

# Genome-wide association mapping dissects the selective breeding of determinacy and photoperiod sensitivity in common bean (*Phaseolus vulgaris* L.)

Kate E. Denning-James <sup>1,2</sup> Caspar Chater,<sup>2,3</sup> Andrés J. Cortés  <sup>4,5</sup> Matthew W. Blair,<sup>6</sup> Diana Peláez,<sup>4</sup> Anthony Hall  <sup>1</sup> José J. De Vega  <sup>1,\*</sup>

<sup>1</sup>Earlham Institute, Norwich, NR4 7UZ, UK

<sup>2</sup>Royal Botanic Gardens, Kew, Richmond TW9 3AE, UK

<sup>3</sup>Department of Plants, Photosynthesis and Soil, School of Biosciences, The University of Sheffield, Sheffield S10 2TN, UK

<sup>4</sup>Corporación Colombiana de Investigación Agropecuaria (AGROSAVIA)—C.I. La Selva, Rionegro 054048, Colombia

<sup>5</sup>Facultad de Ciencias Agrarias—Departamento de Ciencias Forestales, Universidad Nacional de Colombia—Sede Medellín, Medellín, Colombia

<sup>6</sup>Department of Agricultural and Environmental Sciences, College of Agriculture, Tennessee State University, 3500 John A Merritt Blvd, Nashville, TN 37209, USA

\*Corresponding author: Email: jose.devega@earlham.ac.uk

The common bean (*Phaseolus vulgaris* L.) is a legume pulse crop that provides significant dietary and ecosystem benefits globally. We investigated 2 key traits, determinacy and photoperiod sensitivity, that are integral to its management and crop production, and that were early selected during the domestication of both Mesoamerican and Andean gene pools. Still, significant variation exists among common bean landraces for these traits. Since landraces form the basis for trait introgression in prebreeding, understanding these traits' genetic underpinnings and relation with population structure is vital for guiding breeding and genetic studies. We explored genetic admixture, principal component, and phylogenetic analyses using whole-genome sequencing to define subpopulations and gene pools. We used genome-wide association mapping (GWAS) to identify marker-trait associations in a diversity panel of common bean landraces. We observed a clear correlation between these traits, gene pool, and subpopulation structure. We found extensive admixture between the Andean and Mesoamerican gene pools in some regions. We identified 13 QTLs for determinacy and 10 QTLs for photoperiod sensitivity and underlying causative genes. Our study identified known and novel causative genes and a high proportion of pleiotropic effects for these traits in common bean, and likely translatable to other legume species.

**Keywords:** common bean; legume; determinacy; photoperiod; GWAS; domestication; Plant genetics and genomics

## Introduction

The common bean is a global staple that provides significant dietary and economic services by improving health and nutrition while helping to reduce poverty, specifically in developing countries. Common beans have also been labeled as one of the essential crops to mediate climate change due to their lower environmental impact and protection of food and nutritional security (Foyer et al. 2016). Common beans are cultivated mainly as grain legumes, but the immature seeds, pods, and leaves are also eaten (Blair et al. 2010; Ganesan and Xu 2017). There are hundreds of varieties, and the prevailing type grown in a country depends on market preferences (Rawal and Navarro 2019). Common beans are rich in essential dietary components, such as protein, minerals, fiber, and micronutrients (Patto et al. 2015; Blair, Izquierdo, et al. 2013; Castro-Guerrero et al. 2016; Ganesan and Xu 2017), and protect against some forms of malnutrition, including stunting in children and micronutrient deficiencies (Jha et al. 2015; Suarez-Martinez et al. 2016; Ganesan and Xu 2017; Bernardi et al. 2023). As legumes, common beans have a symbiotic relationship with nitrogen-fixing bacteria, allowing them to fix

atmospheric nitrogen and enhance nitrogen levels in the soil, thereby reducing the need for expensive chemical fertilizers while improving yields (Mylona et al. 1995; Cusworth et al. 2021; Mupangwa et al. 2021; Phiri and Njira 2023). Despite its widespread usability, trait segregation within and among bean landraces is still widespread, especially for critical agronomic traits such as growth habit and photoperiod.

The common bean underwent 2 separate domestications resulting in 2 gene pools: Andean and Mesoamerican. In addition, there are different races, intermediate species, and admixed accessions due to genetic isolation, fragmentation, and artificial selection for different morphological traits. The gene pools of common beans grow in a large variety of environments in the neotropics. These ecogeographic conditions, together with isolation by distance, have disrupted the gene flow between wild and domesticated common beans, and between the different gene pools (Santalla et al. 2004; Beebe et al. 2012). Consequently, there are large differences in their life history traits, morphology, and genetics (Gepts and Debouck 1991; Broughton et al. 2003; Beebe et al. 2012; Bitocchi et al. 2017). Another difference is cultivars are commonly autogamous and annual, while wild common beans and

Received on 20 January 2025; accepted on 03 April 2025

© The Author(s) 2025. Published by Oxford University Press on behalf of The Genetics Society of America.

This is an Open Access article distributed under the terms of the Creative Commons Attribution License (<https://creativecommons.org/licenses/by/4.0/>), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

related species can be perennial and allogamous (Debouck et al. 1993; Schier et al. 2019; Chacon-Sánchez et al. 2021).

Photoperiod insensitivity and determinacy arose separately in both gene pools during the domestication of common beans, likely co-selected by growers (Weller et al. 2019; Repinski et al. 2012). Wild common beans tend to be indeterminate and photoperiod sensitive, requiring a particular day length to flower. Indeterminate growth is advantageous in the wild due to competition with surrounding vegetation, while photoperiod sensitivity (PS) was likely reinforced by divergent natural selection and local adaptation. On the other hand, photoperiod insensitivity was selected (likely unconsciously) as cultivated common beans were spread along a greater range of latitudes and environments. Determinacy, a developmental feature that causes common beans to have a terminal inflorescence when switching to a reproductive state (Cavalcante et al. 2020), optimized agricultural management and harvesting efficiency. Determinate common beans tend to have a bush growth habit with reduced branching and vining abilities compared with the indeterminate varieties (Kwak et al. 2012), therefore translocating biomass resources into an increased fitness output. While indeterminate and photoperiod sensitive landraces are common, the combined selection for photoperiod insensitivity and determinacy resulted in common bean varieties with shorter flowering periods, earlier maturation, and easier management during harvesting (Daba et al. 2016; González et al. 2016). Photoperiod insensitivity and determinacy are advantageous traits from an agronomical point of view due to earlier harvesting and shorter exposure to unfavorable weather patterns under climate change, consequently providing better food security for communities (Perez et al. 2020; Botero and Barnes 2022).

Modern breeding programs are moving beyond a yield-centered paradigm to target resistance to biotic and abiotic stress, and also nutritional quality (Singh and Schwartz 2010; Assefa et al. 2019; Caproni et al. 2020; Kachinski et al. 2022). Landraces and crop wild relatives offer a promising reservoir of genetic diversity for these traits by introgression from the landraces into the elite genetic background (Tai et al. 2014; Hu et al. 2021; Suarez, Polania et al. 2021; Suarez, Urban, et al. 2021). However, understanding the genetic diversity, population structure, patterns of adaptations, and how these correlate with determinacy and photoperiod insensitivity is required to guarantee the retention of these key domesticated traits within future breeding cycles, given their association with crop management and production (Beebe et al. 2012).

Common beans in Colombia are diverse regarding growth habits and PS. Colombia is the northernmost part of the Andean gene pool and south of the Mesoamerican and may act as a region of confluence between them. Consequently, it has been proposed that the region has a large amount of admixture and introgressive hybridization (Tohme et al. 1996; Blair et al. 2007; Blair, Cortes, et al. 2013; Leitao, Bicho, et al. 2021). Admixture and hybridization lead to introgressions from differential parental origins, introducing new alleles and novel epistatic interaction into a population, allowing for new trait combinations that could merge exotic variation from diverse germplasm with more agronomically desirable traits such as determinacy and photoperiod insensitivity.

Considering the above hypothesis, we characterized 144 representative landraces from Colombia and neighboring countries, together with controls from other regions, using whole-genome re-sequencing. We utilized genome-wide association mapping (GWAS) to identify significant SNPs for photoperiod insensitivity and determinacy in this diversity panel. The novelty of this work lies in that prior research commonly focused on the Mesoamerican diversity rather than the Andean, due to the

greater genetic diversity in the former, and had ignored admixed materials as an essential source of variation. Furthermore, research has rarely utilized whole-genome sequencing of common bean accessions to undertake a GWAS on determinacy and photoperiod insensitivity phenotypes. Instead, previous work has mostly used QTL mapping and low-density marker panels, resulting in poor resolution (Kwak et al. 2008; González et al. 2016; García-Fernández et al. 2021).

## Materials and methods

### Diversity panel

The diversity panel was comprised of 144 genotypes mainly from Colombia and surrounding countries in Central and South America (Fig. 1). The panel contained accessions from elite backgrounds, landraces, heirlooms, weedy, and wild materials. The material was sourced from the International Centre for Tropical Agriculture (CIAT)'s genebank, the Leibniz Institute of Plant Genetics and Crop Plant Research (IPK)'s genebank, and heirlooms bought from the catalogs from "Jungle Seeds" (JungleSeeds 2020) and (Beans and Herbs 2020) in 2020. The panel was chosen to include control accessions from the Andean and Mesoamerican gene pools and races, while representing diverse seed coat colors and varying genetic backgrounds from Colombia and neighboring countries to focus on putatively admixed varieties.

### Genotyping

The genotypes were whole genome re-sequenced using Illumina short reads. The accessions were grown at the Norwich Research Park (Norwich, UK) in 2021 until the expansion of the first true leaf, after which they were snap-frozen (~50–100 mg). The genomic DNA extraction for short-read sequencing from each accession was completed using a Qiagen DNAeasy kit (Qiagen, Germany). The DNA concentration of the samples was quantified for quality control using the Tecan Plate Read Infinite F200 Pro for a fluorometry-based assay. The sequencing of the samples was completed by Genomic services at Earlham Institute (Norwich, UK). LITE libraries, a cost-effective low-volume variant of the standard Illumina TruSeq DNA protocol, were constructed for the 144 accessions and were sequenced using 2 NovaSeq 6000 S4 v 1.5 flow cells with 150 bp paired-end reads, following the protocol in (Kirkwood et al. 2021).

### Phenotyping

All 144 common bean accessions were evaluated at the Norwich Research Park (Norwich, UK) in temperature-controlled glasshouses. The experiments were conducted in 2 seasons; summer 2022 with long daylength (16:8) and winter 2023 with short daylength (12:12). The accessions were organized in a randomized block design with 3 or 2 replications, respectively. Management was conducted according to recommendations for common bean cultivation.

The diversity panel was characterized for the days to flowering (DTF), seed size (SS), weight of 100 seeds (E100\_SW; estimated based on the weights of seeds harvested and projected to 100 seeds), determinacy (D; terminal flower bud presence) (Cavalcante et al. 2020), and PS (flowering in none, 1 or both seasons). DTF was split into the 2 seasons due to PS in certain accessions and PS was characterized in 3 ways for the GWAS.

The statistical analysis of variance (1-way ANOVA) of the phenotypic data was done in R, then the Pearson's correlation coefficient was calculated and visualized using the R package "corrplot" (Wei and Simko 2021).



**Fig. 1.** Distribution of the 127 common beans with location data that were used in this study. The coordinates of the capital city were used for those without coordinate data. Produced with QGIS.

## Preprocessing genotype data

The raw sequence reads were processed with TrimGalore (v. 0.5.0) (Krueger et al. 2023) to remove adapters and poor-quality reads, and then quality checked using FastQC (Wingett and Andrews 2018) and MultiQC (Ewels et al. 2016). The trimmed reads were aligned to the Andean reference genome, *Phaseolus vulgaris* G19833, v2.1 (Schmutz et al. 2014) downloaded from Phytozome (Goodstein et al. 2012) with BWA-MEM (v 0.7.13) (Li and Durbin 2009) and “-M -R” to add read group information and allow compatibility with GATK. SAMtools (v 1.7) combined, compressed, and sorted the aligned files (Danecek et al. 2021). Picardtools (<https://broadinstitute.github.io/picard/>) (v 2.1.1) marked duplicates and BamTools indexed the alignments (Barnett et al. 2011). The percentage of alignments were calculated at this stage. The genotype data were divided into 10 Mbp regions (Garrison and Marth 2012) (v 1.0.2) to run the Genome Analysis ToolKit (GATK v 4.2) haplotype caller with default parameters (Van der Auwera and O’Connor 2020). This identified 20.2 million variant loci (~17.1 M SNPs and ~3.4 M indels).

## Population structure analysis

The resulting VCF file from GATK using the Andean reference (“Andean VCF”) was filtered further with BCFtools to retain calls with a minimum depth of 5 reads per variant call (FMT/DP  $\geq$  5), a

locus call quality over 30, maximum missing calls per locus of 5%, to keep only biallelic SNP locus, and for a minor allele frequency over 2%. The resulting VCF had ~9 million SNP loci. Then, the VCF was filtered for a maximum heterozygosity of 20% per locus using TASSEL 5 (v. 20230314) (Bradbury et al. 2007). This was then filtered for linkage disequilibrium (LD) (based on LD decay) and thinned with a window size of 10 bps using BCFtools prune.

The population structure of the panel was analyzed using ADMIXTURE (v 1.3.0) (Alexander and Lange 2011) on a subset of 88,786 SNP loci. ADMIXTURE was run for K = 2 to K = 10 and the ideal number of K was determined using the cross-validation error. Accessions were allocated a group when their membership coefficient (q) was greater than 0.7. Plotting was completed in R using the packages “ggplot2” (Ginestet 2011).

## Genome-wide association study

The “Andean VCF” from GATK was filtered with BCFtools (v 1.12) (Danecek et al. 2021) for biallelic loci, a minor allele frequency of 1% and thinned with a window size of 5 bp. To understand the genetic relationship between accessions, we used a principal component analysis (PCA) generated with GAPIT v.3 (Wang and Zhang 2021) on a subset of 2,572,124 loci.

A genome-wide association study investigated marker-trait association for determinacy and photoperiod insensitivity phenotypes

using GAPIT v.3 (Wang and Zhang 2021) with 3 principal components. We ran with the models Bayesian-information and Linkage-disequilibrium Iteratively Nested Keyway (BLINK) (Huang et al. 2019), Fixed and random model Circulating Probability Unification (FarmCPU) (Liu et al. 2016), and Mixed Linear Model (MLM) (Zhang et al. 2010). BLINK and FarmCPU were identified as the best multi-locus models for different heritability levels, improving statistical power (Huang et al. 2019; Merrick et al. 2022; Cebeci et al. 2023). While MLM was chosen for single-locus analysis as a baseline for comparison to BLINK and FarmCPU.

