generating 2-AP (Bradbury et al, 2008). Hence, 2-AP can be produced enzymatically via glycolysis and polyamine degradation pathways or non-enzymatically via direct formation of 2-AP. In the direct synthesis pathway (BADH2 independent pathway), glutamate is converted to the precursor of proline that reacts with methylglyoxal to produce 2-AP (Huang et al, 2008). In aromatic rice, proline, ornithine and glutamate act as nitrogen sources, GABald, 1-pyrroline and Δ^1-pyrroline act as a source of pyrroline ring, and methylglyoxal provides carbon for 2-AP synthesis (Prodhan and Shu, 2020).

Genetic regulation of aroma in scented rice

Mutations of *Badh2* gene exploration of allelic variant locus

The aroma gene identification was carried out by Bradbury et al (2005), and the role and function of *badh2* of 2-AP biosynthesis were suggested by Bradbury et al (2008) and Chen et al (2008). After the discovery of the *Badh2* gene, many studies have been conducted to explore the allelic variants at the *Badh2* locus (Sakthivel et al, 2009; Ghosh and Roychoudhury, 2020). The *Badh2* gene consists of 14 introns and 15 exons, which codes a protein with 503 amino acids. By comparing the significant variations between aromatic and non-aromatic rice, Bradbury et al (2005) detected the major mutations in the *badh2* gene, such as an 8 bp deletion and 3 SNPs in exon 7. Shao et al (2011) revealed a 7 bp deletion in exon 2 and 803 bp deletion between exon 4 and 5. In addition, Shi et al (2014) and Ootsuka et al (2014) reported single nucleotide deletion in intron 1, exon 1 splice sites, promoter and 5′-untranslated regions. Similarly, various mutations in the *Badh2* gene locus were reported by Sakthivel et al (2009). Hence, mutations in the coding or regulatory regions of the *Badh2* gene result in BADH with no biological activity, generating

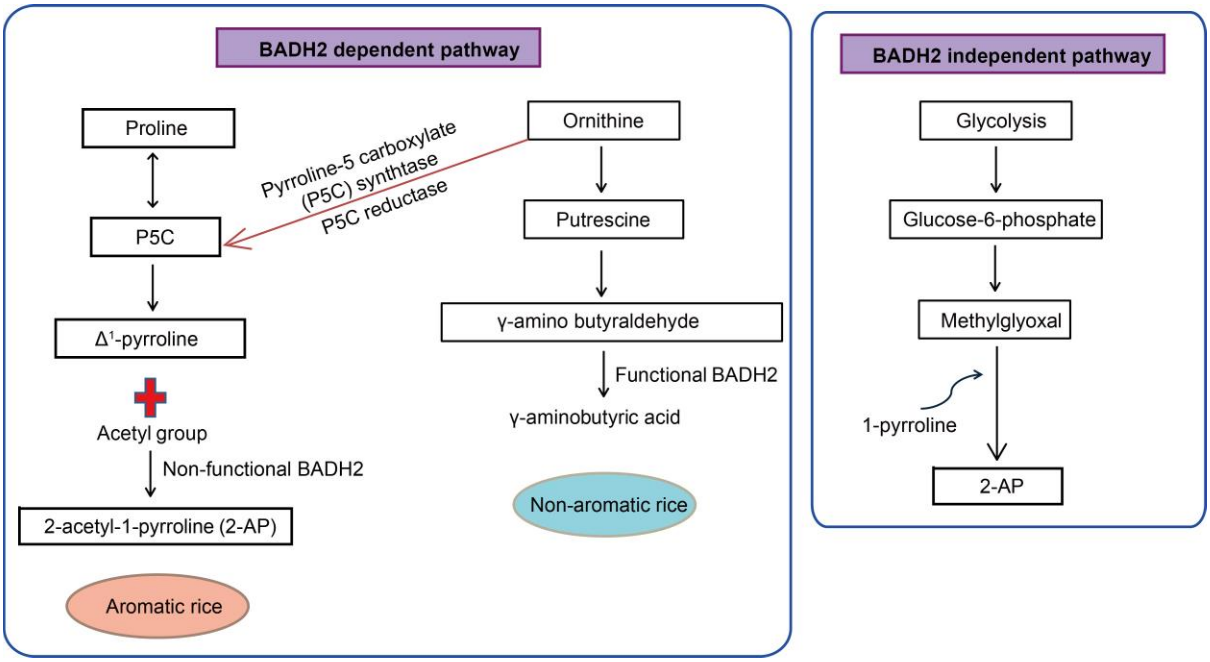

Fig. 1. 2-Acetyl-1-pyrroline (2-AP) biosynthetic pathway (BADH2 dependent and BADH2 independent) for aroma production in aromatic rice.

fragrance in aromatic rice (Peng et al, 2018). These studies suggested the existence of gene or allele level diversity for aroma in the fragrant rice gene pool (Kovach et al, 2009; Ghosh and Roychoudhury, 2020).

Peng et al (2018) reported that a single recessive gene (*fgr*) on chromosome 8 controls flavor and fragrance in rice, which has been mutated and expresses only in homozygous recessive conditions (Ahn et al, 1992). Subsequently, many researchers revealed the complexity of aroma and reported that the inheritance of aroma is regulated by one to three dominant or recessive genes or by QTLs (Chen et al, 2006; Amarawathi et al, 2008). The *fgr* gene encodes BADH homolog 2 (badh2), and an 8-bp deletion was reported in the exon 7 region of chromosome 8, which causes loss of *Badh2* protein function, resulting in fragrance formation in aromatic rice, such as Basmati and Jasmine (Sakthivel et al, 2009; Peng et al, 2018). Therefore, it seems that the *Badh2* gene is associated with the *fgr* gene, which regulates the aroma in aromatic rice (Peng et al, 2018).

