



Current Status and Future Prospects of Head Rice Yield

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Abstract: Global warming poses a serious threat to food security because of its impacts on thermosensitive food crop production. Rice is of paramount significance due to the world's three-billionpopulation dependence on it as a staple food. It is well established that the high temperatures at day or night times during the grain-filling period can reduce rice grain yield, although the intriguing impact of high temperatures on head rice yields (HRY) is poorly discussed. This is because high and stable HRY is vital to meet the demand for rice grain, which is a staple food for many developing and developed nations. Hence, identifying the novel heat-tolerant rice germplasm with higher head rice yields may help mitigate a critical problem threatening global food security resulting from climate change. This review addresses the key factors, including pre-and-post-harvest scenarios related to overall reductions in the HRY and how grain molecular composition can play a significant role in determining head rice yields. Moreover, the underlying genetics of head rice is discussed as and possible mechanism to breach the complexity of HRY before identifying the key alleles and genomic regions related to the reduction in the HRY. Future research should focus on understanding the mechanisms of tolerating heat stress in rice by combining modern statistical, physiological, and molecular techniques to increase HRY. This may include high-throughput phenotyping techniques, mapping quantitative loci affecting HRY loss processes and genomic prediction using a broad wild and cultivated rice germplasm.

Keywords: climate change; high temperatures; rice; head rice yields; agronomy; soil moisture; pre-and-post harvest factors; physiology; grain molecular composition and quantitative genetics

1. Introduction

Freshly harvested rice (*Oryza sativa* L.) grains, known as "paddy" or "rough" rice, are usually milled before human consumption. Paddy typically comprises 20% husk, 11% bran (aleurone layer) and 69% starchy endosperm [1–3]. Milling involves de-hulling the paddy and polishing, where the bran layer and part of the embryo are removed from brown rice to produce broken and un-broken (whole grain) starchy endosperm kernels, known as polished rice [1]. Polishing is important because brown rice, produced after the removal of the indigestible husk tissue, contains lipids and fatty acids in the bran layer, which is problematic for long-term grain storage. They hydrolyze and oxidize to form aldehydes and ketones, making the rice grain rancid over long-term storage periods [4,5].

In the context of the global rice production pattern, head rice yields derive from the paddy (Table 1). Head rice yield is typically affected by the milling operations (dehulling and polishing) and could result in grain breakage. The whole grain portion of the polished white rice—the head rice yield—is typically around 60–65% of the paddy yield [6,7]. Head rice is used for human consumption, while broken kernels are used for animal feed, rice



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Copyright: © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). flour, and the brewing industry [8]. The degree to which the aleurone layer (bran) and embryo are removed in the polishing process has implications for the quality of the milled product and depends on the milling intensity, length of time the rice is milled and grain shape. For these reasons, milling time and intensity are generally optimized for individual rice cultivars [9] to maximize head rice yield while meeting market requirements [10–12].

Table 1. Production patterns of head rice yields (million metric tons) across the globe in major rice-producing regions Source: [13].

Countries	Head Rice Yields (Million Metric Tons)
China	148.30
India	122.27
Indonesia	35.30
Bangladesh	34.60
Vietnam	27.38
Thailand	18.86
Burma	12.60
Philippines	12.42
Pakistan	8.42
Brazil	8

Other factors include grain moisture during harvesting and drying [14], and methods used to dry down the grain/paddy (hot air or infrared drying) [15-17] have a critical impact on head rice yield [14]. In addition, seasonal conditions have been linked to higher grain breakage during milling [18-20]. High day/night temperatures, especially during gametogenesis and early anthesis, result in substantial grain yield losses [9]. Moreover, heat stress during early and late grain filling periods affects the grain yields and milling outturn [14]. Grain breakage during milling is higher in immature grains [21], and it is therefore likely that seasonal conditions affect the uniformity of grain-filling or reduce the number of immature grains at harvest, increasing head rice yields. Further, some lines of evidence suggest that rice grain molecular components (starch, seed storage proteins, starch lipids) may be linked to grain breakage during milling [22–25]. Therefore, in addition to reviewing known factors that influence head rice yields, we review the key molecular components of rice grains, rice grain chalkiness and the impact of seasonal conditions (including temperature) on grain molecular composition, chalkiness, and the uniformity of grain-filling, with the view that these factors may ultimately have consequences on head rice yield.

This review discusses the potential impact of high temperature on HRY in respect to pre-and-post harvest scenarios. This review further resolves the effect of heat stress on losses during milling operations associated with the reductions of HRY and elaborates on genetic variation for the response of HRY and component traits, including grain molecular composition, which could be exploited to map quantitative trait loci (QTLs) or singlenucleotide polymorphisms (SNPs).

2. Factors Affecting Head Rice Yields

2.1. Rice Grain Size and Shape

There is wide variation in rice grain size and shape, which has necessitated the construction of a system to classify the rice grains by size and shape. Rice grain is generally grouped into one of the four grain length categories—short, medium, long and extralong/slender grain (Figure 1), where short grains are ≤ 5.50 mm in length, medium grains are 5.51–6.60 mm, long grains are 6.61–7.5 mm and extra-long/slender grains are >7.5 mm in length [26].

