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Combination of meta-analysis of QTL and GWAS to uncover the genetic architecture of seed yield and seed yield components in common bean

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Abstract

Increasing seed yield in common bean could help to improve food security and reduce malnutrition globally due to the high nutritional quality of this crop. However, the complex genetic architecture and prevalent genotype by environment interactions for seed yield makes increasing genetic gains challenging. The aim of this study was to identify the most consistent genomic regions related with seed yield components and phenology reported in the last 20 years in common bean. A meta-analysis of quantitative trait locus (QTL) for seed yield components and phenology (MQTL-YC) was performed for 394 QTL reported in 21 independent studies under sufficient water and drought conditions. In total, 58 MQTL-YC over different genetic backgrounds and environments were identified, reducing threefold on average the confidence interval (CI) compared with the CI for the initial QTL. Furthermore, 40 MQTL-YC identified were co-located with 210 SNP peak positions reported via genome-wide association (GWAS), guiding the identification of candidate genes. Comparative genomics among these MQTL-YC with MQTL-YC reported in soybean and pea allowed the identification of 14 orthologous MQTL-YC shared across species. The integration of MQTL-YC, GWAS, and comparative genomics used in this study is useful to uncover and refine the most consistent genomic regions related with seed yield components for their use in plant breeding.

1 | INTRODUCTION

Common bean (*Phaseolus vulgaris* L.) is one of the most important legumes for direct human consumption around the word (Siddiq & Uebersax, 2022). Dry beans are a nutrient-dense food, rich in protein, fiber, and micronutrients, and dry bean consumption has been associated with health benefits in the prevention of cardiovascular disease, diabetes, and obesity (Didinger et al., 2022). The rich nutritional profile of dry bean, along with the crop's productivity under limited water make it an appealing food security crop for climate resilience (Medendorp et al., 2022; Siddiq & Uebersax, 2022). Legumes have up to sevenfold less greenhouse gas emissions compared with many other crops such as wheat and canola (Jeuffroy et al., 2013), and improve the soil quality through symbiotic

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Abbreviations: CI, Confidence interval; cM, Centimorgan; DF, Days to flowering; DPM, Days to maturity; GWAS, Genome-wide association; HI, Harvest index; Mb, Megabases; MQTL, Meta-analysis of QTL; MQTL-YC, Meta-analysis of QTL for seed yield components; PDPL, Pods per plant; PHI, Pod harvest index; QTL, Quantitative trait locus; QTN, Quantitative trait nucleotides; SDPD, Seeds per pod; SW, Seed weight; YDSD, Seed yield.

nitrogen fixation and increasing soil carbon content (Jensen et al., 2012), which highlight the value of dry bean as a crop to improve agricultural and dietary sustainability.

Seed yields have incrementally increased in new dry bean cultivars over time and genetic gains have not plateaued (Vandemark et al., 2015). The use of new breeding tools could help continue that trend by more efficiently stacking positive alleles. Seed yield is a quantitative trait that is controlled by numerous genes with small effects. Due to its complexity, seed yield has been divided into yield components, including number of pods per plant (PDPL), seed size, and number of seeds per pod (SDPD). Adams (1967) was the first to describe the interaction among these three yield components, where the increase in one of these three traits often resulted in a reduction of the others. Since dry bean has specific market class requirements for seed weight (SW), changing this component is generally not a viable option to increase seed yield (Kelly, 2018). The total number of PDPL and SDPD are more relevant for breeding within market classes, due to rigid seed size criteria.

Other traits associated with seed yield are related to dry matter partitioning toward seed, including pod harvest index (PHI) and harvest index (HI) (Assefa et al., 2013; Nabateregga et al., 2019; Polania, Poschenrieder et al., 2016). These traits are important indicators of yield potential under drought and non-drought conditions. Under drought, the allocation of resources to reproductive growth is reduced, leading to flower and pod abortion in susceptible genotypes, while drought-tolerant genotypes continue the partition into the seed (Hageman & Volkenburgh, 2021). Phenology traits such as days to flowering and maturity are also associated with seed yield and may have different influence under drought or non-drought conditions. While longer days to maturity may be beneficial to increase seed yield under water suf-ficient conditions, under drought conditions, short growing cycle minimizes exposure to terminal drought, leading to better yield performance (Beebe et al., 2013; Keller et al., 2020; Vandemark et al., 2015). Environmental factors such as latitude, photoperiod, and temperature influence seed yield and yield component traits, and the identification of alleles for local versus broad adaptation will support genetic gains (MacQueen et al., 2021).

For the last 20 years, quantitative trait locus (QTL) and genome-wide association studies (GWAS) have been used to uncover the genetic architecture of seed yield components, and hundreds of associated genomic regions have been identified. QTL analysis is a powerful tool to uncover the genetic architecture of complex traits. This technique comes with some limitations, including low allelic diversity and low recombination in mapping populations, which is reflected in a limited number of loci and recombination assessed on QTL analyses, resulting in QTL covering large genomic regions containing many genes (Brachi et al., 2010). GWAS includes diverse populations that ensure a higher allelic diversity than bi-parental populations and historic recombination events that overcome the two main limitations of QTL analysis (Korte & Farlow, 2013). GWAS has been reported to be a promising approach to identify quantitative trait nucleotides (QTN) associated with causative loci (Cano-Gamez & Trynka, 2020). Nevertheless, most GWAS studies are underpowered due to the limited population size and the small effect of causative loci in quantitative traits as seed yield (Evangelou & Ioannidis, 2013).

Core Ideas

- 743 genomic regions associated with seed yield components and phenology were positioned on reference genome v2.1.
- 51 MQTL-YC were supported by QTL/GWAS identified under drought and non-drought conditions.
- Combining QTL and GWAS is a powerful approach to identify candidate genes in common bean.
- 14 MQTL-YC identified in common bean were identified as orthologous to MQTL-YC reported in soybean and pea.

Although substantial efforts have been made to uncover the genetic architecture of seed yield components in dry bean through QTL and QTN, this information is challenging to use in breeding due to the lack of standardized phenotyping and molecular makers, as well as genetic background and environmental effects that arise in multiple studies (Bernardo, 2008). Additionally, in species with more than one reference genome version, such as common bean, QTL and QTN physical position vary depending on the reference genome version used in each study. Since many market classes of dry beans are bred around the world, the extrapolation of information generated among breeding programs may be limited (Vandemark et al., 2015). The Meta-QTL analysis (MQTL) is an approach that can overcome these limitations by integrating QTL from independent studies to identify and refine the most consistent QTL (Goffinet & Gerber, 2000; Izquierdo et al., 2018; Soriano & Alvaro, 2019), and the co-localization of QTN within MQTL regions leads to the identification of candidate loci with potential use in plant breeding (Bilgrami et al., 2022; Shariatipour et al., 2021).

The goals of this study were to: (i) perform a MQTL to uncover the genomic control of seed yield in dry bean, (ii) assess the co-localization of QTN within MQTL-YC, (iii) identify the physical position in the *P. vulgaris* v2.1 reference genome for all the QTL and QTN included in the analysis, and (iv) evaluate the genomic collinearity of MQTL-YC regions of dry bean with MQTL and MGWAS reported in soybean, pea, and rice. This work will help to better understand the genetic architecture of seed yield in dry bean, and will assess the potential to combine MQTL, GWAS, and comparative genomics to identify and refine the most stable MQTL-YC regions for their use in plant breeding.

2 | MATERIALS AND METHODS

2.1 | Seed yield and yield components QTL and QTN

A detailed literature search was carried out on common bean QTL and GWAS related to yield and yield components traits under sufficient water and drought conditions from 2000 to 2021. All QTL and GWAS except those lacking proper QTL-related information, genetic map information, and those reported under other stress different than drought were used in the MQTL and QTN co-localization analyses. Based on these criteria, 394 QTL and 349 QTN for seed yield (YDSD) and five yield component traits—HI, PHI, PDPL, SDPD, and SW—and two phenology traits, including days to flower (DF), days to maturity (DPM), were identified from 24 biparental, 1 multiparent, and 10 diversity panels of common bean from 21 QTL and 11 GWAS, including Andean, Middle Ameri-can, and wild germplasm (Table 1). The crop ontology for agricultural data for common bean was used as reference to unify the name of traits (https://cropontology.org/term/CO_335:ROOT).

The molecular markers with the highest test statistics associated with QTL were regarded as the estimated location of QTL for each reported association. When the position of the peak markers was not reported, the flanking marker position was used. If the position of the peak marker were not reported and flanking markers were on a different chromosome, the QTL were not used. When the physical location of markers were not reported in the studies, we searched for the amplicon sequences on the Legume Information System (Dash et al., 2016) (Table S1). When the SNP physical position were reported on *P. vulgaris* v1 genome, we extracted the 600 bp surrounding sequence of *P. vulgaris* v1 (Table S2). The amplicons and surrounding sequences were used for the Basic Local Alignment Search Tool (BLAST) analysis against the *P. vulgaris* v2.1 genome for detecting the physical position. The number of QTL and QTN associated with yield and yield components were visualized graphically via R package ggplot2 3.3.5 (Wickham, 2009).