GAPIT was run on the whole panel (144 accessions) and on the Andean subpanel (as defined at K2 ADMIXTURE; 108 accessions). To run BLINK, GAPIT completed the analysis with the option “Random.model = TRUE” as not to calculate  $R^2$  for phenotypic variance explained values after GWAS. The quantile-quantile (QQ) plots were used to understand the suitability of the models to the data. Plotting was completed in R using the package ‘ggplot2’ (Ginestet 2011).

## Selecting significant loci, candidate gene mining, and functional annotation

Significant marker-trait associations (MTAs) were investigated further when they had a  $-\log_{10}(P\text{-value})$  over 7 and were confirmed by 2 models from GAPIT. QTLs were defined as  $\pm 100$  kbp from the MTA based on the estimated LD decay distances in common bean diversity panels and by using a  $r^2 = 0.25$  cutoff (estimated decay as 114 kb) (Moghaddam et al. 2016; Valdisser et al. 2017; Campa et al. 2018; Raggi et al. 2019; Wu et al. 2020, 2024; Ugwuanyi et al. 2022; Reinprecht et al. 2023). This is shorter than the calculated recombination rate in common bean of 3.72 cM/Mb (Bhakta et al. 2015). LD decay was estimated for the diversity panel (mean  $R^2 = 0.27$ ) and subpopulation at  $K = 2$  (Andean mean  $R^2 = 0.21$ , Mesoamerican mean  $R^2 = 0.2$ ) using PopLDdecay software following Wu et al. (2020) (Zhang et al. 2019).

Identified loci were compared with the Andean reference genome, *Phaseolus vulgaris* G19833 v2.1 in JBrowse (Schmutz et al. 2014; Diesh et al. 2023) while considering “highimpact” mutations identified by SnpEff (Cingolani et al. 2012). Once genes were identified, their putative function was explored using PhytoMine (Goodstein et al. 2012) (*Phaseolus vulgaris* v.2), BLAST (Camacho et al. 2009) against the nonredundant protein database at NCBI, and finally against the TAIR database if no gene function could be identified in close relatives (Hualla et al. 2001). The loci were compared with previous studies and literature. PulseDB was used for comparison, particularly for QTLs and markers related to developmental and flowering phenotypes (Humanann et al. 2019). QTLs and markers were mapped to the reference genome to estimate the conversion from cM to Mb in JBrowse.

## Results

### Population structure

The diversity panel split into the 2 gene pools, the Andean and Mesoamerican (Figs. 2a and 3a). At K6 (Fig. 2b), the Mesoamerican group split into 2 subpopulations (M1 and M2), while the Andean subgroup split into 4 subpopulations. Two of these subpopulations included only accessions from Colombia and were named C1 and C2. A subpopulation containing accessions from Colombia and Ecuador/Peru was named C-EP. The remaining subpopulation was named A1. In the PCA (Fig. 3a), PC1 explained 38.8% of the variation in our diversity splitting the 2 gene pools, while PC2 accounted for 5.06% of the variation, splitting the Mesoamerican subgroups (M1

and M2) and separating C-EP from the other Andean subgroups. A total of 11 accessions were classified as admixed between the Andean and Mesoamerican gene pools (Admx\_AM), as they had an ancestry composition lower than 70% from either of the origins ( $q < 0.7$ ). The Admx\_AM accessions were all indeterminate and produced a variety of seed sizes. Seven were landraces and 2 were wild. There was also a mix of photoperiod sensitive and insensitive accessions.

The Colombian subgroups (C1 and C2; Fig. 2b) contained medium and large seeded landraces. However, the subpopulations distinguished by determinacy; C1 contained mainly insensitive determinate accessions while C2 contained sensitive indeterminate accessions. The A1 group contained large and medium seeded landraces that were mainly photoperiod insensitive. The C-EP population contained accessions from Ecuador, Peru, and Colombia. This group contained large-seeded indeterminate landraces and also included accessions from races previously identified to be from the Andean gene pool. The Mesoamerican subgroups (M1 and M2; Fig. 2b) were also distinguished by phenotypic data. They both contained indeterminate and determinate accessions; however, M1 was mainly medium seeded while M2 was mainly small seeded. This is summarized in Table 1 and Supplementary Table 1.

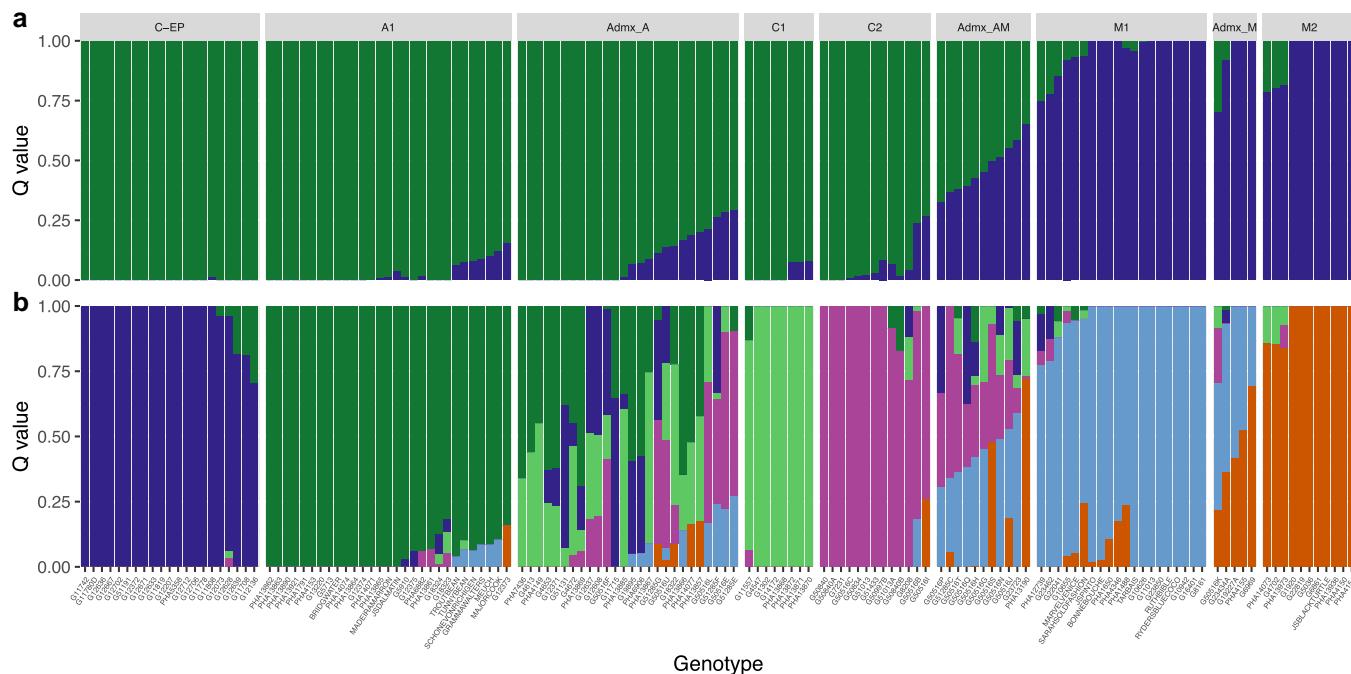
Colombian accessions can be found within all the subgroups and admixed groups at  $K = 6$  (Fig. 2b). While the admixture accessions are mainly from Colombia, while 1 sample is a wild “Ecuador” accession.

The Andean accessions had a lower proportion of heterozygous sites ( $<0.1$ ) than the Mesoamerican accessions, which were more heterozygous (Fig. 3b). The 6 highly heterozygous accessions ( $>25\%$  of the loci) were found within the Andean X Mesoamerican hybrid (Admixed-AM) subpopulation (Fig. 3b) and were from Colombia. Finally, the outlier accession with the lowest alignment to the Andean reference genome and low proportion of heterozygous sites was a wild accession from Ecuador.

### Phenotypic variation and correlations

The correlation coefficient was estimated for each pair of traits (Fig. 4), averaged over 2 seasons or studied in both years. There was a positive correlation between DTF from winter and summer ( $r = 0.57$ ). Both DTF were negatively correlated with PS [ $r = -0.72$  (DTF\_S22),  $r = -0.77$  (DTF\_W23)] and D [ $r = -0.35$  (DTF\_S22),  $r = -0.43$  (DTF\_W23)]. Population structure at either 2 or 6 ancestries (K2, K6) was positively correlated with D [ $r = 0.32$  (K6),  $r = 0.37$  (K2)] but negatively correlated with SS [ $r = -0.44$  (K6),  $r = -0.4$  (K2)] and E100\_SW [ $r = -0.37$  (K6),  $r = -0.47$  (K2)]. SS was not correlated with DTF\_S22, DTF\_W23, D, or PS ( $r = -0.13$ ,  $r = -0.07$ ,  $r = -0.12$ ,  $r = 0.09$ ). However, E100\_SW was positively correlated with PS ( $r = 0.18$ ) and SS ( $r = 0.87$ ) but negatively correlated with DTF\_S22 ( $r = -0.22$ ). Then D and PS were positively correlated ( $r = 0.45$ ).

Figure 5, a–c showed the distributions of the phenotyping for traits E100\_SW, S22\_DTF, and W23\_DTF, respectively. The seed weights (Fig. 5a) were normally distributed, while the DTF in summer and winter (Fig. 5, b and c) were binomial distributions; the peaks were around 42- and 54-days postsowing in summer, and around 70- and 90 days in winter. When analyzing the phenotypes by subpopulation, we can see that C-EP (Fig. 2b) did not flower during winter in the UK, W23\_DTF, as was mainly photoperiod sensitive. This is further supported by the correlation plot (Fig. 4). Furthermore, determinacy, photoperiod insensitivity, and DTF are correlated. The determinate accessions flower earlier than the indeterminate, supporting the binomial distribution.



**Fig. 2.** Analysis of the population structure of 144 accessions belonging to our diversity panel focusing on Colombia at  $K = 2$ , Andean or Mesoamerican groups a) and  $K = 6$  b). (C-EP) accessions mainly from Peru, then Ecuador and Colombia; (A1) Andean accessions from a variety of South American countries; (C1) mostly determinate Colombian landraces; (C2) indeterminate Colombian landraces; (M1) mainly medium seeded\*\* from Central America and Colombia; (M2) mainly small seeded\*\* from Central America and Colombia. (Admx\_AM) Andean X Mesoamerican hybrids; (Admx\_A) and (Admx\_M) admixed accessions between subpopulations (ancestry composition  $q < 0.7$  at  $K = 6$ ). \*\* $P < 0.01$  using a 2-tailed student t-test with unequal variance.

## GWAS for determinacy

The GWAS was performed using the models BLINK, FarmCPU, and MLM with GAPIT (Fig. 6, a and b). The QQ plots (Fig. 6, c and d) provided evidence that the selected models were well fitted to identify significant MTAs for the dataset. We identified 13 MTAs with a significant  $P$ -value ( $-\log_{10}(P\text{-value}) > 7$ ), corresponding to 13 QTLs. We focused on 7 significant MTAs that were identified for the whole panel based on the criteria laid out in the methods (vertical lines in Fig. 6). The 7 QTLs were found on chromosomes Pv01, Pv07, Pv08, Pv09, and Pv10 (Table 2). Five of the 7 QTLs were also identified for the Andean subset.

Putative candidate genes were identified for determinacy based on the significant MTAs and corresponding QTL windows. The identified genes and QTLs are listed in Supplementary Tables 2 and 3.

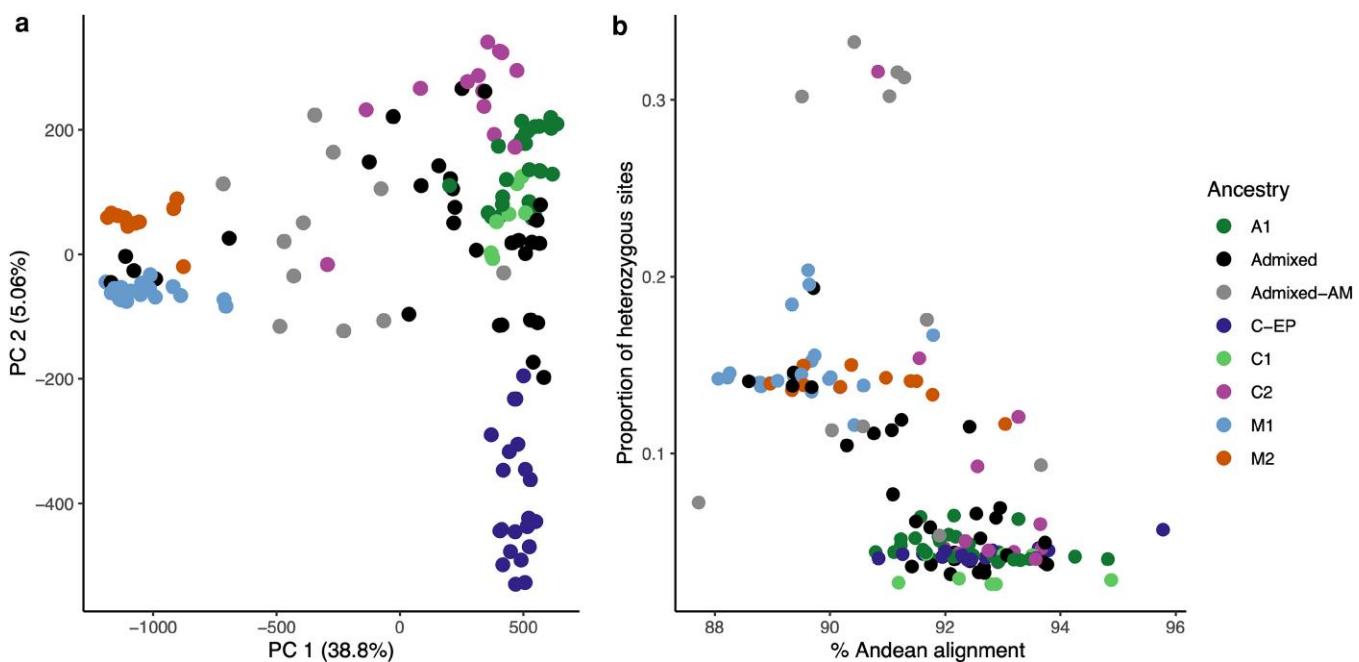
## GWAS for PS

The GWAS was performed using the BLINK and FarmCPU models with GAPIT (Fig. 7, a and b). The QQ plots (Fig. 7, c and d) provide evidence that the selected models are fitted to identify significant MTAs for the dataset. We identified 10 QTLs ( $-\log_{10}(P\text{-value}) > 7$ ). We focused on 6 QTLs for the whole panel based on criteria laid out in the methods. The MTAs were found on chromosomes Pv04, Pv05, Pv07, Pv08, and Pv09 (vertical lines in Fig. 7). Six QTLs were identified for the Andean subset panel in Chromosomes Pv05, Pv07, Pv08, Pv09, and Pv11. The QTL in Pv04 and Pv09 were found in the full dataset only. The QTL in Pv9 and Pv11 were found in the Andean subset only. Candidate genes were identified for the significant MTAs and their corresponding QTLs. The identified genes and QTLs are listed in Supplementary Tables 2 and 3.

