

Genome-Wide Association Study of Grain Quality Traits in Rice Detected Genomic Regions of High-Quality Rice for Increasing Rice Consumption

Jawaher Alkahtani

Department of Botany and Microbiology, College of Science,
King Saud University, Riyadh, Saudi Arabia.

<http://dx.doi.org/10.13005/bbra/2988>

(Received: 07 March 2022; accepted: 21 June 2022)

This review describes the current status of genome-wide association study (GWAS) of the major cereal crop in rice (*Oryza sativa* L.) concentrate on the rice quality traits that related to the consumers demand. These rice quality traits that also become major concern in the rice industry and determine the rice consumption value, including grain length, grain width, grain length to width ratio, grain weight, amylose content, protein content, as well as gelatinization temperature. One of the primary objective in the rice breeding program is to increase rice grain quality based on the consumption demands. Rice grain quality preferences influenced by countries and cultures. genome-wide association study has an important role in increasing the rice quality based on the consumers demand because this method identified many crucial genomic regions of important traits. genome-wide association study has many advantages correlated with reducing genotyping cost and research time, increasing mapping resolution and larger allele number. Meanwhile, genome-wide association study has two main limitations related to population size and the number of markers. There are many software packages for data analysis in genome-wide association study. The most commonly software that was used in genome-wide association study especially in these crops is TASSEL because frequently updated. Recently, many research papers concentrated on genome-wide association study in rice quality traits. A total of 121, 138, 81, 60, 18, 6, and 5 QTLs for grain length, grain width, grain length to width ratio, grain weight, amylose content, protein content, and gelatinization temperature; respectively have been identified by genome-wide association study in different rice populations for almost twelve years (2010 until 2022). genome-wide association study analysis accelerated identification of genetic regions, candidate genes within these genomic regions and their metabolomic analysis correlated to the rice quality traits. Developing high-quality rice varieties that meet consumer preferences and increasing global population demands can be accelerated by genome-wide association study.

Keywords: Genome-Wide Association Study (GWAS); Genomic Regions, Rice Consumption; Rice Quality Traits.

Rice (*Oryza sativa* L.) as the primary staple food for half of the global population, with increasing the living standard of rice consumers,

the demand of premium rice grain quality is increasing along with the climate change, agricultural land limitation, and also growing

*Corresponding author E-mail: jsalqahtani@ksu.edu.sa



population up to 9 billion expected by 2050^{1,2,3,4,5,6,7,8}. Therefore, identification of genomics regions related to the rice grain quality traits has become a primary objective in the rice breeding program and receiving big attention from rice consumers and producers. Genome-wide association study (GWAS) by using diverse rice population and large number of molecular markers have successfully detected genomic regions related to the rice grain quality traits. These grain quality traits belong to the complex quantitative traits that are regulated by multiple genes and affected by environmental conditions^{9,10,11}. Recently, rice grain quality traits including appearance quality (grain length, grain width, grain length to width ratio, grain weight, and percent chalkiness), nutritional quality (protein content, lipid content, minerals, vitamins, and phenols), cooking and eating quality (amylose content, gelatinization temperature, and gel consistency), and milling quality (brown rice recovery, milled rice recovery, and head rice recovery) become the major considerations of rice producers for capturing consumers demands of high-quality rice in the rice marketplace^{12,13,14,15,16}.

The most crucial rice grain quality trait that effect rice market acceptability is related to the grain appearance^{17,18,19}. Rice grain appearance also influence the rice yield that associated with grain length, grain width, and grain weight^{20,21,22}. Grain length and grain width define grain shape and size^{23,24}. Slender rice grain consider having grain length to width ratio of three and above^{25,26}. Rice grain quality preferences differs among the countries and cultures²⁷. Rice consumers in India, Southern China, Pakistan, Bangladesh, Sri Lanka, Southeastern Asian countries, and USA prefer slender and long grains with texture fluffy to harder, and contain intermediate to high amylose content. Meanwhile, rice consumers in Japan, South Korea, and Northern China prefer short and round grain with soft and sticky texture, and also with low amylose content^{28,29,30}.

An undesirable trait of the rice quality is grain chalkiness that reduce palatability, cooking and eating quality of cooked rice³¹. Grain chalkiness is an opaque area in the back, core, and belly of the rice grain. Chalky rice grains are prone to breakage during milling due to loosely packed, large, and round starch granules³². Percentage of

rice grain with chalkiness also influence market acceptability^{32,33}. Rice grain with more than 2% chalkiness is not accepted by rice market^{34,35}. The rice price with different grain appearance varies among regions^{36,37}. The most rice market prefer rice grains with translucent endosperms³⁸.

Eating and cooking quality of rice grain associated with cooked rice textures as stickiness and firmness, and also the easiness of cooking. Eating and cooking quality of rice influenced by the grain composition, including starch (80-85%), protein (4-10%), and lipid (1%) that showed high variation among rice varieties^{28,39}. Rice starch consist of two components, amylose and amylopectin that associated with texture, gel consistency, pasting viscosity, and gelatinization temperature^{40,41}. Amylose content influences the physicochemical characteristics of starch that influence eating and cooking properties⁴². Cooked rice texture and processing characteristics are influenced by amylose content and gelatinization temperature³³. Gelatinization temperature showed a strong correlation with the cooking time⁴³. Rice grain that has high gelatinization temperature needs longer cooking times, more water, and less sticky texture compared to low gelatinization temperature rice^{44,45}. According to the rice consumers preferences, the high-quality rice cultivars has low to intermediated gelatinization temperature^{46,47}. Based on the amylose content, rice grain can be classified into waxy (0-20%), low waxy (12-20%), intermediate waxy (20-25%), and high waxy (25-33%)^{48,49}. One of the rice quality trait that associated with higher rice price is aroma. Jasmine and Basmati rice belong to the aromatic rice that contain phenolic compound 2-acetyl-1-pyrroline (2-AP) which correlated with rice fragrance, such as popcorn-like aroma, milky aromas, sweet nutty, and cracker-like roasted^{27,49,50,51}.

Rice grain quality traits determine the rice price and rice grain market classes in commercial markets. Advanced molecular breeding methods such as GWAS supported by the development of next-generation sequencing methods and -omics technologies led to identify genomic regions associated with the rice grain quality traits effectively^{47,52,53,54}. By understanding the genetic architecture of the rice quality traits could increase breeding efficiency to develop rice variety with high-quality based on rice consumers

in competitive rice commercial markets that can satisfy rice consumers. In this review, emphasis on the crucial rice quality traits based on the rice consumers preferences, including grain length (GL), grain width (GW), grain length to width ratio (RGLW), grain weight (GWT), amylose content (AC), protein content (PC), and also gelatinization temperature (GT).

Phenotypic Variation and Correlation of Grain Quality Traits in Rice

A wide range of phenotypic variation, normal distributions, and also transgressive segregants were observed for all evaluated grain quality traits, including GL, GW, RGLW, GWT, AC, PC, GT, and also ECQ suggesting that these traits were quantitatively inherited^{55, 56}. Transgressive segregant formation is important for rice quality traits improvement due to the availability of novel alleles and genes for improving the quality traits^{17, 57, 58, 59}. Wide ranges of phenotypic variations were present in the GL of rice from 6 until 12 cm^{17, 21, 22, 34, 36, 57, 60, 61, 62, 63, 64, 65, 66, 67}; GW with range 2-4 cm^{17, 21, 22, 34, 36, 57, 60, 61, 62, 64, 65, 68}; range of RGLW from 2-3.5^{17, 21, 34, 36, 47, 57, 62, 64, 67}; GWT range 23-27 g^{21, 61, 62, 64, 65, 66}; AC range 0.8-661%^{31, 47, 60, 61, 69}; range of PC 0.5-12%^{61, 69}; and also GT range 60-70°C^{47, 60, 61}. Therefore, understanding the genetic architecture of phenotypic variation in rice quality traits by using GWAS method is important for improving the rice quality based on the rice consumers preferences.

Low to high correlations were observed among the rice quality traits. Positive and strong correlations were detected between GL and GWT suggesting that GL has the strongest effect on grain weight than the other rice grain quality traits^{13, 23, 57}. Meanwhile, GW more contributes on the grain thickness. GL showed low and negatively correlated with GW. Additionally, GL has moderate and positive correlation with RGLW. Positive and very weak correlations were found between GWT and RGLW^{17, 57, 70}. GL and GW were all showed strong and positive correlation with RGLW and GWT. Low correlation detected between grain appearance traits (GL, GW, RGLW, and GWT) and AC. Correlation between grain appearance (GL, GW, RGLW, and GWT) and GT also low³⁶. Pairwise correlation analysis among the quality traits showed that all of the correlations are similar across the years^{36, 71}. Based on these

results suggesting that long grain rice would have lower GW, higher GW and RGLW. Therefore, it is possible to develop rice varieties with different rice grain shape according to the consumers preferences in the different rice markets.

