

New genomic regions in dry bean (*Phaseolus vulgaris* L.) associated with stem diameter, plant height and other plant architecture traits

Oscar Rodríguez

Universidad Distrital Francisco José de Caldas

Jayanta Roy

North Dakota State University

Didier Murillo

North Dakota State University

Kristin Simons

North Dakota State University

Nusrat Khan

North Dakota State University

Jose C. Figueroa-Cerna

North Dakota State University

Juan M. Osorno

juan.osorno@ndsu.edu

North Dakota State University

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Abstract

Growth habit is one of the most important domestication traits in dry bean (*Phaseolus vulgaris* L.). In the U.S. for example, Type II indeterminate upright plant varieties have allowed farmers to switch from historic two-pass harvest to one-pass direct harvest. Previous work suggested a stem diameter of 5.6 mm as threshold to select Type II architecture genotypes suitable for direct combining. This study aimed to validate the correlation between stem diameter and other agronomic traits using lines comprising various market classes from a public breeding program. It also assesses if stem diameter could be used to select genotypes that combine high seed yield and upright architecture. GWAS was also used to identify genomic regions related to plant height and stem diameter. Mean stem diameter among breeding lines was 7.7 mm, higher than the proposed threshold. Stem diameter showed no significant GxE interactions and the highest broad-sense heritabilities were for regular-darkening pinto (pinto) and slow darkening (SD) pinto. Plant height was the most relevant trait for seed yield variation in black, great northern, and navy beans. In contrast, both plant height and stem diameter are required to explain part of seed yield variability and selecting upright plants for pinto, red/pink, and SD-pinto. GWAS revealed significant regions located on chromosomes Pv03, Pv07, and Pv11 depending on trait and race used. A 40.7–40.8 Mb interval on Pv07 was associated with both plant height and stem diameter, suggesting further studies on indeterminate upright dry bean plant architecture should focus on this region.

Introduction

Growth habit is one of the primary traits that has dramatically changed in dry bean (*Phaseolus vulgaris* L.) from the wild relative to its domesticated form (Smartt 1976). Wild beans had a climbing growth habit as an adaptation to an environment in which trees and shrubs were competitors for light but also helped as a support. Wild bean plants were branched and had many nodes, long and weak internodes, and twining ability (Gepts and Debouck 1991). The domestication process generated new environmental conditions for dry bean. Hence, new growth habits appeared due to reduced competition for light; therefore, less excessive growth was required. These new conditions led to the selection of cultivars that matured earlier, dried down synchronously, and had a compact growth habit with fewer branching and nodes. In Mesoamerica, for example, dry beans were traditionally grown alongside maize (*Zea mays* L.) and squash (*Cucurbita* spp.) in a multi-crop system called “Milpa”, which provided support for climbing beans (Zizumbo-Villarreal and Colunga-García, 2010). Subsequent breeding mostly focused on the selection of upright plants that do not need any external support from trees or trellises. These selected genotype plants had stout stems, fewer nodes, shorter internodes, and reduced twining (Gepts and Debouck 1991), which later helped in the introduction of monocropping. In general, a loss of genetic diversity is observed when comparing wild to cultivated dry bean. However, the opposite is observed for growth habit (Kelly 2001). While most wild beans tend to climb (Gepts 1998), cultivated beans display a wider range of growth habits (Kelly 2001). This growth habit has been related to three factors: the presence of axial or terminal inflorescence, stem length, and twining ability (Norton 1915). This higher diversity led to different classifications. The simplest one is the differentiation between determinate (apical growth ends up in an inflorescence) and indeterminate plants (apical growth continues

vegetatively, no terminal inflorescence, and all inflorescences are axillary) (Ojehomon and Morgan 1969). A more detailed classification is based on indeterminate or determinate growth habit, stem stiffness, and climbing ability. Based on this, Singh (1982) classified beans into four growth habits namely, Type I, II, III, and IV. Thus, growth habit could be considered an important distinguishing criterion for differentiating dry bean germplasm (Beebe et al. 2000). This trait and other morphological, agronomic, and molecular traits were used to classify dry bean in two major gene pools, Middle-American and Andean. Each gene pool has different races, within Middle American, races Durango/Jalisco, Mesoamerica, and Guatemala are found. While races Chile, Nueva Granada, and Peru belong to the Andean gene pool (Singh 1989; Singh et al. 1991; Beebe et al. 2000).

Breeding for upright plant architecture has significantly expanded dry bean production in the midwestern states (Singh et al. 2007). Today, Type II indeterminate growth is highly preferred across U.S. and for most dry bean market classes because the pods do not touch the ground which improved white mold avoidance, and reduced losses during harvest (Eckert et al. 2011). The only exceptions would be determinate growth habit Andean cultivars such as kidney, cranberry, and yellow market classes plants which usually maintain an upright bushy growth across most environments. Different traits related to upright plant selection have been described (Denis and Adams 1978; Adams 1982). However, stem diameter, plant height, branch angle, and pod distribution have been suggested as the most important and reliable traits to select plants with upright Type II architecture due to their high correlation with this trait (Acquaah et al. 1991, 1992; Moura et al. 2013). In addition, different grading scales for plant architecture have been generated, some of them combine traits such as plant height, growth habit and architecture, producing a range of qualitative values to select (Collicchio et al. 1997; Kelly and Adams 1987; Melo 2009). However, these scales are subjective and require training to reduce errors and ensure accurate scoring. Therefore, a key consideration for the breeder is to determine if a trait used for selection can be easily measured (Acquaah et al. 1992), requiring less effort, time, and resources to obtain reliable data. Silva et al. (2013) determined stem diameter and mean plant height are highly correlated to plant architectural grade. Additionally, the authors found that stem diameter was controlled by additive effects, which was confirmed by Oliveira et al. (2015). These findings suggest that stem diameter is more precise and accurate than simply applying a plant architecture scale. In addition to stem diameter, plant height is another highly relevant trait for upright plant selection (Schwartz et al. 1987). Mulube (2017) found that plant height, stem diameter, number of pods per plant, and seed yield are the most important traits related to mechanical harvest. In the US pinto bean cultivars, plant height was increased from a mean of 34 cm in 1965 to a mean of 57 cm by 2008, likely due to the introgression of Mesoamerica race germplasm with upright Type II architecture (Vandemark et al. 2014). This strategy has been used to achieve upright architecture in market classes where this characteristic is uncommon (Kelly 2001). Introgression of Mesoamerica race Type II growth habit into Type III race Durango market classes (e.g. pinto and great northern) resulted in Durango race Type II cultivars (Kelly and Adams 1987).

The importance of plant height and stem diameter for selecting genotypes with upright plant architecture was further confirmed by Soltani et al. (2016) with the Durango Diversity Panel (DDP). Stem diameter was highly correlated with plant height ($r = 0.80$), and both traits showed moderate correlations

with seed yield ($r = 0.42$) and ($r = 0.40$), respectively. Therefore, stem diameter and plant height could be essential traits in selecting genotypes with upright architecture. Indeed, a stem diameter value of 5.6 mm has been suggested as a threshold to choose plants with reduced lodging and improved Type II architecture suitable for mechanical direct harvest (Soltani et al. 2016).

Besides its phenotypic importance, understanding the genetic control of growth habit is essential to detect possible regions or genes related to the trait of interest as genomic tools increase accuracy of selection. Kornegay et al. (1992) suggested a simple genetic control for growth habit, with Type I or determinate recessively inherited, and indeterminate (semi-climbing and climbing types) as dominant. Jung et al. (1996) suggested the *Fin* locus was the determinacy gene and linked with the photoperiod sensitivity gene (*ppd*) which possibly exerted pleiotropic effects on twining. Single gene inheritance for growth habit and pleiotropic relationships with flowering, maturity, and branch angle were confirmed by Tar'an et al. (2002) and Repinski et al. (2012). Using Mesoamerican and Andean germplasm as parents, Kolkman and Kelly (2003) confirmed the *Fin* gene was located on chromosome Pv01. *Fin* is considered a homolog of the *TFL1* (Terminal flower 1) in Arabidopsis (Repinski et al. 2012). Another QTL for growth habit in chromosome Pv07 was found for small-seeded (navy) genotypes, also associated with flowering, branching pattern, lodging, and disease severity index (Kwak et al. 2008). These findings suggest different determinacy origins, the Andean gene pool as the primary source to determinate growth habit (related to *Fin* gene) and the Middle-American pool as the source of indeterminate growth habit.

Using the Middle-American Diversity Panel (MDP), which includes genotypes with different growth habits, Moghaddam et al. (2016) found a strong signal in chromosome Pv01 associated with Type I genotypes. However, when only Type II and Type III genotypes were used in the GWAS analysis, the most significant peak was observed on chromosome Pv07. Meta-analyses by MacQueen et al. (2020) and Izquierdo et al. (2023) identified strong signals on Pv01 and Pv07, with additional associations on Pv03, Pv06, Pv08, and Pv11 linked to phenology and architectural traits (growth habit, plant height) using both Andean and Middle American germplasm.

The molecular function of some genes related to growth habit include regulation by plant hormones auxin, cytokinins and gibberelins (Yoshida et al. 2018; McKim 2020), transcription factors and proteins related to these mechanisms such as WD-40, F-box (Ho et al. 2008); and growth-regulating factors (GRFs) with roles in stem and leaf development (Omidbakhshfard et al. 2015; Piya et al. 2020). Floral activators and floral inhibitors (Jin et al. 2021; Krylova et al. 2021) and Ring/U-box protein related to Ubiquitin ligase genes in response to abiotic and biotic stresses (Zhang et al. 2020; Kim et al. 2021) were others identified.

Despite these advances and several efforts to understand the relationship among plant height, stem diameter, and upright plant selection, there is still a gap to a fuller understanding of how stem diameter and plant height jointly influence upright architecture in commercial breeding programs and within/among different market classes. Moreover, integrating phenotypic and genomic data could

enhance upright plant selection strategies in the commercial breeding program Therefore, this study aimed to validate the correlation between stem diameter and other agronomic traits such as plant height and seed yield among others using breeding lines from a public breeding program. Additionally, it sought to investigate stem diameter as a criterion to select genotypes that combine high seed yield and upright architecture. Furthermore, the study aimed to identify genomic regions related to the traits of stem diameter and plant height using a genome wide association study (GWAS) approach.