## Discussion

We delimited subpopulations in a panel of 144 accessions, initially divided by domestication event into the 2 Andean and the Mesoamerican gene pools (Figs. 2 and 3) (Blair, Cortes, et al. 2013; Kami et al. 1995). The Mesoamerican gene pool is generally more diverse (Mamidi et al. 2013; Schmutz et al. 2014) with less influence from domestication bottlenecks. Furthermore, the Mesoamerican gene pool within our diversity panel is also more heterozygous, suggesting that the Andean gene pool has undergone fewer outcrossing events. These crosses between gene pools occur during common bean dissemination, breeding programs and selection based on market preferences (Hoyos-Villegas et al. 2017; de Almeida et al. 2020; Botero et al. 2021; Bellucci et al. 2023). However, care needs to be taken when utilizing market sampling information. This is highlighted by the 2 "Peruvian" accessions collected from markets that fall with the Mesoamerican subpopulation (Supplementary Table 1).

Admixture was commonly observed in the panel, including 26 admixed Andean accessions, 5 admixed Mesoamerican accessions, and 11 Mesoamerican  $\times$  Andean accessions. This supports our initial hypothesis that Colombia and neighbouring countries hold large common bean variation, including hybrids between both gene pools (Gori et al. 2022; Myers et al. 2000; Pironon et al. 2020). The wider crosses between gene pools compared with within gene pools resulted in a larger observed heterozygosity in the hybrid accessions, supporting the outcrossing events and movement between gene pools. One implication of this study is that admixed Colombian hybrid landraces bridge Andean and Mesoamerican gene pools, and novel allelic and epistatic interactions likely filtered out deleterious effects (Cichy et al. 2015) due to stronger purifying selection with increased recombination. After all, recombination increases local effective



**Fig. 3.** a) Principle component analysis (PCA) plot of PC1 against PC2. b) Proportion of heterozygous sites against the percentage of read pair alignment to the Andean reference genome G19833 (Schmutz et al. 2014). The colors illustrate the population structure of our diversity panel.

**Table 1.** Phenotypic characteristics associated with each subpopulation.

Subpopulation	Gene pool	Determinacy	Photo. sen.	Seed size	Origin
C1	Andean	Mainly determinate	Insensitive	Mainly large	Colombia and Ecuador
C2	Andean	Indeterminate	Mainly sensitive	Mainly large	Colombia
A1	Andean	Both	Mainly insensitive	Mainly large	South America, Heirlooms, Colombia
C-EP	Andean	Indeterminate	Sensitive	Large	Colombia, Ecuador, Peru
Admix_A	Andean	Mainly indeterminate	Both	Mainly large	Colombia and South America
M1	Mesoamerican	Mainly indeterminate	Both	Mainly medium**	Central America, Colombia, Heirlooms, Peru
M2	Mesoamerican	Mainly indeterminate	Mainly insensitive	Mainly small**	Central America, Colombia
Admix_M	Mesoamerican	Mainly indeterminate	Insensitive	Small and medium	Colombia, Brazil, Heirlooms, Central America
Admix_AM	AxM hybrids	Indeterminate	Mainly sensitive	Mainly medium	Colombia and Ecuador

population size ( $N_e$ ) and limits Hill–Robertson interference (Hill and Robertson 2007). This suggests the Colombian hybrids have promising potential for breeding. However, the diversity panel may also be biased and underestimating their prevalence in other regions due to the large number of Colombian accessions in our diversity panel.

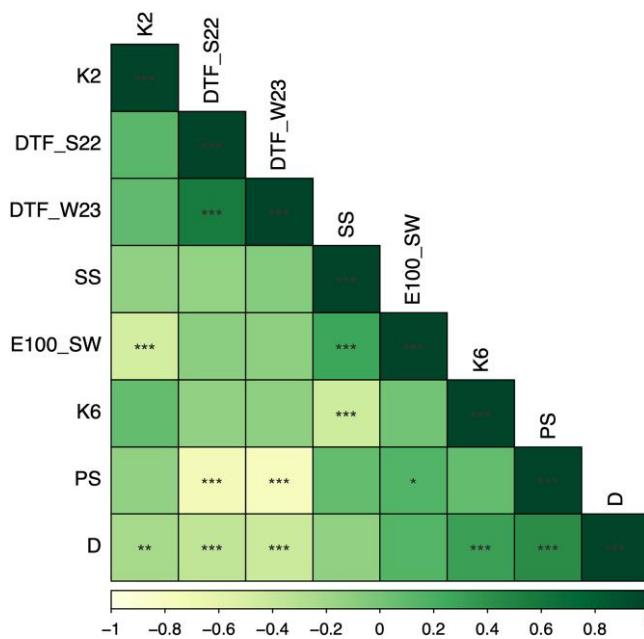
We observed some traits associated with demography, including determinacy and PS: C1 and C2 shared origin but could be separated by ancestry admixture analysis, and were characterized by different determinacy, as C1 contained mainly determinate accessions, and C2 mainly indeterminate accessions. Furthermore, the population structure suggests that Colombian farmers have not selected varieties based on the seed characteristics studied (e.g. SS) (Botero et al. 2021).

Indeterminate and photoperiod sensitive landraces were common, despite the combined selection for photoperiod insensitivity and determinacy resulting in common bean varieties with shorter flowering periods (DTF) and easier management. Prior research supports the correlation between DTF and phenotypes such as seed weight, determinacy and growth habit (Tar'an et al. 2002; Moghaddam et al. 2016; Hoyos-Villegas et al. 2017; Elias et al.

2021; Vargas et al. 2021). These phenotypes are related to apical meristems and floral development (Sablowski 2007).

We observed the distribution of DTF values, in either summer or winter, were bimodal, i.e. had 2 peaks (Fig. 5, b and c). This likely occurred due to the determinate types flowering first and then followed by the indeterminate beans (Coelho et al. 2023). The distribution also correlates to growth habits as bush types typically flower earlier than climbing types (Ugwuanyi et al. 2022). Figure 2a supports that PS arose during domestication in both gene pools (Weller et al. 2019).

The Andean accessions within our diversity panel were large and medium seeded while the Mesoamerican accessions were small and medium sized, which supports previous research (Blair et al. 2009). Among the Mesoamerican accessions, the Mesoamerican race is characterized by small-seeds, while the Durango–Jalisco race is characterized by medium seeds (Beebe et al. 2000; Zhang et al. 2008; Blair et al. 2009; Giordani et al. 2022). We could not separate our diversity panel into subpopulations matching these races due to a lack of Mesoamerican diversity in the panel, a limited genetic component for the SS trait, or introgressions occurring in the Mesoamerican Colombian accessions.



**Fig. 4.** Pearson correlation coefficients among five agronomic traits and population structure measured in 144 common bean genotypes grown at the Norwich Research Park, Norwich, UK in 2022 and 2023. K6, K6 subgroups from ADMIXTURE; K2, K2 subgroups from ADMIXTURE; D, determinacy; PS, photoperiod sensitivity; SS, seed size; E100\_SW, estimated weight of 100 seeds; DTF\_W23, DTF from winter 2023; DTF\_S22, DTF from summer 2022. \* $P < 0.05$ ; \*\* $P < 0.01$ ; \*\*\* $P < 0.001$ .

Interestingly, Ecuador accessions are often separated from Andean subgroups, suggesting that they are members of the PhI group or a possible sister species *Phaseolus debouckii* (Chacon-Sanchez et al. 2007; Rendon-Anaya et al. 2017). Further to this, the wild Ecuador accession is separated from both gene pools (Figs. 2 and 3), suggesting a separate ancestry originating from Ecuador or Peru (Bitocchi et al. 2012; Bitocchi et al. 2017). Finally, the C-EP group (Fig. 2b) are mainly photoperiod sensitive (Fig. 5f), possibly due to a different domestication history or due to their quatorial provenance not necessitating evolution under fluctuating photoperiods.

By leveraging this diversity panel and its trait segregation across the demographic stratification, we prioritized 13 QTLs for determinacy and 10 QTLs for PS. Four of the QTLs for PS, and 4 for determinacy, were also identified only for the Andean subset, but not the whole panel. The Andean gene pool has adapted to lower latitudes than the Mesoamerican pool, resulting in differential selection for PS between the 2 gene pools. The LD was estimated as 114 kb from an  $R^2$  cutoff of 0.25, this value is consistent with WGS data of diversity panels rather than breeding populations (Campa et al. 2018; Diniz et al. 2018; Reinprecht et al. 2023; Ambachew et al. 2024). LD in common beans is impacted by the evolutionary and breeding history of the accessions in the diversity panel; therefore, a 200 kb region accounts for the higher resolution of WGS as well as allowing for LD (Moghaddam et al. 2016; Valdisser et al. 2017).

During this study we completed analysis with the Andean reference genome (Schmutz et al. 2014). This reference genome was selected for being the most complete at the time of analysis and because our panel has a higher proportion of Andean accessions based on population structure analysis (Fig. 2). The accessions also had higher alignments to the Andean reference genome ( $92.5\% \pm 1$  and  $89.9\% \pm 1.1\%$  for the Andean and Mesoamerican

subpopulations, respectively) and no difference in metrics to the Mesoamerican reference genomes (Supplementary Table 1).

## QTLs and candidate genes associated with determinacy

### Three QTLs in chromosome 1

We identified a determinacy QTL in chr 1 -Pv01- (D1.4-D1.6; Table 2), identified in other studies (Moghaddam et al. 2016; da Silva et al. 2018; Kamfwa et al. 2019; Sedlar et al. 2020; Vargas et al. 2021; Keller et al. 2022) as a hotspot of allelic variation, named the Fin locus. The Fin locus has been mapped to ~44.5 Mb (Pérez-Vega et al. 2010; Kamfwa et al. 2019). This co-segregates with an upstream gene, TFL1y (Phvul.001G189200), a candidate gene for flowering, vegetative growth, rate of plant production, and determinacy (Kwak et al. 2008, 2012; Repinski et al. 2012; Cichy et al. 2015; González et al. 2016; Campa et al. 2018; Delfini et al. 2021). Consequently, the Fin locus has pleiotropic effects due to associations with many development traits such as determinacy, shoot biomass, DTF, days to maturity, plant architecture, embryo abortion, number of pods per plant, number of seeds per plant (seed yield and weight), and disease resistance (Miklas et al. 2001; González et al. 2016; Delfini et al. 2021; Soler-Garzón et al. 2024). However, segregation for this QTL hotspot in Pv01 may prove difficult in breeding programs due to these pleiotropic effects (Vargas et al. 2021).

Further candidate genes have been identified in this QTL, such as Phvul.001G192200. This gene is an ortholog of LIGHT-REGULATED WD1 (LWD1), a gene involved in the circadian rhythm pathway (Wu et al. 2008; Moghaddam et al. 2016; Delfini et al. 2021), or Phvul.001G192300, which is an ortholog of SPINDLY (SPY). SPY interacts with genes in the reproductive pathway (Tseng et al. 2004; Moghaddam et al. 2016; da Silva et al. 2018) and has been associated with days to maturity (Reinprecht et al. 2023).

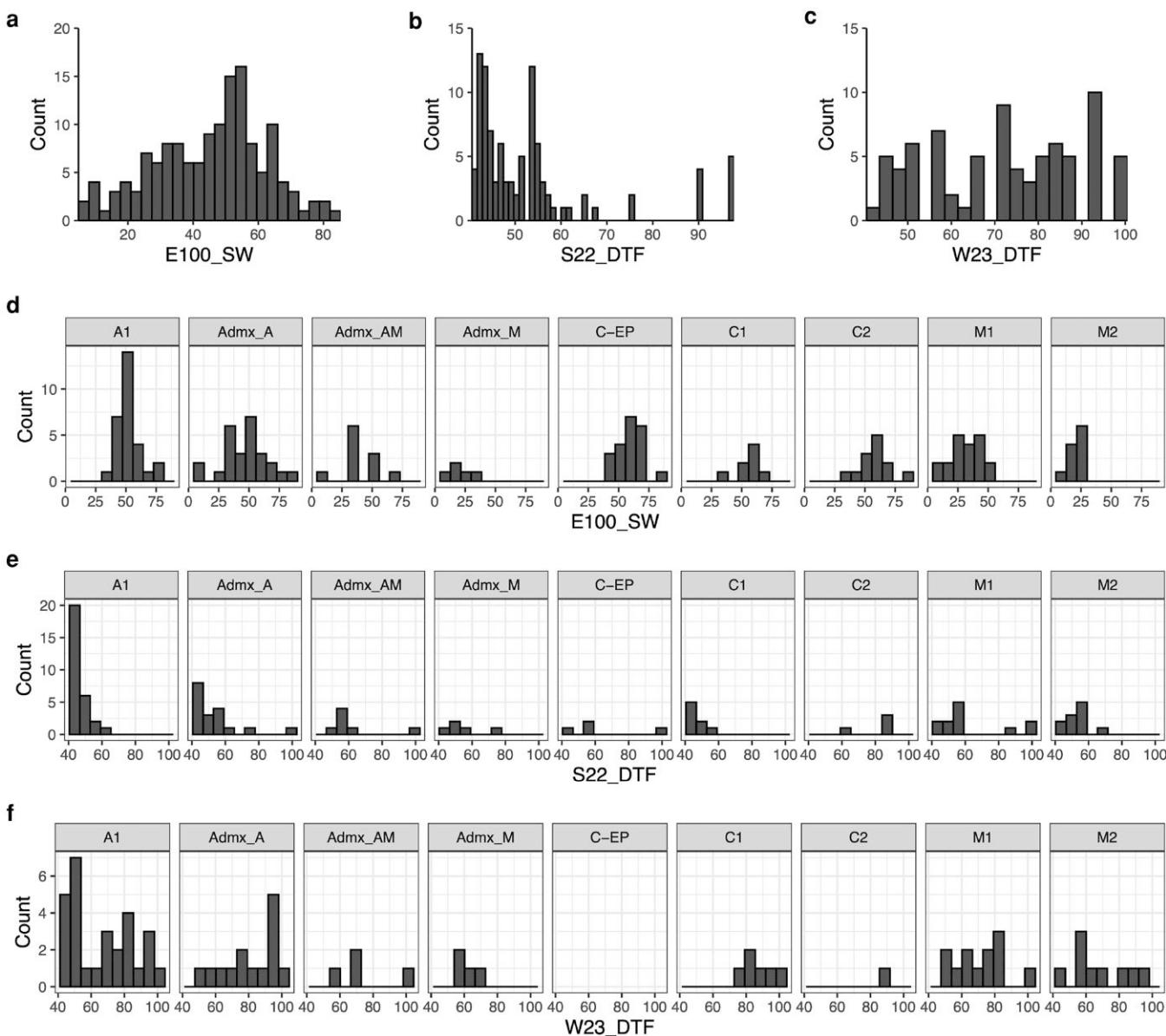
Another QTL we identified on Pv01 (D1.3; Table 2) contains the gene Phvul.001G168700. This gene is related to the phytochrome interacting factor 1 (PIF1) transcription factor isoform X1 in the legume *Vigna radiata* (Bateman et al. 2023). This bHLH transcription factor is involved in many light-dependent pathways in plant development and interacts with circadian clock genes (Kim et al. 2016).

