



Morphological and simple sequence repeat (SSR)-based diversity of *Capsicum* germplasm characterizes population structure and enables marker-assisted selection for *Phytophthora capsici* resistance

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Abstract *Capsicum annuum* is a globally important crop with rich genetic diversity that underpins breeding for productivity and disease resistance. In this study, we assessed 485 accessions representing a diverse *Capsicum* germplasm set, predominantly *Capsicum annuum* with a limited representation of related wild species using agro-morphological traits and simple sequence repeat markers to explore diversity, structure, and trait variation. Phenotypic

evaluation of 352 accessions was conducted under field conditions during the 2024 summer season, where data were recorded on eight quantitative and four qualitative traits. Genetic characterization on the whole collection was performed using 24 polymorphic SSR markers selected for their known linkage to *Phytophthora capsici* resistance. A total of 308 alleles were detected post-binning, with an average of 12.83 alleles per locus and high polymorphism information content (mean PIC=0.80). STRUCTURE analysis revealed three major genetic clusters (K=3), supported by the Evanno ΔK method and consistent with clustering observed in Principal Component Analysis (PCA) and Neighbor-Joining (NJ). The clusters comprised predominantly *C. annuum* accessions, but also included individuals from *C. baccatum*, *C. chinense*, and other species, suggesting historical introgression and admixture. Phenotypic variation largely aligned with molecular groupings, supporting the complementary use of morphological and marker-based data. The high allelic diversity and defined population structure observed in this study provide a valuable foundation for genetic improvement, association mapping, and core collection development in *Capsicum*. In addition, the choice of *Phytophthora*-linked SSR markers provides an important platform for future association mapping and marker-assisted selection studies aimed at improving disease resistance in *Capsicum*.

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preserve pepper germplasms (Mongkolporn and Taylor 2022).

One effective strategy for conserving and utilizing pepper diversity is the establishment of core collections, which capture maximum genetic variation with a minimum number of accessions. These subsets facilitate the identification of valuable traits for stress tolerance, disease resistance, and nutritional quality, making them highly relevant to breeding programs (Zewdie et al. 2004). Targeted sampling in centers of origin and diversity helps preserve unique alleles while enabling the development of climate-resilient cultivars (Scaladaferro et al. 2018; Smith et al. 2024). Constructing core collections requires integrating morphological and molecular data to ensure comprehensive representation of variation (Kim et al. 2018). Among these traits, fruit shape holds both taxonomic and commercial significance, and in *C. annuum* populations, fruit morphology shows high heritability and strong correlations with genetic markers (Nankar et al. 2020; Hong et al. 2020; Brilhante et al. 2024). Utilizing this integrated phenotypic–genotypic framework is particularly critical for addressing devastating diseases such as *Phytophthora capsici*, which threatens pepper production worldwide and necessitates the need for resistance-oriented germplasm characterization.

In peppers, *P. capsici* causes root, crown, and fruit rot, with the most severe yield losses occurring in warm, humid production regions (Barksdale et al. 1984; Lee et al. 2008). Conventional control methods are limited by the pathogen's ability to persist in the soil for years and rapidly adapt to fungicides. Consequently, breeding for host resistance has become a priority, and marker-assisted selection (MAS) plays a central role in accelerating this process. Over the past two decades, multiple molecular marker systems have been applied to identify and map resistance loci, including Simple Sequence Repeats (SSRs), Amplified Fragment Length Polymorphisms (AFLPs), and Single Nucleotide Polymorphism (SNP) markers. Although SNPs dominate current high-throughput genotyping platforms due to their abundance and genome-wide coverage, SSRs generally exhibit higher polymorphism information content (PIC) per locus, making them particularly powerful for assessing allelic richness and genetic diversity. In the context of this study, SSR markers were particularly suitable because their multi-allelic nature enables detection of

allelic richness within a diverse germplasm collection, while their prior linkage to *Phytophthora capsici* resistance allows direct integration of diversity assessment with resistance-oriented breeding objectives. This high informativeness, combined with their established linkage to resistance loci, underscores the continued relevance of SSRs in *Capsicum* diversity studies. Polymorphic markers for accurate genetic analysis and resistant plant selection have been identified (Lee et al. 2004), and high-density SSR mapping has revealed major QTLs for *P. capsici* resistance on chromosomes P5 and P11 (Minamiyama et al. 2007). Additional QTLs linked to foliar blight and root rot resistance have been reported (Truong et al. 2013), whereas AFLP markers associated with resistance have been developed (Thabuis et al. 2004). Bulk segregant analysis (BSA) has pinpointed candidate genes and tightly linked SSRs (Liu et al. 2014; Truong et al. 2013), and further mapping studies have identified tightly linked markers controlling resistance traits (Wang et al. 2016). Recent genotyping-by-sequencing-based SNP (GBS-SNP) approaches have identified candidate genes for multi-locus resistance, in which resistance is governed by multiple quantitative trait loci (QTLs) distributed across the genome and contributing partial and additive effects (Kaur et al. 2024; Mohammad Bagheri et al. 2022), and SSR-based studies have reported significant associations between specific alleles and resistance to root rot and foliar blight symptoms (Xu et al. 2016; Bukhari et al. 2024). Collectively, these studies have produced a robust toolbox of trait-linked markers that allow breeders to rapidly screen germplasm, introgress resistance alleles, and pyramid multiple QTLs for durable resistance. Integrating such markers into large, genetically diverse collections provides the opportunity to simultaneously assess population structure and resistance gene distribution, thereby supporting targeted breeding for *P. capsici* resistance.

In this context, the present study aims to evaluate genetic and morphological relationships among diverse pepper accessions for the development of a representative core collection (hereafter referred to as UGA-Capsi-Core) and to characterize fruit shape-based diversity groupings using standardized morphological descriptors. The UGA-Capsi-Core collection was assembled through informed selection to capture broad diversity in geographic origin, fruit morphology, and breeding relevance, while

maintaining representation of elite lines, landraces, and wild relatives available through collaborating programs. A set of SSR markers previously reported to be linked to *P. capsici* resistance was intentionally employed to genotype the collection with a dual objective. First, these markers enabled robust assessment of genetic diversity and population structure across a morphologically diverse *Capsicum* germplasm collection. Second, their established association with resistance loci allowed direct evaluation of the distribution of resistance-linked alleles within the collection, thereby facilitating the identification of accessions with potential breeding value for *P. capsici* resistance. This targeted marker selection integrates diversity characterization with resistance-oriented breeding objectives, rather than serving as a general genome-wide diversity survey. The resulting dataset provides a foundation for future resistance screening to *P. capsici* and targeted breeding applications.

