

ORIGINAL ARTICLE



Assessment of genotypic variability and genome-wide association analysis of cooking time and canning quality traits in common bean (*Phaseolus vulgaris* L.)

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Abstract

Developing improved common bean varieties with short cooking time (CT) and good canning quality traits (CQTs) is very key for accelerating bean consumption among the urban and middle-class population. The objective of this study was to assess the genotypic variability and identify single nucleotide polymorphism (SNP) markers associated with CT and CQTs in common bean. A total of 250 common bean accessions were evaluated under field conditions for two seasons using alpha lattice design with two replications. Three months post-harvest, the dry bean grains were evaluated for CT and CQTs. Significant variation was observed among the 250 common bean accessions tested for both traits. CT ranged from 51 to 215 min, with 11 genotypes cooking in less than 60 min. The percentage total CQTs' score ranged from 41% to 84% with 31 genotypes scoring 76% and above. Forty-seven significant GWAS signals were detected for CT on chromosomes Pv01, Pv04, Pv05 and Pv11 and CQTs on Pv01, Pv02, Pv03, Pv04, Pv05, Pv06, Pv07, Pv08, Pv10 and Pv11, respectively. Positional candidate genes including Phvul.005G161200 on chromosome Pv05, Phvul.007G2803001 and Phvul.007G280700 on chromosome Pv07 were associated with seed coat colour retention of the canned beans. Besides their usefulness in breeding research, the identified bean genotypes with shorter CT and good CQTs could enhance bean consumption and processing industries.

KEYWORDS

assessment, correlations, GWAS, SNP markers

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1 | INTRODUCTION

Common bean provides a source of low-fat proteins and micronutrients affordable to the most vulnerable groups, especially children under 5, women of reproductive age and patients with HIV and AIDS. Beans have the highest level of mineral content among legumes, including iron, zinc, copper, phosphorus and aluminium. They also provide starch, dietary fibre, folic acid and vitamin B (Imran et al., 2014; UNDP, 2012). Consumption of beans is associated with health benefits that include reduced risk of diabetes, heart disease and colon and prostate cancers plus the mitigation of obesity (Câmara et al., 2013; Ganesan & Xu, 2017; Nchanji & Ageyo, 2021). In addition, they contain an extensive array of flavonoids such as anthocyanins, proanthocyanins, flavonols, phenolic acids and isoflavones (Granito et al., 2008; Lin et al., 2008). Beans can serve as a functional food because they contain several bioactive compounds such as enzyme inhibitors, lectins, phytates, oligosaccharides and phenolic substances that play metabolic roles in humans and animals that frequently consume them (Díaz-Batalla et al., 2006; Suárez et al., 2023).

However, global per capita consumption of beans is estimated at 2.58 kg/year, hence low (Anon, 2020), and this is attributed to the high energy requirements for cooking beans in terms of fuel, water and time (UNDP, 2012). Previous studies conducted on the CT of beans reported that it can vary depending on the growth environment, variety, length of storage, method of cooking and the quantity used (Arruda et al., 2012; Daher & Braybrook, 2015). Globally, 40% of households depend on wood as a source of fuel for cooking, yet the woodlands and trees have been seriously exhausted due to widespread deforestation (WEO, 2010). The scarcity of wood fuel has caused some households substitute beans with foods that have lower energy requirements for cooking, though these often lack essential nutritional benefits (Stephy et al., 2013). Another common practice among bean consumers is to cook beans once in large amounts and warm the leftovers later, while in some communities, the bean seed coat is removed with ash before cooking and then mashed (Egeru et al., 2014). Therefore, the development of improved bean genotypes with fast or rapid cooking properties would accelerate consumption among smallholder farmers, and additional beans with high canning quality traits will drive industrial processing and subsequently increase consumption.

In order to increase genetic gain in CT and CQTs, understanding the genetic control of these traits is critical. Previous studies on the genetic control of CT suggest qualitative nature of the trait, controlled by a few genes with relatively small and cumulative effects (Elia et al., 1997; Mukai, 2017). However, other studies have reported that two dominant genes control CT and that it is highly heritable with high narrow sense heritability estimates of 0.74–0.90 (Elia et al., 1997; Jacinto-Hernandez et al., 2003). On the other hand, CQT's mechanisms have been reported to be quantitative in nature (Hosfield et al., 1984; Posa-Macalincag et al., 2002; Walters et al., 1997; Wassimi et al., 1990).

The recent advances in genomics and computational approaches have enhanced mapping of quantitative trait loci (QTL) and genomic regions associated with variations for complex and quantitative traits (Kamfwa et al., 2015). The current genotyping tools have led to the

discovery of thousands of SNP markers across various species at a reasonable cost, including use of combined genome complexity reduction with next-generation sequencing through RADSeq (Willing et al., 2011), genotype by sequencing (GBS) (Elshire et al., 2011) and DArTseq strategies (Cruz et al., 2013). A few thousand SNPs are currently available for the common bean, thus allowing the exploration of genetic diversity and population structure (Rodríguez et al., 2015; Valdisser et al., 2016). Currently, genome-wide association study (GWAS) is the most popular method used to understand the genetic basis of complex traits in a diverse population, since it provides new insights into the genetic architecture of complex traits (Thorwarth et al., 2017). During GWAS analysis, population structure and kinship among genotypes can be corrected for crops with complex domestication history including beans to reduce spurious associations between significant markers and traits, hence making GWAS the best approach for association mapping study for these traits (Agarwal, 2014). In addition, the diverse nature of populations used in association studies enables assemble of alleles from across a large number of genotypes, and this is critical for discovery of alleles with both large and small genetic effects associated with important plant traits (Mamidi et al., 2013; Moghaddam et al., 2016). GWAS has been conducted on common beans using different materials and genotyping platforms to find genetic associations for key traits. These include days to flowering and seed yield (Kamfwa et al., 2015), resistance to anthracnose and angular leaf spot (Perseguini et al., 2016; Zuiderveen et al., 2016), cooking time (Cichy et al., 2015), the nutritional quality of cooked dry beans (Katuuramu et al., 2018), genetic traits associated with production traits; days to flowering, the *Macrophomina phaseolina* disease, SPAD index and days to maturity in both heat and drought stress environments (Dramadri et al., 2021; Oladzad et al., 2019), days to maturity, growth habit, canopy height, lodging and seed yield (Moghaddam et al., 2016).

In a previous study consisting of 206 common bean accessions of the Andean Diversity Panel (ADP), several significant single nucleotide polymorphisms (SNPs) associated with CT were reported on Pv02, Pv03 and Pv06, respectively (Cichy et al., 2015). Additional evaluation of 430 accessions of the ADP resulted in identification of additional significant SNPs on Pv03, Pv04, Pv06, Pv07, Pv08 and Pv11 (Bassett et al., 2020), and on Pv10 using 220 accessions freshly harvested and stored for 4 months at 35°C and 50% RH for accelerating aging (Wanjohi et al., 2023). In another study, 10 QTLs were identified for CT in TZ-27 (slow cooking) and TZ-37 (fast cooking) recombinant inbred line (RIL) population on chromosomes Pv01, Pv02, Pv03, Pv05, Pv06, Pv10 and Pv11, and three QTLs, namely, CT3.1 on Pv03, CT6.1 on Pv06 and CT11.2 on Pv11, were stable across multiple environments (Berry et al., 2020). In a recent study, six QTLs for CT were identified using a RIL population between *Ervilha* and P1527538 on Pv02, Pv05, Pv08 and Pv10 (Bassett et al., 2021).

For canning quality traits, 35 QTLs were identified from a recombinant inbred population of 100 lines for seed coat lustre, hydration coefficient, washed drain coefficient, water uptake, anthocyanin concentration of soak water and appearance near the ASP gene on chromosome 7 and QTLs for colour and seed appearance on Pv 04, 05, 06 and 07 (Cichy et al., 2014). From a study of 96 RILs derived from a

cross between the black cultivar Tagguar and cultivar 115M, colour retention following processing was associated with loci on B1, B2, B5, B8 and B11 and texture with QTL on B6 and B11. Visual appearance was associated with QTL on B5 and B8, while washed drain weight was associated with QTL on B3 and two separate regions on B10 (Wright & Kelly, 2011). From the evaluation of 148 RILs derived from two recombinant inbred populations crossed between dark red kidney cultivars (Montcalm and California Dark Red Kidney 82), a QTL for appearance and splitting was detected on linkage group 1 (LG1) (Posa-Macalincag et al., 2002). Further studies on the genetics of cooking time and canning quality traits could allow feasible application of MAS for the two traits reducing the requirement for the tedious and expensive phenotyping processes by the two traits. Therefore, the objective of this study was to assess the genotypic variability for CT and CQTs among diverse common bean accessions and identify SNP markers that are associated with the two traits.

2 | MATERIALS AND METHODS

2.1 | Genetic materials

The study comprised 250 accessions, of which 75 were collections from the regional canning nursery coordinated by the PABRA/CIAT network, 13 ADP lines from Michigan State University and 162 from the released varieties, local germplasm and elite breeding lines from within and across other countries whose statuses for the two traits were not known. Details of the accessions, country of origin and reaction to the two traits are given in Table S1.

2.2 | Experimental site

This study's field trials were conducted at Rwebitaba Zonal Agricultural Research and Development Institute (ZARDI) in western Uganda. The institute is situated at 041°36.81 N, 30 19°57.76E, with an elevation of 1531 m above sea level (masl), and it receives a bimodal rainfall

regime from March to June as the first season and September to December as the second season. The soils range from highly weathered ferralsols to young andosols. After assembling the germplasm, an adaptation and seed multiplication trial was conducted on-station at the National Crops Resources Research Institute (NaCRRI) to test for suitability to Ugandan climatic conditions and to generate sufficient seeds to undertake cooking time and canning quality evaluations. NaCRRI is located in central Uganda at latitude 0°32'N and longitude 32°53'E, with an altitude of 1150 masl. The institute falls in a bimodal rainfall region with March to May as the first season and September to December as the second season with a mean annual rainfall of 1270 mm and a mean temperature of 22.5°C.

2.3 | Experimental design

Subsequently, two experiments were established using an alpha lattice design with two replications at Rwebitaba ZARDI during the 2019B and 2020A seasons. In both experiments, the seed was sown at a spacing of 10 cm between plants and 50 cm between rows in a plot of four rows each of 2 m. The experiments were rain-fed and received a total of 978 mm of rain in 2019B, while a total of 383.7 mm was received in the first season of 2020A, and the minimum and maximum temperatures in 2019B were 15.1 and 25.1°C, respectively, while in 2020A, it was 15.98 and 26.5°C. Other recommended agronomic practices were done to ensure the growth of the trial, including weeding, staking and spraying against fungal diseases and pests, but no inorganic fertilizer was added. A schematic summary of materials and methods is given in Figure 1.

2.4 | Evaluation of common bean genotypes for cooking time and canning quality traits

2.4.1 | Cooking time

An automated Mattson cooker apparatus was used to estimate cooking time according to Wang and Daun (2005). At harvest, yield per

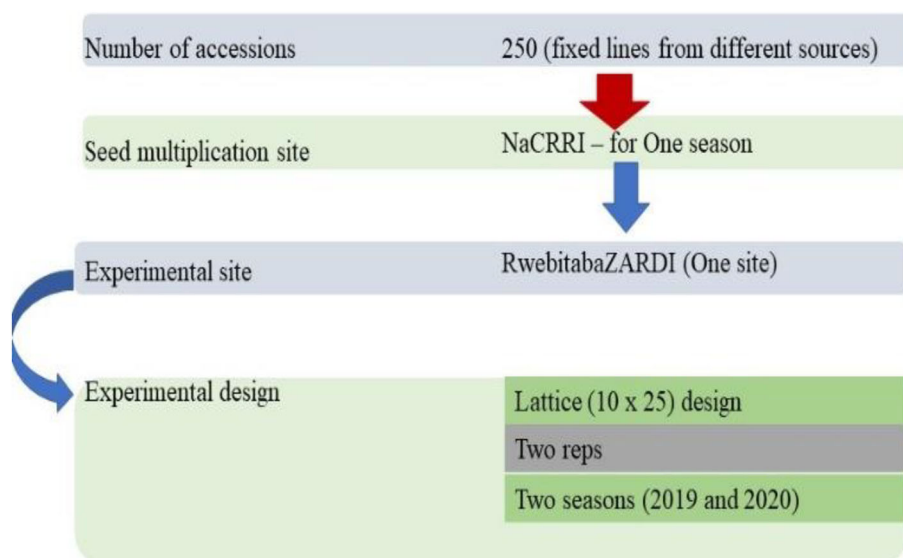


FIGURE 1 Schematic summary of materials and methods. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13172)]

plot, seed coat colour and seed size were determined. The seed from each plot was then sun-dried for 2 days and later stored at room temperature for 3 months. After this period, the moisture content for each seed sample entry was determined using a 6095 moisture analyzer (SINARTM AgriProto, made in England) to ensure that all were within the suitable processing moisture range of 12%–16% (Vanderleia et al., 2017). Beginning with replication 1, a sample of 25 uniform and healthy seeds were randomly picked from each entry. These were soaked in distilled water at room temperature ($22 \pm 2^\circ\text{C}$) for 16 h in sealed glass bottles, ensuring that the beans were entirely covered with water. Afterwards, the water was drained from all samples while retaining the seeds in sealed bottles to safeguard against moisture loss through evaporation. Twenty-five seeds per accession were then positioned into the 25 holes of the Mattson cooker (one seed per hole), ensuring that the piercing tip of the 90-g rod (plunger) was in contact with the surface of the seed. These were then placed in a 5-L beaker containing 4 L of boiling distilled water, and the hot plate was set at 350°C . When the seed became sufficiently tender, the plunger penetrated the seed and dropped through the hole in the saddle, with the time automatically recorded on the computer. The top of the dropped plunger would appear lower than the top of the others that had not yet dropped, making it easy to determine when the plunger penetrated its corresponding seed. Testing for cooking time was considered complete when the 20th plunger fell, though the cooking trial was allowed to continue until all the 25 plungers dropped. The time taken for each sample to cook was automatically recorded on a computer.