Molecular aspect of fragrance in scented rice

A single recessive gene (*Badh2*) and many QTLs may also govern the aroma trait (Sakthivel et al, 2009; Prodhan and Shu, 2020). First QTL mapping was carried out by Lorieux et al (1996) on chromosomes 4 and 12 for rice fragrance. Till now, a few specific aroma-related QTLs have been reported. The genetic mapping and map-based cloning lead to the interpretation of the number of candidate genes associated with aroma, and to date, *OsBadh2* or *badh2* gene on chromosome 8 is considered the candidate gene controlling aroma in rice (Prodhan and Shu, 2020).

Table 2 lists the potential candidate genes related to the aroma of scented rice. In Basmati rice varieties, three QTLs on chromosomes 3, 4 and 8 controlling aroma were identified by Amarawathi et al (2008). Further, it was also reported that two QTLs on chromosomes 3 and 4, together with *Badh2* on chromosome 8, control fragrance in rice (Amarawathi et al, 2008; Peng et al, 2018). The locus *aro4-1* on chromosome 4 related to the *badh1* gene also control aroma (Sakthivel et al, 2009). It has been suggested that *Badh1* and *Badh2* are homologous genes, and rice gene *Badh1* is also homologous to the *Badh1* gene of sorghum and barley (Bradbury et al, 2008; Peng et al, 2018). However, He et al (2015) revealed that *Badh1* is positively correlated with salinity resistance at the germination stage of rice and the mutations reported in *Badh1* are less as compared with those reported in the *Badh2* gene (Peng et al, 2018). Therefore, the *OsBadh1* gene located on *aro4-1* QTL shows a molecular function similar to *OsBadh2*. Some pieces of evidence also suggested that at the *aro4-1* locus, along with the *OsBadh1* gene, a cluster of eight other

Table 2. Potential candidate genes and their tissue specific expression associated with aroma in rice.

Candidate gene	Chr	Response to stress	Tissue specificity	Protein interaction	Subcellular localization	Reference
OsBadh1	8	Submergence, anoxia, salinity	Flowers, roots before flowering	Glutamate synthase	Peroxisome, chloroplast, cytoplsam, nucleus	Amarawathi et al, 2008; Pachauri et al, 2014
OsBadh2	3, 4 and 8	Anoxia, salinity, submergence	Flower buds, flowers	Glutamate synthase	Chloroplast, peroxisome, cytoplasm, nucleus	IRGSP, 2005
OsP5CS1	5	Salinity, anoxia, osmoregulation	Milk grains, flower buds	Ferredoxin-dependent glutamate synthase	Chloroplast, endoplasmic reticulum, nucleus, cytoplasm, mitochondria, plasma membrane, extracellular, vacuole	Kaikavoosi et al, 2015
OsP5CS2	5	Osmoregulation, anoxia, salinity	Flower buds, flowers	Glutamate synthase	Chloroplast, extracellular, nucleus, vacuole	Kaikavoosi et al, 2015
OsGlyI	5	Salinity, anoxia	Flower buds, leaves before flowering		Chloroplast, cytoplasm	Talukdar et al, 2017
OsGlyII	3	Anoxia, salinity	Flowers, flower buds	Glyoxalase	Cytoplasm, chloroplast, nucleus, extracellular	Huang et al, 2008; Pachauri et al, 2014
OsGlyIII	3	Salinity, anoxia	Leaves and roots before flowering	Ferredoxin-nitrite reductase	Chloroplast, peroxisome, cytoplasm, Golgi apparatus	Huang et al, 2008; Pachauri et al, 2014

Chr, Chromosome; BADH, Betaine aldehyde dehydrogenase; P5CS, Δ(1)-pyrroline-5-carboxylate synthetase; GLY, Glyoxalase.

genes controls the expression of aroma. This might be assumed *OsBadh1* as candidate gene underlying *aro4-1* aroma QTL for its similar molecular function of *OsBadh2* gene (Prodhan and Shu, 2020). Another locus *aro3-1* on chromosome 3 detected by Amarawathi et al (2008) is considered a minor QTL and plays a complementary role with *aro4-1*. Talukdar et al (2017) identified that the *OsGlyI* gene, located in the region between RM169 and RM430 on chromosome 5, is involved in rice aroma through methylglyoxal. Hence, based on previously reported QTLs (Bradbury et al, 2005; Yi et al, 2009; Fitzgerald et al, 2010; Pachauri et al, 2014), *OsBadh2* (IRGSP and Sasaki, 2005) along with *OsBadh1* (Amarawathi et al, 2008; Pachauri et al, 2014), *Glyoxalase I/II/III* (Huang et al, 2008), and *Δ^1-Pyrroline-5- carboxylate synthetase* (Kaikavoosi et al, 2015) genes are considered to be also associated with the generation of aroma and high concentrations of 2-AP. Imran et al (2022) reported that transcriptional factors are also associated with aroma production, and more than 26 transcription factor families are identified, which are related to the molecular regulation of 2-AP biosynthesis in scented rice. Imran et al (2022) also detected key aroma-related genes significantly up-regulated, such as *P5CS*, *OAT*, *P5CR* and *PDH*, and they also found that transcription factors, such as WRKY, MYB, NAC, bHLH, bZIP, GATA and AP2 in the promoter region, play an important role during 2-AP regulation. Similarly, Bao et al (2021) revealed that *P5CS2*, *DAO5* and *BADH2* gene expression patterns are consistent with the accumulation pattern of 2-AP, indicating that these genes are the node genes of 2-AP biosynthesis in aromatic rice.