Materials and methods

Plant materials

The UGA-Capsi-Core collection is comprised of a total of 485 accessions, and it predominantly comprises of *C. annuum* (473), with a few other species including *C. chinense* (4), *C. baccatum* L. var. *pendulum* (3), *C. chacoense* (1), *C. flexuosum* (1), *C. frutescens* (1), *C. galapagoense* (1), and *C. rhomboideum* (1). The germplasm accessions evaluated for trait characterization comprise a total of 352 accessions collected from global gene banks and subsequently 133 additional accessions were acquired from international collaborators, expanding the collection to 485 accessions. Each accession was assigned a unique UGA ID (e.g., UGA-CAPS-001 to UGA-CAPS-485). Among 485 pepper accessions comprising the UGA-Capsi-Core collection, 352 accessions were evaluated for morphological traits, while all 485 accessions were genotyped using SSR markers previously reported to be linked to *P. capsici* (PCAP) resistance. While all 485 accessions were genotyped using SSR markers previously reported to be linked to *Phytophthora capsici* (PCAP) resistance, only the initial 352 accessions were included in the morphological trait evaluation due to the delayed arrival of the remaining

133 accessions, which were received after the summer 2024 breeding trial was over.

Experimental design

The experiment was conducted at the University of Georgia's Tifton Vegetable Park (TVP) in Tifton, Georgia, USA (31.4298° N, 83.5277° W) situated at an elevation ranging from 90–120 m above the mean sea level. A total of 352 accessions were evaluated using a randomized complete block design (RCBD) with two replications.

Seed preparation and production: A total of 25 seeds were counted from each original seed packet and treated with Tri-Sodium Phosphate (TSP) to prevent Pepper Mild Mottle Virus (PMMoV) infection. The treated seeds were then stored in labeled packets at 4 °C until sowing. Around 20 seeds were planted per accession in a ProMix BX soil in standard 242 count pepper seedling trays. Each tray was planted with 20 accessions and were labeled with accession number (UGA-CAPS-001 to UGA-CAPS-020) and tray number.

Transplanting and crop management: When the seedlings were around eight weeks old, each accession was transplanted into two replications in the field. Each replication had eight plants. Plant beds were 6ft apart, with two rows of plants per bed and 1 foot between plants within the row. 1000 lbs of 5–10–15 granular preplant fertilizer was applied and incorporated into the soil providing 50 lbs of nitrogen, 100 lbs phosphate and 150 lbs potash per acre. The soil was fumigated with Pic-Clor 60 and covered with totally impermeable film. Transplanting occurred 4 weeks after fumigation. Weekly fertilization with 7–0–7 liquid fertilizer was provided with providing 15 lbs of nitrogen and potash per acre per week for 10 weeks. The total seasonal nitrogen applied with granular pre-plant and weekly fertigation was 200lbs/acre. Preventative sprays of copper and manzate (active ingredient: Mancozeb) were applied to control bacterial leaf spot, while chlorothalonil (active ingredient: Chlorothalonil) and approvia top (active ingredient: Benzovindiflupyr also known as Solatenol) were applied to control anthracnose. Insecticides were applied as needed with radiant (active ingredient: Spinetoram) to control thrips and agrimek (active ingredient: Abamectin) to control broadmites.

Quantitative trait evaluation

Eight quantitative and four qualitative morphological and phenological traits were recorded throughout the season on 330 accessions that germinated successfully from the 352 sown. The quantitative traits included were germination percentage, plant vigor, days to flowering, days to maturity, plant height, main stem height, lodging percentage, and number of lobes. Germination percentage was calculated based on 20 seedlings. Plant vigor was measured two weeks after the germination and was assessed using a scale of 1 (poor), 3 (low), 5 (moderate), 7 (good), and 9 (excellent). The scale value of 1 represented extremely poor-looking or small plants, or no plants sprouted in an accession. The scale value of 3 indicated slightly better performance than 1. The scale value of 5 represented the moderate range, with plants appearing quite healthy and of medium height. The scale value of 7 denoted a plant that was close to ideal, appearing healthy with good height and leaf growth. Plants were assigned a scale value of 9 if they were outstanding, very tall and healthy, with almost every plant in an accession germinating and exhibiting consistent size and quality. Days to flowering were recorded when 50% of the plants flowered by minus the date of transplanting. Similarly, days to maturity was also observed based on the harvest date minus the transplanting date. Plant height was measured using a meter stick positioned at the soil level, recording the highest point of the plant in centimeters, including flowers, leaves, or main stems. Main stem height was determined similarly, measuring up to the point of bifurcation. Lodging data was recorded by visually assessing each plant for leaning or falling and categorizing the degree of lodging as 0° (no lodging), 25° (minor lodging), 45° (medium lodging), or 90° (complete lodging). Observations were systematically documented for each accession. The number of lobes was determined based on visual counting for each accession. Due to the delayed seeding and transplanting, yield data could not be collected as fruits across accessions were starting to mature, ripen and rot with the high temperatures. However, more comprehensive trait characterization of UGA-Capsi-Core (485 accessions) has been undertaken in summer 2025 and will be repeated in summer 2026.

Qualitative trait evaluation

The qualitative traits included plant growth habit, leaf shape, fruit position, and fruit color. Plant growth habit was categorized based on the structural characteristics into three types: prostrate, erect, and compact (Supplementary Fig. 1). Prostrate plants exhibited branches or main stems spread horizontally along the ground, presenting a trailing appearance. Erect plants displayed upright growth with main stems and branches growing vertically without significant inclination. Compact plants demonstrated dense, closely packed growth with short internodes and limited branch spreading. Leaf shape was classified into three distinct categories: deltoid, ovate, and lanceolate. Deltoid leaves possessed an equilateral triangular shape with broad bases and pointed apices. Ovate leaves were egg-shaped, being broader at the base and narrowing toward the apex. Lanceolate leaves were narrow and elongated, tapering at both ends to form a lance-like appearance.

Fruit position was assessed using three descriptors: pendant, where the fruit is suspended in a manner reminiscent of a pendant in a necklace; erect, where the fruits, instead of hanging, project straight upward from the plant; and intermediate, where the fruit orientation is neither erect nor pendant. Immature fruit color was recorded by evaluating each accession and categorizing the peppers as green (G) or yellow (Y), based on visual observation. Among the plants per plot, the average color of the peppers per accession was documented, with priority given to the predominant color.

SSR marker analysis

DNA isolation

Seedlings were raised in trays under greenhouse conditions during the winter season of 2024. At the three-leaf stage, young leaf tissues were collected from all 485 accessions for genomic DNA extraction. DNA was isolated using the Qiagen DNeasy Plant Pro Kit, following the manufacturer's protocol. DNA concentration and purity were measured using a NanoDrop™ Lite Spectrophotometer (Thermo Fisher Scientific, USA), and DNA integrity was verified by agarose gel electrophoresis. Only high-quality DNA

samples (473 accessions) with acceptable A260/A280 ratios were used for downstream PCR amplification.

Polymerase chain reaction (PCR)

A total of 31 SSR primers were selected for genotyping based on publicly available reports indicating their linkage to genomic regions associated with resistance to *Phytophthora capsici* and related pathogenic traits in *Capsicum* (Table 1). PCR amplification was performed using *Promega GoTaq® G2 Green Master Mix* in a 20 µL reaction volume. The thermal cycling conditions included an initial denaturation at 95 °C for 5 min, followed by 30 cycles of denaturation at 94 °C for 30 s, annealing (53–63 °C) for 30 s, and extension at 72 °C for 30 s. A final extension was performed at 72 °C for 5 min. The annealing temperature was optimized individually for each primer within this range.

