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Genetics, Biochemistry and Biophysical Analysis of Anthocyanin in Rice (*Oryza sativa L.*)

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Abstract. Rice (*Oryza sativa L.*) is the primary staple food for half of the world population. It is generally classified based on the grain color into black, red, purple, brown, green, and white. These colored rice are determined by the composition and concentration of anthocyanin pigments in different layers of aleurone, pericarp, and seed coat. Anthocyanins are also accumulated in various tissues of the rice plants, mostly in the grain, but are also presents in leaves, leaf sheath, floral organ, and hull. The type and concentration of the anthocyanins in rice tissues are influenced by the cultivars and developmental stages. Anthocyanin-enriched rice is related to the health effects, including antioxidant, antibacterial, and anti-inflammation activities that potentially use as functional food ingredients, dietary supplements, and natural colorants. Structural and regulatory genes are involved in anthocyanin biosynthesis of rice. Various molecular biology techniques have been applied to improve productivity, nutritional contents, and market value of pigmented rice. This review focused on the genetics, biochemistry and biophysical analysis of anthocyanin in rice that will facilitate rice breeding program to develop new high-yield pigmented rice varieties.

Keywords: rice, anthocyanins, genetics, biochemistry, biophysics

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1. Introduction

Rice (*Oryza sativa L.*) has become the major staple food for almost half of the global population due to the nutrients composition, including carbohydrate, protein, oil components, and other micronutrients [1-5]. There are various kinds of rice are consumed that can be classified based on the grain color into black, red, purple, brown, green, and white [6-9]. White rice is generally consumed, while pigmented rice, such as black, red, purple, and brown contain natural pigment anthocyanins that accumulate in the particular layers of the seed coat, pericarp, and aleurone [10-18]. Total anthocyanins in each pigmented rice varieties are diverse in the range of 0-493 mg/100 g [19]. Black rice is the most common pigmented rice in the market due to their sensory characteristics and organoleptic properties, such as good taste, fragrant aroma, fluffiness texture, high nutrition values, and positive health effects [20-27]. China is the biggest black rice producer followed by Sri Lanka, Indonesia, India, Philippines, Bangladesh, Malaysia, Thailand, and Myanmar [17]. Pigmented rice genotypes have been cultivated in Asia for a long time, such as Chinese black rice, Indonesian black rice, and Thai black rice [20]. Anthocyanins of the pigmented rice has the potential to be applied as a dietary supplements, functional food ingredient, and natural colorant for food, beverages, and pharmaceutical products. Anthocyanins show positive effects for the human health, including antioxidant, antibacterial, anti-inflammatory, anticancer, anti-diabetic, antitumor, anti-allergic agents, anticarcinogenic, anti-atherosclerosis, and others [23], [28-37], [38-40]. Consequently, anthocyanins play important roles in preventing human diseases, such as atherosclerosis [12], [28], [41], diabetes [42-44], and cancer [45-49]. In the rice plants, anthocyanins involve in pollination to attract the insects, UV-B protection, hormone responses regulation, photo-perception in autumn leaves, stabilize photosynthetic activity, biotic and abiotic stress defense system [50-59].