Materials and methods

Plant material

Two hundred and thirty-three (233) advanced dry bean breeding lines from the Nort Dakota State University (NDSU) dry bean breeding program and 28 cultivars commonly grown in North Dakota were evaluated across 3 growing seasons from 2020 to 2022. The lines are from the six major market classes in the U.S. including black, navy, great northern, red, pink, regular-darkening pinto (pinto), and slow-darkening (SD) pinto (Table 1).

Table 1
Number of breeding lines and cultivars evaluated in 2020, 2021, and 2022.

Race	Market Class	Total number of lines evaluated (with checks)	Total Number of Environments (Year x Location)
Mesoamerica	Black	45	8
	Navy	44	9
Durango / Jalisco	Great Northern	55	9
	Red and Pink	32	9
	Pinto	32	9
	SD Pinto	53	9
	Total	261	53

Field experiments

Breeding lines and check cultivars were evaluated in separate advanced yield trials (AYT) within each market class, except for red and pinks which were grown within the same trial because they are considered genetically close. Trails were established at four representative locations in North Dakota – Hatton, Johnstown, Carrington, and Prosper, during the growing seasons (May-September) of the years 2020, 2021, and 2022. These locations are representative of the major dry bean growing areas within the state. For each year, the number of genotypes evaluated varied, because different AYT lines from the

breeding program were included annually. The number of environments (location by market class) varied between 8 and 9. The trials followed the standard management practices used by the dry bean farmers in the Red River Valley of North Dakota (Kandel and Endres 2019), with the exception of controlling for natural disease pressure. Each field trial was conducted in a randomized complete block design (RCBD) with three replications. The experimental plots consisted of 2 rows; each row had a length of 3.65 m, spaced 0.76 m apart, for a total plot area of 5.54 m².

Morpho-agronomic traits data collection

The following traits were measured:

Plant height: The distance in cm from the soil surface and the top of the canopy at bloom, 50% of plants at pod setting, without stretching out the plant.

Stem diameter: Measured in mm by randomly selecting two plants per plot with a caliper brand tool shop model SKU 243–2377, right above the soil surface at maturity (80% of the pods and leaf area dry).

Seed size: Expressed as 100-seed weight: the weight of 100 seeds in g.

Seed yield: The seed yield at harvest in kg ha⁻¹. **Maturity:** Days to maturity when 80% of the pods and leaf area dry, in days after planting (DAP) (Soltani et al. 2016).

Phenotypic Data analysis

Data analysis was performed with SAS 9.4 (SAS Institute, Cary, NC, USA) to display numerical data distribution with histograms and detect outliers within boxplots, which were removed from the analysis. This dataset is unbalanced since all the breeding lines were not evaluated in the same years. Homogeneity of variances was performed using the “10x rule”. In this test, trials were considered homogeneous if the largest error variance was not 10 times larger than the smallest one (Patterson and Silvey 1980). After confirming homogeneity of variances, for each market class, the MIXED procedure was conducted in SAS 9.4 to perform a combined analysis of variance (ANOVA). Given the unbalanced nature of the dataset, the Best Linear Unbiased Predictor (BLUP) was obtained for all the recorded traits. The sources of variation used were genotype, environment, genotype x environment (GxE), and blocks nested within each environment. Environment was considered as the combination between location and year. The genotype effect was considered fixed, while the remaining terms were considered random. The probability of observing differences between group means was tested at significance levels of 0.05 and 0.01.

Heritability estimates

Variance components were obtained using covtest in PROC MIXED with SAS 9.4, considering genotype, environment and GxE as random effects. Using covariance estimates, the broad-sense heritability based on the entry mean was calculated (Fehr 1991).

$$H^2 = \frac{\sigma_G^2}{\sigma_G^2 + \sigma_{\frac{GE}{e}}^2 + \sigma_{\frac{E}{re}}^2}$$

Where,

σ_G^2 = Genotypic variance

σ_{GE}^2 = Genotype x environment variance

σ_E^2 = Environmental variance

e = number of environments

r = number of replicates

Correlation analysis with agronomic traits

Pearson's correlation coefficients were calculated to determine the strength and direction of the linear relationship between pairs of quantitative traits. Correlation coefficients and matrices were calculated and plotted using the functions *cor.matix ()* and *corrplot ()* from the *corrplot* package in R (Wei and Simko 2017).

Regressions

Simple and multiple linear regression analyses were performed to confirm a cause-and-effect relationship among the different independent variables and seed yield. Plant height, stem diameter, maturity, and seed weight were considered as independent variables, while seed yield was the dependent variable. The R function *lm ()* was used. Each independent trait was considered for simple regression, while combinations of the most relevant independent traits were considered for the multiple linear regressions.

Principal component analysis (PCA)

Principal component analysis was performed using the function *PCA* in R package *FactoMineR* (Husson et al. 2023). This analysis was performed for the whole data set, using all market classes and within each market class.

Genetic material, DNA extraction, and GBS libraries generation

A total of 544 advanced breeding lines evaluated between the years 2020, 2021, and 2022, were used to develop a representative panel comprising multiple dry bean market classes. For DNA collection, two dry bean seeds for each line were planted and the first trifoliate leaf from a single plant was taken and placed in a single well on a plate of 96 wells. Liquid nitrogen was used to preserve the collected samples. DNA was isolated using the Mag-Bind® Plant DNA Plus kit (Omega Bio-Tek, Norcross, Georgia, USA) and quantified using Nanodrop. GBS libraries were developed using the optimized two-enzyme protocol [MseI and Taqα1] protocol described by Schröder et al. (2016). Six GBS libraries were sequenced in paired-end runs (2 x 150 bp) using Illumina HiSeq 2500 sequencing system at the HudsonAlpha institute for Biotechnology (Huntsville, AL, USA).

Sequence data processing and SNP Calling

Low quality reads (quality threshold < 20) and reads with less than 80 bp length were discarded using SICKLE software (Joshi and Fass 2011). The filtered reads were mapped to the *P. vulgaris* reference genome UI111 v1.1 (available at: https://phytozome-next.jgi.doe.gov/info/PvulgarisUI111_v1_1) using Burrows-Wheeler Alignment Tool (BWA-mem) (Li, 2013). Subsequently, SAMtools (Li et al. 2009) were used to sort and index the mapping results. Read group information was added using Picard tools (<http://broadinstitute.github.io/picard>). SNP calling was performed using the *MultisampleVariantsDetector* module embedded in the NGSEPcore_4.2.0 software with the *-maxAlnsPerStartPos* 100 parameter (Tello et al. 2023). Multiallelic SNPs were discarded and SNPs with a minimum read depth ≥ 3 , were selected. Further filtering was done to remove genotypes that had more than 75% missing sites, resulting in a total of 508 genotypes. SNPs with less than 25% missing sites and 10% heterozygotes were imputed using Beagle v5.4 (Browning et al. 2018). Finally, a subset of 214 genotypes with a total of 80,578 high quality SNPs after applying 5% minor allele frequency (MAF), were used for the GWAS analysis. However, after applying same quality filtering with 5% MAF, a total of 72,494 and 41,799 SNPs were used for GWAS analysis for the 132 Durango and 82 MA race genotypes, respectively.

Single trait and multi-trait GWAS

Genome-wide association analyses for stem diameter and plant height were conducted using GEMMA v0.98.1 (Genome-wide Efficient Mixed Model Analysis: Zhou and Stephens 2012). The analysis was performed for combined datasets (all 214 genotypes) and separately for Durango race and Mesoamerican race genotypes. Two models were implemented: i) the mixed linear model (GEMMA-MLM) including population structure (PCA) and relatedness (kinship matrix), and ii) efficient mixed-model analysis (EMMA) (efficient mixed-model analysis) in which only kinship matrix was included. The first two PCA calculated by *prcomp* () function in R was used as a covariate. The kinship matrix was computed using the centered relatedness procedure in GEMMA. The lower mean square deviation (MSD) (Mamidi et al. 2011) and q-q plots were considered to select the best model for further analysis. The

significant threshold of P -value with multiple testing correction was calculated following the method proposed by Li and Ji, (2005), to declare association between SNPs and trait of interest. This method uses the eigenvalues of the correlation matrix between the SNPs to calculate the effective number of independent loci (M_{eff}). The significance threshold was calculated as $\alpha_p = 1 - (1 - \alpha_e)^{1/M_{eff}}$, where the experiment-wise error rate was $\alpha_e = 0.05$. For significant SNPs, the proportion of phenotypic variance explained (PVE; R^2) was calculated using the genABEL package available in R (Aulchenko et al. 2007; R Core Team 2015). Manhattan plots were generated using the R function *mhplot()* (Zhao 2007).

Additionally, a multi-trait GWAS was performed in GEMMA v0.98.1 using both plant height and stem diameter as response variables. The analysis was performed across the full panel as well as within each race. The GEMMA-MLM model was implemented for both traits, incorporating the first two principal components (PCA) and kinship matrix to account for population structure and relatedness.

Search for putative candidate genes

Common bean UI111 v1.1 genome annotation was scanned for potential candidate genes present within the ± 50 Kb genomic regions from the significant peak SNPs. This range was selected based on the average LD blocks, which is ~ 100 kb. Genes within a region were investigated through available literature search and their putative biological functions. The potential candidate genes were selected based on their potential relationship to stem diameter and plant height metabolic pathways.

Haplotype block analysis

Haplotype blocks were constructed surrounding the significant SNPs for the respective chromosome according to the solid spine method of linkage disequilibrium (LD) and the extended spine if $D' > 0.8$ implemented in the Haploview v4.1 software (Barrett et al. 2005). This method considers that the first and last markers in a haplotype block are in strong LD with all intermediate markers, thereby providing more robust block boundaries.

Results

Evaluation of traits across locations

Genotype, environment, and GxE effects were highly significant ($P \leq 0.01$), either on the combined or for the market class analyses, for nearly all traits in the study. GxE was significant ($P \leq 0.05$) for plant height, in great northern, and red and pinks. Stem diameter did not exhibit a significant GxE for the pinto and SD-pinto market classes while this interaction was significant ($P \leq 0.05$) for the other market classes (Table 2).