Gel electrophoresis

Amplified products were resolved on 3% agarose gels (SeaKem® ME Agarose) stained with GelRed® Nucleic Acid Gel Stain and visualized under UV illumination. Gel images were captured using G:Box Syngene and analyzed using GeneTools 4.3.17.0.

Allele binning and genetic diversity analysis

Allele binning was carried out using TANDEM v1.09 (Matschiner and Salzburger 2009), based on the expected SSR repeat motifs for each primer. The binned allele data were exported and analyzed in RStudio v4.4.2 to compute fundamental genetic diversity parameters. These included the number of alleles per locus (N_a), major allele frequency, observed heterozygosity (H_o), expected heterozygosity (H_e), and polymorphism information content (PIC). Custom R scripts were used to perform the calculations and summarize the diversity metrics across all loci and accessions.

Population structure analysis

Population structure among the 473 diverse *Capsicum* accessions was inferred using a Bayesian model-based clustering approach implemented in STRUCTURE v2.3.4 (Pritchard et al. 2000).

Genotyping was performed using a subset of 24 highly polymorphic SSR markers. The admixture model with correlated allele frequencies was applied to account for potential gene flow and shared ancestry among subpopulations. Each STRUCTURE run consisted of a burn-in period of 100,000 iterations followed by 250,000 Markov Chain Monte Carlo (MCMC) repetitions to ensure convergence of the parameter estimates. STRUCTURE was executed for hypothetical population numbers (K) ranging from 1 to 10, with 10 independent replicates per K to assess the stability and consistency of clustering patterns. The most likely number of genetic clusters (K) was determined using the ΔK method described by Evanno et al. (2005), as implemented in STRU CTURE HARVESTER (Earl and vonHoldt 2012). The alignment of replicate runs and graphical visualization of population assignments were carried out using CLUMPAK (Kopelman et al. 2015). The ΔK plot revealed a distinct peak at $K=3$, indicating that three genetically differentiated clusters provided the best fit for the data. Accordingly, $K=3$ was selected as the optimal number of clusters for subsequent interpretation and visualization of population structure.

Statistical analysis

Morphological trait data were processed, summarized, and visualized in RStudio v4.4.2 using the packages ‘dplyr’ (Wickham et al. 2023), ‘tidyr’ (Wickham & Girlich 2023), ‘ggplot2’ (Wickham 2016), and ‘corrplot’ (Wei & Simko 2021). Descriptive statistics, analysis of variance (ANOVA), heritability, Pearson’s correlation coefficients were calculated, and correlation matrices were visualized using corrplot. SSR diversity analyses were conducted using the packages ‘adegenet’ (Jombart 2008), ‘dplyr’ (Wickham et al. 2023), ‘ape’ (Paradis & Schliep 2019), ‘ggtree’ (Yu et al. 2017), and ‘ggplot2’ (Wickham 2016) for dendrogram construction, visualization, and summary statistics. For phenotypic data, PCA was performed using the packages ‘stats’, ‘FactoMineR’ (Lê et al. 2008), and ‘factoextra’ (Kassambara & Mundt 2020). For molecular data, PCA was performed using ‘adegenet’ (Jombart 2008) and ‘poppr’ (Kamvar et al. 2014).

Table 1 List of SSR markers used in the current study

S.No	Marker Name	Forward sequence (5' to 3')	Reverse sequence (3' to 5')	Annealing temp (C°)	Reference
1	SSR9	CAAGCACCTACAAATGCA AAAT	CCGGATGAGAAAACCTGC TACT	60	Kim et al. (2008)
2	SSR3	TTTCCAAGCACCTACAAA TGC	CCGGATGAGAAAACCTGC TACT	55	Kim et al. (2008)
3	HpmsE034	AAACCGCTTGGAATAAA GGTGCT	CCACTCCAGTTTGTATCA TCTCCA	55	Kumar et al. (2021)
4	HpmsE062	ATTTTTGCCCAAATGTC AACG	AAACGTTGGGGGTGGAGA TTG	55	Kumar et al. (2021)
5	ZL6726	TCCAGCCATCCATTATTT CAT	ATCCCGAACTGCCAATAA TTA	55	Wang et al. (2016)
6	HpmshsMADS	TGCTTTCAAAACAATTTG CATGG	GCGTCTAATGCAAAACAC ACATTAC	55	Minamiyama et al. (2007)
7	CAMS089	AACAGCGCTGATCCTTTACC	CAACATCACAGTGGCAGA AGA	55	Minamiyama et al. (2006)
8	U196349	CCTGGGAGAGGAGTCCTA CA	GCAAGAAACAGCGCCTTT AG	55	Mallard et al. (2013)
9	U198114	TTGGGCTCAATTAAACCA TACA	GCACCCCTTGATTGAGAG AA	55	Mallard et al. (2013)
10	U197890	CCATATGGTCCTCCTCCAGA	CTTCAACCACTTCGGCAAT	55	Mallard et al. (2013)
11	CONTIG1896	CATAACACAACCCAATTG CAGAACC	GTCCTACACTTGTTACAG CTGCC	55	Liu et al. (2014)
12	CAMS319	TCGAAATCAATACTCCTC CTTCCC	CATAACACAACCCAATTG CAGAACC	55	Minamiyama et al. (2007)
13	907,783	CTCACGCGTTGTTCTTAA AAGGTT	GGCACAACAATAGTCACA ACGG	55	Liu et al. (2014)
14	CaRP-5130	CATAACACAACCCAATTG CAGAACC	GAGACTAAGAAAGTTGGA CGCC	55	Liu et al. (2014)
15	CaNB-5170	TTCGATCCACACCATCATCT	TCCTTCAATGGCTTTCCATC	55	Mallard et al. (2013)
16	EPMS 331	AACCCAATCCCCTTATCCAC	GCATTAGCAGAAGCCATTTG	53	Nagy et al. (2007)
17	EPMS 342	CTGGTAGTTGCAAGAGTA GATCG	ATGATCTTTGACGACGAGGG	53	Nagy et al. (2007)
18	EPMS 376	ACCCACCTTCATCAACAACC	ATTTGTGGCTTTTCGAAACG	50	Nagy et al. (2007)
19	EPMS 399	GTCTTCTCGCCGACAAGTC	TTCAAAAATCATGAGCAG CG	53	Nagy et al. (2007)
20	EPMS 404	TCTCTCTCTACATCTCTC CGTTG	TGTCGTTCGTCGACGTACTC	50	Nagy et al. (2007)
21	EPMS 418	ATCTTCTTCTCATTTCTC CCTTC	TGCTCAGCATTAAACGACGTC	53	Nagy et al. (2007)
22	EPMS 441	GCACGAGGAAAGAGAGAG ACATAG	TCAACGGATTCACTCTTCCC	53	Nagy et al. (2007)
23	EPMS 480	AGGAACGGCAGTCTTGCT AG	GATGCTAGGTCTGGATTC CTG	53	Nagy et al. (2007)
24	EPMS 501	AATCCTCCAAATCCACCCTC	ATTCGATTGCTTGCTCCTTG	53	Nagy et al. (2007)
25	EPMS 542	ATCCACTTCCCCATTATCCC	TGGATGATCGAGTTGACTGG	53	Nagy et al. (2007)
26	GPMS29	CAGGCAATACGGAGCATC	TGTGTGCTTCTTGACGAC	53	Nagy et al. (2007)
27	GPMS112	TCCCTCAGCAGCAACAATTT	GTCGGGCTCTTTGATTGTGT	50	Nagy et al. (2007)
28	GPMS117	GATGTTAGGTCCGTGCTTCG	AAGCCCCATGGAAGTTATCC	53	Nagy et al. (2007)
29	Hpms1-1	TCAACCCAATATTAAGGT CACTTCC	CCAGGCGGGGATTGTAGA TG	53	Lee et al. (2004)