Rice grain size and shape are largely determined by genetics and a few quantitative trait loci (QTLs). Rice grain size and shape are identified in Table 2. For example, the QTL GS3 (Table 2) plays a major effect on QTL for rice grain length and weight and a minor effect on QTL for rice grain width and thickness [27,28]. GL3.1 regulates the grain

length and weight, while qgl3 has a favorable effect on grain length, filling and weight [29]. GW2 increases spikelet hull width and accelerates the grain-filling rate, grain width and weight [30]. However, none of the QTLs for grain length and width (Table 2) have been directly linked to head rice yield.



Figure 1. Rice grain diversity in size (thickness) and shape (length, width and length-to-width ratio). Source: [31].

Plant Material	QTL	Traits	Cloning	Chromosome Number	References
Rice	lk3	Grain length		3	[32]
Rice	gw3.1, gw3.2, gw9.1	Grain weight		3	
Rice	gw3.1	Grain weight	Fine mapped	3	[22]
Rice	GS3	grain length and weight	cloned	3	[33]
Rice	GW2	Control grain width and weight	cloned	2	[34]
Rice	Lk-4	Grain length	Fine mapped	4	[35]
Rice	GW5	Grain width and weight	Fine mapped	5	[36]
Rice	DEP1	Reduce length of panicle for better grain-filling		1	[37]
Rice	qGL7	Grain length and size		7	[38]
Rice	ĜL3.1	Grain length and weight	cloned	3	[39]
Rice	qGL4b	Grain length and weight		4	[40]
Rice	qSS7	Length, width and weight		7	[41]
Rice	GW1, GS3, GS7	Grain weight and size	Fine mapped	1, 3, 7	[42]
Rice	GW7	Grain width	OsSNB	7	[43]
Rice	GW2, Gl12	Grain length and width	Fine mapped	2, 12	[44]
Rice	TGW6	Thousand grain weight	cloned	6	[45]
Rice	qgl3	Grain length, filling and weight	cloned	3	[46]
Rice	* Srs5	Cell elongation		5	[47]
Rice	GS2	Grain weight	cloned	2	[48]
Rice	GS5-1, GS5-2	Grain width, filling and weight		5	[49]
Rice	* BG1	Seed weight	الم سماد	1	[50]
Rice	* BG1	Source-size sink and heading date	cioned	1	[50]
Rice	GLW7	Grain length	Cloned OsSPL13	7	[51]
Rice	GL1.3	Grain length and weight	Fine mapped	1	[52]
Rice	GL-6	Grain length	Fine mapped	6	[53]
Rice	TGW12	Grain weight	Fine mapped	12	[54]
Rice	MQTL3.1	Grain weight	Meta QTL	3	[55]

Table 2. Quantitative traits loci of rice grain size and shape.

* Indicates artificial mutants.

Head rice yield varies with the shape and size of the rice grain, but contradictory findings have been reported. For example, [56,57] observed higher head rice yield in

short grains than in medium and long grains. In contrast, [58,59] found higher head rice yields in medium-grain cultivars than in short- and long-grain cultivars. The contradictory findings could be due to the seasonal environmental conditions where rice cultivars were grown and/or factors beyond physiological maturity or may be due to genetics. However, ultimately, the reason for the discrepancy still needs to be solved.

2.2. Rice Grain Molecular Composition

Rice grain is mainly composed of starch (89–92%), seed storage proteins (6–8%) and lipids (1–2%) [60,61], and these components largely determine the rice grain functional properties, including gelatinization temperature, gelatinization index, flour viscosity and RVA (rapid viscos analyzer) pasting properties [62,63]. The roles of starch, lipids and seed storage proteins have been widely studied from a cooking and eating perspective. However, the role of these grain components in determining the head rice yield still needs to be determined despite several studies demonstrating a potential association between one or more of these components and grain breakage, as reviewed below.

2.2.1. Starch

Starch, the dominant component of the rice grain endosperm, is a polymer composed of glucose monomers and is found in one of two types: amylose (0–30%) or amylopectin (75–80%) [64]. Amylose is primarily a linear molecule joined by α 1-4 links while amylopectin has α 1-6 linkages in addition to α 1-4 links [65]. The α 1-6 linkage creates a branched structure, and these structural differences affect physio-chemical properties such as solubil-ity: amylopectin is water soluble, while amylose is not soluble in water. Structural analysis of starch granules [66] shows that amylose molecules reside between the amylopectin molecules (Figure 2), and their relative concentration is important for starch stability.



Figure 2. Schematic representation of different structural levels of the starch granule and the involvement of amylose and amylopectin in developing starch molecules [64].

Amylose is synthesized by a granule-bound starch synthase (GBSSI) coded by the waxy gene (Waxy/wx) [67] while amylopectin is synthesized by (Sbe) starch synthase branching and debranching enzymes [68,69]. DNA sequence differences within the rice starch synthesis structural genes generate allelic diversity, which results in rice starch composition differences. However, any of the changes caused by Wx and Sbe genes have not been linked to head rice yield.

