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QTL Analysis in Sorghum (*Sorghum bicolor L. Moench*): A Review

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Abstract

Sorghum is a Gramineae crop with two sets of chromosomes (2n = 2x = 20). Sorghum has a euchromatin and heterochromatin size of about 252 Mbp and 460 Mbp, respectively. QTL analysis determines the region in the genome that controls a quantitative character phenotype. The methods of analysis include SMA, SIM, CIM, and MQM. Genotyping generally uses molecular markers with a high polymorphism, such as RFLP, AFLP, SSR, SNP, and DArT. QTL analysis has been conducted on sorghum crops for various purposes and traits. The analyzed agronomic traits were plant height, days to flowering, 1000 grain weight, and seed length. The grain quality, including mineral content (Fe and Zn), starch, fat, fibre, protein, and carotenoid content, can be analyzed. Disease resistance that can be analyzed is resistance to leaf spot and anthracnose. Several QTLs were co-localized between traits and between populations. The data that has been obtained can be used for the preparation of the QTL consensus.

Keywords: Chromosome, gene annotation, linkage, pleiotropy, RILs

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Introduction

Sorghum is a cereal crop taxonomically close to rice, corn, hanjeli, and wheat. Sorghum has advantages in adaptability and productivity on marginal land. Sorghum can be used for rice, flour, sugar, and alcohol (Sirappa, 2003). Sorghum has the potential to become a raw material for the sorghum industry. Sorghum has the potential to become a raw material for the flour industry, which has only been sourced from wheat. According to FAO (2016), sorghum production in Asia until 2016 reached 7.9 million tons. Meanwhile, Kristamtini *et al.* (2024) explained that sorghum productivity reached 3.7 tons ha-1 after adjusting the planting distance. The sorghum genome is composed of 2 sets of chromosomes, which contain 20 chromosomes (2n = 2x = 20) (Price et al., 2005), with a euchromatin size of about 252 megabase pairs (Mbp) and a heterochromatin size of about 460 Mbp (Paterson et al., 2009).

Quantitative trait loci (QTL) analysis identifies genomic regions that control a specific phenotype, especially quantitative characters. Quantitative traits are polygenic and can influence the environment (Pierce, 2019). The QTL analysis generally uses populations of recombinant inbred lines (RILs). However, the analysis can also use backcross populations, F2 populations, near-isogenic lines (NILs), and double haploid populations (Gupta et al., 2013). A QTL can be defined as a genomic region associated with or responsible for a quantitative trait. It can be measured by comparing genotype variation with phenotype variation. QTL can be a single gene or a group of genes but are generally polygenic and have different effects on phenotypic variation. Analysis methods include single marker analysis (SMA), simple interval mapping (SIM), composite interval mapping (CIM), and multiple QTL mapping (MQM). The SMA method is used to see the association of a single marker to a QTL, but the SIM, CIM, and MQM methods are used to see the location of the QTL on the genome.

The aim of this review is to synthesize and meta-analyze identified QTLs across multiple studies to pinpoint stable genomic 'hotspots'—specifically on chromosomes 6, 7, and 9—that govern plant height, flowering time, and grain yield. By identifying these

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consistent loci, this review provides a strategic map for marker-assisted selection (MAS) to accelerate the development of high-performing sorghum cultivars.

The Use of QTL Analysis for Agronomical Traits

Plant Height Traits

The QTL analysis for plant height traits discussed in this paper is the analysis produced by Bai et al., (2017) and Govindarajulu et al., (2021). Bai et al., (2017) analyzed the F6:8 RILs population resulting from the cross of the Rio genotype, which has a high performance (313-336 cm) against BTx623, which has a relatively short performance (114-125 cm). Genotyping was conducted using 118 SSR markers and 8 INDEL markers. The analysis used the inclusive composite interval mapping (ICIM) method. Based on the results of the analysis, a total of 6 QTLs were found and suspected to control plant height traits. The QTL were distributed in the sorghum genome on chromosome 3 (qPH3-1, qPH3-2), chromosome 6 (qPH6-1, qPH6-2), chromosome 7 (qPH7-1), and chromosome 9 (qPH9-1). The QTL found they could explain about 2.53%-40.43% of the phenotypic diversity of plant height traits. Govindarajulu et al., (2021) use a population of F3:5 RILs resulting from a cross between S. propinquum, which is a plant with an average height of 227 cm, and Tx7000 which is a plant with an average height of 96 cm. Genotyping was carried out using SNP markers, further analyzed by the MQM method. Based on the analysis results, QTL was found on chromosome 7 at around 58.26-66.59 cM and chromosome 9 at around 64.83-72.19 cM (Table 1). The QTL found they could explain about 7.38%-30.55% of the diversity of plant height phenotypes. Similar with that Lu *et al.* (2022) conducted a study on plant height (PH) using selfing between Scattered Ear Sorghum and Red Hull Sudangrass and found four QTLs (qPH-7-1 to qPH-7-4) on chromosome 7 and revealed that these QTLs had phenotypic variation rates exceeding 10%.

The QTLs found were different in each experimental environment. Bai et al., (2017) conducted a multi-season experiment from 2013-2015, while Govindarajulu et al., (2021) conducted multi-location experiments, namely two field experiments (2016-2017) and one greenhouse experiment (2014). Lu *et al.* (2022), performed at two locations in Inner Mongolia, China, over two years (2021 and 2022). Theses study suggesting that the PH trait at this locus was relatively stable across different environments. This indicates that the identified QTL locus is a dominant factor in controlling plant height. The QTL found are also known to overlap or co-localize with genes found previously. On chromosome 7, the QTL co-localized with the Dw3 gene (Sobic.007G163800), which controls auxin transport. Similarly, on chromosome 9, several QTL co-localized with the Dw1 gene (Sobic.009G229800), which is known to reduce cell proliferation activity in internodes. Based on the results of the analysis, it was found that the highest phenotypic diversity explained by QTL (PVE) was found on chromosome 7. It may suggest that the Dw3 gene and QTL on chromosome 7 have a more significant influence on controlling plant height traits in sorghum. QTL was also found on chromosome 6. Based on Zhang et al., (2015) and Hilley et al., (2017), the Dw2 gene (Sobic.006G067700) that controls the synthesis of protein kinase regulators for internode length activity in sorghum stems is located on chromosome 6.