Table 1 (continued)

S.No	Marker Name	Forward sequence (5' to 3')	Reverse sequence (3' to 5')	Annealing temp (C°)	Reference
30	Hpms1-117	ACCCAAATTTGCCTTGTT GAT	AATCCATAACCTTATCCC ATAAA	50	Lee et al. (2004)
31	Hpms2-2	GCAAGGATGCTTAGTTGG GTGTC	TCCCAAAATTACCTTGCA GCAC	53	Lee et al. (2004)

Results

Agronomical and fruit quality trait characterization among and across varietal groups

The pepper collection used in the current study comprised accessions representing diverse fruit types and agro-morphological traits evaluated during the summer 2024. Based on the observed fruit diversity, we classified the UGA-Capsi-Core collection (330 accessions) into six different varietal groups (VGs): banana (45 accessions), bell (24 accessions), Italian frier (22 accessions), mini bell (61 accessions), mini sweet (91 accessions), and specialty peppers (87 accessions) (Fig. 1). specialty peppers mainly were comprised hot peppers including jalapeno, serrano, cayenne,

habanaro among others. Agronomical and fruit quality traits were assessed, focusing on parameters such as germination percentage, plant vigor, plant and main stem height, days to flowering and maturity, lodging, and fruit morphological characteristics. This collection displayed notable phenotypic diversity, emphasizing its potential for breeding and genetic improvement of pepper cultivars.

Across all varietal groups (VGs), the average germination rate was 62.4%, with the highest mean germination observed in mini sweet accessions (68.9%), followed by Italian frier (64.3%) (Table 2). The lowest germination rate was recorded in banana peppers (52.1%). Plant vigor was highest in banana accessions (5.49) and lowest in bell peppers (4.17). Days to flowering revealed limited variability, ranging from 6 to

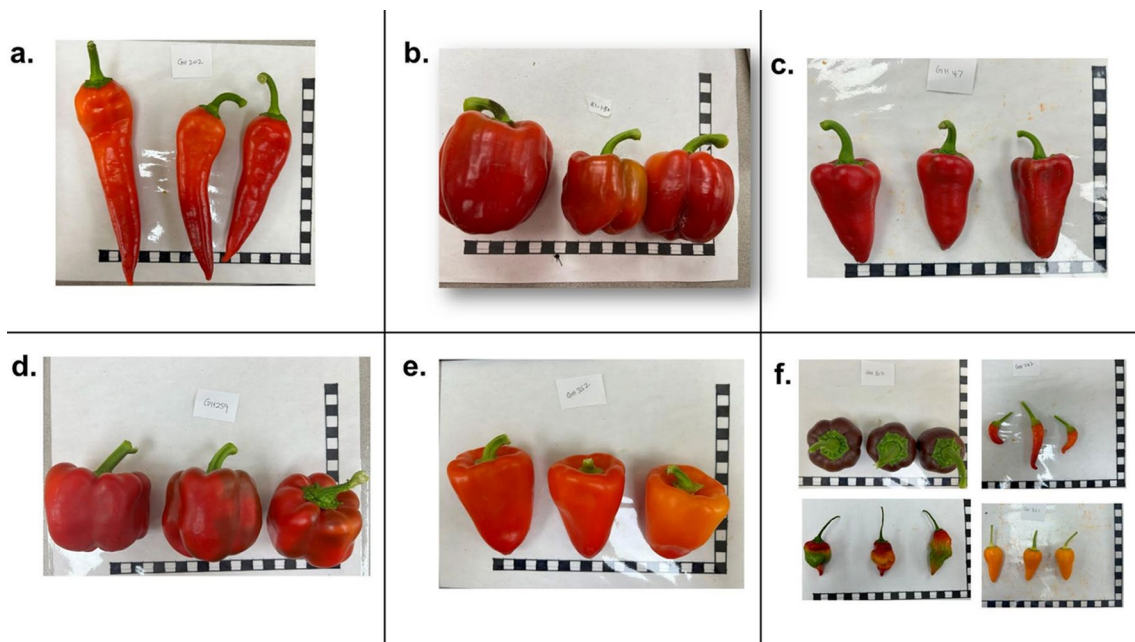


Fig. 1 Morphological diversity in fruit characteristics across the six varietal groups. **a** banana **b** bell **c** Italian frier, **d** mini bell **e** mini sweet **f** specialty peppers

Table 2 Descriptive statistics of quantitative traits between accessions evaluated during Summer 2024

Group	Trait	Min	Mean	Max	CV	SD
Across	Germination	5	62.42	100	38.28	23.9
	Plant Vigor	0	4.66	9	32.74	1.53
	Days to Flowering	6	25.83	56	44.15	11.4
	Number of Lobes	1	2.35	4	50.5	1.19
	Plant Height	14	38.24	75	23.81	9.11
	Main Stem Height	7	16.3	46.5	25.21	4.11
	Lodging	0	23.58	90	65.24	15.39
	Days to Maturity	71	74.78	83	3.23	2.41
Banana	Germination	5	52.11	95	48.33	25.18
	Plant Vigor	1	5.49	9	32	1.76
	Days to Flowering	6	27.88	56	51.15	14.26
	Number of Lobes	1	1.05	3	30.62	0.32
	Plant Height	18.5	39.79	62	20	7.96
	Main Stem Height	10.5	17.55	29.7	21.3	3.74
	Lodging	0	25.02	57.5	52.17	13.05
	Days to Maturity	71	73.84	77	2.24	1.65
Bell	Germination	25	59.38	100	33.17	19.7
	Plant Vigor	3	4.17	7	27.71	1.15
	Days to Flowering	11	20.78	28	20.83	4.33
	Number of Lobes	1	3.53	4	18.88	0.67
	Plant Height	23.3	34.22	46.8	18.22	6.23
	Main Stem Height	10	14.98	24.5	20.18	3.02
	Lodging	0	24.02	62.5	78.44	18.84
	Days to Maturity	71	74.7	77	3.03	2.26
Italian Frier	Germination	20	64.32	95	35.98	23.14
	Plant Vigor	3	5.45	9	33.42	1.82
	Days to Flowering	11	24.9	56	38.32	9.54
	Number of Lobes	1	1.15	3	46	0.53
	Plant Height	25	40.19	56.3	18.52	7.44
	Main Stem Height	11	16.63	24.5	20.11	3.34
	Lodging	0	28.42	57.5	49.53	14.08
	Days to Maturity	71	74.86	77	3.16	2.36
Mini Bell	Germination	10	60.08	100	34.45	20.7
	Plant Vigor	3	4.31	7	27.83	1.2
	Days to Flowering	6	25.11	56	36.25	9.1
	Number of Lobes	1	3.44	4	17.38	0.6
	Plant Height	16	35.02	52	17.45	6.11
	Main Stem Height	7.3	15.4	24	18.23	2.81
	Lodging	0	19.78	78.8	72.11	14.26
	Days to Maturity	75.55	83	2.85	2.15	75.55