Genetic improvement of aromatic rice through conventional and molecular breeding

Improving aromatic rice cultivars or transferring aroma trait through traditional or conventional breeding approaches is difficult because of the significant environmental impacts and limited narrow- sense heritability of the traits. Although conventional approaches can produce high-yielding rice cultivars, the quality attributes of these cultivars are not sufficiently high as those of indigenous Basmati types (Vemireddy et al, 2021). In 1989, the Indian Agricultural Research Institute (IARI) introduced PB1, the first semi-dwarf, photoperiod-insensitive, and high-yielding Basmati variety in India, which contributes 60% of all Basmati rice exports. From 1995 to 2007, PB1 completely transformed Basmati rice production in India (Siddiq et al, 2012). Furthermore, many high-yielding Basmati varieties were improved and released in India, including Pusa Sugandha 2, Pusa Sugandha 3 and Pusa Sugandha 5. PB1121 was developed by crossing Pusa 614-1-2 and Pusa 614-2-4-3 [advanced breeding lines obtained from Basmati 370 and type 3 (traditional Basmati variety)]. It fetches a market value of > 20.8 billion USD in foreign export and accounts for 70% of the cultivated area of total Basmati cultivation in India (Singh V K et al, 2018; Vemireddy et al, 2021). PB1121 is characterized by extra-long slender grains and exceptional cooking quality. Furthermore, IARI also developed the first semi-dwarf aromatic hybrid rice variety (RH10) in the worldwide, which is a high-yielding and super-fine-grain variety (Vemireddy et al, 2021). Khao Dawk Mali 105 (KDML105) was the first Jasmine rice released in Thailand. Furthermore, RD6 (waxy variety) and RD15 (early maturing) were developed from the mutagenesis of KDML105, constituting approximately > 70% of the cultivation area for its abiotic stress (drought, salinity, and acid sulfate soils) tolerance (Vanavichit et al, 2018; Vemireddy et al, 2021).

Since conventional breeding methods are technically more challenging, less consistent and labor-intensive, molecular marker-based easy and inexpensive breeding approaches are considered (Table 3) (Siangliw et al, 2003; Samal et al, 2019; Sun et al, 2023). Pusa 1460 (improved PB1 variety in terms of bacterial blight resistance) was developed from the cross of IRBB55 and PB1, integrating *Xa13* and *Xa21* genes, by molecular-assisted breeding (Gopalakrishnan et al, 2008). Singh et al (2018) developed bacterial blight tolerant rice (Pusa Basmati 1718) by integrating *Xa13* and *Xa21* genes using molecular breeding methods. Other aromatic rice varieties with advanced bacterial blight-tolerance were developed, including IC-R28, IC-R32, IC-R42 and IC-R68 (Baliyan et al, 2018). In 2006, RD33, the first blast-resistant variety of Jasmine rice, which is photoperiod-insensitive, was released in Northern and Northeast Thailand (Vemireddy et al, 2021). Furthermore, KDML105 was employed to produce biotic and abiotic stress-tolerant varieties using molecular breeding by incorporating various genes. For instance, HM80, a submergence-tolerant variety, was produced from IR49830-7-1-2-2 and KDML105 (Siangliw et al, 2003), and HM812 (bacterial blight tolerant) was produced from IR1188 and KDML105 (Korinsak et al, 2009). It was found that HM84 was an improved KDML105 in terms of tolerances to drought, salinity, brown planthopper, and bacterial-blight (Vanavichit et al, 2018; Vemireddy et al, 2021). Singh V K et al (2018) improved the salinity resistance in PB1 by integrating *Saltol* QTL (for salt resistance) at the seedling stage through molecular breeding. In addition to conventional and molecular breeding approaches, there have been a few attempts of using genetic engineering techniques, such as RNAi technology, to decrease *OsBADH2* expression levels and consequently elevate 2-AP levels in rice. For instance, a 20-fold increase in 2-AP content was achieved using RNAi technology in Nipponbare (Ashokkumar et al, 2020). Recently, CRISPR/Cas9-mediated gene editing technology is also utilized to enhance 2-AP levels by creating novel alleles of *OsBADH2* gene (Ashokkumar et al, 2020).

Perspective

Aromatic rice is popular for its strong aroma and quality traits, such as cooking quality, long and slender grain, and grain elongation after cooking, and its suitable taste fetches a premium price. 2-AP is the major compound for aroma production. However, a few other volatile compounds have also been associated with aroma production. *OsBadh2* along with *OsBadh1*, *OsGly* and *OsP5C5* are responsible for aroma production and high concentrations of 2-AP in aroma rice. In the last four decades, the emphasis has primarily been on improving rice yield potential to feed the world's growing population. Hence, around the globe, high-yielding varieties have quickly replaced the locally cultivated low-yielding fragrant rice varieties with excellent quality traits. Improvement

Table 3. QTLs/genes incorporated/transferred to improve aromatic rice.