2.4.2 | Canning quality traits

Before the actual canning process, water absorption capacity, which is determined by the hydration coefficient (HC), was carried out. Weighed samples from each plot with a dry weight of approximately 100 g were placed in nylon mesh bags and soaked in distilled water for 16 h. Water was removed, and the bean samples were drained adequately. The hydration coefficient was calculated as the ratio of the soaked beans' weight to the weight of the dry sample. Canning was done in glass jars following the modified Michigan State University (MSU) bean canning protocol. After cooking, the glass jars were cooled under running water from a tap and then stored on shelves for a month before evaluation.

2.4.3 | Parameters for canning quality traits

For CQT evaluations, the brine and seeds were poured onto a wide plate together, though each was viewed separately. The canned beans were evaluated for the following aspects: (1) clumping, (2) colour retention, (3) appearance, (4) viscosity (brine clarity), (5) bean splitting and (6) free starch. A panel of eight trained personnel used a rating scale of 1–5, where 1 = *poor/severe* and 5 = *excellent*, based on the modified MSU bean canning protocol.

2.4.4 | Washed drained solids and washed drain coefficient

After the evaluations, the canned sample was poured onto a sieve, and the beans were washed with clean tap water, followed by rinsing and allowing them to drain properly. Then, the washed beans were weighed to assess the net weight of the canned beans (washed drain solids). The coefficient for washed drained solids was determined by dividing the washed drained solids' weight by the soaked weight of the sample.

2.4.5 | Phenotypic data analysis

Statistical analysis for GWAS was performed using best linear unbiased predictors (BLUPs), which minimize environmental, and seasonal effects. The 'lme4' package in R (Bates et al., 2014) was used to determine and extract the random effects (BLUPs) of the phenotypic traits using the simple linear model for one environment:

$$Y_{ijk} = \mu + R_i + R(B) + G + \varepsilon_{ijk} \quad (1)$$

The BLUP analysis across seasons for traits were calculated based on following statistical model:

$$Y_{ijk} = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} + R(B)k + \varepsilon_{ijk} \quad (2)$$

where for Equations (1) and (2), Y_{ijk} is the trait of interest, μ is the mean effect, α is the effect of the i th genotype, β is the effect of the j th season, $\alpha\beta$ is the effect of the interaction between genotype i and season j and $R(B)$ is random effect of blocks nested with reps, respectively.

2.4.6 | Broad-sense heritability for individual seasons

Broad-sense heritability in individual seasons was calculated using the equation below:

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_e^2}{n_{reps}}} \quad (3)$$

where σ_g^2 and σ_e^2 are the genotype and error variance components, respectively, and n_{reps} is the number of replications.

2.4.7 | Broad-sense heritability across seasons

Broad-sense heritability across seasons was calculated as

$$H^2 = \frac{\sigma_g^2}{\sigma_g^2 + \frac{\sigma_{seas}^2}{n_{seas}} + \frac{\sigma_e^2}{n_{seas} * n_{reps}}} \quad (4)$$

where the new term σ_{seas}^2 is the genotype-by-season interaction variance component and n_{seas} is the number of seasons conducted.

2.4.8 | Phenotypic and genetic correlations

Pairwise trait and environment Pearson correlations were computed in the R statistical program. Genetic correlation between traits was calculated as $\rho_g = \frac{\sigma_g(jj')}{\sigma_g(j)\sigma_g(j')}$, where $\sigma_g(jj')$ is the arithmetic mean of all pairwise genotypic covariances between trait j and j' and $\sigma_g(j)\sigma_g(j')$ is the arithmetic average of all pairwise geometric means among the genotypic variance components of the traits.

2.4.9 | Genotyping of common bean genotypes

Common bean leaf samples were obtained from tender leaves of 217 genotypes one and half months after planting for DNA extraction and placed into 96 well plates. The samples were genotyped using Diversity Array Technology (DArT) sequencing. The TANBead Plant extraction kit was used for DNA extraction, which ranged from 50 to 100 ng/μL. The quality and quantity of the DNA were checked on 0.8% agarose, and libraries were constructed according to Kilian et al. (2012). DArTseq complexity reduction was performed through the digestion of genomic DNA and ligation of barcoded adapters, followed by PCR amplification of adapter-ligated fragments. Libraries were sequenced using single-read sequencing runs for 77 bases, while next-generation sequencing was carried out using HiSeq 2500. DArTseq markers' scoring was done by DArTsoft14, an in-house pipeline for scoring markers that is based on algorithms, using various levels of barcoding of individual samples and novel classification algorithms from both leading commercial sequencing platforms and "open access" instruction. SNP markers were scored in a binary fashion, 1 and 0, respectively, indicating the presence or absence of the restriction fragment in the genomic representative of each sample, as described by Wenzl et al. (2004). SNP markers were aligned to the reference genome of common bean v9 to identify chromosome positions. To include only high-quality markers, 153,000 SNPs were filtered using TASSEL version 5.0 for duplicates, monomorphic markers and minor allele frequency at a threshold of 0.05 and for genotypes missing more than 10% of data. A total of 11,094 SNPs were retained and used for principal component analysis (PCA) and association analyses. The kinship matrix was calculated using the scaled identity by descent method in Tassel.

2.4.10 | PCA and clustering

PCA was performed using *factoextra* and *vegan* packages in R (R Core Team, 2020) to determine the genetic relationship between the 217 common bean genotypes used in this study. Genetic distance between genotypes was calculated using Roger's genetic distance (Rogers, 1972) and a dendrogram generated from these genetic distance matrices with the neighbour-joining method in PowerMarker version 3.25 (Liu & Muse, 2005). The resulting trees

were visualized using MEGA version 11 (Tamura et al., 2011). The SNP's contribution to the trait based on the observed alleles was plotted using the 'gg plots' and their confidence statistics calculated with 'rstatistix' in R.

2.4.11 | Marker trait association analysis

The best linear unbiased predictions (BLUPs) extracted from the phenotypic data for CT and CQTs and genotypic data consisting of 11,094 SNP markers from the 217 genotypes were used for conducting genome-wide association study (GWAS) analysis. This included BLUPs for CT, seven CQTs and transformed data for clumping and hydration coefficient. The GWAS analysis was conducted using the FarmCPU (Fixed and random model Circulating Probability Unification) model implemented in the R package rMVP (Yin et al., 2021). Kinship matrix and principal components (PCs) computed in TASSEL program (Traits Association and Evolution by Linkage) (Bradbury et al., 2007) were included in the GWAS model to account for the relatedness among genotypes and population stratification (Liu et al., 2016). To declare that an SNP marker was significantly associated with a trait, we used the Bonferroni cut-off threshold at $\alpha = .05$.

2.4.12 | Identification of possible candidate genes

In order to identify positional candidate genes near to significant GWAS peaks, candidate genes within ± 100 kb window of the significant SNP markers were considered, and this was within the linkage disequilibrium decay rate for common bean, characteristic of highly self-pollinated species like *Phaseolus vulgaris* (Flint-Garcia et al., 2003; Patishtan et al., 2018). In addition, the function of the putative candidate gene was related to regulating cooking time and canning quality traits using the online JBrowse tool on Phytozome v. 12.1 (Goodstein et al., 2012).

3 | RESULTS

Significant differences were observed among the genotypes for yield and yield component traits (Table S2). The number of pods per plant (PDPL) ranged from 2 to 30 with a grand mean of 10.4. The number of seeds per pod ranged from 2 to 10, with a grand mean of 3.8. The seed yield per hectare ranged from 133 to 4333 kg/ha with a grand mean of 1380 (Table S2). There were a low non-significantly positive correlation between seed coat size and cooking time and a significantly negative correlation with seed coat colour (Table S3).

3.1 | Genotypic variability for cooking time

Significant variation in cooking time observed among the 250 dry bean genotypes evaluated in this study (Table 1) ranged from 47.1 to 187.2 minutes (min) in the first season of 2019B and 46.9 to 264.1 min

TABLE 1 Mean squares for CQT and CT for 250 common bean genotypes evaluated at Rwebitaba ZARDI for two seasons of 2019B and 2020A in Uganda.

Traits		FS	Clup	App	Col	Vis	WDS	WDC	HC	Slt	CT
SOV	df										
Heritability		0.49	0.48	0.54	0.63	0.54	0.38	0.68	0.47	0.68	0.62
Seas	1	2.33*	0.18	1.41	4.97***	42.51***	328.4	0.04	8.80***	66.45***	2925
Rep	1	0.57	0.26	3.12**	7.89***	9.80**	70	0.23***	0.56*	0.38	62281***
Bl	9	0.8	2.10***	0.89*	0.76**	0.59	2592.5*	0.03*	0.22	1.92***	4542***
Geno	249	1.23**	1.25***	1.18***	0.99***	2.6***	2821**	0.03***	0.21***	1.88***	2498***
Seas:Rep	1	2.33*	0.24	10.42***	4.73***	1.32	6253.4*	0.01	0.49	7.17***	10876***
Seas:Bl	9	1.14*	0.87	0.27	0.43	2.28*	1565.3	0.03	0.13	0.56	722***
Rep:Bl	9	0.49	0.52	0.65	0.62*	1.75	1393.2	0.01	0.06	0.46	1796*
Seas: Geno	242	0.91***	0.85***	0.84***	0.51***	1.99***	2129.1***	0.03***	0.19***	0.97***	1180***
Seas:Rep:Bl	9	0.78	0.62	0.71	0.43	1.24	2332.7	0.03	0.06	0.93*	954
Residuals	448	0.49	0.48	0.40	0.26	0.42	1322.1	0.02	0.14	0.433	799

Abbreviations: Clup, clumping; Col, colour retention; CT, cooking time; FS, free starch; G, genotype; G × S, genotype × season; HC, hydration coefficient; ns, not significant; REP, replication; REP (BLK), blocks nested with replication; S, season; Slt, splitting; Vis, viscosity; SOV, source of variation; He, Heritability App is the appearance; WDC, washed drain coefficient; WDC, washed drain coefficient; WDS, washed drain solids; WDS, washed drain solids.

*Significant at the .05 probability level.

**Significant at the .01 probability level.

***Significant at the .001 probability level.

TABLE 2 Means of the 11 highest and lowest cooking genotypes averaged across two seasons.

Low CT genotypes			High CT genotypes		
Rank	Genotype	CT (min)	Rank	Genotypes	CT (min)
1	SMR 159	51.56	250	BANJA 2	215.88
2	SMR 133	56.35	249	NABE 16	164.41
3	SER 384	56.36	248	VCB 81013	16.08
4	220ALB	58.23	247	RAZ11	159.23
5	234 ALB	58.29	246	Awash 1	159.21
6	SMC 153	58.42	245	UGD.008	158.94
7	SMC 208	58.75	244	MBC 52	158.08
8	G-90	59.38	243	71GERM	155.54
9	138ALB	59.41	242	215ALB	154.61
10	IZO 201543	59.44	241	ADP 522	154.2
11	RAZ42	59.75	240	Narobean7	152.84
	GM	94.09			
	SED	24.3			

in the second season of 2020A with a mean of 96.1. Combined analysis from the two seasons showed cooking time ranging from 51 to 215 min, with a mean of 94.1 min. Table 2 shows the mean performance of the 11 best- and 11 worst-performing genotypes.