Genome-Wide Association Study of Grain Quality Traits in Rice

A powerful tool and an effective approach to identify loci associated with the rice grain quality traits is a GWAS^{21, 72, 73, 74, 75, 76, 77, 78, 79, 80}. Developing rice varieties with desired characteristics of rice to satisfy rice consumers could be more effective by using GWAS^{45, 81, 82, 83, 84, 85, 86, 87, 88, 89, 90, 91, 92, 93, 94}. The first GWAS associated with rice grain quality traits were conducted by Huang *et al.* (2010)⁶⁰ by using 517 rice diverse landraces that genotyped by ~3.6 million SNPs. GWAS detected major and minor quantitative trait loci (QTLs) correlated with the grain quality traits. GWAS also fine mapped of QTLs that lead to identify genes regulated QTLs of grain quality traits and guide to develop rice varieties with high-quality grains to satisfy the rice consumers preferences^{47, 95, 96, 97, 98, 99, 100, 101, 102, 103, 104, 105, 106, 107, 108, 109, 110, 111, 112, 113, 114, 115, 116, 117, 118}.

In this review article, we will explore the recent development of identification of genomic regions associated with the rice grain quality traits from 2010 until 2022. These rice grain quality traits including grain length (GL), grain width (GW), grain length to width ratio (RGLW), grain weight (GWT), amylose content (AC), protein content (PC), and also gelatinization temperature (GT).

Grain rice appearance such as GL, GW, and RGLW belong to the most stable quality traits and have high heritability¹¹⁹. A lot of GWAS have been done for grain rice appearance traits (GL, GW, and RGLW) compared to the others quality traits (GWT, AC, PC, and GT). Based on the GWAS analysis, a lot of QTLs have been detected for GL, GW, and RGLW (Table 1). A total of 121, 138, 81, 60, 18, 6, and 5 QTLs for GL, GW, RGLW, GWT, AC, PC, and GT; respectively have been identified by GWAS in different rice populations for almost twelve years (2010 until 2022). Many QTLs showed pleiotropic effects that control more than one quality traits on one loci. QTLs for GL more distributed on chromosome 3 than others. Meanwhile, chromosome 5 harbored more QTLs for GW. Many QTLs for RGLW displayed pleiotropic effects with QTLs for GL and GW

Table 1. Genome wide association studies of grain quality traits in rice

Grain Quality Traits	Population	Sample Size	Background Markers	Loci	Chromosome	Year	References
Grain length	Diverse landraces	517	~3.6 million SNPs	5	3, 3, 3, 5, and 11	2010	(Huang <i>et al.</i> , 2010) ⁶⁰
	<i>Indica</i> and <i>Japonica</i> Landraces and elite accessions	950	1,345,417 SNPs	7	3, 6, and 7	2012	(Huang <i>et al.</i> , 2012) ⁶¹
	<i>Indica</i> rice accessions	529	4,358,600 SNPs	-	1, 2, 3, 4, and 7	2014	(Yang <i>et al.</i> , 2014) ⁶²
	Diverse inbred lines	272	9,340 SNPs and 12,926 DArT	8	2, 3, 5, 7, 9, and 11	2015	(Qiu <i>et al.</i> , 2015) ¹⁷
	Diverse <i>indica</i> accessions	1,568	700,000 SNPs	-	3, 5, and 10	2016	(McCouch <i>et al.</i> , 2016) ⁶³
	Diverse accessions	469	3,951 SNPs	8	2, 3, 4, 5, 8, and 12	2016	(Feng <i>et al.</i> , 2016) ²¹
	Hybrid	258	22,488 SNPs	14	2, 3, 4, 6, 7, 8, and 9	2017	(Verma <i>et al.</i> , 2017) ³⁴
	Temperate <i>Japonica</i>	100	1,663,267 SNPs	34	3	2019	(Chen <i>et al.</i> , 2019) ⁶⁴
	<i>Indica</i> multiparent advanced generation intercross (MAGIC) populations	203	365,710 SNPs	1	3	2020	(Changrong <i>et al.</i> , 2020) ²²
	Diverse accessions	378	55K array-based SNP	3	3 and 7	2020	(Ponce <i>et al.</i> , 2020) ⁵⁷
Grain width	Diverse accessions	183	39,40,165 SNPs	15	1, 3, 4, 5, 7, 8, 9, 10, and 12	2020	(Roy <i>et al.</i> , 2020) ⁶⁵
	Diverse accessions	760	488,973 SNPs	14	1, 3, 5, 6, 7, 8, 10, and 11	2021	(Qiu <i>et al.</i> , 2021) ³⁶
	Hybrid rice lines	404	56K SNP chip	12	1, 3, 4, 5, 6, 7, 10, 11, and 12	2022	(Yu <i>et al.</i> , 2022) ⁶⁷
	Diverse landraces	517	~3.6 million SNPs	2	5 and 5	2010	(Huang <i>et al.</i> , 2010) ⁶⁰
	<i>Indica</i> and <i>Japonica</i> Landraces and elite accessions	950	1,345,417 SNPs	4	12	2012	(Huang <i>et al.</i> , 2012) ⁶¹
	<i>Indica</i> rice accessions	529	4,358,600 SNPs	-	1, 2, 3, 5, 6, 7, 9, and 11	2014	(Yang <i>et al.</i> , 2014) ⁶²
	Diverse <i>indica</i> accessions	272	9,340 SNPs and 12,926 DArT	5	4, 5, 7, 10, and 11	2015	(Qiu <i>et al.</i> , 2015) ¹⁷
	Diverse accessions	469	3,951 SNPs	4	1, 2, 4, and 5	2016	(Feng <i>et al.</i> , 2016) ²¹
	Wild rice and diverse accessions	258	22,488 SNPs	18	1, 3, 4, 5, 6, 7, 8, 9, 10, and 11	2017	(Verma <i>et al.</i> , 2017) ³⁴
	Hybrid	570	>1.9 million SNPs	33	2, 4, and 5	2018	(Zheng <i>et al.</i> , 2018) ⁶⁸
Temperate <i>Japonica</i> Diverse accessions	Hybrid	100	1,663,267 SNPs	34	5	2019	(Chen <i>et al.</i> , 2019) ⁶⁴
	Temperate <i>Japonica</i>	203	365,710 SNPs	3	3, 5, and 9	2020	(Changrong <i>et al.</i> , 2020) ²²
	Diverse accessions	183	39,40,165 SNPs	9	1, 3, 4, 6, 7, and 10	2020	(Roy <i>et al.</i> , 2020) ⁶⁵

<i>Indica</i> multiparent advanced generation intercross (MAGIC) populations	378	55K array-based SNP	3	5, 7, and 8	2020	(Ponce <i>et al.</i> , 2020) ⁵⁷
Diverse accessions	760	488,973 SNPs	23	1, 2, 3, 4, 5, 6, 7, 8, 9, 11, and 12	2021	(Qiu <i>et al.</i> , 2021) ³⁶
Landraces and elite accessions	529	4,358,600 SNPs	-	3, 5, 6, and 8	2014	(Yang <i>et al.</i> , 2014) ⁶²
<i>Indica</i> rice accessions	272	9,340 SNPs and 12,926 DaRT	6	1, 3, 5, 7, and 11	2015	(Qiu <i>et al.</i> , 2015) ¹⁷
Diverse <i>indica</i> accessions	469	3,951 SNPs	5	2, 3, 4, 5, and 10	2016	(Feng <i>et al.</i> , 2016) ²¹
Diverse accessions	258	22,488 SNPs	13	1, 2, 3, 4, 5, 7, 9, 10, 11, and 12	2017	(Verma <i>et al.</i> , 2017) ³⁴
Hybrid	100	1,663,267 SNPs	34	3 and 5	2019	(Chen <i>et al.</i> , 2019) ⁶⁴
<i>Indica</i> multiparent advanced generation intercross (MAGIC) populations	378	55K array-based SNP	4	3, 5, 7, and 8	2020	(Ponce <i>et al.</i> , 2020) ⁵⁷
Diverse rice accessions	284	SNPs	1	7	2021	(Cruz <i>et al.</i> , 2021) ⁴⁷
Diverse accessions	760	488,973 SNPs	11	1, 2, 3, 5, 6, 7, and 10	2021	(Qiu <i>et al.</i> , 2021) ³⁶
Hybrid rice lines	404	56K SNP chip	7	1, 4, 7, and 9	2022	(Yu <i>et al.</i> , 2022) ⁶⁷
<i>Indica</i> and <i>Japonica</i> Landraces and elite accessions	950	1,345,417 SNPs	2	2 and 7	2012	(Huang <i>et al.</i> , 2012) ⁶¹
Diverse <i>indica</i> accessions	529	4,358,600 SNPs	-	1, 2, 3, 4, 6, 7, 9, and 10	2014	(Yang <i>et al.</i> , 2014) ⁶²
Hybrid	469	3,951 SNPs	10	1, 3, 4, 5, 7, and 11	2016	(Feng <i>et al.</i> , 2016) ²¹
Diverse accessions	183	1,663,267 SNPs	34	3	2019	(Chen <i>et al.</i> , 2019) ⁶⁴
Diverse landraces	517	39,401,165 SNPs	14	1, 4, 5, 7, 8, 9, 10, and 11	2020	(Roy <i>et al.</i> , 2020) ⁶⁵
<i>Indica</i> and <i>Japonica</i> Diverse rice accessions	950	~3.6 million SNPs	3	6, 6, and 6	2010	(Huang <i>et al.</i> , 2010) ⁶⁰
Diverse rice accessions	284	1,345,417 SNPs	4	6 and 12	2012	(Huang <i>et al.</i> , 2012) ⁶¹
Diverse rice accessions	526	SNPs	3	6	2021	(Cruz <i>et al.</i> , 2021) ⁴⁷
Diverse rice accessions	217	42,446 SNPs	1	9	2021	(Verma <i>et al.</i> , 2021) ⁶⁹
<i>Indica</i> and <i>Japonica</i> Diverse rice accessions	950	872,556 SNPs	7	1, 4, 7, 8, 10, and 11	2022	(Alpuerto <i>et al.</i> , 2022) ³¹
Diverse rice accessions	526	1,345,417 SNPs	5	6, 7, and 11	2012	(Huang <i>et al.</i> , 2012) ⁶¹
Diverse rice accessions	517	42,446 SNPs	1	12	2021	(Verma <i>et al.</i> , 2021) ⁶⁹
Diverse landraces	950	~3.6 million SNPs	1	6	2010	(Huang <i>et al.</i> , 2010) ⁶⁰
<i>Indica</i> and <i>Japonica</i> Diverse rice accessions	284	1,345,417 SNPs	3	7	2012	(Huang <i>et al.</i> , 2012) ⁶¹
Diverse rice accessions	284	SNPs	1	6	2021	(Cruz <i>et al.</i> , 2021) ⁴⁷