Developed improved variety	Target trait	Parent	QTL/gene used	Reference
HM80	Submergence resistance	IR49830-7-1-2-2 and KDML105	*Sub1*	Siangliw et al, 2003
Pusa 1460	Bacterial blight tolerance	IRBB55 and Pusa Basmati 1	*xa13* and *Xa21*	Gopalakrishnan et al, 2008
HM812	Bacterial blight tolerance	IR1188 and KDML105	*Xa21*, *xa5*, *xa33*(t), *xa34*(t) and *qBB11*	Korinsak et al, 2009
IC-R28, IC-R68, IC-R32 and IC-R42	Bacterial blight tolerance	IRBB60 and CSR30	*Xa21*, *xa13* and *xa5*	Baliyan et al, 2018
Pusa Basmati 1	Salt tolerance	FL478 and Pusa Basmati 1	*Saltol* QTL	Singh V K et al, 2018
Pusa Basmati 1718	Bacterial blight tolerant	SPS97 and PB1121	*xa13* and *Xa21*	Singh V P et al, 2018
HM84	Brown planthopper, blast resistant, and salinity and drought tolerance	Abhaya, Rathu Heenati and KDML105	*Sub1A*, *Xa21*, *xa5*, *BphQ12*, *Bph32*, *Bph3* and *BLQ1*	Vanavichit et al, 2018
Two superior BC_2F_1 recombinants	Semi-dwarf and blast tolerance	Pusa Basmati 1637 and Ranbir Basmati	*Pi9* and *sd1*	Samal et al, 2019
Improved Kalanamak lines	Semi-dwarf trait	CSR10 and Kalanamak	*Sd1*	Srivastava et al, 2019

of locally adopted short and medium-grain aromatic rice genotypes is a primary goal of breeding. Further research is required to analyze the relationship among 2-AP, other volatile compounds, aroma genes, and genes associated with the eating and cooking qualities of rice. A molecular breeding strategy is required to understand the association between aroma biology and quality traits and to achieve the production of high-quality rice for sustained food security. Finally, the application of novel technologies, such as Omics and CRISPR/Cas9 gene editing, must be applied to enhance the aroma and quality of aromatic rice available globally for nutritional and food security.

ACKNOWLEDGEMENT

The authors are grateful to University Grant Commission, New Delhi, India for providing Non-National Eligibility Test fellowship.

REFERENCES

Ahn S N, Bollich C N, Tanksley S D. 1992. RFLP tagging of a gene for aroma in rice. *Theor Appl Genet*, **84**(7): 825–828.

Amarawathi Y, Singh R, Singh A K, Singh V P, Mohapatra T, Sharma T R, Singh N K. 2008. Mapping of quantitative trait loci for basmati quality traits in rice (*Oryza sativa* L.). *Mol Breed*, **21**(1): 49–65.

Anik A R, Talukder R K. 2002. Economic and financial profitability of aromatic and fine rice production in Bangladesh. *Bangladesh J Agric Econ*, **25**(2): 103–113.

Ashokkumar S, Jaganathan D, Ramanathan V, Rahman H, Palaniswamy R, Kambale R, Muthurajan R. 2020. Creation of novel alleles of fragrance gene *OsBADH2* in rice through CRISPR/Cas9 mediated gene editing. *PLoS One*, **15**(8): e0237018.

Baliyan N, Malik R, Rani R, Mehta K, Vashisth U, Dhillon S, Boora K S. 2018. Integrating marker-assisted background analysis with foreground selection for pyramiding bacterial blight resistance genes into Basmati rice. *C R Biol*, **341**(1): 1–8.

Bao G G, Ashraf U, Wan X R, Zhou Q, Li S Y, Wang C L, He L X, Tang X R. 2021. Transcriptomic analysis provides insights into foliar zinc application induced upregulation in 2-acetyl-1-pyrroline and related transcriptional regulatory mechanism in fragrant rice. *J Agric Food Chem*, **69**(38): 11350–11360.

Bergman C J, Delgado J T, Bryant R, Grimm C, Cadwallader K R, Webb B D. 2000. Rapid gas chromatographic technique for quantifying 2-acetyl-1-pyrroline and hexanal in rice (*Oryza sativa* L.). *Cereal Chem J*, **77**(4): 454–458.

Bounphanousay C, Jaisil P, Sanitchon J, Fitzgerald M, Hamilton N S. 2008. Chemical and molecular characterization of fragrance in black glutinous rice from Lao PDR. *Asian J Plant Sci*, **7**(1): 1–7.

Bradbury L M T, Fitzgerald T L, Henry R J, Jin Q S, Waters D L E. 2005. The gene for fragrance in rice. *Plant Biotechnol J*, **3**(3): 363–370.

Bradbury L M T, Gillies S A, Brushett D J, Waters D L E, Henry R J. 2008. Inactivation of an aminoaldehyde dehydrogenase is responsible for fragrance in rice. *Plant Mol Biol*, **68**(4/5): 439–449.

Buttery R G. 1982. 2-Acetyl-1-pyrroline: An important aroma component of cooked rice. *Chem Ind*, **12**: 958–959.

Caicedo A L, Williamson S H, Hernandez R D, Boyko A, Fledel-Alon A, York T L, Polato N R, Olsen K M, Nielsen R, McCouch S R, Bustamante C D, Purugganan M D. 2007. Genome-wide patterns of nucleotide polymorphism in domesticated rice. *PLoS Genet*, **3**(9): 1745–1756.