Flowering Time Traits

The QTL analysis for flowering time traits that will be discussed in this paper is the analysis produced by Awika et al., (2017), Bai et al., (2017), Kong et al., (2018) and Govindarajulu et al., (2021). Population mapping in Bai et al., (2017) and Govindarajulu et al., (2021) is the same as the previous explanation, where Rio is a plant with a flowering time of 91-93 days after planting (HST), BTx623 67-69 HST, Tx7000 around 50-71.2 HST, and S. propinquum which is unable to flower. Awika et al., (2017) used a population of F12 RILs resulting from a cross between Tx642 and Tx7000 in a multi-site experiment (3 field experiments and one greenhouse experiment). Genotyping was conducted using nucleotide base sequencing data as markers, followed by QTL analysis using the CIM method. Based on the analysis results, 2 QTL could be identified for flowering time traits located on chromosome 8 (FTcx-8-15) and chromosome 10 (FTcx-10-35). The QTL found they could explain about 8.12%-11.76% of the flowering time variances.

Based on the analysis by Bai et al., (2017), a total of 2 QTL that are thought to control flowering age traits were found on chromosome 6 (qFT6-1, qFT6-2) with a PVE value of 30.58%-42.47%. Kong et al., (2018) found as many 7 QTL: Chromosome 1 (qFL1,1 and qFL1.2), chromosome 3 (qFL3.1), chromosome 4 (qFL4.1), chromosome 6 (qFL6.1), chromosome 8 (qFL8.1) and chromosome 9 (qFL9.1). Theses QTL These QTLs are able to explain **7**-11**%** of the phenotypic variation. Govindarajulu et al., (2021) also found as many as 4 QTL spread on chromosome 2 (qFL2.17S), chromosome 3 (qFL3.17S), chromosome 6 (qFL6.14GH), and chromosome 9 (qFL9.17S). These QTLs were able to explain about 11.72%-15.23% of the phenotypic diversity of flowering age. Four literature sources identified a total of 15 QTLs influencing flowering time, with chromosome 6 exhibiting the most QTLs. Certain QTLs on chromosome 6 were found to co-localize with the Ma1 gene (SbPRR37), a known regulator of sorghum's transition from vegetative to reproductive growth Cuevas et al., (2016). The region around 45 Mb on chromosome 6 also emerged as a significant hotspot for inflorescence length, linking it to both plant height and flowering (Zhang et al., 2015). Interestingly, QTLs on chromosome 3 also co-localized with the gene (Sobic.003G295300) responsible for phosphatidylethanolamine-binding protein (PEBP) synthesis, which is also implicated in sorghum flowering.

The 1000-Grain Weight Traits

The QTL analysis for the 1000-grain weight traits that will be discussed in this paper were Bai et al., (2017), Boyles et al., (2017) and Zou et al., (2020). The mapping population in Bai et al., (2017) is the same as the previous explanation, where Rio has a 100-grain weight of about 1.77-2.14 g or 1000-grain weight of about 17.7-21.4 g, and BTx623 has a 100-grain weight of about 2.10-2.48 g or 100-grain weight of about 21.0-24.8g. Based on the analysis, 2 QTLs were found on chromosomes 7 (qHGW7-1) and 9 (qHGW9-1) with PVE values ranging from 9.10%-20.67%.

Boyles et al., (2017) analyzed two populations of F4:5 RILs. Population 1 resulted from a cross between BTx642 (1000-grain weight = 30.9 g) and BTxARG-1 (1000-grain weight = 30.9 g) 24.3-25.9g. Population 2 crossed BTxARG-1 and P850029 (1000-grain weight = 27 g). Genotyping was carried out using SNP markers, which were then analyzed using the SIM method. Based on the analysis, 6 QTL were found on chromosome 1 (BT/P-TGW-1a, P-TGW-1b), chromosome 2 (BT-TGW-2), chromosome 5 (P-TGW-5), chromosome 6 (BT-TGW-6), and chromosome 8 (BT-TGW-8). These QTLs explained about 5.30%-17.60% of the phenotypic diversity of 1000-grain weight.

Zou et al., (2020) used a population of F8 RILs resulting from a cross between genotypes 654 (1000 grain weight = 27.44 g) and LTR108 (1000 grain weight = 50.10 g) in a 4-year multi-season experiment. Genotyping was conducted using nucleotide base sequencing data as markers, followed by QTL analysis using the CIM method. Based on the analysis, 9 QTL were found on chromosomes 1, 3, 6, 7, and 8, with PVE values ranging from 4.10%-12.0% (Table 1). The total number of 1000-grain weight QTL based on the three works of literature was 14 QTL spread almost throughout the sorghum genome. In addition, Zou et al. (2020) tried to introduce the qTGW1a locus into the rice genome to analyze the function of the locus by overexpression method. However, the results showed that the introduced gene caused a decrease in 1000-grain weight in rice. The genes controlling the 1000-grain weight trait are pretty complex.

Seed Length Traits

The QTL analysis for seed length traits discussed in this paper is the analysis produced by Zou et al. (2020) and Takanashi et al., (2021). Takanashi et al. (2021) used a population of F7 RILs resulting from a cross between BTx623 with a seed length of about 4.3 mm and NOG with a seed length of about 4.7 mm in a multi-season experiment (2015-2016). Genotyping was conducted using SNP markers and QTL analysis using the CIM method. Based on the analysis, only one QTL was found on chromosome 4 with a PVE value of 7.92%. This QTL co-localized with the orthologous PGL2 gene (Sobic.004G237000) in rice and the Gln-4 gene (Sobic.004F247000) in maize.