### QTL D7.1 in chromosome 7

The QTL at Pv07 (D7.1) was identified in the whole and Andean panel. The QTL contains the gene Phvul.007G244700. This is related to a transcriptional corepressor, Leunig-homolog in *Vigna radiata* (Bateman et al. 2023). In *Arabidopsis*, Luenig-homologs have functional redundancy with Leunigs (LUGs), and are involved in embryo and floral development (Sitaraman et al. 2008). This QTL has been associated with SS, seed weight, and growth habit (Kwak et al. 2008; da Silva et al. 2018; Elias et al. 2021; Keller et al. 2022), suggesting it may have pleiotropic effects.

### QTL D8.2 in chromosome 8

The QTL identified on Pv08 (D8.2; Table 2) for determinacy has previously been identified for plant architecture (da Silva et al. 2018). However, no gene with a clear function was identified. We have, however, identified a possible candidate gene for further investigation; Phvul.008G170000. This encodes a putative fantastic 4 (FAF) domain-containing protein. In *Arabidopsis*, FAF proteins regulate shoot meristem size and architecture (Wahl et al. 2010).



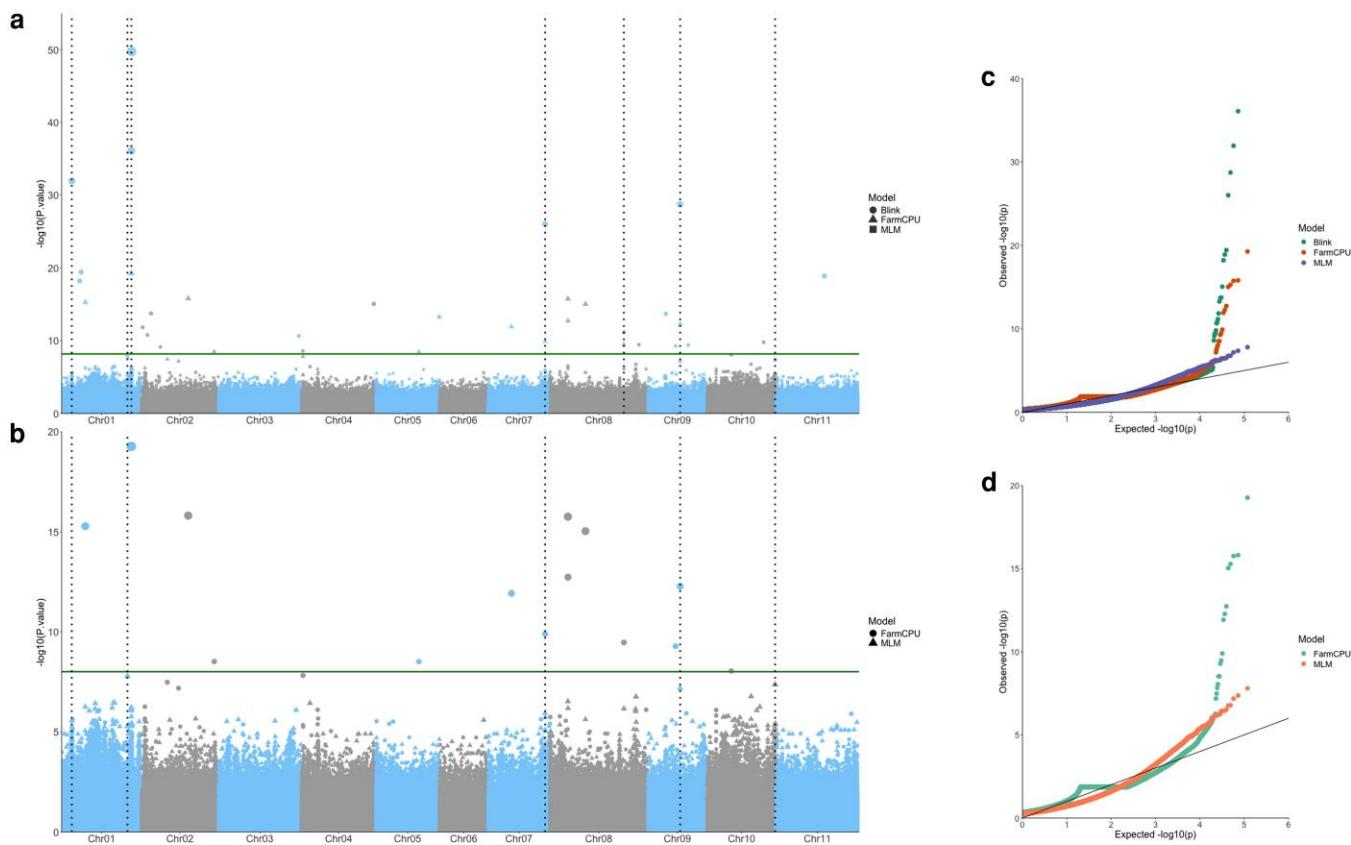
**Fig. 5.** Frequency distribution of seed weight and days to flower traits evaluated in 2 seasons in a common bean diversity panel. a) E100\_SW, estimated weight of 100 seeds; b) phenological DTF in the summer 2022 (S22\_DTF) and c) in the winter 2023 (W23\_DTF) at the Norwich Research Park, excluding those which did not flower. The distributions were split into the subpopulations from K6 ADMIXTURE. d) E100\_SW\*\*\*; e) S22\_DTF\*\*\*; f) W23\_DTF\*. Completed a 1-way ANOVA for E100\_SW, S22\_DTF, and W23\_DTF. \*P < 0.05; \*\*P < 0.01; \*\*\*P < 0.001.

#### QTL D9.1 in chromosome 9

The QTL D9.1 in chr 9 was identified in the whole and Andean panel. Nearby QTLs have been identified for yield and determinacy (Kamfwa et al. 2015; Campa et al. 2018). The gene *Phvul.009G138100* is found within this QTL and contains the significant MTA found by GAPIT (Wang and Zhang 2021). This gene has an insertion that possibly affects function (Cingolani et al. 2012). This gene is uncharacterized in common bean but has homology to the root meristem growth factor 9 from *Glycine soja* (Goodstein et al. 2012; Bateman et al. 2023). This growth factor is expressed in the roots and flowers, regulating and maintaining apical meristems, and therefore both root and floral development, SS, and leaf architecture (Chen et al. 2019; Shinohara 2021). Although it has previously been identified as a candidate gene associated with Mesoamerican domestication (Schmutz et al. 2014), we found the QTL in the Andean panel, suggesting that it has also played a role in the Andean domestication event.

#### QTL D10.1 in chromosome 10

The QTL on Pv10 (D10.1) is located near QTLs for plant height and number of nodules and near genes associated with metabolic changes during domestication, once again suggesting pleiotropic effects (Delfini et al. 2021; de Souza et al. 2023). Three of the genes within this region encode bHLHLZip proteins: *Phvul.010G158500*, *Phvul.010G158300*, and *Phvul.010G158200*. These bHLH transcription factors may be involved in the regulation of flowering genes (Zhou et al. 2019). The gene *Phvul.010G158500* displays nonsynonymous modifications in our panel, including insertions, deletions, and other variants linked to frameshift mutations and gained stop codons (Cingolani et al. 2012). Homology to *Vigna angularis* suggests this gene may be related to the transcription factor bHLH25, and possibly linked to a circadian rhythm-associated protein (Goodstein et al. 2012).



**Fig. 6.** Manhattan plots highlighting markers significantly associated with determinacy on (a) the whole panel and b) the Andean subpanel. The analyses were completed with GAPIT and the models are FarmCPU, BLINK, or MLM (Huang et al. 2019; Liu et al. 2016; Wang and Zhang 2021; Zhang et al. 2010). The X-axis represents the genomic position of markers and the Y-axis is the  $-\log_{10}$  of the P-values for association with the phenotype. The vertical lines correspond to QTLs found by at least 2 models. Point size correlates to  $-\log_{10}(P\text{-value})$ . Quantile-quantile (QQ) plots are provided for c) the whole panel and d) the Andean panel.

## Candidate genes for PS

### QTL PS4.1 in chromosome 4

One QTL for PS was found on Pv04 (PS4.1; Table 2) from the analysis on the whole panel. Within this QTL, 4 genes were identified, 3 of which (*Phvul.004G110200*, *Phvul.004G110301*, and *Phvul.004G110000*) have nonsynonymous mutations such as a stop lost, stop gained, or a frameshift mutation in our panel (Cingolani et al. 2012). However, the genes are uncharacterized.

### Two QTLs in chromosome 5

Two QTLs were identified in Pv05: PS5.2 for the Andean panel and PS5.1 for the whole panel. PS5.2 overlaps with a previously identified QTL for seed weight, DTF, and pod weight (Arriagada et al. 2022; Reinprecht et al. 2023). However, this previous analysis with a limited number of markers did not identify a candidate gene. Based on sequence homology with *Vigna radiata*, we identified the gene *Phvul.005G077000*, which encodes a proton gradient regulation 5 (PGR5) protein (Bateman et al. 2023). PGR5 is involved in plant growth under different light conditions due to interactions with Photosystem I, and consequently putatively associated with differentiating PS in our panel (Munekage et al. 2002). The QTL PS5.1 contained 2 genes, one of which, *Phvul.005G076300*, may encode a bidirectional sugar transporter, named SWEET protein. Evidence suggests SWEET proteins have essential roles in plant development, including in reproductive organs and bud growth (Gautam et al. 2022).

### Two QTLs in chromosome 7

Two QTLs were also identified on Pv07. PS7.1 and PS7.2, both in the Andean and the whole panel. The QTL PS7.2 contains the genes *Phvul.007G157400* and *Phvul.007G156200*. Homology with *Arabidopsis* suggests that *Phvul.007G157400* encodes a BANQUE3 BHLH161 protein. BANQUE3 is negatively regulated by APETALA3 and PISTILLATA in petals and is involved in light-regulated responses and flowering time (Huala et al. 2001; Mara et al. 2010). *Phvul.007G156200* may encode the BHLH transcription factor PIF4 (Phytochrome Interacting Factor 4) based on homology with *Vigna radiata* and *Glycine soja* (Goodstein et al. 2012; Bateman et al. 2023). PIF4 is a downstream signaling component integrating environmental cues such as light (Bateman et al. 2023).

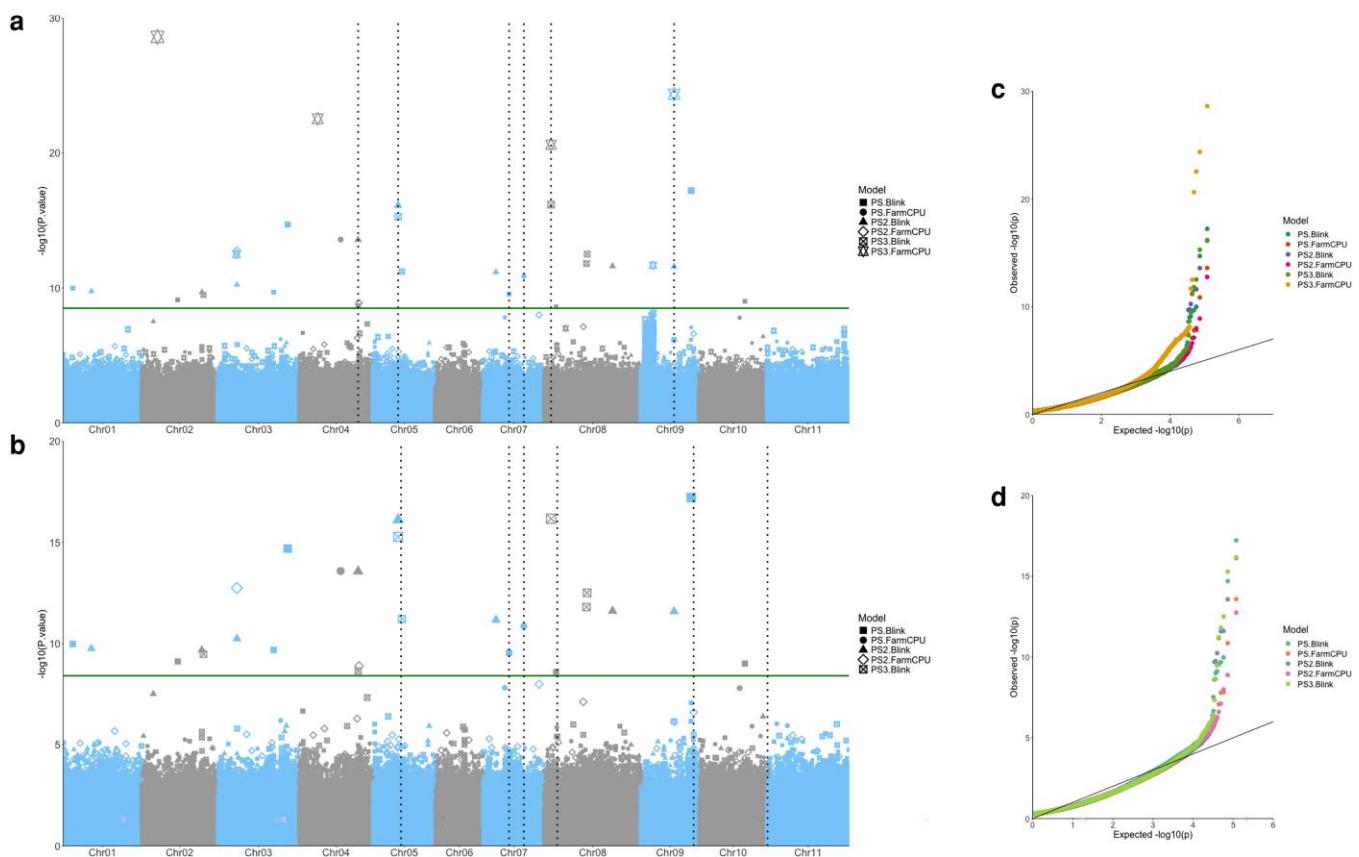
The QTL PS7.1 overlaps with a previously identified QTL for plant production traits (González et al. 2016). The QTL includes the gene *Phvul.007G117400* which encodes a putative JUMONJI domain-containing protein (Goodstein et al. 2012). JUMONJI proteins are involved in multiple plant developmental processes such as flowering and leaf senescence (Gan et al. 2014; Liu et al. 2019; Yamaguchi 2021; Xin et al. 2024). *Phvul.007G117400*'s homology with a JUMONJI16 orthologue in *Vigna radiata* also supports this role (Bateman et al. 2023).