Chakraborty D, Deb D, Ray A. 2016. An analysis of variation of the aroma gene in rice (*Oryza sativa* L. subsp. *indica* Kato) landraces. *Genet Resour Crop Evol*, **63**(6): 953–959.

Chen S H, Wu J, Yang Y, Shi W W, Xu M L. 2006. The *fgr* gene responsible for rice fragrance was restricted within 69 kb. *Plant Sci*, **171**(4): 505–514.

Chen S H, Yang Y, Shi W W, Ji Q, He F, Zhang Z D, Cheng Z K, Liu X N, Xu M L. 2008. *Badh2*, encoding betaine aldehyde dehydrogenase, inhibits the biosynthesis of 2-acetyl-1-pyrroline, a major component in rice fragrance. *Plant Cell*, **20**(7): 1850–1861.

Chen Y B, Wang Z D, Wang C R, Li H, Huang D Q, Zhou D G, Zhao L, Pan Y Y, Gong R, Zhou S C. 2022. Comparisons of metabolic profiles for carbohydrates, amino acids, lipids, fragrance and flavones during grain development in *indica* rice cultivars. *Rice Sci*, **29**(2): 155–165.

Dela Cruz N, Khush G S. 2000. Rice grain quality evaluation procedures. *In*: Singh R K, Singh U S, Khush G S. Aromatic Rices. New Delhi, India: Oxford and IBH Publishing Co Pvt. Ltd: 15–28.

Fitzgerald T L, Lex Ean Waters D, Brooks L O, Henry R J. 2010. Fragrance in rice (*Oryza sativa*) is associated with reduced yield under salt treatment. *Environ Exp Bot*, **68**(3): 292–300.

Fukuoka S, Suu T D, Ebana K, Trinh L N, Nagamine T, Okuno K. 2006. Diversity in phenotypic profiles in landrace populations of Vietnamese rice: A case study of agronomic characters for conserving crop genetic diversity on farm. *Genet Resour Crop Evol*, **53**(4): 753–761.

Garris A J, Tai T H, Coburn J, Kresovich S, McCouch S. 2005. Genetic structure and diversity in *Oryza sativa* L. *Genetics*, **169**(3): 1631–1638.

Ghosh P, Roychoudhury A. 2020. Aromatic rice: Biochemical and molecular basis of aroma production and stress response. *In*: Roychoudhury A. Rice Research for Quality Improvement: Genomics and Genetic Engineering. Singapore: Springer: 373–408.

Glaszmann J C. 1987. Isozymes and classification of Asian rice varieties. *Theor Appl Genet*, **74**(1): 21–30.

Gopalakrishnan S, Sharma R K, Anand Rajkumar K, Joseph M, Singh V P, Singh A K, Bhat K V, Singh N K, Mohapatra T. 2008. Integrating marker assisted background analysis with foreground selection for identification of superior bacterial blight resistant recombinants in Basmati rice. *Plant Breed*, **127**(2): 131–139.

Grimm C C, Champagne E T, Lloyd S W, Easson M, Condon B, McClung A. 2011. Analysis of 2-acetyl-1-pyrroline in rice by HSSE/GC/MS. *Cereal Chem*, **88**(3): 271–277.

He Q, Yu J, Kim T S, Cho Y H, Lee Y S, Park Y J. 2015. Resequencing reveals different domestication rate for *BADH1* and *BADH2* in rice (*Oryza sativa*). *PLoS One*, **10**(8): e0134801.

Hien N L, Ahmad Sarhadi W, Oikawa Y, Hirata Y. 2007. Genetic diversity of morphological responses and the relationships among Asia aromatic rice (*Oryza sativa* L.) cultivars. *Tropics*, **16**(4): 343–355.

Hinge V, Zanan R, Rashmi D, Nadaf A. 2019. Aroma volatiles as biomarkers for characterizing rice (*Oryza sativa* L.): Flavor types and their biosynthesis. *In*: Verma D K, Srivastav P P. Science and Technology of Aroma, Flavor and Fragrance in Rice. Florida, USA: Apple Academic Press: 200–269.

Hinge V R, Patil H B, Nadaf A B. 2016. Aroma volatile analyses and 2AP characterization at various developmental stages in Basmati and non-Basmati scented rice (*Oryza sativa* L.) cultivars. *Rice*, **9**(1): 38.

Hofmann T, Schieberle P. 1998. 2-Oxopropanal, hydroxy-2-propanone, and 1-pyrrolineImportant intermediates in the generation of the roast-smelling food flavor compounds 2-acetyl-1-pyrroline and 2-acetyltetrahydropyridine. *J Agric Food Chem*, **46**(6): 2270–2277.

Hu X Q, Lu L, Guo Z L, Zhu Z W. 2020. Volatile compounds, affecting factors and evaluation methods for rice aroma: A review. *Trends Food Sci Technol*, **97**: 136–146.

Huang T C, Teng C S, Chang J L, Chuang H S, Ho C T, Wu M L. 2008. Biosynthetic mechanism of 2-acetyl-1-pyrroline and its relationship with Δ^1-pyrroline-5-carboxylic acid and methylglyoxal in aromatic rice (*Oryza sativa* L.) callus. *J Agric Food Chem*, **56**(16): 7399–7404.