The importance of starch in determining head rice yield is somewhat unclear (Table 3). A temperature stress study [70] reported that head rice yields declined with increasing night-time temperature as amylopectin carbon chain lengths increased. In contrast, another study [63] found no association between amylose:amylopectin ratios and head rice yield

across a range of rice cultivars. Similar conflicting results have been reported for the relationship between amylose and grain chalkiness, a trait linked to reduced head rice yields, discussed in Section 2.2.4 below.

Table 3. Quantitative traits loci for endosperm starch and their importance in rice grain quality.

Plant Material	QTL	Traits	Chromosome Number	References	
Seven indica (T65,N8,108,C8669,C8005,221,T65wx), three glaberrima (W025,GM1,GM2)	Wx gene (Wx ^a , Wx ^b)	Amylose	6	[67]	
Kinmaze and its mutant lines	Flo-2	Regulates RBE1 gene for starch synthesis	6		
Japonica	Soluble starch synthase	Starch		[71]	
132 DH population via anther culture of F ₁ hybrid between ZYQ8 (indica) and JX17 (japonica)	qAC-5, Wx	Amylose content	5,6		
, , , , , , , , , , , , , , , , , , , ,	GBSSI, GBSSII, SSI, SSIIa, SSIIb, SSIIc, SSIIIa, SSIIIb, SSICa, SSIVb	Starch synthase under temperature stress	6, 7, 6, 6, 2, 10, 8, 4, 1, 5		
	BEI, BEIIb,	Branching enzyme	6, 2		
Nipponbare Koshiibuki Tentakaku	ISA1, ISA3, PUL	Debranching enzyme	8, 9, 4		
Sasanishiki and Hatsuboshi	Amy1A, Amy2A, Amy3A, Amy3C, Amy3D, Amy3E, Amy4A	Alpha-Amylase	2, 6, 9, 9, 8, 8, 1	[72]	
	Ramy1	Transcription factor for amylase gene	1		
Nipponbare	Flo-2	Starch quality and grain size	6	[73]	
chromosome segment substitution lines of a cross between 9311 and Nipponbare	starch paste viscosity characteristics	Rapid viscos analyzer profile of rice genotypes	1, 2, 4, 5, 6, 8, 10	[74]	

^a indicates the allele a produces the larger amount of amylose; ^b indicates the allele b produces smaller amount of amylose.

2.2.2. Seed Storage Proteins

Seed storage proteins in rice endosperm are composed of glutelins (60–80%), prolamins (20–30%) and globulins (5–6%) [60]. Seed storage proteins are traditionally defined by their solubility, where glutelins are soluble in dilute acid or base, prolamins in aqueous alcohol solutions, and globulins in salt solutions. These seed storage proteins, referred to as protein body I (PB-I) and protein body II (PB-II) (Figure 3), are embedded between the starch granules, helping them to bind [75]. Prolamins are found within PB-I and have molecular masses of 10, 13 and 16 kDa [60,61,75]. The 13 kDa prolamins are the dominant component of PB-I and are further classified based on Cys residues [76]. The Cys-poor prolamins have one cysteine residue per molecule, while the Cys-rich have five to nine cysteine residues per molecule. Prolamins accumulate within the smooth endoplasmic reticulum [77], which then mature and form PB-I.

Globulins and glutelins are deposited into protein storage vacuoles, which then mature and form PB-II. Approximately 15 glutelin coding genes are divided based on DNA sequence into four gene families: GluA, GluB, GluC and GluD [78–80]. Globulin is dominated by a protein derived from a single-copy α -globulin encoding gene [81]. Several studies have reported the QTLs for seed storage proteins, but none for rice grain seed storage proteins (Table 4) have been linked to head rice yield.



Figure 3. Transmission electron microscope (TEM) image of 'Protein body I (PB-I; where prolamins accumulate within the smooth endoplasmic reticulum)' and Protein body-II (PB-II, where globulins and glutelins are accumulated into protein storage vacuoles)' in matured rice endosperm. Source [75].

Table 4. Quantitative traits loci for rice grain proteins.