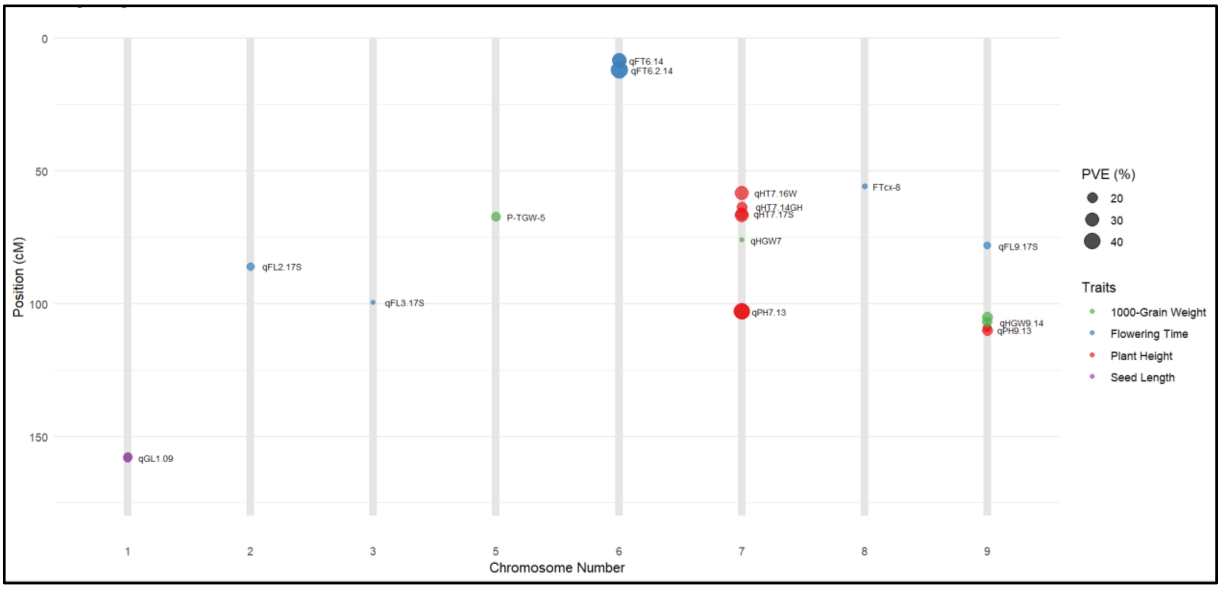

Figure 1. Genetic Map of High-Impact QTLs (PVE > 10%) for Agronomic Traits in Sorghum

The mapping population in Zou et al. (2020) is the same as the previous explanation, where genotype 654 has a seed length of about 4,504 ± 0.181 mm and genotype LTR108 has a seed length of about 4,951 ± 0.183 mm. Based on the results of QTL analysis, 10 QTLs were found to control the seed length trait. The QTL were distributed on chromosome 1 (qGL1), chromosome 2 (qGL2a, qGL2b, qGL2c), chromosome 3 (qGL3a, qGL3b), chromosome 6 (qGL6a, qGL6b, qGL6c), and chromosome 7 (qGL7). These QTLs were able to explain 3.0%-17.0% of the variation in seed length phenotype, with the largest PVE being the QTL on chromosome 1.

Co-localization and Pleiotropic Effects of Agronomic QTLs

The genomic landscape of major-effect QTLs in sorghum is illustrated in Figure 1, highlighting significant genomic hotspots where multiple agronomic traits converge (Singh et al., 2025). Co-localization between QTL of different traits indicates pleiotropy, a phenomenon where a single gene influences multiple phenotypic traits. This creates genetic correlations that play a crucial role in shaping selection patterns and the response to selection in correlated traits (Saltz et al., 2017). Notably, the genomic overlap at the *Dw1* locus on Chromosome 9 significantly impacts plant height, stem volume, and stem biomass yield, suggesting a common genetic mechanism underlying plant architecture and yield efficiency.

By filtering for major-effect loci (PVE > 10%), chromosomes 1, 6, 7, and 9 emerge as the primary drivers of sorghum architecture and yield components:

a. Chromosome 7 (Plant Height & Grain Weight): This chromosome is a dominant regulator for plant height, with stable QTLs like qPH7-1 explaining up to 40.43% of phenotypic variation. High-impact grain weight QTLs, such as qHGW7, also co-localize in this region.
b. Chromosome 6 (Flowering Time Hotspot): Major-effect flowering time QTLs, including qFT6-1 and qFT6-2, are clustered on this chromosome, with PVE values reaching as high as 42.47%.
c. Chromosome 1 (Seed Length Stability): Stable seed length QTLs (qGL1) are consistently found on chromosome 1 across four consecutive years (2009–2012), explaining up to 17% of phenotypic variance.
d. Chromosome 9 (Trait Convergence): This chromosome exhibits significant convergence between plant height (qPH9), flowering time (qFL9), and grain weight (qHGW9), with PVE values ranging from 11.2% to 20.67%.

To emphasize the most necessary data for breeding selection, the specific parameters for these major-effect and stable loci (PVE > 10%) are summarized in Table 1., while the full comprehensive dataset is provided in the Supplementary Tabel.

Table 1. Summary of High-Impact and Stable QTLs for Agronomic Traits in Sorghum (PVE > 10%)

Trait	Chromosome	Position (cM)	Max PVE (%)	Major QTL Identified
Plant Height	7	103	40.43%	qPH7-1-2015
Flowering Time	6	12	42.47%	qFT6-2-2015
1000-Grain Weight	9	105	20.67%	qHGW9-1-2015
Seed Length	1	157.8	17.00%	qGL1-2012

The Use of QTL Analysis for Grain Quality Traits

Fe and Zn Content

QTL analysis in sorghum is also used to determine QTL related to grain quality traits. Fe and Zn content is one of the aspects studied related to grain quality in sorghum to increase functional food consumption. Kotla et al., (2019) conducted QTL analysis for Fe and Zn content in sorghum grains with the F6 RILs mapping population from the crossing of genotypes 296B and PVK 801. Genotype 296B had a Fe content of 26.00-46.33 mg/kg and Zn content of 14.63-26.44 mg/kg, while genotype PVK 801 had a Fe content of 28.20-49.40 mg/kg and Zn content of 16.46-30.43 mg/kg. The experiment was conducted at 3 locations and two seasons, resulting in 6 experimental environments. SSR, DArT, and SNP markers were used for genotyping, followed by QTL analysis using the CIM method.