Table 2 (continued)

Group	Trait	Min	Mean	Max	CV	SD
Mini Sweet	Germination	5	68.9	100	34.43	23.72
	Plant Vigor	3	4.56	9	31.81	1.45
	Days to Flowering	6	24.44	56	46.46	11.35
	Number of Lobes	1	2.59	4	36.07	0.93
	Plant Height	14	37.4	69.7	25.4	9.5
	Main Stem Height	7	15.63	46.5	28.1	4.39
	Lodging	0	24.62	90	63.8	15.71
Specialty Pepper	Days to Maturity	71	75.42	83	3.57	2.69
	Germination	10	62.99	100	39.36	24.79
	Plant Vigor	0	4.53	9	32.76	1.48
	Days to Flowering	11	28.35	56	43.19	12.24
	Number of Lobes	1	1.95	4	58.43	1.14
	Plant Height	15.3	41.36	75	25.87	10.7
	Main Stem Height	8	17.34	31.8	27.59	4.78
	Lodging	0	23.08	75	68.04	15.7
	Days to Maturity	71	74.04	83	3.12	2.31

56 days, with bell tending to flower later (20.78 days) compared to specialty peppers (28.3 days). The days to flowering were calculated from the date of transplanting. Because transplanting was delayed for 2 weeks, plants were physiologically older at transplanting, resulting in fewer days to flowering being recorded compared to the typical range (40–55 days). Notable differences in plant height were observed, with specialty peppers (41.4 cm) and Italian frier (40.2 cm) exhibiting the tallest plants, while bell peppers were the shortest (34.2 cm). Main stem height followed a similar trend, with banana recording the tallest stems (17.6 cm) and bell the lowest (15.0 cm). Lodging rates varied widely, with Italian frier showing the highest mean (28.4%) and mini bell the lowest (19.8%). Days to maturity were highly consistent across groups, ranging from 71 to 83 days, though mini bell (75.56 days) and mini sweet (75.43 days) matured slightly later than banana (73.8 days). Fruit quality traits showed substantial variation, particularly in the number of lobes. The highest mean number of lobes per fruit was observed in bell peppers (3.53), whereas banana accessions recorded the lowest (1.05) (Fig. 2).

The ANOVA revealed highly significant variation ($p < 0.001$) among varietal groups for most traits, including germination, plant vigor, days to flowering,

number of lobes, plant height, main stem height, and days to maturity (Table 3). Lodging also showed significant differences across groups, though at a lower level ($p < 0.05$). Replication effects were generally non-significant, except for plant height and lodging, which exhibited strong replication effects ($p < 0.001$). The relatively large residual variances observed for certain traits, such as lodging and plant height, suggest that environmental factors may contribute substantially to variation. Overall, these results confirm considerable genetic diversity in agro-morphological and fruit quality traits across the *Capsicum* germplasm, highlighting their potential value for breeding programs targeting productivity, adaptability, and fruit quality improvement.

The estimates of genetic variance, heritability, and variability parameters revealed substantial differences across traits (Table 4). Broad-sense heritability (H^2) was estimated using variance components derived from replicated field evaluations of accessions, rather than from progeny-based inheritance. High broad-sense heritability was observed for number of lobes ($H^2 = 76.5\%$), accompanied by high genetic ($GCV = 46.0\%$) and phenotypic ($PCV = 52.5\%$) coefficients of variation, indicating strong genetic control and potential for effective selection. Plant vigor exhibited moderate

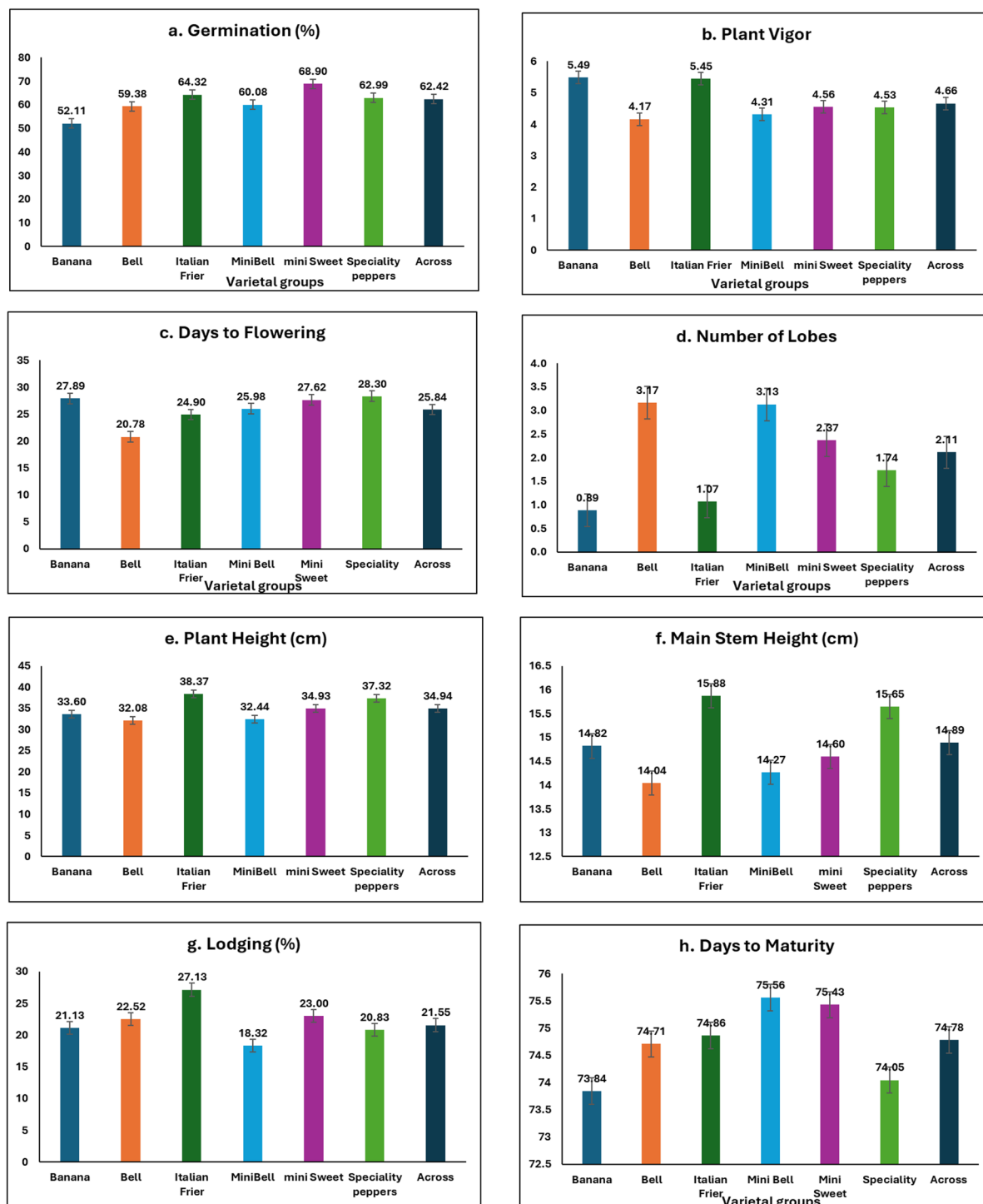


Fig. 2 Mean values of quantitative traits for each UGA-Capsi-Core varietal groups: **a** Germination (%) **b** Plant vigor **c** Days to flowering **d** Number of lobes **e** Plant height **f** Main stem height **g** Lodging (%) **h** Days to maturity