Plant Material	QTL	Traits	Chromosome Number	References
210 F ₁₀ RIL population derived from <i>Zhenshan</i> 97 (maternal) and Minghui 63 (paternal)	Markers (C922, C1016, R1629 RM228, R19, C909B, TEL3, R496)	Protein %	1, 4, 8, 10, 3, 11, 12	[82]
312 Double haploids from BC3F1 i.e., derived from <i>Caiapo</i> (Brazillian, long grain) × <i>Oryza glaberrima</i> , IRGC 103544	Pro1, pro2, pro6, pro11	Protein %	1, 2, 6, 11	
81 DH lines from the F1 hybrid of a cross between <i>Gui 630 (indica)</i> × 02428 (<i>japonica</i>)	qRPC-1, qRPC-4, qRPC6, qRPC-7, qRPC-10	Protein content	1, 4, 6, 7, 10	[83]
71 RILs derived from a cross	qGLB-1, qGLB-2.1, aGLB-2,2, aGLB-5	Globulin	1, 2, 2, 5	
between Asominori \times IR24	qPLA-1, qPLA-3, qPLA-10	Prolamin	1, 3, 10	[84]
	qGLT-2, qGLT-10, qGLT-11, qGLT-12	Glutelin	2, 10, 11, 12	
Two BC3F2 populations, NILs and 197 accessions (<i>indica and japonica</i>)	* qPC1	Glutelins, prolamins, globulins, albumins and starch. encodes a putative amino acid transporter OsAAP6	1	[85]
25 BC1F1 lines were developed by crossing "ARC 10075" × Naveen	qGPC1.1, qSGPC2.1, qSGPC7.1	Grain protein content	1, 2, 7	[86]
Mutants rice lines	rice asparagine synthetase 1	Grain protein content and grain yield	1	[87]
193 recombinant inbred lines were developed by crossing <i>Japonica rice</i> <i>Nipponbare</i> with <i>Indica super rice</i> YK17	qPC6, qPC7 and qGLU6	Crude protein and protein contents	6,7	[88]

* Only this gene has been cloned.

2.2.3. Starch Lipids

Typically, brown rice is composed of 1–2% lipids [89–91], which are generally classified as non-starch lipids and starch lipids [92–94], as shown in Figure 4. The non-starch lipids are found in the bran and embryo that are removed during milling, while starch lipids are located within the starchy endosperm portion of the rice grain. The starch lipids are chiefly composed of surface lipids, lysophosphatidyl choline, free fatty acids and lysophosphatidyl ethanolamine [95]. The surface lipids contain surface acylglycerols that are hydrolyzed through lipase action into free fatty acids [4,96] and are considered important for grain cracking during milling. For example, [22] observed high amounts of surface lipids in polished broken kernels compared to head rice (whole-grain polished kernels). Puroindoline proteins in wheat are lipid-binding proteins that play a key role in



determining wheat hardness and flour milling yield [97], a trait that is analogous to grain breakage in rice. Several studies in rice have reported the QTLs for lipid contents (Table 5), but none of these have been linked definitively to head rice yields.

Figure 4. Distribution and illustration of starch and non-starch lipids. Source [94].

Table 5. Quantitative traits loci for grain lipids in rice.

Plant Material	QTL	Traits	Chromosome Number	References
81 DH lines from the F1 hybrid of a cross between Gui 630 (<i>indica</i>) × 02428 (<i>japonica</i>)	qRFC-1, qRFC-2, qRFC-5	Fat content	1, 2, 5	[98]
71 RIL cross of Asominori (<i>japonica</i>) × IR24 (<i>indica</i>)	qFC-1-2, qFI-1-2, qFC-2-2, qFI-2, qFC-4, qFI-4, qFC-9, qFI-9	Fat contents and fat index	1, 1, 2, 2, 4, 4, 9, 9	[99]
190 DH lines, derived From anther culture of an F1 hybrid between <i>Wuyujing2 (japonica)</i> × <i>Zhanshen 97B (indica)</i> .	qCFC1a, qCFC1c, qCFC3a, qCFC3c, qCFC5abc, qCFC6a, qCFC7ac, qCFC7b, qCFC8b, qCFC9a	Fat content in brown rice	1, 1, 3, 3, 5, 6, 7, 7, 8, 9	[100]
RIL population derived from <i>Xieqingzao B × Milyang 46</i>	qFC-3, qFC-5, qFC-6, qFC-8	Crude fat content	3, 5, 6, 8	[101]
 190 DH lines derived from F1 hybrid Wuyujing2 (japonica) × Zhanshen 97B (indica). BCF1 developed by crossing DH with both parents: 149 from Zhanshen 97B and 143 from Wuyujing2 	qCFC5 detected in both populations: DH and BCF1	Crude Fat content	5	
120 DH lines developed by anther culture, F1 cross <i>Samgang</i> \times <i>Nagdong</i>	qLC6.1, qLC7.1, qLC9.1	Lipid content brown rice	6, 7, 9	[102]

Plant Material	QTL	Traits	Chromosome Number	References
	qFC7.1 and qFC7.2 pal4, ara5, oil3 encodes enzymes:	Crude fat content brown rice	7	[103]
	Ketoacyl–ACP Synthase I(KAS I), Ketoacyl–CoA Synthase (FAE1)		4, 5, 3	
182 backcross inbred lines (BILs), backcross (" <i>Koshihikari</i> " × " <i>Kasalath</i> ") and 39 chromosome segment substitution lines (CSSL)	pal6, ste4, ole1, oil1 encodes enzymes: Acyl-ACP Thioesterase (FatB), Acyl-CoA Thioesterase, ER 2-Lysophosphatidate Acyltransferase (LPAAT)	Fatty acid composition	6, 4, 1	[104]
	myr2-2, lin6-1, ole6, lin6-2 encode enzyme: Acyl–CoA:Diacylglycerol Acyltransferase (DGAT)		2, 6, 6	
133 DH lines cross Cheongcheong × Nagdong	qLip-3, qLip-6	Lipid contents brown rice	3,6	[105]
533 diverse <i>O. sativa</i> accessions Rice mutant population	PAL6, LIN6, MYR2, and ARA6 OsLTPL23	Oil biosynthesis in rice Lipid transfer protein	2,6 1,2	[106] [107]

Table 5. Cont.

