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Genetic mapping of loci associated with yield and their components in black common bean (*Phaseolus vulgaris* L.)

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Abstract

The increase in world population linked to climate change leads to the need to develop more productive and more adapted cultivars of food species. Quantitative trait loci (QTLs) mapping is a useful tool although, interaction between genotype and the environment is still a challenge. In this study, we sought to identify QTL related to grain yield and the production components in common beans (*Phaseolus vulgaris* L.) supported by QTL × environment interaction. Two hundred eight recombinant inbred lines obtained from the Awauna UEM × IPR88 Uirapuru common bean cross were evaluated in 2017, 2018, and 2019 in field conditions under a 15 × 15 triple lattice experimental design. QTL mapping was estimated using genotypic means and a genetic linkage map with 288 single nucleotide polymorphism markers. Five QTLs associated with plant height (PH), number of pods per plant (NPP), first pod height (FPH), 100-seed weight (SW), and grain yield per plant (GYP) were identified on chromosomes Pv01, Pv04, Pv08, and Pv10. Interestingly, three of these QTLs were co-localized for more than one trait, where the QTL for PH, NPP, and GYP co-locate on Pv01, the QTL for PH and FPH co-locate on Pv04, and the QTL for NPP and SW co-locate on Pv08. In turn, on Pv10, two distinct QTLs were found for SW. The identification of these QTLs stands out in Brazil since relatively little research is directed at this economically important commercial group. It is noteworthy that the molecular markers found linked to the QTLs must later be validated to be used in a multi-trait marker-assisted selection.

Plain Language Summary

Mapping studies identify genomic regions using molecular markers. Quantitative trait loci (QTLs) mapping in plants is used to understand the inheritance patterns

Abbreviations: FPH, first pod height; GYP, grain yield per plant; NPP, number of pods per plant; NSP, number of seeds per pod; PVE, explained phenotypic variation; QTL, quantitative trait locus; RILs, recombinant inbred lines; SNP, single nucleotide polymorphism; SW, 100-seed weight.

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and genetic architecture of quantitative traits and identify molecular markers linked to quantitative traits. Interaction between genotype and the environment led to identification of different QTLs. In this study, we aimed to identify QTL related to grain yield and the production components in black common bean recombinant inbred line population supported by QTL × environment interaction. Five QTLs associated with plant height, number of pods per plant, first pod height, 100-seed weight, and grain yield per plant were identified on chromosomes Pv01, Pv04, Pv08, and Pv10. These findings contribute to the development of improved strategies for breeding common bean cultivars, ensuring sustainable bean production.

1 | INTRODUCTION

According to projections, the global population is expected to reach 10.9 billion by the year 2100. As a result, various sectors of society are increasingly focused on achieving food security. A key implication of this population increase is a greater demand for agricultural expansion, which requires more intensive land use. This shift calls for the adaptation of existing crop varieties or the development of new, more productive cultivars to meet the growing food needs (Garrett et al., 2018).

Climate change requires the development of cultivars that can adapt to diverse and changing environmental conditions. The common bean (*Phaseolus vulgaris* L.) is an important crop with significant nutritional benefits. It provides essential amino acids, complex carbohydrates, dietary fiber, unsaturated fats, vitamins, and minerals. Moreover, it contains bioactive compounds with potential health benefits, including hypocholesterolemic, antiatherogenic, anticarcinogenic, and hypoglycemic properties (Celmeli et al., 2018; Kotue et al., 2018).

One of the major challenges faced by plant breeding programs is the variation in genotype performance across different environments, commonly referred to as genotype by environment interaction (G × E interaction; Singamsetti et al., 2021). Identifying the underlying causes of G × E interaction and integrating this knowledge into breeding strategies requires extensive multi-environment experiments, which demand large sample populations and considerable financial investment (A. A. Elias et al., 2016).

Mapping studies identify genomic regions using molecular markers (Kromdijk et al., 2014). Quantitative trait loci (QTLs) mapping in plants helps uncover the inheritance patterns and genetic architecture of quantitative traits, aiding the identification of functional markers that can be used for selecting complex traits (Bernardo, 2008). However, most identified QTLs account for less than half of the total genetic variation; this can be attributed to the presence of numerous undetected minor QTL and epistatic interactions within the mapping process (Boopathi, 2020). As a result, the interaction between QTL and environmental factors (QTL × E interaction) involves additional complexity, requiring more advanced statistical approaches to accurately assess and quantify these effects (Kromdijk et al., 2014).

Several researchers have made significant contributions to mapping QTL in common beans. González et al. (2016) identified important QTL for plant height (PH) and the number of pods per plant (NPP) on chromosome Pv01. Similarly, Delfini et al. (2021) found QTLs associated with PH, the NPP, and 100-seed weight (SW) on Pv01, as well as QTL for PH and the height of the first pod on Pv04. Langat et al. (2019) focused on mapping QTL related to drought tolerance in an F_2 population of common beans. They found QTL for the NPP on Pv01, QTL for SW on Pv08 and Pv10, and QTL for grain yield on Pv01. Mir et al. (2021) identified QTL for the NPP on Pv01 and Pv08, QTL for SW on Pv08 and Pv10, and QTL for grain yield per plant (GYP) on Pv01. These studies collectively highlight chromosome Pv01 as a significant locus for traits related to PH, the number of pods, and grain yield, with other QTL identified on chromosomes Pv04, Pv08, and Pv10. Cordoba-Novoa et al. (2022) conducted an investigation for the genetic variability and structural characteristics of traits related to transpiration, stomatal regulation, and water utilization within Mesoamerican common bean germplasm. They successfully identified QTLs on chromosomes Pv01 and Pv07, as well as candidate genes and regulatory elements associated with tolerance to abiotic stress, including various transcription factors. Arriagada et al. (2023) performed a meta-QTL (MQTL) analysis encompassing 667 QTLs derived from 21 distinct studies with the aim of discerning reliable genomic regions linked to yield-related traits in common bean. Their comprehensive analysis unveiled 42 MQTLs, characterized by confidence intervals that were 3.41 times more precise than those of the original QTL, thereby enhancing the accuracy of mapping. Notably, among these MQTLs, 28 were correlated with both yield and phenological traits, highlighting their significant potential applicability in breeding programs. In a similar vein, Njau et al. (2024) identified 44 QTLs pertinent to pod quality and yield traits within a recombinant inbred line (RIL) population originating from a Vanilla × MCM5001 snap × dry bean cross. The QTLs associated with pod quality were localized on chromosomes Pv01, Pv02, Pv03, Pv04, Pv06, and Pv07, whereas those associated with pod yield were discerned on chromosome Pv08.

Traits controlled by multiple loci are often heavily influenced by environmental factors, making it crucial to assess QTL responses across various environments (A. A. Elias et al., 2016). QTL analysis allows researchers to determine the number and location of key genetic regions, as well as to explore the interactions among loci and identify essential genes and their functions (Li et al., 2015). Yuste-Lisbona et al. (2014) discovered five QTLs with only individual additive effects, six with only epistatic effects, and 12 that exhibited both types of effects for pod traits. Hoyos-Villegas et al. (2016) conducted a study over two agricultural years and identified QTL associated with seed yield, seed size, days to flowering, days to maturity, number of seeds, and PH.

Sandhu et al. (2018) evaluated an RIL population at two locations in southern Manitoba over the years 2014–2016 and found QTL associated with seed hydration and hardness, traits that impact cooking quality. Geravandi et al. (2020) identified QTL linked to seed size and yield-related traits. González et al. (2016) evaluated an RIL population across various environments and identified QTL that control the number of days to flowering as a function of increasing degree-days. J. C. F. Elias et al. (2021) examined RILs grown under both drought and non-drought conditions for 2 years and identified 16 QTLs across chromosomes Pv01, Pv02, Pv03, Pv05, Pv07, Pv08, Pv09, Pv10, and Pv11. These studies highlight the complex genetic basis of common bean traits, demonstrating the presence of both single-locus and epistatic QTL and the importance of environmental interaction. They also underscore the need for multi-environmental studies to capture the full range of QTL effects, which is critical for plant breeding and the development of improved cultivars.

The present study aimed to map QTL related to production components, as well as interaction between QTL and the environment within a RIL population of black common bean derived from a cross between Awauna UEM × IPR88 Uirapuru.