3.2 | Genotypic variability for canning quality traits

Canning quality traits that included clumping, splitting, visual appeal, seed coat colour retention, brine clarity (viscosity) and free starch

revealed significant differences among the genotypes for all traits (Table 1). Clumping scores ranged from 1.2 to 4.8, with 207 genotypes scoring 3 and above. Splitting scores ranged from 1.2 to 5, with 151 genotypes attaining average to excellent scores. Scores for visual appeal ranged from 1.4 to 4.6, with 148 genotypes recording scores of 3 and above. Colour retention scores ranged from 2.3 to 4.9, with 241 genotypes obtaining scores that were average to excellent performance. Free starch scores ranged from 1.8 to 4.4, with 207 genotypes performing average to excellent. Viscosity scores ranged from 1.4 to 4.4, with 90 genotypes attaining average to excellent scores. The highest score was 5, so 4 and above was taken to be excellent and 2.5 as average. Total canning scores ranged from 12.39 to 25.24, with 30 being the maximum. Table 3 shows 11 genotypes with the highest and lowest total canning score percentages.

3.3 | Hydration coefficient

A total of 216 genotypes exhibited the required industrial processing hydration coefficient of 1.8 and above (Balasubramanian et al., 2000). Apart from ADP 0521, Kahura, 71 Germ, NUS17 and ADP 430, the remaining 39 genotypes that performed well for canning quality traits recorded the minimum recommended hydration coefficient of 1.8.

3.4 | Washed drained weight and washed drained co-efficient

Highly significant differences were obtained for washed drained solids among the genotypes tested, ranging from 158.9 to 317.8 g, with

TABLE 3 Means of the 11 best and least performing genotypes for canning averaged A cross two seasons.

Best performing genotypes				Least performing genotypes			
Rank	Geno	T.score	%ge	Rank	Geno	T.score	%ge
1	KK8	25.24	84	250	110GERM	12.39	41.3
2	NABE 3	25.15	84	249	ADP 0098	12.56	41.9
3	KAHURA	24.4	81	248	NABE 9 C	12.69	42.3
4	SMR-53	24.32	81	247	SCR 26	13.07	43.6
5	AB136	24.18	81	246	SMR 116	13.37	44.6
6	SER 384	24.02	80	245	NAVY 87	13.62	45.4
7	ADP 0521	23.95	80	244	DRM-6-11-1	13.83	46.1
8	CAL 96	23.92	80	243	MUTIKE	14.01	46.7
9	135GERM	23.74	79	242	IZO 201543	14.09	47
10	RAZ11	23.72	79	241	NABE 13	14.1	47
11	SMR 135	23.6	79	240	94GERM	14.2	47.3

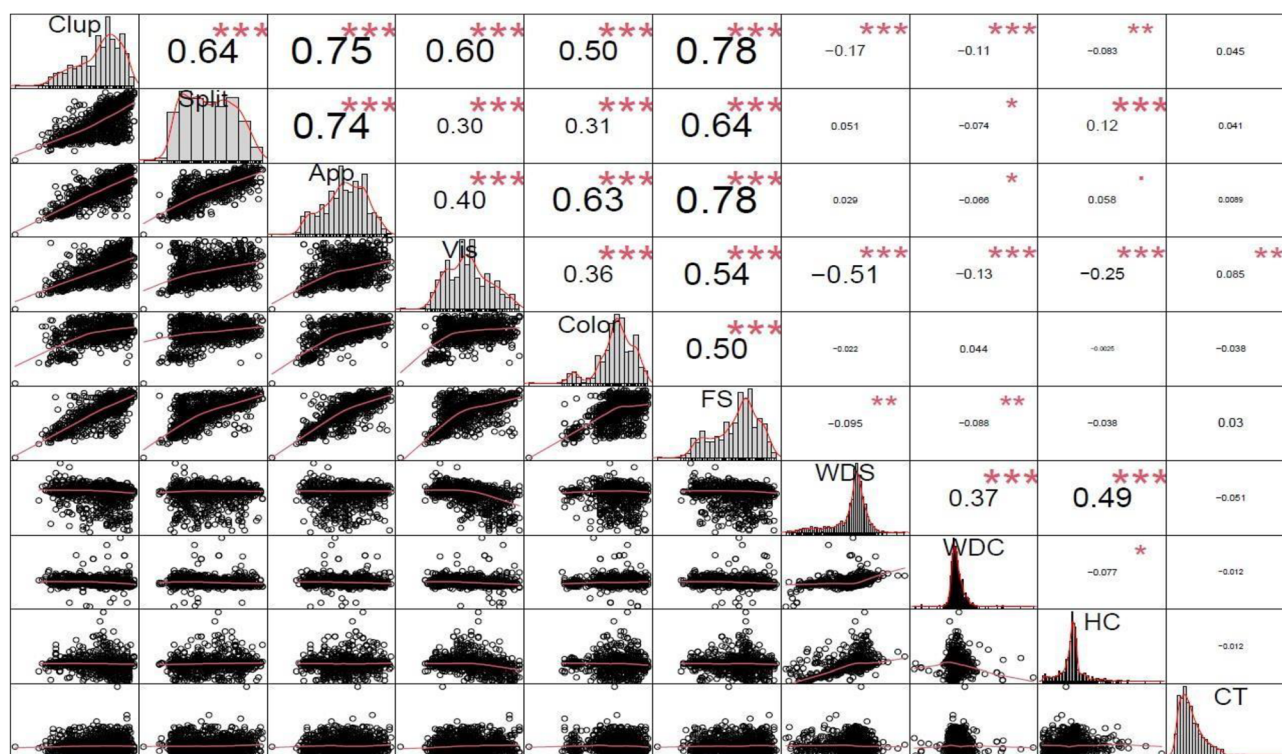


FIGURE 2 Pearson correlation coefficients among mean variables for CT and CQTs among common bean genotypes evaluated at Rwebitaba ZARDI for two seasons of 2019B and 2020A in Uganda. APP, appearance; CLP, clumping; colour, colour retention; CT, cooking time; FS, free starch; HC, hydration coefficient; SPL, splitting; VIS, viscosity; WDC, washed drained coefficient; WDS, washed drained solids. *Significant at the .05 probability level. **Significant at the .01 probability level. ***Significant at the .001 probability level. ns. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13172)]

272 genotypes weighing at least 240 g, which is typical of a sample that is equivalent to 90 g of a dry bean sample (Balasubramanian et al., 2000).

3.5 | Washed drain coefficient

Washed drain coefficient ranged from 1.0 to 1.7, with 33 genotypes recording a ratio of at least 1.4 and above.

3.6 | Phenotypic correlations

The results from phenotypic correlations between cooking time and canning quality parameters are given in Figure 2. According to the results, clumping gave high and significant correlations with splitting, visual appeal, viscosity and free starch (.64***, .75***, .60***, .78***), while its correlation with seed coat colour retention was medium (.50***). The correlation of clumping with cooking time was low, non-significant but positive, while the correlations with water absorption

parameters (HC, WDC and WDS) were negative but highly significant (Figure 2). Splitting had high and highly significant correlations with visual appeal and free starch (.74*** and .64***). Its correlations with viscosity, seed coat colour retention and hydration coefficient were low but highly significant (Figure 2). Visual appeal was highly significantly correlated with seed coat colour retention and free starch (.63***, .78***) and moderately correlated with viscosity. Viscosity gave moderate but highly significant correlations with seed coat colour retention and free starch and very low and negative correlations with water absorption parameters. Seed coat colour retention gave moderate but highly significantly positive correlation with free starch (.50***). Washed drained solids gave moderately highly significant correlations with washed drained coefficient and hydration coefficient (.37*** and .49***).

3.7 | Genetic correlations

Genetic correlations between cooking time and canning quality parameters are shown in Table 4. The data showed differing correlations within and among the various parameters. Clumping showed highly positive and significant correlations with splitting, visual appeal and free starch (.72***, .96***, .99**). The correlations of clumping with viscosity and cooking time were medium but highly significant (.4***, .45***) and negative but highly significant with washed drained solids and washed drained coefficient (−.39***, −.71**). Splitting showed high and significant positive correlations with visual appeal and free starch (.79***, .56***) moderate with hydration coefficient and cooking time (.39*** and .37***). Visual appeal correlated highly significantly with free starch, hydration coefficient and moderate with

seed coat colour retention (.87***, .84*** and .53***) and showed low but significantly positive correlations with viscosity and cooking time (.28**, .33**). Viscosity showed medium to high positive significance in its correlations to colour, free starch and cooking time (.33***, .46***, .64***). The correlations of viscosity with WDS, WDC and HC were low and negative though significant (−1.00***, −.37***, −1.00***). Colour showed high and highly significant genetic correlation (1.00***) with hydration coefficient. Free starch showed high and highly significant correlations with cooking time (.62***) and negative significance in correlation to WDS and WDC (−.39**, −.38). There were a significantly positive correlation of washed drained solids to hydration coefficient and a low and non-significant negative correlation to cooking time. Finally, high and significantly negative correlation was obtained between cooking time and hydration coefficient (−.82***) (Table 4).

3.8 | PCA and clustering

The PCA results revealed 66.6% of the total genetic variation, which was explained by the first two axes of the PCA (Figure S3 and Table 5). The first axis explained 62.3% of the genetic variation, while the second axis explained 4.3% of the total genetic variation. The distribution of the genotypes based on SNP markers and PCA showed moderate diversity among the genotypes based on their origin. The graph revealed two major clusters indicating genotypes grouping into Mesoamerican and Andean gene pools with a few admixtures (Figure 3).

The cluster analysis based on the Euclidean distance matrix, classified the 217 common bean genotypes into two major clusters. The

TABLE 4 Genotypic correlations between cooking time and canning quality parameters.

Traits	Clu	Slt	App	Vis	Col	FS	WDS	WDC	HC
Slt	.72***								
App	.964***	.79***							
Vis	.4***	−.2***	.28***						
Col	.17***	−.08***	.53***	0.33***					
FS	.99**	.56***	.87***	0.46***	0.28***				
WDS	−.39***	.14***	—	—	—	—			
			.06***	1.00***	0.03NS	.39***			
WDC	−.71***	−.4	—	—	0.12NS	—	0.28***		
			.27***	0.37***	—	.38***			
HC	.08NS	.39***	.84***	—	1.00***	—	1.00***	.68***	
				1.00***	—	.01NS			
CT	.45***	.37***	.33***	0.64***	0.02NS	.62***	—	—	—
							0.44***	.11NS	.82***

Note: Total score shows the sum total from visual ratings performed on canned beans for 6 traits using a scale of 1–5 where 1 was the least and 5 highest score, the sum total being 30.

Abbreviations: App 866, appearance; Clu, clumping; col, colour; FS, free starch; HC, hydration coefficient; ns, nonsignificant; Slt, splitting; TS, total score; Vis, viscosity; WDC, washed drained coefficient; WDS, washed drained solids.

*Significance at 0.05.

**Significance at 0.01.

***Significance at 0.001.

first cluster consisted of two sub-clusters, the first having 19 genotypes, while the second had 79. This group/cluster consisted of genotypes mainly from the Andean gene pool. The first sub-cluster in the second main cluster consisted of the smallest number of individuals (9), while the second sub-division had the highest number of individuals (110). This cluster mainly consisted of genotypes from the Mesoamerican gene pool (Figure 4).

3.9 | Genome-wide association analysis

A total of 47 associations between all the traits tested were identified as being significant across the 11 chromosomes (Table 6). Figures 5 and 6 display the Manhattan plots that show a rectangular representation of the thousands of values across the genome by chromosome for the studied traits and QQ plots, which show the quantile distribution of $-\log_{10}$ of the observed p -values on the Y-axis versus the quantile distribution of the $-\log_{10}$ of expected p -values on the x-axis. The blue shaded areas in the QQ plots indicate the 95% confidence interval under the null hypothesis, while the blue dots are the observed SNPs. The dots in Manhattan plots above the threshold lines indicate the significant markers. A shows Manhattan and QQ plots for cooking time, B for hydration coefficient, C for general appearance of canned beans, D seed coat colour retention, E clumping and F splitting, while in Figure 6, G is for free starch, H for viscosity, I for washed drain solids and J for washed drained coefficient.

TABLE 5 First 20 principal components of 217 genotypes based on DArTseq markers.