Imran M, Liu Y H, Shafiq S, Abbas F, Ilahi S, Rehman N, Ahmar S, Fiaz S, Baran N, Pan S G, Mo Z W, Tang X R. 2022. Transcriptional cascades in the regulation of 2-AP biosynthesis under Zn supply in fragrant rice. *Physiol Plant*, **174**(3): e13721.

IRGSP (International Rice Genome Sequencing Project). 2005. The map-based sequence of the rice genome. *Nature*, **436**: 793–800.

Itani T. 2002. Agronomic characteristics of rice cultivars collected from Japan and other countries. *Jpn J Crop Sci*, **71**: 68–75. (in Japanese with English abstract)

Itani T, Tamaki M, Hayata Y, Fushimi T, Hashizume K. 2004. Variation of 2-acetyl-1-pyrroline concentration in aromatic rice grains collected in the same region in Japan and factors affecting its concentration. *Plant Prod Sci*, **7**(2): 178–183.

Kaikavoosi K, Kad T D, Zanan R L, Nadaf A B. 2015. 2-Acetyl-1-pyrroline augmentation in scented *indica* rice (*Oryza sativa* L.) varieties through Δ(1)-pyrroline-5-carboxylate synthetase (P5CS) gene transformation. *Appl Biochem Biotechnol*, **177**(7): 1466–1479.

Kamath S, Stephen J C, Suresh S, Barai B K, Sahoo A K, Reddy K R, Bhattacharya K R. 2008. Basmati rice: Its characteristics and identification. *J Sci Food Agric*, **88**(10): 1821–1831.

Khush G S. 2000. Taxonomy and origin of rice. *In*: Singh R K, Singh U S, Khush G S. Aromatic Rices. New Delhi, India: Oxford and IBH Publishing Co Pvt. Ltd: 5–13.

Kiani G, Nematzadeh G A, Ghareyazie B, Sattari M. 2012. Pyramiding of *cry1Ab* and *fgr* genes in two Iranian rice cultivars Neda and Nemat. *J Agric Sci Technol*, **14**: 1087–1092.

Kishor D S, Seo J, Chin J H, Koh H J. 2020. Evaluation of whole-genome sequence, genetic diversity, and agronomic traits of Basmati rice (*Oryza sativa* L.). *Front Genet*, **11**: 86.

Korinsak S, Sriprakhon S, Sirithanya P, Jairin J, Korinsak S, Vanavichit A, Toojinda T. 2009. Identification of microsatellite markers (SSR) linked to a new bacterial blight resistance gene *xa33*(t) in rice cultivar 'Ba7'. *Maejo Int J Sci Technol*, **3**(2): 235–247.

Kovach M J, Calingacion M N, Fitzgerald M A, McCouch S R. 2009. The origin and evolution of fragrance in rice (*Oryza sativa* L.). *Proc Natl Acad Sci USA*, **106**(34): 14444–14449.

Kumari A, Kumar J, Kumar A, Gaur A K. 2019. Physico-chemical and epigenetic aspects towards revealing aroma biology in *Oryza sativa* L. *Genome Gene Ther Int J*, **3**(1): 000111.

Lorieux M, Petrov M, Huang N, Guiderdoni E, Ghesquière A. 1996. Aroma in rice: Genetic analysis of a quantitative trait. *Theor Appl Genet*, **93**(7): 1145–1151.

Luo H W, He L X, Du B, Pan S G, Mo Z W, Yang S Y, Zou Y B, Tang X R. 2022. Epoxiconazole improved photosynthesis, yield formation, grain quality and 2-acetyl-1-pyrroline biosynthesis of fragrant rice. *Rice Sci*, **29**(2): 189–196.

Maraval I, Sen K, Agrebi A, Menut C, Morere A, Boulanger R, Gay F, Mestres C, Gunata Z. 2010. Quantification of 2-acetyl-1-pyrroline in rice by stable isotope dilution assay through headspace solid-phase microextraction coupled to gas chromatography-tandem mass spectrometry. *Anal Chim Acta*, **675**(2): 148–155.

Mathure S V, Jawali N, Thengane R J, Nadaf A B. 2014. Comparative quantitative analysis of headspace volatiles and their association with BADH2 marker in non-basmati scented, basmati and non-scented rice (*Oryza sativa* L.) cultivars of India. *Food Chem*, **142**: 383–391.

Nadaf A, Mathure S, Jawali N. 2016. Quality parameter assessment in scented rice cultivars. *In*: Nadaf A, Mathure S, Jawali N. Scented Rice (*Oryza sativa* L.) Cultivars of India: A Perspective on Quality and Diversity. New Delhi, India: Springer: 31–56.

Nagaraju J, Kathirvel M, Kumar R R, Siddiq E A, Hasnain S E. 2002. Genetic analysis of traditional and evolved Basmati and non-Basmati rice varieties by using fluorescence-based ISSR-PCR and SSR markers. *Proc Natl Acad Sci USA*, **99**(9): 5836–5841.

Nematzadeh G A, Karbalaie M T, Farrokhzad F, Ghareyazie B. 2000. Aromatic rices of Iran. *In*: Singh R K, Singh U S, Khush G S. Aromatic Rices. New Delhi, India: Oxford and IBH Publishing Co Pvt. Ltd: 191–200.

Ootsuka K, Takahashi I, Tanaka K, Itani T, Tabuchi H, Yoshihashi T, Tonouchi A, Ishikawa R. 2014. Genetic polymorphisms in Japanese fragrant landraces and novel fragrant allele domesticated in northern Japan. *Breed Sci*, **64**(2): 115–124.