### Two QTLs in chromosome 8

One of the QTLs found in Pv08 is PS8.1 from the whole panel. This QTL has been associated with determinacy (Campa et al. 2018), seed weight (Elias et al. 2021), DTF (Raggi et al. 2019), and pod

**Table 2.** QTLs for determinacy and photoperiod sensitivity.

Name	Chromosome	Start	End	Trait	Panel
D1.1	Chr01	6,512,000	6,521,000	Determinacy	Andean + Whole
D1.2	Chr01	11,363,000	11,372,000	Determinacy	Andean
D1.3	Chr01	42,404,000	42,413,000	Determinacy	Andean + Whole
D1.4	Chr01	44,856,000	44,847,000	Determinacy	Whole
D1.5	Chr01	44,932,000	44,941,000	Determinacy	Andean + Whole
D1.6	Chr01	45,098,000	45,107,000	Determinacy	Whole
D2.1	Chr02	24,821,000	24,830,000	Determinacy	Andean
D3.1	Chr03	25,608,000	25,617,000	Determinacy	Andean
PS4.1	Chr04	38,316,000	38,325,000	Photo sensitivity	Whole
PS5.1	Chr05	16,423,000	16,432,000	Photo sensitivity	Whole
PS5.2	Chr05	18,321,000	18,330,000	Photo sensitivity	Andean
PS7.1	Chr07	16,829,000	16,838,000	Photo sensitivity	Andean + Whole
PS7.2	Chr07	26,485,000	26,494,000	Photo sensitivity	Andean + Whole
D7.1	Chr07	36,860,000	36,869,000	Determinacy	Andean + Whole
PS8.1	Chr08	4,234,000	4,243,000	Photo sensitivity	Whole
D8.1	Chr08	7,440,000	7,449,000	Determinacy	Andean
PS8.2	Chr08	8,320,000	8,329,000	Photo sensitivity	Andean
D8.2	Chr08	47,582,000	47,591,000	Determinacy	Whole
D9.1	Chr09	20,814,000	20,823,000	Determinacy	Andean + Whole
PS9.1	Chr09	21,640,000	21,649,000	Photo sensitivity	Whole
PS9.2	Chr09	34,445,000	34,454,000	Photo sensitivity	Andean
D10.1	Chr10	43,762,000	43,771,000	Determinacy	Andean + Whole
PS11.1	Chr11	204,000	213,000	Photo sensitivity	Andean



**Fig. 7.** Manhattan plots highlighting markers significantly associated with photoperiod insensitivity on (a) the whole panel and b) the Andean subpanel. The analyses were completed with GAPIT and the models FarmCPU, BLINK, or MLM (Zhang et al. 2010; Liu et al. 2016; Huang et al. 2019; Wang and Zhang 2021). The X-axis represents the genomic position of markers and the Y-axis is the  $-\log_{10}$  of the P-values for association with the phenotype. The vertical lines correspond to QTLs found by at least 2 models. Point size correlates to  $-\log_{10}(P\text{-value})$ . Quantile-quantile (QQ) plots are provided for c) the whole panel and d) the Andean panel.

number (Kamfwa et al. 2015). Due to the marker technology used, the QTL for seed weight was large so had low resolution (Elias et al. 2021). Our results (Fig. 4) suggest a correlation between DTF,

determinacy, and PS under the same QTL. The significant MTA for this QTL was within the gene *Phvul.008G048300*. However, the function of this gene is currently unclear.

The other QTL found on Pv08 is PS8.2, which has previously been identified for seed weight (Blair et al. 2006). Genes within this QTL include *Phvul.008G085000*, *Phvul.008G084500*, *Phvul.008G084900*, and *Phvul.008G084100*. *Phvul.008G085000* is homologous to *gibberellin 2-oxidase 8* in *Arabidopsis* (Huala et al. 2001). Gibberellin oxidases may respond to light intensity, and can therefore be related to PS (Zhang et al. 2022). *Phvul.008G084100* is homologous to *CLAVATA3* in *Arabidopsis*, a gene that regulates shoot and floral meristem development (Clark et al. 1995; Hirakawa 2021). *Phvul.008G084900* is homologous to genes encoding ovate family proteins (OFPs). OFPs appear to be sensitive to light stimuli (Shahzaib et al. 2024). *Phvul.008G084500* has homology with *RAVEN/INDETERMINATE DOMAIN5* in *Arabidopsis*, which is linked to GA signaling pathways as well as other plant developmental pathways (Sanchez-Corriñero et al. 2019; Aoyanagi et al. 2020). *Phvul.008G085000* and *Phvul.008G084900* also both contain insertions or deletions with high-impact nonsynonymous mutations which, therefore, possibly affect function (Cingolani et al. 2012).

### Two QTLs in chromosome 9

A QTL was identified on Pv09 in the Andean panel (PS9.1). This was near a QTL associated with grain yield (Elias et al. 2021), postharvest index (Sedlar et al. 2020), shoot biomass (Kamfwa et al. 2019), SS (da Silva et al. 2018), DTF, and yield (Blair et al. 2006). Genes within the QTL included *Phvul.009G229100*, *Phvul.009G229200*, *Phvul.009G229700*, and *Phvul.009G229900*. *Phvul.009G229100* is homologous to PIN3 transcription factor genes, involved in regulating root and shoot growth (Goodstein et al. 2012; Haga and Sakai 2012). Homology with *Arabidopsis* suggests *Phvul.009G229200* and *Phvul.009G229700* are involved in root growth (Huala et al. 2001), and that *Phvul.009G229900* encodes a HAB1 (*Hypersensitive To Aba1*) homology to ABI (*Abscisic Acid-Insensitive*)1 gene involved in ABA signal transduction, which is regulated by circadian rhythm (Leitao, Santos, et al. 2021; Kamrani et al. 2022). The other QTL in PV09 (PS9.2) was found in the whole panel and included the gene *Phvul.009G145100*, which was also related to an ABA response gene in *Arabidopsis*. A nearby QTL to PS9.2 was previously identified for DTF (Keller et al. 2022).

### QTL PS11.1 in chromosome 11

The QTL at PV11 (PS11.1) was near a QTL for seed weight (da Silva et al. 2018) and a QTL for disease resistance (Banoo et al. 2020). This may be due to pleiotropic effects or low resolution of the previous analysis with a limited number of markers. Within this QTL is the gene *Phvul.011G004000* which encodes a putative PHD finger protein. PHDs have been found to be involved in the regulation of flowering time (Zhou et al. 2019; Qian et al. 2021). Other genes within the QTL are related to root or shoot growth. For example, homology of *Phvul.011G003200* and *Phvul.011G003400* implicates them in processes involved in root meristem development (Huala et al. 2001). *Phvul.011G003700* is an uncharacterized gene in common bean but homology with *Arabidopsis* suggests it may be associated with phytochrome interacting factor 7 (PIF7) to regulate hypocotyl elongation (Huala et al. 2001; Leivar et al. 2008). However, there are many genes within this QTL and further research is needed to clearly distinguish a candidate gene.

## Conclusion

Our common bean panel contains genetic diversity from the Andean (4 subgroups) and Mesoamerican (2 subgroups) gene pools. Including accessions from Colombia that contain introgressive hybridization and admixture diversity from the Andean and Mesoamerican gene

pools. There was a systematic association between the population structure and agronomic traits such as determinacy and PS. In this study we identified genomic regions which are connected to known and novel putative candidate genes involved in developmental and reproductive pathways. We found 13 QTLs associated with determinacy and 10 QTLs associated with PS. One known QTL was the *Fin* locus on Pv01 for determinacy known for its pleiotropic effects in plant development. While other putative candidate genes were identified due to homology with *Glycine soja*, *Vigna* species and *Arabidopsis*. This includes *Phvul.008G170000* that encodes a putative FAF domain-containing protein. Consequently, GWAS are important in identifying MTAs and candidate genes, especially when accounting for population structure. By linking candidate genes to phenotypes, we hope more targeted precision breeding approaches can be adopted to improve common bean traits under climate change. Nevertheless, this current study and previous ones highlight that for some genes and genomic regions, this will be difficult due to the high proportion of pleiotropic effects in common beans.

## Data availability statement

We thank CIAT's Genebank and IPK's Genebank for their generous provision of germplasm. Germplasm held in the CIAT and IPK collections is available on request. Raw reads are deposited in the SRA under accession PRJEB81566. The scripts used in this study are publicly available in Github (<https://github.com/DeVegaGroup/KDJ-CBeans>).

Supplemental material available at G3 online.

## Acknowledgments

The authors would like to acknowledge the support of the Norwich Bioscience Institutes Research Computing team, Horticultural Services at the John Innes Centre, and the Technical Genomics group at the Earlham Institute, as well as the Genebank personnel at the International Centre of Tropical Research (CIAT) in Colombia and IPK in Germany. All the authors contributed and approved this manuscript.

## Funding

KED-J is supported by the Biotechnology and Biological Sciences Research Council (UKRI-BBSRC) to the Norwich Research Park Doctoral Training program (#2578607). This research was partially funded by the British Council throughout the "2019 Newton Fund Institutional Links binational Bioeconomy" call in grant ID 527023146 to AJC and JJDV. This study was also partially funded by the Biotechnology and Biological Sciences Research Council (BBSRC), part of UK Research and Innovation (UKRI), to the Earlham Institute's Grant "Decoding Biodiversity" (BBX011089/1), and its constituent work package BBS/E/ER/230002B (Decode WP2 Genome Enabled Analysis of Diversity to Identify Gene Function, Biosynthetic Pathways, and Variation in Agri/Aquacultural Traits). Funding was also received from the BBSRC through the "Core Strategic Programme Grant" BB/CSP1720/1 (Genomes to Food Security) and its constituent work package BBS/E/T/000PR9818 (WP1 Signatures of Domestication and Adaptation), as well as the BBSRC-funded "Core Capability Grant" BB/CCG1720/1.

## Conflicts of interest

The author(s) declare no conflict of interest.