2 | MATERIALS AND METHODS

2.1 | Plant material

In this study, common bean RILs were generated via artificial intragenic (Mesoamerican) hybridizations between the cultivars Awauna UEM (female) and IPR88 Uirapuru (male) within a controlled greenhouse environment at the Núcleo de Pesquisa Aplicada à Agricultura (Nupagri-UEM). A total of 208 progenies were produced using the Single Seed Descent method, progressing through generations until reaching the $F_{2:5}$ stage. Subsequently, the RIL population ($F_{2:6}$, $F_{2:7}$, and $F_{2:8}$) underwent phenotypic evaluations in field conditions at Centro de Treinamento em Irrigação (CTI-UEM). Both facilities are part of the Universidade Estadual de Maringá-UEM, situated in Maringá, in the Northwestern region of the state of Paraná, Brazil.

Awauna UEM is a black common bean cultivar product of the Nupagri-UEM Common Bean Breeding Program. It derives from the crossing of the cultivar FT Nobre and the SEL 1308 line. Noteworthy characteristics of this cultivar include an average maturation period of 71 days from emergence to harvest, resistance to lodging, and a yield potential of 3400 kg ha^{-1}, particularly suited for the southern region of the country. Moreover, it exhibits resistance to angular leaf spot (*Pseudocercospora griseola*), common bean mosaic virus (BCMV), and most of the Brazilian endemic races of *Colletotrichum lindemuthianum*, owing to the presence of the *Co-4*^{2} anthracnose resistance allele.

IPR88 Uirapuru, a member of the black commercial group of common bean cultivars, is the result of breeding efforts of the Common Bean Improvement Program of the Agronomic Institute of Paraná. Its genetic lineage traces back to a combination of traditional cultivars, including BAC 29, PR1711/3, NEP2/2, Puebla 173, and ICA Pijao. Phenotypically, IPR88 Uirapuru exhibits wide adaptability across the primary production regions of Paraná, with optimal size for mechanical harvesting, an average growth cycle of 86 days, and a yield potential of 2407 kg ha^{-1}. Additionally, it demonstrates tolerance to water deficit and high temperatures. Furthermore, it is resistant to BCMV, rust (*Uromyces phaseoli*), and powdery mildew (*Erysiphe polygoni*) (Moda-Cirino et al., 2001).

Core Ideas

- Genetic mapping of the loci using recombinant inbreeding lines.
- Quantitative trait loci (QTLs) mapping and a genetic linkage map with 288 single nucleotide polymorphism markers.
- Five QTLs associated yield and their components on Pv01, Pv04, Pv08, and Pv10 chromosomes.
- QTL related to grain yield and the production components in common bean supported by QTL environment interaction.
- Genetic mapping of Awauna UEM × IPR88 Uirapuru population of black common bean.

2.2 | Field trial design, evaluation of productivity, and morpho-agronomic traits

A total of 208 RILs, the parent varieties Awauna UEM and IPR88 Uirapuru, and control cultivars, including BRS Esteio, FT Noble, FT Soberano, FT 120, Crioulo, and CHP996524, were evaluated. These assessments spanned three agricultural years, from August to November of 2017, 2018, and 2019, within the experimental fields of CTI-UEM. Each experimental unit comprised a 2.0 m row, spaced 0.5 m apart, accommodating 24 plants. The experimental design was a triple lattice arrangement of 15×15.

The following agronomic traits were evaluated: PH: the distance from the soil surface to the tip of the leaves measured in centimeters; NPP: calculated as the total number of pods per plot divided by the number of plants within the plot; number of seeds per pod (NSP): determined by counting the seeds from 10 randomly selected pods within a plot; first pod height (FPH): determined by averaging the heights (in centimeters) of five plants at maturity, measured from the cotyledonary scar to the base of the first pod; SW: the weight of a sample containing 100 seeds expressed in grams; GYP: calculated by dividing the total mass of plant seeds by the number of plants within the effective plot area, considering a moisture content of 13%.

2.3 | Phenotypic data analysis

The phenotypic data from each trial underwent analysis using SELEGEN software (Resende, 2016) and the R software (R Core Team, 2013), utilizing the ggplot2 package (Wickham, 2016). Within the R environment, we generated frequency density curves to illustrate the quantitative characteristics of the evaluated traits. Additionally, genetic and phenotypic correlation analyses were conducted, and scatter plots. These visualizations aimed to elucidate the potential influence of co-localized QTLs across different traits (Figure S1).

The prediction of genotypic values was performed via best linear unbiased predictor (BLUP), while estimates of variance components for random factors were derived through the restricted maximum likelihood method. Phenotypic data from each year (2017, 2018, and 2019) were independently analyzed using mixed models, specifically employing mathematical Model 1. In evaluating the genotype by environment (G × E) interaction, the Harmonic Mean of the Relative Performance of Genotypic Values (Model 2) was employed. The G × E interaction, both between pairs of agricultural years and across all 3 years, was treated as the environmental component for QTL mapping purposes, denoted as "Combination of agricultural years."

The significance of model effects was assessed using the likelihood ratio test (LRT), facilitating a deviance analysis (ANADEV). Goodness of fit was determined by comparing models with and without genotype effects and genotype-environment interactions. This comparison involved subtracting the deviance of the model without the effect from the deviance of the complete model, subsequently evaluating it against the chi-square value (χ^2) with 1 degree of freedom at 1% and 5% probability levels (Resende & Duarte, 2007). Mathematically, this can be expressed as follows:

$$\mathrm{LRT} = -2\ln\left(\frac{\text{ML of reduced model}}{\text{ML of complete model}}\right)$$

where ln represents the Naperian logarithm and ML is the maximum likelihood estimation.

$$\text{Model 1}: y = x_r + z_g + w_b + e$$

$$\text{Model 2}: y = x_r + z_g + w_b + T_i + e$$

where y is the data vector; r is the replication effect vector (assumed as fixed) added to the overall mean; g is the genotypic effect vector (assumed as random); b is the block effect vector (assumed as random); i is the genotype environment interaction effects (random); e is the error or residuals value (random). The uppercase letters represent the incidence matrices for the aforementioned effects.

2.4 | Genotyping of the RILs using BARCBean6K_3 BeadChip

Genomic DNA extraction was performed on the 208 RILs ($F_{2:8}$ generation) and their parental lines (Awauna UEM and IPR88 Uirapuru) using the DNeasy plant mini kit (Qiagen) in accordance with the manufacturer's guidelines. The extracted DNA was then quantified using a 1.5% agarose gel (Agarose SFR, Amresco) in TBE buffer (tris-borate-ethylenediamine tetraacetic acid) and visualized by staining with 1 g mL^{-1} Sybr Green (Sigma-Aldrich).

The DNA samples were screened with 5398 SNP (single nucleotide polymorphism) DNA markers using the BARCBean6K_3 Illumina BeadChip, employing the Infinium HD assay ultra-protocol (Illumina, Inc.). Fluorescence intensity measurements were obtained by imaging the BeadChip with the Illumina beadarray reader. Automatic allele calling for each locus was carried out using the GenomeStudio Genotyping Module v1.8.4 software (Illumina), followed by visual inspection. Errors in allele calling due to improper cluster identification were corrected, resulting in a final set of 800 SNPs.

Following quality assessment of SNPs using the GenomeStudio software, we employed a Microsoft Excel electronic spreadsheet to execute the filtering process. This involved excluding monomorphic SNPs present in both parental lines, Awauna UEM and IPR88 Uirapuru, as well as those with missing data exceeding 5% and a minimum allele frequency below 30%. Furthermore, SNP markers were mapped to their respective chromosomes and assigned nomenclature deposited at the National Center for Biotechnology Information database.

2.5 | Genetic mapping and QTL analysis

The QTL analysis, conducted on the new adjusted genotypic means of the phenotypic traits evaluated across the years 2017, 2018, and 2019, as well as the combination of agricultural years, was carried out using the QTL software IciMapping Version 4.2 (Meng et al., 2015). This software employs the inclusive composite interval mapping (ICIM) method, integrating both the BIP and MET analysis modules in the appropriate sequence. These modules enable the mapping of QTL with additive effects in individual environments and QTL with environmental interactions across multiple environments (Li et al., 2015).

Significance of QTLs was determined using the 1000-permutation test for each trait in QTL IciMapping, establishing the LOD threshold at $p = 0.05$. The peak LOD score was considered as the location of the QTL. For QTLs with additive effect genes, a 1 cM scan step was utilized, with a probability of 0.001 for inserting variables in stepwise regression. Detection and declaration of putative QTLs relied on a minimum LOD score of three in individual settings and a minimum LOD score of 4.5 in multi-environmental analyses (α: 0.05; Li et al., 2015).