2.2 | Conversion of physical to cM positions

The estimated location for all SNP markers in BARCBean6K_1 and BARCBean6K_2 chips and QTL and QTN were converted to cM position in the Stampede x Red Hawk reference map based on physical position for the molecular markers on the *P. vulgaris* v2.1 genome (Schmutz et al., 2014; Song et al., 2015) using a special version of cM converter for common bean (http://mapdisto.free.fr/cMconverter/). For the projection of QTL, the confidence interval (CI) of 95% was estimated in the position where the molecular marker with the highest LOD value was reported for each QTL. The formulas were $CI = 530/(N \times R^2)$ for backcross (BC), and $CI = 163/(N \times R^2)$ for recombinant inbred line (RIL) populations (Guo et al., 2006), where N is the population size and R^2 is the proportion of phenotypic variance of the QTL. If the CI was beyond the end of a chromosome, the CI was cut off at the end of that chromosome. The QTN were projected into the reference map to allow the comparison of GWAS and the MQTL analysis.

2.3 | MQTL analysis and QTN co-localization

The MQTL analysis for yield and yield components (MQTL-YC) was conducted in BioMercator v4.2 software (Sosnowski et al., 2012), and the best model of MQTL-YC was chosen according to the prevalent value among Akaike Informa-tion Criterion (AIC), corrected Akaike Information criterion (AICc and AIC3), Bayesian Information Criterion, and aver-age weight of evidence criteria. The CI of the MQTL-YC was defined as the most likely region but when QTL that belong to MQTL-YC were out of the CI, we used the extreme QTL peaks as boundaries for further analyses. QTL, QTN, and MQTL-YC were visualized graphically via Circos (Krzywinski et al., 2009).

2.4 | Ortho-MQTL analysis

The *P. vulgaris* v2.1 (Schmutz et al., 2014) genome was compared to the *Glycine max* Wm82.a2.v1 (Schmutz et al., 2010), *Pisum sativum* v1a (Kreplak et al., 2019), and *Oryza sativa* v7 (Ouyang et al., 2007) genomes using the phyton version of MCScan (https://github.com/tanghaibao/jcvi/wiki/MCscan). To detect ortho-MQTLs between common bean and the other crops, we used the MQTL and MGWA analysis reported for soybean (Shook et al., 2021), pea (Klein et al., 2020), and rice (Khahani et al., 2021) to identify the physical position on the genomes of regions associated with seed yield, seed yield-components, and phenology. Then we filtered out the syntenic blocks that were out of MQTL-YC identified on common bean. The EnsemblPlants database (Bolser et al., 2016) was used to identify the candidate and orthologous genes among species and the paralogous genes in common bean.

TABLE 1 Summary of QTL and GWAS used in the MQTL analysis for seed yield, yield components, and phenology in dry bean.

Reference	Germplasm	Gene pool	Type	Size	Env	QTL-QTN	Analysis
Blair et al. (2006)	Cerinza x G24404	AxW	BC	157	N	21	QTL
Wright & Kelly (2011)	Jaguar x 115 M	M	RIL	96	N	3	QTL
Mkwaila et al. (2011)	Tacana x PI318695	MxW	BC	30	N	1	QTL
Mkwaila et al. (2011)	Tacana x PI313850	MxA	BC	30	N	6	QTL
Galeano et al. (2012)	DP	A	DP	80	D-N	60	GWA
Asfaw et al. 2012)	BAT477 x DOR364	M	RIL	97	D-N	7	QTL
Blair et al. (2012)	BAT477 x DOR364	M	RIL	113	D-N	10	QTL
Checa & Blair (2012)	G2333 x G19839	MxA	RIL	84	N	3	QTL
Blair & Izquierdo (2012)	Cerinza x G10022	AxW	BC	138	N	8	QTL
Mukeshimana et al. (2014)	SEA5 x CAL96	MxA	RIL	125	D-N	30	QTL
Cichy et al. (2014)	Black Magic x Shiny Crow	M	RIL	100	N	5	QTL
Trapp et al. (2015)	Buster x Roza	M	RIL	140	D-N	27	QTL
Kamfwa et al. (2015)	ADP	A	DP	237	N	9	GWA
Villordo-Pineda et al. (2015)	Pinto Villa x Pinto Saltillo	M	RIL	282	D-N	34	SMA
Moghaddam et al. (2016)	MDP	M	DP	280	N	11	GWA
Hoyos-Villegas et al. (2016)	Merlot x SER48/55/94	M	RIL	76,36,48	N	9	QTL
Hoyos-Villegas et al. (2017)	SNAD	M	DP	96	D-N	2	GWA
Heilig et al. (2017)	Puebla 152 x Zorro	M	RIL	122	N	8	QTL
Diaz et al. (2018)	BAT 881 X G21212	M	RIL	95	D-N	4	QTL
da Silva et al. (2018)	Ruda x AND277	MxA	RIL	376	N	16	QTL
Resende et al. (2018)	DP	M-A	DP	188	N	4	GWA
Sandhu et al. (2018)	BK004-001 x H68-4	M	RIL	85	N	17	QTL
Onziga et al. (2019)	Portillo x Red Hawk	A	RIL	97	D-N	3	QTL
Nabateregga et al. (2019)	BRB 191 × SEQ 1027	A	RIL	128	D-N	7	QTL
Berny Mier Y Teran et al. (2019)	ICA Bunsi x SXB405	M	RIL	226	D-N	122	QTL
Geravandi et al. (2020)	Goli x AND1007	MxA	RIL	100	N	13	QTL
Wu et al. (2020)	SCAAS	M-A	DP	683	N	83	GWA
Keller et al. (2020)	VEF	A	DP	481	D-N	19	GWA
Diaz et al. (2020)	MAGIC	M	MAGIC	636	D	42–50	QTL-GWA
Mir et al. (2021)	DP	M-A	DP	96	N	34	GWA
Nkhata et al. (2021)	DP	M-A	DP	99	N	43	GWA
Diaz et al. (2022)	SCR16xSMC40	M	RIL	100	D-N	10	QTL
Diaz et al. (2022)	SMC33xSCR16	M	RIL	100	D-N	6	QTL
Diaz et al. (2022)	SMC44xSCR9	M	RIL	100	D-N	16	QTL

Abbreviations: QTL, quantitative trait locus; GWAS, genome-wide association studies; MQTL, meta-analysis of QTL. Germplasm: ADP, Andean diversity panel; MDP, Middle American diversity panel; SNAD, subset of North American diversity panel; SCAAS, subset Chinese academy of agriculture sciences; DP, diversity panel; VEF, vivero equipo frijol; MAGIC, multiparent advanced generation intercross. Type: RIL, recombinant inbred lines; BC, backcross; MAGIC, multiparent advanced generation intercross; DP, diversity panel. Gene pool: A, Andean; M, Middle American; W, wild. Environment: D, drought; N, non-drought.

3 | RESULTS

3.1 | Distribution of yield and yield-components QTL and QTN

Hundreds of molecular markers related to seed yield, yield components, and phenology have been reported in common bean. To uncover the most consistent genomic regions associated with seed yield, five yield components, and two phenology traits under sufficient water and drought conditions, a total of 394 QTL from 24 biparental and one multi-parental population were used. The populations included two Andean, and 15 Middle American intra-gene pool, five inter-gene pool, one Middle American × wild, and two Andean × wild bean populations. These populations were field grown under sufficient water and/or drought conditions from 1999 to 2017 and were reported in 21 studies (Table 1; Table S3). From the 394 QTL, 223 were identified under sufficient water and