## Literature cited

- Alexander DH, Lange K. 2011. Enhancements to the admixture algorithm for individual ancestry estimation. *Bmc Bioinformatics*. 12(1):246. doi:[10.1186/1471-2105-12-246](https://doi.org/10.1186/1471-2105-12-246).
- Ambachew D, Londono JM, Castillo NR, Asfaw A, Blair MW. 2024. Genetic diversity, linkage disequilibrium, and population structure in a common bean reference collection. *Agronomy*. 14(5): 985. doi:[10.3390/agronomy14050985](https://doi.org/10.3390/agronomy14050985).
- Aoyanagi T, Ikeya S, Kobayashi A, Kozaki A. 2020. Gene regulation via the combination of transcription factors in the indeterminate domain and gras families. *Genes (Basel)*. 11(6):613. doi:[10.3390/genes11060613](https://doi.org/10.3390/genes11060613).
- Arriagada O, Arévalo B, Cabeza RA, Carrasco B, Schwember AR. 2022. Meta-qt1 analysis for yield components in common bean (*phaseolus vulgaris* l.). *Plants (Basel)*. 12(1):117. doi:[10.3390/plants12010117](https://doi.org/10.3390/plants12010117).
- Assefa T, Mahama AA, Brown AV, Cannon EKS, Rubyogo JC, Rao IM, Blair MW, Cannon SB. 2019. A review of breeding objectives, genomic resources, and marker-assisted methods in common bean (*phaseolus vulgaris* l.). *Mol Breed*. 39(2):1–23. doi:[10.1007/s11032-018-0920-0](https://doi.org/10.1007/s11032-018-0920-0).
- Banoo A, Nabi A, Rasool RS, Mahiya-Farooq, Shah MHD, Ahmad M, Sofi PA, Aasiya-Nabi, Itoo H, Sharma PN, et al. 2020. North-western himalayan common beans: population structure and mapping of quantitative anthracnose resistance through genome wide association study. *Front Plant Sci*. 11:571618. doi:[10.3389/fpls.2020.571618](https://doi.org/10.3389/fpls.2020.571618).
- Barnett DW, Garrison EK, Quinlan AR, Strömberg MP, Marth GT. 2011. Bamtools: a c++ api and toolkit for analyzing and managing bam files. *Bioinformatics*. 27(12):1691–1692. doi:[10.1093/bioinformatics/btr174](https://doi.org/10.1093/bioinformatics/btr174).
- Bateman A, Martin MJ, Orchard S, Magrane M, Ahmad S, Alpi E, Bowler-Barnett EH, Britto R, Cukura A, Denny P, et al. 2023. Uniprot: the universal protein knowledgebase in 2023. *Nucleic Acids Res*. 51(D1):D523–D531. doi:[10.1093/nar/gkac1052](https://doi.org/10.1093/nar/gkac1052).
- Beans and herbs. 2020. [accessed 2020]. <https://www.beansandherbs.co.uk/>.
- Beebe S, Rao I, Mukankusi C, Buruchara R. 2012. Improving resource use efficiency and reducing risk of common bean production in Africa, Latin America, and the Caribbean. In: Hershey Clair H, editor. Eco-Efficiency: From vision to reality. Vol. 8. Centro Internacional de Agricultura Tropical (CIAT). p. 1–18. <https://cgspage.cgiar.org/items/57ddcb4c-35a3-486a-ad28-eddd57443d41>.
- Beebe S, Skroch PW, Tohme J, Duque MC, Pedraza F, Nienhuis J. 2000. Structure of genetic diversity among common bean landraces of middle American origin based on correspondence analysis of rapd. *Crop Sci*. 40(1):264–273. doi:[10.2135/cropsci2000.401264x](https://doi.org/10.2135/cropsci2000.401264x).
- Bellucci E, Benazzo A, Xu CM, Bitocchi E, Rodriguez M, Alseekh S, Di Vittori V, Gioia T, Neumann K, Cortinovis G, et al. 2023. Selection and adaptive introgression guided the complex evolutionary history of the European common bean. *Nat Commun*. 14(1):1908. doi:[10.1038/s41467-023-37332-z](https://doi.org/10.1038/s41467-023-37332-z).
- Bernardi C, Macri G, Biagi M, Miraldi E, Finetti F, Trabalzini L. 2023. In vitro digestion of *phaseolus vulgaris* l. Cooked beans induces autophagy in colon cancer cells. *Foods*. 12(4):839. doi:[10.3390/foods12040839](https://doi.org/10.3390/foods12040839).
- Bhakta MS, Jones VA, Vallejos CE. 2015. Punctuated distribution of recombination hotspots and demarcation of pericentromeric regions in *phaseolus vulgaris* l. *PLoS One*. 10(1):e0116822. doi:[10.1371/journal.pone.0116822](https://doi.org/10.1371/journal.pone.0116822).
- Bitocchi E, Nanni L, Bellucci E, Rossi M, Giardini A, Zeuli PS, Logozzo G, Stougaard J, McClean P, Attene G, et al. 2012. Mesoamerican origin of the common bean (*phaseolus vulgaris* l.) is revealed by sequence data. *Proc Natl Acad Sci U S A*. 109(14):E788–E796. doi:[10.1073/pnas.1108973109](https://doi.org/10.1073/pnas.1108973109).
- Bitocchi E, Rau D, Bellucci E, Rodriguez M, Murgia ML, Gioia T, Santo D, Nanni L, Attene G, Papa R. 2017. Beans (*phaseolus* spp.) as a model for understanding crop evolution. *Front Plant Sci*. 8:722. doi:[10.3389/fpls.2017.00722](https://doi.org/10.3389/fpls.2017.00722).
- Blair MW, Chaves A, Tofino A, Calderon JF, Palacio JD. 2010. Extensive diversity and inter-gene pool introgression in a world-wide collection of indeterminate snap bean accessions. *Theor Appl Genet*. 120(7):1381–1391. doi:[10.1007/s00122-010-1262-4](https://doi.org/10.1007/s00122-010-1262-4).
- Blair MW, Cortes AJ, Penmetsa RV, Farmer A, Carrasquilla-Garcia N, Cook DR. 2013. A high-throughput snp marker system for parental polymorphism screening, and diversity analysis in common bean (*phaseolus vulgaris* l.). *Theor Appl Genet*. 126(2):535–548. doi:[10.1007/s00122-012-1999-z](https://doi.org/10.1007/s00122-012-1999-z).
- Blair MW, Diaz LM, Buendia HF, Duque MC. 2009. Genetic diversity, seed size associations and population structure of a core collection of common beans (*phaseolus vulgaris* l.). *Theor Appl Genet*. 119(6):955–972. doi:[10.1007/s00122-009-1064-8](https://doi.org/10.1007/s00122-009-1064-8).
- Blair MW, Diaz JM, Hidalgo R, Diaz LM, Duque MC. 2007. Microsatellite characterization of andean races of common bean (*phaseolus vulgaris* l.). *Theor Appl Genet*. 116(1):29–43. doi:[10.1007/s00122-007-0644-8](https://doi.org/10.1007/s00122-007-0644-8).
- Blair MW, 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. *Theor Appl Genet*. 112(6):1149–1163. doi:[10.1007/s00122-006-0217-2](https://doi.org/10.1007/s00122-006-0217-2).
- Blair MW, Izquierdo P, Astudillo C, Grusak MA. 2013. A legume biofortification quandary: variability and genetic control of seed coat micronutrient accumulation in common beans. *Front Plant Sci*. 4:275. doi:[10.3389/fpls.2013.00275](https://doi.org/10.3389/fpls.2013.00275).
- Botero H, Barnes AP. 2022. The effect of enso on common bean production in Colombia: a time series approach. *Food Secur*. 14(6): 1417–1430. doi:[10.1007/s12571-022-01290-z](https://doi.org/10.1007/s12571-022-01290-z).
- Botero H, Barnes AP, Perez L, Rios D, Ramirez-Villegas J. 2021. The determinants of common bean variety selection and diversification in Colombia. *Ecol Econ*. 190:107181. doi:[10.1016/j.ecolecon.2021.107181](https://doi.org/10.1016/j.ecolecon.2021.107181).
- Bradbury PJ, Zhang Z, Kroon DE, Casstevens TM, Ramdoss Y, Buckler ES. 2007. Tassel: software for association mapping of complex traits in diverse samples. *Bioinformatics*. 23(19):2633–2635. doi:[10.1093/bioinformatics/btm308](https://doi.org/10.1093/bioinformatics/btm308).
- Broughton WJ, Hernández G, Blair M, Beebe S, Gepts P, Vanderleyden J. 2003. Beans (*phaseolus* spp.)—model food legumes. *Plant Soil*. 252(1):55–128. doi:[10.1023/A:1024146710611](https://doi.org/10.1023/A:1024146710611).
- Camacho C, Coulouris G, Avagyan V, Ma N, Papadopoulos J, Bealer K, Madden TL. 2009. Blast+: architecture and applications. *BMC Bioinformatics*. 10(421). doi:[10.1186/1471-2105-10-421](https://doi.org/10.1186/1471-2105-10-421).
- Campa A, Murube E, Ferreira JJ. 2018. Genetic diversity, population structure, and linkage disequilibrium in a Spanish common bean diversity panel revealed through genotyping-by-sequencing. *Genes (Basel)*. 9(11):518. doi:[10.3390/genes9110518](https://doi.org/10.3390/genes9110518).
- Caproni L, Raggi L, Talsma EF, Wenzl P, Negri V. 2020. European landrace diversity for common bean biofortification: a genome-wide association study. *Sci Rep*. 10(1):19775. doi:[10.1038/s41598-020-76417-3](https://doi.org/10.1038/s41598-020-76417-3).
- Castro-Guerrero NA, Isidra-Arellano M, Mendoza-Coatl DG, Valdez Lopez O. 2016. Common bean: a legume model on the rise for unraveling responses and adaptations to iron, zinc, and phosphate deficiencies. *Front Plant Sci*. 7:600. doi:[10.3389/fpls.2016.00600](https://doi.org/10.3389/fpls.2016.00600).
- Caivalcante AG, Lemos LB, Meirelles FC, Caivalcante ACP, de Aquino LA. 2020. Thermal sum and phenological descriptions of growth