because of their strong phenotypic correlations. QTLs for GWT mostly distributed on chromosome 7. Due to their high phenotypic correlations, QTLs for AC and GT also showed pleiotropic effects on chromosome 6. QTLs for PC distributed equally on chromosome 6, 7, 11, and 12.

Many genes regulating the rice grain quality traits have been cloned. About four genes controlling GL have been cloned, including *PGL1* (LOC_Os03g07510) on chromosome 3, *PGL2* (LOC_Os02g51320) on chromosome 2, *GL3.1* (LOC_Os03g44500) on chromosome 3, and *GL7/GW7* (LOC_Os07g41200) on chromosome 7^{66, 120, 121}. Two genes controlling GW have been cloned, including *GW2* (LOC_Os02g14720) on chromosome 2 and *GW8* (LOC_Os08g41940) on chromosome 8^{23, 122}. Genes regulating GWT that have been cloned were *GW5* (LOC_Os05g09520) on chromosome 5, *GW6a* (LOC_Os06g44100) on chromosome 6, *TGW6* (LOC_Os06g41850) on chromosome 6, and *HGW* (LOC_Os06g06530) on chromosome 6^{123, 124, 125}. The major gene regulating AC and GT is *Wx* on chromosome 6^{126, 127, 128, 129, 130, 131, 132, 133, 134, 135}. Rice which contain high AC is beneficial to be consumed by diabetic people due to their low glycemic index^{9, 31}. These cloned genes could be effectively and efficiently used for developing high-quality rice varieties.

Environmental Stresses and Rice Grain Quality Traits

All of the rice grain quality traits, including GL, GW, RGLW, GWT, AC, PC, and GT classified as quantitative traits that controlled by multiple genes and largely affected by various environmental conditions^{32, 36, 65}. Environmental factors that significantly affected rice grain quality traits are high-noon temperature (HNT), drought, and diseases^{138, 139, 140, 141, 142}. Under HNT conditions during reproductive grain filling stages, amylose biosynthesis was down-regulated and increase percent chalkiness of the grain, and also declining grain dimensions (grain shape and size). This chalky grains decrease the grain appearance due to grains are prone to break during milling and decrease sensory characteristics^{143, 144}. The price of broken rice grains is 50% lower than unbroken grains^{145, 146}. Genetic improvement of rice varieties by using GWAS method are needed to develop high-quality of rice varieties in the climate change

conditions and limited agricultural land, and also significantly growing population.

CONCLUSIONS

This review article provides an insight of genetic basis of rice grain quality traits by using GWAS method to develop high-quality of rice varieties based on the rice consumers preferences. GWAS has made a great progress to provide gene resources to increase rice quality traits. Many QTLs associated with the rice grain quality traits have been identified and a lot of genes controlling grain quality traits have been cloned during twelve years (2010 until 2022). The results of this study provide important information of the genomic information associated with the rice grain quality traits to improve rice grain quality characteristics. Validation of the specific genes to improve grain quality is necessary by using transgenic strategy, gene editing techniques, gene expression analyses, and fine-mapped based cloning.

REFERENCES

1. Food and Agriculture Organization of the United Nations. Increasing crop production sustainably. The perspective of biological processes. Food and Agricultural Organization of the United Nations. 2009. <http://www.fao.org/docrep/012/i1235e/i1235e00.htm> (accessed 20 May 2022).
2. Godfray, C.H., J.R. Beddington, I.R. Crute, L. Haddad, D. Lawrence, J.F. Muir, et al. Food security: The challenge of feeding 9 billion people. *Science*, 2010;**327**:812–818. doi:10.1126/science.1185383
3. Yu, Y., R.A. Wing, and J. Li. Grain quality. In: Q. Zhang and R.A. Wing, editors, Genetics and genomics of rice. Springer, New York. 2013.p. 237–254.
4. Mohanty, S. Rice facts. Trends in global rice consumption. *Rice Today*, 2013; **12**: 44–45.
5. Hsiaoping, C. 2005. Rice is life: Scientific perspectives for the 21st century. In: K. Toriyama, K.L. Heong, and B. Hardy, editors, Proceedings of the World Rice Research Conference, Tokyo and Tsukuba, Japan. 4–7 Nov. 2004. IRRI, Philippines. p. 497–499.
6. Zader, A. Technologies of quality: The role of the Chinese state in guiding the market for rice. *EASTS*, 2011;**5**:461–477. doi:10.1215/18752160-1458155