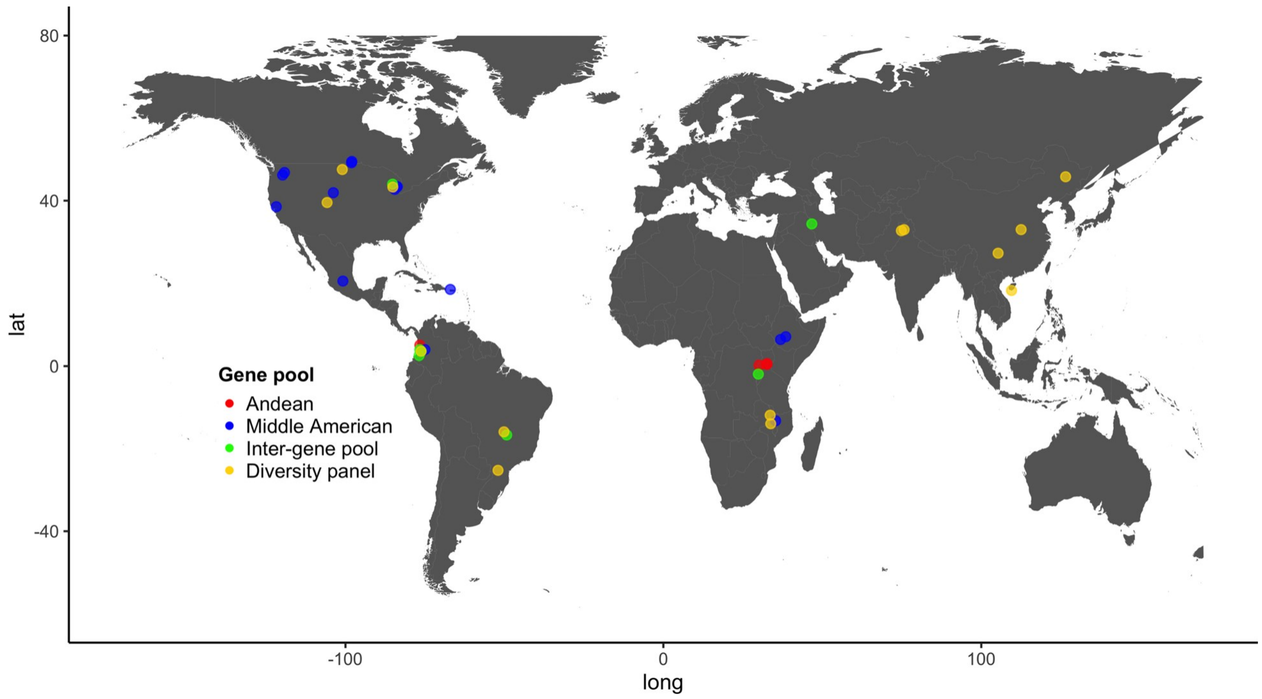

FIGURE 1 Geographic distribution of QTL and GWAS used for the MQTL and co-localization analyses. GWAS, genome-wide association studies; QTL, quantitative trait locus; MQTL, meta-analysis of QTL.

171 under drought conditions. The QTL reported for SW, DF, YDSD, and PHI were the most common QTL reported in the studies representing 34%, 20%, 16%, and 13% of total QTL, respectively.

Furthermore, a total of 349 QTN were compiled for seed yield, five yield components, and two phenology traits from 10 GWAS and one biparental population study that used a simplified method derived from GWAS, a single-marker analysis (SMA). The SMA and GWAS included germplasm of Andean and Middle American gene pools. The populations were field grown under sufficient water and/or drought conditions from 2009 to 2019 and were reported in 11 studies. (Table 1; Table S4). From the 349 QTN, 217 were identified under sufficient water, 79 under drought, and 53 under combined analysis of both conditions. The QTN reported for DF, DPM, SW, and YDSD were the most common representing 31%, 17%, 17%, and 14% of total QTN, respectively.

The QTL, SMA, and GWAS were conducted at 35 different locations distributed in 13 countries around the world (Figure 1). The distribution of QTL and QTN were unevenly distributed across the eleven chromosomes of common bean (Figure 2). Chromosome Pv01 have the highest number of QTL (69) and QTN (56) and chromosome Pv10 and Pv09 have the lowest number of QTL and QTN (15) (Figure 2).

3.2 | Meta-QTL analysis

The physical position of 394 initial QTL were converted to cM using the recombination estimated in the Stampede x Red Hawk map. Stampede x Red Hawk map has a total length of 1042.2 cM and an average distance among SNP of 0.17 cM (Song et al., 2015). The MQTL analysis confined 373 (95%) of initial QTL into 58 MQTL for yield, yield components, and phenology (MQTL-YC) supported by at least two QTL identified in different populations, environments, or traits (Table 2; Table S5). The number of MQTL-YC per chromosome ranged from three on chromosome Pv10 to eight on chromosome Pv01 (Figure 3). The Meta-QTL analysis allowed a 3.2 reduction on average of the CI (3.8 cM) in comparison to the average CI of initial QTL (12 cM). The MQTL-YC with the largest physical sizes were MQTL-YC1.2 (14.7 Mb), MQTL-YC3.3 (21.3 Mb), MQTL-YC4.2 (11.6 Mb), MQTL-YC6.1 (8.52 Mb), MQTL-YC7.5 (28.51 Mb), and MQTL-YC8.3 (42.2 Mb), all of them within the pericentromeric regions.

Further support for 40 MQTL-YC was obtained by the co-localization of 210 QTN reported for seed yield, yield components, and phenology in common bean. Since most of the QTN do not fall into coding regions and the link-age disequilibrium can affect the co-localization, QTN were considered co-localized if they were within the CI of MQTL-YC or within the boundaries of QTL peaks that support each MQTL-YC (Table 2; Table S6). The co-located QTN led to the identification of 42 candidate genes that have been related with flowering, circadian clock, root elongation, plant shoot branching, plant growth, leaf development, photoperiod, seed weight, seed development, seed yield and seed yield components in several species including common bean, Arabidopsis, rice, soybean, ryegrass, and maize

TABLE 2 Description of detected MQTL-YC.

					N of pop QTL-QTN	Traits	Env	GP	Lat
MQTL-YC1.1	10.4	2.4	2.4	12–7	7–3	DF, DPM, HI, PHI, SW, YDSD	D6, N13	B	B
MQTL-YC1.2	27.4	0.6	11.4	11–16	4–6	DF, DPM, PDPL, SDPD, SW, YDSD	D15, N10, C2	B	B
MQTL-YC1.3	41.9	1.3	29.8	5–0	1–0	DF	D3, N2	M	Temp
MQTL-YC1.4	51.0	2.0	37.1	11–3	5–2	DF, DPM, PHI, SW, YDSD	D7, N7	B	B
MQTL-YC1.5	58.5	3.7	42.8	4–1	1–1	DF, DPM	D2, N3	M	Trop
MQTL-YC1.6	65.8	1.2	45.0	4–6	3–2	DF, DPM, SW, YDSD	D1, N9	M	B
MQTL-YC1.7	74.5	1.2	47.2	16–6	4–2	DF, DPM, PHI, SW, YDSD	D4, N18	B	B
MQTL-YC1.8	115.7	1.9	51.2	5–3	2–2	PHI, SDPD	D4, N4	M	B
MQTL-YC2.1	27.2	5.0	1.8	5–0	3–0	PDPL, SDPD, SW	D2, N3	M	B
MQTL-YC2.2	41.8	3.5	2.9	8–2	5–2	DF, HI, SW, YDSD	D2, N7, C1	B	B
MQTL-YC2.3	58.6	2.4	8.3	7–0	2–0	DPM, PHI, SW, YDSD	D4, N3	M	Temp
MQTL-YC2.4	71.9	2.4	71.8	5–0	1–0	DF	D3, N2	M	Temp
MQTL-YC2.5	93.5	3.7	30.7	6–12	3–4	DF, PDPL, PHI, SDPD, SW, YDSD	D5, N13	B	B
MQTL-YC2.6	120.5	5.3	41.0	5–2	2–2	DF, DPM, PHI, SW	D5, N2	M	B
MQTL-YC2.7	161.4	0.4	47.7	5–2	2–1	PHI, SW	D5, N2	M	B
MQTL-YC3.1	4.8	5.4	1.0	3–1	3–1	DF, PHI, SW, YDSD	D2, N2	M	B
MQTL-YC3.2	37.4	4.4	3.6	9–0	2–0	PDPL, SW, YDSD	D4, N5	B	B
MQTL-YC3.3	67.5	3.2	31.4	5–5	4–5	DF, DPM, PDPL, SW, YDSD	D1, N9	B	B

(Continues)

TABLE 2 (Continued)