Table 2. QTL analysis for Fe and Zn content in sorghum grains

QTL identity	Chromosome	Position (cM)	LOD (%)	AE (%)	PVE (%)
ICRISAT 12-13 (E1)					
qfe6.1(E1)	6	90.4	4.6	0.84	5.44
qfe7.1(E1)	7	42.9	3.6	0.87	5.82
qfe7.2(E1)	7	123.5	4.3	0.81	5.09
qzn7.1(E1)	7	42.9	5.6	0.88	9.42
qzn7.2(E1)	7	54	6.8	0.86	8.8
qzn7.3(E1)	7	57	5.9	0.77	6.96
VNMKV 12-13 (E3)					
qfe7.1(E3)	7	65.5	3.9	0.88	5.19
qzn7.1(E3)	7	64.2	4.9	0.78	5.83
qzn7.2(E3)	7	67.2	4.3	0.75	5.83
ICRISAT 13-14 (E4)					
qfe1.1(E4)	1	107.4	5.5	0.79	6.80
VNMKV 13-14 (E6)					
qfe7.1(E6)	7	61	4.4	0.99	5.66
Combined					
qfe7.2	2	123.5	5.6	0.60	6.7
qzn7.4	7	67.2	4.5	0.53	5.7
qzn7.1	1	55.5	4.5	0.54	5.7

Notes: PVE = phenotypic variances explained. AE = additive effect.
Source: Kotla et al. (2019)

Based on the analysis, 4 QTL for Fe content were found on chromosomes 1, 6, and 7 (Table 2). These QTLs were able to explain 5.09%-6.80% of the phenotypic variation in Fe content. In addition, 4 QTL for Zn content were found scattered on chromosome 7 with a range of PVE values of 4.3%-6.8%. QTL with the most significant PVE values were qfe7.1 (6.7%) and qzn7.1(E1) (9.42%) located on chromosome 7. It indicates that Fe and Zn content are controlled by genes located on chromosome 7 with potential candidate genes CYP71B34 and ZFP8. Furthermore, a co-localization analysis of QTL with annotated genes in the gene bank database was conducted. Based on the analysis, it was found that QTL qfe7.2 co-localized with genes that play a role in Fe ion transport, while QTL qzn7.1 and qzn7.4 co-localized with genes that play a role in Zn ion transport (Table 3).

Starch, Protein, Fiber, and Lipid Content:

Other aspects of grain quality in sorghum are starch, protein, fibre and lipid content. Some of the literature used in this discussion are Sukumaran et al., (2012), Boyles et al., (2017b), Rhodes et al., (2017), and Patil et al., (2019). The QTLs that have been analyzed are spread across the sorghum genome. In this discussion, we will discuss the co-localization of QTL between starch, protein, fibre, and lipid content traits (Table 4). On chromosome 2, co-localization occurred between QTL for fibre, starch, and lipid content in the range of 60.82-73.41 Mbp. On chromosome 4, co-localization occurred between fibre, starch, protein, and lipid content QTL in the range of 56.50-60.16 Mbp. On chromosome 5, co-localization occurred between starch and protein content QTL in the range of 0.44-2.05 Mbp. On chromosome 6, co-localization occurred between lipid, protein and starch content QTL in the range of 1.61-44.09 Mbp. On chromosome 10, co-localization occurred between starch and protein QTL in the range of 1.80-53.79 Mbp. Co-localization between QTL of different traits indicates pleiotropy, which can be supportive or inhibitory depending on the correlation between traits in a gene (Mitteldorf, 2019). In addition, co-localization also occurred between fat content QTL from different populations on chromosome 6 in the range of 45.75-48.82 Mbp. Co-localization between QTL from the same trait and different populations can be used as a basis for determining QTL consensus on a trait and supporting the candidate gene approach. Ayalew et al., (2022) detected starch content QTLs on chromosomes 9 and 10 by evaluating a RTx430 x SC35 recombinant inbred line (RIL) population in six environments across Hays and Manhattan.

Table 3. Position of QTL and Putative Genes Associated With QTL Of Fe and Zn Content in Sorghum Grains

QTL	Chromosome	Position (cM)	LOD (%)	AE (%)	PVE (%)	Marker position (bp)	Accession ID	Position (bp)	Description
qfe7.2	7	123.5	5.6	0.6	6.7	2340000-4593373	Sb07g003000	3191492-3193591	*electron carrier/heme binding/iron ion binding/monooxygenase/ oxygen binding*
qzn7.4	7	67.2	4.5	0.53	5.7	54837270-54659732	Sb07g0211300	54829074-54830555	*zinc ion binding*
qzn7.1	7	55.5	4.5	0.54	5.7	56915197-56741980	Sb07g021910	56151914-56153758	*zinc finger family protein*
							Sb07g022160	56501258-56504350	*protein binding/zinc ion binding*
							Sb07g022165	56514545-56515453	*protein binding/zinc ion binding*
							Sb07g022570	57198318-57199295	*nucleic acid binding/transcription factor/zinc ion binding*

Source: Kotla et al. (2019)

Table 4. Co-Localization of QTL For Starch, Protein, Fibre, and Lipid Content in Grain Sorghum