In QTL classification, the following criteria were applied: a main QTL is defined by a minimum LOD score of five and a proportion of the total explained phenotypic variation (total PVE) exceeding 10%; a stable QTL exhibits a LOD score greater than three in at least two environments; and a specific QTL is characterized by a minimum LOD score of five and significant QTL × E interaction. QTLs were named according to the guidelines proposed by Miklas and Porch (2010) for QTL naming in common bean. Finally, using MapChart 2.3 (Voorrips, 2002), the QTLs were visually depicted on genetic linkage maps for *P. vulgaris* developed using the RIL population Awauna UEM × IPR88 Uirapuru.

3 | RESULTS

3.1 | Phenotypic performance of RILs and assessment of experimental quality

Evaluation of the RIL population at the field conditions for three crop years provided an opportunity to account for their phenotypic performance under a variety of environmental conditions (Table 1 and Table S1). Despite the phenotypic similarity in terms of averages between parents and RILs, these showed a wide range of extreme values (max and min), denoting a substantial transgressive segregation and indicating that both parents carry genes that contribute to the variation of traits.

Observing the pattern of data distribution (Figure S1), the inference about the asymmetry reveals that there is a certain disturbance in the data distribution due to the complementary gene interaction in the traits PH, NPP, FPH, and GYP, as well as duplicated gene interaction in the traits NSP and SW (Table 1). Obviously, such interactions are not mutually exclusive events, as they are polygenic traits.

Another important information provided by the frequency distribution in phenotypic classes concerns kurtosis. All evaluated traits reveal some form of gene interaction, especially the NPP, NSP, SW, and GYP for both showing, at some point, leptokurtic behavior of the data distribution (Table 1).

The selective accuracy values obtained with the experimental data (Table S2) were, on average, >70%, being considered, therefore, high and consistent with the need for data required for the purpose of QTL mapping.

3.2 | Genetic correlation between the evaluated traits

In the partition of the effects involved in the differential expression of the correlated traits, it was observed that, under the experimental conditions, the genetic effects played a major role in the correlations, since most of the traits, at some point, were genetically associated with each other in greater or lesser degree (Table 2).

The genotypic correlation coefficients of PH were significant and positive with all traits, except for the NSP, which was not significant. The NPP showed a significant and positive correlation with all traits; however, its correlation with the NSP was negative. The SW had a significant and negative correlation with the NSP, but it was positively correlated with the height of the first pod and GYP. (Table 2).

Although the high estimates of genetic correlation observed indicate the presence of pleiotropy, the contrast is not true, as different pleiotropic loci can result in positive or negative covariances between traits, which can cancel each other out. In other words, pleiotropic effects of different genes that affect pairs of traits may not lie in a single direction for each trait and, therefore, will not result in significant genetic correlations between them (Mackay et al., 2009).

The phenotypic correlation and its respective graphical representation, the scatter plot (Figure S1), evidenced the important role of the G × E interaction in the associated pairs, since the genotypic correlation only partially reflected the phenotypic correlation. Of the 11 pairs of significant

TABLE 1 Descriptive statistics of the traits plant height, number of pods per plant, number of seeds per pod, first pod height, 100-seed weight and grain yield per plant of the 208 common bean recombinant inbred lines (RILs) from Awauna UEM × IPR88 Uirapuru cross in the agricultural years 2017, 2018, and 2019.

Traits	Mean	SD	CV%	Max	Min	Skew	Inf.S	Kurt	Inf.K
Plant Height									
2017	58.11	8.09	13.93	64.86	53.23	0.50	(+)	−0.10	Meso
2018	58.35	7.80	13.37	64.37	53.66	0.48	(+)	0.10	Meso
2019	61.71	8.00	12.97	67.75	57.64	0.31	(+)	0.05	Meso
No. of pods per plant									
2017	12.84	2.04	15.92	19.58	8.15	0.34	(+)	−0.13	Meso
2018	13.06	2.34	17.96	19.92	2.36	−0.43	(−)	0.90	Lepto
2019	12.73	1.85	14.52	18.74	8.77	0.30	(+)	0.01	Meso
No. of seeds per pod									
2017	5.56	0.74	13.24	7.33	4.00	−0.16	Sym	−0.23	Meso
2018	5.82	0.62	10.57	7.33	4.00	−0.61	(−)	0.45	Lepto
2019	5.78	0.66	11.41	7.00	4.00	−0.21	(−)	−0.12	Meso
First pod height							**f.S**		
2017	18.11	2.29	12.62	24.86	13.23	0.50	(+)	−0.10	Meso
2018	18.35	1.97	10.73	24.37	13.66	0.48	(+)	0.10	Meso
2019	17.16	1.63	9.51	22.44	13.16	0.52	(+)	0.10	Meso
100-Seed weight									
2017	24.60	2.21	9.00	32.18	15.84	−0.01	Sym	0.62	Lepto
2018	25.74	2.34	9.11	32.60	15.04	−0.43	(−)	0.90	Lepto
2019	24.45	2.49	10.18	32.11	15.22	−0.53	(−)	0.80	Lepto
Grain yield per plant									
2017	15.24	2.04	13.42	21.98	10.55	0.34	(+)	−0.13	Meso
2018	15.74	2.00	12.70	22.99	11.44	0.45	(+)	0.40	Lepto
2019	15.13	1.85	12.22	21.14	11.17	0.30	(+)	0.01	Meso

Abbreviations: CV%, coefficient of variation of the phenotypic data; Inf.K, inference about the kurtosis; Inf.S, inference about the skewness; Kurt, kurtosis of the phenotypic data; Lepto, leptokurtic; Max, maximum of the phenotypic data from the RILs; Meso, mesokurtic; Min, minimum of the phenotypic data from the RILs; Skew, skewness of the phenotypic data. (+), (−), and Sym means positive asymmetric, negative asymmetric, and symmetric, respectively.

genotypic correlations (Table 2), only six remained at a phenotypic level, either the pairs: FPH and NPP; MS and NPP; GYP and NPP; NSP and MS; FPH and MS; and GYP and MS (Figure S1). In part, the explanation of the observed is supported by the premise that the interaction between pleiotropic loci and environments can alter the genetic effects of traits according to the environment, leading to differences in covariances between traits and consequent changes in correlations due to imposed environmental differences (Pavličev & Cheverud, 2015).

3.3 | Deviation analysis and detection of G × E interaction

Deviation analysis showed a significant difference between the RILs and a significant G × E interaction (α: 1% and 5%) for all evaluated traits, years, and combination of years (Table S3). Therefore, it was necessary to adjust the phenotypic means using BLUPs, mitigating environmental effects that reduce the range of population variation that would restrict QTL detection. Furthermore, the new averages avoid confusion between environmental effects and QTL, resulting in consistent values of PVE.

3.4 | Genetic mapping

This study involved genotyping 208 RILs derived from the Awauna UEM × IPR88 Uirapuru cross using 5398 SNPs (Table S4). Following the filtering process, a total of 288 SNP markers were selected for mapping procedures (Table 3). The mapping of the Awauna UEM × IPR88 Uirapuru population spanned 590.3 cM, with an average marker distance of

TABLE 2 Genetic correlation coefficient of the traits plant height (PH), number of pods per plant (NPP), number of seeds per pod (NSP), first pod height (FPH), 100-seed weight (SW), and grain yield per plant (GYP) of the 208 common bean recombinant inbred lines (RILs) to the agricultural years 2017, 2018, and 2019.

Traits	Agricultural year	PH	NPP	NSP	FSH	SW
NPP	2017	0.066	–	–	–	–
	2018	0.162**	–	–	–	–
	2019	0.999**	–	–	–	–
NSP	2017	−0.107	0.034	–	–	–
	2018	−0.031	−0.224**	–	–	–
	2019	0.128	0.130	–	–	–
FPH	2017	0.999**	0.066	−0.107	–	–
	2018	0.999**	0.162**	−0.031	–	–
	2019	0.399**	0.396**	0.118	–	–
SW	2017	0.158*	0.185**	0.107	0.158*	–
	2018	0.162**	0.999**	−0.224**	0.162**	–
	2019	0.314**	0.316**	−0.014	0.427**	–
GYP	2017	0.066	0.999**	0.034	0.066	0.185**
	2018	0.130*	0.230**	0.052	0.130	0.230**
	2019	0.999**	0.999**	0.130	0.196	0.316**

** and * effects at 1% and 5% probability by *t* test, respectively.

TABLE 3 Distribution of SNPs markers on the linkage map constructed from the recombinant inbred line (RIL) population Awauna UEM × IPR88 Uirapuru.