Table 2
Statistic parameters for all traits within each market class across eight to nine environments

		Combined	Black †	Great northern	Navy	Pinto	Red and Pinks	SD-pinto
F Values								
Stem Diameter	G	2.7 ***	1.9 ***	1.4 *	2.0 ***	5.2 ***	3.4 ***	3.5 ***
	E	51.2 ***	18.0 ***	12.7 ***	41.4 ***	13.1 ***	10.4 ***	19.2 ***
	G x E	1.3 ***	1.2 *	1.3 *	1.3 *	0.8 n.s.	1.4 *	1.1 n.s.
Plant Height	G	3.4 ***	1.6 *	4.9 ***	2.7 ***	6.4 ***	5.3 ***	2.7 ***
	E	69.0 ***	29.8 ***	36.3 ***	14.7 ***	9.0 ***	29.2 ***	37.7 ***
	G x E	2.05 ***	1.6 ***	1.3 *	1.5 ***	1.8 ***	1.3 *	1.8 ***
Maturity	G	2.4 ***	3.0 ***	3.7 ***	2.9 ***	3.4 ***	2.2 ***	5.1 ***
	E	55.2 ***	36.0 ***	43.7 ***	11.7 ***	24.5 ***	62.6 ***	26.2 ***
	G x E	3.3 ***	2.4 ***	2.2 ***	2.7 ***	2.3 ***	2.3 ***	1.5 **
Seed Weight	G	133.5 ***	18.5 ***	12.8 ***	12 ***	10.7 ***	11.2 ***	7.9 ***
	E	118.5 ***	117.1 ***	48.2 ***	18.9 ***	52.6 ***	31.6 ***	37.9 ***
	G x E	2.9 ***	2.0 ***	2.2 ***	2.1 ***	2.5 ***	2.2 ***	2 ***
Seed Yield	G	2.7 ***	2.5 ***	5.5 ***	2.9 ***	1.9 **	5.4 ***	2.8 ***
	E	49.2 ***	57.0 ***	30.0 ***	12.2 ***	12.8 ***	17.7 ***	39.5 ***
	G x E	2.7 ***	1.7 ***	2.4 ***	1.7 ***	2.6 ***	1.8 ***	1.5 ***

G: Genotype, E: Environment and G X E: Genotype x Environment interaction. *** *P* value < 0.0001; ***P* value < 0.01; * *P* value < 0.05; n.s. non significant. † For black, eight environments were evaluated, for the remaining market classes nine environments were taken.

Mean values by market class

Means values for plant height were between 49.3 cm for great northern and 53.6 cm for pinto genotypes. Stem diameter mean values across all market classes ranged between 7.6 and 8.0 mm (Table 3). The most common value for stem diameter among market classes was 7.6 mm, observed in black, navy, great northern, and red/pink. The highest mean stem diameter for pinto with 8.0 mm was significantly higher than the remaining market classes.

According to the mean separation values for plant height, pinto and red/pink had the highest plant height with 53.6 and 52.3 cm, respectively. In addition, these two market classes showed the highest seed yield with 1827 kg ha⁻¹ for red/pink and 1754 kg ha⁻¹ for pinto. In most cases, pintos showed either the highest or some of the highest values for stem diameter, plant height, and seed yield.

Table 3
Means for agronomic traits across environments (2020–2022)

	Stem diameter	Plant height	Maturity	100-Seed weight	Seed yield
Market Class	Mean				
	Mm	cm	d	g	kg ha ⁻¹
Combined	7.7	50.9	102	28.4	1662
Pinto	8.0 a	53.6 a	101 bc	35.0 b	1754 b
SD Pinto	7.7 b	50.2 cd	102 ab	35.7 a	1664 c
Red and Pinks	7.6 b	52.3 b	103 a	31.3 d	1827 a
Black	7.6 b	50.4 c	103 a	19.0 e	1694 bc
Navy	7.6 b	51.0 c	101 c	17.9 f	1582 d
Great Northern	7.6 b	49.3 d	101 c	34.0 c	1539 d
LSD	0.12	0.91	1.03	0.37	67.44

Mean with different letters indicate significantly different Market Classes (LSD test $P < 0.05$)

Heritabilities

The heritability estimates for stem diameter ranged between 0.43 for great northern and 0.87 for pinto (Table 4). The two market classes with the highest heritability were pinto and SD-Pinto (0.84), which also showed non-significant GxE interactions for the trait. Heritability for plant height, ranged between 0.46 for black and 0.89 for pinto and red/pink. Except for black, all market classes showed heritability higher than 0.70 for this trait.

Table 4
Broad-sense heritability values for each market class

	Heritability (H^2)						
	Combined	Black	Great Northern	Navy	Pinto	Red and Pinks	SD Pinto
Stem diameter	0.75	0.58	0.43	0.63	0.87	0.82	0.84
Plant height	0.81	0.46	0.88	0.74	0.89	0.89	0.78
Maturity	0.73	0.74	0.84	0.76	0.81	0.73	0.91
Seed weight	0.99	0.96	0.96	0.95	0.94	0.95	0.93
Seed yield	0.75	0.69	0.89	0.76	0.56	0.89	0.79

H^2 : Broad sense heritability using entry-mean.

Correlations among traits

Among all market classes, all correlations were significant except plant height and seed weight. The two most important correlations were plant height and seed yield ($r = 0.5$); plant height and stem diameter (0.4). Conversely, stem diameter and seed yield had a low correlation value (0.2). In both analyses, combined and within market classes, the most important correlation was found between plant height and seed yield. Small differences were observed among market classes for this correlation, with navy (0.6), showing the highest value. In contrast, pinto, red/pink, and SD-pinto shared the lowest correlation value of 0.4 (Fig. 1). Likewise, plant height and stem diameter were positively correlated. Great northern, pinto, and SD-pinto scored the lowest value of 0.3, while the highest were found for navy (0.5), red/pink, and black (0.4). In contrast to the combined analysis, higher correlation values between stem diameter and seed yield were found within market classes. Maturity and seed yield were negatively correlated for red/pink and SD-pinto (-0.3), while the remaining market classes showed weak negative or non-significant correlations (Fig. 1).

X for non-significant correlation. PH: Plant height, SD: Stem diameter, MAT: Maturity, SW: Seed weight and Y: Plant yield.

Regressions

Simple linear regressions for the combined data set, plant height, stem diameter, maturity, and seed weight explained 24.1%, 8.9%, 2.7%, and 0.1% of seed yield variation, respectively (Table 5). In addition, multiple linear regressions that were performed using the three most important traits showed that, plant height + stem diameter (25.6%) explained most of seed yield variation; adding maturity to the model explained less variation than considering only plant height. In conclusion, plant height and stem diameter explained most of the seed yield variation.

When regressions were performed within each market class, two main patterns were observed. The first pattern was detected for black, great northern, and navy, where plant height explained more than 24.4% of seed yield variation. In contrast, stem diameter only explained between 4.7 to 8.5% of the variation. For black and navy when plant height and stem diameter were used in multiple regressions, plant height was the only significant trait. Conversely, for great northern, both were significant and explained 24.0% and 7.3% of the variation, respectively. However, when a model including plant height + stem diameter was used, variation reached 26.3%. In this group, plant height was the most important trait explaining 24.4% of yield variation.

The second pattern was observed for pinto, red/pink, and SD-pinto, in which plant height explained less variation than the previous group, with values of 15.1% for pinto, 16.5% for red/pink, and 20.9% for SD-pinto (Table 5). In contrast, stem diameter explained between 10.6 and 11.7%, suggesting a higher relevance of this trait for this group. In all market classes within this pattern, the model plant height + stem diameter showed an increase on the explained variation in comparison to the single use of plant height data. For this group, plant height was also the most important trait, however, it explained a smaller variation in seed yield. In contrast, stem diameter was relevant, explaining around 11% of the variation (Table 5).

Table 5
Linear and multiple regressions between the traits of study and seed yield

Trait	Combined	Black	Navy	Great	Pinto	Red	SD-pinto
Simple linear regression							
% of variation explained							
Plant height (PH)	24.1	29.1	36.2	24.4	15.1	16.5	20.9
Stem diameter (SD)	8.9	4.7	8.5	7.3	10.6	11.7	11.0
Maturity (MAT)	2.7	4.4	0.1 *	0.0 *	1.8	8.3	11.9
100-Seed weight (SW)	0.1	0.7	4.6	0.5	- 0.2 *	0.3 *	- 0.1 *
Multiple linear regression							
PH + SD	25.6	29.0 *	36.2 **	26.3	19.0	20.0	24.5
PH + MAT	23.2	29.9	35.1	24.0 *	16.3	18.3	23.2
SD + MAT	10.5	7.9 *	8.6 *	8.1 *	12.8	18.0	19.7
PH + SD + MAT	24.7	29.8 *	35.0 **	26.4 *	20.7	22.5	26.8

Simple linear regression: * n.s. non significant. **Multiple regression:** **Black:** *SD non-significant. **Great northern:** *MAT non-significant. **Navy:** **SD non-significant and *MAT non-significant.

Principal component analysis

When the PCA for the combined phenotypic analysis was performed, PC1 and PC2 explained 41.9% and 20.4% of the variation, respectively, reaching a total of 62.3% of the variation (Fig. 2). Stem diameter, seed yield, and plant height were clustered, but plant height was the closer vector to seed yield. Maturity and seed weight appear to have an opposite relationship. These last two variables showed no relationship with stem diameter, seed yield, and plant height. When this analysis was performed within each market class, there were some similarities to correlations and regressions results. However, some changes regarding the distribution of the variables were found. Similar to the combined analysis, seed weight and maturity were not clustered with plant height, stem diameter, or seed yield in most market classes. Nevertheless, some differences were observed for each market class and race. Within the Mesoamerican race, plant height, stem diameter, and seed yield were clustered together. However, a closer relationship between plant height and stem diameter was present in black compared to navy. For black beans, these two traits had almost the same vector length and direction (Fig. 2).

For great northern and red/pink beans, a close relationship was observed between plant height and stem diameter (Fig. 3). Nevertheless, for great northern these traits were also highly associated with seed yield. Differences for plant height and stem diameter were observed in pinto and SD-pinto (Fig. 3). In these cases, and especially for SD-pinto beans, the vectors of these two variables were not in the same direction. Maturity for pinto was not related to any of the two principal components (Fig. 3).