PC	Eigenvalue	Proportion of total	Cumulative proportion
1	1095.29701	.62254	.62254
2	75.19397	.04274	.66528
3	40.00086	.02274	.68801
4	37.5154	.02132	.70933
5	25.6679	.01459	.72392
6	20.30879	.01154	.73547
7	16.95231	.00964	.7451
8	16.66759	.00947	.75457
9	12.71614	.00723	.7618
10	11.70629	.00665	.76846
11	10.5648	.006	.77446
12	9.80499	.00557	.78003
13	9.44193	.00537	.7854
14	8.61132	.00489	.79029
15	8.35343	.00475	.79504
16	8.05103	.00458	.79962
17	7.67161	.00436	.80398
18	7.20494	.0041	.80807
19	6.58504	.00374	.81182
20	6.36185	.00362	.81543

3.10 | Candidate gene identification

Following the criteria described in the methodology for candidate gene identification, different putative genes were identified.

3.11 | Cooking time

This study identified protein families associated with cooking time: calcium-dependent protein kinase 29 (0.054 Mbs), LYR family of Fe/S cluster biogenesis protein (0.045 Mbs), RING/U-box superfamily protein (0.024 Mbs), PAM domain (PCI/PINT-associated module protein) (0.014 Mbs), expansion 11 (0.0085 Mbs), Peroxidase superfamily protein (0.0044 Mbs) downstream and cinnamyl alcohol dehydrogenase 9 (0.0057 Mbs), winged-helix DNA-binding transcription factor family protein (0.012 Mbs) upstream of marker 8197930-29-C/T on position 220257 on chromosome 1. Plastid movement impaired1 (0.046 Mbs), Kunitz trypsin inhibitor 1 (0.039 Mbs), Kunitz family trypsin and protease inhibitor protein (0.018 Mbs) on position 42699013 upstream of marker 3380308-18-C/T located on position 42699013 on chromosome 4. Tetratricopeptide repeat (TPR)-like superfamily protein (0.013 Mbs), Pentatricopeptide repeat (PPR) superfamily protein (0.0059 Mbs) upstream of marker 8214410-24-G/T on chromosome 5. Alpha/beta-Hydrolases superfamily protein (0.012 Mbs) downstream and Hyaluronan/mRNA binding family protein (0.034 Mbs), RAS 5 (0.041 Mbs) upstream of marker 100067613-41-T/A on chromosome 11 on position 4098223.

3.12 | Splitting

The study identified gene proteins associated with the splitting of canned beans; polynucleotidyl transferase, ribonuclease H-like superfamily protein (0.035 Mbs), glycerol-3-phosphate acyltransferase 9 (0.013 Mbs) downstream of marker 3381147-50-T/G on position 35636714 on chromosome 2. Alpha/beta-hydrolase superfamily protein (0.0046 Mbs), bromo-adjacent homology (BAH) domain-containing protein (0.0071 Mbs), transducin/WD40 repeat-like superfamily protein (0.023 Mbs), HCO3-transporter family (0.039 Mbs) near marker 3371346-13-C/A on position 39993624 on chromosome 5. NAD (P)-binding Rossmann-fold superfamily protein (0.023 Mbs), WRKY DNA-binding protein 33 (0.018 Mbs), UDP-glycosyltransferase 73B4 (0.0093 Mbs), UDP-glucosyl transferase 73B5 (0.006 Mbs), UDP-glucosyl transferase 73B3 (0.0014 Mbs) from marker 16652736-57-A/G on chromosome 8. Cleavage and polyadenylation specificity factor 73 kDa subunit-II (0.0189 Mbs), Zinc finger C3HC4 type (RING finger) family protein (0.047 Mbs) on chromosome 3 from marker 8215692-14-A/C on position 1768057.

3.13 | Clumping

Ankyrin repeat family protein (0.045 Mbs), zinc ion binding; DNA binding (0.021 Mbs), MYB domain protein 15 (0.021 Mbs), threonine

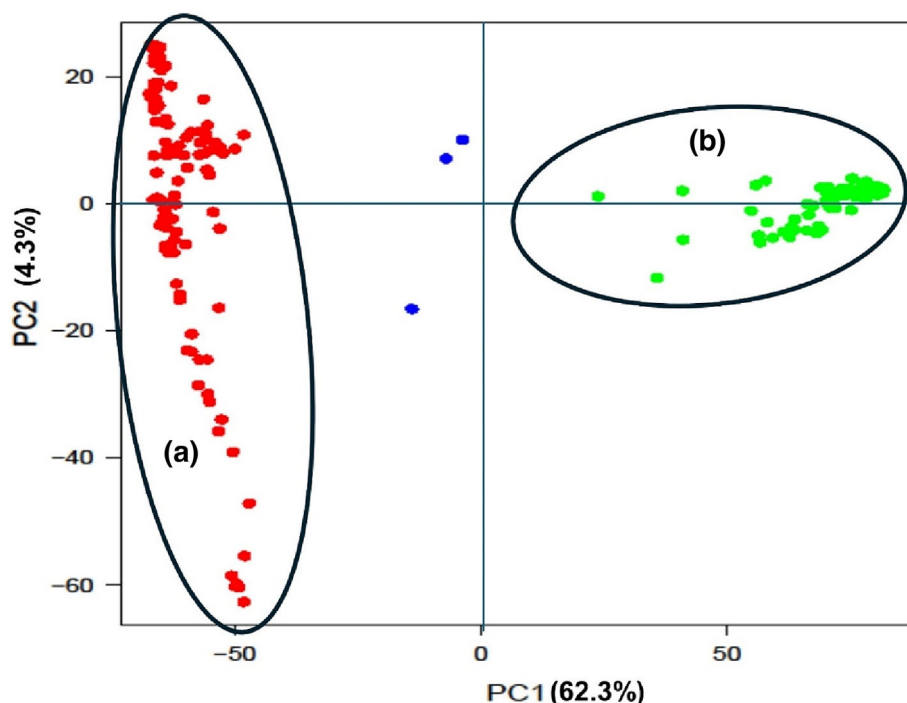


FIGURE 3 Principal component analysis for 217 genotypes used in the study. [Color figure can be viewed at wileyonlinelibrary.com]

aldolase 1(0.012Mbs), calcium-binding EF-hand family protein (0.055 Mbs) upstream of marker 3379517-59-A/T at position 21465564 on chromosome 6.

3.14 | Hydration coefficient

Putative gene proteins associated with hydration coefficient included CYCLIN D4;1 (0.024 Mbs) and phosphofructokinase 5 (0.037 Mbs) upstream of marker 100046828-37-C/T on position 29985761 on chromosome 2 and F-box and associated interaction domains-containing protein (0.025 Mbs) upstream of marker 3377243-6-T/G on position 14349477 on chromosome 3.

3.15 | Free starch

Gene proteins associated with free starch included calmodulin-binding receptor-like cytoplasmic kinase 3 (0.018 Mbs), voltage-gated chloride channel family protein (0.013 Mbs), calcium-dependent lipid-binding (CaLB domain) family protein (0.012 Mbs) upstream of marker 3381325-64-T/A on position 39242152 on chromosome 3. Heptahelical protein 4 (0.0025 Mbs) upstream, endoplasmic reticulum-type calcium-transporting ATPase 3 (0.015 Mbs), serine carboxypeptidase-like 19 (0.043 Mbs) downstream of marker 3380001-48-A/G on position 12473537 on chromosome 9. Glycosyl hydrolase 9B18 (0.054 Mbs), GATA transcription factor 7 (0.038 Mbs), chalcone and stilbene synthase family protein (0.02 Mbs), exportin 1A (0.020 Mbs), subtilase family protein (0.013 Mbs), SH3 domain-containing protein (0.012 Mbs), squalene synthase 1(0.007 Mbs) upstream, MATE efflux family protein (0.008 Mbs), terminal EAR1-like 1 (28.95 Mbs), xylulose kinase-1

(0.041 Mbs) downstream of marker 3373103-6-A/G on position 3636660 on chromosome 11.

3.16 | Viscosity

Gene proteins that were identified for viscosity included receptor kinase 3 (0.040 Mbs), S-locus lectin protein kinase family protein (0.006 Mbs), upstream, calcium-binding E F-hand family protein (0.011 Mbs), NADH dehydrogenase 5A (0.043 Mbs) downstream of marker 3377726-42-C/T on position 26029285 on chromosome 7. CRINKLY4 related 1(0.014 Mbs) upstream of marker 3380996-25-T/C on position 34334689 on chromosome 7. Transducin/WD40 repeat-like superfamily protein (0.050 Mbs), O-fucosyltransferase family protein (0.024 Mbs), pentatricopeptide repeat (PPR-like) superfamily protein (17 Mbs) upstream, Zn-dependent exopeptidases superfamily protein (0.021 Mbs), starch branching enzyme 2.2 (0.030 Mbs) downstream of marker 3366305-54-C/A on position 1846051 on chromosome 9. Ethylene responsive element binding factor 4(0.044 Mbs), Yippee family putative zinc-binding protein (0.024 Mbs) upstream and Ankyrin repeat family protein (0.026 Mbs) downstream of marker 8211994-35-A/T on position 46189666 on chromosome 11.

Possible candidate genes for seed coat colour retention, visual appeal, washed drain weight and washed drained coefficient are summarized in Table 7.

3.17 | SNP allele contribution to cooking time reduction and good canning quality traits

Two SNPs were considered per trait, that is, for cooking time and each canning quality trait. For cooking time, the SNPs on

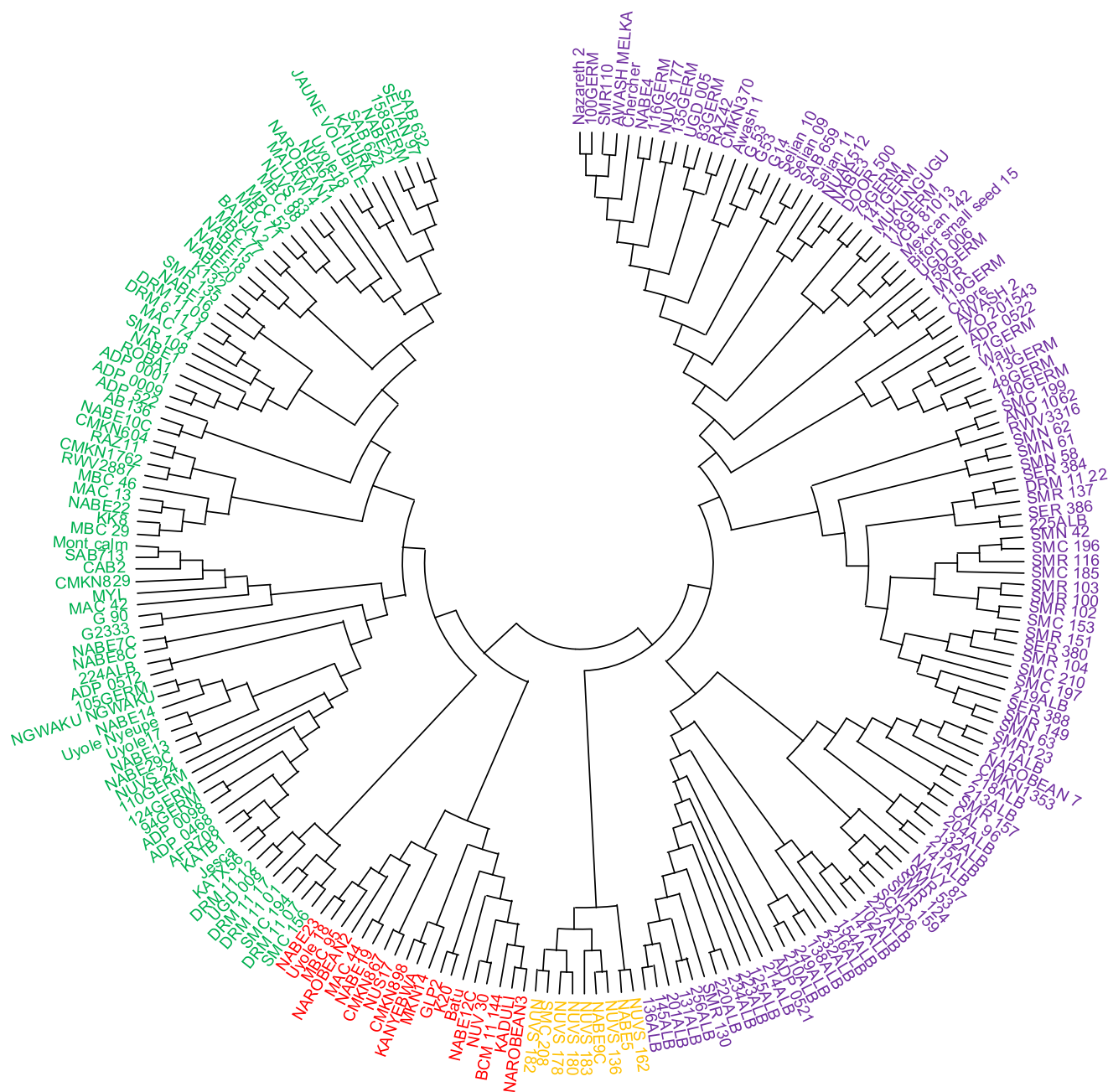


FIGURE 4 Clustering of 217 genotypes used in the study. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13172)]

chromosomes 1 and 2 were considered. Further dissection of the two SNPs revealed that accessions with the favourable allele CC and AA for markers 819730-29-CT on chromosome 1 and 3378984-64-AG on chromosome 2, respectively, had more genotypes with low cooking times (Figure 7a,b). Marker 8214903.10-CT for clumping, the unfavourable allele TT, contributed significantly to higher scores, while with SNP 3371448-36-TC, it is the favourable allele TT that contributed to high scores (Figure 7c,d). SNP marker 3384089-68-C/A, for free starch, the favourable allele CC, significantly contributed to high scores of 3 and above, while for marker 3380001-48-AG, it is the unfavourable allele GG that contributed to high scores (Figure 7e,f). Marker X100046828.37 CT and X3377243.6 TG, for

hydration coefficient, both the favourable and unfavourable alleles, had almost the same means though for X100046828.37CT, the favourable allele, had more genotypes, and for marker X3377243.6TG, it was the unfavourable allele that had more (Figure 8g,h). Marker 100045471-42-T/A for washed drained solids, the heterozygote TA, had accessions with more high values though few. For SNP marker 8212753-63-G/A, still the heterozygote GA gave high values, with the favourable allele GG, performing slightly better than the unfavourable allele AA, though AA had more accessions (Figure 8i,j). For marker X3378758.35T/A for washed drained coefficient, allele mean performance was almost similar, but most genotypes again had the favourable allele, while for marker