2.2.4. Chalkiness

Chalkiness refers to an opaque area of the rice endosperm instead of a translucent endosperm in non-chalky rice. Chalkiness is considered a highly undesirable trait because the chalky appearance lowers the marketability of rice and causes significant milling losses [108–115].

Chalkiness is a highly undesirable trait that favors grain cracking during milling operations (dehusking and polishing), which ultimately reduces head rice yields [113]. The reason for the development of chalky grains has not been fully resolved yet [116]. Therefore, the following points need to be considered regarding the effect of rice crop physiology coupled with high-temperature stress for chalkiness.

- (1) High-temperature stress during grain filling [69,113,117] was considered a major contributing factor to the development of chalky grains.
- (2) However, other seasonal conditions such as wetting and drying cycles, are also associated with the development of chalky grains [118,119].
- (3) Previous literature also suggested that loosely packed starch molecules cause chalkiness, possibly due to variations in amylose content [108,120,121].
- (4) Other studies suggested that amylose and chalkiness are negatively correlated [113,114,122,123].
- (5) Environmental factors such as temperature, transpiration rate of canopy and evaporation rate contribute to developing chalkiness. Therefore, future studies are required to investigate which factors, environmental and genetic (in the context of Table 6), contribute to developing the chalky grains and finding the possible link between the rice grain molecular components and chalkiness.

Table 6. Quantitative traits loci for chalkiness in rice grain.

Plant Material	QTL	Traits	Chromosome Number	References
132 DH population via anther	Ratio of white-core kernels to total number of observed kernels	qPGWC-8, qPGWC-12	8, 12	
ZYQ8 (<i>indica</i>) and JX17 (japonica)	Ratio square of the white core to square of white-core kernel.	qSWC-3	3	
241 $F_{2:3}$ segregating population	C161-R753, RG360-C734a, RG528-C1447, R1952-C226, R2625-C223	Chalkiness in milled rice	3	[124]
238 F_{10} (Recombinant Inbred lines)	RG360-C734a, R1245-R1789, RG360-C734a, Wx-R1952	Brown rice white belly (First two marker intervals), brown rice white core (Second two marker intervals)	3	

Plant Material	QTL	Traits	Chromosome Number	References
66 CSSL lines (BC3F1), derived	qPGWC-8, qPGWC-9, qPGWC-1, qPGWC-7	Percentage of grains with chalkiness (PGWC)	1, 5, 5, 6, 10	
from the cross Asominori IR24	qACE-8, qACE-2, qACE-9	Area of chalky endosperm (ACE)	8,9	[125]
(Asominori recurrent parent)	qDEC-8, qDEC-9, qDEC-1a, qDEC-1b, qDEC-2	Degree of endosperm chalkiness (DEC)	5, 7, 5, 6	
NIL (near-isogenic lines), Transgenic	Chalk 5	Increased chalkiness	8, 9, 1	[126]
two single-segment substitution lines	qPGC5, qPGC6	Lower percentage of chalkiness	5,6	[127]
184 BC5F2 lines were developed by crossing <i>indica</i> cultivar J23B (the recurrent parent) and a <i>japonica</i> cultivar BL130	qWCR4	White core rate	4	[128]
Meta QTL analysis	64 MetaQTL	Grain chalkiness	1, 2, 3, 4, 5, 6, 7, 9, 10, 11, 12	[129]

 Table 6. Cont.

2.3. Rice Plant Morphology and Grain Breakage

During milling operations, immature and partially filled grains are easily broken, leading to reduced head rice yields [9,14,57,58]. The extent to which grains are filled with assimilates during grain filling is driven by source-sink relationships and plant morphological traits. These morphological traits include synchrony in tillering, panicle architecture and the annual/perennial nature of a rice cultivar, which alters the source–sink relationships [21]. For example, the GIF1 (grain incomplete filling 1) gene is associated with perennial nature in rice and downregulates the cell wall invertase that restricts carbon partitioning to grains during the early stages of grain filling, leading to immature or partially filled grains [14,130]. This gene appears to have arisen in cultivated rice (O. sativa) through introgression from the perennial wild rice O. rufipogon [130]. Panicle architecture also influences the rate and uniformity of grain filling within and between the panicles. For example, panicle length greater than 22% of plant height is associated with higher uniformity of grain filling within panicles [131]. The shorter panicle length to plant phytomass ratio could increase grain filling and development uniformity within and between the panicles, which could potentially increase head rice yield [57]. If genes controlling panicle architectural traits that are associated with more uniform grain filling could be identified, a pyramiding of these genes with genes associated with reduced perennial nature and more synchronous tillering into elite rice lines may help to lower the number of immature or partially filled grains, leading to higher head rice yields.