Chromosome	No. of markers	Starting marker	Ending marker	Map length (cM)	Density[a]
1	30	ss715645919	ss715648161	93.98	3.13
2	39	ss715648504	ss715646370	15.83	0.41
3	17	ss715646392	ss715647338	83.51	4.91
4	22	ss715646899	ss715640244	86.09	3.91
5	35	ss715651063	ss715645454	59.93	1.71
6	24	ss715646671	ss715650275	53.16	2.22
7	12	ss715649072	ss715646021	7.22	0.60
8	29	ss715646515	ss715648623	84.30	2.91
9	28	ss715646185	ss715649931	23.86	0.85
10	28	ss715641336	ss715639844	61.27	2.19
11	24	ss715640322	ss715649886	21.14	0.88
Entire genome	288	–	–	590.293	x̄: 2.05

[a] Density refers to marker density in cM/marker.

2.05 cM. The number of markers ranged from 12 to 39 per chromosome.

3.5 | QTL mapping

Utilizing Inclusive Composite Interval QTL mapping within individual environments, we identified a total of five QTLs associated with PH, NPP, FPH, SW, and GYP on chromosomes Pv01, Pv04, Pv08, and Pv10 (Figure 1; Table 4).

Our study revealed the ss715646884 marker, situated at 46,961,454 bp on chromosome Pv01 associated with PH, NPP, and GYP. Similarly, marker ss715649973 (at 1,575,721 bp) on chromosome Pv04 was found in close proximity to the peak of the QTL for both PH and FPH. Noteworthy findings emerged on Pv08, where markers ss715646109 (at 58,231,277 bp) and ss715646101 (at 58,006,525 bp) were linked to the QTLs for NPP and SW. Moreover, Pv10 unveiled two distinct QTLs for SW, associated with markers ss715650584 (at 40,255,828 bp) and ss715641827 (at

TABLE 4 Quantitative trait loci (QTL) for agronomic traits identified in the common bean recombinant inbred line (RIL) population Awauna UEM × IPR88 Uirapuru cultivated under field conditions in Maringá, PR, in the agricultural years of 2017, 2018, and 2019 and combined.

Trait	QTL	Year	Chr.	Peak	SNP left	SNP right	QTL interval	Nearest SNP	LOD	PVE	Add
Plant height	PH4^{AU}	2017	4	7	ss715649973	ss715647823	4.35–12.03	ss715649973	3.33	2.03	−1.00
	PH4^{AU}	2018	4	7	ss715649973	ss715647823	4.35–12.03	ss715649973	3.20	2.43	−0.89
	PH1^{AU}	2019	1	29	ss715646884	ss715645259	24.09–42.43	ss715646884	3.47	8.88	0.26
No. of pods per plant	NPP8^{AU}	2018	8	14	ss715647389	ss715646109	8.85–17.40	ss715646109	10.95	11.23	0.41
	NPP8^{AU}	2018	8	19	ss715646109	ss715646101	17.40–23.04	ss715646109	10.67	11.30	0.42
	NPP1^{AU}	2019	1	31	ss715646884	ss715645259	24.09–42.43	ss715646884	3.70	9.60	0.26
	NPP1^{AU}	Comb	1	37	ss715646884	ss715645259	24.09–42.43	ss715645259	4.72	10.13	0.53
First pod height	FPH4^{AU}	2017	4	7	ss715649973	ss715647823	4.35–12.03	ss715649973	3.35	2.20	−1.03
	FPH4^{AU}	2018	4	7	ss715649973	ss715647823	4.35–12.03	ss715649973	3.32	2.62	−0.93
	FPH4^{AU}	2019	4	8	ss715649973	ss715647823	4.35–12.03	ss715649973	3.79	2.00	−0.79
100-Seed weight	SW8^{AU}	2017	8	21	ss715646109	ss715646101	17.40–23.04	ss715646101	9.61	14.25	0.48
	SW8^{AU}	2018	8	19	ss715646109	ss715646101	17.40–23.04	ss715646109	12.58	12.67	0.51
	SW10^{AU}	2018	10	25	ss715645516	ss715650584	21.1–26.87	ss715650584	3.02	2.76	0.31
	SW8^{AU}	2019	8	21	ss715646109	ss715646101	17.40–23.04	ss715646101	7.75	13.95	0.45
	SW8^{AU}	Comb	8	20	ss715646109	ss715646101	17.40–23.04	ss715646109	8.34	8.27	0.72
	SW10^{AU}	Comb	10	25	ss715645516	ss715650584	21.1–26.87	ss715650584	2.96	2.95	0.56
	SW10.2^{AU}	Comb	10	35	ss715641827	ss715649351	29.06–55.08	ss715641827	3.41	7.60	0.88
Grain yield per plant	GY1^{AU}	2019	1	32	ss715646884	ss715645259	24.09–42.43	ss715646884	2.98	7.87	0.23
	GY1^{AU}	Comb	1	36	ss715646884	ss715645259	24.09–42.43	ss715645259	2.97	6.78	0.38

Abbreviations: Add, estimated additive effect of QTL at the current scanning position; Chr., chromosome; Comb, combination of agricultural years; LOD, logarithm of the odds score calculated from single marker analysis; Peak, peak of QTL position in cM; PVE (%), phenotypic variation explained by QTL at the current scanning position; SNP, single nucleotide polymorphism; Year, agricultural year.

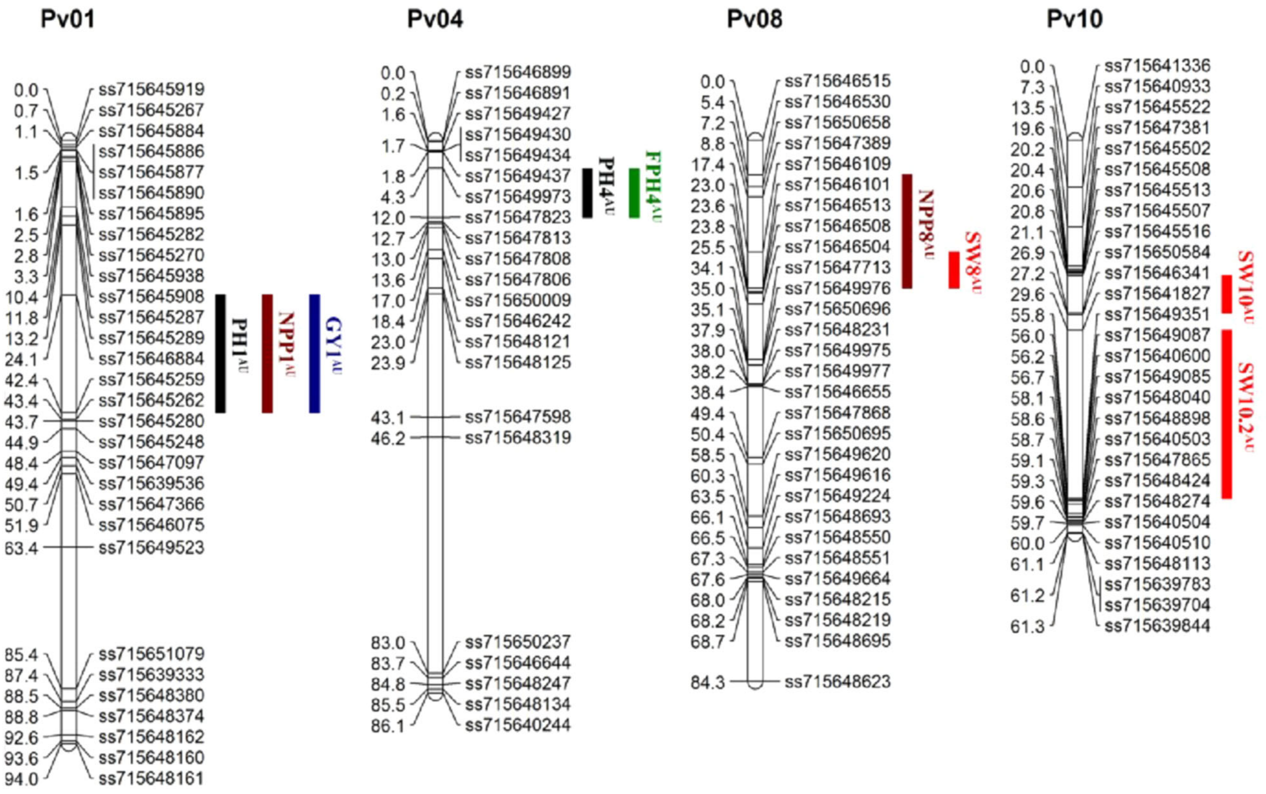

FIGURE 1 Genetic linkage map showing the quantitative trait loci (QTL) mapped on the chromosomes of the Awauna UEM × IPR88 Uirapuru population. Distances between markers are indicated in cM.