Anthocyanins are water-soluble natural pigments classified to the phenolic compounds of flavonoids group which responsible for attractive colors, such as purple, red or brown in different tissues of the rice plants with various concentration and composition of anthocyanins [60-64]. There are six anthocyanin types, including malvidin, peonidin, cyanidin, delphinidin, petunidin, and pelargonidin [65]. Different combinations of anthocyanins lead to different colors, the higher anthocyanins concentration and combination, the blacker the color. The concentration and composition of anthocyanins in the rice plants are vary depend on the rice variety and developmental stages [66-68]. The common anthocyanin types in the pigmented rice are cyanidin-3-glucoside, while the minor is peonidin-3-glucoside [69-70]. Anthocyanins are important secondary metabolites in the rice plants and accumulate in various tissues and organs that related to photosynthesis, reproduction, and defense, such as pericarp, aleurone, awn, leaf blade, leaf sheath, palea, lemma, internode, stigma, apiculus, and root [71-74]. Different level of purple color are identified in these tissues and organs of the rice plants. For example, purple and red rice contain 20 times higher concentrations of the anthocyanin in their aleurone layer compared with brown rice [75]. Black rice contain higher total antioxidant capacity compared to red rice; black rice have 0.5-2.5% while red rice only 0.03-0.1% [76]. The purple pigmentation is regulated by the allelic variation of genes, the co-segregation of the alleles do not always happen [72]. Anthocyanin biosynthesis is controlled by the structural and regulation genes, and the stability of the anthocyanins also influenced by the environmental conditions, including temperature, pH value, lights, enzymes, oxygen, and metallic ions [51], [77-84]. Anthocyanin biosynthesis can be enhanced by environmental modification, such as maintaining temperature ranging from 22 to 27oC and light intensity between 301-600 lx. Maintaining the stability of anthocyanins is a crucial factor in food and pharmaceutical industry [85]. Accumulation of anthocyanins in the rice plants are depend on the rice developmental stages, including seedling, vegetative, reproductive, and mature stages. During maturity stage, black rice contains higher anthocyanins in the aleurone layer compared with grain filling stage [75].

Anthocyanins have been used in human diet for centuries as herbal medicines to cure several health problems, such as cold, diarrhea, and hypertension. Recently, anthocyanins are being applied as natural colorant of food and beverages, and also dietary supplements due to their attractive colors and health benefits. In the United States, estimated anthocyanins consumption is around 12.5 mg/day [86]. Black rice as the common pigmented rice in the market that contain various combinations of anthocyanins, such as cyanidin-3-glucoside, peonidin-3-glucoside, and petunidin-3-glocoside in the aleurone layer of the rice grain [13], [17], [70], [76], [87-88]. Cyanidin-3-glucoside is the most anthocyanins composition in black rice around 631 mg/100 g, while peonidin-3-glucoside is around 363 mg/100 g [13], [70], [88-89]. Southeastern Asian countries are the primary producer of black rice. Recently, California also produces black rice due to high market demand [90]. European countries that cultivate black rice are Italy and Greece [23]. In Asian countries such as Thailand, China, Indonesia, India, Korea, and Japan, black rice is usually combine with white rice to increase the flavor [12], [91-94]. The color of cooked black rice become regal purple [95]. Black rice is usually use as food ingredients in fried rice, paella, risotto, porridge, bread, pasta, and rice cake [96-97]. Black rice also become an important material to produce alcoholic beverages with red color. There are many varieties of black rice, including short and long grains, glutinous and non-glutinous rice, early and late maturity period [98-100]. Red rice is generally used as a natural colorant in ice cream, bread, and liquor [11], [101]. Pigmented rice also contains higher concentration of micronutrients, such as iron, manganese, and zinc in the grain compared to white rice [102-107]. These pigmented rice has a potential to decrease malnutrition around the world [66]. Many studies have been reported the nutritional values of black and red rice [23], [41], [108-111]. Powdered anthocyanins extracts from black rice was produced with spray-drying and freeze-drying processes of Italian black rice that contain rich anthocyanins and antioxidant activity [112]. These powdered anthocyanins are more stable from environmental conditions of storage and food processing, including temperature, pH value, and lights that give high economic value to use for functional foods and pharmaceuticals products [6], [79], [113-114].

In China, red rice has been approved by the Chinese Ministry of Health as a food colorant in soybean products, meat, and fish [115]. Meanwhile, in United States, Canada, European Union, Japan, Australia, New Zealand, and South Africa restrict anthocyanins as a food colorant [116]. Red rice is commonly use as food colorants and dietary supplements in China due to attractive and high stability color from high light exposure, pH changes, and heat conditions; good taste and flavor; cheap; high availability; and high yield rice variety [117]. The anthocyanin concentration in red rice is lower than black rice around 1.5 to 9.4 mg/100 g [70], [118]. Fermented rice as a dietary supplement to decrease cholesterol accumulation of the blood circulation has been marketed in China. Red rice as a herbal medicine to treat cardiovascular disease and abdominal pain [11].