7. Khush, G.S. What it will take to feed 5.0 billion rice consumers in 2030. *Plant Mol Biol.*, 2005;**59**:1–6
8. Maqsood, A., Khan, Z.I., Ahmad, K., Akhtar, S., Ashfaq, A., Malik, I.S., Sultana, R., Nadeem, M., Alkahtani, J., Dwiningsih, Y., & Elshikh, M. Quantitative evaluation of zinc metal in meadows and ruminants for health assessment: implications for humans. *Environmental Science and Pollution Research*, 2022;**29**:21634–21641. doi: 10.1007/s11356-021-17264-1
9. Fitzgerald, M.A., S.R. McCouch, and R.D. Hall. Not just a grain of rice: The quest for quality. *Trends Plant Sci.*, 2009;**14**:133–139. doi:10.1016/j.tplants.2008.12.004
10. Atwell S., Huang Y. S., Vilhjalmsson B. J., Willems G., Horton M., Li Y., Meng D., Platt A., Tarone A. M., Hu T. T., Jiang R., Mulyati N. M., Zhang X., Amer M. A., Baxter I., Brachi B., Chory J., Dean C., Debieu M., de Meaux J., Ecker J. R., Faure N., Kniskern J. M., Jones J. D. G., Michael T., Nemri A., Roux F., Salt D. E., Tang C., Todesco M., Traw M. B., Weigel D., Marjoram P., Borevitz J. O., Bergelson J., Nordborg. Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature*, 2010;**465**(3). doi:10.1038/nature08800
11. Zhu X. M., Shao X. Y., Pei Y. H., Guo X. M., Li J., Song X. Y., Zhao M. A. Genetic Diversity and Genome-Wide Association Study of Major Ear Quantitative Traits Using High-Density SNPs in Maize. *Front. Plant Sci.* 2018;**9**:966. doi:10.3389/fpls.2018.00966
12. Xing, Y., Tan, Y., Hua, J., Sun, X., Xu, C., and Zhang, Q. Characterization of the main effects, epistatic effects and their environmental interactions of QTLs on the genetic basis of yield traits in rice. *Theor. Appl. Genet.* 2002; **105**: 248–257. doi:10.1007/s00122-002-0952-y
13. Tan, Y. F., Xing, Y. Z., Li, J. X., Yu, S. B., Xu, C. G., and Zhang, Q. F. Genetic bases of appearance quality of rice grains in Shanyou 63, an elite rice hybrid. *Theor. Appl. Genet.*, 2000;**101**: 823–829. doi:10.1007/s001220051549
14. Dwiningsih Y., Kumar A., Thomas J., Gupta C., Ruiz, C., Baisakh N., Pereira A. QTLs analysis and identification of candidate genes for flag leaf characteristics related to grain yield in US RIL rice population under drought conditions. American Society of Agronomy (ASA), Crop Science Society of America (CSSA), Soil Science Society of America (SSSA) International Annual Meeting, Salt Lake City, UT. 2021b.
15. Yang W., Guo Z., Huang C., Wang K., Jiang N., Feng H., Chen G., Liu Q., Xiong L. Genome-wide association study of rice (*Oryza sativa* L.) leaf traits with a high-throughput leaf scorer. *Journal of Experimental Botany*, 2015;**66**: 18. doi:10.1093/jxb/erv100
16. Yano K., Yamamoto E., Aya K., Takeuchi H., Lo P. C., Hu L., et al. Genome-wide association study using whole-genome sequencing rapidly identifies new genes influencing agronomic traits in rice. *Nat. Genet.* 2016;**48**: 927-934. doi:10.1038/ng.3596
17. Qiu X, Pang Y, Yuan Z, Xing D, Xu J, Dingkuhn M, et al. Genome-Wide Association Study of Grain Appearance and Milling Quality in a Worldwide Collection of Indica Rice Germplasm. *PLoS ONE*, 2015;**10**(12): e0145577. doi:10.1371/journal.pone.0145577
18. Zheng, T.Q., Xu, J.L., Li, Z.K., Zhai, H.Q., Wan, J.M. Genomic regions associated with milling quality and grain shape identified in a set of random introgression lines of rice (*Oryza sativa* L.). *Plant Breeding*, 2007;**126**:158-163
19. Dwiningsih, Y., Kumar, A., Thomas, J., Yingling, S., & Pereira, A. Identification of QTLs associated with drought resistance traits at reproductive stage in K/Z RILs rice population. 5th Annual Meeting of the Arkansas Bioinformatics Consortium AR-BIC 2020, Bioinformatics in Food and Agriculture. 2020a.
20. Huang, R., Jiang, L., Zheng, J., Wang, T., Wang, H., Huang, Y., Hong, Z. Genetic bases of rice grain shape: so many genes, so little known. *Trends Plant Sci.*, 2013;**18**:218–226
21. Feng, Y., Lu, Q., Zhai, R., Zhang, M., Xu, Q., Yang, Y., Wang, S., Yuan, X., Yu, H., Wang, Y., & Wei, X. Genome wide association mapping for grain shape traits in indica rice. *Planta*. 2016. doi:10.1007/s00425-016-2548-9
22. Changrong, Y., Hengming, L., Wei, D., Jinwen, Z., Yuran, X., Anyu, G. Yonggang, L., Wei, N., Shengli, S., Hua, A., Ying, L., Lihua, Z., Xuebao, Y., Ju, L., Guangde, L., Zhenghe, L., Wei, P., Dinghong, Z., & Xiaolin, L. Genome-wide association study on agronomic traits of temperate japonica rice (*Oryza sativa* L.). *Crop Breeding and Applied Biotechnology*, 2020; **20**:1. doi:10.1590/1984-70332020v20n1a1
23. Wang, S., Wu, K., Yuan, Q., Liu, X., Liu, Z., Lin, X., Qian, Q., Zhang, G. and Fu, X. Control of grain size, shape and quality by OsSPL16 in rice. *Nature Genetics*, 2012;**44**: 950-954.
24. Dwiningsih, Y. Molecular genetic analysis of drought resistance and productivity traits of rice genotypes. University of Arkansas, Fayetteville, USA. 2020.
25. Jain, S., Jain, R. K., & McCouch, S. R. Genetic analysis of Indian aromatic and quality rice

- (*Oryza sativa* L.) germplasm using panels of fluorescently-labeled microsatellite markers. *Theoretical and Applied Genetics*, 2004;**109**: 965–977. doi:10.1007/s00122-004-1700-2
26. Fan, C., Xing, Y., Mao, H., Lu, T., Han, B., Xu, C., Li, X., & Zhang, Q. GS3, a major QTL for grain length and weight and minor QTL for grain width and thickness in rice, encodes a putative transmembrane protein. *Theoretical and Applied Genetics*, 2006;**112**: 1164–1171. doi:10.1007/s00122-006-0218-1
 27. Custodio, M.C., Cuevas, R.P., Ynion, J., Laborte, A.G., Velasco, M.L., and Demont, M. Rice quality: how is it defined by consumers, industry, food scientists, and geneticists? *Trends Food Sci. Technology*, 2019;**92**:122–137. doi:10.1016/J.TIFS.2019.07.039.
 28. Sreenivasulu N., Zhang C., Tiozon R.N., and Liu Q. Post-genomics revolution in the design of premium quality rice in a high-yielding background to meet consumer demands in the 21st century. *Plant Comm.* 2022;**3**: 100271.
 29. Ge, X., Khan, Z.I., Chen, F., Akhtar, M., Ahmad, K., Ejaz, A., Ashraf, M.A., Nadeem, M., Akhtar, S., Alkahtani, J., Dwiningsih, Y., & Elshikh, M.S. A study on the contamination assessment, health risk and mobility of two heavy metals in the soil-plants-ruminants system of a typical agricultural region in the semi-arid environment. *Environmental Science and Pollution Research*, 2021;**29**: 14584–14594. doi:10.1007/s11356-021-16756-4
 30. Bradbury P. J., Zhang Z., Kroon D. E., Casstevens T. M., Ramdoss Y., Buckler E. S. TASSEL: Software for association mapping of complex traits in diverse samples. *Bioinformatics*, 2007;**23**:2633-2635.
 31. Alpuerto, J.B.B.; Samonte, S.O.P.B.; Sanchez, D.L.; Croaker, P.A.; Wang, Y.-J.; Wilson, L.T.; Christensen, E.F.; Tabien, R.E.; Yan, Z.; Thomson, M.J. Genomic Association Mapping of Apparent Amylose and Protein Concentration in Milled Rice. *Agronomy*, 2022, **12**: 857. doi:10.3390/agronomy12040857
 32. Dwiningsih Y., Kumar A., Thomas J., Ruiz C., Alkahtani J., Al-hashimi A., Pereira A. Identification of Genomic Regions Controlling Chalkiness and Grain Characteristics in a Recombinant Inbred Line Rice Population Based on High-Throughput SNP Markers. *Genes*, 2021a;**12**(1690). doi:10.3390/genes12111690
 33. Chen, M. H., Bergman, C. J., Pinson, S. R. M., & Fjellstrom, R. G. Waxy gene haplotypes: Associations with pasting properties in an international rice germplasm collection. *Journal of Cereal Science*, 2008;**48**: 781–788. doi:10.1016/j.jcs.2008.05.004
 34. Verma, D.K., Srivastav, P.P. Proximate composition, mineral content and fatty acids analyses of aromatic and non-aromatic Indian rice. *Rice Sci.*, 2017;**24**(1):21–31
 35. Zhou H., Li P., Xie W., Hussain S., Li Y., Xia D., Zhao H., Sun S., Chen J., Ye H., Hou J., Zhao D., Gao G., Zhang Q., Wang G., Lian X., Xiao J., Yu S., Li X., He Y. Genome-wide Association Analyses Reveal the Genetic Basis of Stigma Exsertion in Rice. *Mol. Plant.*, 2017;**10**:634-644.
 36. Qiu, X., Yang, J., Zhang, F., Niu, Y., Zhao, X., Shen, C., Chen, K., Teng, S., & Xu, J. Genetic dissection of rice appearance quality and cooked rice elongation by genome-wide association study. *The Crop Journal*, 2021;**9**:1470-1480. doi:10.1016/j.cj.2020.12.010
 37. Dwiningsih, Y., Kumar, A., Thomas, J., Yingling, S., & Pereira, A. Molecular genetic analysis of drought resistance and productivity in US rice cultivars. Plant and Animal Genome XXVII Conference (January 12-16, 2019). 2019a.
 38. Lin, Z., Zheng, D., Zhang, X., Wang, Z., Lei, J., Liu, Z., Li, G., Wang, S., & Ding, Y. (2016). Chalky part differs in chemical composition from translucent part of japonica rice grains as revealed by a notched belly mutant with white-belly. *Journal of the Science of Food and Agriculture*, 2016;**96**: 3937–3943. doi:10.1002/jsfa.7793
 39. Dwiningsih, Y., Kumar, A., Thomas, J., Gupta, C., Ruiz, C., Alkahtani, J., Baisakh, N., & Pereira, A. Identification and expression of abscisic acid-regulated genes in US RIL rice population under drought conditions. 82nd Meeting of Southern Section of the American Society of Plant Biologists. 2021b.
 40. Buenafe, R.J.Q., Kumanduri, V., and Sreenivasulu, N. Deploying viscosity and starch polymer properties to predict cooking and eating quality models: a novel breeding tool to predict texture. *Carbohydr. Polym.* 2021. **260**:117766. doi:10.1016/J.CARBPOL.2021.117766.
 41. Tian, Z., Qian, Q., Liu, Q., Yan, M., Liu, X., Yan, C., Liu, G., Gao, Z., Tang, S., Zeng, D., et al. Allelic diversities in rice starch biosynthesis lead to a diverse array of rice eating and cooking qualities. *Proc. Natl. Acad. Sci.* 2009;**106**:21760–21765. doi:10.1073/PNAS.0912396106.
 42. Li, H. and Gilbert, R. Starch molecular structure: the basis for an improved understanding of cooked rice texture. *Carbohydr. Polym.*, 2018;**195**:9–17. doi:10.1016/J.CARBPOL.2018.04.065.
 43. Waters, D. L. E., Henry, R. J., Reinke, R. F., & Fitzgerald, M. A. Gelatinization temperature of rice explained by polymorphisms in starch