GWAS

The Bonferroni-Holm correction for multiple testing proved too conservative, as it assumes all tests are independent. However, many SNPs might be linked due to their physical proximity or other associated factors, meaning they are not truly independent. Consequently, applying this stringent threshold resulted in no significant associations being detected for any traits. Therefore, *P*-value threshold to declare significant marker trait associations was determined using the Li and Ji (2005) method. Based on this method, the *P*-value thresholds corresponding to a 5% experiment-wise error rate were: 1.61×10^{-4} (LOD = 3.8) for the combined analyses (single trait and multi-trait), 4.27×10^{-4} (LOD = 3.4) for the Mesoamerican race, and 2.67×10^{-4} (LOD = 3.6) for the Durango race.

Plant height

For plant height, significant peaks were found on chromosomes Pv03 and Pv07 (Fig. 4). The major GWAS signal was located on Pv07, with the lead SNP S07_40778504 located within a 40.7–40.8 Mb genomic interval. In this region, five SNPs surpassed the 1.58×10^{-5} (LOD = 4.8) threshold.

Within this interval, gene model PvUI111.07G214700, annotated as a growth-regulating factor was identified as a strong candidate gene (Table 6). Additional genes in these regions included those encoding serine/threonine-protein kinase, ring/zinc finger protein, E3 ubiquitin-protein ligase MGRN1 (MGRN1), SF98-Membrane associated ring fingers, and leucine rich repeats.

Table 6
Candidate genes on chromosomes Pv03 and Pv07 for plant height

Chr	Region	SNP	Peak	Putative Genes	Gene Function
Pv03	36.7 – 36.9 Mb	S03_36917109	3.22 $\times 10^{-5}$	PvUI111.03G154900.1 PvUI111.03G157000.1 and PvUI111.03G157100.1	Serine/Threonine-Protein Kinase F-box associated domain (FBA_3)
Pv07	40.7 – 40.8 Mb	S07_40778587	1.05 $\times 10^{-5}$	PvUI111.07G214700.1 (1 copy .2) PvUI111.07G213900.1 (1 copy.2) and PvUI111.07G213300.1 PvUI111.07G213500.1 PvUI111.07G213800.1 PvUI111.07G214300.1	Growth-regulating factor related-3-related Serine/Threonine-protein kinase ring/Zinc Finger Protein Jackdaw E3 ubiquitin-protein ligase MGRN1 (MGRN1) SF98-Membrane associated ring finger. Leucine Rich Repeat (LRR_1), (LRRNT_2), and (LRR_8)

The second most important peak SNP, S03_36917109, was identified on Pv03 with a *P*-value of 3.22×10^{-5}

(LOD = 4.5). A cluster of 16 SNPs within the 36.7–36.9 Mb region exceeded the *P*-value threshold of 5.68×10^{-5} (LOD = 4.2). Notable gene models such as PvUI111.03G154900 related to a serine/threonine protein kinase; PvUI111.03G157000 and PvUI111.03G157100, both associated with an F-box associated domain (FBA-3), were the most relevant and considered as candidate genes governing plant height. Collectively, the significant SNPs explained 39% of the phenotypic variation for plant height, with the Pv07 significant region alone accounting for 16.6% of the variation.

When GWAS analyses were conducted separately by race, four significant SNPs were detected in the Durango race. One SNP (S06_3623485) on Pv06 and three SNPs on Pv03, located between 36.8–37.2 Mb interval, corresponding to the same genomic region detected in the combined plant height GWAS analysis. For race Mesoamerica, 27 significant SNPs were found, distributed on chromosomes Pv01 (1), Pv05 (7), and Pv07 (17) (Fig. 5). The strongest signals with majority of the significant SNPs (7) were identified at ~ 40.7 Mb on Pv07, overlapping with the combined analysis. Additionally, five SNPs were detected on Pv07 around 2.2 Mb, highlighting the relevance of these genomic regions for plant height regulation.

GWAS results pointed to chromosomes Pv03 (36.8–37.2 Mb) and Pv07 (40.7–40.8 Mb) as the most important genomic regions related to plant height for dry bean. These genomic regions were simultaneously detected in both races as well as in combined GWAS analyses.

Stem diameter.

GWAS identified two highly significant genomic regions located on Pv11 and Pv07 for stem diameter when all the genotypes were combined (Fig. 6). The most significant SNP was observed on Pv11, where the peak SNP (S11_8564171) was located around 8.5 Mb ($P = 1.42 \times 10^{-5}$; LOD = 4.8). This region harbored two candidate genes with a possible relationship with stem diameter, PvUI111.11G089600.1, a cyclin-dependent kinase regulatory subunit (CKS1) and PvUI111.11G089800.1, an apoptosis inhibitor//Ring//U-Box domain-containing protein.

On Pv07, two major genomic regions were detected, spanning 33.5–34.7 Mb (23 SNPs) and 40.7 Mb (5 SNPs). Haplotype block analysis revealed four distinct haplotype blocks: The first block (Block 1) extends about 379 Kb from 33.4 to 33.7 Mb consisting of five significant SNPs. The other three blocks were Block 2: 33.7 Mb (1 SNP; ~139 Kb); Block 3: 34.5–34.6 Mb (17 SNPs); Block 4: 35.7 Mb (1 SNP). An additional block of five significant SNPs clustered around 40.7 Mb spanned a 112 Kb haplotype block. Collectively, these significant genomic regions explained 56.2% of the phenotypic variation in stem diameter.

Among these, the Pv07 region spanning 34.5–34.6 Mb (Block 3) was the most significant containing several functionally relevant gene models: PvUI111.07G159600 (gibberellin receptor GID1), PvUI111.07G159700 (WD repeat containing protein), and PvUI111.07G159800 (leucine rich repeat protein) (Table 7). Another significant region at 33.5 Mb, with five significant SNPs, contained two notable gene models: PvUI111.07G153300 (defense-related protein containing SCP domain) and PvUI111.07G153400 (PPR repeat family protein). Notably, the 40.7 Mb region on Pv07 was significantly associated with stem diameter, overlapped with the major regions identified for plant height, suggesting a shared genetic control for upright plant architecture.

Table 7
Candidate genes for stem diameter found on chromosomes Pv11 and Pv07.

Chr	Region	SNP	Peak	Genes	Genes Function
Pv07	33.5 Mb	S07_33538378	7.85×10^{-5}	PvUI111.07G153300.1 PvUI111.07G153400.1	Defense-related protein containing SCP domain PPR repeat (PPR) // PPR repeat family (PPR_2)
Pv07	34.5–34.6 Mb	S07_34570692	3.11×10^{-5}	PvUI111.07G159600.1 PvUI111.07G159700.1 (1 copy) PvUI111.07G159800.1	Gibberellin receptor GID1 (GID1) WD repeat-containing protein 23 (WDR23) Leucine Rich Repeat (LRR_1) (LRRNT_2)
Pv07	40.7 Mb	S07_40778429	1.47×10^{-5}		Same region as plant height
Pv11	8.5–8.9 Mb	S11_8564171	1.42×10^{-5}	PvUI111.11G089600.1 PvUI111.11G089800.1 (1 Copy)	Cyclin-dependent kinase regulatory subunit CKS1 (CKS1) Inhibitor of apoptosis //Ring//U-Box domain-containing protein.

When stem diameter GWAS was performed separately by race, the MLM was identified as the best-fitting model for both Durango and Mesoamerican races. In the Durango race, significant regions for stem diameter were detected on Pv07 and Pv11, with 67 and 3 significant SNPs, respectively. The significant SNPs found on Pv11 overlapped with those identified in the combined analysis. On Pv07, 67 significant SNPs were distributed in the 31.4–31.8 Mb (5 SNPs), 32.4–32.9 (36 SNPs), 33–33.1 (16 SNPs), and 34.5–34.6 Mb (10 SNPs) genomic regions. Most of these intervals coincided with those found in the combined analysis. In the Mesoamerica race, 11 significant SNPs were found exclusively on chromosome Pv07, with seven SNPs clustered around 2.2 Mb. This region was also observed in the Mesoamerican plant height analysis.

Overall, GWAS results indicate that multiple genomic regions on Pv07 contribute to stem diameter variation. The 2.2 Mb and 40.7 Mb genomic regions are primarily related to the Mesoamerican race, while the 33.5–33.6 Mb and 34.5–34.6 Mb regions are associated with the Durango race.

Multi-trait GWAS

Single-trait GWAS analyses identified overlapping genomic regions associated with both plant height and stem diameter, suggesting potential pleiotropic effects. Therefore, a multi-trait GWAS was conducted to

detect common genomic loci influencing both traits simultaneously.

In combined panel, the multi-trait GWAS detected significant signals on chromosomes Pv03, Pv05, Pv07, and Pv11 (Fig. 7). Notably, the significant signals on Pv07 and P11 overlapped with those detected in the single-trait GWAS for both plant height and stem diameter. The genomic region at 40.7–40.8 Mb on Pv07, consistently detected across multiple analyses, indicates shared genetic control underlying the two traits.

Similar patterns were also observed in the race-specific multi-trait GWAS analyses. In the Durango race, multi-trait GWAS detected major peaks Pv03, Pv05, Pv07, and Pv11 (Fig. 8). Consistent with the single-trait GWAS, significant genome regions were located on Pv07 spanning between 31.6–33.1 Mb (54 SNPs) and on Pv11 at 8.5 Mb, both associated with stem diameter. For the Mesoamerican race, significant associations were detected on Pv01, Pv05, Pv06, Pv07, and Pv08 (Fig. 9). The peak genomic region spanning 40.7–40.8 Mb on Pv07 was simultaneously detected in both single-trait and multi-trait GWAS analysis, confirming the importance of this locus in governing plant height and stem diameter in Mesoamerican genotypes.

Discussion

The present study highlights the importance of key agronomic traits for seed yield and upright plant selection in dry bean. Using a combined analysis and six different market classes, from two races, allowed a better understanding of the different traits used for plant selection. Among all traits studied, both plant height and stem diameter were the most important for seed yield and upright plant selection. Nevertheless, their importance changed based on the race and the market class evaluated. Therefore, the discussion will focus on these traits. GWAS analyses further elucidated the genetic architecture underlying these traits, offering valuable opportunities to develop markers for breeding programs aimed at optimizing beneficial ideotype development.