TABLE 6 Chromosome (CHR), SNP marker, position, allele, effects and *p*-values for CT and CQT traits with 11,094 SNP markers measured on 217 common bean genotypes evaluated at Rwebitaba ZARDI for two seasons of 2019B and 2020A in Uganda.

Trait	CHR	SNP marker	Position (bp)	Position (Mb)	Allele	Effect	<i>p</i> -value
Cooking time (CT)	Pv01	8197930-29-C/T	220257	0.22	C/T	16.84	1.50×10^{-11}
	Pv02	3378984-64-A/G	47065562	47.07	A/G	14.27	3.95×10^{-08}
	Pv04	3380308-18-C/T	42699013	42.7	C/T	9.97	1.41×10^{-10}
	Pv05	8214410-24-G/T	6894731	6.89	G/T	-8.28	2.46×10^{-06}
	Pv11	10006761341-T/A	4098223	4.10	T/A	12.63	5.08×10^{-07}
	Pv11	3378635-13-T/A	13255190	13.26	T/A	-14.8	1.01×10^{-07}
Splitting (SPL)	Pv02	3381147-50-T/G	35636714	35.64	T/G	0.34	1.18×10^{-06}
	Pv03	8215692-14-A/C	1768057	1.77	A/C	-0.30	1.44×10^{-06}
	Pv05	3382955-62-T/C	35563055	35.56	T/C	-0.13	3.43×10^{-06}
	Pv05	3371346-13-C/A	39993624	39.99	C/A	-0.12	1.02×10^{-06}
	Pv08	16652736-57-A/G	9096595	9.10	A/G	0.58	1.14×10^{-09}
Appearance (APP)	Pv07	3380009-30-C/A	40002118	40.00	C/A	-0.08	7.06×10^{-09}
	Pv08	3375092-60-A/T	19877614	19.88	A/T	-0.06	7.14×10^{-07}
Hydration coefficient (HC)	Pv02	10004682837-C/T	29985761	29.99	C/T	0.01	4.61×10^{-07}
	Pv03	3377243-6-T/G	14349477	14.35	T/G	-0.01	4.16×10^{-06}
Free starch (FS)	Pv03	3381325-64-T/A	39242152	39.24	T/A	-0.06	3.62×10^{-07}
	Pv09	3380001-48-A/G	12473537	12.47	A/G	-0.14	2.78×10^{-07}
	Pv10	3384089-68-C/A	38009682	38.01	C/A	-0.08	1.81×10^{-07}
	Pv11	33731036-A/G	3636660	3.64	A/G	0.07	8.46×10^{-07}
Colour retention (CRT)	Pv05	3371324-22-T/A	38895075	38.91	T/A	-0.26	1.36×10^{-06}
	Pv07	3380009-30-C/A	40002118	40.00	C/A	-0.13	6.66×10^{-13}
	Pv10	3374054-31-T/C	3927915	3.93	T/C	0.13	1.55×10^{-08}
Clumping (CLP)	Pv06	3379517-59-A/T	21465564	21.47	A/T	-0.46	5.25×10^{-07}
	Pv08	3377655-36-A/T	5445838	5.45	A/T	-0.43	2.05×10^{-06}
	Pv08	3380216-67-C/T	49367321	49.37	C/T	0.42	7.86×10^{-07}
	Pv09	3370112-61-T/C	30956309	30.96	T/C	-1.27	4.39×10^{-07}
	Pv09	8214903-10-C/T	35444094	35.44	C/T	0.49	1.33×10^{-09}
	Pv10	3371448-36-T/C	2421470	2.42	T/C	-0.98	5.74×10^{-11}
	Pv11	3380017-63-A/G	11508668	11.51	A/G	-0.52	1.06×10^{-07}
Viscosity (VIS)	Pv02	3373587-14-C/A	716712	0.72	C/A	0.08	1.49×10^{-11}
	Pv05	3377726-42-C/T	26029285	26.03	C/T	0.10	2.03×10^{-09}
	Pv05	338347323-T/C	40,060,914	40.06	T/C	-0.05	1.01×10^{-07}
	Pv07	3380996-25-T/C	34,334,689	34.33	T/C	-0.08	3.16×10^{-10}
	Pv09	3366305-54-C/A	1846051	1.85	C/A	0.13	1.21×10^{-09}
	Pv11	8211994-35-A/T	46189666	46.19	A/T	-0.05	2.03×10^{-10}
Washed drained solids (WDS)	Pv02	100045471-42-T/A	2860645	2.86	T/A	-7.84	9.14×10^{-11}
	Pv02	3381813-54-T/C	45802683	45.8	T/C	2.5	3.27×10^{-06}
	Pv03	3377056-35-G/A	44809022	44.81	G/A	4.7	3.68×10^{-06}
	Pv04	3377113-44-C/T	528752	0.53	C/T	6.91	3.92×10^{-07}
	Pv10	8212753-63-G/A	4758010	4.76	G/A	3.54	3.22×10^{-09}
	Pv11	8208249-10-G/A	1845255	1.85	G/A	-4.81	1.81×10^{-08}
Washed drained coefficient (WDC)	Pv01	3372952-8-G/A	1297032	1.3	G/A	0.02	2.12×10^{-07}
	Pv02	3378758-35-T/A	33343706	33.34	T/A	0.01	1.15×10^{-07}
	Pv02	16653066-62-A/G	44451311	44.45	A/G	-0.01	3.94×10^{-06}
	Pv04	336623352-C/G	3442	0.0003	C/G	0.02	2.88×10^{-10}
	Pv08	8208893-55-G/A	1134429	1.13	G/A	0.02	3.98×10^{-10}
	Pv09	100048109-39-C/A	26228908	26.23	C/A	-0.02	8.55×10^{-07}

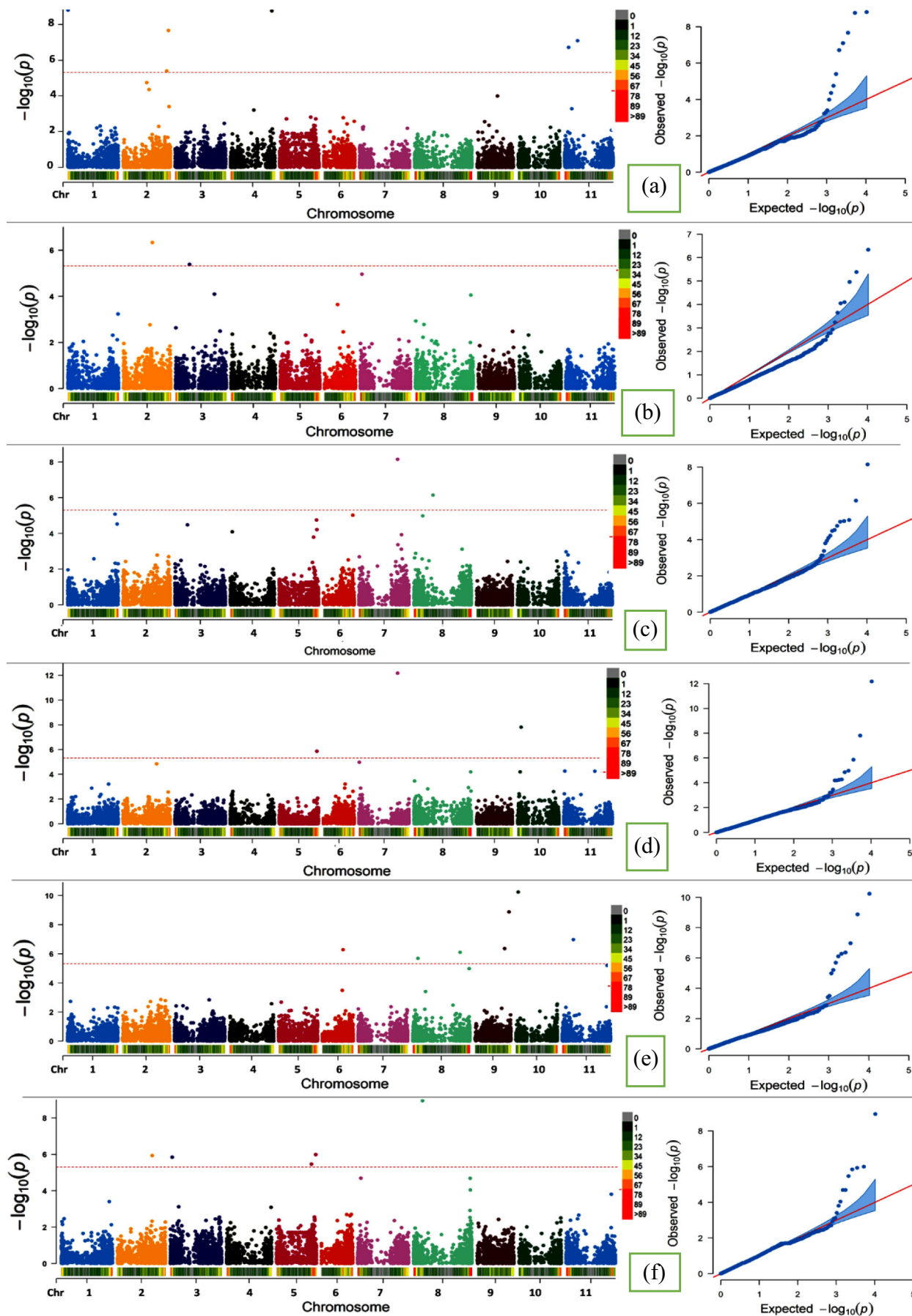


FIGURE 5 Manhattan plots showing significant single nucleotide polymorphisms (SNPs) and their p -values from genome-wide association study using FarmCPU model for (a) cooking time (CT) on Pv01, Pv02, Pv04, Pv05 and Pv11; (b) hydration coefficient (HC) on Pv02 and Pv03; (c) appearance (APP) on Pv07 and Pv08; (d) colour retention (CRT) on Pv05, Pv07 and Pv10; (e) clumping (CLP) on Pv06, Pv08, Pv09, Pv10 and Pv11; (f) splitting (SPL) on Pv02, Pv03, Pv05 and Pv08; red line is the significance threshold of $P = 1.03 \times 10^{-5}$ after Bonferroni correction of $\alpha = .05$. [Color figure can be viewed at wileyonlinelibrary.com]