					N of pop QTL-QTN	Traits	Env	GP	Lat
MQTL-YC3.4	82.3	2.0	39.6	9–11	5–4	DF, DPM, SDPD, SW, YDSD	D8, N12	B	B
MQTL-YC3.5	88.4	2.2	41.7	10–1	6–1	DF, DPM, SW, YDSD	D1, N9, C1	B	B
MQTL-YC3.6	115.7	0.8	46.4	8–3	5–2	DF, HI, SW, YDSD	D3, N8	B	B
MQTL-YC4.1	4.2	2.6	0.5	7–6	6–5	DF, DPM, PHI, SDPD, SW, YDSD	D4, N8, C1	B	B
MQTL-YC4.2	48.5	3.0	12.6	7–5	3–3	DF, PDPL, SW, YDSD	D4, N8	B	B
MQTL-YC4.3	77.9	7.7	41.2	3–7	2–3	DF, DPM, PDPL, SW, YDSD	D4, N6	B	B
MQTL-YC4.4	98.9	3.4	43.6	4–0	1–0	PHI, SDPD	D1, N3	M	Temp
MQTL-YC4.5	127.8	1.0	45.4	6–6	4–2	DF, DPM, SDPD, YDSD	D1, N10, C1	B	B
MQTL-YC5.1	11.6	12.0	1.0	2–4	2–3	DPM, PHI, SW	D1, N4, C1	B	B
MQTL-YC5.2	49.3	3.3	4.7	13–0	3–0	DF, PHI, SDPD, YDSD	D7, N6	B	B
MQTL-YC5.3	59.9	2.8	12.4	5–0	1–0	SW	D3, N2	M	Temp
MQTL-YC5.4	102.6	1.5	39.2	8–2	4–1	DF, DPM, PHI, SDPD, SW, YDSD	N8, C2	B	B
MQTL-YC6.1	30.8	3.4	12.2	6–11	3–3	DF, DPM, HI, PDPL, SDPD, SW, YDSD	D10, N7	B	B
MQTL-YC6.2	43.0	1.7	18.7	10–1	2–1	DF, PHI, SW, YDSD	D7, N4	M	B
MQTL-YC6.3	51.6	3.4	19.6	5–0	3–0	DF, SW	D2, N3	B	Trop
MQTL-YC6.4	62.6	2.3	21.0	4–0	4–0	DPM, PHI, SW	N4	B	Trop
MQTL-YC6.5	87.3	0.5	26.8	9–11	4–5	DF, DPM, PHI, SW, YDSD	D7, N11, C2	B	B
MQTL-YC7.1	15.4	4.8	1.9	8–3	4–2	DF, DPM, SW, YDSD	D5, N6	M	B
MQTL-YC7.2	40.3	2.6	5.5	4–0	4–0	SDPD, SW, YDSD	D2, N2	B	B
MQTL-YC7.3	46.3	5.1	7.2	2–1	2–1	PHI, SW	D2, C1	B	Trop
MQTL-YC7.4	55.0	6.8	8.9	2–0	1–0	PHI, SDPD	D2	M	Trop
MQTL-YC7.5	63.9	0.3	27.0	31–20	5–8	DF, DPM, PDPL, PHI, SDPD, SW, YDSD	D23, N22, C6	B	B

(Continues)

TABLE 2 (Continued)

					N of pop QTL-QTN	Traits	Env	GP	Lat
MQTL-YC8.1	9.4	1.9	1.0	7–5	4–4	DF, DPM, PHI, SW, YDSD	D6, N6	M	B
MQTL-YC8.2	25.2	5.7	3.1	2–0	2–0	DPM, SW	N2	M	Temp
MQTL-YC8.3	72.7	3.7	44.5	9–7	6–4	DF, DPM, PDPL, PHI, SDPD, SW, YDSD	D6, N10	B	B
MQTL-YC8.4	103.6	2.3	54.0	3–0	3–0	SDPD, SW, YDSD	D2, N1	M	Trop
MQTL-YC8.5	141.3	0.0	59.5	9–10	6–6	DF, DPM, PDPL, SDPD, SW, YDSD	D2, N16, C1	B	B
MQTL-YC9.1	2.6	4.3	1.9	2–2	2–1	DPM, PDPL, SW	N4	A	B
MQTL-YC9.2	31.8	6.2	14.3	4–3	3–2	DF, HI, PHI, SW, YDSD	D1, N6	B	B
MQTL-YC9.3	64.9	5.6	23.7	7–1	4–1	DF, DPM, SW	D2, N6	B	B
MQTL-YC9.4	84.2	5.8	26.6	3–1	2–1	DF, YDSD	D1, N2, C1	B	B
MQTL-YC9.5	90.8	3.5	29.5	2–0	1–0	DF, DPM	N2	A	Trop
MQTL-YC9.6	97.4	1.8	31.1	5–0	1–0	SW	D3, N2	M	Temp
MQTL-YC10.1	9.5	4.7	2.7	5–4	3–3	DPM, PDPL, PHI, SW, YDSD	D3, N5, C1	M	B
MQTL-YC10.2	85.8	8.4	40.9	3–7	3–2	DPM, PDPL, SDPD, YDSD	D3, N7	B	B
MQTL-YC10.3	96.9	1.0	41.7	3–0	3–0	HI, SDPD, YDSD	D1, N2	B	B
MQTL-YC11.1	5.9	3.3	0.6	9–2	3–2	DF, SW, YDSD	D5, N6	B	B
MQTL-YC11.2	46.5	6.3	5.7	6–0	2–0	DF, SW	D4, N2	M	B
MQTL-YC11.3	76.5	29.2	38.7	2–8	1–6	DF, DPM, PDPL, SW, YDSD	D3, N6, C1	B	B
MQTL-YC11.4	104.7	1.2	49.7	3–2	2–2	DF, PHI, YDSD	D2, N3	M	B

Abbreviations: MQTL-YC, meta-analysis of QTL for seed yield components. DPM, days to maturity; DF, days to flowering; HI, harvest index; PDPL, pods per plant; SDPD, seeds per pod; PHI, pod harvest index; SW, seed weight; YDSD, seed yield. Environment (Env): drought (D), non-drought (N), and combined (C) conditions. Germplasm (GP): MQTL-YC with effects in Andean (A), Middle American (M), and both (B) gene pools. Latitude (Lat): MQTL-YC with effects in temperate (Tem), tropical (Trop), and both latitudes.

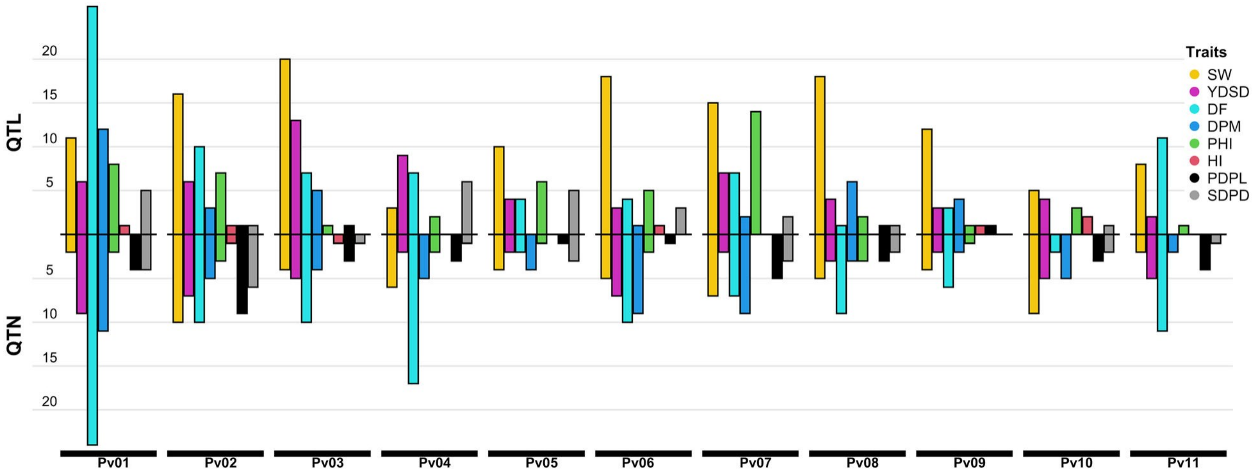

FIGURE 2 The number and distribution of QTL and QTN associated with seed yield, yield components, and phenology in common bean. DF, days to flowering; DPM, days to maturity; PHI, pod harvest index; HI, harvest index; PDPL, pods per plant; SDPD, seeds per pod; SW, seed weight; YDSD; seed yield; QTL, quantitative trait locus; QTN, quantitative trait nucleotides.

(Table S7). The well-known *fin* (Phvul.001G189200) and *Ppd* (Phvul.001G221100) genes are in MQTL-YC1.6 and MQTL-YC1.7, respectively, and several QTN were reported around them, which show the potential of QTN to narrow down genomic regions to identify candidate genes.

3.3 | MQTL-YC across yield components and phenology

Multiple yield component and phenology QTL/QTN were identified within individual MQTL-YC (Figure 4). In total, 38 out of 58 MQTL-YC included QTL/QTN for YDSD. The co-localization of QTL/QTN for seed yield components with YDSD ranged from 68% (PHI) to 100% (HI). The QTL/QTN for DF, DPM, PHI, SW, and YDSD most frequently co-localized within MQTL-YC; however, this could be a result of the higher number of QTL/QTN reported for these traits as compared to HI, PDPL, and SDPD (Figure 4). PDPL has been reported to be critical for YDSD in dry bean (Kelly, 2018). QTL/QTN for PDPL had 93% co-localization with SW and 53% with SDPD. Interestingly, the co-localization of QTL/QTN for PDPL with QTL/QTN for partitioning traits (HI [7%], PHI [27%]) was lower compared to SDPD (HI [33%], PHI [47%]) and SW (HI [83%], PHI [80%]). QTL/QTN for phenology traits (DF, DPM) showed a high co-localization frequency with the other traits, ranging for DPM from 53% (SDPD) to 87% (SW).

The co-localization of different traits could be explained by pleiotropy or linkage disequilibrium among causative loci. Although it is challenging to distinguish between them (Chebib & Guillaume, 2021), some MQTL-YC seem to have pleiotropy caused by major QTL, for example, MQTL-YC1.6 comprising the *fin* locus that controls growth habit (Figure 5a), while others such as MQTL-YC3.5 seems to be controlled by tightly linked loci (Figure 5b). MQTL-YC1.6 and MQTL-YC3.5 are both associated with DF, DPM, YDSD, and SW. However, in MQTL-YC1.6 all the QTL/QTN related to DF, DPM, and YDSD are surrounding the *fin* loci, while in MQTL-YC3.5 the QTL are clustered by trait.