Stem diameter

Across all market classes, stem diameter averaged 7.7 mm, with pinto showing the thickest stem (8.0 mm), significantly greater than other market classes. These values are higher than the ones found by Oliveira et al. (2015) (5.1 mm) and Moura et al. (2013) (5.4 mm) who mainly used Type III cultivars. Our results were similar to the ones found by Brothers and Kelly, (1993) and Mulube, (2017) who observed diameters ranging from 5.7 and 8.3 mm in crosses involving either small or medium seed sizes or Andean genotypes. Most importantly, the stem diameter in this study surpass the 5.6 mm threshold proposed by Soltani et al. (2016) for selecting upright cultivars. Values from our study were even greater than the thickest stems found by these authors, 5.7 mm in Type II plants, and 5.0 mm in Type III plants. Soltani et al. (2016) used a diverse panel of genotypes (Durango Diversity Panel – DDP), which included old and new germplasm and several cultivars with growth type III. In contrast, our study used elite/advanced lines from a public breeding program in which selection for upright plant architecture is a

routine selection component of the breeding pipeline. Thus, it is not surprising that selection for upright architecture within the breeding program may have indirectly increased stem diameter.

Stem diameter showed no significant GxE interaction for pinto and SD-pinto, indicating high phenotypic stability across environments (Fehr 1991). Similar stability was reported by Mulube, (2017) and Oliveira et al. (2015) for released cultivars. In contrast, Moura et al. (2013) and Soltani et al. (2016), observed significant GxE interaction when analyzing panels with contrasting growth habits. Nevertheless, Soltani et al. (2016), showed non-significant GxE when the analysis was performed within Type II and III growth habits separately. These findings suggests that GxE effects diminishes within populations with similar architecture, highlighting the need for pattern-specific evaluations within populations.

Heritability estimates also showed differences among market classes. Pinto (0.87) and SD-pinto (0.84) showed the highest heritability. This reinforces the stability and reliability of the trait for selecting upright plants especially in these two market classes. These values are comparable to those reported by Silva et al. (2013) (0.81) and Oliveira et al. (2015) (0.75–0.77); but substantially higher those obtained by Soltani et al. (2016), who found a broad-sense heritability of 0.33 and found higher heritability values for Type II compared to Type III plants. This could be explained by the inherent nature of stiff-stem and upright plants in Type II compared to Type III plants, which have prostate habit and weaker stems (Singh et al. 1991). However, in this study, Durango market classes showed higher heritability values than Mesoamerican. It could show that breeding efforts to select upright plants likely are changing traits in different market classes (Kelly, 2001), one of them could be stem diameter.

Plant height

Plant height had a highly significant GxE interaction across all market classes, indicating lower stability compared to stem diameter. Mulube, (2017), Moura et al. (2013) and Soltani et al. (2016) also reinforced that plant height is more environment-sensitive. Heritability values differed among market classes, ranging from 0.46 in black to 0.89 for red/pinks. However, most heritability values were above 0.75. These results are higher than the 0.66 reported by Soltani et al. (2016), and the 0.6 found by Oliveira et al. (2015). Mean plant height exceeded 49 cm across all market classes, with pinto and red/pink reaching 53.6 and 52.3 cm, respectively. These values were higher than the mean of completely upright, Type II plants (42.3 cm), or Type III (33.3), reported by Soltani et al. (2016). Silva et al. (2013) also observed taller and thicker Type II (6.3 mm and 50 cm) than Type III plants (5.3 mm and 38 cm), suggesting that differences of 12 cm in plant height and 1 mm in stem diameter could imply a change in growth habit. This contrasts with our results given that some Durango/Jalisco market classes are showing taller and thicker plants. This shows again a likely influence of the breeding efforts to bring these characteristics from Mesoamerican to Durango races (Kelly, 2001). In spite of the significant GxE interaction for plant height, its heritability was high, which confirms its importance for plant architecture. Thus, plant height and stem diameter could be considered as appropriate selection traits for dry bean, although their use in combination would depend on the market class undergoing selection.

Relationships between stem diameter, plant height and other traits

Plant height showed a stronger correlation with seed yield than stem diameter in this study. In contrast, Soltani et al. (2016), found that plant height (0.42) and stem diameter (0.4) were equally correlated with seed yield. Within market classes, plant height and yield were also significantly correlated, however, its magnitude changed based on the market class. For black, navy, and great northern, correlation values were higher than 0.5. Plant height and stem diameter correlation ranged between 0.3 and 0.5 across all market classes and was stronger for Mesoamerican market classes black (0.4) and navy (0.5). Higher correlation values of 0.8 for this combination of traits was found by Silva et al. (2013) and Soltani et al. (2016). Then, this study confirms a positive correlation between plant height, stem diameter, and seed yield; however, their magnitude will vary based on the market class. The correlations between stem diameter and plant height, plant height and seed yield tended to be higher in Mesoamerican market classes compared to Durango/Jalisco. This could be related to inherent traits nature for each race, but also to breeding efforts to bring upright characteristic from Mesoamerican into Durango (Kelly, 2001).

Regression analyses further confirmed correlations results regarding the observed two patterns. In black, navy, and great northern market classes, plant height explained more than 24.4% of seed yield variation, while stem diameter showed non-significant or minor effects. Interestingly, great northern beans were more closely related to Mesoamerican than Durango/Jalisco, likely due to the use of navy beans as parents to generate early upright great northern cultivars (McClean et al. 2018). In addition, comparisons between pinto and great northern DNA sequence data have shown differences between these two market classes regarding selection hotspots for plant architecture (unpublished data). In contrast, pinto, red/pink, and SD-pinto showed similar contributions of plant height and stem diameter to seed yield, reflecting dual role of these traits in upright architecture. Tall plants prevent pods contact with soil, while thicker stem provide structural support (Acquaah et al. 1992).

Historical trends support these findings, Vandemark et al. (2014) documented significant increase in plant height (34 cm to 57 cm) in pinto cultivars released after 1980, coinciding with the shift from prostrate Type III to upright Type II architecture. However, no-significant differences were found for navy, likely, due to their common upright architecture. Our study further indicates that stem diameter was increased mainly in pinto cultivars, likely due to the indirect selection for upright architecture. According to Soltani et al. (2016) an increase in stem diameter and plant height could result from converting Type III genotypes (thinner stems) to Type II (stiff stem). Changes in plant height in the newly released pinto cultivars have allowed a more efficient direct harvest for these cultivars (Eckert et al. 2011). While Soltani et al. (2016) suggested a 5.6 mm threshold for stem diameter, our results indicate that this benchmark may need revision for commercial breeding programs and for specific market classes, given historic differences in growth habits. Stem diameter was a stable and heritable trait, which explained a high amount of variation in the seed yield of Durango/Jalisco market classes such as pinto and SD-pinto.

It is suggested to continue selecting for this trait and plant height in these market classes. In contrast, plant height is a reliable trait for upright selection in the Mesoamerican market classes.

Genetic architecture of plant height

GWAS results for plant height revealed significant regions on chromosomes Pv07 and Pv03. On Pv07, the region close to 40.7 Mb, has several plant growth-related genes, including PvUI111.07G214700, which encodes a growth-regulating factor (GRF). GRFs are plant-specific transcription factor that controls cell expansion (size) and proliferation (number), influencing stem and leaf development (Omidbakhshfard et al. 2015). In rice (*Oryza sativa* L.), they play important roles in stem growth and development (Wang et al. 2018) and coordinate levels of defense and plant development hormones in opposite directions (Omidbakhshfard et al. 2015). Under normal conditions, GRF1/GRF3 invest energy in plant growth. Under stress conditions, they inhibit growth directing resources to stress tolerance processes (Piya et al. 2020).

The second major region found on Pv03 (36.7–36.9 Mb) includes gene models related to serine/threonine-protein kinases and F-box associated domains. According to Kuzbakova et al. (2022), these kinases have been associated with plant height. For instance, in soybean (*Glycine max* L.), a serine/threonine-protein phosphatase is encoded by the gene GmPP1-like. Mutants of this gene show shorter internode length and height. Gene model PvUI111.03G157000.1 was also found in this region, encoding an F-box domain, with protein destruction functions (Ho et al. 2008). F-box domains, create dimers to regulate auxins, gibberellins (GA), jasmonate (JA), and ethylene expressions (Prigge et al. 2016).

Combined and race-specific single trait and multi-trait GWAS analysis confirmed the relevance of Pv03 (36 Mb) and Pv07 (40.7 Mb), with Pv03 (36 Mb) and Pv06 (3.6 Mb) significant for Durango, and Pv07 (40.7 Mb) was highly relevant for Mesoamerican races. These findings support previous report of MacQueen et al. (2020) that several chromosomes could be related to plant height and highlight Pv03 and Pv07 as key targets for marker-assisted selection.

Genetic architecture of stem diameter

For stem diameter, the most important peak was located on chromosome Pv11 (8.5 and 8.9 Mb), which includes PvUI111.11G089600 encoding a cyclin-dependent kinase regulatory subunit (CKS1). CKS1 proteins, regulate the cell cycle affecting growth and development (Tamirisa et al. 2017). A second most important peak on Pv07 (34.5 and 34.6 Mb) harbors gene model PvUI111.07G159600 encodes a gibberellin receptor GID1, which interacts with DELLA proteins, to modulate GA signaling repressors (Yoshida et al. 2018).

A highly relevant finding is the region around 40.7 Mb on Pv07, detected for both plant height and stem diameter traits. This region contains genes related to growth regulating factors, serine/threonine protein

kinase, E3 ubiquitin-protein ligase, membrane associated ring finger and leucine rich repeats. According to (Wang et al. 2018), the growth regulating factors are not only related to plant height but to stem thickness. In rice, similar pleiotropic loci named *Ideal Plant architecture* (IPA1) have been reported, encoding OsSPL14 (SQUAMOSA PROMOTER BINDING PROTEIN-LIKE 14), which controls plant height, stem diameter, tiller numbers and number of productive tillers (Jiao et al. 2010). Thus, Pv07 (40.7 Mb) becomes interesting and important target for further indeterminate growth plant architecture studies.