- synthase. *Plant Biotechnology Journal*, 2006;**4**:115–122. doi:10.1111/j.1467-7652.2005.00162.x
44. Nakata, M., Miyashita, T., Kimura, R., Nakata, Y., Takagi, H., Kuroda, M., Yamaguchi, T., Umemoto, T., and Yamakawa, H. MutMapPlus identified novel mutant alleles of a rice starch branching enzyme I1b gene for fine-tuning of cooked rice texture. *Plant Biotechnol. J.*, 2018;**16**:111–123. doi:10.1111/PBI.12753.
 45. Zhang Z., Zhao H., Li W., Wu J., Zhou Z., Zhou F., Chen F., Lin Y. Genome-wide association study of callus induction variation to explore the callus formation mechanism of rice. *Journal of Integrative Plant Biology*, 2018;**61**(11). doi:10.1111/jipb.12759
 46. Pang, Y., Ali, J., Wang, X., Franje, N. J., Revilleza, J. E., Xu, J., & Li, Z. Relationship of rice grain amylose, gelatinization temperature and pasting properties for breeding better eating and cooking quality of rice varieties. *PLOS ONE*, 2016;**11**. doi:10.1371/journal.pone.0168483
 47. Cruz, M., Arbelaez, J. D., Loaiza, K., Cuasquer, J., Rosas, J., & Graterol, E. Genetic and phenotypic characterization of rice grain quality traits to define research strategies for improving rice milling, appearance, and cooking qualities in Latin America and the Caribbean. *Plant Genome*. 2021;e20134. <https://doi.org/10.1002/tpg2.20134>
 48. Lu, Z. H., Sasaki, T., Li, Y. Y., Yoshihashi, T., Li, L. T.e, & Kohyama, K. Effect of amylose content and rice type on dynamic viscoelasticity of a composite rice starch gel. *Food Hydrocoll.*, 2009;**23**:1712–1719. doi:10.1016/j.foodhyd.2009.01.009
 49. Dwiningsih, Y., Thomas, J., Kumar, A., Gupta, C., Ruiz, C., Yingling, S., Crowley, E., & Pereira, A. Molecular genetic analysis of drought resistance and productivity mechanisms in rice. Plant and Animal Genome XXVIII Conference, January 11-15, 2020. 2020b.
 50. Jie, Y., Shi, T., Zhang, Z., and Yan, Q. Identification of key volatiles differentiating aromatic rice cultivars using an untargeted metabolomics approach. *Metabolites*, 2021;**11**:528. doi:10.3390/METABO11080528.
 51. Zhao, Q., Xue, Y., and Shen, Q. Changes in the major aroma active compounds and taste components of Jasmine rice during storage. *Food Res. Int.* 2020. Ottawa, Ont 133. doi:10.1016/J.FOODRES.2020.109160.
 52. Hickey, L. T., Hafeez, A. N., Robinson, H., Jackson, S. A., Leal-Bertioli, S. C. M., Tester, M., Gao, C., Godwin, I. D., Hayes, B. J., & Wulff, B. B. H. Breeding crops to feed 10 billion. *Nature Biotechnology*, 2019;**37**:744–754. doi:10.1038/s41587-019-0152-9
 53. Crossa, J., Pérez-Rodríguez, P., Cuevas, J., Montesinos-López, O., Jarquín, D., de los Campos, G., Burgueño, J., González-Camacho, J. M., Pérez-Elizalde, S., Beyene, Y., Dreisigacker, S., Singh, R., Zhang, X., Gowda, M., Roorkiwal, M., Rutkoski, J., & Varshney, R. K. Genomic selection in plant breeding: Methods, models, and perspectives. *Trends in Plant Science*, 2017;**22**: 961–975. doi:10.1016/j.jtplants.2017.08.011
 54. Dwiningsih Y., Thomas J., Kumar A., Gupta C., Crowley E., Ruiz C., Pereira A. Drought stress response in US recombinant inbred line of rice population. National Science Foundation (NSF) 26th National Conference 2019. 2019b;**26**(76):127.
 55. Dwiningsih, Y., Kumar, A., Thomas, J., Yingling, S., & Pereira A. Molecular genetic analysis of drought resistance and productivity in K/Z RIL rice population. Arkansas Bioinformatics Consortium 2019. 2019c
 56. Chen, W., Gao, Y., Xie, W., Gong, L., Lu, K., Wang, W., et al. Genome-wide association analyses provide genetic and biochemical insights into natural variation in rice metabolism. *Nat. Genet.*, 2014;**46**: 714-721. doi:10.1038/ng.3007
 57. Ponce, K., Zhang, Y., Guo, L., Leng, Y. and Ye, G. Genome-Wide Association Study of Grain Size Traits in Indica Rice Multiparent Advanced Generation Intercross (MAGIC) Population. *Front. Plant Sci.* 2020;**11**:395. doi:10.3389/fpls.2020.00395
 58. Yu, J., Pressoir, G., Briggs, W. H., Bi, I. V., Yamasaki, M., Doebley, J. F., McMullen, M. D., Gaut, B. S., Nielsen, D. M., Holland, J. B., Kresovich, S., Buckler, E. S. A unified mixed-model method for association mapping that accounts for multiple levels of relatedness. *Nat. Genet.* 2006;**38**:203-208.
 59. Wang, S., Wu, K., Yuan, Q., Liu, X., Liu, Z., Lin, X., Zeng, R., Zhu, H., Dong, G., Qian, Q., Zhang, G., & Fu, X. Control of grain size, shape and quality by OsSPL16 in rice. *Nature Genetics*, 2012;**44**: 950–954. doi:10.1038/ng.2327
 60. Huang, X., Wei, X., Sang, T., Zhao, Q., Feng, Q., Zhao, Y., et al. Genome-wide association studies of 14 agronomic traits in rice landraces. *Nat. Genet.* 2010;**42**:961-967. doi:10.1038/ng.695
 61. Huang, X. H., Zhao, Y., Wei, X. H., Li, C. Y., Wang, A. H., Zhao, Q., et al. Genome-wide association study of flowering time and grain yield traits in a worldwide collection of rice germplasm. *Nat Genet.* 2012;**44**(31):329.
 62. Yang, N., Lu, Y., Yang, X., Huang, J., Zhou,