3.4 | MQTL-YC across gene pool and latitude

From the 373 QTL contained in the MQTL-YC, the parental sources originated from wild, Andean, and Middle American gene pools for 9, 68, and 296 QTL, respectively. Additionally, from the 210 QTN that co-located with MQTL-YC, 53 and 57 were reported in Andean and Middle American populations, respectively. The remaining 100 QTN were reported in diversity panels including both gene pools. In total, 327 associations were identified in tropical (<30 degrees north latitude), and 253 in temperate (> 30 degrees north latitude) regions. Out of the total number of MQTL-YC, two were specific for Andean, 22 for Middle American, and 34 have sources from both gene pools. In total, 31 MQTL-YC were supported by QTL/QTN identified in both gene pools and latitudes, which suggests that these regions could have effects across wide genetic backgrounds, independent of latitude (Table 2).

3.5 | MQTL-YC related with drought

In total, 51 out of 58 MQTL-YC were supported by QTL/QTN identified under both non-drought and drought conditions,

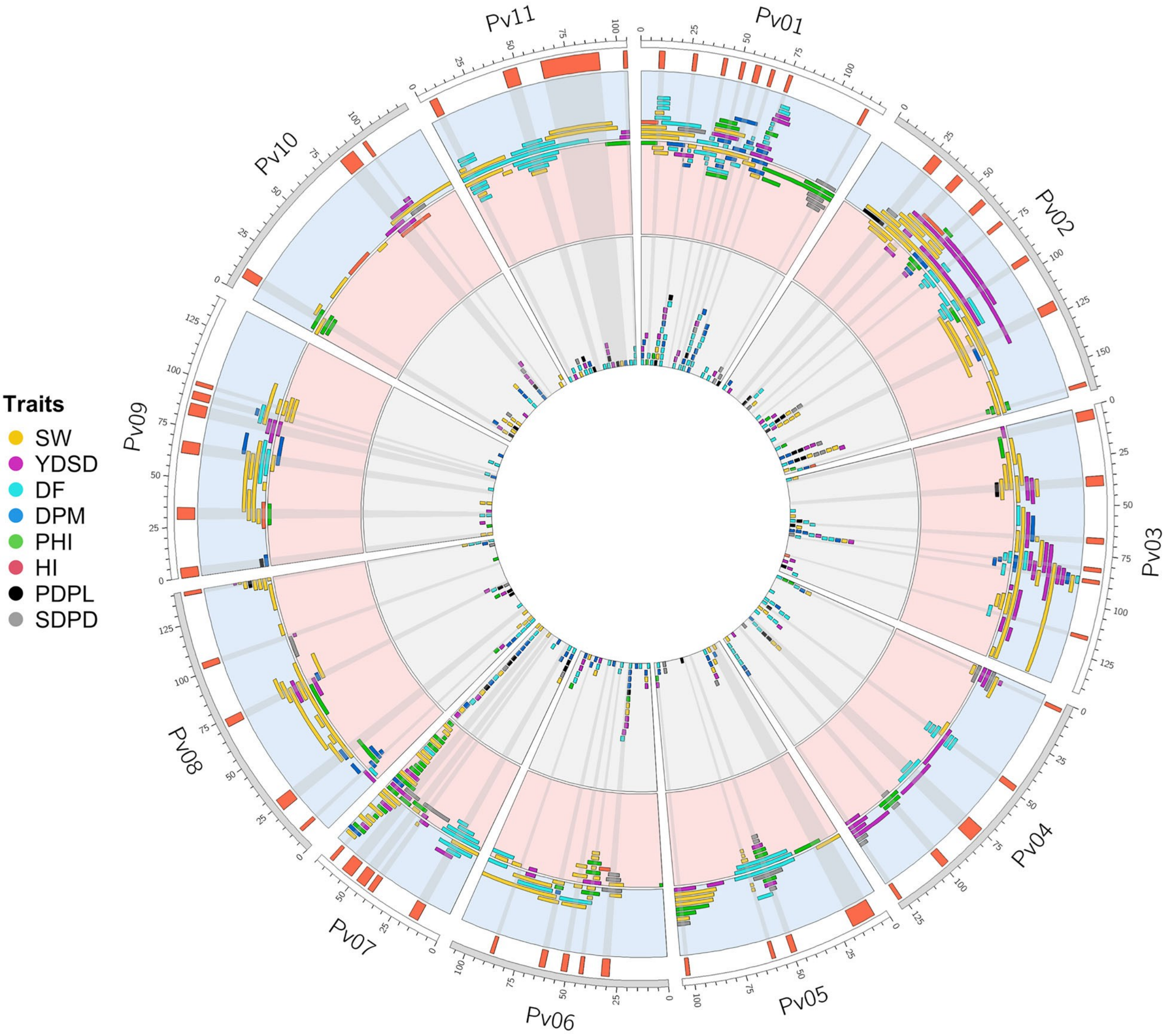

FIGURE 3 Circus plot showing distribution of MQTL-YC, QTL and QTN associated with yield, yield components, and phenology in common bean. The outermost circle indicates the length in cM on the reference genetic map Stampede x Redhawk. The second circle indicates the MQTLs with 95% confidence intervals. The third circle displays the QTLs. The fourth circle displays the QTN. QTL, quantitative trait locus; QTN, quantitative trait nucleotides; MQTL-YC, meta-analysis of QTL for seed yield components; SW, seed weight; YDSD; seed yield; DF, days to flowering; DPM, days to maturity; PHI, pod harvest index; HI, harvest index; PDPL, pods per plant; SDPD, seeds per pod.

which supports the hypothesis that breeding for both conditions simultaneously is possible. However, five out of those 51 (MQTL-YC1.4, MQTL-YC6.1, MQTL-YC6.5, MQTL-YC7.5, and MQTL-YC8.3) appear to be relevant for drought due to the high number (> 6) of QTL/QTN in this environment and their association with partitioning. All these MQTL-YC were supported by QTL/QTN identified in both gene pools and latitudes (Table S8).

3.6 | Ortho-MQTL analysis

Genomic synteny was evaluated among the MQTL-YC identified in dry bean and MQTL studies for pea (Klein et al., 2020) and rice (Khahani et al., 2021) and a MGWAS study for soybean (Shook et al., 2021). In total, 43 MQTL-YC identified in this study showed synteny blocks (ortho-MQTL-YC) with genomic regions associated with seed yield components in pea and/or soybean (Tables S9 and S10), and 14 ortho-MQTL-YC were identified across legumes (Table 3; Figure 6). Among the ortho-MQTL-YC, the MQTL-YC3.6 was the only one that showed synteny with genomic regions associated with yield components in rice (Tables S9 and S10). In total, 38 out of the 43 ortho-MQTL-YC showed signatures of selection in common bean (Schmutz et al., 2014; Wu et al., 2020), which indicated that these are conserved regions in the genome (Table S11).

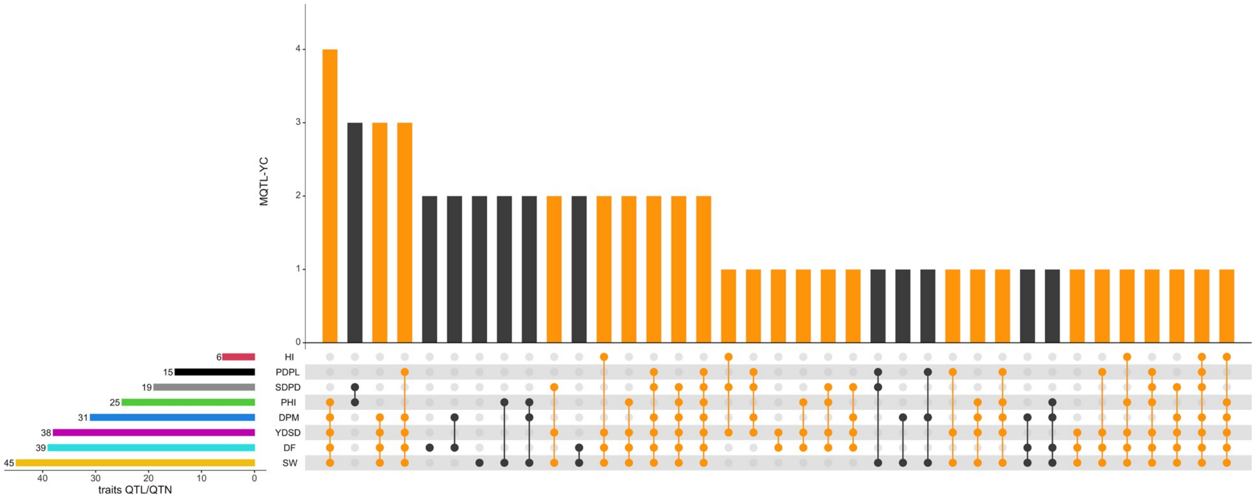

FIGURE 4 Upset plot showing the interaction among traits within the 58 MQTL-YC. The number of MQTL-YC in which each trait was reported are displayed as horizontal bars in the lower-left corner. The number of intersections are shown as vertical bars, with those including YDSD QTL/QTN highlighted in orange. The QTL/QTN traits involved in each intersection are identified with connected circles, with those including YDSD QTL/QTN highlighted in orange. DPM, days to maturity; DF, days to flowering; HI, harvest index; PDPL, pods per plant; SDPD, seeds per pod; PHI, pod harvest index; SW, seed weight; QTL, quantitative trait locus; QTN, quantitative trait nucleotides; MQTL-YC, meta-analysis of QTL for seed yield components; YDSD, seed yield.