Traits	Population	Pop. size	Environment	Chromosome	QTL range (Mbp)	QTL Position (Mbp)	Source
Fibre	Sureño/RTx430	113	CC-2012	2	61.21-61.67	61.58	[1]
Protein	BTx642/BTxARG-1	191	SC, TX-2015	2	60.82-73.41	63.14-63.15	[2]
Lipid	BTx642/BTxARG-1	191	TX-2014	2	61.96-63.87	63.35	[2]
Fibre	Sureño/RTx430	113	WE-2012, Combined	4	56.50-59.56	57.6-58.83	[1]
Lipid	SAP	265	Combined	4	57.40-60.07	57.6-57.7	[3]
Protein	SAP	265	Combined	4	57.40-60.07	57.6-57.7	[3]
Starch	Diverse Panel	269	KS-2007	4	57.43-60.16	-	[4]
Starch	Sureño/RTx430	113	HW-2012	5	1.47-2.05	1.59	[1]
Protein	BTx642/BTxARG-1	191	SC-2014	5	0.44-1.62	1.42	[2]
Lipid	Sureño/RTx430	113	HW-2012, Combined	6	41.38-42.64	42.41-42.44	[1]
Protein	BTxARG-1/P850029	279	TX-2015	6	6.56-44.05	41.45	[2]
Starch	BTxARG-1/P850029	279	SC, TX-2015	6	1.61-44.09	42.83	[2]
Lipid	Sureño/RTx430	113	HW-2012	6	47.51-48.82	47.57	[1]
Lipid	BTxARG-1/P850029	279	SC-2014	6	45.75-48.61	48.61	[2]
Starch	Sureño/RTx430	113	WE-2012, Combined	10	7.51-8.48	7.77	[1]
Protein	Sureño/RTx430	113	WE-2012, Combined	10	7.51-8.48	7.77	[1]
Starch	BTx642/BTxARG-1	191	SC, TX-2015	10	1.80-53.79	8.54-8.63	[2]

Notes: [1] Patil et al. (2018) [2] Boyles et al. (2017) [3] Rhodes et al. (2017) [4] Sukumaran et al. (2012)

QTL Analysis for Disease Resistance Traits

Resistance to Leaf Spot Traits

The QTL analysis can also determine QTLs associated with disease resistance traits. Kimball et al., (2019) conducted QTL analysis for sorghum resistance to leaf spot disease. The mapping populations comprised two F5:6 RILs, BTx623/SC155-14E and BTx623/BTx642. Testing took place in two experimental seasons (2016 and 2017), focusing on leaf spot disease severity and Flg22 hypersensitive response. The BTx623 genotype exhibited relative resistance compared to BTx642, while being relatively more susceptible than SC155-14E. Genotyping was performed using SNP markers, and QTL analysis was carried out using the CIM method. According to the analysis, seven leaf spot disease QTLs were identified, distributed across chromosomes 3, 4, 5, 6, and 9 (see Table 6). Notably, on chromosome 5, QTL qTLS5 occupies the same position as the major gene controlling leaf spot resistance, ds1 (Kawahigashi et al., 2011). Furthermore, three QTLs were identified for Flg22 hypersensitive response on chromosomes 4, 6, and 8.

Resistance to Anthracnose

Patil et al., (2017) conducted a QTL analysis for sorghum resistance to leaf spot disease. The mapping populations used were two F4:5 RILs, BTx623/SC155-14E and BTx623/SC414-12E. Testing was conducted in 6 experimental environments by looking at anthracnose disease severity on the leaves. The BTx623 genotype was susceptible compared to the SC155-14E and SC414-12E genotypes. Genotyping was conducted using SNP markers and QTL analysis using the CIM and ICIM methods. In the BTx623/SC414-12E population, QTL for anthracnose resistance was found on chromosome 2 in all environments.

In contrast, QTLs on chromosomes 4 and 5 were specific to particular environments, indicating the influence of environmental factors on anthracnose resistance in sorghum. In the BTx623/SC155-14E population, QTLs were detected on chromosomes 4 and 9 (refer to Table 7). The QTL on chromosome 9 remained consistent across all test environments. Furthermore, this QTL on chromosome 9 is suggested to be associated with genes regulating various processes such as cell death, sesquiterpene biosynthesis, response to wounding, ubiquitin protein, oxidative stress response, flavonol biosynthesis, and chitinase biosynthesis.

Table 6. QTL Analysis for Leaf Spot Resistance and Hypersensitive Response Traits of Flg22

QTL	Population	Chr.	Position (cM)	Range (cM)	LOD	AE	R^2 (%)
TLS							
qTLS3-2016	BTx623/SC155-14E	3	11.41	6.6–21.2	3.46	−0.25	11.64
qTLS3-2017	BTx623/SC155-14E	3	12.91	11.4–17.9	4.78	−0.27	15.54
qTLS3-ac	BTx623/SC155-14E	3	10.61	5.3–18.6	4.84	−0.22	14.88
qTLS4-2017	BTx623/SC155-14E	4	103.41	101.2–106.6	3.27	0.22	11.49
qTLS4-ac	BTx623/SC155-14E	4	103.41	101.2–106.8	4.82	0.23	15.95
qTLS5-2016	BTx623/BTx642	5	125.31	124.2–126.4	38.3	−0.93	65.65
qTLS5-2017	BTx623/BTx642	5	125.31	123.3–129	22	−0.51	43.99
qTLS5-ac	BTx623/BTx642	5	125.31	123.8–126.8	39.7	−0.74	71.12
qTLS6-2016	BTx623/BTx642	6	49.01	42.6–56.0	3.2	0.19	3.08
qTLS9.1-2017	BTx623/BTx642	9	315.81	315.5–317.9	2.6	0.22	3.92
qTLS9.2-2017	BTx623/BTx642	9	329.31	324.3–334.5	5.2	0.39	8.34
qTLS9.3-2017	BTx623/BTx642	9	346.41	342.9–354.7	2.8	−0.27	4.39
qTLS9.1-ac	BTx623/BTx642	9	316.81	315.7–320.4	8.3	0.45	8.87
Flg22							
qflg22.4-run2	BTx623/SC155-14E	4	19.41	8.9–26.5	2.92	−0.29	10.13
qflg22.4-run1	BTx623/BTx642	4	139.21	138.3–148.8	3.15	0.24	7,39
qflg22.6-run1	BTx623/SC155-14E	6	73.31	72.8–81.5	3.19	−0.22	11.28
qflg22.6-ac	BTx623/SC155-14E	6	72.41	65.2–73.3	2.72	−0.22	10.16
qflg22.8-run2	BTx623/SC155-14E	8	68.71	64.7–70.4	3.72	−0.24	17.35

Notes: TLS = target leaf spot. Chr. = chromosome.
Source: Kimball et al. (2019)