- Y., Ali, F., Wen, W., Liu, J., Li, J., Yan, J. Genome wide association studies using a new nonparametric model reveal the genetic architecture of 17 agronomic traits in an enlarged maize association panel. *PLoS Genet.* 2014; **10**:9:004573. doi:10.1371/journal.pgen.1004573
63. McCouch, S. R., Wright, M. H., Tung, C., Maron, L. G., McNally, K. L., Fitzgerald, M., Singh, N., DeClerck, G., Perez, F. A., Korniliev, P., Greenberg, A. J., Naredo, M. E. B., Mercado, S. M. Q., Harrington, S. E., Shi, Y., Branchini, D. A., Kuser-Falcao, P. R., Leung, H., Ebana, K., Yano, M., Eizenga, G., McClung, A., Mezey, J. Open access resources for genome-wide association mapping in rice. *Nature Communication*, 2016; **7**:10532. doi:10.1038/ncomms10532
64. Chen J., Zhou H., Xie W., Xia D., Gao G., Zhang Q., Wang G., Lian X., Xiao J., He Y. Genome-wide association analyses reveal the genetic basis of combining ability in rice. *Plant Biotechnology*, 2019; **12**:2211-2222. doi:10.1111/pbi.13134
65. Roy, N., Kabir, A.H., Zahan, N., Mouna, S.T., Chakravarty, S., Rahman, A.H., & Bayzid, M.S. (2020). Genome wide association studies on 7 yield-related traits of 183 rice varieties in Bangladesh. *bioRxiv*. doi:10.1101/2020.11.22.393074
66. Wang S, Li S, Liu Q, Wu K, Zhang J, Wang S, Wang Y, Chen X, Zhang Y, Gao C, Wang F, Huang H and Fu X. The OsSPL16-GW7 regulatory module determines grain shape and simultaneously improves rice yield and grain quality. *Nature Genetics*, 2015; **47**: 949-954.
67. Yu, P., Ye, C., Li, L., Yin, H., Zhao, J., Wang, Y., Zhang, Z., Li, W., Long, Y., Hu, X., Xiao, J., Jia, G., & Tian, B. Genome-wide association study and genomic prediction for yield and grain quality traits of hybrid rice. *Research Square*. 2022. doi:10.21203/rs.3.rs-1355596/v1
68. Zheng X. M., Gong T., Ou H. L., Xue D., Qiao W., Wang J., Liu S., Yang Q., Olsen K. M. Genome-wide association study of rice grain width variation. *Genome*, 2018; **61**:233-240. doi:10.1139/gen-2017-0106
69. Verma, R.K., Chetia, S.K., Sharma, V., Baishya, S, Sharma, H., & Modi, M.K. GWAS to spot candidate genes associated with grain quality traits in diverse rice accessions of North East India. *Molecular Biology Reports*, 2021. doi:10.1007/s11033-021-07113-2
70. Xu, F., Sun, X., Chen, Y., Huang, Y., Tong, C., and Bao, J. Rapid identification of major QTLs associated with rice grain weight and their utilization. *PLoS One*, 2015; **10**:e0122206. doi: 10.1371/journal.pone.0122206
71. Dwiningsih, Y., Thomas, J., Kumar, A., Gupta, C., Yingling, S., Basu, S., & Pereira, A. Circadian expression patterns of the HYR gene. *Arkansas Bioinformatics Consortium* 2018, 7(11): 34.
72. Price A. L., Patterson N. J., Plenge R. M., Weinblatt M. E., Shadici N. A., Reich, D. Principal components analysis corrects for stratification in genome-wide association studies. *Nature Genetics*, 2006; **38**(8). doi:10.1038/ng1847
73. Purcell S., Neale B., Todd-Brown K., Thomas L., Ferreira M. A., Bender D., Maller J. et al. PLINK: a tool set for whole-genome association and population-based linkage analyses. *Am. J. Human Genet.* 2007; **81**:559-575.
74. Brachi B., Morris G. P., Borevitz J. O. Genome-wide association studies in plants: the missing heritability is in the field. *Genome Biology*, 2011; **12**(232).
75. Wen Y. J., Zhang H., Ni Y. L., Huang B., Zhang J., Feng J. Y., et al. Methodological implementation of mixed linear models in multi-locus genome-wide association studies. *Brief. Bioinform.* 2018; **19**:700-712. doi:10.1093/bib/bbw145
76. Wu T. T., Chen Y. F., Hastie T., Sobel E., Lange K. Genome-wide association analysis by lasso penalized logistic regression. *Bioinformatics*, 2009; **25**:714-721. doi:10.1093/bioinformatics/btp041
77. Wang Q., Tian F., Pan Y., Buckler E. S., Zhang Z. A SUPER Powerful Method for Genome Wide Association Study. *PLoS ONE*, 2014; **9**(9): 107684. doi:10.1371/journal.pone.0107684
78. Lippert C., Listgarten J., Liu Y., Kadie C. M., Davidson R. I., Heckerman D. FaST linear mixed models for genome-wide association studies. *Nature Methods*, 2011; 8833-835.
79. Crowell S., Korniliev P., Falcao A., Ismail A., Gregorio G., Mezey J., McCouch S. Genome-wide association and high-resolution phenotyping link *Oryza sativa* panicle traits to numerous trait-specific QTL clusters. *Nature Communications*, 2016; **7**:10527. doi:10.1038/ncomms10527
80. Zhu D., Kang H., Li Z., Liu M., Zhu X., Wang Y., Wang D., Wang Z., Liu W., Wang G. A genome-wide association study of field resistance to *Magnaporthe oryzae* in rice. *Rice*, 2016; **9**:44. doi:10.1186/s12284-016-0116-3
81. Zhang Z., Ersoz E., Lai C. Q., Todhunter R. J., Tiwari H. K., Gore M. A. Mixed linear model approach adapted for genome-wide association studies. *Nat. Genet.* 2010; **42**: 355-360. doi:10.1038/ng.546
82. Han Z., Zhang B., Zhao H., Ayaad M., Xing Y. Genome-Wide Association Studies Reveal that

- Diverse Heading Date Genes Respond to Short and Long Day Lengths between Indica and Japonica Rice. *Front. Plant Sci.* 2016;**7**:1270. doi:10.3389/fpls.2016.01270
83. Ma X., Feng F., Wei H., Mei H., Xu K., Chen S., Li T., Liang X., Liu H., Luo L. Genome-Wide Association Study for Plant Height and Grain Yield in Rice under Contrasting Moisture Regimes. *Front. Plant Sci.* 2016;**7**:1801. doi:10.3389/fpls.2016.01801
84. Biscarini F., Cozzi P., Casella L., Riccardi P., Vattari A., Orasen G., Perrini R., Tacconi G., Tondelli A., Biselli C., Cattivelli L., Spindel J., McCouch S., Abbruscato P., Vale G., Piffanelli P., Greco R. Genome-Wide Association Study for Traits Related to Plant and Grain Morphology, and Root Architecture in Temperate Rice Accessions. *PLoS ONE*, 2016;**11**(5):0155425. doi:10.1371/journal.pone.0155425
85. Bai A., Zhao H., Huang Y., Xie W., Han Z., Zhang B., Guo Z., Yang L., Dong H., Xue W., Li G., Hu G., Hu Y., Xing Y. Genome-wide association analysis reveals different genetic control in panicle architecture between *Indica* and *Japonica* rice. *The Plant Genome*, 2016;**9**(2).
86. Shi Y., Gao L., Wu Z., Zhang X., Wang M., Zhang C., Zhang F., Zhou Y., Li Z. Genome-wide association study of salt tolerance at the seed germination stage in rice. *BMC Plant Biology*, 2017;**17**: 92. doi:10.1186/s12870-017-1044-0
87. Yu J., Zao W., He Q., Kim T. S., Park Y. J. Genome-wide association study and gene set analysis for understanding candidate genes involved in salt tolerance at the rice seedling stage. *Mol Genet Genomics*, 2017;**292**(1391). doi:10.1007/s00438-017-1354-9
88. Volante A., Desiderio F., Tondelli A., Perrini R., Orasen G., Biselli C., Riccardi P., Vattari A., Cavalluzzo D., Urso S., Ben Hassen M., Fricano A., Piffanelli P., Cozzi P., Biscarini F., Sacchi G. A., Cattivelli L., Valè G. Genome-Wide Analysis of japonica Rice Performance under Limited Water and Permanent Flooding Conditions. *Front. Plant Sci.* 2017;**8**:1862. doi:10.3389/fpls.2017.01862
89. Dilla-Ermita C. J., Tandayu E., Juanillas V. M., Detras J., Lozada D. N., Dwiyantri M. S., Cruz C. V., Mbanjo E. G. N., Ardales E., Diaz M. G., Mendioro M., Thomson M. J., Kretzschmar T. Genome-wide association analysis tracks bacterial leaf blight resistance loci in rice diverse germplasm. *Rice*, 2017;**10**(8). doi:10.1186/s12284-017-0147-4
90. Cui Y., Zhang F., Zhou Y. The application of multi-locus GWAS for the detection of salt-tolerance loci in rice. *Frontiers in Plant Science*, 2018;**9**:1464. doi:10.3389/fpls.2018.01464
91. Dong H., Zhao H., Li S., Han Z., Hu G., Liu C., Yang G., Wang G., Xie W., Xing Y. Genome-wide association studies reveal that members of bHLH subfamily 16 share a conserved function in regulating flag leaf angle in rice (*Oryza sativa*). *PLoS Genet.* 2018;**14**(4):1007323. doi:10.1371/journal.pgen.1007323
92. Guo Z., Yang W., Chang Y., Ma X., Tu H., Xiong F., Jiang N., Feng H., Huang C., Yang P., Zhao H., Chen G., Liu H., Luo L., Hu H., Liu Q., Xiong L. Genome-Wide Association Studies of Image Traits Reveal Genetic Architecture of Drought Resistance in Rice. *Mol. Plant.* 2018;**11**: 789-805. doi:10.1016/j.molp.2018.03.018
93. Yang M., Lu K., Zhao F. J., Xie W., Ramakrishna P., Wang G., Du Q., Liang L., Sun C., Zhao H., Zhang Z., Liu Z., Tian J., Huang X-Y., Wang W., Dong H., Hu J., Ming L., Xing Y., Wang G., Xiao J., Salt D. E., Lian X. Genome-wide association studies reveal the genetic basis of ionic variation in rice. *The Plant Cell*, 2018;**30**:2720-2740. doi:10.1105/tpc.18.0037
94. Patishtan J., Hartley T. N., de Carvalho R. F., Maathuis F. J. M. Genome-wide association studies to identify rice salt-tolerance markers. *Plant, Cell and Environment*, 2018;**41**:970-982. doi:10.1111/pce.12975
95. Xu F., Bao J., He Q., Park Y. Genome-wide association study of eating and cooking qualities in different subpopulations of rice (*Oryza sativa* L.). *BMC Genomics*, 2016;**17**:663. doi:10.1186/s12864-016-3000-z
96. Yuan J., Wang X., Zhao Y., Khan N. U., Zhao Z., Zhang Y., Wen X., Wang F., Li Z. Genetic basis and identification of candidate genes for salt tolerance in rice by GWAS. *Nature Scientific Reports*, 2020;**10**:9958. doi:10.1038/s41598-020-66604-7
97. Ren M., Huang M., Qiu H., Chun Y., Li L., Kumar A., Fang J., Zhao J., He H., Li X. Genome-wide association study of the genetic basis of effective tiller number in rice. *Rice*, 2021;**14**:56. doi:10.1186/s12284-021-00495-8
98. Courtois B., Audebert A., Dardou A., Roques S., Ghneim- Herrera T., Droc G., Froulin J., Rouan L., Goze E., Kilian A., Ahmadi N., Dingkuhn M. Genome-Wide Association Mapping of Root Traits in a Japonica Rice Panel. *PLoS ONE*, 2013;**8**(11):78037. doi:10.1371/journal.pone.0078037
99. Norton G.J., Douglas A., Lahner B., Yakubova E., Guerinot M. L., Pinson S. R. M., Tarpley L., Eizenge G. C., McGrath S. P., Zhao F. J., Islam M. R., Islam S., Duan G., Zhu Y., Salt