Analysis of biosynthesis, storage, and transportation mechanisms in anthocyanins have been achieved a significant progress due to the development of molecular biology. These progress give a positive impact on the food industry, pharmaceuticals, flavors, rice breeding program [119-121]. Identification of physicochemical properties, quantification, and extraction of anthocyanins in the rice plants was based on Ultraviolet-Visible (UV-Vis) absorption spectrophotometer, High Performance Liquid Chromatography (HPLC), mass spectrometry, liquid chromatography, and paper chromatography [101], [104], [122-124]. Based on the UV-Vis absorption spectrophotometer data, anthocyanins show maximum absorption range in the region 500-535 nm of the blue spectrum; malvidin at 530 nm, peonidin at 517-520 nm, cyanidin at 512-520 nm, delphinidin at 525 nm, petunidin at 526-529 nm, and pelargonidin at 502-506 nm [70]. By identification of phytochemical properties of anthocyanins in pigmented rice gives insights to the application of pigmented rice as health promotion agents [122], [125-126]. Based on the genetic analysis of pigmentation in pigmented rice, there are three genes that regulates the pigmentation, including Ra, Rc, and Rd genes. The intensity of the pigmented rice coloration is influenced by the presence of genes and the genes status (dominant or recessive). Ra genes regulated purple pericarp, which purple color is dominant and white color is recessive. Brown pericarp is produced when Rc gene presence and Rd gene absence. Both of the genes, Rc and Rd genes are presence produce red pericarp. Meanwhile, if only Rd gene presence, it will not produce any color [99], [127-128]. The alleles segregation of coloration in pigmented rice also presence, for example F2 population of the crossing between black rice and white rice varieties showed three phenotypes; black, brown, and white color with the segregation ratio 9:3:4.

Pigmented rice cultivation since ancient time and in 1970s become more popular due to the development of genetic engineering [129]. The famous pigmented rice varieties in Korea are dark red Heugjinjubyeo, dark purple Heugnambyeo, dark blue Jakwangdo, red brown Sanghaehyeolla, black purple Hongmi, and dark red-purple Kilimheugmi [130]. The quality of pigmented rice varieties have been improve by employing recent technologies, including genome sequencing, gene expression analysis, gene editing, and omics technologies [102], [131-134]. High-yield pigmented rice varieties have been developed by applying the characteristics of grain pigmentation inheritance, tagging the key genes that controlled the rice quality traits, and identifying markers of these rice quality traits [135-136]. The advanced pigmented rice varieties can be developed by understanding the molecular basis of anthocyanin biosynthesis in several organs of the rice plants [50]. In Japan, improved pigmented rice variety was developed by crossing black rice variety 'Okunomurasaki' with high quality-white rice variety 'Koshihikari' [137]. In Kazakhstan, adapted pigmented rice variety was developed by crossing pigmented and non-pigmented rice varieties [138]. In Thailand, a new deep purple rice variety 'Riceberry' was developed by crossing between non-glutinous purple rice and an aromatic white jasmine rice variety [139-140]. Brazil has been released two advanced pigmented rice varieties; the red rice 'Rubi' and the black rice 'Onix' [141]. In China, biofortified purple endosperm rice called 'Zijingmi' with high anthocyanins concentration was developed by editing anthocyanin biosynthesis [142]. New foods and beverages from pigmented rice also have been develop by using improved processing technologies. This review provides an update information on the genetics, biochemistry and biophysical analysis of anthocyanin in pigmented rice that will facilitate rice breeding program to develop improved pigmented rice varieties.