- stages of the common bean according to the bbch scale. Ann Appl Biol. 176(3):342–349. doi:[10.1111/aab.12571](https://doi.org/10.1111/aab.12571).
- Cebeci Z, Bayraktar M, Gökçe G. 2023. Comparison of the statistical methods for genome-wide association studies on simulated quantitative traits of domesticated goats (*capra hircus l.*). Small Rumin Res. 227:107053. doi:[10.1016/j.smallrumres.2023.107053](https://doi.org/10.1016/j.smallrumres.2023.107053).
- Chacon-Sanchez MI, Martinez-Castillo J, Duitama J, Debouck DG. 2021. Gene flow in *phaseolus* beans and its role as a plausible driver of ecological fitness and expansion of cultigens. Front Ecol Evol. 9:618709. doi:[10.3389/fevo.2021.618709](https://doi.org/10.3389/fevo.2021.618709).
- Chacon-Sanchez MI, Pickersgill B, Debouck DG, Arias JS. 2007. Phylogeographic analysis of the chloroplast dna variation in wild common bean (*phaseolus vulgaris l.*) in the americas. Plant Systematics and Evolution. 266(3–4):175–195. doi:[10.1007/s00606-007-0536-z](https://doi.org/10.1007/s00606-007-0536-z).
- Chen F, Yang YZ, Luo XF, Zhou WG, Dai YJ, Zheng C, Liu WG, Yang WY, Shu K. 2019. Genome-wide identification of grf transcription factors in soybean and expression analysis of gmgrf family under shade stress. BMC Plant Biol. 19(1):269. doi:[10.1186/s12870-019-1861-4](https://doi.org/10.1186/s12870-019-1861-4).
- Cichy KA, Porch TG, Beaver JS, Cregan P, Fourie D, Glahn RP, Grusak MA, Kamfwa K, Katuuramu DN, McClean P, et al. 2015. A diversity panel for andean bean improvement. Crop Sci. 55(5):2149–2160. doi:[10.2135/cropsci2014.09.0653](https://doi.org/10.2135/cropsci2014.09.0653).
- Cingolani P, Platts A, Wang LL, Coon M, Nguyen T, Wang L, Land SJ, Lu XY, Ruden DM. 2012. A program for annotating and predicting the effects of single nucleotide polymorphisms, snpeff. Fly (Austin). 6(2):80–92. doi:[10.4161/fly.19695](https://doi.org/10.4161/fly.19695).
- Clark SE, Running MP, Meyerowitz EM. 1995. Clavata3 is a specific regulator of shoot and floral meristem development affecting the same processes as clavata1. Development. 121(7):2057–2067. doi:[10.1242/dev.121.7.2057](https://doi.org/10.1242/dev.121.7.2057).
- Coelho AP, de Faria RT, Lemos LB, dos Reis MAM, Filla VA, Bertino AMP. 2023. Irrigation management of common bean cultivars with contrasting growth habits. Scientia Agricola. 80:e20220038. doi:[10.1590/1678-992x-2022-0038](https://doi.org/10.1590/1678-992x-2022-0038).
- Cusworth G, Garnett T, Lorimer J. 2021. Agroecological break out: legumes, crop diversification and the regenerative futures of UK agriculture. J Rural Stud. 88:126–137. doi:[10.1016/j.jrurstud.2021.10.005](https://doi.org/10.1016/j.jrurstud.2021.10.005).
- Daba K, Warkentin TD, Bueckert R, Todd CD, Tar'an B. 2016. Determination of photoperiod-sensitive phase in chickpea (*cicer arietinum l.*). Front Plant Sci. 7:478. doi:[10.3389/fpls.2016.00478](https://doi.org/10.3389/fpls.2016.00478).
- Danecek P, Bonfield JK, Liddle J, Marshall J, Ohan V, Pollard MO, Whitwham A, Keane T, McCarthy SA, Davies RM, et al. 2021. Twelve years of samtools and bcftools. Gigascience. 10(2): giab008. doi:[10.1093/gigascience/giab008](https://doi.org/10.1093/gigascience/giab008).
- da Silva LC, de Souza TLPO, Cruz CD, Carneiro PCS, Silva FFE, de Barros EG, Vianello RP, da Fonseca CEL, Song QJ, Cregan PB, et al. 2018. Linkage fine-mapping and qtls affecting morpho-agronomic traits of a mesoamericanxandean ril common bean population. Euphytica. 214(12):1–15. doi:[10.1007/s10681-018-2299-8](https://doi.org/10.1007/s10681-018-2299-8).
- de Almeida CP, Paulino JFD, Carbonell SAM, Chiorato AF, Song QJ, Di Vittori V, Rodriguez M, Papa R, Benchimol-Reis LL. 2020. Genetic diversity, population structure, and andean introgression in Brazilian common bean cultivars after half a century of genetic breeding. Genes (Basel). 11(11):1298. doi:[10.3390/genes11111298](https://doi.org/10.3390/genes11111298).
- Debouck DG, Toro O, Paredes OM, Johnson WC, Gepts P. 1993. Genetic diversity and ecological distribution of *phaseolus-vulgaris* (*Fabaceae*) in northwestern south-America. Econ Bot. 47(4): 408–423. doi:[10.1007/BF02907356](https://doi.org/10.1007/BF02907356).
- Delfini J, Moda-Cirino V, Neto JD, Zeffa DM, Nogueira AF, Ribeiro LAB, Ruas PM, Gepts P, Gonçalves LSA. 2021. Genome-wide association study identifies genomic regions for important morpho-agronomic traits in mesoamerican common bean. Front Plant Sci. 12:748829. doi:[10.3389/fpls.2021.748829](https://doi.org/10.3389/fpls.2021.748829).
- de Souza LP, Bitocchi E, Papa R, Tohge T, Fernie AR. 2023. Decreased metabolic diversity in common beans associated with domestication revealed by untargeted metabolomics, information theory, and molecular networking. Plant J. 115(4):1021–1036. doi:[10.1111/tpj.16277](https://doi.org/10.1111/tpj.16277).
- Diess C, Stevens GJ, Xie PT, Martinez TD, Hershberg EA, Leung A, Guo E, Dider S, Zhang JJ, Bridge C, et al. 2023. Jbrowse 2: a modular genome browser with views of synteny and structural variation. Genome Biol. 24(1):74. doi:[10.1186/s13059-023-02914-z](https://doi.org/10.1186/s13059-023-02914-z).
- Diniz AL, Giordani W, Costa ZP, Margarido GRA, Persegui JM, Benchimol-Reis LL, Chiorato AF, Garcia AAF, Vieira MLC. 2018. Evidence for strong kinship influence on the extent of linkage disequilibrium in cultivated common beans. Genes (Basel). 10(1):5. doi:[10.3390/genes10010005](https://doi.org/10.3390/genes10010005).
- Elias JCF, Gonçalves-Vidigal MC, Bisneta MV, Valentini G, Vidigal PS, Gilio TAS, Moda-Cirino V, Song QJ. 2021. Genetic mapping for agronomic traits in iapar 81/lp97–28 population of common bean (*phaseolus vulgaris l.*) under drought conditions. Plants (Basel). 10(8):1568. doi:[10.3390/plants10081568](https://doi.org/10.3390/plants10081568).
- EWels P, Magnusson M, Lundin S, Kaller M. 2016. Multiqc: summarize analysis results for multiple tools and samples in a single report. Bioinformatics. 32(19):3047–3048. doi:[10.1093/bioinformatics/btw354](https://doi.org/10.1093/bioinformatics/btw354).
- Foyer CH, Lam HM, Nguyen HT, Siddique KHM, Varshney RK, Colmer TD, Cowling W, Bramley H, Mori TA, Hodgson JM, et al. 2016. Neglecting legumes has compromised human health and sustainable food production. Nat Plants. 2(8):16112. doi:[10.1038/nplants.2016.112](https://doi.org/10.1038/nplants.2016.112).
- Gan ES, Xu YF, Wong JY, Goh JG, Sun B, Wee WY, Huang JB, Ito T. 2014. Jumonji demethylases moderate precocious flowering at elevated temperature via regulation of *flc* in *arabidopsis*. Nat Commun. 5(1):5098. doi:[10.1038/ncomms6098](https://doi.org/10.1038/ncomms6098).
- Ganesan K, Xu BJ. 2017. Polyphenol-rich dry common beans (*phaseolus vulgaris l.*) and their health benefits. Int J Mol Sci. 18(11):2331. doi:[10.3390/ijms18112331](https://doi.org/10.3390/ijms18112331).
- García-Fernández C, Campa A, Garzón AS, Miklas P, Ferreira JJ. 2021. Gwas of pod morphological and color characters in common bean. BMC Plant Biol. 21(1):184. doi:[10.1186/s12870-021-02967-x](https://doi.org/10.1186/s12870-021-02967-x).
- Garrison E, Marth G. 2012. Haplotype-based variant detection from short-read sequencing. arXiv 1207.3907. <https://doi.org/10.48550/arXiv.1207.3907>, preprint: not peer reviewed.
- Gautam T, Dutta M, Jaiswal V, Zinta G, Gahlaut V, Kumar S. 2022. Emerging roles of sweet sugar transporters in plant development and abiotic stress responses. Cells. 11(8):1303. doi:[10.3390/cells11081303](https://doi.org/10.3390/cells11081303).
- Gepts P, Debouck D. 1991. Origin, domestication, and evolution of the common bean (*phaseolus vulgaris l.*). In: van Schoonhoven A, Voysest O, editors. Common Beans: Research for Crop Improvement. C.A.B. Int.; Wallingford, UK: CIAT; Cali, Colombia. p. 7–53.
- Ginestet C. 2011. Ggplot2: elegant graphics for data analysis. Journal of the Royal Statistical Society Series a-Statistics in Society. 174(1):245–246. doi:[10.1111/j.1467-985X.2010.00676\\_9.x](https://doi.org/10.1111/j.1467-985X.2010.00676_9.x).
- Giordani W, Gama HC, Chiorato AF, Garcia AAF, Vieira MLC. 2022. Genome-wide association studies dissect the genetic architecture of seed shape and size in common bean. G3 (Bethesda). 12(4):jkac048. doi:[10.1093/g3journal/jkac048](https://doi.org/10.1093/g3journal/jkac048).
- González AM, Yuste-Lisbona FJ, Saburido S, Bretones S, De Ron AM, 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. *Front Plant Sci.* 7:1940. doi:[10.3389/fpls.2016.01940](https://doi.org/10.3389/fpls.2016.01940).
- Goodstein DM, Shu SQ, Howson R, Neupane R, Hayes RD, Fazo J, Mitros T, Dirks W, Hellsten U, Putnam N, et al. 2012. Phytozome: a comparative platform for green plant genomics. *Nucleic Acids Res.* 40(D1):D1178–D1186. doi:[10.1093/nar/gkr944](https://doi.org/10.1093/nar/gkr944).
- Gori B, Ulian T, Bernal HY, Diazgranados M. 2022. Understanding the diversity and biogeography of Colombian edible plants. *Sci Rep.* 12(1):7835. doi:[10.1038/s41598-022-11600-2](https://doi.org/10.1038/s41598-022-11600-2).
- Haga K, Sakai T. 2012. Pin auxin efflux carriers are necessary for pulse-induced but not continuous light-induced phototropism in *Arabidopsis*. *Plant Physiol.* 160(2):763–776. doi:[10.1104/pp.112.202432](https://doi.org/10.1104/pp.112.202432).
- Hill WG, Robertson A. 2007. The effect of linkage on limits to artificial selection (reprinted). *Genet Res (Camb.)*. 89(5–6):311–336. doi:[10.1017/S001667230800949X](https://doi.org/10.1017/S001667230800949X).
- Hirakawa Y. 2021. Clavata3, a plant peptide controlling stem cell fate in the meristem. *Peptides.* 142:170579. doi:[10.1016/j.peptides.2021.170579](https://doi.org/10.1016/j.peptides.2021.170579).
- Hoyos-Villegas V, Song QJ, Kelly JD. 2017. Genome-wide association analysis for drought tolerance and associated traits in common bean. *Plant Genome.* 10(1):2015.12.0122. doi:[10.3835/plantgenome2015.12.0122](https://doi.org/10.3835/plantgenome2015.12.0122).
- Hu TS, Chitnis N, Monos D, Dinh A. 2021. Next-generation sequencing technologies: an overview. *Hum Immunol.* 82(11):801–811. doi:[10.1016/j.humimm.2021.02.012](https://doi.org/10.1016/j.humimm.2021.02.012).
- Huala E, Dickerman AW, Garcia-Hernandez M, Weems D, Reiser L, LaFond F, Hanley D, Kiphart D, Zhuang MZ, Huang W, et al. 2001. The *Arabidopsis* information resource (TAIR): a comprehensive database and web-based information retrieval, analysis, and visualization system for a model plant. *Nucleic Acids Res.* 29(1):102–105. doi:[10.1093/nar/29.1.102](https://doi.org/10.1093/nar/29.1.102).
- Huang M, Liu XL, Zhou Y, Summers RM, Zhang ZW. 2019. Blink: a package for the next level of genome-wide association studies with both individuals and markers in the millions. *Gigascience.* 8(2):giy154. doi:[10.1093/gigascience/giy154](https://doi.org/10.1093/gigascience/giy154).
- Humann J, Jung S, Cheng C-H, Lee T, Zheng P, Frank M, McGaughey D, Scott K, Buble K, Yu J, et al. 2019. Cool Season Food Legume Genome Database: A Resource for Pea, Lentil, Faba Bean and Chickpea Genetics, Genomics and Breeding. Paper Presented at: International Plant and Animal Genome Conference; San Diego, CA, USA.
- Jha AB, Ashokkumar K, Diapari M, Ambrose SJ, Zhang HX, Tar'an B, Bett KE, Vandenberg A, Warkentin TD, Purves RW. 2015. Genetic diversity of folate profiles in seeds of common bean, lentil, chickpea and pea. *J Food Compost Anal.* 42:134–140. doi:[10.1016/j.jfca.2015.03.006](https://doi.org/10.1016/j.jfca.2015.03.006).
- Jungleseeds. 2020. Seed catalogue [accessed 2020 Jun]. <https://jungleseeds.co.uk/>
- Kachinski WD, Avila FW, Dos Reis AR, Muller MML, Mendes MC, Petranski PH. 2022. Agronomic biofortification increases concentrations of zinc and storage proteins in common bean (*Phaseolus vulgaris* L.) grains. *Food Res Int.* 155:111105. doi:[10.1016/j.foodres.2022.111105](https://doi.org/10.1016/j.foodres.2022.111105).
- Kamfwa K, Cichy KA, Kelly JD. 2015. Genome-wide association study of agronomic traits in common bean. *Plant Genome.* 8(2):2014.09.0059. doi:[10.3835/plantgenome2014.09.0059](https://doi.org/10.3835/plantgenome2014.09.0059).
- Kamfwa K, Cichy KA, Kelly JD. 2019. Identification of quantitative trait loci for symbiotic nitrogen fixation in common bean. *Theor Appl Genet.* 132(5):1375–1387. doi:[10.1007/s00122-019-03284-6](https://doi.org/10.1007/s00122-019-03284-6).
- Kami J, Velasquez VB, Debouck DG, Gepts P. 1995. Identification of presumed ancestral DNA-sequences of phaseolin in *Phaseolus vulgaris*. *Proc Natl Acad Sci U S A.* 92(4):1101–1104. doi:[10.1073/pnas.92.4.1101](https://doi.org/10.1073/pnas.92.4.1101).
- Kamrani YY, Shomali A, Aliniaefard S, Lastochkina O, Moosavi-Nezhad M, Hajinajaf N, Talar U. 2022. Regulatory role of circadian clocks on aba production and signaling, stomatal responses, and water-use efficiency under water-deficit conditions. *Cells.* 11(7):1154. doi:[10.3390/cells11071154](https://doi.org/10.3390/cells11071154).
- Keller B, Ariza-Suarez D, Portilla-Benavides AE, Buendia HF, Aparicio JS, Amongi W, Mbiu J, Msolla SN, Miklas P, Porch TG, et al. 2022. Improving association studies and genomic predictions for climbing beans with data from bush bean populations. *Front Plant Sci.* 13:830896. doi:[10.3389/fpls.2022.830896](https://doi.org/10.3389/fpls.2022.830896).
- Kim J, Kang H, Park J, Kim W, Yoo J, Lee N, Kim J, Yoon TY, Choi G. 2016. Pif1-interacting transcription factors and their binding sequence elements determine the in vivo targeting sites of pif1. *Plant Cell.* 28(6):1388–1405. doi:[10.1105/tpc.16.00125](https://doi.org/10.1105/tpc.16.00125).
- Kirkwood M, Vohra P, Bawn M, Thilliez G, Pye H, Tanner J, Chintooan-Uta C, Branchu P, Petrovska L, Dallman T, et al. 2021. Ecological niche adaptation of *Salmonella typhimurium* u288 is associated with altered pathogenicity and reduced zoonotic potential. *Commun Biol.* 4(1):498. doi:[10.1038/s42003-021-02013-4](https://doi.org/10.1038/s42003-021-02013-4).
- Kwak M, Toro O, Debouck DG, Gepts P. 2012. Multiple origins of the determinate growth habit in domesticated common bean (*Phaseolus vulgaris*). *Ann Bot.* 110(8):1573–1580. doi:[10.1093/aob/mcs207](https://doi.org/10.1093/aob/mcs207).
- Kwak M, Velasco D, Gepts P. 2008. Mapping homologous sequences for determinacy and photoperiod sensitivity in common bean (*Phaseolus vulgaris*). *J Hered.* 99(3):283–291. doi:[10.1093/jhered/esn005](https://doi.org/10.1093/jhered/esn005).
- Leitao ST, Bicho MC, Pereira P, Paulo MJ, Malosetti M, Araujo SD, van Eeuwijk F, Patto MCV. 2021. Common bean SNP alleles and candidate genes affecting photosynthesis under contrasting water regimes. *Hortic Res.* 8(1):4. doi:[10.1038/s41438-020-00434-6](https://doi.org/10.1038/s41438-020-00434-6).
- Leitao ST, Santos C, Araújo SD, Rubiales D, Vaz Patto MC. 2021. Shared and tailored common bean transcriptomic responses to combined Fusarium wilt and water deficit. *Hortic Res.* 8(1):149. doi:[10.1038/s41438-021-00583-2](https://doi.org/10.1038/s41438-021-00583-2).
- Leivar P, Monte E, Al-Sady B, Carle C, Storer A, Alonso JM, Ecker JR, Quail PH. 2008. The *Arabidopsis* phytochrome-interacting factor pif7, together with pif3 and pif4, regulates responses to prolonged red light by modulating phyB levels. *Plant Cell.* 20(2):337–352. doi:[10.1105/tpc.107.052142](https://doi.org/10.1105/tpc.107.052142).
- Li H, Durbin R. 2009. Fast and accurate short read alignment with Burrows-Wheeler transform. *Bioinformatics.* 25(14):1754–1760. doi:[10.1093/bioinformatics/btp324](https://doi.org/10.1093/bioinformatics/btp324).
- Liu P, Zhang SB, Zhou B, Luo X, Zhou XF, Cai B, Jin YH, Niu D, Lin JX, Cao XF, et al. 2019. The histone H3K4 demethylase jmj16 represses leaf senescence in *Arabidopsis*. *Plant Cell.* 31(2):430–443. doi:[10.1105/tpc.18.00693](https://doi.org/10.1105/tpc.18.00693).
- Liu X, Huang M, Fan B, Buckler ES, Zhang Z. 2016. Iterative usage of fixed and random effect models for powerful and efficient genome-wide association studies (vol 12, e1005767, 2016). *PLoS One.* 11(3):e1005767. doi:[10.1371/journal.pgen.1005767](https://doi.org/10.1371/journal.pgen.1005767).
- Mamidi S, Rossi M, Moghaddam SM, Annad D, Lee R, Papa R, McClean PE. 2013. Demographic factors shaped diversity in the two gene pools of wild common bean *Phaseolus vulgaris* L. *Heredity (Edinb).* 110(3):267–276. doi:[10.1038/hdy.2012.82](https://doi.org/10.1038/hdy.2012.82).
- Mara CD, Huang TB, Irish VF. 2010. The floral homeotic proteins aptala3 and pistillata negatively regulate the genes implicated in light signaling. *Plant Cell.* 22(3):690–702. doi:[10.1105/tpc.109.065946](https://doi.org/10.1105/tpc.109.065946).
- Merrick LF, Burke AB, Zhang ZW, Carter AH. 2022. Comparison of single-trait and multi-trait genome-wide association models and inclusion of correlated traits in the dissection of the genetic architecture of a complex trait in a breeding program. *Front Plant Sci.* 12:772907. doi:[10.3389/fpls.2021.772907](https://doi.org/10.3389/fpls.2021.772907).