- D. E., Meharg A. A., Price A. H. Genome Wide Association Mapping of Grain Arsenic, Copper, Molybdenum and Zinc in Rice (*Oryza sativa* L.) Grown at Four International Field Sites. *PLoS ONE*, 2014;**9**(2):89685. doi:10.1371/journal.pone.0089685
100. Wu J., Feng F., Lian X., Teng X., Wei H., Yu H., et al. Genome-wide Association Study (GWAS) of mesocotyl elongation based on re-sequencing approach in rice. *BMC Plant Biol.* 2015;**15**(218). doi:10.1186/s12870-015-0608-0
101. Wang Q., Xie W., Xing H., Yan J., Meng X., Li X., Fu X., Xu J., Lian X., Yu S., Xing Y., Wang G. Genetic architecture of natural variation in rice chlorophyll content revealed by a genome-wide association study. *Mol Plant.* 2015;**8**(6). doi:10.1016/j.molp.2015.02.014
102. Talukdar P., Douglas A., Price A. H., Norton G. J. Biallelic and Genome Wide Association Mapping of Germanium Tolerant Loci in Rice (*Oryza sativa* L.). *PLoS ONE*, 2015;**10**(9):0137577. doi:10.1371/journal.pone.0137577
103. Begum H., Spindel J. E., Lalusin A., Borromeo T., Gregorio G., Hernandez J., Virk P., Collard B., McCouch S. R. Genome-Wide Association Mapping for Yield and Other Agronomic Traits in an Elite Breeding Population of Tropical Rice (*Oryza sativa*). *PLoS ONE*, 2015;**10**(3):0119873. doi:10.1371/journal.pone.0119873
104. Nawaz Z., Kakar K. U., Li X., Li S., Zhang B., Shou H., Shu Q. Genome-wide association mapping of quantitative trait loci (QTLs) for contents of eight elements in brown rice (*Oryza sativa*). *Journal of Agricultural and Food Chemistry*, 2015;**63**:8008-8016. doi:10.1021/acs.jafc.5b01191
105. Kumar V., Singh A., Mithra S. V. A., Krishnamurthy S. L., Parida S. K., Jain S., Tiwari K. K., Kumar P., Rao A. R., Sharma S. K., Khurana J. P., Singh N. K., Mohapatra T. Genome-wide association mapping of salinity tolerance in rice (*Oryza sativa*). *DNA Research*, 2015;**22**(2). doi:10.1093/dnares/dsu046
106. Liang S., Wu L., Ren G., Zhao X., Zhou M., McNeil D., Ye G. Genome-wide association study of grain yield and related traits using a collection of advanced *indica* rice breeding lines for irrigated ecosystems. *Field Crop Research*, 2016;**193**:70-86. doi:10.1016/j.fcr.2016.03.008
107. Norton G. J., Travis A. J., Douglas A., Fairley S., De Paiva Alves E., Ruang-areerate P., Naredo M. E. B., McNally K. L., Hossain M., Islam M. R., Price A. H. Genome Wide Association Mapping of Grain and Straw Biomass Traits in the Rice Bengal and Assam Aus Panel (BAAP) Grown Under Alternate Wetting and Drying and Permanently Flooded Irrigation. *Front. Plant Sci.* 2018;**9**:1223. doi:10.3389/fpls.2018.01223
108. Jiang S., Wang D., Yan S., Liu S., Liu B., Kang H., Wang G. L. Dissection of the genetic architecture of rice tillering using a genome-wide association study. *Rice*, 2019;**12**(43):3 doi:10.1186/s12284-019-0302-1
109. Tang W., Ye J., Yao X., Zhao P., Xuan W., Tian Y., Zhang Y., Xu S., An H., Chen G., Yu J., Wu W., Ge Y., Liu X., Li J., Zhang H., Zhao Y., Yang B., Jiang X., Peng C., Zhou C., Terzaghi W., Wang C., Wan J. Genome-wide associated study identifies NAC42-activated nitrate transporter conferring high nitrogen use efficiency in rice. *Nature Communications*, 2019;**10**:5279. doi:10.1038/s41467-019-13187-1
110. Zhiguo E., Chen C., Yang J., Tong H., Li T., Wang L., Chen H. Genome-wide analysis of fatty acid desaturase genes in rice (*Oryza sativa*). *Nature Research*, 2019;**9**:19445. doi:10.1038/s41598-019-55648-z
111. Bollinedi H., Yadav A. K., Vinod K. K., Gopala Krishnan S., Bhowmick P. K., Nagarajan M., Neeraja C. N., Ellur R. K., Singh A. K. Genome-Wide Association Study Reveals Novel Marker-Trait Associations (MTAs) Governing the Localization of Fe and Zn in the Rice Grain. *Front. Genet.* 2020;**11**:213. doi:10.3389/fgene.2020.00213
112. Liu S., Zhong H., Meng X., Sun T., Li Y., Pincon S. R. M., Chang S. K. C., Peng Z. Genome-wide association studies of ionomic and agronomic traits in USDA mini core collection of rice and comparative analyses of different mapping methods. *BMC Plant Biology*, 2020;**20**(441). doi:10.1186/s12870-020-02603-0
113. Volante A., Tondelli A., Desiderio F., Abbruscato P., Menin B., Biselli C., Casella L., Singh N., McCouch S. R., Tharreau D., Zampieri E., Cattivelli L., Vale G. Genome wide association studies for *japonica* rice resistance to blast in field and controlled conditions. *Rice*, 2020;**13**(71). doi:10.1186/s12284-020-00431-2
114. Sattayachiti W., Wanchana S., Arikiti S., Nubankoh P., Patarapuwadol S., Vanavichit A., Darwell C. T., Toojinda T. Genome-wide association analysis identifies resistance loci for bacterial leaf streak resistance in rice (*Oryza sativa*). *Plants*, 2020;**9**:1673. doi:10.3390/plants9121673
115. Zhang H., San M. L., Jang S. G., Lee J. H., Kim N., Lee A. R., Park S., Cao F. Y., Chin J. H., Kwon S. W. Genome-wide association study of root system development at seedling stage in rice. *Genes*, 2020;**11**(1395). doi:10.3390/genes11121395