16,330,477 bp). The co-occurrence of QTLs for different traits suggests potential pleiotropy or closely linked genes (Haggard et al., 2015). Furthermore, QTL mapping for PH, FPH, NPP, and SW revealed consistent performance across the experimental years, underscoring stability in trait expression.

3.5.1 | QTL for PH

QTLs associated with PH were detected on chromosomes Pv01 and Pv04. The peak of the QTL PH1^{AU} on Pv01 was located at 4.91 cM from the marker ss715646884 (46,961,454 bp), based on data from the 2019 assay, explaining 8.9% of the phenotypic variation. QTL mapping on Pv04 (PH4^{AU}) revealed consistent identification across both the 2017 and 2018 datasets, positioned at 2.65 cM from marker ss715649973 (1,575,721 bp). This QTL accounted for over 2.0% of the phenotypic variation in each year.

3.5.2 | QTL for NPP

QTLs associated with NPP were identified on chromosomes Pv01 and Pv08. The QTL on Pv01 (NPP1^{AU}) was detected in 2019 and across the combination of agricultural years, within the interval delimited by markers ss715646884 (46,961,454 bp) and ss715645259 (50,130,201 bp). This QTL explained 9.6% and 10.1% of the phenotypic variation, respectively, in each year. Intriguingly, this QTL overlaps with the region where QTLs for PH and GYP were also found. On Pv08, the NPP8^{AU} QTL was identified in 2018, spanning the region between markers ss715647389 (59,483,302 bp) and ss715646109 (at 58,231,277 bp). This QTL explained 11.2% and 11.3% of the phenotypic variation in each respective year.

3.5.3 | QTL for FPH

On chromosome Pv04, the QTL FPH4^{AU} was consistently identified across all years (2017, 2018, and 2019), positioned at 2.65 cM from marker ss715649973 (1,575,721 bp). This QTL explained >2.0% of the phenotypic variation in each year. Intriguingly, this QTL coincides with the QTL identified for PH.

3.5.4 | QTL for seed weight (SW)

QTLs associated with SW were detected on chromosomes Pv08 and Pv10. On Pv08, the QTL SW8^{AU} was consistently identified across all years (2017, 2018, and 2019) and in the combination of agricultural years. It spanned the interval between markers ss715646109 (at 58,231,277 bp) and ss715646101 (at 58,006,525 bp), explaining 14.2%, 12.7%, 13.9%, and 8.3% of the phenotypic variation in each respective analysis. Notably, this QTL coincides with the QTL found for NPP. On Pv10, two distinct QTLs were identified. The QTL SW10^{AU} was detected in 2018, and across the combination of agricultural years, it was positioned at 1.87 cM from marker ss715650584 (at 40,255,828 bp), explaining 2.7% and 2.9% of the phenotypic variation, respectively. Additionally, the QTL SW10.2^{AU} was identified in the combination of agricultural years, spanning the interval between markers ss715641827 (at 16,330,477 bp) and ss715649351 (at 61,114,365 bp), explaining 7.6% of the phenotypic variation.

3.5.5 | QTL for GYP

The QTL GY1^{AU}, located on chromosome Pv01 between the markers ss715646884 and ss715645259 at positions 46,961,454 bp and 50,130,201 bp, was identified both in 2019 and across the combination of agricultural years. It explains from 6.8% to 7.9% of the phenotypic variation and coincides with the region where QTLs for PH and NPP were also found.

4 | DISCUSSION

4.1 | Correlation

The observed genetic correlations between NPP and GYP across all years, as well as between PH and NPP, and PH and GYP in 2018 and 2019 (Table 2), suggest the presence of pleiotropic loci or loci located in tightly linked regions of the genome, as noted by Haggard et al. (2015). This implies that a greater number of shared QTL could lead to larger values of genetic correlation (Gardner & Latta, 2007). Indeed, QTL co-localization for correlated variables has been documented in various studies (Briñez et al., 2017; García-Fernández et al., 2021; Mukeshimana et al., 2014; Nabateregga et al., 2019; Sedlar et al., 2020; Trapp et al., 2015).

4.2 | QTL mapping

4.2.1 | PH trait

In the study, putative QTLs were identified for the PH trait on both chromosome Pv01 (PH1^{AU}) and chromosome Pv04 (PH1^{AU}). Notably, on chromosome Pv01, a co-localized QTL was discovered for PH, NPP, and GYP in close proximity to the marker ss715646884 (46,961,454 bp). This finding was supported by a significant and positive genetic correlation coefficient among these traits. Interestingly, González et al. (2016) also reported similar co-localization for these three traits.

Stable QTLs for both PH and FPH were consistently mapped together at the beginning of chromosome Pv04, near the marker ss715649973 (1,575,721 bp). Notably, this QTL stands out for its stability across multiple years, exhibiting non-significant QTL × E interaction (Table S5). Furthermore, these traits demonstrated a consistent genetic correlation across all assays. It is worth mentioning that the primary genetic influence driving the increase in PH originates from the parental line Awauna UEM.

PH plays a crucial role in the common bean crop, influencing the formation of yield components (Fang et al., 2020). An upright growth habit and lower susceptibility to lodging are vital factors for facilitating both manual and mechanized harvesting processes. Moreover, optimal PH facilitates cultivation practices, minimizing harvest losses and the incidence of diseases. This, in turn, allows for increased harvest frequency per year by reducing the crop cycle (Mendes et al., 2009).

Several studies have consistently mapped QTLs for the PH trait on chromosomes Pv01 and Pv04 (Delfini et al., 2021; J. C. F. Elias et al., 2021; González et al., 2016; Silva et al., 2018). Additionally, Tar'an et al. (2002), Blair et al. (2006), Checa and Blair (2008), and Chavarro and Blair (2010) have reported QTLs for the PH trait on both Pv01 and Pv04 in their respective studies.

Indeed, comparing results across different studies can be challenging due to variations in populations and marker technologies utilized. Despite methodological differences, the consistent identification of QTLs on Pv01 across multiple studies underscores the robustness of this genetic region's association with the PH trait in common bean crops.

4.2.2 | NPP trait

In the NPP trait, putative QTLs were identified on both chromosome Pv01 (NPP1^{AU}) and Pv08 (NPP8^{AU}). Once more, our study revealed a QTL on Pv01, which was co-localized with QTLs for PH, NPP, and GYP in close proximity to the marker ss715646884 (46,961,454 bp).

This stable QTL, NPP1^{AU}, exceeds the contribution to the increase in NPP derived from the parental line IPR88 Uirapuru, as indicated by the additivity values. Despite exhibiting QTL × environment interaction (Table S5), the predominant portion of the phenotypic variation is attributed to additive effects (A), with minimal environmental influence. This observation confirms the authenticity of the QTL, suggesting its reliability in genetic prediction across diverse environments. Consequently, markers such as ss715646884 emerge as compelling candidates for multi-trait marker-assisted selection strategies.

On chromosome Pv08, we detected a QTL co-localized for both the NPP and SW in close proximity to marker ss715646109 (58,231,277 bp). Notably, NPP and SW exhibited a consistent genetic correlation across all assays. Additive effects predominantly influenced both traits, with the increase in NPP attributed to the parental line IPR88 Uirapuru and the increase in SW attributed to Awauna UEM. This QTL demonstrated no significant QTL × environment interaction, underscoring its importance for marker-assisted selection strategies (Table S5).

Several studies have consistently mapped QTLs for NPP trait on chromosomes Pv01 and Pv08. Mukeshimana et al. (2014) and Langat et al. (2019) mapped QTLs associated with drought tolerance in common bean and identified QTLs for NPP on Pv01. Similarly, González et al. (2016) and Delfini et al. (2021) also identified significant QTLs for NPP on Pv01. Additionally, Vargas et al. (2021) and Mir et al. (2021) also mapped QTLs for NPP on chromosomes Pv01 and Pv08. Cordoba-Novoa et al. (2022) conducted a comprehensive analysis of the genetic variability and underlying architecture of traits pertinent to transpiration, stomatal regulation, and the overall water utilization of the whole plant within Mesoamerican common bean germplasm. They successfully identified specific genomic regions located on Pv01 and Pv07 that are significantly associated with critical traits, such as the mean normalized transpiration rate and the essential fraction of transpirable soil water.