heritability ($H^2 = 21.1\%$) with moderate variability

(GCV = 11.5%; PCV = 25.1%), suggesting some

scope for genetic improvement. Germination, days to flowering, and lodging displayed very low heritability values ($H^2 < 10\%$), coupled with low to moderate genetic variability, reflecting strong environmental influence and limited potential for direct selection. Notably, lodging showed the lowest heritability ($H^2 = 3.7\%$) despite high phenotypic variation ($PCV = 45.9\%$), highlighting its strong dependence on environmental conditions. Overall, the

results indicate that number of lobes is the most reliable trait for selection, while plant vigor may offer moderate breeding gains. In contrast, traits such as lodging and germination are less heritable and require careful management of environmental effects or integration with molecular tools for effective improvement.

Table 3 Analysis of variance (ANOVA) for eight quantitative traits across UGA-Capsi-Core varietal groups

Trait	Source	df	Mean Square (MS)	F-value	p-value	Significance
Germination	Group	5	3707.23	6.77	<0.001	***
	Rep	1	0	0	ns	ns
	Residual	653	547.91	—	—	—
Plant Vigor	Group	5	24.15	11.13	<0.001	***
	Rep	1	0.03	0.01	ns	ns
	Residual	652	2.17	—	—	—
Days to Flowering	Group	5	593.97	4.69	<0.001	***
	Rep	1	0	0	ns	ns
	Residual	603	126.51	—	—	—
Number of Lobes	Group	5	82.86	115.38	<0.001	***
	Rep	1	0.23	0.31	ns	ns
	Residual	586	0.72	—	—	—
Plant Height	Group	5	778	10.31	<0.001	***
	Rep	1	1051.35	13.93	<0.001	***
	Residual	596	75.47	—	—	—
Main Stem Height	Group	5	107.88	6.68	<0.001	***
	Rep	1	0.7	0.04	ns	ns
	Residual	596	16.15	—	—	—
Lodging	Group	5	602.42	2.67	0.021	*
	Rep	1	5170.2	22.94	<0.001	***
	Residual	596	225.36	—	—	—
Days to Maturity	Group	5	64.67	11.97	<0.001	***
	Rep	1	0	0	ns	ns
	Residual	653	5.4	—	—	—

*** $p < 0.001$; ** $p < 0.01$;

* $p < 0.05$; ns = non-significant

Table 4 Genetic variance, heritability, and coefficients of variation for eight quantitative traits in pepper accessions
 σ^2_g = genetic variance;
 σ^2_p = phenotypic variance; H^2 = broad-sense heritability;
GCV = genotypic coefficient of variation;
PCV = phenotypic coefficient of variation

Trait	Mean	σ^2_g	σ^2_p	H^2	GCV (%)	PCV (%)
Germination	62.42	27.94	301.4	9.3	8.47	27.81
Plant Vigor	4.66	0.29	1.37	21.1	11.55	25.12
Days to Flowering	25.84	5.31	68.48	7.8	8.92	32.03
Number of Lobes	2.35	1.17	1.53	76.5	45.96	52.54
Plant Height	38.24	7.31	45.04	16.2	7.07	17.55
Stem Height	16.3	0.94	9.01	10.5	5.96	18.41
Lodging	23.58	4.3	117.02	3.7	8.79	45.87
Days to Maturity	74.78	0.46	3.16	14.7	0.91	2.38

Qualitative traits characterization among and across varietal groups

A comprehensive analysis of qualitative traits was conducted across the pepper accession collection to assess genetic diversity and phenotypic variation. Four primary morphological descriptors were evaluated: plant growth habit (PGH), fruit position (FP), fruit color, and leaf shape (Supplementary Fig. 2; Table 5). Analysis of qualitative traits revealed significant variations among pepper accessions. Plant growth habit showed a statistically significant association demonstrating substantial diversity in plant architectural characteristics across the studied germplasm. Fruit positioning exhibited the most pronounced genetic differentiation, with an extremely high significance. This robust association indicates substantial diversity in fruit placement among the accessions, suggesting considerable genetic variation in this trait.

Fruit color presented a marginally significant association, revealing subtle genetic variations in color characteristics. Although less pronounced than other traits, this trend suggests potential for further exploration in breeding programs focused on color-specific varieties. Leaf shape analysis showed no statistically significant association, indicating relative conservation of leaf morphology across the studied accessions (Table 5). This result suggests that leaf shape may be a more stable trait within the examined pepper germplasm collection. These findings underscore the genetic diversity present in pepper germplasm, particularly in traits related to plant architecture and fruit characteristics. Such variation provides valuable insights for future breeding strategies.

Multivariate analysis

Principal component analysis (PCA)

Principal component analysis (PCA) was performed on the eight quantitative traits to explore the patterns

Table 5 Results of Pearson's Chi-squared tests for qualitative traits in UGA-Capsi-Core pepper accessions

Trait	χ^2	df	p-value
Plant Growth Habit	38.07	20	**
Leaf Shape	6.26	10	–
Fruit Position	84.28	20	***
Fruit Color	16.48	10	–

of morphological variation among the 330 *Capsicum* accessions. The first two principal components (PC1 and PC2) together explained 42.57% of the total variation, with PC1 accounting for 26.65% and PC2 for 15.93% (Fig. 3a and b). PC1 was strongly influenced by plant height (29.4%) and stem height (27.9%), followed by plant vigor (12.9%) and number of lobes (12.4%), suggesting this axis mainly represented variation in plant architecture and vigor. PC2 was dominated by days to flowering (24.8%) and days to maturity (22.7%), indicating that this axis largely captured phenological differences among accessions (Supplementary Fig. 3; Table S1).

The PCA scatter plot revealed that accessions from different varietal groups (banana, bell, Italian frier, mini bell, mini sweet, and specialty pepper) were dispersed across quadrants without distinct clustering, although some overlap was evident (Fig. 3a). Group means along PC1 and PC2 suggested subtle tendencies: banana and specialty peppers generally loaded positively on PC1, while bell and Italian frier accessions tended toward negative loadings. However, no sharp group separation was observed, reflecting the admixed diversity within the UGA-Capsi-Core collection. Overall, PCA highlighted that architectural traits (plant and stem height) and phenological traits (days to flowering and maturity) were the major contributors to variation, while other traits like lodging and germination played smaller roles. These results reinforce the complexity of morphological diversity and the necessity of integrating molecular marker data for clearer population structure resolution.