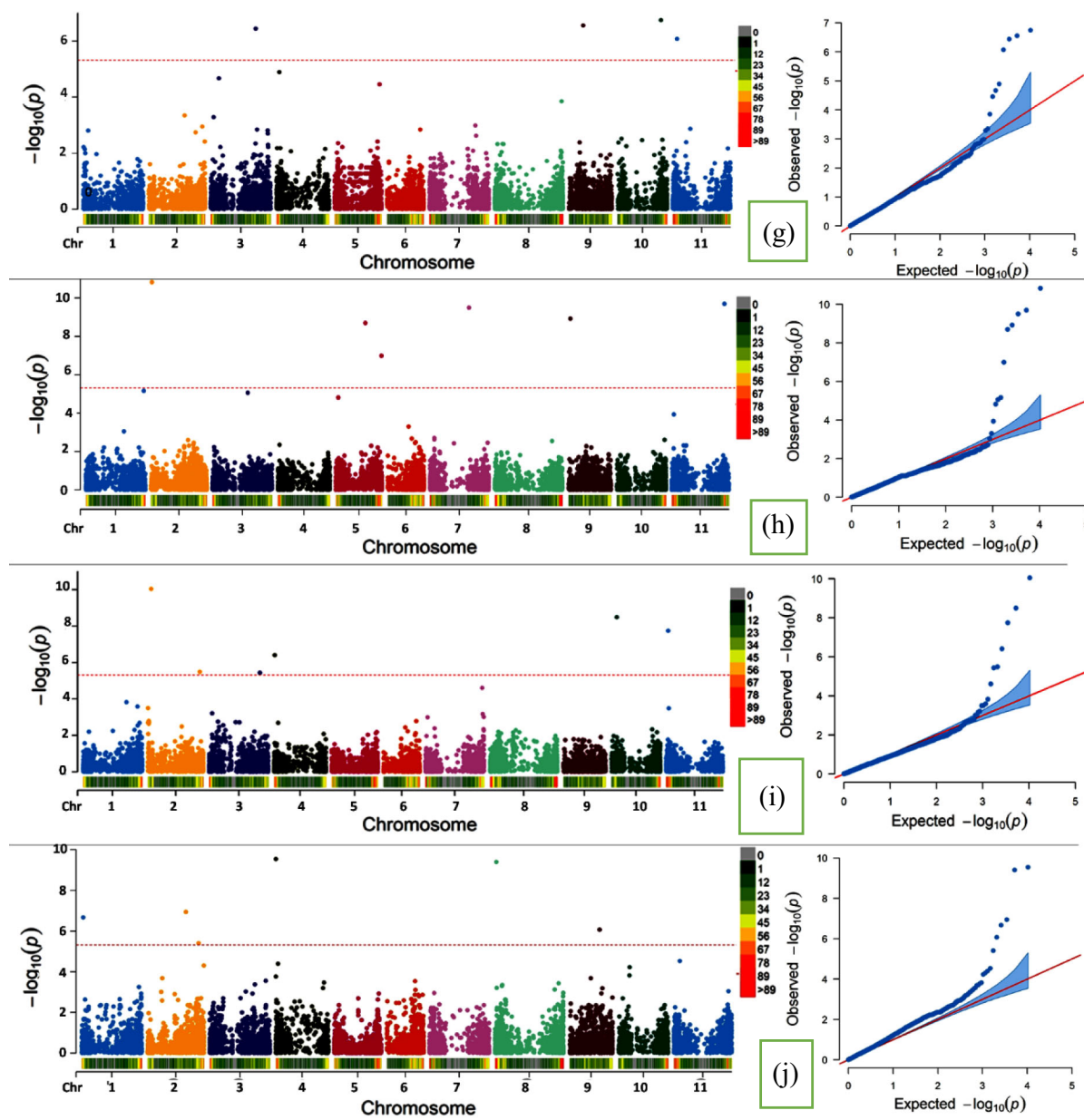
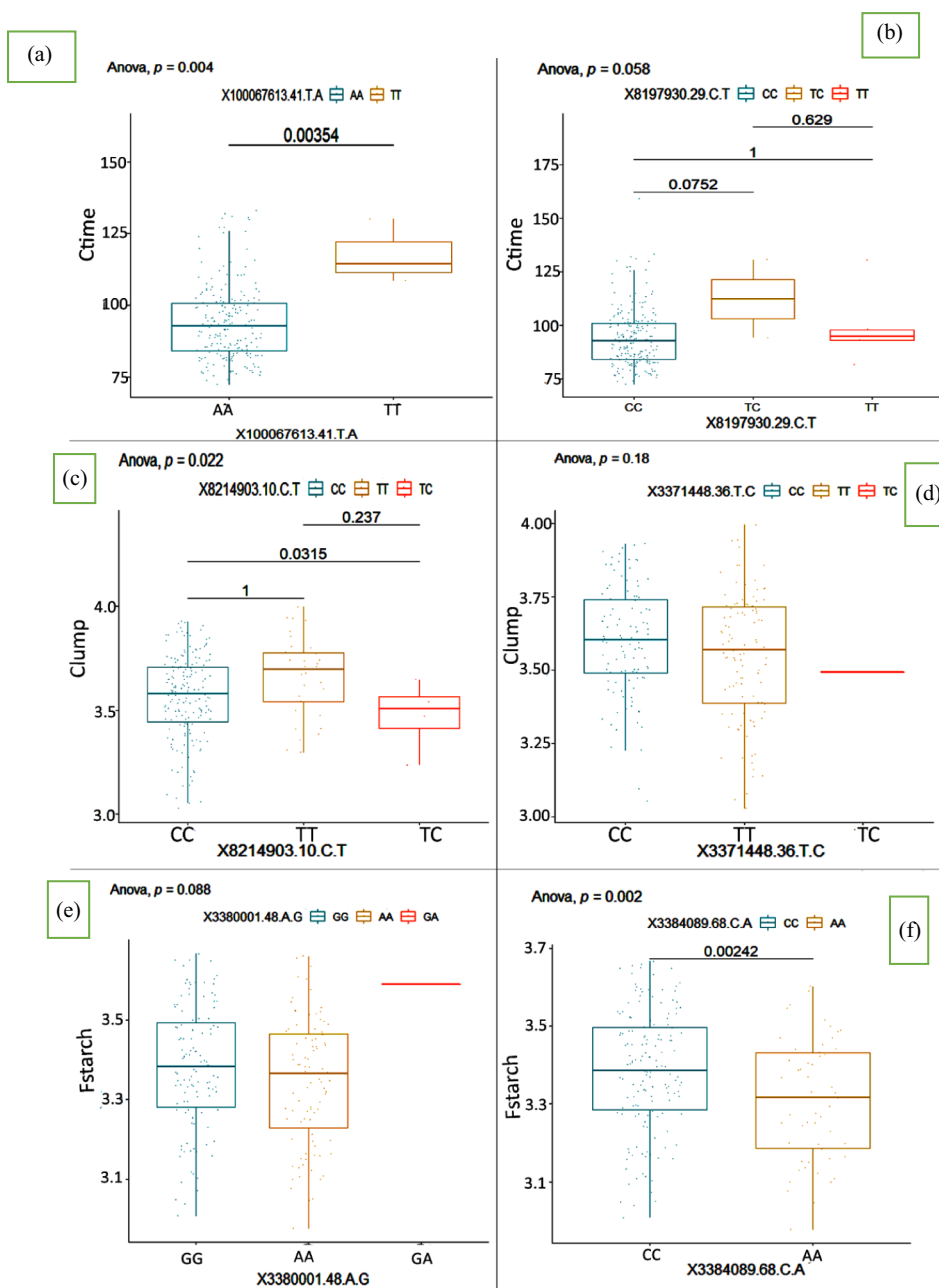


FIGURE 6 Manhattan plots showing significant single nucleotide polymorphisms (SNPs) and their p -values from genome-wide association study using FarmCPU model for (g) free starch (FS) on Pv03, Pv09, Pv10 and Pv11; (h) viscosity (VIS) on Pv02, Pv05, Pv07, Pv09, and Pv11; i, washed drained solids (WDS), on Pv02, Pv03, Pv04, Pv10 and Pv11; (j) washed drained coefficient (WDC) on Pv01, Pv02, Pv04, Pv08 and Pv09. The red line is the significance threshold of $P = 1.03 \times 10^{-5}$ after Bonferroni correction of $\alpha = .05$. [Color figure can be viewed at wileyonlinelibrary.com]

X8208893 GA, genotypes with at least a copy of the unfavourable allele had high washed drained coefficient scores (Figure 8k,l). Both SNPs for viscosity, the unfavourable alleles, contributed slightly higher than the favourable allele to giving high viscosity scores (Figure 9m,n). With SNP 821560092-74-A/C for splitting on chromosome 3, the

favourable allele AA contributed more to the accessions with higher scores, while for marker 16652736-57-A/G on chromosome 8, it is the unfavourable allele GG together with the heterozygote that contributed to accessions with higher scores (Figure 9o,p). For appearance, marker X3375092.60.AT, the heterozygous allele had slightly

FIGURE 7 Allele trait contribution for cooking time, clumping and free starch. Boxplots showing the effect of significant markers associated with hydration coefficient on chromosomes 2 and 3 (g,h), washed drained solids on chromosome 2 and 10 (i,j) and washed drained coefficient on chromosome 2 and 8 (k,l). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13172)]



higher means though most genotypes had the unfavourable allele. For marker X3380009.30 CA, the favourable allele gave more genotypes and with slightly higher means (Figure 9q,r).

Boxplots showing the effect of significant markers associated with cooking time (CT) on chromosomes 1 and 2 (a,b), clumping on chromosomes 9 and 11 (c,d) and free starch on chromosomes 9 and 10. The letters on the x-axis represent allele variants (A, C, G and T).

4 | DISCUSSION

4.1 | Cooking time

Bean consumers worldwide, especially those in developing countries, are generally concerned about cooking time because it increases fuel

consumption, yet besides being an environmental burden, the use of fuel wood, which is the primary fuel source for most families, is becoming increasingly scarce and unaffordable and exposes cooks especially women and children to smoke-related health hazards (Maryanna et al., 2010). In most studies, cooking time has been assessed within the first month of harvesting, which disregards the fact that beans are typically consumed 3–5 months after harvesting. Factors influencing the time required for cooking beans vary with the variety, their growing environment, cooking method used, the quantity used, condition and length of grain storage (Arruda et al., 2012). Cooking time of common beans increases with storage duration, and freshly harvested beans have been shown to cook two to four times faster than beans stored for 6 months (Coelho et al., 2007). Rousseau et al. (2020) reported that common beans stored under optimum conditions (35°C and 80% RH) for 8 weeks required significantly longer