Chromosome Pv07 could be related to indeterminate growth in dry bean

Our current findings reinforce the critical role of chromosome Pv07 in plant architecture and growth habit. Genes such as *PvTFL1y* or *Fin* locus on Pv01 and *PvTFL1z* (likely a duplication of the first one) on Pv07 (Krylova et al. 2021; Kwak et al. 2008) have been related to plant height. Genes on Pv01, are associated with determinant Andean genotypes (Cichy et al. 2015; Resende et al. 2018), whereas Pv07 could be related to indeterminacy in the Middle American gene pool, particularly in navy (Kolkman and Kelly, 2003). This suggests two distinct domestication processes, one on Pv01 for Andean (determinant) and another on Pv07 for Mesoamerican (indeterminant). Our GWAS results could confirm an indeterminacy region on Pv07. This region was suggested by Moghaddam et al. (2016) who used Type I, II, and III plants and confirmed a determinacy region on Pv01. However, it was only found when Andean determinate genotypes were present. When Andean cultivars were removed, peaks on Pv04, Pv06, Pv07, and Pv11 appeared. Being the peaks on Pv07, (46.11 Mb) and (35.42 Mb) the most relevant. Similarly, our results showed significant regions on Pv03, Pv07, and Pv11 using indeterminate Durango and Mesoamerica germplasm. Notably, the genomic region 40.7 Mb on Pv07, was significant for plant height and stem diameter. This region was also validated and identified by multi-trait GWAS analysis. However, genome comparisons showed that this region is different to the one found by Moghaddam et al. (2016) on Pv07 (46 Mb), which was mapped based on G19833v2.1 reference genome (Schmutz et al. 2014). Recent findings by Beagley et al. (2025), further support this by identifying Pv07 regions associated with stem elongation of the first five nodes independent of flowering time, which consistent with the results. Candidate genes identified in our study, such as PvUI111.07G141800 and PvUI111.07G153300 located at 31.4 Mb and 33.5 Mb, respectively, share 100% similarity with G19833v2.1 genome homologs Phvul.007G149432 and Phvul.007G161200, respectively reported by Beagley et al. (2025) and are implicated in stem elongation. These findings highlight Pv07 as a hotspot for growth habit regulation, with potential pleiotropic effects on plant height, stem diameter and node elongation.

Domestication process likely led to different growth habits. For instance, due to maize's late arrival to the Andes some mutations were generated to give Andean plants own support. In contrast, the use of maize in Middle America, allowed the bean plants to climb (Koinange et al. 1996). However, it is possible that some Middle American climbing Type IV plants adapted to less support conditions, generating Type III plants. This could be partially shown by Tobar-Piñon, (2020) who found higher admixture between Guatemalan climbing beans (Type IV) and Durango/Jalisco race (Type III and IV) than with Mesoamerican race (Type II). Likely a plant biomass reduction was required to adapt to temperature and

altitude variations, changing from Type IV to Type II progressively. Evidence suggests that Pv07 could be highly relevant for indeterminate dry bean germplasm growth habit. Similar to dry bean, soybean has growth habits such as determinate, indeterminate, and semideterminate, which are mastered by two genes (*Dt1* and *Dt2*), *Dt1* controls determinacy, and *Dt2*, semideterminacy (Ping et al. 2014; Clark and Ma 2023). *Dt2* is related to branch number (Virdi et al. 2023), generates differences in height and diverse degrees of stem termination, with pleiotropic effects on node number and internode length (Kou et al. 2021). It is possible that within the indeterminate dry bean germplasm, there are genes controlling specific height or vine length, having therefore a similar function to *Dt2*. This region could be located on Pv07 and could be important to improve traits such as first pod height, plant stature, and mechanical harvesting, which are key for dry bean commercialization.

Our GWAS analyses revealed multiple Pv07 regions contributing to stem diameter variation (2.2 Mb, 33.5–34.6 Mb, and 40.7 Mb), with race-specific associations: 2.2 Mb and 40.7 Mb for Mesoamerica and 33.5–33.6 Mb and 34.5–34.6 Mb for Durango. In general, regions on Pv07 not only can help to understand differences among indeterminant growth habits grown in the US (Type II and III); but could also help to trace their domestication traits. Only a few studies available related to stem diameter genetics have been reported. Therefore, the effect of intervals located mainly on Pv07 is an important result of this study. This is one of the few studies that show genetic architecture and field importance of stem diameter and plant height. Collectively, Pv07 significant regions explained 56.2% genetic variation for stem diameter and 16.6% for plant height, underscoring its central role in indeterminate architecture. These regions could help explain differences in Type II and III growth habits in beans with indeterminant growth habits. These findings provide a foundation for developing functional markers for fine-mapping and cloning causative genes, enabling targeted breeding for upright plants with thicker stems-traits essential for mechanical harvesting and improved yield stability.

Conclusions

Overall, stem diameter was larger for current advanced lines than values suggested by Soltani et al. (2016) of 5.6 mm., indicating that selection for upright architecture within the breeding program may have indirectly increased stem diameter. Stem diameter showed the highest heritability values in pinto and SD-pinto. Additionally, non-significant GxE interaction was found in these market classes. This suggests that it is a stable and heritable trait for selection of upright plant architecture, especially in these two market classes. Plant height could be a better indicator for seed yield than stem diameter in black, great northern, and navy. While both plant height and stem diameter are required to continue selecting upright and high-yielding plants for pinto, red/pink and SD-pinto. Specially, considering that these three last market classes tend to have a Type III prostrate genetic background. For both plant height and stem diameter there is a shared genetic effect in an interval centered on region centered at 40.7 Mb at Pv07. This common region is related to growth regulating factors, serine/threonine protein kinase, E3 ubiquitin-protein ligase, membrane associated ring finger, and leucine rich repeat. Most of these gene models have relation to plant growth and disease avoidance, which makes this region an

interesting area to continue with further investigation and exploit by developing functional molecular markers to assist bean breeding for selecting bean genotypes with improved plant architecture.

Declarations

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Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

Author Contribution Statement

Oscar Rodriguez: Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing - original draft

Jayanta Roy: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - review & editing

Philip E. McClean: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing - review & editing

Didier Murillo: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - review & editing

Kristin Simons: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - review & editing

Nusrat Khan: Data curation, Formal analysis, Investigation, Methodology, Software, Supervision, Validation, Visualization, Writing - review & editing

Jose Figueroa: Data curation, Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing - review & editing

Juan Osorno: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

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Figures

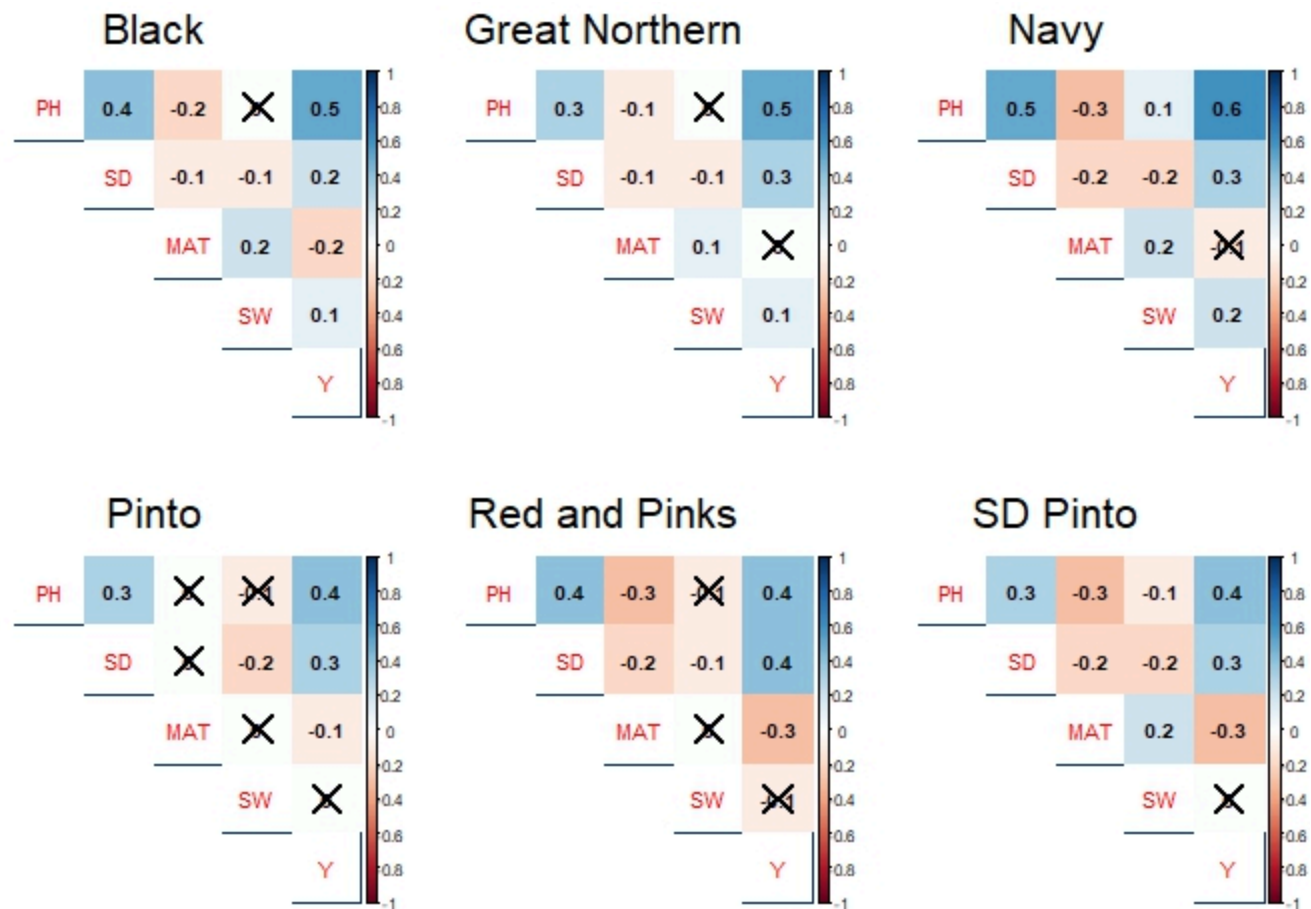


Figure 1

Pearson's correlations among traits within each market class

X for non-significant correlation. PH: Plant height, SD: Stem diameter, MAT: Maturity, SW: Seed weight and Y: Plant yield.