Table 7. QTLs for Resistance to Anthracnose in Sorghum

QTL	Population	Chr.	Position (cM)	Range (cM)	LOD	PVE	AE
qANP2-2013-GA	BTx623/SC414-12E	2	106.4	105.70–106.80	5.31	17	−0.93
qANP2-2015-CS	BTx623/SC414-12E	2	100.7	99.00–101.20	4	7	−0.27
qANP2-2015-GA	BTx623/SC414-12E	2	126.6	121.80–129.80	5.04	11	−0.61
qANP2-Comb	BTx623/SC414-12E	2	121.6	119.60–128.20	4.69	9	−0.28
qANP4-2013-GA	BTx623/SC414-12E	4	118.9	118.00–122.40	3.59	10	0.72
qANP4-2015-GA	BTx623/SC414-12E	4	112.2	102.90–116.20	5.53	14	0.81
qANP4-Comb	BTx623/SC414-12E	4	112.2	100.00–119.50	3.31	6	0.27
qANP4-2012-CS	BTx623/SC155-12E	4	83.7	80.80–90.30	3.71	5	0.58
qANP4-2013-GA	BTx623/SC155-12E	4	92.2	91.60–93.30	6.24	16	1.1
qANP4-2015-CS	BTx623/SC155-12E	4	98.2	97.20–99.20	4.14	9	0.54
qANP4-2015-GA	BTx623/SC155-12E	4	98.2	95.70–99.20	3.71	9	0.51
qANP4-Comb	BTx623/SC155-12E	4	86.1	84.70–87.40	4.3	7	0.41
qANP5-2012-CS	BTx623/SC414-12E	5	108.2	108.20–120.20	8.74	25	0.9
qANP5-2013-CS	BTx623/SC414-12E	5	117.2	116.60–118.10	14.35	39	1.41
qANP5-2015-CS	BTx623/SC414-12E	5	119.9	116.60–124.80	12.41	31	0.55
qANP5-Comb	BTx623/SC414-12E	5	117.2	116.90–118.10	8.62	20	0.45
qANP9-2011-CS	BTx623/SC155-12E	9	0.9	0.20–2.00	5.8	19	0.31
qANP9-2012-CS	BTx623/SC155-12E	9	0.9	0.00–2.10	21.55	42	1.55
qANP9-2013-CS	BTx623/SC155-12E	9	1.6	0.00–1.70	27.65	62	2.16
qANP9-2013-GA	BTx623/SC155-12E	9	0.9	0.00–2.10	8.43	24	1.31
qANP9-2015-CS	BTx623/SC155-12E	9	0.9	0.40–4.80	8.85	23	0.74
qANP9-2015-GA	BTx623/SC155-12E	9	0.9	0.60–2.60	9.55	26	0.83
qANP9-Comb	BTx623/SC155-12E	9	0.9	0.60–1.80	17.37	40	0.97

Notes: PVE = phenotypic variances explained. AE = additive effect
Source: Patil et al., (2017)

Conclusions

QTL analysis in sorghum can be utilized to determine QTL for agronomic characters, seed quality, and disease resistance. One method widely used for QTL analysis is the CIM method because it can determine the position of QTL on the sorghum genome. Some widely used markers for QTL analysis in sorghum are SSR markers, SNPs, and nucleotide base sequencing-based markers. In agronomic characters, some QTLs co-localized between characters. It suggests that there is an indication of pleiotropy in the gene or QTL controlling the trait. The same thing was found in the characteristics of sorghum seeds' starch, protein, fibre and lipid content. Co-localization between the same traits in different mapping populations can be used as a consensus of QTL for a particular trait. Co-localization of QTL to an annotated gene can be used as a marker for selecting a particular trait. The data that has been obtained can be used to develop QTL consensus for several characters at once through meta-QTL analysis. In addition, the data collected needs to be increased so that the QTL meta-analysis can provide better and more precise mapping.

References

Awika, H. O., Hays, D. B., Mullet, J. E., Rooney, W. L., & Weers, B. D. (2017). QTL mapping and loci dissection for leaf epicuticular wax load and canopy temperature depression and their association with QTL for staygreen in Sorghum bicolor under stress. *Euphytica*, *213*(9), 207. https://doi.org/10.1007/s10681-017-1990-5

Ayalew, H., Peiris, S., Chiluwal, A., Kumar, R., Tiwari, M., Ostmeyer, T., Bean, S., & Jagadish, S. V. K. (2022). Stable sorghum grain quality QTL were identified using SC35 × RTx430 mapping population. *Plant Genome 15*(3). https://doi.org/10.1002/tpg2.20227

Bai, C., Wang, C., Wang, P., Zhu, Z., Cong, L., Li, D., Liu, Y., Zheng, W., & Lu, X. (2017). QTL mapping of agronomically important traits in sorghum (*Sorghum bicolor* L.). *Euphytica, 213*. https://doi.org/10.1007/s10681-017-2075-1

Bernardino, K. C., Pastina, M. M., Menezes, C.

B., de Sousa, S. M., Maciel, L. S., Jr, G. C., Guimarães, C. T., Barros, B. A., da Costa e Silva, L., Carneiro, P. C. S., Schaffert, R. E., Kochian, L. V, & Magalhaes, J. V. (2019). The genetic architecture of phosphorus efficiency in sorghum involves pleiotropic QTL for root morphology and grain yield under low phosphorus availability in the soil. *BMC Plant Biology*, *19*(1), 87. https://doi.org/10.1186/s12870-019-1689-y

Boyles, R. E., Pfeiffer, B. K., Cooper, E. A., Zielinski, K. J., Myers, M. T., Rooney, W. L., & Kresovich, S. (2017a). Quantitative trait loci mapping of agronomic and yield traits in two grain sorghum biparental families. *Crop Science*, *57*(5), 2443–2456. https://doi.org/https://doi.org/10.2135/cropsci2016.12.0988

Boyles, R. E., Pfeiffer, B. K., Cooper, E. A., Zielinski, K. J., Myers, M. T., Rooney, W. L., & Kresovich, S. (2017b). Genetic dissection of sorghum grain quality traits using diverse and segregating populations. *TAG. Theoretical and Applied Genetics. Theoretische Und Angewandte Genetik*, *130*(4), 697–716. https://doi.org/10.1007/s00122-016-2844-6