2. Discussion

2.1 Anthocyanins in Rice Grains

Anthocyanins is mainly accumulated in the pericarp of the rice grains (Figure 1). Purple bran color showed the highest total anthocyanin (2874 cyanidin 3-O-glucoside equivalent (CGE)/100g) followed by black (1884 CGE/100 g), red (8.78 CGE/100g), and brown (3.09 CGE/100g). These rice bran color has been reported to be correlated to the seed dormancy, red bran color rice have a longer dormant compare to the white rice [143]. Based on the quantitative trait loci (QTL) analysis, one QTL qSD7/qPC7 that regulated rice bran color and seed dormancy was identified on chromosome 7 [144]. Anthocyanin contents in the rice pericarp were significantly influenced by environmental conditions and rice developmental stages (Figure 2). Rice developmental stages influence the anthocyanin concentration in caryopsis that shows gradual color changes at each developmental stage. The anthocyanin level increases as the increasing developmental stages and gradual grain filling. At 8-14 days after flowering (DAF), anthocyanins start accumulate in the caryopsis. At the milk stage, caryopsis becomes black and at the maturity stage (35-45 DAF) is the highest anthocyanins concentration accumulate in the caryopsis. The gradual changes of the anthocyanin concentration correlated with the gene expression that control anthocyanin biosynthesis [145]. During maturity stage, the gene expression level of OsDFR, OsF3H, OsAns, and OsCHS are increasing [146]. The anthocyanin accumulation in black rice also influenced by photosynthetic activity.

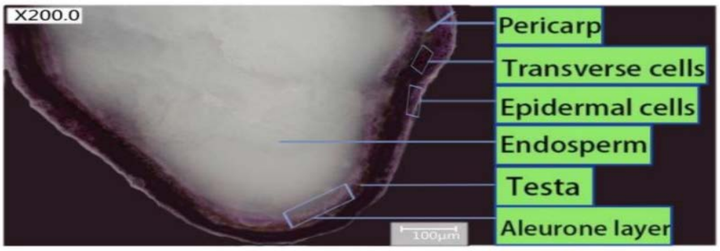

Figure 1. Cross-section of black rice grain showing anthocyanin accumulation in pericarp [66]

Anthocyanin is synthesized on the endoplasmic reticulum, transported through the Golgi apparatus, and accumulated in the vacuole cells of vegetative and generative organs. Anthocyanin biosynthesis is influenced by environmental conditions, such as salinity, drought, abscisic acid (ABA), and rice diseases [147-149]. Black rice pigmentation is regulated by key activator loci for anthocyanin (KALA), such as Kala1, Kala3 or MYB3, and Kala4 [137]. Based on the QTL analysis, Kala1 was identified on chromosome 1 between SSR markers RM7405 and RM7419, Kala3 on chromosome 3 between RM15191 and RM3400, and Kala4 on chromosome 4 between RM1354 and RM7210. LOC_Os04g0557500 within Kala4 region controls the purple color in the rice pericarp. Anthocyanin concentration in the rice pericarp can be enhanced by overexpress LOC_ Os04g0557500 [20]. Red rice pericarp is controlled by a QTL rg7.1 on chromosome 7 and LOC_Os07g11020 was identified within the QTL region [150]. LOC_Os07g11020 encodes a bHLH TF. Two genes PURPLE PERICARP A (Pp, Prpa and Prp1) on chromosome 1 and PURPLE PERICARP B (Pb, Prpb and Prp2) on chromosome 4 are regulates the purple color of rice pericarp [151-155].

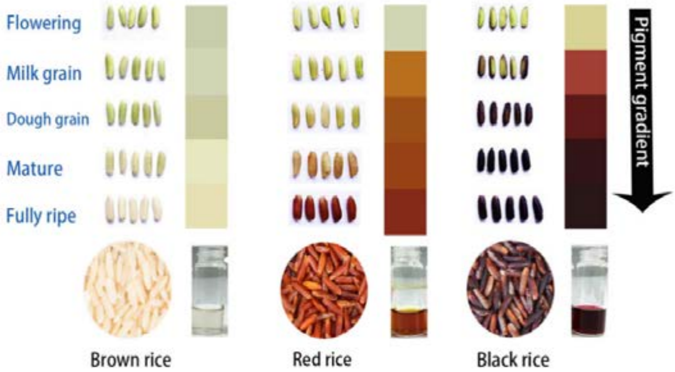

Figure 2. Pigment gradient in brown rice, red rice, and black rice during developmental stages [66]