2.4. Pre-Harvest Factors That Affect Head Rice Yield

2.4.1. Temperature

Rice is highly sensitive to high-temperature stress (day/night), especially during gametogenesis and early anthesis (booting up to 50% flowering) stages, and heat stress during these stages results in substantial grain yield losses [6,19,132–136]. Heat stress during early grain filling downregulates the starch synthase and prolamin genes, which affects rice grain quality and yield [137]. The development of chalky grain, a main factor that has been reported that reduces head rice yields, is a result of high-temperature stress during grain-filling periods [18,19,69,118,138–144]. Other than this, rice grain functional properties such as setback viscosity, porosity, gelatinization temperature, pasting value and alkali spreading values are affected by high day and night-time temperatures [19], but whether any changes to these parameters are associated with the increased grain cracking during milling is not known.

2.4.2. Soil Moisture during Grain Filling

Soil moisture showed a considerable effect in altering the grain yield across the cereal crops following grain-filling stages in rice [145,146] and wheat [147]. Soil moisture level

might affect the source-to-sink relationships where the remobilization of pre-stored carbon and nitrogen assimilates either increased or decreased from the source (vegetative parts) to the sink (grain) under soil moisture stress. However, agronomic practices, such as post-anthesis (50% days after flowering) soil drying, have the potential to increase the amount of carbon partitioning from the flag leaf to grains by regulating key plant hormones such as abscisic acid, cytokinins in leaves [148–153] and trans-zeatin-type cytokinins in the roots [154]. Grain-filling period proved to be the dominant factor that influences head rice yields [14]; therefore, soil drying practice during mid- and late grain-filling periods upregulated the starch branching and debranching enzymes (SuSase, AGPase, SSS, GBSS, SBE) and genes (SuS2, SuS3, SuS4, AGPS2b, AGPL1, AGPL2, SSSIIb, SSSIIc, GBSSI, GBSSII, SBEI, and SBEIIb) [69]. There is a possibility to investigate the effect of post-anthesis soil drying during the grain-filling periods (mid-and-late grain filling) that influence head rice yields by altering carbon partitioning from the flag leaf to developing grains.

2.4.3. Nitrogen

Nitrogen plays a key role in determining grain yield and protein contents [24]. Nitrogen fertilizer application typically leads to increasing grain protein content, albeit this is not always the case, and substantial genotype \times environment interactions were observed [155–162]. The importance of nitrogen fertilizer application across various growth stages of rice plants (ranging from vegetative growth phases to gametogenesis and grain filling periods) in terms of rice grain cracking has not been extensively studied. However, some field studies reported nitrogen fertilizer application before flowering increased the amount and density of seed storage proteins and reduced chalkiness, which coincided with reducing grain cracking during milling operations [163–165].

2.5. Factors beyond Physiological Maturity Affecting Head Rice Yield

Head rice yield may vary with relative humidity (RH) or vapour pressure deficit (VPD), but contradictory findings have been reported. For example, [118] observed a lower head rice yield under high relative humidity and a high negative correlation between RH and HRY (r = -0.693). In contrast, [23,129] found a very weak positive correlation between RH and HRY (r = 0.168) over two-crop growing seasons across multiple growing locations. Both studies measured the RH following the entire period, grain ripening, and maturity stages (from heading/50% flowering to harvesting). The contradictory findings could be due to variation in grain moisture content at harvesting that has a confounding impact on HRY.

Paddy harvesting is normally recommended at moisture contents of about 20–25%, as a slow drying process from these levels down to around 14% (used for milling) helps to reduce fissuring and grain breakage during milling operations [16,17]. Generally, paddy drying involves the use of flat beds in hot air and/or infrared radiation chambers to reduce the grain moisture content to around 14% for dehusking and polishing [166,167]. The temperature of hot air and infrared chambers is recommended at 55 °C or less, selected based on the rice grain glass transition temperature, which is about 60 °C [14,16]. Glass transition temperature is defined as the state when polymers of starchy rice endosperm shift from soft rubbery material to hard glassy material and vice versa. Therefore, the paddy drying at or below the temperature of 55 °C makes the starchy endosperm soft and rubbery, which assists in reducing the fissuring and grain cracking during milling operations [168,169].

During milling operations, the degree of milling strongly affects head rice yield [11,12]. The degree of milling reflects how many passes are required for polishing [168]. Generally, a lower degree of milling achieves higher head rice yields and favours the retention of key nutrients in the polished grain [10]. The optimum degree of milling is generally different for short-, medium- and long-grain cultivars [169]; therefore, each grain type is recommended to be milled separately.

2.6. Genetics of Head Rice Yield

As discussed above, a wide range of rice plant morphological traits, grain size and shape, and grain molecular composition components such as chalkiness and seed storage proteins have been associated with head rice yield. Genetic variation exists for many of these traits, and the associated genes and QTLs that contribute to these traits have been identified (Table 7). However, it needs to be clarified if any of these QTL/genes have led to quantifiable improvements in breeding programs and thus to enhanced head rice yields. Given the range of environmental (temperature) and nutritional (nitrogen) factors that are associated with head rice yield, many of the mapped QTLs may be specific to the given environment (Table 7) under which the phenotyping was conducted and may not be robust across environments.