116. Rakotoson T., Dusserre J., Letourmy P., Frouin J., Ratsimiala I. R., Rakotoarisoa N. V., Cao T. V., Brocke K. V., Ramanantsoanirina A., Ahmadi N., Raboin L. M. Genome-wide association study of nitrogen use efficiency and agronomic traits in upland rice. *Rice Science*, 2021;28, **4**: 379-390. doi:10.1016/j.rsci.2021.05.008
117. Chen C., Travis A. J., Hossain M., Islam M. R., Price A. H., Norton G. J. Genome-wide association mapping of sodium and potassium concentration in rice grains and shoots under alternate wetting and drying and continuously flooded irrigation. *Theoretical and Applied Genetics*, 2021;134:2315-23334. doi:10.1007/s00122-021-03828-9
118. Le T. D., Gathignol F., Vu H. T., Nguyen K. L., Tran L. H., Vu H. T. T., Dinh T. X., Lazennec F., Pham X. H., Véry A. A., et al. Genome-Wide Association Mapping of Salinity Tolerance at the Seedling Stage in a Panel of Vietnamese Landraces Reveals New Valuable QTLs for Salinity Stress Tolerance Breeding in Rice. *Plants*, 2021;10(1088). doi:10.3390/plants10061088
119. Zhang G., Wang R., Ma J., Gao H., Deng L., Wang N., Wang Y., Zhang J., Li K., Zhang W., Mu F., Liu H., Wang Y. Genome-wide association studies of yield-related traits in high-latitude japonica rice. *BMC Genomic Data*, 2021;22(39). doi:10.1186/s12863-021-00995-y
120. Qi P, Lin Y, Song X, Shen J, Gao J and Lin H. The novel quantitative trait locus GL3.1 controls rice grain size and yield by regulating Cyclin-T1;3. *Cell Research*, 2012;22:1666-1680.
121. Heang D and Sassa H. Antagonistic actions of HLH/bHLH proteins are involved in grain length and weight in rice. *PLoS ONE*, 2012;7: e31325.
122. Song X, Huang W, Shi M, Zhu M and Lin H. A QTL for rice grain width and weight encodes a previously unknown RING-type E3 ubiquitin ligase. *Nature Genetics*, 2012; **39**: 623-630.
123. Song X, Kuroha T, Ayano M, Furuta T, Jacobsen S and Ashikari M. Rare allele of a previously unidentified histone H4 acetyltransferase enhances grain weight, yield, and plant biomass in rice. *Proceedings of the National Academy of Sciences USA*, 2015; **112**: 76-81.
124. Ishimaru K, Hirotsu N, Madoka Y, Miyagawa H and Katoh E. Loss of function of the IAA-glucose hydrolase gene TGW6 enhances rice grain weight and increases yield. *Nature Genetics*, 2013; **45**: 707-711.
125. Li J, Chu H, Zhang Y, Mou T, Wu C, Zhang Q and Xu J. The rice HGW gene encodes a ubiquitin-associated (UBA) domain protein that regulates heading date and grain weight. *PLoS ONE*, 2012;7:e34231.
126. Su Y, Rao Y, Hu S, Yang Y, Gao Z, Zhang G, Liu J, Hu J, Yan M, Dong G, Zhu L, Guo L, Qian Q, Zeng D. Map-based cloning proves qGC-6, a major QTL for gel consistency of japonica/indica cross, responds by waxy in rice (*Oryza sativa* L.). *Theor Appl Genet.*, 2011;123:859-867
127. Lapitan VC, Redona ED, Abe T, Brar DS. Mapping of quantitative trait loci using a double-haploid population from the cross of indica and japonica cultivars of rice. *Crop Sci.*, 2009;49:1620-1628.
128. Fan CC, Yu XQ, Xing YZ, Xu CG, Luo LJ, Zhang QF. The main effects, epistatic effects and environmental interactions of QTLs on the cooking and eating quality of rice in a doubled-haploid line population. *Theor Appl Genet.*, 2005;110:1445-1452.
129. Wan XY, Wan JM, Su CC, Wang CM, Shen WB, Li JM, Wang HL, Jiang L, Liu SJ, Chen LM, Yasui H, Yoshimura A. QTL detection for eating quality of cooked rice in a population of chromosome segment substitution lines. *Theor Appl Genet.*, 2004;110:71-79.
130. Aluko G, Martinez C, Tohme J, Castano C, Bergman C, Oard JH. QTL mapping of grain quality traits from the interspecific cross *Oryza sativa* × *O. glaberrima*. *Theor Appl Genet.*, 2004;109:630-639
131. Septiningsih EM, Trijatmiko KR, Moeljopawiro S, McCouch SR. Identification of quantitative trait loci for grain quality in an advanced backcross population derived from the *Oryza sativa* variety IR64 and the wild relative *O. rufipogon*. *Theor Appl Genet.*, 2003;107:1433-1441.
132. Lanceras JC, Huang ZL, Naivikul O, Vanavichit A, Ruanjaichon V, Tragoonrung S. Mapping of genes for cooking and eating qualities in Thai jasmine rice (KDML105). *DNA Res.*, 2000;7:93-101.
133. He P, Li SG, Qian Q, Ma YQ, Li JZ, Wang WM, Chen Y, Zhu L. Genetic analysis of rice grain quality. *Theor Appl Genet.*, 1999;98: 502-508.
134. Tan YF, Li JX, Yu SB, Xing YZ, Xu CG, Zhang Q. The three important traits for cooking and eating quality of rice grains are controlled by a single locus in an elite rice hybrid, Shanyou 63. *Theor Appl Genet.*, 1999;99:642-648.
135. Dwiningsih, Y., Kumar, A., Thomas, J., & Pereira, A. Identification drought-tolerance rice variety for reducing climatic impacts on rice production. Fulbright Enrichment Seminar Climate Change, Estes Park, Colorado, USA. 2017.
136. Fitzgerald, M.A.; Rahman, S.; Resurreccion, A.P.; Concepcion, J.; Daygon, V.D.; Dipti,

- S.S.; Kabir, K.A.; Klingner, B.; Morell, M.K.; Bird, A.R. Identification of a Major Genetic Determinant of Glycaemic Index in Rice. *Rice* 2011;**4**:66–74.
137. Qiu, X., Yang, J., Zhang, F., Niu, Y., Zhao, X., Shen, C., Chen, K., Teng, S., & Xu, J. Genetic dissection of rice appearance quality and cooked rice elongation by genome-wide association study. *The Crop Journal*, 2021;**9**:1470-1480. doi:10.1016/j.cj.2020.12.010
138. Dwiningsih Y., Rahmaningsih M., Alkahtani J. Development of single nucleotide polymorphism (SNP) markers in tropical crops. *Advance Sustainable Science, Engineering and Technology*, 2020c;**2**(2).
139. Sitarasi, R., Nallal, U.M., Razia, M., Chung, W.J., Shim, J., Chandrasekaran, M., Dwiningsih, Y., Rasheed, R.A., Alkahtani, J., Elshikh, M.S., Debnath, O., & Ravindran. Inhibition of multi-drug resistant microbial pathogens using an ecofriendly root extract of *Furcraea foetida* silver nanoparticles. *Journal of King Saud University-Science*, 2022;**34**(2): 101794. doi: 10.1016/j.jksus.2021.101794
140. Yamakawa, H.; Hirose, T.; Kuroda, M.; Yamaguchi, T. Comprehensive Expression Profiling of Rice Grain Filling-Related Genes under High Temperature Using DNA Microarray. *Plant Physiol.*, 2007; **144**: 258–277.
141. Dwiningsih Y., Kumar A., Thomas J., Ruiz C., Alkahtani J., Baisakh N., Pereira A. Quantitative trait loci and candidate gene identification for chlorophyll content in RIL rice population under drought conditions. *Indonesian Journal of Natural Pigments*, 2021c;**3**(2):54-64. doi:10.33479/ijnp.2021.03.2.54
142. Rashid Z., Sofi M., Harlapur S. I., Kachapur R. M., Dar Z. A., Singh P. K., Zaid P. H., Vivek B. M., Nair S. K. Genome-wide association studies in tropical maize germplasm reveal novel and known genomic regions for resistance to Northern corn leaf blight. *Scientific Reports*, 2020; **10**. doi:10.1038/s41598-020-78928-5
143. Del Rosario, A.R.; Briones, V.P.; Vidal, A.J.; Juliano, B.O. Composition and endosperm structure of developing and mature rice kernel. *Cereal Chem.* 1968; **45**: 225–235.
144. Dwiningsih Y, Thomas J, Kumar A, et al. Identification of QTLs and Candidate Loci Associated with Drought-Related Traits of the K/Z RIL Rice Population. *Research Square*; 2022. doi: 10.21203/rs.3.rs-1609741/v1.
145. Childs, N. Rice Yearbook 2016. USDA ERS. Available online: www.ers.usda.gov/data-products/rice-yearbook.aspx (accessed on 19 May 2022).
146. Yang W., Zhao J., Zhang S., Chen L., Yang T., Dong J., Fu H., Ma Y., Zhou L., Wang J., Liu W., Liu Q., Liu B. Genome-wide association mapping and gene expression analysis reveal the negative role of *OsMYB21* in regulating bacterial blight resistance in rice. *Rice*, 2021;**14**(58). doi:10.1186/s12284-021-00501-z