Transgenic pigmented rice varieties were developed by using transgene stacking system that have higher nutritional and medical values for food and pharmaceutical industries [137]. Anthocyanin concentration in the rice pericarp can be improved by using this genetic engineering technique that can be enhanced their antioxidant activity and seed dormancy period [162]. By enhancing the anthocyanin concentration in the rice pericarp may enhance the abiotic and biotic resistance [50]. Important genes regulating the anthocyanin biosynthesis, such as CHS (chalcone synthase), F3H (flavanone 3]3-hydroxylase), DFR (dihydroflavanol), and ANS1 (anthocyanin synthase) were identified by using whole genome sequencing and transcriptomic sequencing in the pigmented rice plants [156]. Pigmented rice produce lower yield and lower grain weight than white rice varieties [157-158]. Lower grain yield of pigmented rice due to the anthocyanin deposition that reduce chlorophyll content in spikelet, decrease photosynthetic rate and also grain filling rate [159]. The accumulation of anthocyanin in pericarp of the pigmented rice cause lower grain weight [145]. The lower grain yield and decreased grain size in black rice near isogenic lines (NILs) population was identified in Japan [137].

2.2 Anthocyanins in Rice Floral Organs

Floral organs of the rice plants including stigma and apiculus showing red, purple, or brown color because of anthocyanins accumulation (Figure 3). These obvious color is important in pollination to attract insects and other animals but does not apply in the rice plants due to self-pollination. Anthocyanins content in the floral organs also important as protective agents from ultraviolet radiation and strong light intensity, and also become defense system from abiotic and biotic stresses including salinity, drought, cold, heat, and diseases [160-162]. The specific color of stigma and apiculus is important for rice taxonomy [73], [163-164]. Investigation about purple stigma and apiculus started in 1957 [165]. OsB2 is an important gene regulating anthocyanin biosynthesis in floral organs of the rice plants. The variation color of apiculus is regulated by locus C, OsC1 [50].

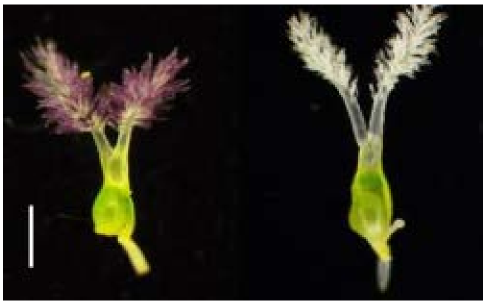

Figure 3. Purple and white stigma of the rice plants [73]

The variation color of apiculus and stigma are regulated by several QTL regions. Diverse color of apiculus is controlled by C-gene located between SSR markers RM19552-RM19565 [166-167]. Purple apiculus is regulated by Pa-6 and red apiculus is coordinated by OSC [163], [166]. Purple stigma is controlled by Ps-4(t) located in RM253, RM111, and RM6917 [168]. The first purple stigma gene OsC1 was identified on chromosome 6. Based on the map-based cloning strategy, two genes OsC1 and OsDFR that responsible for the purple color of stigma and apiculi were identified in pigmented indica rice cultivar Xieqingzao. A R2R3-MYB transcription factor is encoded by OsC1 on chromosome 6, while a dihydroflavonol 4-reductase is encoded by OsDFR. OsPa gene responsible for apiculi color and OsPs gene regulating the stigma color were identified by transcriptional expression analysis and CRISPR/Cas9. Variety color of stigma and apiculus can be produced by gene interaction of OsC1, OsDFR, OsPa, and OsPs. The purple color of stigma and apiculi is the result of genes interaction OsC1, OsPa or OsPs , and OsDFR. Brown apiculi can be produced by gene interaction OsC1 and OsPa. Knock-out of OsDFR resulting straw-white color stigma [169].