4.2.3 | FPH trait

In the FPH trait, a putative stable QTL, FPH4^{AU}, was uniquely mapped to chromosome Pv04. The primary genetic contribution to the increase in FPH was attributed to the parental line Awauna UEM. This trait demonstrated genetic correlation with other evaluated traits, across all assays, except with the NSP and GYP. Moreover, besides being stable over the years, the QTL FPH4^{AU} identified on this chromosome for FPH, co-localized with PH, showed no significant QTL × environment interaction. Therefore, these QTLs are highly desirable in breeding programs as they offer greater reliability for marker-assisted selection (Table 1 and Table S5).

The FPH trait has received considerable attention in common bean breeding programs, particularly with the modernization of crop management and the increase in large-scale production. There is a growing need for plants with higher and more uniform pod insertion to facilitate mechanized harvesting. Despite this, relatively few studies have mapped QTLs for FPH on chromosome Pv04. Beattie et al. (2003), in their investigations into mapping QTLs for a common bean ideotype, identified QTLs for FPH on Pv04. Similarly, more recently, Delfini et al. (2021) also reported mapping QTLs for FPH on this chromosome. These findings underscore the importance of further research in this area to facilitate the development of common bean varieties with improved FPH characteristics.

4.2.4 | Seed weight trait (SW)

In SW trait, putative QTLs were identified on chromosomes Pv08 and Pv10. Specifically, on Pv08, we consistently identified a QTL for SW across all evaluated crop years, as well as in the combined analysis, co-localized with NPP near the marker ss715646109 (58,231,277 bp). It is noteworthy that SW and NPP exhibited a genetic correlation in all assays. Both traits were primarily influenced by additive effects, with the increase in SW attributed to Awauna UEM and the increase in NPP attributed to IPR88 Uirapuru. While this QTL did show significant QTL × environment interaction, the partition of total (PVE; 12.10) indicated that additive effects (11.49) outweighed the effects of the genotype-by-environment interaction (0.61), confirming its importance for assisted selection (Table S5).

On Pv10, we identified two QTL for SW. The SW10^{AU}, linked to the marker ss715650584 (40,255,828 bp), exhibited QTL × E interaction (Table S5); however, the majority of the phenotypic variation is attributed to additive effects (A) with small environment influence, and therefore confirmed that it is a true QTL. In turn, the QTL SW10.2^{AU}, linked to the marker ss715641827 (16,330,477 bp), did not show significant QTL × E interaction and therefore is desirable in breeding programs, as it is more reliable for assisted selection (Table 1 and Table S5). The genetic contribution to the increase in the SW derives from the parental UEM × IPR88 Uirapuru.

It is indeed quite common for various studies to map QTLs related to SW on chromosomes Pv08 and Pv10 in common bean. Silva et al. (2018), Kamfwa et al. (2018), and Nabateregga et al. (2019) also reported QTLs on Pv08 associated with this trait. Lei et al. (2020) and J. C. F. Elias et al. (2021) mapped QTLs for SW on Pv10. Similarly, Trapp et al. (2015), Sandhu et al. (2018), Langat et al. (2019), Murube et al. (2020), Valdisser et al. (2020), Vargas et al. (2021), and Mir et al. (2021) identified QTLs for SW on Pv08 and Pv10.

The stability observed in the majority of the identified QTLs across multiple years, coupled with their relatively modest phenotypic contribution, suggests the involvement of numerous loci with small effects in governing the expression of these traits. This finding aligns with the insights provided by Luo et al. (2020), indicating that the genetic architecture underlying these traits may be characterized by the cumulative impact of multiple minor effect loci.

4.2.5 | GYP trait

In the GYP trait, we identified a single putative QTL situated on chromosome Pv01. Remarkably, this QTL, designated as GY1^{AU}, was co-localized for GYP, PH, and NPP in close proximity to the marker ss715646884 (46,961,454 bp). The genetic correlation observed among PH, NPP, and GYP (Table 2) underscores the significance of uncovering co-located QTL governing these traits. Notably, this stable QTL, GY1^{AU}, demonstrates a greater contribution to the enhancement of GYP, surpassing the additive effects derived from the UEM × IPR88 Uirapuru parental lines, as evidenced by the additivity values (Table 4). Cordoba-Novoa and Hoyos-Villegas (2024) discerned loci correlated with agronomic characteristics such as flowering time, maturation rate, and yield in Middle American common beans, with loci located on Pv02 and Pv04 demonstrating interaction effects on both flowering time and yield. Furthermore, they underlined the significance of epistatic interactions among genomic regions to facilitate the optimal stacking of advantageous alleles aimed at enhancing yield outcomes. Importantly, the utilization of Pv03 and Pv08 as reference loci could lead to yield enhancement, while the allocation of markers on Pv01 and Pv04 as reference and alternative loci, respectively, would further augment yield efficiency.

Several studies have mapped QTL for grain yield on chromosome Pv01, underscoring the significance of our findings (Briñez et al., 2017; L. M. Diaz et al., 2018; Langat et al., 2019; S. Diaz et al., 2020). Additionally, research by Sedlar et al. (2020), Valdisser et al. (2020), Delfini et al. (2021), and Mir et al. (2021) has consistently mapped QTL related to grain yield on chromosome Pv01. Arriagada et al. (2023) executed a meta-QTL (MQTL) analysis aimed at discerning robust genomic regions correlated with yield-related characteristics in common bean. They elucidated that 28 MQTL were linked to both yield and phenological characteristics, underscoring their applicability for breeding programs.

The clustering of QTL for GYP, PH, and NPP in close proximity on Pv01 highlights the potential significance of this chromosomal region for commercial bean breeders (Geravandi et al., 2020). Such co-localized QTL clusters offer promising targets for marker-assisted selection, enabling the simultaneous improvement of multiple agronomic traits and thereby enhancing overall crop productivity and performance.

In conclusion, this study marks a substantial progression in the genetic characterization of the RIL population derived from the Awauna UEM × IPR88 Uirapuru cross. Utilizing 288 polymorphic SNP markers and comprehensive phenotypic data, we identified consistent QTL associated with key agronomic traits. A total of five QTL linked to PH, NPP, FPH, SW, and GYP were detected across chromosomes Pv01, Pv04, Pv08, and Pv10. Notably, three QTL exhibited co-localization for multiple traits, indicating potential pleiotropic effects or close genetic linkage. On chromosome Pv01, a QTL was identified that simultaneously influenced PH, NPP, and GYP. Similarly, chromosome Pv04 harbored QTL affecting both PH and FPH, while Pv08 contained QTL linked to NPP and SW. Finally, two distinct QTLs associated with SW were identified on Pv10. QTL mapping in individual environments successfully identified co-located, main, and relatively stable QTL, while multi-environment QTL mapping confirmed their relative importance. This comprehensive mapping QTL in the Awauna UEM × IPR88 Uirapuru population holds significant implications for common bean breeding programs, particularly for the Black commercial group in Brazil, which has historically received limited research attention despite its economic importance.

AUTHOR CONTRIBUTIONS

Deivid Lincoln Reche: Conceptualization; data curation; formal analysis; investigation; methodology; software; writing—original draft. **Maria Celeste Gonçalves-Vidigal**: Conceptualization; funding acquisition; investigation; project administration; software; supervision; visualization; writing—review and editing. **Pedro Soares Vidigal Filho**: Conceptualization; data curation; investigation; project administration; resources; supervision; validation; visualization. **Mariana Vaz Bisneta**: Conceptualization; data curation; methodology; supervision; validation; visualization; writing—original draft; writing—review and editing. **Giselly Figueiredo Lacanallo**: Data curation; methodology; visualization. **Alessandro A. Brito dos Santos**: Data curation; methodology. **Abner Pais dos Santos**: Data curation; investigation.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All data generated or analyzed during this study are included in this published article.