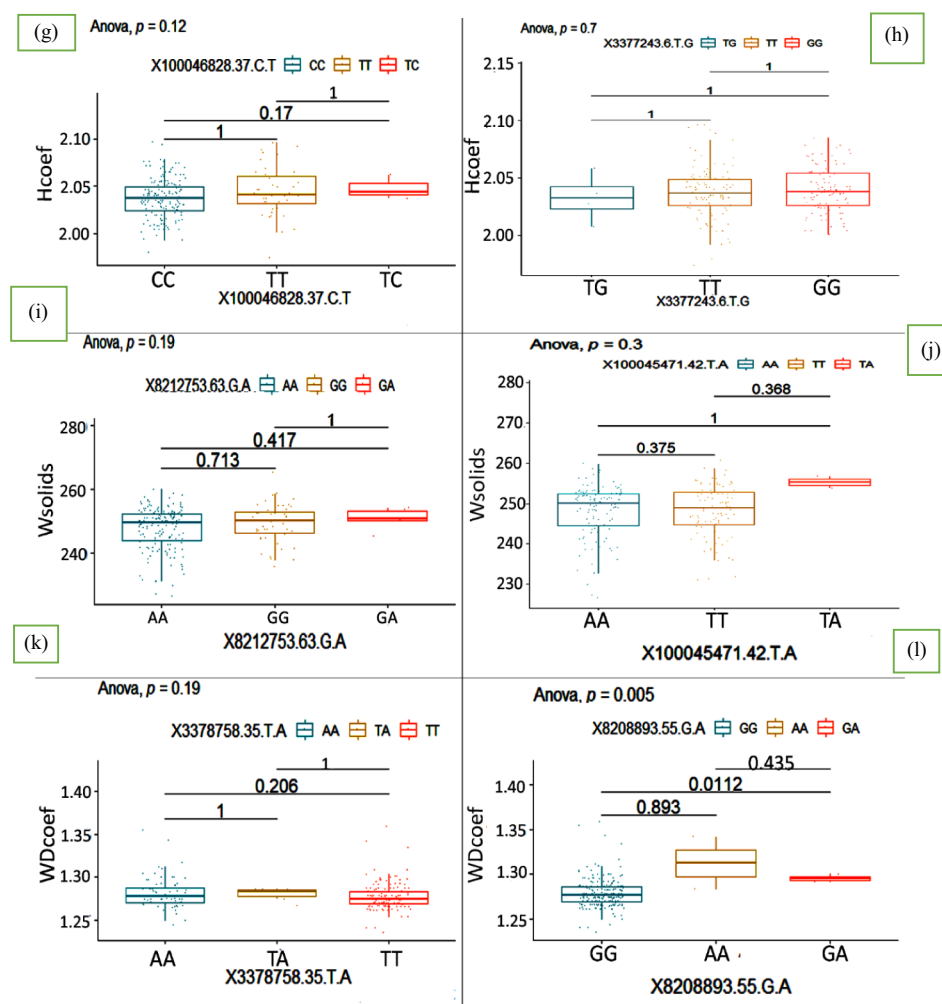


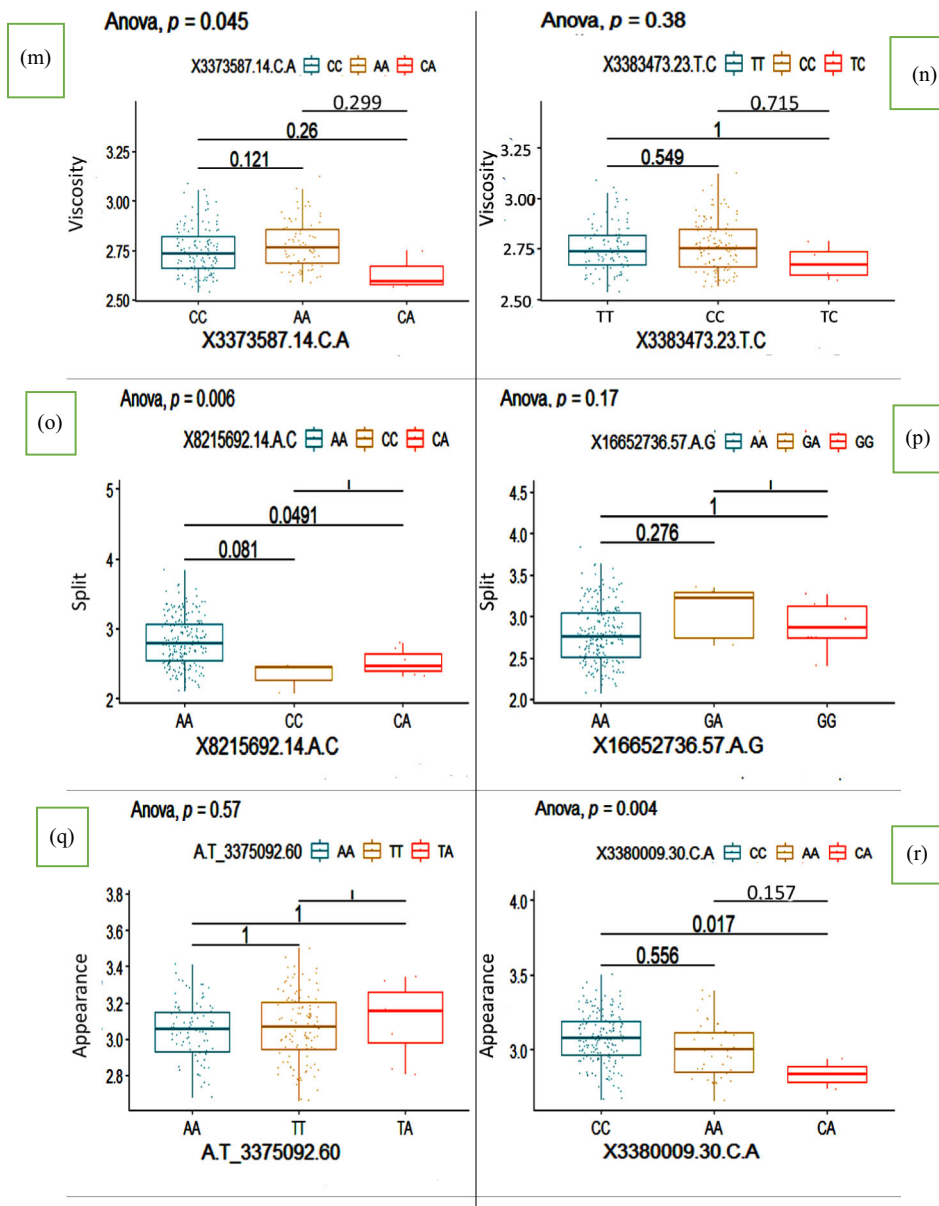
FIGURE 8 Allele trait contribution to hydration coefficient, washed drained solids and washed drained coefficient. Boxplots showing the effect of significant markers associated with viscosity on chromosomes 2 and 5 (m,n), splitting on chromosomes 3 and 8 (o,p) and appearance on chromosomes 7 and 8 (r,s). [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com/doi/10.1111/pbr.13172)]

cooking times than those freshly harvested. Beans that cook in 1 h can cook 2–3 h as they age (Hernández-Unzón & Ortega-Delgado, 1989), a phenomenon often referred to as ‘hard to cook’. Therefore, the current study used a Mattson pin-drop cooker to measure the cooking time of beans stored for 3 months. Evaluating the cooking time at this point after harvest targets those regions where beans are planted once or twice a year and thus consumed for approximately 5 months or more after harvest before the next season's fresh beans are ready.

The combined analysis across two seasons revealed highly significant differences for cooking time among the 250 genotypes tested (Table 1). These estimations were slightly higher than those obtained from previous studies conducted in Uganda, Tanzania and Kenya, in which the genotypes were evaluated within a month after harvesting. In Katuuramu et al.'s (2018) test of 18 genotypes, the cooking time ranged from 25 to 97 min. Mukai, 2017 evaluated 152 bean genotypes and cooking time ranged from 42 to 104 min, Syombua Syanda (2019) evaluated 11 bean genotypes and cooking time ranged from 28 to 81 min, while Amongi et al., 2021 reported 29–89 for small seeded white and 34–65 min for large seeded white. High cooking time values obtained in this current study for some varieties and lines such as kanyebwa, Nabe 3, Nabe 15, Nabe

16, Nabe 19, Masindi yellow short, KATB1 and KATB9 are in agreement with the high values obtained by Mukai (2017), though some varieties such as Nabe 4, Nabe 12C, Roba 1, CAB2, Awash melka and Awash 1, which were reported by Mukai (2017) and Amongi et al. (2021) to be short cooking within few weeks after harvesting, gave high cooking time in the current study. However, two genotypes, Nabe 6 and SAB713 that cooked in a short time after harvesting, still maintained an average cooking time of slightly higher than 60 min even when tested 3 months after harvesting. Storage time and conditions impact cooking time through changes in phytic acid content, enzyme activity, seed coat permeability, pectin solubility, cell wall content and thickness, oxidation of phenolic compounds and membrane deterioration (Daher & Braybrook, 2015; Shiga et al., 2009). These genotypes could be tested further for possible utilization by farmers who store beans for about 6 months before the next new harvest. Genotypes SMR 159, SMR 133, SER 384, 220ALB, 234 ALB, SMC 153, SMC 208, G-90, 138ALB, IZO 201543 and RAZ42, cooked in less than an hour and thus could be utilized by farmers who entirely depend on their bean farm, produce and have to consume these beans for a long period of about 5 months since they exhibited averagely shorter cooking times when tested 3 months after harvesting. Processors can store the beans

FIGURE 9 Allele contribution to the mean performance of viscosity, splitting and general appearance of the canned beans. [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]



from these lines and utilize until the new season's harvest without spending a lot of fuel and time in processing and/or importation costs. Most of the lines that cooked fast are small-seeded, a trait that is not desired by most Ugandan consumers; these lines can be utilized by breeders to improve the long cooking bean varieties but have other consumer desirable traits. There were negative phenotypic and genotypic correlations between water absorption capacity measured by the hydration coefficient and the other water absorption traits: HC (−.01 and −.82***), WDS (−.41* and −.44***) and WDC (−.01 and −.11***), respectively, with cooking time. Several studies have indicated an inverse relationship between cooking time and water absorption as with the current study (Bassett et al., 2020; Bellido et al., 2006; Chigwedere et al., 2019; Cichy et al., 2015). The negative correlations suggest that fast-cooking beans absorbed more water than slow-cooking ones; thus, water absorption should be a useful predictor of cooking time in beans.

4.2 | Canning

Though good quality traits for canning beans are desired by consumers, processors and plant breeders, preferences vary from one end-user to another. While consumers are mostly concerned about the texture and overall visual appeal of the processed bean (Alemu, 2018; Khanal et al., 2015; Wassimi et al., 1990), processors seek out for beans that absorb more water, expand rapidly and uniformly during soaking and blanching, can cook quickly and have a high hydration coefficient and washed drained weight. A high hydration coefficient is important to processors as good water absorption by a bean variety potentially increases the number of cans obtained from a unit of dry bean seeds and thus increases the bean variety's economic return for the processor. Another trait with economic significance is the percent washed drained solids, which refers to the mass of the processed beans after being rinsed and drained (Hosfield et al., 1984; Hosfield &

TABLE 7 Positional candidate genes near most significant marker for colour retention (CRT), washed drain weight (WDS) and washed drained coefficient (WDC).

Trait	SNP and position	Chromosome	Candidate gene	Distance from SNP (Mb)	Gene annotation
Colour retention (CRT)	3380009-30-C/A (400002118)	Pv07	Phvul.007G280300.1	0.032 Mb downstream	Encodes AUX/IAA transcriptional regulatory family protein
	3380009-30-C/A		Phvul.007G280100.1	0.04 Mb downstream	NAD(P)H dehydrogenase 18
	3380009-30-C/A		Phvul.007G280700.2	0.05 Mb downstream	Basic helix-loop-helix (bHLH) DNA-binding superfamily protein
	3371324-22-T/A (38895075)	Pv05	Phvul.005G161200.1	0.04 Mb upstream	DOF zinc finger protein 1
Washed drain coefficient (WDC)	8208893-55-G/A (1134429)	Pv08	Phvul.008G013200.1	0.049 Mb down stream	Delta (3), delta(2)-enoyl CoA isomerase 1
	8208893-55-G/A		Phvul.008G013300.1	0.041 Mb down steam	Subtilase family protein
	8208893-55-G/A		Phvul.008G013400.1	0.029 Mb downstream	Phospholipase D beta 1
	8208893-55-G/A		Phvul.008G013800.1	0.014 Mb downstream	Homolog of X-ray repair cross complementing 3 (XRCC3)
	8208893-55-G/A		Phvul.008G013900.1	0.017 Mb upstream	Pentatricopeptide repeat (PPR) superfamily protein
	8208893-55-G/A		Phvul.008G014000.1	0.022 Mb upstream	WUSCHEL-related homeobox
	8208893-55-G/A		Phvul.008G014200.1	0.027 Mb upstream	Mitochondrial editing factor
	8208893-55-G/A		Phvul.008G014300.1	0.037Mbs	Ras-related small GTP-binding family protein
Washed drain solids (WDS)	8208893-55-G/A		Phvul.008G014400.1	0.046 Mbs	2-Oxoglutarate dehydrogenase, E1 component
	100045471-42-T/A (2860645)	Pv02	Phvul.002G026800.2	0.049 Mb downstream	Brassinosteroid signalling positive regulator (BZR1) family protein
	100045471-42-T/A		Phvul.002G026900.1	0.039 Mb downstream	UDP-glucosyltransferase 72E1
	100045471-42-T/A		Phvul.002G027000.1	0.026 Mb downstream	Aminopeptidase P1
	100045471-42-T/A		Phvul.002G027100.1	0.022 Mb upstream	Quinone reductase family protein
	100045471-42-T/A		Phvul.002G027200.1	0.008 Mb upstream	Homeobox protein 40

Uebersax, 1980). The hydration coefficient of 1.8 and above is considered optimum, as is a washed-drained solids weight of 240–280 g for 90 g of initial solids, according to the MSU's protocol. Other physical characteristics assessed during processing are visual appeal, grain size, splitting, clumping and colour of the drained grains and brine (Merwe et al., 2006; White & Howard, 2013). In this study, 216 genotypes obtained the optimum hydration coefficient of above 1.8, implying that they are capable of absorbing enough water and expanding to produce more can yield during processing. One hundred seventy-two genotypes attained a washed drained solids weight of 240 g and above, and 13 genotypes exceeded 280 g. A low washed drained solids value may indicate excessive loss of solids during processing and leads to an increased degree of clumping of beans at the bottom

of the can after processing and during storage, which is undesirable. The weight of washed drained solids is important to canners because it indicates the degree of hydration during soaking, blanching and processing (Hosfield et al., 1984). Washed drain coefficients ranged from 1.0 to 1.7, with 33 genotypes giving a ratio of 1.4 and above, which is the industrial recommended value. Other good performing genotypes included 19 that scored 4.5 and above for clumping and 7 that scored 4 and above for visual appeal, while 14 scored 4 and above for free starch. Among the 14 genotypes that scored 4.5 and above for colour retention, seven are small white seeded, six red maroon and one red mottled. In a study by Derese and Shimelis (2012), awash melka and awash 1 showed excellent canning qualities, while Chercher was average. In the total score of all canning traits observed in this study, all

the three above-mentioned genotypes scored 60% or more, with Awash melka and Awash 1 being among those that performed well for colour retention. Mukankusi et al. (2022) reported Awash Melka, Awash 1, CAB 2 and G 90 as some of the genotypes that retained excellent seed coat colour after canning in their study. Ten genotypes scored 4 and above for viscosity, including Mexican 142, also reported by Warsane and Kimani (2014) as having been the best canning variety in Kenya for several years. Among the genotypes that performed well for CQTs, six of them, including SAB 659, Nabe 12 C, KK8, MAC 44, Nabe 21 and Biofort small seeds 15, were also reported to have performed well in the studies conducted by Mukankusi et al. (2022) and Amongi et al. (2021), suggesting that the testing procedure was consistent and that these genotypes are potential candidates for canning quality trait improvement.