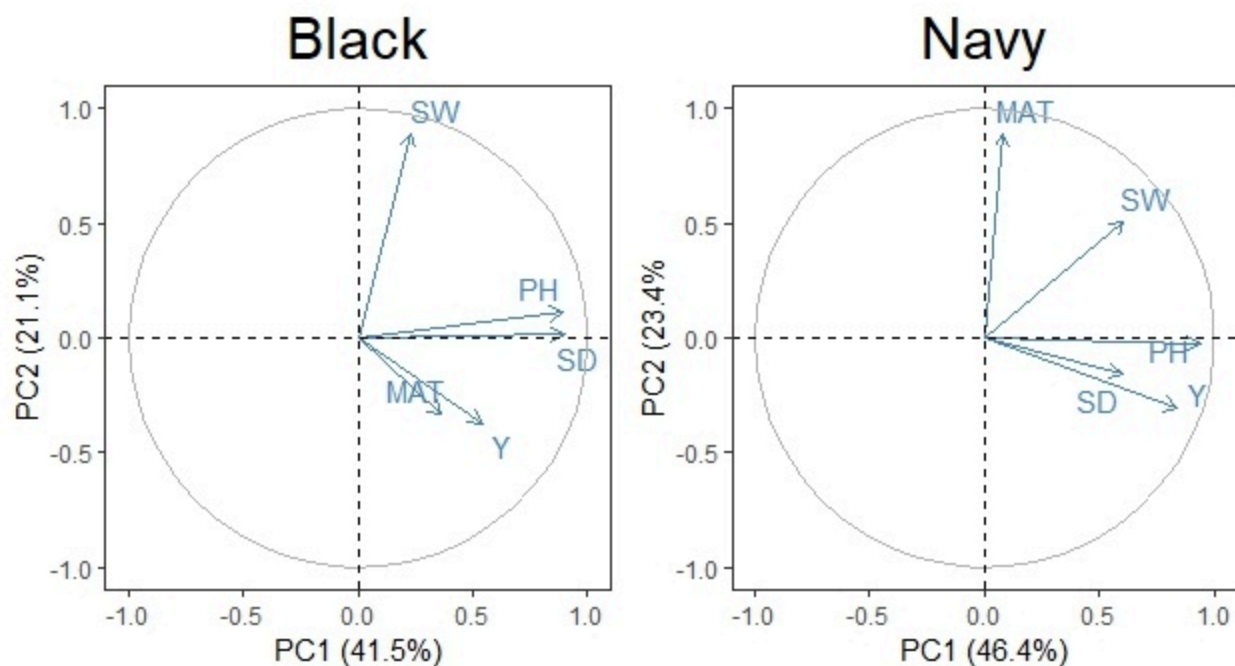


Figure 2

PCA Analysis for all traits in Mesoamerica race (black and navy). PH: Plant height, SD: Stem diameter, MAT: Maturity, SW: Seed weight and Y: Seed yield.

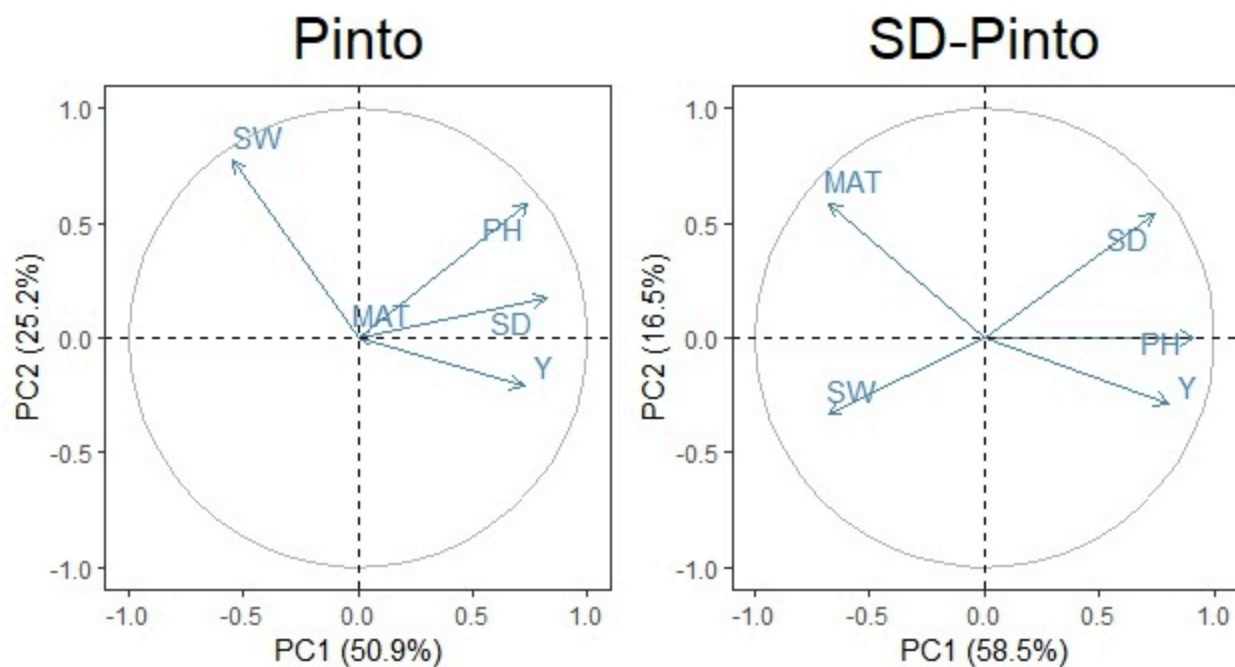


Figure 3

PCA Analysis for all traits in Durango/Jalisco race (Pinto and SD-pinto). PH: Plant height, SD: Stem diameter, MAT: Maturity, SW: Seed weight and Y: Seed yield.

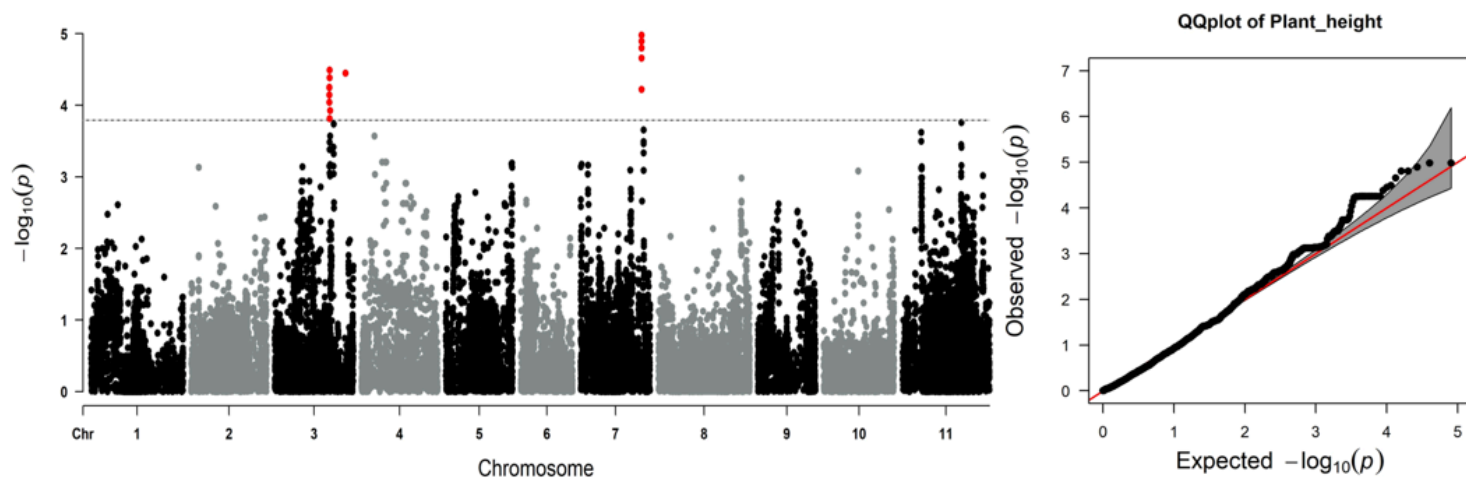


Figure 4

Manhattan plot and q-q plot for plant height using MLM in GEMMA

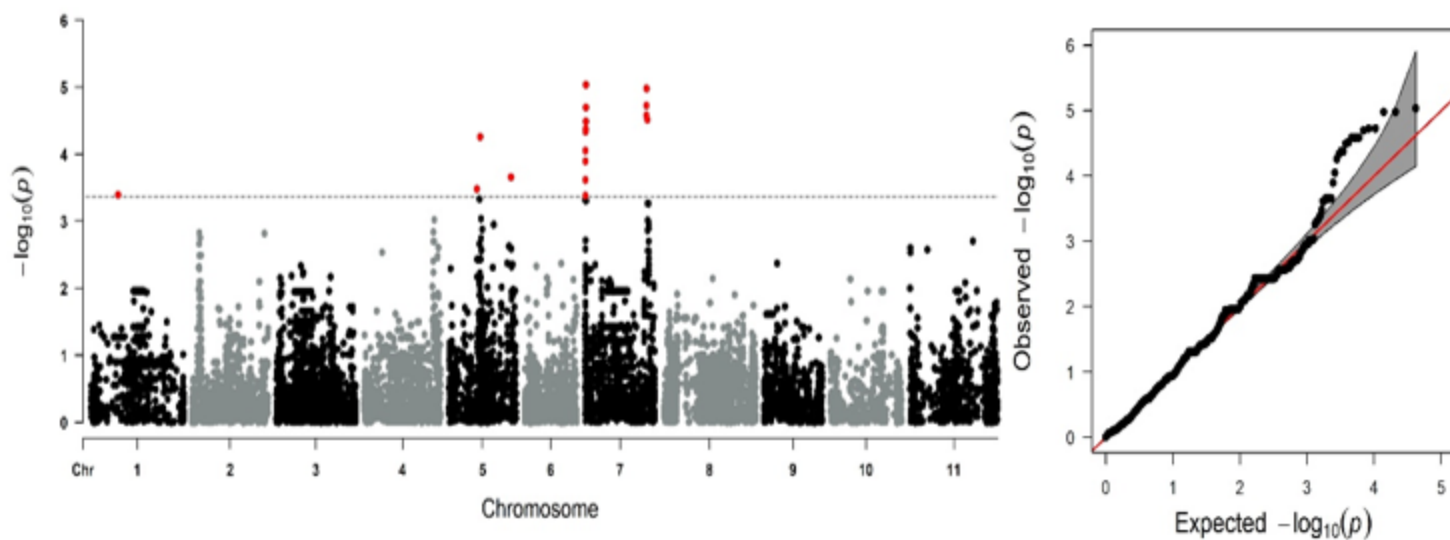


Figure 5

Manhattan and q-q plot for plant height within Mesoamerican race using MLM in GEMMA