Pachauri V, Singh M K, Singh A K, Singh S, Shakeel N A, Singh V P, Singh N K. 2010. Origin and genetic diversity of aromatic rice varieties, molecular breeding and chemical and genetic basis of rice aroma. *J Plant Biochem Biotechnol*, **19**(2): 127–143.

Pachauri V, Mishra V, Mishra P, Singh A K, Singh S, Singh R, Singh N K. 2014. Identification of candidate genes for rice grain aroma by combining QTL mapping and transcriptome profiling approaches. *Cereal Res Commun*, **42**(3): 376–388.

Peng B, Zuo Y H, Hao Y L, Peng J, Kong D Y, Peng Y, Nassirou T Y, He L L, Sun Y F, Liu L, Pang R H, Chen Y X, Li J T, Zhou Q Y, Duan B, Song X H, Song S Z, Yuan H Y. 2018. Studies on aroma gene and its application in rice genetics and breeding. *J Plant Stud*, **7**(2): 29.

Prasad G S V, Padmavathi G, Suneetha K, Madhav M S, Muralidharan K. 2020. Assessment of diversity of Indian aromatic rice germplasm collections for morphological, agronomical, quality traits and molecular characters to identify a core set for crop improvement. *CABI Agric BioSci*, **1**: 13.

Prodhan Z H, Shu Q Y. 2020. Rice aroma: A natural gift comes with price and the way forward. *Rice Sci*, **27**(2): 86–100.

Ramaiah K, Rao M V. 1953. Rice Breeding and Genetics. New Delhi, India: Indian Council of Agricultural Research.

Roy S, Banerjee A, Basak N, Kumar J, Mandal N P. 2020. Aromatic rice. *In*: de Oliveira A C, Pegoraro C, Viana V E. The Future of Rice Demand: Quality Beyond Productivity. Cham: Springer: 251–282.

Sakthivel K, Sundaram R M, Shobha Rani N, Balachandran S M, Neeraja C N. 2009. Genetic and molecular basis of fragrance in rice. *Biotechnol Adv*, **27**(4): 468–473.

Samal P, Pote T D, Krishnan S G, Singh A K, Salgotra R K, Rathour R. 2019. Integrating marker-assisted selection and doubled haploidy for rapid introgression of semi-dwarfing and blast resistance genes into a basmati rice variety 'Ranbir Basmati'. *Euphytica*, **215**: 149.

Sansenya S, Hua Y L, Chumanee S. 2018. The correlation between 2-acetyl-1-pyrroline content, biological compounds and molecular characterization to the aroma intensities of Thai local rice. *J Oleo Sci*, **67**(7): 893–904.

Shan Q W, Wang Y P, Chen K L, Liang Z, Li J, Zhang Y, Zhang K, Liu J X, Voytas D F, Zheng X L, Zhang Y, Gao C X. 2013. Rapid and efficient gene modification in rice and *Brachypodium* using TALENs. *Mol Plant*, **6**(4): 1365–1368.

Shao G N, Tang A, Tang S Q, Luo J, Jiao G A, Wu J L, Hu P S. 2011. A new deletion mutation of fragrant gene and the development of three molecular markers for fragrance in rice. *Plant Breed*, **130**(2): 172–176.

Shi Y Q, Zhao G C, Xu X L, Li J Y. 2014. Discovery of a new fragrance allele and development of functional markers for identifying diverse fragrant genotypes in rice. *Mol Breed*, **33**(3): 701–708.

Siangliw M, Toojinda T, Tragoonrung S, Vanavichit A. 2003. Thai jasmine rice carrying QTLch9 (*Sub*QTL) is submergence tolerant. *Ann Bot*, **91**(S2): 255–261.

Siddiq E A, Vemireddy L R, Nagaraju J. 2012. Basmati rices: Genetics, breeding and trade. *Agric Res*, **1**(1): 25–36.

Singh R K, Singh U S, Khush G S, Rohilla R. 2000. Genetics and biotechnology of quality traits in aromatic rices. *In*: Singh R K, Singh U S, Khush G S. Aromatic Rices. New Delhi, India: Oxford and IBH Publishing Co Pvt. Ltd: 47–70.

Singh S P, Singh M K, Kumar S, Sravan U S. 2019. Cultivation of aromatic rice: A review. *In*: Hasanuzzaman M. Agronomic Crops. Singapore: Springer: 175–198.

Singh V K, Singh B D, Kumar A, Maurya S, Krishnan S G, Vinod K K, Singh M P, Ellur R K, Bhowmick P K, Singh A K. 2018. Marker-assisted introgression of *Saltol* QTL enhances seedling stage salt tolerance in the rice variety Pusa Basmati 1. *Int J Genom*, **2018**: 8319879.

Singh V P. 2000. Basmati rice of India. *In*: Singh R K, Singh U S, Khush G S. Aromatic Rices. New Delhi, India: Oxford and IBH Publishing Co Pvt. Ltd: 135–154.

Singh V P, Singh A K. 2010. Role of Indian agricultural research institute in collection, acquisition, evaluation, enhancement, utilization and conservation of rice germplasm. *In*: Sharma S D, Rap P. Genetic Resources of Rice in India. New Delhi, India: Today and Tomorrow's Printers and Publications: 135–150.