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REFERENCES

Arriagada, O., Arévalo, B., Cabeza, R. A., Carrasco, B., & Schwember, A. R. (2023). Meta-QTL analysis for yield components in common bean (*Phaseoulus vulgaris* L.). *Plants*, *12*, 117. https://doi.org/10.3390/plants12010117

Beattie, A. D., Larsen, J., Michaels, T. E., & Pauls, K. P. (2003). Mapping quantitative trait loci for a common bean (*Phaseolus vulgaris* L.) ideotype. *Genome*, *46*, 411–422. https://doi.org/10.1139/g03-015

Bernardo, R. (2008). Molecular markers and selection for complex traits in plants: Learning from the last 20 years. *Crop Science*, *48*, 1649–1664. https://doi.org/10.2135/cropsci2008.03.0131

Blair, M. W., Iriarte, G., & Beebe, S. (2006). QTL analysis of yield traits in an advanced backcross population derived from a cultivated Andean × wild common bean (*Phaseolus vulgaris* L.) cross. *Theoretical and Applied Genetics*, *112*, 1149–63. https://doi.org/10.1007/s00122-006-0217-2

Boopathi, N. M. (2020). QTL analysis. In *Genetic mapping and marker assisted selection: Basics, practice and benefits* (2nd ed., pp. 516). Springer. https://doi.org/10.1007/978-981-15-2949-8

Briñez, B., Perseguini, J. M. K. C., Rosa, J. S., Bassi, D., Gonçalves, J. G. R., Almeida, C., Paulino, J. F. D. C., Blair, M. W., Chioratto, A. F., Carbonell, S. A. M., Valdisser, P. A. M. R., Vianello, R. P., & Benchimol-Reis, L. L. (2017). Mapping QTL for drought tolerance in a SEA 5×AND 277 common bean cross with SSRs and SNP markers. *Genetics and Molecular Biology*, *40*, 813–823. https://doi.org/10.1590/1678-4685-GMB-2016-0222

Celmeli, T., Sari, H., Canci, H., Sari, D., Adak, A., Eker, T., & Toker, C. (2018). The nutritional content of common bean (*Phaseolus vulgaris* L.) landraces in comparison to modern varieties. *Agronomy*, *8*, 166. https://doi.org/10.3390/agronomy8090166

Chavarro, M. C., & Blair, M. W. (2010). QTL analysis and effect of the fin locus on tropical adaptation in an inter-gene pool common bean population. *Tropical Plant Biology*, *3*, 204–218. https://doi.org/10.1007/s12042-010-9058-x

Checa, O. E., & Blair, M. W. (2008). Mapping QTL for climbing ability and component traits in common bean (*Phaseolus vulgaris* L.). *Molecular Breeding*, *22*, 201–215. https://doi.org/10.1007/s11032-008-9167-5

Cordoba-Novoa & Hoyos-Villegas. (2024). Genetic architecture of ideotype-related traits in middle American beans through single trait, multi-trait and epistatic genome-wide analyses. *agriRxiv*, Article 20240338132. https://doi.org/10.31220/agriRxiv.2024.00265

Cordoba-Novoa, H., Zhang, B., Guo, Y., Aslam, M. M., Fristchi, F. B., & Hoyos-Villegas, V. (2022). Whole plant transpiration responses of common bean (*Phaseolus vulgaris*L.) to drying soil: Water channels and transcription factors. *BioRxiv*, Article 509270. https://doi.org/10.1101/2022.09.23.509270

Da Silva, L. C., De Souza, T. L. P. O., Cruz, C. D., Carneiro, P. C. S., E Silva, F. F., De Barros, E. G., Vianello, R. P., Da Fonseca, C. E. L., Song, Q., Cregan, P. B., & De Souza Carneiro, J. E. (2018). Linkage fine-mapping and QTL affecting morpho-agronomic traits of a Mesoamerican × Andean RIL common bean population. *Euphytica*, *214*, 1–15. https://doi.org/10.1007/s10681-018-2299-8

Delfini, J., Moda-Cirino, V., Dos Santos Neto, J., Zeffa, D. M., Nogueira, A. F., Ribeiro, L. A. B., Ruas, P. M., Gepts, P., & Gonçalves, L. S. A. (2021). Genome-wide association study identifies genomic regions for important morpho-agronomic traits in Mesoamerican common bean. *Frontiers in Plant Science*, *12*, 748829. https://doi.org/10.3389/fpls.2021.748829

Diaz, L. M., Ricaurte, J., Tovar, E., Cajiao, C., Terán, H., Grajales, M., Polanía, J., Rao, I., Beebe, S., & Raatz, B. (2018). QTL analyses for tolerance to abiotic stresses in a common bean (*Phaseolus vulgaris* L.) population. *PLoS One*, *13*, e0202342. https://doi.org/10.1371/journal.pone.0202342

Diaz, S., Ariza-Suarez, D., Izquierdo, P., Lobaton, J. D., De La Hoz, J. F., Acevedo, F., Duitama, J., Guerrero, A. F., Cajiao, C., Mayor, V., Beebe, S. E., & Raatz, B. (2020). Genetic mapping for agronomic traits in a MAGIC population of common bean (*Phaseolus vulgaris* L.) under drought conditions. *BMC Genomics*, *21*, Article 799. https://doi.org/10.1186/s12864-020-07213-6

Elias, A. A., Robbins, K. R., Doerge, R. W., & Tuinstra, M. R. (2016). Half a century of studying genotype by environment interactions in plant breeding experiments. *Crop Science*, *56*, 2090–2105. https://doi.org/10.2135/cropsci2015.01.0061

Elias, J. C. F., Gonçalves-Vidigal, M. C., Vaz Bisneta, M., Valentini, G., Vidigal Filho, P. S., Gilio, T. A. S., Moda-Cirino, V., & Song, Q. (2021). Genetic mapping for agronomic traits in IAPAR 81/LP97-28 population of common bean (*Phaseolus vulgaris* L.) under drought conditions. *Plants*, *10*, 1568. https://doi.org/10.3390/plants10081568

Fang, Y., Liu, S., Dong, Q., Zhang, K., Tian, Z., Li, X., Li, W., Qi, Z., Wang, Y., Tian, X., Song, J., Wang, J., Yang, C., Jiang, S., Li, W.-X., & Ning, H. (2020). Linkage analysis and multi-locus genome-wide association studies identify QTNs controlling soybean plant height. *Frontiers in Plant Science*, *11*, Article 9. https://doi.org/10.3389/fpls.2020.00009

García-Fernández, C., Campa, A., Garzón, A. S., Miklas, P., & Ferreira, J. J. (2021). GWAS of pod morphological and color characters in common bean. *BMC Plant Biology*, *21*, Article 184. https://doi.org/10.1186/s12870-021-02967-x

Gardner, K. M., & Latta, R. G. (2007). Shared quantitative trait loci underlying the genetic correlation between continuous traits. *Molecular Ecology*, *16*, 4195–209. https://doi.org/10.1111/j.1365-294X.2007.03499.x

Garrett, R. D., Koh, I., Lambin, E. F., le Polain de Waroux, Y., Kastens, J. H., & Brown, J. C. (2018). Intensification in agriculture-forest frontiers: Land use responses to development and conservation policies in Brazil. *Global Environmental Change*, *53*, 233–243. https://doi.org/10.1016/j.gloenvcha.2018.09.011

Geravandi, M., Cheghamirza, K., Farshadfar, E., & Gepts, P. (2020). QTL analysis of seed size and yield-related traits in an inter-genepool population of common bean (*Phaseolus vulgaris* L.). *Scientia Horticulturae*, *274*, 109678. https://doi.org/10.1016/j.scienta.2020.109678

González, A. M., Yuste-Lisbona, F. J., Saburido, S., Bretones, S., De Ron, A. M., Lozano, R., & Santalla, M. (2016). Major contribution of flowering time and vegetative growth to plant production in common bean as deduced from a comparative genetic mapping. *Frontiers in Plant Science*, *7*, 1940. https://doi.org/10.1016/j.scienta.2020.109678

Haggard, J. E., Johnson, E. B., & St Clair, D. A. (2015). Multiple QTL for horticultural traits and quantitative resistance to *Phytophthora infestans* linked on *Solanum habrochaites* chromosome 11. *G3 Genes|Genomes|Genetics*, *5*, 2219–233. https://doi.org/10.1534/g3.114.014654

Hoyos-Villegas, V., Song, Q., Wright, E. M., Beebe, S. E., & Kelly, J. D. (2016). Joint linkage QTL mapping for yield and agronomic traits in a composite map of three common bean RIL populations. *Crop Science*, *56*(5), 2546–2563. https://doi.org/10.2135/cropsci2016.01.0063

Kamfwa, K., Beaver, J. S., Cichy, K. A., & Kelly, J. D. (2018). QTL mapping of resistance to bean weevil in common bean. *Crop Science*, *58*, 2370–2378. https://doi.org/10.2135/cropsci2018.02.0106

Kotue, T. C., Marlyne, J. M., & Wirba, L. Y. (2018). Nutritional properties and nutrients chemical analysis of common beans seed. *MOJ Biology and Medicine*, *3*, 41–47. https://doi:10.15406/mojbm.2018.03.00074

Kromdijk, J., Bertin, N., Heuvelink, E., Molenaar, J., De Visser, P. H. B., Marcelis, L. F. M., & Struik, P. C. (2014). Crop management impacts the efficiency of quantitative trait loci (QTL) detection and use:

Case study of fruit load x QTL interactions. *Journal of Experimental Botany*, *65*, 11–22. https://doi.org/10.1093/jxb/ert365