Table 7. Quantitative traits loci for percentage head rice yield (the amount of whole grain polished white rice of the paddy from which it is derived and then multiplied by 100).

Plant Material	QTLs	Chromosome Number	References	Climate Zone
212 RILs developed by crossing Lemont (<i>iavonica</i>) × Teging (<i>Indica</i>)	QHr6, QHr7	6,7	[170]	Temperate zone (China)
312 double haploids of an interspecific cross of O. sativa \times O. glaberrima.	hr1,hr3,hr6,hr8, hr11	1, 3, 6, 8	[171]	Tropical Zone (Columbia; Tropic of Cancer)
165 F6 RILs of a cross between Asominori (<i>japonica</i>) × IR24 (<i>indica</i>).	qMHP-1,MHP-3, qMHP-5	1, 3, 5	[172]	Temperate zone (Japan)
190 DH lines from the cross of Zhenshan 97 (<i>indica</i>) × WYJ-2 (<i>japonica</i>)	RM570-RM85 RM38-RM25	3, 8	[83]	Temperate zone (China)
254 BC4F1 of a cross between Teqing (<i>Indica</i>) × Lemont (<i>Japonica</i>)	QHr1, QHr5, QHr6	1, 5, 6	[173]	Temperate zone (China)
137 F_{11} RILs developed from a cross of two long-grain rice Cypress (<i>japonica</i>) ×	hr6	6	[174]	Temperate zone (USA)
286 F8 RILs developed from a cross between Chuan7 (<i>Indica</i>) and	qHRR-3 RM6283 and RM16 *	3 3	[175]	Temperate zone (China)
$154 \text{ BC}_3\text{F}_2$ derived from cross between Koshihikari (iaponica) and Nona Bokra (<i>Indica</i>)	qHRP-1, qHRP-6, qHRP-8	1, 6, 8	[176]	Temperate zone (China)
MY1: 129 RILs derived from (Cypress ×	qhr_6.1, qhr_9.1 (MY1)	6,9	[177]	Temperate zone (USA)
and MY2: 298 RILs (Cypress × LaGrue) grown in 2006, 2007 on four locations)	qhr_1.1, qhr_5.1, qhr_9.1, qhr_10.1 (MY2)	1, 5, 9, 10	[]	,
231 RILs derived from L-204 (<i>japonica</i>) × 01Y110 (<i>japonica</i>)	qhr_6.1, qhr_6.2, qhr_8.1, qhr_9.1, qhr_9.2, qhr_10.1, qhr_11.1	6, 8, 9, 10, 11	[178]	Temperate zone (USA)
258 rice accessions (<i>Indica, japonica, aus, aromatic</i>)	qHMRR3, qHMRR9	3,9	[179]	Temperate zone (China)
529 plants F2 population were developed by crossing Koshihikari (<i>japonica</i>) with Nona Bokra, (<i>indica</i>)	HRY10	10	[116]	Temperate zone (China)

* This study also looked at the traits of grain length and grain length to width ratio, in addition to head rice yield.

2.6.1. QTL Mapping for Head Rice Yield

The genetics of head rice yield has not been fully resolved, and the prediction power of QTL mapping requires trait variation decomposition to determine whether it is due to the main effect QTL (QTL \times QTL, QTL \times epistatic) and/or environmental (QTL \times environment, epistatic \times environment) effects. In the case of head rice yield, the environmental effects are not only confined to field variation but are also linked to variation associated with storage and milling operations. Dehusking and polishing (milling operations) are two distinct processes, and grain breakage during each step could be associated with head rice yield. Various QTLs for head rice yield have been reported, with most found on chromosomes 1 and 6 (Table 7). However, none of the studies listed in Table 7 clarify whether these are linked to grain breakage during the dehusking or polishing step. Therefore, "QTL \times milling environment" could be included as a separate parameter while performing QTL mapping for head rice yield.

A further consideration is that the embryo is diploid, while the endosperm is triploid, and the present QTL models are designed for a diploid inheritance, with no software available for triploid inheritance. The development of triploid models that could be used to capture the associated endosperm variation in relation to head rice yield may be beneficial.

2.6.2. GWAS (Genome-Wide Association Mapping)

Genome-wide association mapping is a recently developed tool in plant breeding that can capture the variation associated with candidate genes and/or SNPs to related traits. GWAS is based on linkage disequilibrium to identify trait–SNP association underlying complex traits. In rice breeding, the use of GWAS for head rice yield is limited. Most of the studies sampled their materials from the 3000 resequenced rice genome populations with population sizes ranging between 200 and 404 *indica* or *japonica* rice accessions [180–187]. These studies combined detected over one hundred loci associated with head rice yield and chalkiness-related traits distributed throughout the rice genome. However, none of these QTL overlapped among different studies with interval distance between any two adjacent QTL > 0.5 Mbp, except for one chalkiness QTL on the beginning of chromosome 3 that was detected in *japonica* [185] and *indica* germplasm [186]. This indicates that these studies detected environment-specific QTL.