4.3 | Phenotypic and genetic correlations for canning quality traits

Information on phenotypic and genotypic correlations supplies plant breeders with useful evidence for predicting the performance of traits in early generation lines (Lu & Chang, 1996). This association gives breeders an insight into how a change in one trait may be related to or affect other traits. The relationships that can be recognized between various canning traits influence both the choice of markers for MAS and the traits that may be best suited for improvement by traditional selection methods. Results from this study indicate positive and significant phenotypic correlations between visual appeal and clumping, colour retention, free starch and splitting. There were similar correlations between clumping and free starch, splitting and viscosity (Figure 2). Furthermore, splitting significantly and positively correlated with free starch and free starch with viscosity. These results suggest that lines selected based on one of these traits should also have acceptable values for the other and thus can be used to predict the performance of the other trait without wasting resources to measure all the traits. Lu and Chang (1996) reported a high significantly positive correlation between clumping and viscosity. Posa-Macalincag et al. (2002) reported high correlations between visual appeal and splitting and low positive phenotypic and negative genotypic correlation between visual appeal and washed drained solids (.04 and -1^{***}). This agrees with Walters's et al. (1997) reporting that in selecting for high visual appeal, one should expect low values for WDS. We observed negative correlations between water absorption capacity as measured by the hydration coefficient and clumping ($-.08$) and free starch ($-.039$). Thus, when selecting beans with a high hydration coefficient, poor scores for clumping and free starch should be expected.

4.4 | PCA and clustering

The first two PCs revealed a high genotypic variation (66.6%), suggesting that there is no need for higher number of components to be

able to discriminate the genotypes. In this case, 3 or 4 would be enough. Previous studies reported a few PCs (2–5) being able to explain most of the variation observed among common bean genotypes for different traits (Girgel, 2021; Rezene et al., 2011). The 217 bean accessions used in the study clustered into two main groups indicating two gene pools—Andean and Mesoamerican gene pools (Schmutz et al., 2014)—with a few admixtures, for example, Nabe 4 and CAL 96, which are Andean clustered with the Mesoamerican. Nkhata et al. (2020) reported CAL 96 clustering with the Mesoamerican. Clustering revealed moderate diversity among the accessions, which can be utilized for the improvement of the traits being studied.

4.5 | Genome-wide association studies

The ability to envisage genetic factors that confer important traits in plants requires an understanding of the specific genomic region underlying the phenotype. We used GWAS to evaluate the association between each genotyped marker and phenotypes of 217 individual common bean *Phaseolus vulgaris* accessions that were tested for cooking time and nine canning quality traits. Forty-eight significant SNPs that are associated with the 10 phenotypic traits distributed across all the 11 chromosomes were detected. Among six significant associations observed for cooking time, the association found on chromosome one at position 220257 was the most significant (1.50E-11) (Table 6). Previous studies have identified significant associations for cooking time on chromosome 1; Garcia et al. (2012) studied F2: 4 and F2:5 populations and identified QTLs on chromosome 1 at 70.95.8, 149.169.9, 48.9-69.9 and 70.295.2 cM, while Sadohara et al. (2022) identified an association on the same chromosome at position 1528388. The same study identified markers for water uptake on chromosome 2 at position 49223533. Meanwhile, the current study identified a marker for water uptake on the same chromosome at position 21985761. In Bassett et al. (2021), two markers for cooking time were identified on chromosome 2 at positions 44116993 and 47982820, which are 2.9 Mbs downstream and 0.9 Mbs upstream, respectively, of the marker identified in the current study. While Berry et al. (2020) identified QTLs for cooking time on chromosome 11 from two different environments on positions 51-62 and 96-107cM, respectively, the current study identified two significant markers on the same chromosome at positions 4108223 and 13265190, respectively. Four significant markers were identified on chromosome 2 for cooking time on positions 37679737, 38662923, 48072125 and 48100200 by Cichy et al. (2015); in the current study, we identified a SNP 3378984-64-A/G on position 47065562, which is 0.9 Mbs, 8.4 Mbs downstream and 1.0 and 1.03 Mbs upstream, respectively, from the ones identified by Cichy et al. (2015). Similarly, Diaz et al. (2021) identified marker Pv2.1_02_46670223_A/G for cooking time on chromosome 2 on position 46670223, which is 0.39 Mbs downstream of marker 3378984-64-A/G with the same alleles as the one identified in the current study. Cichy et al. (2015) reported two significant markers for water absorption on chromosome 3 on positions 33874326 and 33910221, and the current study identified a

significant marker for water uptake at position 14349477 on the same chromosome. This study identified a SNP marker associated with splitting on chromosome 2 at position 35636714, while Posa-Macalincag et al., 2002 identified markers OP15.1150 and OG17.1300 on LG2 that were associated with splitting and general visual appeal. The current study identified significant associations with seed coat colour retention and visual appeal of the canned beans on chromosome 7, and the identification of a marker for colour retention on chromosome 7 is important since the shiny seed coat gene (ASP) is also on this chromosome (Perez-Vega et al., 2010). Studies show that an allele on the P locus on chromosome Pv07 controls the white seed colour (Bassett, 1994; Prakken, 1970), and correspondingly, genetic mapping by Moghaddam et al. (2016) indicated that the P locus is located around 40 Mbs on chromosome Pv07. The marker identified in our study for seed coat colour retention is located on position 40002118, just 0.002 Mbs from the position of the P locus. In the current study, this marker 3380009-30-C/A with the major allele CC exists in all the genotypes that have white seed coat colour. All the genotypes that possess this major allele scored 4 and above out of 5 for seed coat colour retention in canned beans during evaluation. To the best of our knowledge, all the other markers identified in this study, especially for the canning traits whose genetic associations have not been studied including free starch, viscosity, washed drain solids and washed drain coefficient are novel.

4.6 | Candidate genes

Gene Phvul.007G280300.1 with best hit at IG04240.1 located 0.032 Mbs downstream of marker 3380009-30-C/A on chromosome 7 encodes AUX/IAA transcriptional regulatory family protein with *Arabidopsis* define IAA3 SHY2. Auxin has been reported to be involved in ovule and seed development and involved in the pathway that leads to seed coat formation (Batista, 2013). Gene Phvul.007G280100.1 with best hit at 5G43750.1 located 0.04 Mbs downstream of marker 3380009-30C/A on chromosome 7 with *Arabidopsis* define NDH18 encodes NAD(P)H dehydrogenase 18. Dihydroflavonol 4-reductase (DFR: EC1.1.219), which is a pivotal enzyme in anthocyanidins biosynthesis, uses NAD(P) as a cofactor to reduce dihydroflavonol to precursors of anthocyanidins and proanthocyanidins (Kim et al., 2005; Wang et al., 2016). Inhibition of DFR has been reported to reduce anthocyanin accumulation, while over-expression has increased anthocyanin production in tobacco and apple. Anthocyanidins determine the colour of most tissues and organs in plants such as leaves, flowers, fruits and seeds (He & Giusti, 2010). They are the main factors underlying the red, blue and purple colours of certain vegetables, fruits and grains (Burton-Freeman et al., 2019), while proanthocyanidins are primarily found in fruits, nuts, bark, chocolate, wine and some plant seeds and flowers (Ou & Gu, 2013). Gene Phvul.007G280700.2 on chromosome 7 with best hit AT5G43650.1 located at 0.05Mbs with *Arabidopsis* define BHLH92 encodes basic helix-loop-helix (bHLH) DNA-binding superfamily protein. This gene has been reported as the major switch in the flavonoid biosynthesis pathway with the dominant form

allowing the expression of other colour genes, while the recessive allele blocks expression (Quattrocchio et al., 2006). Results from many studies conducted on the function of bHLH show that these proteins are involved in the regulation of various networks or biological and biochemical processes throughout the plant life cycle, including Fe uptake (Ogo et al., 2007), tanshinone biosynthesis (Zhang et al., 2015), petal growth (Szecsi et al., 2006) and the response to drought and salt stress (Mao et al., 2017) (Kavas et al., 2016). Most importantly, many studies have suggested that bHLH proteins are involved in the regulation of fruit development and in anthocyanin biosynthesis in both flowers and fruits (Nakatsuka et al., 2008; Zhao et al., 2017; Xiang et al., 2015; Xu et al., 2017). Anthocyanin has been reported to contribute to red flesh colour, and bHLH genes have been suggested to be involved in the biosynthesis of anthocyanin in some fruit species. Gene Phvul.005G161200.1 on chromosome 5 located at 0.04 Mbs upstream of marker 3371324-22-T/A gave *Arabidopsis* define DOF zinc finger protein 1. The PBF DOF (prolamin binding factor DNA binding with one finger only) transcriptional factor can be an important regulator for seed storage protein, gene expression and colour (Gupta et al., 2011). Cichy et al. (2015) reported genes that included 3 UDP-glucosyl transferases on chromosome Pv06 near SNPs associated with cooking time. This gene family is involved in flavonoid biosynthesis and the development of pigments (Bowles et al., 2005), which is of interest because seed coat colour retention had a positive genetic correlation with cooking time and more so a highly positive significant correlation with hydration coefficient. Again, UDP-glucosyl transferase family of genes 73B4 are found on chromosome 8 near marker 16652736-57-A/G (0.009 Mbs) that was significant for bean splitting. Splitting gave a positive correlation with hydration coefficient, implying that the more water the beans absorb, the more likely they would split. Cooking time had an inverse correlation with hydration coefficient in this study, which is in agreement with previous studies (Bellido et al., 2006; Cichy et al., 2015, Chigwedere et al., 2019; Bassett et al., 2020).

4.7 | Free starch and viscosity

Arabinoxylanase, which is from glycoside hydrolase family protein (Falck et al., 2017), is present in the cell wall of starchy wheat endosperm and, when dissolved, has a relatively high viscosity that has a negative impact on beer production and in the animal intestine (Mu et al., 2010). Viscosity of the canned beans results from splitting of the canned bean grain that leaves free starch in the canning medium. Glycoside hydrolase protein was among the candidate genes identified for free starch located at 54.21 Mbs upstream of marker 3373103-6-A/G on position 3636660 on chromosome 11.

5 | CONCLUSION

High and significant genotypic variability for cooking time and canning quality traits among the 250 genotypes tested was observed. The

11 genotypes that cooked in less than an hour and genotypes that scored 80% and above of the total canning quality trait scores and good water absorption traits can be utilized by consumers and processors in the canning industry. The same genotypes can as well be utilized by bean breeders to improve bean genotypes that have long cooking times and poor canning quality traits but possess other desirable traits. Genotype SER 384 combined both short cooking and good canning characteristics, possessing more advantages to processors and consequently consumers. Genotype SMR-53 presented good canning quality traits and average cooking time and thus could be utilized as well. GWAS identified 47 significant markers for the traits tested and several candidate genes. These markers should be validated in a bi-parental population derived from superior and less superior lines for the two traits and recommend the most suitable for MAS.

AUTHOR CONTRIBUTIONS

Eunice Vasiter Kesiime: Conceptualization; experimental layout; data collection; data analysis and write-up. **Stanley Tamusange Nkalubo:** Conceptualization; data collection and write-up. **Mildred Ochwo Ssemakula:** Conceptualization and write-up. **Isaac Onziga Dramadri:** Conceptualization; data analysis and write-up. **Dorothy Nakimbugwe:** Write-up. **Arfang Badji:** Conceptualization; data analysis and write-up. **Paul Gibson:** Data analysis and write-up. **Richard Edema:** Write-up.

CONFLICT OF INTEREST STATEMENT

None.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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