Langat, C. K., Ombori, O., Cheruiyot, R., Gathaara, M., Karanja, D., & Leley, P. (2019). Mapping of quantitative trait loci (QTL) related to drought tolerance in common bean (*Phaseolus vulgaris* L.) using F_2 population from (KATB1×GLP2). *International Annals of Science*, *8*, 75–86. https://doi:10.21467/ias.8.1.75-86

Lei, L., Wang, L., Wang, S., & Wu, J. (2020). Marker-trait association analysis of seed traits in accessions of common bean (*Phaseolus vulgaris* L.) in China. *Frontiers in Genetics*, *11*, Article 698. https://doi.org/10.3389/fgene.2020.00698

Li, S., Wang, J., & Zhang, L. (2015). Inclusive composite interval mapping of QTL by environment interactions in biparental populations. *PLoS One*, *10*, e0132414. https://doi.org/10.1371/journal.pone.0132414

Luo, Z., Cui, R., Chavarro, C., Tseng, Y., Zhou, H., Peng, Z., Chu, Y., Yang, X., Lopez, Y., Tillman, B., Dufault, N., Brenneman, T., Isleib, T. G., Holbrook, C., Ozias-Akins, P., & Wang, J. (2020). Mapping quantitative trait loci (QTL) and estimating the epistasis controlling stem rot resistance in cultivated peanut (*Arachis hypogaea*). *Theoretical and Applied Genetics*, *133*, 1201–1212. https://doi.org/10.1007/s00122-020-03542-y

Mackay, T. F., Stone, E. A., & Ayroles, J. F. (2009). The genetics of quantitative traits: Challenges and prospects. *Nature Reviews Genetics*, *10*, 565–77. https://doi.org/10.1038/nrg2612

Mendes, F. F., Ramalho, M. A. P., & Abreu, F. B. A. (2009). Índice de seleção para escolha de populações segregantes de feijoeiro comum. *Pesquisa Agropecuária Brasileira*, *44*, 1312–1318. https://doi.org/10.1590/S0100-204İ2009001000015

Meng, L., Li, H., Zhang, L., & Wang, J. (2015). QTL IciMapping: Integrated software for genetic linkage map construction and quantitative trait locus mapping in biparental populations. *The Crop Journal*, *3*, 269–283. https://doi.org/10.1016/j.cj.2015.01.001

Miklas, P. N., & Porch, T. (2010). Guidelines for common bean QTL nomenclature. *Annual Report of the Bean Improvement Cooperative*, *53*, 202–204.

Mir, R. R., Choudhary, N., Bawa, V., Jan, S., Singh, B., Bhat, M. A., Paliwal, R., Kumar, A., Chitikineni, A., Thudi, M., & Varshney, R. K. (2021). Allelic diversity, structural analysis, and Genome-wide association study (GWAS) for yield and related traits using unexplored common bean (*Phaseolus vulgaris* L.) germplasm from Western Himalayas. *Frontiers in Genetics*, *11*, Article 609603. https://doi.org/10.3389/fgene.2020.609603

Moda-Cirino, V., Oliari, L., Lollato, M. A., & Fonseca Júnior, N. S. (2001). IPR 88 Uirapuru: Common bean. *Crop Breeding and Applied Biotechnology*, *1*, 205–206.

Mukeshimana, G., Butare, L., Cregan, P. B., Blair, M. W., & Kelly, J. D. (2014). Quantitative trait loci associated with drought tolerance in common bean. *Crop Science*, *54*, 923–938. https://doi.org/10.2135/cropsci2013.06.0427

Murube, E., Campa, A., Song, Q., McClean, P., & Ferreira, J. J. (2020). Toward validation of QTL associated with pod and seed size in common bean using two nested recombinant inbred line populations. *Molecular Breeding*, *40*, Article 70. https://doi.org/10.1007/s11032-020-01155-3

Nabateregga, M., Mukankusi, C., Raatz, B., Edema, R., Nkalubo, S., & Alladassi, B. M. E. (2019). Quantitative trait loci (QTL) mapping for intermittent drought tolerance in BRB 191 × SEQ 1027 Andean intragene cross recombinant inbred line population of common bean (*Phaseolus vulgaris* L.). *African Journal of Biotechnology*, *18*, 452–461. https://doi.org/10.5897/AJB2019.16768

Njau, S. N., Parker, T. A., Duitama, J., Gepts, P., & Arunga, E. E. (2024). QTL mapping for pod quality and yield traits in snap bean (*Phaseolus vulgaris* L.). *Frontiers in Plant Science*, *15*, 1422957. https://doi.org/10.3389/fpls.2024.1422957

Pavličev, M., & Cheverud, J. M. (2015). Constraints evolve: Context dependency of gene effects allows evolution of pleiotropy. *Annual Review of Ecology, Evolution and Systematics*, *46*, 413–434. https://doi.org/10.1146/annurev-ecolsys-120213-091721

R Core Team. (2013). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. http://www.R-project.org

Resende, M. D. V. (2016). Software selegen-REML/BLUP: A useful tool for plant breeding. *Crop Breeding and Applied Biotechnology*, *16*, 330–339. https://doi.org/10.1590/1984-70332016v16n4a49

Resende, M. D. V., & Duarte, J. B. (2007). Precisão e controle de qualidade em experimentos de avaliação de cultivares. *Pesquisa Agropecuária Tropical*, *37*, 182–194.

Sandhu, K. S., You, F. M., Conner, R. L., Balasubramanian, P. M., & Hou, A. (2018). Genetic analysis and QTL mapping of the seed hardness trait in a black common bean (*Phaseolus vulgaris*) recombinant inbred line (RIL) population. *Molecular Breeding*, *38*, 1–13. https://doi.org/10.1007/s11032-018-0789-y

Sedlar, A., Zupin, M., Maras, M., Razinger, J., Šuštar-Vozlič, J., Pipan, B., & Meglič, V. (2020). QTL Mapping for drought-responsive agronomic traits associated with physiology, phenology, and yield in an andean intra-gene pool common bean population. *Agronomy*, *10*, 225. https://doi.org/10.3390/agronomy10020225

Singamsetti, A., Shahi, J. P., Zaidi, P. H., Seetharam, K., Vinayan, M. T., Kumar, M., Singla, S., Shikha, K., & Madankar, K. (2021). Genotype × environment interaction and selection of maize (*Zea mays* L.) hybrids across moisture regimes. *Field Crops Research*, *270*, 108224. https://doi.org/10.1016/j.fcr.2021.108224

Tar'an, B., Michaels, T. E., & Pauls, K. P. (2002). Genetic mapping of agronomic traits in common bean. *Crop Science*, *42*, 544–556. https://doi.org/10.2135/cropsci2002.5440

Trapp, J. J., Urrea, C. A., Cregan, P. B., & Miklas, P. N. (2015). Quantitative trait loci for yield under multiple stress and drought conditions in a dry bean population. *Crop Science*, *55*, 1596–1607. https://doi.org/10.2135/cropsci2014.11.0792

Valdisser, P. A. M. R., Müller, B. S. F., De Almeida Filho, J. E., Morais Júnior, O. P., Guimarães, C. M., Borba, T. C. O., De Souza, I. P., Zucchi, M. I., Neves, L. G., Coelho, A. S. G., Brondani, C., & Vianello, R. P. (2020). Genome-Wide association studies detect multiple QTL for productivity in mesoamerican diversity panel of common bean under drought stress. *Frontiers in Plant Science*, *11*, 574674. https://doi.org/10.3389/fpls.2020.574674

Vargas, Y., Mayor-Duran, V. M., Buendia, H. F., Ruiz-Guzman, H., & Raatz, B. (2021). Physiological and genetic characterization of heat stress effects in a common bean RIL population. *PLoS One*, *16*, e0249859. https://doi.org/10.1371/journal.pone.0249859

Voorrips, R. E. (2002). Mapchart: Software for the graphical presentation of linkage maps and QTL. *Journal of Heredity*, *93*, 77–78. https://doi.org/10.1093/jhered/93.1.77

Wickham, H. (2016). *Package "ggplot2": Elegant graphics for data analysis*. Springer-Verlag.

Yuste-Lisbona, F. J., González, A. M., Capel, C., García-Alcázar, M., Capel, J., De Ron, A. M., Lozano, R., & Santalla, M. (2014). Genetic analysis of single-locus and epistatic QTL for seed traits in an adapted nuña RIL population of common bean (*Phaseolus vulgaris* L.). *Theoretical and Applied Genetics*, *127*, 897–912. https://doi.org/10.1007/s00122-014-2265-3

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