All previous studies used a single trait mixed linear model to detect associated QTL. Therefore, to detect stable QTL across environments, future studies should adopt more advanced statistical models such as the multi-trait mixed linear model [187,188] or MetaG-WAS model [189,190]. The latter would be more appropriate when raw data cannot be shared among different institutes, as it only requires sharing summary statistics. The major difficulty associated with combining the results of multiple studies is the ability to synchronize the SNPs used in all of them. However, this can be easily solved for a crop such as rice for which a large genomic stock exists in the 3000 resequenced genome projects, which facilitate the imputation from different genotyping platforms to a common high-density genotyping [191] or by imputing missing summary statistics [192], given that grain size and shape are strongly linked to head rice yields. Since milling is generally optimized for each grain shape, it will be interesting in future studies to fit these traits (or preferably the first few principal components of them to avoid their correlations) as covariates to ensure detecting loci for head rice yields that are independent of grain characters.

2.6.3. Genomic Selection

Genomic selection has the advantage of exploiting the whole genetic variation explained by the SNPs over QTL mapping and GWAS, which usually detect a small number of QTL with a large enough effect to pass the significance threshold [193]. However, the cumulative effect of these small numbers of QTL could not be enough to make informative long-term selections for complex quantitative traits. Therefore, QTL with a small effect can be captured with the genomic selection, which usually explains most of the phenotypic variation of the complex traits that are usually controlled by hundreds to thousands of genes. To the best of our knowledge, only two studies were conducted by the same group that investigated the potential of genomic selection to improve head rice yield and grain chalkiness [194,195]. Both studies worked on the same data, which involved 327 *indica* elite rice lines and 309/320 *japonica* elite rice lines. Both populations were phenotyped for multiple seasons in a single location.

The former study [194] investigated the prediction accuracy using two cross-validation schemes (CV1 and CV2) for five traits, including head rice yield and grain chalkiness, using different prediction models that exploit genotype by environment interactions. The *indica* and *japonica* populations were phenotyped in three seasons in a single location. In CV1, they completely masked a subset of the studied accessions to calculate the accuracy of predicting them. This approach mimics the case of introducing new materials to the breeding program. In CV2, they masked random plots across different field trials to mimic the case where different trials have different sets of lines to predict phenotypes for all lines in all trials.

The heritability for head rice yield and chalkiness was considerably high, with 0.87 and 0.63 average values across all seasons for *indica* and *japonica* populations, respectively. The prediction accuracies for the top model ranged between 0.51 and 0.66 for head rice yield and between 0.33 and 0.61 across different seasons for both populations, with average values of 0.56 for head rice yield and 0.44 for chalkiness. Given the small reference population used in the study, the prediction accuracy could be further improved if more data were used to train the prediction equation.

In a later study [195], the authors used the same previous data with two extra seasons for the *japonica* population (a total of five seasons versus only three seasons for the *indica* population) to test the advantage of using environmental covariates simultaneously with their molecular variants in predicting the performance of their population in unobserved environments. Environmental covariates were recorded from the daily weather data for each rice accession on the day it reached a specific developmental stage, e.g., flowering. They used the "one-environment-out" cross-validation scheme in which they dropped the environment from the reference to be predicted. Across different seasons and applied models, the prediction accuracy reached a maximum of 0.5 for head rice yield and 0.3 for chalkiness for the *indica* population, while the accuracies were much higher for the *japonica* population with a maximum of 0.8 for head rice yield and 0.7 for chalkiness. This is not unexpected given that the reference *japonica* population had four seasons while the *indica* reference population had only two seasons. A major drawback of their study is their assumption that the phenology data (such as the flowering date used to calculate the environmental covariates) may not be possible to use for untested environments. Future studies should investigate the effect of predicted phenology traits on the prediction accuracy of untested environments. Alternatively, untested or future climates can be predicted in a more straightforward CGM-WGP, which integrates crop growth models and genomic prediction [196].

3. Conclusions and Outlooks

Several factors potentially affect the yields of head rice, including day and night-time temperatures across various growth stages including vegetative, reproductive, and grain filling periods, nitrogen fertilizer applications at days to 50% flowering and during key grain developmental stages, harvest moisture contents, paddy storage conditions and paddy moisture contents before milling operations (including dehusking and polishing). Among these factors, the temperature is critical because of the predicted changes in day and night-time temperatures expected to arise due to climate change. However, the study of rice crop physiology needs to be accounted for, for a better understanding of the heat stress that affects rice plant yield in terms of grain yields and head rice yields. Moreover, the measure of association is required between chalkiness and several other factors including temperature, nitrogen application and milling operations across the different genetic backgrounds including *japonica*, *temperate japonica*, *indica*, *aus*, *aromatic*, and wild types to develop potential links between chalkiness and GGM-WGP will be required to accelerate the genetic development of head rice yield.

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