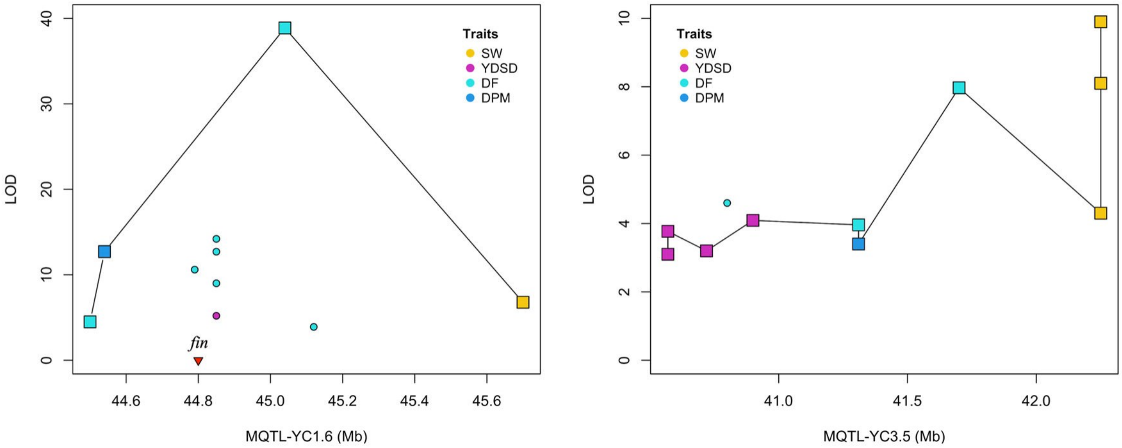

FIGURE 5 Co-localization of QTL and QTN in (a) MQTL-YC1.6 and (b) MQTL-YC3.5. The squares and circles represent QTL and QTN, respectively. The red triangle in MQTL-YC1.6 is the location of the *fin* locus. QTL, quantitative trait locus; QTN, quantitative trait nucleotides; MQTL-YC, meta-analysis of QTL for seed yield components; SW, seed weight; YDSD; seed yield; DF, days to flowering; DPM, days to maturity.

To further explore the 42 candidate genes identified through the co-localization of MQTL-YC and QTN, a search of their orthologous genes in pea, soybean, and rice was conducted, and seven genes associated with yield and yield components were identified in four ortho-MQTL-YC regions. MQTL-YC2.7 contains a protein kinase domain (*Phvul.002G302300* orthologous to the pea *Psat7g020840* gene) and three MADS-box genes (*Phvul.002G309200, Phvul.002G309400, Phvul.002G309500* orthologous to the soybean *Glyma.05G227200* gene). Protein kinase domain genes regulate plant development and seed yield components in rice (Zhou et al., 2016), while MADS-box have been related with seed development and reproductive organ development in species such as *A. thaliana, Glycine max* and *O. sativa* (Gramzow & Theissen, 2010). MQTL-YC3.3 has an orthologous response regulator receiver gene (*Phvul.003G110100* orthologous to the soybean *Glyma.17G030600* gene). Response regulator receiver genes have been related with seed growth and development in soybean (Assefa et al., 2019). Two serine/threonine-protein kinase (STK) genes were identified in MQTL-YC3.6 (*Phvul.003G252400*) and MQTL-YC7.5 (*Phvul.007G174900*). STK genes have been associated with flowering (Deng et al., 2017) and seed weight (Hu et al., 2012) in rice, and in maize the

TABLE 3 Ortho MQTL-YC detected between common bean, soybean and pea.

MQTL	Start (Mb)	End (Mb)	QTL-QTN	GP	MQTL soybean	MQTL pea
MQTL-YC2.1	1.4	1.9	5–0	M	SW_meta	mQTL1.4, mQTL4.3
MQTL-YC2.7	46.8	47.7	5–2	M	DF_ms923	mQTL7.1
MQTL-YC3.1	0.2	2.0	3–1	M	YIELD_il0102	mQTL2.1–2.2
MQTL-YC3.3	11.7	33.0	5–5	B	SW_meta	mQTL4.1, mQTL4.2
MQTL-YC3.4	35.4	40.0	9–11	B	SW_meta	mQTL4.1, mQTL4.2
MQTL-YC3.6	44.3	49.2	8–3	B	YIELD_2il81.2	mQTL4.3
MQTL-YC5.2	4.6	7.2	13–0	B	DF_sojams989	mQTL6.1
MQTL-YC5.4	38.7	39.5	8–2	B	MD_2mn81	mQTL3.4
MQTL-YC7.5	11.1	39.6	31–20	B	DF_il989, MD_il989	mQTL2.1–2.2
MQTL-YC9.2	14.0	15.4	4–3	B	SW_il0102	mQTL3.1
MQTL-YC10.2	40.5	41.3	3–7	B	DF_5il90	mQTL4.5
MQTL-YC11.1	0.4	1.3	9–2	B	DF_ms923	mQTL7.3
MQTL-YC11.3	10.1	45.4	2–8	B	DF_meta, MD_il989, YIELD_mn945	mQTL7.3–7.4
MQTL-YC11.4	49.4	51.8	3–2	M	YIELD_ms967	mQTL4.5

Abbreviations: MQTL-YC, meta-analysis of QTL for seed yield components; MD, maturity date. Germplasm (GP): MQTL-YC with effects in Middle American (M), and both (B) gene pools.

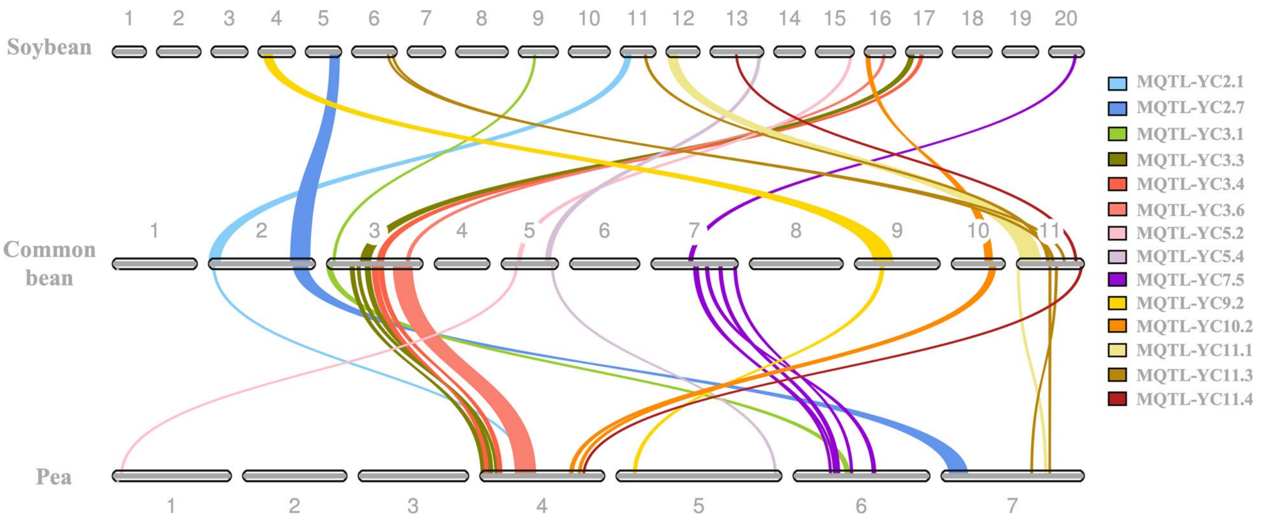

FIGURE 6 Comparative maps of ortho-MQTLs among common bean, soybean and pea. MQTL, meta-analysis of quantitative trait locus; MQTL-YC, meta-analysis of QTL for seed yield components.

overexpression of a STK protein significantly increased grain yield (Jia et al., 2020). The gene *Phvul.003G252400* (49.2 Mb) located in MQTL-YC3.6 has orthologous genes in rice (*LOC_Os02g45054*), soybean (*Glyma.16G141100*), and pea (*Psat4g091880*). Kelly, 2018 suggested the importance of loci in chromosome PV03 related to yield in previous studies, although the loci were not well defined due to the availability of analytical tools when prior studies were reported. Interestingly, QTN associated with YDSD were closely located near both STK paralogous genes (*Phvul.003G252400, Phvul.007G174900*) in MQTL-YC3.6 and MQTL-YC7.5 (Cichy et al., 2014; Resende et al., 2018).