Cuevas, H. E., Zhou, C., Tang, H., Khadke, P. P., Das, S., Lin, Y.-R., Ge, Z., Clemente, T., Upadhyaya, H. D., Hash, C. T., & Paterson, A. H. (2016). The evolution of photoperiod-insensitive flowering in sorghum, a genomic model for panicoid grasses. *Molecular Biology and Evolution*, *33*(9), 2417–2428. https://doi.org/10.1093/molbev/msw120

Endre, A., & Kassahun, B. (2017). Evaluation and association mapping of agronomic traits for drought tolerance in sorghum [*Sorghum bicolor* (L.) *Moench*]. *African Journal of Biotechnology*, *16*(13), 631–642. https://doi.org/10.5897/AJB2016.15400

Gelli, M., Konda, A. R., Liu, K., Zhang, C., Clemente, T. E., Holding, D. R., & Dweikat, I. M. (2017). Validation of QTL mapping and transcriptome profiling for identification of candidate genes associated with nitrogen stress tolerance in sorghum. *BMC Plant Biology*, *17*(1), 123. https://doi.org/10.1186/s12870-017-1064-9

Govindarajulu, R., Hostetler, A. N., Xiao, Y., Chaluvadi, S. R., Mauro-Herrera, M., Siddoway, M. L., Whipple, C., Bennetzen, J. L., Devos, K. M., Doust, A. N., & Hawkins, J. S. (2021). Integration of high-density genetic mapping with transcriptome analysis uncovers numerous agronomic QTL and reveals candidate genes for the control of tillering in sorghum. *G3 Genes|Genomes|Genetics*, *11*(2), jkab024. https://doi.org/10.1093/g3journal/jkab024

Gupta, P., Kulwal, P., & Mir, R. (2013). QTL Mapping: Methodology and Applications in Cereal Breeding. In *Cereal Genomics II* (pp. 275–318). Springer Nature Link. https://doi.org/10.1007/978-94-007-6401-9_11

Hilley, J. L., Weers, B. D., Truong, S. K., McCormick, R. F., Mattison, A. J., McKinley, B. A., Morishige, D. T., & Mullet, J. E. (2017). Sorghum Dw2 encodes a protein kinase regulator of stem internode length. *Scientific Reports*, *7*(1), 4616. https://doi.org/10.1038/s41598-017-04609-5

Kadam, S. ., & Fakrudin, B. (2017). Marker assisted pyramiding of root volume QTLs to improve drought tolerance in rabi sorghum. *Research on Crops*, *18*(4), 683–692. https://doi.org/https://doi.org/10.5958/2348-7542.2017.00114.0

Kawahigashi, H., Kasuga, S., Ando, T., Kanamori, H., Wu, J., Yonemaru, J., Sazuka, T., & Matsumoto, T. (2011). Positional cloning of ds1, the target leaf spot resistance gene against Bipolaris sorghicola in sorghum. *Theoretical and Applied Genetics*, *123*(1), 131–142. https://doi.org/https://doi.org/10.1007/s00122-011-1572-1

Kimball, J., Cui, Y., Chen, D., Brown, P., Rooney, W. L., Stacey, G., & Balint-Kurti, P. J. (2019). Identification of QTL for Target Leaf Spot resistance in Sorghum bicolor and investigation of relationships between disease resistance and variation in the MAMP response. *Scientific Reports*, *9*(1), 1–9. https://doi.org/10.1038/s41598-019-54802-x

Kiranmayee, K. N. S. U., Hash, C. T., Sivasubramani, S., Ramu, P., Amindala, B. P., Rathore, A., Kishor, P. B. K., Gupta, R., & Deshpande, S. P. (2020). Fine-mapping of sorghum stay-green qtl on chromosome10 revealed genes associated with delayed senescence. *Genes*, *11*(9), 1026. https://doi.org/10.3390/genes11091026

Kiyosawa, A., Yonemaru, J., Kawahigashi, H., & Goto, K. (2020). Analysis of quantitative trait loci for fertility restoration in seven F_2 populations derived from sorghum F_1 hybrids bred in Japan. *Breeding Science*, *70*(3), 379–386. https://doi.org/10.1270/jsbbs.19144

Kong, W. Q., Kim, C., Zhang, D., Guo, H., Tan, X., Jin, H., Zhou, C., Shuang, L. S., Goff, V., Sezen, U., Pierce, G., Compton, R., Lemke, C., Robertson, J., Rainville, L., Auckland, S., & Paterson, A. H. (2018). Genotyping by sequencing of 393 sorghum bicolor BTx623 × IS3620C recombinant inbred lines improves sensitivity and resolution of QTL detection. *G3: Genes, Genomes, Genetics*, *8*(8), 2563–2572. https://doi.org/10.1534/g3.118.200173

Kotla, A., Phuke, R., Hariprasanna, K., Mehtre, S. P., Rathore, A., Gorthy, S., Srivastava, R. K., Das, R., Bhanu Prakash, A., Radhika, K., Hash, C. T., Reddy, B. V. S., Patil, J. V, Jabeen, F., Shashikanth, D., Jaganathan, J., Gaddameedi, A., Subhasini, V., Deshpande, S. P., & Kumar, A. A. (2019). Identification of QTLs and candidate genes for high grain Fe and Zn concentration in sorghum [*Sorghum bicolor* (L.) *Moench*]. *Journal of Cereal Science* 90: 102850 https://doi.org/https://doi.org/10.1016/j.jcs.2019.102850

Kristamtini, Widodo, S., Purwaningsih, S., Pustika, A., S, W., Muazam, A., Rachmiwati, Hanifah, A., Pramono, J., Triastono, J., Sahara, D., Sulistyawati, H., Laksono, P., Fahmi, A., & Sutardi. (2024). Sorghum Productivity and Its Farming feasibility in dryland agriculture: genotypic and planting distance insights. *Phyton-International Journal of Experimental Botany*, *93*(5), 1007–1021. https://doi.org/10.32604/phyton.2024.048770