Correlation analysis

The correlation matrix revealed weak to moderate relationships among agro-morphological traits in the UGA-Capsi-Core accessions (Table S2; Supplementary Fig. 4). The strongest positive correlation was observed between plant height and main stem height ($r=0.727$), confirming that taller plants tend to have proportionally taller stems. Germination showed a moderate positive correlation with plant vigor ($r=0.286$), suggesting that higher germination success may contribute to improved overall vigor. Germination also exhibited weak but positive associations with plant height ($r=0.175$) and main stem height ($r=0.183$). Plant vigor was weakly and positively correlated with main stem height ($r=0.169$)

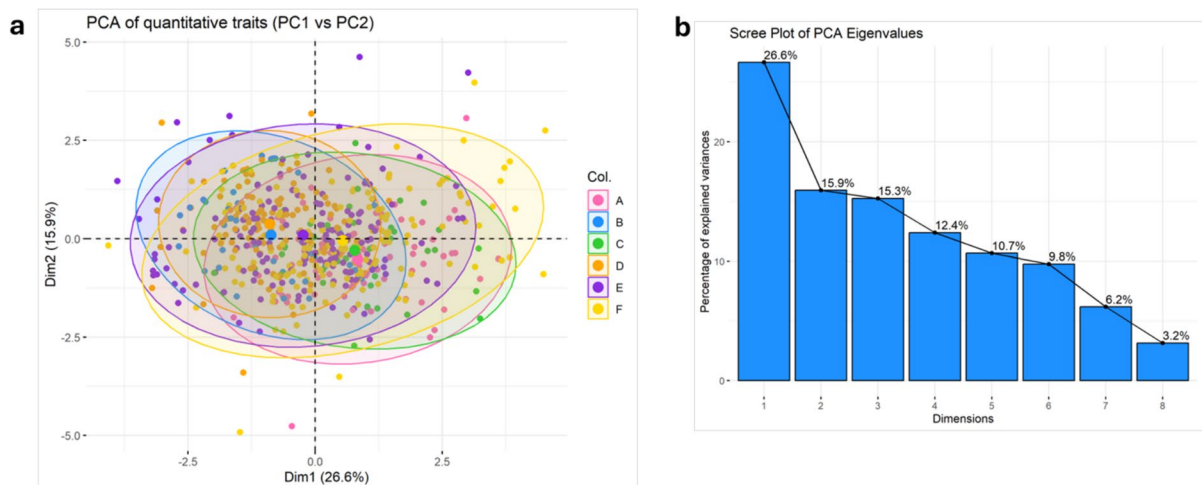


Fig. 3 PCA analysis of UGA-Capsi-Core varietal groups based on eight quantitative traits. **a** PCA of quantitative traits (PC1 vs PC2) A- banana B- bell, C- Italian frier, D- mini bell,

E- mini sweet, F- specialty peppers **b** Scree plot explaining the percentage of explained variance at different dimensions

and lodging ($r=0.197$), though the latter relationship suggests only a slight trend toward more vigorous plants being prone to lodging. In contrast, plant vigor was negatively correlated with number of lobes ($r=-0.274$) and days to maturity ($r=-0.172$), indicating potential trade-offs between vigor and certain developmental or fruit traits. Days to flowering was negatively associated with number of lobes ($r=-0.058$) and days to maturity ($r=-0.175$), though these correlations remained weak. Overall, aside from the strong relationship between plant height and main stem height, most correlations among traits were weak to moderate in strength. These findings highlight the largely independent genetic or environmental regulation of flowering and maturity traits, while germination and vigor relationships underscore the importance of early establishment for plant robustness.

Molecular screening for *Phytophthora capsici* and identification of resistance source

SSR allelic diversity

A total of 24 SSR markers were successfully amplified across 473 *Capsicum* accessions. In total, 311 alleles were detected across all loci before binning, which reduced to 308 distinct alleles after binning (Table 6; Supplementary Fig S5). Only three

markers (SSR9, HpmsE034, and GPMS117) lost a single allele during the binning process, indicating that binning had minimal impact on overall allelic diversity (Fig. 4a; Table S3). The post-binning data was employed for further downstream analysis. The number of alleles per locus ranged from 6 (EPMS542) to 24 (EPMS 342), with an average of 12.83 (Fig. 4b; Table 6). Most of the markers (87.5%) exhibited between 8 and 18 alleles. The major allele frequency ranged from 0.116 (GPMS117) to 0.442 (SSR3). Notably, loci such as GPMS117, EPMS342, and CaNB-5170 exhibited very low major allele frequency (MAF) (<0.17), reflecting high allelic diversity and evenness. Gene diversity values (expected heterozygosity) ranged from 0.729 (SSR9 and SSR3) to 0.923 (GPMS117), with an overall mean of 0.827, indicating substantial heterozygosity within the population. Similarly, PIC values, which reflect both the number and frequency of alleles, ranged from 0.656 (SSR3 and SSR9) to 0.917 (GPMS117), with a mean of 0.80. The three most informative markers were GPMS117 (PIC=0.917), EPMS342 (0.907), and CaNB-5170 (0.888), each showing high gene diversity and a broad allelic spectrum.

Among the markers evaluated, several SSRs previously reported to be linked with *Phytophthora capsici* resistance QTLs on chromosome P5 also exhibited moderate to high allelic diversity and informativeness in the present study. Notably, ZL6726,

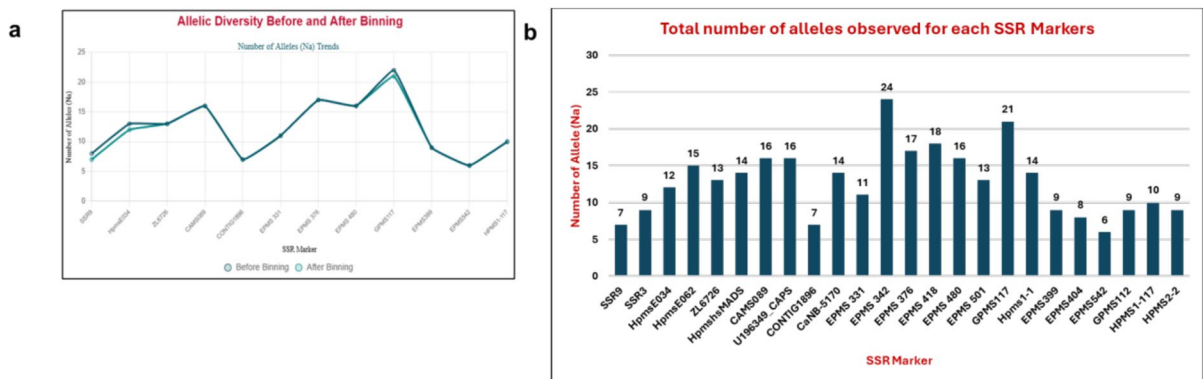
Table 6 SSR-based allelic diversity and Polymorphism Information Content (PIC) among the 24 markers on 473 UGA-Capsi-Core pepper accessions