2.3. Anthocyanins in Rice Leaves

Leaves as the primary organ in photosynthesis promote the biosynthesis of anthocyanin and starch. Anthocyanin accumulation in the rice leaves reduces the efficiency of photosynthetic activity and consequently decrease the rice yield [170]. On the other hand, reducing the anthocyanin concentration in the leaves will increase the photosynthetic activity and subsequently improve rice yield. Consequently, in the rice variety selection process, purple leaf trait become a negative marker [50]. Based on the genomic sequence analysis, accumulation of anthocyanin in the rice leaves is regulated by OsC1 and OsDFR [170]. OsC1 controls cyanidin 3-O-glucoside concentration in the rice leaves [171]. Rb gene on chromosome 1 involves in anthocyanins biosynthesis in the rice leaves was identified by GWAS analysis. LOC_Os04g0577800 and LOC_Os04g0616400 on chromosome 4 also involve in anthocyanin biosynthesis in the purple rice leaves that identified by using bulk segregant and transcriptome analysis [172].

2.4. Anthocyanins in Rice Leaf Sheath

Purple leaf sheath in rice due to the accumulation of anthocyanins. Leaf sheath color trait also become a marker in rice variety selection. The level of anthocyanin accumulation in the leaf sheath also influenced by the developmental growth stages. At V4 stage with 4-leaf, the anthocyanin concentration in the leaf sheath ranging from 0.01 µmol/g until 0.06 µmol/g. The highest concentration of anthocyanins starting at active tillering stage until maturity stage around 1.16 µmol/g [73]. Accumulation of the anthocyanins in the leaf sheath also correlated with defense system to the abiotic stresses, including soil acidity, ultraviolet radiation, and temperature [173-174]. Diverse leaf sheath color is regulated by OsC1 gene that has co-segregation with apiculus color [167]. A mutant rice plant Z418 showing purple leaf sheath which was developed from C418 rice variety with green leaf sheet color by modifying OsC1 gene [175]. OsC1 gene also identified in the F2 population of crossing between purple leaf sheath rice (Tainung 72 / TNG72) and green leaf sheath rice (Taichung Sen 17 / TCS17) [176]. There a segregation in that F2 population with ratio 3:1, 3 for purple leaf sheath and 1 for green leaf sheath, indicating that OsC1 is the dominant gene. Based on the RT-PCR analysis, the gene expression of OsC1 in the leaf sheath tissue started at 5-leaf stages [177]. Another gene that regulating the rice purple leaf sheath is PSH1(t) on chromosome 1 that identified in a recombinant inbred line (RIL) population resulting from crossing rice variety IRBB60 and 9407 [152]. Variation of the leaf sheath color also controlled by two QTLs on chromosome 1 and 6 [73], [178-179]. LOC_Os06g10350 on chromosome 6 as a gene controlling leaf sheath color was also identified by using F2 rice population and 117 markers. LOC_Os06g10350 belong to the MYB family transcription factor.

Variation of leaf sheath color ranging from light to dark purple showing tyran rose, pansy purple, red purple, and blackish purple. Anthocyanin accumulation in the leaf sheath ranged from 1.04 to 42.77

μmol/g, tyran rose color has the least anthocyanin concentration and blackish purple color has the most anthocyanin content (Figure 4). The diverse leaf sheath color also associated with the rice varieties [73].

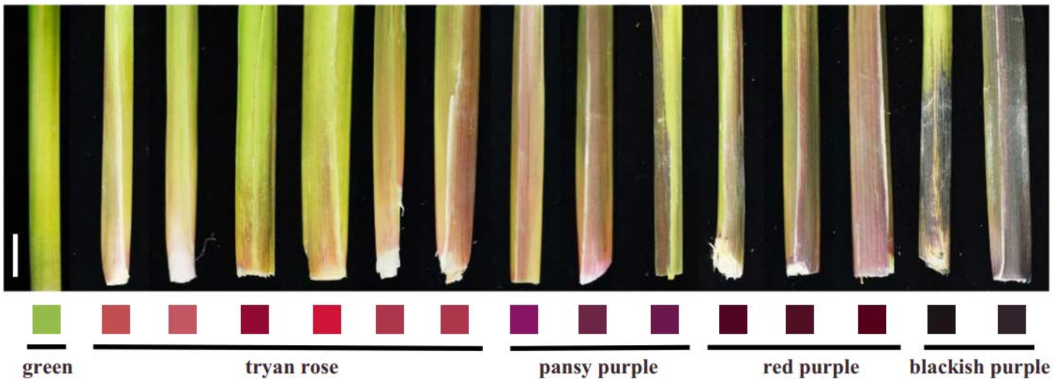

Figure 4. Diverse rice leaf sheath color [73]