- Miklas PN, Johnson WC, Delorme R, Gepts P. 2001. Qtl conditioning physiological resistance and avoidance to white mold in dry bean. *Crop Sci.* 41(2):309–315. doi:[10.2135/cropsci2001.412309x](https://doi.org/10.2135/cropsci2001.412309x).
- Moghaddam SM, Mamidi S, Osorno JM, Lee R, Brick M, Kelly J, Miklas P, Urrea C, Song QJ, Cregan P, et al. 2016. Genome-wide association study identifies candidate loci underlying agronomic traits in a middle American diversity panel of common bean. *Plant Genome.* 9(3):2016.02.0012. doi:[10.3835/plantgenome2016.02.0012](https://doi.org/10.3835/plantgenome2016.02.0012).
- Munekage Y, Hojo M, Meurer J, Endo T, Tasaka M, Shikanai T. 2002. *Pgr5* is involved in cyclic electron flow around photosystem i and is essential for photoprotection in *arabidopsis*. *Cell.* 110(3): 361–371. doi:[10.1016/S0092-8674\(02\)00867-X](https://doi.org/10.1016/S0092-8674(02)00867-X).
- Mupangwa W, Nyagumbo I, Liben F, Chipindu L, Craufurd P, Mukhlani S. 2021. Maize yields from rotation and intercropping systems with different legumes under conservation agriculture in contrasting agro-ecologies. *Agricul Ecosys Environ.* 306: 107170. doi:[10.1016/j.agee.2020.107170](https://doi.org/10.1016/j.agee.2020.107170).
- Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J. 2000. Biodiversity hotspots for conservation priorities. *Nature.* 403(6772):853–858. doi:[10.1038/35002501](https://doi.org/10.1038/35002501).
- Mylona P, Pawłowski K, Bisseling T. 1995. Symbiotic nitrogen-fixation. *Plant Cell.* 7(7):869–885. doi:[10.2307/3870043](https://doi.org/10.2307/3870043).
- Patto MCV, Amarowicz R, Aryee ANA, Boye JI, Chung HJ, Martin-Cabrejas MA, Domoney C. 2015. Achievements and challenges in improving the nutritional quality of food legumes. *CRC Crit Rev Plant Sci.* 34(1–3):105–143. doi:[10.1080/07352689.2014.897907](https://doi.org/10.1080/07352689.2014.897907).
- Pérez-Vega E, Pañeda A, Rodríguez-Suárez C, Campa A, Giraldez R, Ferreira JJ. 2010. Mapping of qtls for morpho-agronomic and seed quality traits in a ril population of common bean (*phaseolus vulgaris* l.). *Theor Appl Genet.* 120(7):1367–1380. doi:[10.1007/s00122-010-1261-5](https://doi.org/10.1007/s00122-010-1261-5).
- Perez L, Rios DA, Giraldo DC, Twyman J, Blundo-Canto G, Prager SD, Ramirez-Villegas J. 2020. Determinants of vulnerability of bean growing households to climate variability in Colombia. *Clim Dev.* 12(8):730–742. doi:[10.1080/17565529.2019.1685931](https://doi.org/10.1080/17565529.2019.1685931).
- Phiri AT, Njira KOW. 2023. Grain legume-based cropping systems' effects on soil organic carbon and nutrient dynamics. *Agric Res.* 12(1):45–52. doi:[10.1007/s40003-022-00619-6](https://doi.org/10.1007/s40003-022-00619-6).
- Pironon S, Borrell JS, Ondo I, Douglas R, Phillips C, Khoury CK, Kantar MB, Fumia N, Gomez MS, Viruel J, et al. 2020. Toward unifying global hotspots of wild and domesticated biodiversity. *Plants-Basel.* 9(9):1128. doi:[10.3390/plants9091128](https://doi.org/10.3390/plants9091128).
- Qian F, Zhao QY, Zhang TN, Li YL, Su YN, Li L, Sui JH, Chen S, He XJ. 2021. A histone h3k27me3 reader cooperates with a family of phd finger-containing proteins to regulate flowering time in *arabidopsis*. *J Integr Plant Biol.* 63(4):787–802. doi:[10.1111/jipb.13067](https://doi.org/10.1111/jipb.13067).
- Raggi L, Caproni L, Carboni A, Negri V. 2019. Genome-wide association study reveals candidate genes for flowering time variation in common bean (*phaseolus vulgaris* l.). *Front Plant Sci.* 10:962. doi:[10.3389/fpls.2019.00962](https://doi.org/10.3389/fpls.2019.00962).
- Rawal V, Navarro DK. 2019. The Global Economy of Pulses. Rome: FAO.
- Reinprecht Y, Schram L, Perry GE, Morneau E, Smith TH, Pauls KP. 2023. Mapping yield and yield-related traits using diverse common bean germplasm. *Front Genet.* 14:1246904. doi:[10.3389/fgene.2023.1246904](https://doi.org/10.3389/fgene.2023.1246904).
- Rendon-Anaya M, Herrera-Estrella A, Gepts P, Delgado-Salinas A. 2017. A new species of *phaseolus* (leguminosae, papilionoideae) sister to *phaseolus vulgaris*, the common bean. *Phytotaxa.* 313(3): 259–266. doi:[10.11646/phytotaxa.313.3.3](https://doi.org/10.11646/phytotaxa.313.3.3).
- Repinski SL, Kwak M, Gepts P. 2012. The common bean growth habit gene *pvtfl1y* is a functional homolog of *arabidopsis* TFL1. *Theor Appl Genet.* 124(8):1539–1547. doi:[10.1007/s00122-012-1808-8](https://doi.org/10.1007/s00122-012-1808-8).
- Sablowski R. 2007. Flowering and determinacy in *arabidopsis*. *J Exp Bot.* 58(5):899–907. doi:[10.1093/jxb/erm002](https://doi.org/10.1093/jxb/erm002).
- Sanchez-Corrión A, Perez-Garcia P, Cabrera J, Silva-Navas J, Perianez-Rodriguez J, Gude I, del Pozo JC, Moreno-Risueno MA. 2019. Root patterning and regeneration are mediated by the quiescent center and involve bluejay, jackdaw and scarecrow regulation of vasculature factors. *bioRxiv* 803973. <https://doi.org/10.1101/803973>, preprint: not peer reviewed.
- Santalla M, Menendez-Sevillano MC, Monteagudo AB, De Ron AM. 2004. Genetic diversity of argentinean common bean and its evolution during domestication. *Euphytica.* 135(1):75–87. doi:[10.1023/B:EUPH.0000009543.46471.72](https://doi.org/10.1023/B:EUPH.0000009543.46471.72).
- Schier HE, Eliot KA, Herron SA, Landfried LK, Migicovsky Z, Rubin MJ, Miller AJ. 2019. Comparative analysis of perennial and annual *phaseolus* seed nutrient concentrations. *Sustainability.* 11(10): 2787. doi:[10.3390/su11102787](https://doi.org/10.3390/su11102787).
- Schmutz J, McClean PE, Mamidi S, Wu GA, Cannon SB, Grimwood J, Jenkins J, Shu SQ, Song QJ, Chavarro C, et al. 2014. A reference genome for common bean and genome-wide analysis of dual domestications. *Nat Genet.* 46(7):707–713. doi:[10.1038/ng.3008](https://doi.org/10.1038/ng.3008).
- Krueger F, James F, Ewels P, Afyonian E, Weinstein M, Schuster-Boeckler B, Hulsemans G, Sclamons. 2023. Felixkrueger/trimgalore: V0.6.10—add default decompression path (0.6.10). Zenodo.
- Sedlar A, Zupin M, Maras M, Razinger J, Sustar-Vozlic J, Pipan B, Meglic 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(2): 225. doi:[10.3390/agronomy10020225](https://doi.org/10.3390/agronomy10020225).
- Shahzaib M, Khan UM, Azhar MT, Atif RM, Khan SH, Zaman QU, Rana IA. 2024. Phylogenomic curation of ovate family proteins (ofps) in the u's triangle of *brassica* l. Indicates stress-induced growth modulation. *PLoS One.* 19(1):e0297473. doi:[10.1371/journal.pone.0297473](https://doi.org/10.1371/journal.pone.0297473).
- Shinohara H. 2021. Root meristem growth factor rgf, a sulfated peptide hormone in plants. *Peptides.* 142:170556. doi:[10.1016/j.peptides.2021.170556](https://doi.org/10.1016/j.peptides.2021.170556).
- Singh SP, Schwartz HF. 2010. Breeding common bean for resistance to diseases: a review. *Crop Sci.* 50(6):2199–2223. doi:[10.2135/cropsci2009.03.0163](https://doi.org/10.2135/cropsci2009.03.0163).
- Sitaraman J, Bui M, Liu ZC. 2008. Leunig homolog and leunig perform partially redundant functions during *arabidopsis* embryo and floral development. *Plant Physiol.* 147(2):672–681. doi:[10.1104/pp.108.115923](https://doi.org/10.1104/pp.108.115923).
- Soler-Garzón A, Mulube M, Kamfwa K, Lungu DM, Hamabwe S, Roy J, Salegwa V, Fourie D, Porch TG, McClean PE, et al. 2024. Gwas of resistance to three bacterial diseases in the andean common bean diversity panel. *Front Plant Sci.* 15:1469381. doi:[10.3389/fpls.2024.1469381](https://doi.org/10.3389/fpls.2024.1469381).
- Suarez-Martinez SE, Ferriz-Martinez RA, Campos-Vega R, Elton-Puente JE, Carbot KD, Garcia-Gasca T. 2016. Bean seeds: leading nutraceutical source for human health. *Cyta-Journal of Food.* 14(1):131–137. doi:[10.1080/19476337.2015.1063548](https://doi.org/10.1080/19476337.2015.1063548).
- Suarez JC, Polania JA, Anzola JA, Contreras AT, Mendez DL, Vanegas JI, Noriega JE, Rodriguez L, Urban MO, Beebe S, et al. 2021. Influence of nitrogen supply on gas exchange, chlorophyll fluorescence and grain yield of breeding lines of common bean evaluated in the Amazon region of Colombia. *Acta Physiologiae Plantarum.* 43(4):1–15. doi:[10.1007/s11738-021-03233-1](https://doi.org/10.1007/s11738-021-03233-1).
- Suarez JC, Urban MO, Contreras AT, Grajales MA, Cajiao C, Beebe SE, Rao IM. 2021. Adaptation of interspecific mesoamerican common bean lines to acid soils and high temperature in the Amazon region of Colombia. *Plants (Basel).* 10(11):2412. doi:[10.3390/plants10112412](https://doi.org/10.3390/plants10112412).

- Tai APK, Martin MV, Heald CL. 2014. Threat to future global food security from climate change and ozone air pollution. *Nat Clim Chang*. 4(9):817–821. doi:[10.1038/nclimate2317](https://doi.org/10.1038/nclimate2317).
- Tar'an B, Michaels TE, Pauls KP. 2002. Genetic mapping of agronomic traits in common bean. *Crop Sci*. 42(2):544–556. doi:[10.2135/cropsci2002.5440](https://doi.org/10.2135/cropsci2002.5440).
- Tohme J, Gonzalez DO, Beebe S, Duque MC. 1996. Aflp analysis of gene pools of a wild bean core collection. *Crop Sci*. 36(5): 1375–1384. doi:[10.2135/cropsci1996.0011183X003600050048x](https://doi.org/10.2135/cropsci1996.0011183X003600050048x).
- Tseng TS, Salomé PA, McClung CR, Olszewski NE. 2004. Spindly and gigantea interact and act in *arabidopsis thaliana* pathways involved in light responses, flowering, and rhythms in cotyledon movements. *Plant Cell*. 16(6):1550–1563. doi:[10.1105/tpc.019224](https://doi.org/10.1105/tpc.019224).
- Ugwuanyi S, Udengwu OS, Snowdon RJ, Obermeier C. 2022. Novel candidate loci for morpho-agronomic and seed quality traits detected by targeted genotyping-by-sequencing in common bean. *Front Plant Sci*. 13:1014282. doi:[10.3389/fpls.2022.1014282](https://doi.org/10.3389/fpls.2022.1014282).
- Valdisser PAMR, Pereira WJ, Almeida JE, Müller BSF, Coelho GRC, de Menezes IPP, Vianna JPG, Zucchi MI, Lanna AC, Coelho ASG, et al. 2017. In-depth genome characterization of a Brazilian common bean core collection using dartseq high-density snp genotyping. *Bmc Genomics*. 18(1):423. doi:[10.1186/s12864-017-3805-4](https://doi.org/10.1186/s12864-017-3805-4).
- Van der Auwera G, O'Connor B. 2020. Genomics in the Cloud: Using Docker, GATK, and WDL in Terra. O'Reilly Media.
- Vargas Y, Mayor-Duran VM, Buendia HF, Ruiz-Guzman H, Raatz B. 2021. Physiological and genetic characterization of heat stress effects in a common bean RIL population. *PLoS One*. 16(4): e0249859. doi:[10.1371/journal.pone.0249859](https://doi.org/10.1371/journal.pone.0249859).
- Wahl V, Brand LH, Guo YL, Schmid M. 2010. The fantastic four proteins influence shoot meristem size in *Arabidopsis thaliana*. *BMC Plant Biol*. 10(1):285. doi:[10.1186/1471-2229-10-285](https://doi.org/10.1186/1471-2229-10-285).
- Wang JB, Zhang ZW. 2021. Gapit version 3: boosting power and accuracy for genomic association and prediction. *Genom Proteomic Bioinformat*. 19(4):629–640. doi:[10.1016/j.gpb.2021.08.005](https://doi.org/10.1016/j.gpb.2021.08.005).
- Wei T, Simko V. 2021. R package ‘Corrplot’: Visualization of a Correlation Matrix. 0.92 ed. [accessed 2024 Jun]. <https://github.com/taiyun/corrplot>
- Weller JL, Schoor JKV, Perez-Wright EC, Hecht V, Gonzalez AM, Capel C, Yuste-Lisbona FJ, Lozano R, Santalla M. 2019. Parallel origins of photoperiod adaptation following dual domestications of common bean. *J Exp Bot*. 70(4):1209–1219. doi:[10.1093/jxb/ery455](https://doi.org/10.1093/jxb/ery455).
- Wingett SW, Andrews S. 2018. FastQ Screen: A tool for multi-genome mapping and quality control. *F1000Research*. 7:1338. doi:[10.12688/f1000research.15931.2](https://doi.org/10.12688/f1000research.15931.2).
- Wu L, Chang YJ, Wang LF, Wang SM, Wu J. 2024. Genome-wide association study dissecting drought resistance- associated loci based on physiological traits in common bean. *J Integr Agric*. 23(11): 3657–3671. doi:[10.1016/j.jia.2024.03.079](https://doi.org/10.1016/j.jia.2024.03.079).
- Wu J, Wang LF, Fu JJ, Chen JB, Wei SH, Zhang SL, Zhang J, Tang YS, Chen ML, Zhu JF, et al. 2020. Resequencing of 683 common bean genotypes identifies yield component trait associations across a north-south cline. *Nat Genet*. 52(1):118–125. doi:[10.1038/s41588-019-0546-0](https://doi.org/10.1038/s41588-019-0546-0).
- Wu JF, Wang Y, Wu SH. 2008. Two new clock proteins, lwd1 and lwd2, regulate arabidopsis photoperiodic flowering. *Plant Physiol*. 148(2):948–959. doi:[10.1104/pp.108.124917](https://doi.org/10.1104/pp.108.124917).
- Xin XY, Li PR, Zhao XY, Yu YJ, Wang WH, Jin GH, Wang J, Sun LL, Zhang DS, Zhang FL, et al. 2024. Temperature-dependent jumonji demethylase modulates flowering time by targeting h3k36me2/3 in. *Nat Commun*. 15(1):5470. doi:[10.1038/s41467-024-49721-z](https://doi.org/10.1038/s41467-024-49721-z).
- Yamaguchi N. 2021. Removal of h3k27me3 by jmj proteins controls plant development and environmental responses in. *Front Plant Sci*. 12:687416. doi:[10.3389/fpls.2021.687416](https://doi.org/10.3389/fpls.2021.687416).
- Zhang XY, Blair MW, Wang SM. 2008. Genetic diversity of Chinese common bean (*phaseolus vulgaris* l.) landraces assessed with simple sequence repeat markers. *Theor Appl Genet*. 117(4):629–640. doi:[10.1007/s00122-008-0807-2](https://doi.org/10.1007/s00122-008-0807-2).
- Zhang C, Dong SS, Xu JY, He WM, Yang TL. 2019. Poplddecay: a fast and effective tool for linkage disequilibrium decay analysis based on variant call format files. *Bioinformatics*. 35(10):1786–1788. doi:[10.1093/bioinformatics/bty875](https://doi.org/10.1093/bioinformatics/bty875).
- Zhang ZW, Ersoz E, Lai CQ, Todhunter RJ, Tiwari HK, Gore MA, Bradbury PJ, Yu JM, Arnett DK, Ordovas JM, et al. 2010. Mixed linear model approach adapted for genome-wide association studies. *Nat Genet*. 42(4):355–360. doi:[10.1038/ng.546](https://doi.org/10.1038/ng.546).
- Zhang CH, Nie X, Kong WL, Deng XX, Sun T, Liu XH, Li YS. 2022. Genome-wide identification and evolution analysis of the gibberellin oxidase gene family in six gramineae crops. *Genes (Basel)*. 13(5):863. doi:[10.3390/genes13050863](https://doi.org/10.3390/genes13050863).
- Zhou AM, Sun HW, Dai SY, Feng S, Zhang JZ, Gong SF, Wang JG. 2019. Identification of transcription factors involved in the regulation of flowering in *Adonis amurensis* through combined RNA-seq transcriptomics and iTRAQ proteomics. *Genes (Basel)*. 10(4):305. doi:[10.3390/genes10040305](https://doi.org/10.3390/genes10040305).

Editor: S. Pearce