4 | DISCUSSION

4.1 | Seed yield and seed yield components QTL and QTN in common bean

QTL and GWAS studies provide rich datasets to understand the genetic architecture of seed yield in common bean that can be used to improve breeding methods and targets. The value of these studies is greatly increased when they are taken collectively as with the MQTL approach. The integration of QTL and GWAS is an effective approach to take advantage of the power of detection of QTL and high resolution of GWAS, narrowing down the number of candidate genes (Bilgrami et al., 2022; Brown et al., 2021). Seed yield is a complex trait that is controlled by many QTL with small affects, and it is strongly affected by environmental conditions. This complex genetic architecture reduces the power to uncover the genomic regions that are associated with seed yield. To address this limitation, we identified seed yield components and phenology traits that have been widely used in QTL and GWAS that have a less complex genetic architecture controlled by fewer genes. Disaggregating complex traits into more simple ones can increase the power to detect the causative loci (Benjamin et al., 2012).

All QTL and QTN evaluated in this study were physically positioned in relation to the *P. vulgaris* reference genome v2.1. This allowed the comparison of genetic maps from: (i) different mapping populations that depend on the num-ber of markers and recombination events to estimate the genetic positions of markers, and (ii) studies that reported the QTL/QTN positions on reference genome v1, since the physical position of markers change in the most updated reference genome v2.1. The identification of physical positions in v2.1. for all QTL (394) and QTN (349) included in this study allowed for the comparison from independent experiments and environments and made an ideal dataset for MQTL analyses due to the high reliability of the physical markers position on the latest genome reference v2.1. One other MQTL analysis for yield and yield components is available in dry beans (Arriagada et al., 2023). However, the MQTL positions of this study were reported using the physical location of the *P. vulgaris* v1 genome on the genetic map Stampede x Red Hawk (Song et al., 2015), which limits the comparison across studies using the latest *P. vulgaris* v2.1 genome.

4.2 | MQTL analysis

The current MQTL analysis included QTL and QTN identified in the last 20 years in dry bean. However, not all the QTL/QTN reported for seed yield components were considered in the analysis because of lack of information to identify their physical position. Additionally, instead of using a consensus map that depends on common markers among individual mapping populations to project the QTL/QTN, we used the recombination rate estimated in the highly saturated Stampede x Red Hawk reference map genotyped with BARCBean6K_1 and BARCBean6K_2 BeadChips that are commonly used for QTL and GWAS in dry bean (Geravandi et al., 2020; Heilig et al., 2017; Moghaddam et al., 2016; Song et al., 2015). The use of the recombination rate in the Stampede x Red Hawk reference map (i) overcomes the need for common markers among individual maps, and (ii) improved the quality of the MQTL because the popula-tion size (267) is up to eightfold compared to the populations included in this study, which translate in a better estimation of the recombination.

This study narrows down the CI of detected MQTL-YC compared to the initial QTL. However, although the Gaussian mixture model implemented in Biomercator has been shown to be a good clustering approach to determine the real number of distinct QTL (Sosnowski et al., 2012; Veyrieras et al., 2007), factors such as population size, number of markers, and QTL effect influence the CI of QTL, which affect the CI of the MQTL (Guo et al., 2006; Visscher & Goddard, 2004). Moreover, other biological factors such as linkage disequilibrium and genomic regulatory elements that can influence gene expression of causative genes could be underestimated by the CI of the MQTL. Although the CI is the most likely region estimated by the Gaussian mixture model, we were conservative and when QTL were out of the CI, we used the extreme QTL to define the MQTL-YC regions. The MQTL-YC with the largest physical sizes were in the pericentromeric regions. The pericentromeres contained 26.5% of the genes identified in common bean, and the average recombination rate is lower (5.1 Mb/cM) compared to euchromatic arms (0.24 Mb/cM) (Schmutz et al., 2014), which explained the large physical size of these MQTL-YC, especially for MQTL-YC7.5 and MQTL-YC8.3 regions with a recombination rate of 9.2 and 6.9 Mb/cM, respectively (Schmutz et al., 2014).

Additional support for MQTL-YC were assessed with the co-localization of QTN associated with seed yield, yield components, and phenology. In this study, 60% (210) of QTN included co-localized with 40 MQTL-YC, which suggest that 40% of QTN could be: (i) false-positive associations related with population structure or (ii) QTN related with rare alleles that are not common in breeding programs. Interestingly, candidate genes associated with selection signatures have been reported on 49 out of 58 MQTL-YC genomic regions in previous studies (Schmutz et al., 2014; Wu et al., 2020) (Table S11).

The validation of candidate genes in dry bean is challenging because the lack of an efficient transformation pipeline and its recalcitrance to in vitro regeneration (Baloglu et al., 2022; Hnatuszko-Konka et al., 2014). However, promising candidate genes were identified by integrating MQTL-YC and reported QTN. The well-known genes *fin* and *Ppd* related with determinacy and photoperiod sensitivity were identified precisely within MQTL-YC with several QTN around them (< 10 kb). We found that focusing on QTN that have co-localization with MQTL-YC is a powerful approach to narrow down the genomic regions leading to the identification of 42 candidate genes. The receptor associated kinase (RAK) *Phvul.006G020700* was closely located to QTN (69 kb) reported for YDSD, SW, and DPM in MQTL-YC6.1. In a study, transgenic plants silenced for RAK presented a reduction of seed number in rice (Zhou et al., 2016). Interestingly, three QTL for SDPD were detected in MQTL-YC6.1, which suggest that the role of *Phvul.006G020700* could be similar in dry bean. MADS-box protein have been related with seed development in Arabidopsis (Gramzow & Theissen, 2010), and three MADS-box protein belonging to MQTL-YC2.7 are closely located to QTN for SW and PHI. In addition, MQTL-YC2.7 comprised QTL for SW and PHI, which provide evidence that this region is related with seed development. Although the 42 candidate genes detected within MQTL-YC can potentially have the same function of orthologous genes, they should be validated, and in the absence of an efficient transformation methodology in dry bean, the integration of functional genomics data such as transcriptomics, proteomics, epigenomics, and comparative genomics can help to pinpoint the causal genes associated with yield (Cano-Gamez & Trynka, 2020; Ghoussaini et al., 2021; Ibrahim et al., 2020).

4.3 | MQTL-YC across yield components

Finding that 51 out of 58 MQTL-YC were supported by QTL/QTN identified under both drought and non-drought conditions supports the hypothesis that yield potential is not exclusive between non-stressful and stressful environments (Beebe et al., 2008; Diaz et al., 2018), and genes related to traits such as photosynthate translocation, phenology, plant architecture, seed, and development could help to increase seed yield in both conditions. The MQTL-YC could be classified into two groups depending on whether they are related to phenology. 46 MQTL-YC are related to phenology (DF and/or DPM), and 12 have no QTL/QTN identified for DF or DPM. Overall, increasing days to maturity allows plants to produce more biomass and have more time for seed filling increasing partitioning, seed size and seed number leading to high seed yield under sufficient water conditions. However, under drought conditions, the tendency of positive correlation between seed yield with DF and DPM changes to negative due to abortion of flowers, pods and seeds caused by water stress, especially under terminal drought in drought susceptible lines. The antagonistic effect between DF and DPM with YDSD under drought conditions was observed with the susceptible (MIB778) and drought tolerant parents (SEN56 and ALB213) in a MAGIC population, where loci from MIB778 consistently increase DF and DPM, while loci of SEN56 and ALB213 increase SW and YDSD (S. Diaz et al., 2020). Remarkably, some drought tolerant lines had increased yield in non-stressed conditions as well as slightly earlier maturity, suggesting genetic effects of crop efficiency that do not depend on a longer vegetative period (Beebe et al., 2008). The previous finding is supported by five MQTL-YC (1.2, 2.3, 3.3, 6.5, 7.5) where QTL for YDSD and DF/DPM were identified in the same population and loci from drought-tolerant lines increased YDSD while reducing phenology traits (DF and/or DPM) (Teran et al., 2019; Diaz et al., 2020; Trapp et al., 2015; Wright & Kelly, 2011). Additionally, phenology is affected by differences in photoperiod, represented by long-day and short-day in temperate and tropical regions, respectively. Photoperiod sensitivity is under oligogenic control and has effects in the reproductive development (Weller et al., 2019). In a cross between an adapted and a photoperiod sensitive landrace, the long-day treatment reduced the internode length, increasing the number of PDPL compared to short-day on dry bean (González et al., 2021). The differences between photoperiod sensitivity and reproductive development in high latitudes are related to local adaptation, and the higher number of pods reported by Gonzalez et al. (2021) could be beneficial for seed yield in temperate regions.