2.5. Anthocyanins in Rice Hulls

Colored rice hulls which are black and red due to the accumulation of anthocyanins [36]. About 15% of the rice varieties are colored hull and the most rice varieties (85%) have white-hulled. Colored rice hull responsible to protect rice grain from oxidative stress [180]. China and Japan have been cultivated rice variety with colored hulls since ancient time due to the health positive effects. Recently, rice variety with colored hulls are cultivated in South Asia countries, United States, Italy, and Greece [181]. The type of anthocyanin in the purple rice hull is cyanidin 3-O-glucoside with concentration 2.8 mg/g [182]. Lemma and palea of the rice hull are associated with the rice floral organs and seed characteristics including grain length, grain width, and grain weight [183-188]. The highest anthocyanins accumulation is in purple hulls. Rice hull has been treated as one of residue material from the rice plants, but right now colored rice hull is become antioxidant and anti-cancer sources. Straw-white hull correlated with non-shattered rice grains and became an important marker during rice domestication [189].

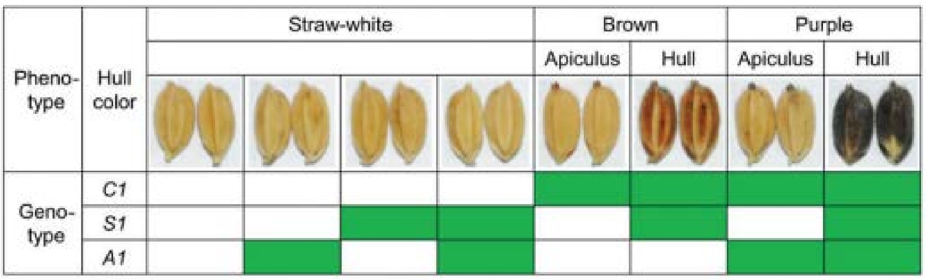

Figure 5. C-S-A gene system of rice hull pigmentation [182]

Methanol extracts of colored rice hulls from rice variety Heuginju with black hull, WD-3 with purple hull, Jeoginju with red hull, and Ilpum with light-brown showed significantly high anti-cancer and antioxidant activities. Black hull of Heuginju showed the highest anti-cancer and antioxidant activities compared to the others colored hulls [190]. Acetone extract of rice hull contain procyanidins [36]. Based on the molecular, genetic, metabolic, and phylogenetic analysis; colored rice hulls were regulated by C-S-A gene system, which C1 encoding MYB transcription factor and become gene that produce color, S1 encoding bHLH protein and acting as a tissue specific regulator, A1 encoding dihydroflavonol reductase and only express when C1 co-ordinate with S1 (Figure 5). Brown hull color is formed when A1 is not expressed. One QTL responsible for black hull trait is on chromosome 4 [191]. Gene Phr1 on chromosome 4 encoding polyphenol oxidase is found to be responsible for black hull color of rice [192-193]. Black hull is also regulated by Bh4 gene on chromosome 4. Another genes that responsible for black hull are Bh-a, Bh-b, and Bh-c as complementary genes [194]. Two QTLs qHC4 and qHC7 also responsible for black hull coloration, these QTLs were identified by using an F2 population of crossing between SS18-2 and EM93-1 [194].

3. Conclusions

Pigmented rice has been popular among rice consumers and increasing demand of pigmented rice have become motivation for rice breeder to develop high yield pigmented rice. Anthocyanin is a source of functional food ingredients, natural colorants, pharmaceuticals, and other industrial biochemical products with the high health benefits. Anthocyanin accumulation in the rice plants can be enhanced by genetic molecular techniques and environmental regulation. Advanced pigmented rice varieties with enhanced anthocyanins content have been developed. To fulfill the consumer increasing demand, it is important to explore deeply the genetic bases of pigmented rice in order to enhance pigmented rice quality, sensory properties, and nutritional content. In this review provides important information for rice breeder to develop high quality pigmented rice based on consumer demand.

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