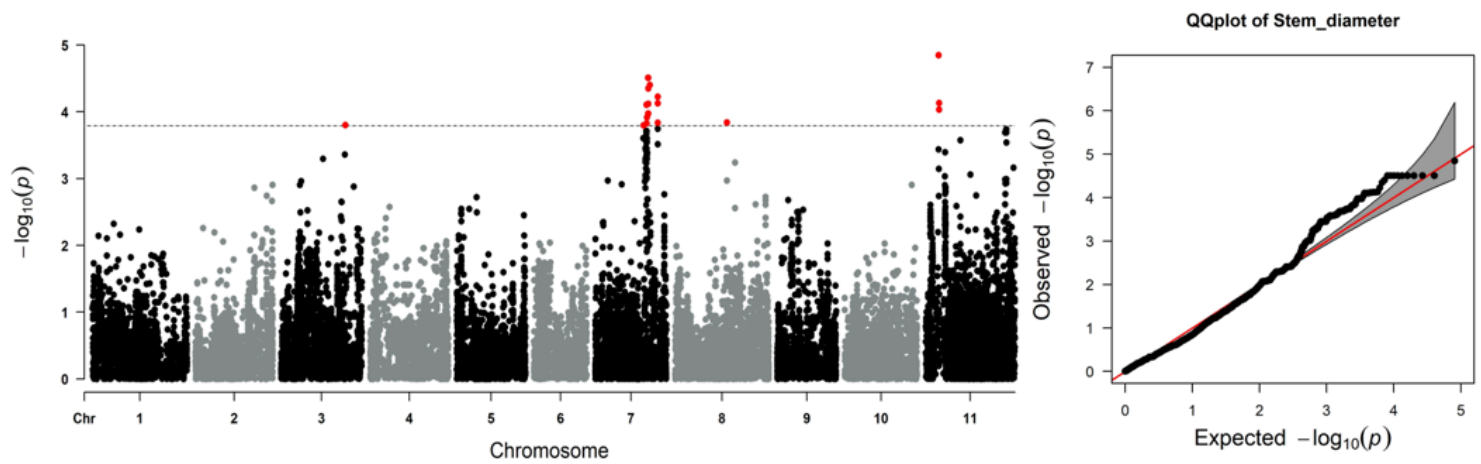


Figure 6

Manhattan and q-q plot for stem diameter using MLM in GEMMA

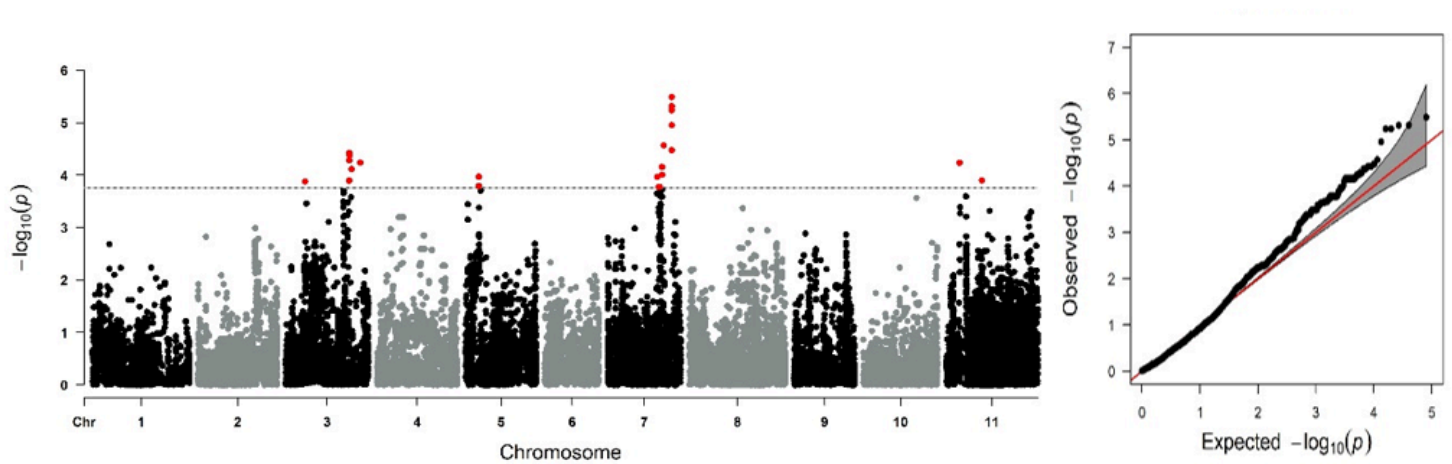


Figure 7

Manhattan and q-q plot for a multi-trait analysis using MLM in GEMMA

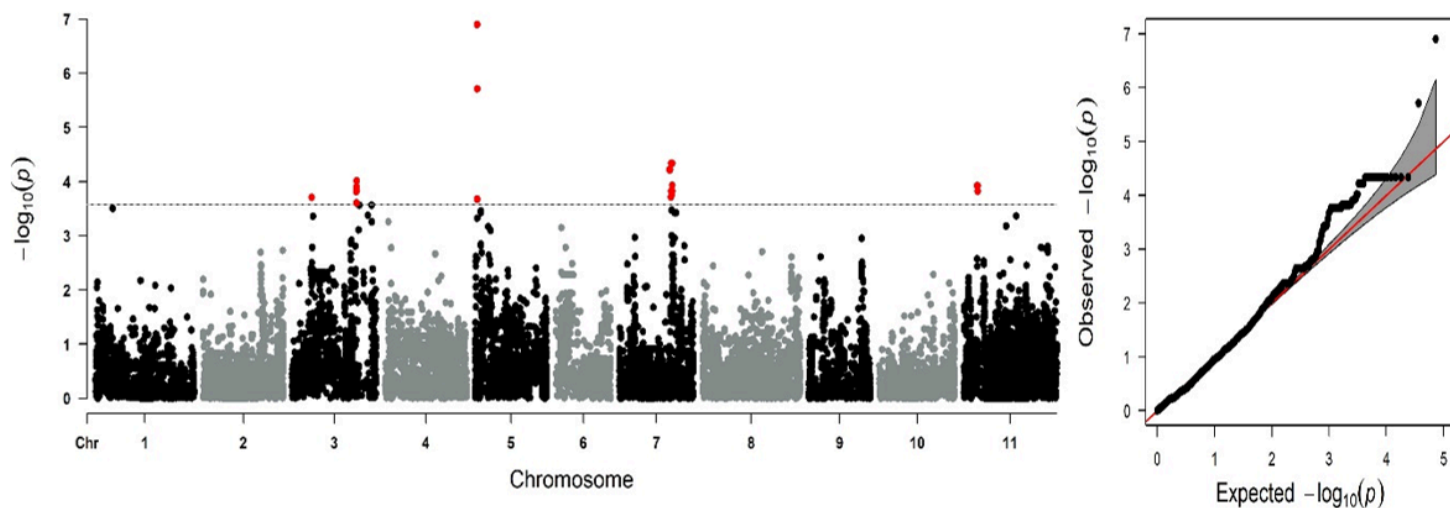


Figure 8

Manhattan and q-q plot for a multi-trait analysis within Durango race using MLM in GEMMA

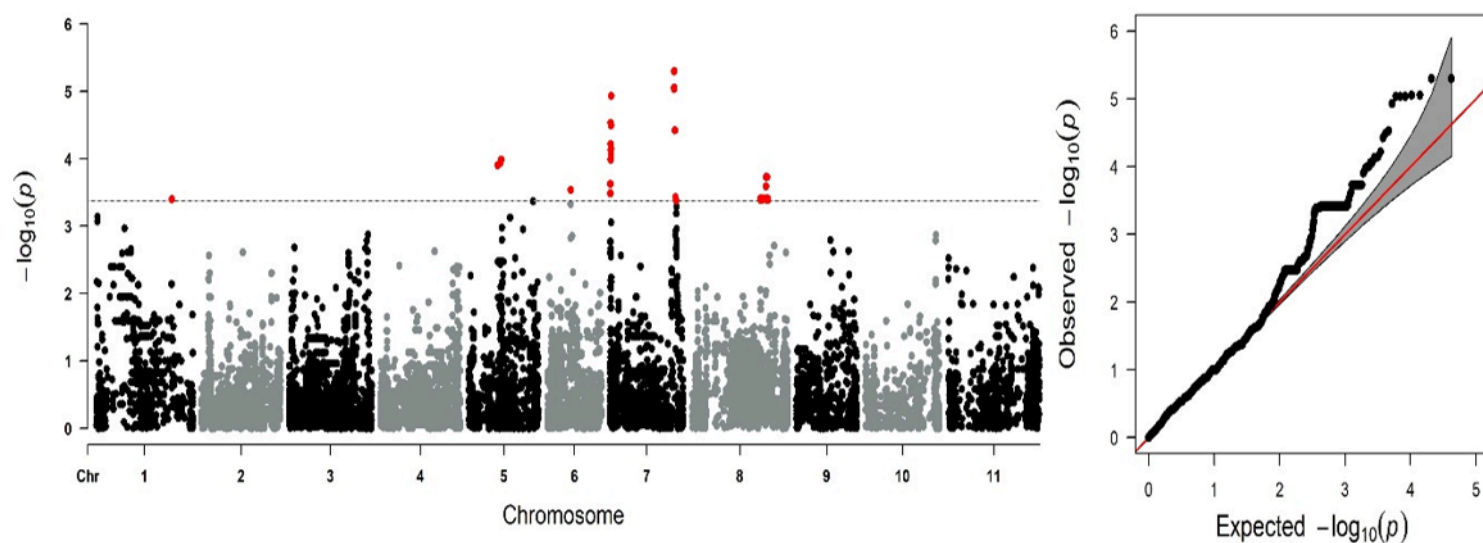


Figure 9

Manhattan and q-q plot for a multi-trait within Mesoamerica race using MLM and GEMMA