The most consistent MQTL-YC was determined by the number of supported QTL/QTN and the number of different genetic backgrounds where the associations were reported. We used the following criteria to identify the most robust MQTL-YC in common bean: (i) MQTL-YC with QTL/QTN in at least five populations, and (ii) MQTL-YC with at least one QTL/QTN for YDSD. Based on these criteria, we identified 28 MQTL-YC that could be used in common bean breeding to increase seed yield (Table S8). Interestingly, 27 of these MQTL-YC were supported by QTL/QTN reported with effect in both low and high latitudes and both water supplies, and from them, 23 were supported by QTL/QTN with both gene-pools as sources while the reminder four were supported by QTL/QTN where the sources were Middle American genotypes. The MQTL-YC5.4 was the only robust MQTL-YC that was supported for QTL/QTN under sufficient water conditions alone, which reinforced the hypothesis that genetic gain for seed yield is achievable for both drought and non-drought simultaneously.

These robust MQTL-YC could be used to deploy marker-assisted selection strategies. It is important to consider that all these MQTL-YC included phenological traits. However, QTL with high additivity for DF and DPM (> 2 days) were in general reported in crosses (i) between parents of different growth habit (Trapp et al., 2015), (ii) including photoperiod sensitive material field grown in temperate regions (Heilig et al., 2017), and (iii) including wild accessions (Blair et al., 2006), which suggest that increasing seed yield using these MQTL-YC in adapted germplasm with similar growth habit should not increase significantly DPM. Besides, breeders in temperate regions should look closely at the MQTL-YC1.7 comprising the *Ppd* locus controlling photoperiod sensitivity, which in a dominant state could increase DF and even produce non-flowering plants under long-day environments such in temperate regions (Weller et al., 2019).

Among the detected MQTL-YC in this study, 12 MQTL-YC are unrelated with phenology, and although they do not fulfill our criteria to be labeled as robust MQTL-YC, these MQTL-YC have the potential to improve seed yield with-out increasing DF and DPM. As the number of different populations supporting each MQTL-YC reflects their potential use in a wide genetic background, we believe that the MQTL-YC unrelated with phenology with QTL/QTN identified in at least three populations could be consider for breeding decisions.

4.4 | MQTL-YC related with drought

Drought is one of the most important abiotic stress in common bean around the world, and it is expected to affect more growing areas under future climate change scenarios (Beebe et al., 2008; Hummel et al., 2018). Under drought conditions, susceptible dry beans cultivars slow vegetative growth and seed filling while increasing flower and pod abortion, and tolerant genotypes maintain high vegetative growth and seed filling, which suggest that high partitioning efficiency into seeds is a good indicator of drought tolerance (Hageman & Volkenburgh, 2021). In the populations used in this analysis, drought tends to reduce the number of pods and seeds per plant (Diaz et al., 2022), while increasing SW (Diaz et al., 2018), which could be explained by less competition for nutrients due to lower number of seeds the during seed filling period.

Although the reported correlation between SW with PHI is not strong (Diaz et al., 2022), and sometimes negative (Kamfwa et al., 2015), we identified that 80% (25) of the MQTL-YC that involved QTL for PHI overlap with QTL reported for SW. Furthermore, a strong correlation between PHI and seed number has been reported (Teran et al., 2019; Diaz et al., 2022), indicating that sink strength is higher for seed number than for seed weight. However, the number of seeds per pod is more sensitive to abiotic stresses such as drought and heat, (Teran et al., 2019; Diaz et al., 2022), which could lead to partitioning in a reduced number of seeds increasing the seed size under drought stress (Diaz et al., 2020; Mukeshimana et al., 2014). Middle American genotypes tend to have more pods, more seeds and a greater ability to mobilize photosynthates to pod production and seed filling compared with Andean genotypes (Kelly, 2001; Polania, Rao et al., 2016), while Andean cultivars tend to have larger seeds than Middle American (Kelly, 2001). These differeces may explain the higher suceptibility of Andean cultivars to drougtht compared to Middle American genotypes (Polania, Rao et al., 2016). The larger number of seeds and pods in Middle American genotypes could work as a buffer under drougth conditions when plants are subjected to seed and pod abortion. This would result in higher seed yield compare to Andean genotypes with larger seeds and pods. Although all the robust MQTL-YC but one identified in this study have QTL/QTN identified under drought conditions, five MQTL-YC appear to be more relevant for drought. These include, MQTL-YC1.4, MQTL-YC6.1, MQTL-YC6.5, MQTL-YC7.5, and MQTL-YC8.3 which originate from 6 to 23 QTL/QTN identified under drought. These MQTL-YC are associated with phenology (DF, DPM) and partitioning (HI, PHI), traits that are related with drought tolerance.

4.5 | MQTL-YC related with domestication

Complex traits such as seed yield are controlled by many QTL with small effects across the genome. Although major QTL could contribute to the variation of complex traits, most of them have been fixed due domestication (Bernardo, 2008; Doebley, 2006). In previous studies involving landraces and wild germplasm, several major QTL for DF, DPM, PDPL, and SW belonging to MQTL-YC regions were identified (Blair & Izquierdo, 2012; Blair et al., 2006; Checa & Blair, 2012; Geravandi et al., 2020). The highest additivity for each trait was 11.4 g for SW, 4 days for DF, 3 days for DPM, and five pods for PDPL,. Taking into account that the definition of additivity is half of the difference between the two homozygous in biparental populations (Li et al., 2011), the effect of these regions is large. However, QTL for the same traits reported in crosses between adapted cultivars show that the effect is 10-fold lower, which reflects the effect of domestication in common bean.

Furthermore, we identified that 58% (34) of the MQTL-YC are supported by QTL identified in both gene pools. This could indicate that selection pressure for yield led to focus-ing on similar genomic regions in both gene pools. Schmutz et al. (2014) reported that less than 10% of the genes related with domestication were similar between both gene pools. However, this proportion could be underestimated due to the lack of demographic information in that study to control false positive regions with low genetic diversity (Bitocchi et al., 2017). Additionally, although Schmutz et al. (2014) reported that more than 90% of the genes related to domestication in dry beans were gene pool specific most are located in close physical proximity, and domestication candidate genes for both gene pools were located within 22 out of 34 MQTL-YC supported by QTL identified in both gene pools, which give additional support to these regions in the control of domestication traits such as seed yield components (Tables S11 and S12).

4.6 | Comparative genomic analysis

Comparative genomics is a useful approach to identify orthologous loci that have been reported in other species as causative loci. In this study, we compared the genome of common bean with soybean, pea, and rice genomes to identify orthologous MQTL (ortho-MQTL) across species. Since the genomic regions of 49 MQTL-YC were reported with signatures of selection (Schmutz et al., 2014; Wu et al., 2020), it was reasonable to hypothesize that similar legumes as pea and soybean could present ortho-MQTL regions that control seed yield. Yield components and phenology have been under human selection to increase seed production in crops, leading to the selection of similar phenotypic features in different species, and these set of traits have been described as part of the domestication syndrome (Pickersgill, 2018), which is the most evident case of convergent evolution in plants (Rau et al., 2019). We identified several ortho-MQTL across legumes with signature of selection in dry bean which could indicate a convergent evolution of seed yield components in legumes. As defined by Pickersgill, 2018, convergent evolution can be produced by different non-homologous genes or by different mutations in homologous genes. Additionally, using the co-localization of QTN and the synteny with related species, we identified seven candidate genes that are within the MQTL-YC regions, in the proximity of GWA peaks and have orthologous genes related to yield components in other species, which suggest that employing QTN, and comparative genomics could be useful for identifying causal loci in MQTL-YC regions.

5 | CONCLUSIONS

In this study, we described a genome-wide landscape for the most consistent genomic regions associated with seed yield, yield components, and phenology through QTL and GWAS identified over the last two decades in common bean. All QTL and QTN were positioned on *P. vulgaris* reference genome v2.1, thereby allowing for inclusion of results from older studies.

The robust MQTL-YC supported by at least five populations reported in this study should be considered for dry bean breeding to increase seed yield. The MQTL-YC regions could be used to develop markers for marker-assisted selection and also into genomic selection models to assess their potential as fixed variables to increase the prediction accuracies (Izquierdo et al., 2018; McGowan et al., 2021). Functional genomics can be useful to identify candidate genes and to understand the interaction among genes in these genomic regions and their effect on seed yield. Furthermore, we found that the integration of QTL, GWAS and genomic information available from other legumes and related crops could help to improve our understanding of the genetic architecture of seed yield in dry bean.

AUTHOR CONTRIBUTION

Paulo Izquierdo: conceptualization; data curation; formal analysis; methodology; visualization; writing—original draft. **James D. Kelly**: Writing—review and editing. **Stephen E. Beebe**: Writing—review and editing. **Karen Cichy**: conceptualization; funding acquisition; project administration; resources; supervision; writing—review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

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