Singh V P, Singh A K, Mohapatra T, Gopala Krishnan S, Ellur R K. 2018. Pusa Basmati 1121: A rice variety with exceptional kernel elongation and volume expansion after cooking. *Rice*, **11**: 19.

Srivastava D, Shamim M, Mishra A, Yadav P, Kumar D, Pandey P, Khan N A, Singh K N. 2019. Introgression of semi-dwarf gene in Kalanamak rice using marker-assisted selection breeding. *Curr Sci*, **116**(4): 597–603.

Sun P Y, Zhang W H, Zhang L, Shu F, He Q, Xu N, Peng Z R, Zeng J, Fang P P, Deng H F. 2023. Development and application of a novel functional marker for fragrance in rice. *Rice Sci*, **30**(3): 176–180.

Talukdar P R, Rathi S, Pathak K, Chetia S K, Sarma R N. 2017. Population structure and marker-trait association in indigenous aromatic rice. *Rice Sci*, **24**(3): 145–154.

Tama R A Z, Begum I A, Alam M J, Islam S. 2015. Financial profitability of aromatic rice production in some selected areas of Bangladesh. *Int J Innov Appl Stud*, **12**(1): 235–242.

Tanchotikul U, Hsieh T C Y. 1991. An improved method for quantification of 2-acetyl-1-pyrroline, a "popcorn"-like aroma, in aromatic rice by high-resolution gas chromatography/mass spectrometry/selected ion monitoring. *J Agric Food Chem*, **39**(5): 944–947.

van Quoc G, Huynh K, Nguyen C T T, Nguyen L H, van Nguyen M, Nguyen N T, Vo C T, Swee K Y. 2023. Novel deletion in exon 7 of *Betaine Aldehyde Dehydrogenase 2* (*BADH2*). *Rice Sci*, **30**(2): 104–112.

Vanavichit A, Yoshihashi T, Wanchana S, Areekit S, Saengsraku D, Kamolsukyunyong W. 2005. Cloning of *Os2AP*, the aromatic gene controlling the biosynthetic switch of 2-acetyl-1-pyrroline and gamma aminobutyric acid (GABA) in rice. *In*: 5th International Rice Genetics Symposium. Manila, the Philippines: IRRI: 44.

Vanavichit A, Kamolsukyeunyong W, Siangliw M, Siangliw J L, Traprab S, Ruengphayak S, Chaichoompu E, Saensuk C, Phuvanartnarubal E, Toojinda T, Tragoonrung S. 2018. Thai hom Mali rice: Origin and breeding for subsistence rainfed lowland rice system. *Rice*, **11**(1): 20.

Vemireddy L R, Tanti B, Lahakar L, Shandilya Z M. 2021. Aromatic rices: Evolution, genetics and improvement through conventional breeding and biotechnological methods. *In*: Hossain M A, Hassan L, Iftekharudaula K M, Kumar A, Henry R. Molecular Breeding for Rice Abiotic Stress Tolerance and Nutritional Quality. NY, USA: John Wiley & Sons Ltd: 341–357.

Verma D K, Mohan M, Yadav V K, Asthir B, Soni S K. 2012. Inquisition of some physico-chemical characteristics of newly evolved basmati rice. *Environ Ecol*, **30**(1): 114–117.

Verma D K, Mohan M, Asthir B. 2013. Physicochemical and cooking characteristics of some promising basmati genotypes. *Asian J Food Agro-Ind*, **6**(2): 94–99.

Verma D K, Mohan M, Prabhakar P K, Srivastav P P. 2015. Physico-chemical and cooking characteristics of Azad basmati. *Int Food Res J*, **22**(4): 1380–1389.

Verma D K, Srivastav P P. 2017. Proximate composition, mineral content and fatty acids analyses of aromatic and non-aromatic Indian rice. *Rice Sci*, **24**(1): 21–31.

Verma D K, Srivastav P P, Nadaf A. 2019. Aromatic rice from different countries: An overview. *In*: Verma D K, Srivastav P P. Science and Technology of Aroma, Flavour and Fragrance in Rice. Florida, USA: Apple Academic Press: 35–58.

Wakte K, Zanan R, Hinge V, Khandagale K, Nadaf A, Henry R. 2017. Thirty-three years of 2-acetyl-1-pyrroline, a principal basmati aroma compound in scented rice (*Oryza sativa* L.): A status review. *J Sci Food Agric*, **97**(2): 384–395.

Yang D S, Shewfelt R L, Lee K S, Kays S J. 2008. Comparison of odor-active compounds from six distinctly different rice flavor types. *J Agric Food Chem*, **56**(8): 2780–2787.

Yang S Y, Zou Y B, Liang Y Z, Xia B, Liu S K, Ibrahim M, Li D Q, Li Y Q, Chen L, Zeng Y, Liu L, Chen Y, Li P, Zhu J W. 2012. Role of soil total nitrogen in aroma synthesis of traditional regional aromatic rice in China. *Field Crops Res*, **125**: 151–160.

Yi M, Nwe K T, Vanavichit A, Chai-arree W, Toojinda T. 2009. Marker assisted backcross breeding to improve cooking quality traits in Myanmar rice cultivar Manawthukha. *Field Crops Res*, **113**(2): 178–186.

Yoshihashi T. 2002. Quantitative analysis on 2-acetyl-1-pyrroline of an aromatic rice by stable isotope dilution method and model studies on its formation during cooking. *J Food Sci*, **67**(2): 619–622.

(Managing Editor: WANG Caihong)