Lu, Q., Yu, X., Wang, H., Yu, Z., Zhang, X., & Zhao, Y. (2022). Quantitative trait locus mapping for important yield traits of a sorghum-sudangrass hybrid using a high-density single nucleotide polymorphism map. *Frontiers in Plant Science*, *13*, 1–17. https://doi.org/10.3389/fpls.2022.1098605

Mace, E. S., Singh, V., Van Oosterom, E. J., Hammer, G. L., Hunt, C. H., & Jordan, D. R. (2012). QTL for nodal root angle in sorghum (*Sorghum bicolor* L. *Moench*) co-locate with QTL for traits associated with drought adaptation. *TAG. Theoretical and Applied Genetics*, *124*(1), 97–109. https://doi.org/10.1007/s00122-011-1690-9

Mitteldorf, J. (2019). What is antagonistic pleiotropy? *Biochemistry. Biokhimiia*, *84*(12), 1458–1468. https://doi.org/10.1134/S0006297919120058

Paterson, A. H., Bowers, J. E., Bruggmann, R., Dubchak, I., Grimwood, J., Gundlach, H., Haberer, G., Hellsten, U., Mitros, T., Poliakov, A., Schmutz, J., Spannagl, M., Tang, H., Wang, X., Wicker, T., Bharti, A. K., Chapman, J., Feltus, F. A., Gowik, U., … Rokhsar, D. S. (2009). The *Sorghum bicolor* genome and the diversification of grasses. *Nature*, *457*(7229), 551–556. https://doi.org/10.1038/nature07723

Patil, N. Y., Klein, R. R., Williams, C. L., Collins, S. D., Knoll, J. E., Burrell, A. M., Anderson, W. F., Rooney, W. L., & Klein, P. E. (2017). Quantitative Trait Loci Associated with Anthracnose Resistance in Sorghum. *Crop Science*, *57*(2), 877–890. https://doi.org/https://doi.org/10.2135/cropsci2016.09.0793

Patil, N. Y., Pugh, N. A., Klein, R. R., Martinez, H. S., Martinez, R. S., Rodriguez-Herrera, R., Rooney, W. L., & Klein, P. E. (2019). Heritability and quantitative trait loci of composition and structural characteristics in sorghum grain. *Journal of Crop Improvement*, *33*(1), 1–24. https://doi.org/10.1080/15427528.2018.1536006

Phuong, N., Afolayan, G., Stützel, H., Uptmoor, R., & El-Soda, M. (2019). Unraveling the genetic complexity underlying sorghum response to water availability. *PLOS ONE*, *14*(4), e0215515. https://doi.org/10.1371/journal.pone.0215515

Pierce, B. (2019). *A Conceptual Approach* (7th ed.). W.H. Freeman.

Price, H. J., Dillon, S. L., Hodnett, G., Rooney, W. L., Ross, L., & Johnston, J. S. (2005). Genome evolution in the genus Sorghum (Poaceae). *Annals of Botany*, *95*(1), 219–227. https://doi.org/10.1093/aob/mci015

Rhodes, D. H., Hoffmann, L., Rooney, W. L., Herald, T. J., Bean, S., Boyles, R., Brenton, Z. W., & Kresovich, S. (2017). Genetic architecture of kernel composition in global sorghum germplasm. *BMC Genomics*, *18*(1), 1–8. https://doi.org/10.1186/s12864-016-3403-x

Ritter, K. B., Jordan, D. R., Chapman, S. C., Godwin, I. D., Mace, E. S., & Lynne McIntyre, C. (2008). Identification of QTL for sugar-related traits in a sweet × grain sorghum (*Sorghum bicolor* L. *Moench*) recombinant inbred population. *Molecular Breeding*, *22*(3), 367–384. https://doi.org/10.1007/s11032-008-9182-6

Saltz, J. B., Hessel, F. C., & Kelly, M. W. (2017). Trait Correlations in the Genomics Era. *Trends in Ecology & Evolution*, *32*(4), 279–290. https://doi.org/10.1016/j.tree.2016.12.008

Singh, A., Newton, L., Schnable, J. C., & Thompson, A. M. (2025). Unveiling shared genetic regulators of plant architectural and biomass yield traits in sorghum. *Journal of Experimental Botany*, *76*(6), 1–32. https://doi.org/https://doi.org/10.1093/jxb/eraf012

Sirappa, M. (2003). Prospek pengembangan sorgum di Indonesia sebagai komoditas alternatif untuk pangan, pakan, dan industri. *Prospek Pengembangan Sorgum Di Indonesia Sebagai Komoditas Alternatif Untuk Pangan, Pakan, Dan Industri* 22(4): 133–140.

Sukumaran, S., Xiang, W., Bean, S. R., Pedersen, J. F., Kresovich, S., Tuinstra, M. R., Tesso, T. T., Hamblin, M. T., & Yu, J. (2012). Association mapping for grain quality in a diverse sorghum collection. *The Plant Genome* 5(3). https://doi.org/https://doi.org/10.3835/plantgenome2012.07.0016

Takanashi, H., Shichijo, M., Sakamoto, L., Kajiya-Kanegae, H., Iwata, H., Sakamoto, W., & Tsutsumi, N. (2021). Genetic dissection of QTLs associated with spikelet-related traits and grain size in sorghum. *Scientific Reports* 11(1): 9398. https://doi.org/10.1038/s41598-021-88917-x

Zhang, D., Kong, W., Robertson, J., Goff, V. H., Epps, E., Kerr, A., Mills, G., Cromwell, J., Lugin, Y., Phillips, C., & Paterson, A. H. (2015). Genetic analysis of inflorescence and plant height components in sorghum (Panicoidae) and comparative genetics with rice (Oryzoidae). *BMC Plant Biology* 15(1): 1–15. https://doi.org/10.1186/s12870-015-0477-6

Zou, G., Zhai, G., Yan, S., Li, S., Zhou, L., Ding, Y., Liu, H., Zhang, Z., Zou, J., Zhang, L., Chen, J., Xin, Z., & Tao, Y. (2020). Sorghum qTGW1a encodes a G-protein subunit and acts as a negative regulator of grain size. *Journal of Experimental Botany* 71(18): 5389–5401. https://doi.org/10.1093/jxb/eraa277