Marker	Na	Major_Allele_Freq	Gene_Diversity	PIC
SSR9	7	0.371	0.729	0.656
SSR3	9	0.442	0.729	0.656
HpmsE034	12	0.241	0.858	0.838
HpmsE062	15	0.252	0.839	0.813
ZL6726	13	0.266	0.829	0.8
HpmsHMA5	14	0.222	0.877	0.862
CAMS089	16	0.182	0.869	0.852
U196349_CAPS	16	0.209	0.89	0.878
CONTIG1896	7	0.332	0.754	0.694
CaNB-5170	14	0.165	0.898	0.888
EPMS 331	11	0.196	0.872	0.856
EPMS 342	24	0.149	0.914	0.907
EPMS 376	17	0.221	0.892	0.88
EPMS 418	18	0.222	0.831	0.803
EPMS 480	16	0.162	0.89	0.877
EPMS 501	13	0.164	0.886	0.872
GPMS117	21	0.116	0.923	0.917
Hpms1-1	14	0.233	0.852	0.83
EPMS399	9	0.342	0.78	0.732
EPMS404	8	0.253	0.827	0.797
EPMS542	6	0.304	0.763	0.707
GPMS112	9	0.327	0.784	0.737
HPMS1-117	10	0.304	0.806	0.769
HPMS2-2	9	0.322	0.764	0.709

which is tightly linked to the major resistance locus *CaPhyto* on chromosome P5, displayed 13 alleles with a gene diversity of 0.829 and a PIC value of 0.800. Additional P5-associated markers, including SSR9, SSR3, U196349_CAPS, CONTIG1896, and CaNB-5170, showed PIC values ranging from 0.656 to 0.888 and gene diversity values between 0.729 and 0.898, indicating substantial allelic variation within resistance-associated genomic regions. In particular, CaNB-5170 and U196349_CAPS exhibited high informativeness (PIC=0.888 and 0.878, respectively), comparable to or exceeding the collection-wide average. These results demonstrate that SSR markers linked to major *P. capsici* resistance loci on chromosome P5 are highly polymorphic and informative in the UGA-Capsi-Core germplasm, supporting their utility for simultaneous population structure analysis and resistance-oriented breeding applications. Minor or isolate-specific resistance QTLs have also been reported on chromosome P11 in previous studies; however, specific SSR loci on P11 are less consistently defined and were therefore not individually assigned in this analysis.

STRUCTURE analysis

Bayesian model-based clustering of 473 *Capsicum* accessions, using 24 SSR markers, revealed clear evidence of population structure. Analysis using STRUCTURE v2.3.4, based on simulations from K=1 to 10, identified K=3 as the most likely number of genetic clusters (Fig. 5a). This was supported by a sharp peak in ΔK values calculated via the method of Evanno et al. (2005) and visualized using STRUCTURE HARVESTER. At K=3,

**Fig. 4** a Allele variation observed before and after binning b Total number of alleles observed for each marker in the current study

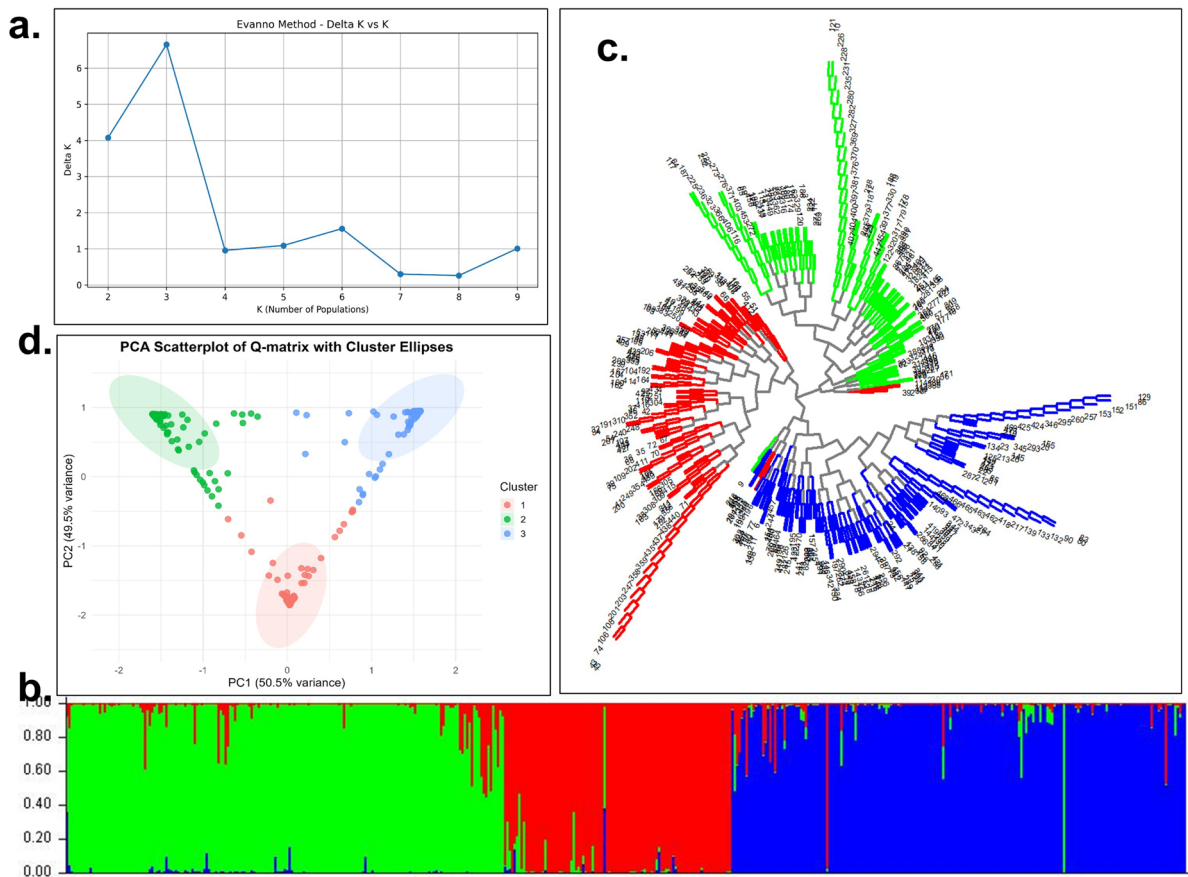


Fig. 5 **a** Inferred population structure of 473 accessions. Distribution of the accessions to different populations is indicated by the color code. Numbers on the y-axis show the subgroup membership, and the x-axis shows the different accessions. **b**

Delta K values for different numbers of populations assumed (K) in the STRUCTURE analysis **c** NJ tree compared the classification of inferred populations **d** Principal component analysis (PCA)

the STRUCTURE bar plot showed that accessions were grouped into three genetically distinct clusters (Fig. 5b). Outputs from replicate runs at $K=3$ were aligned using CLUMPP-compatible files to ensure consistent cluster assignment across iterations. The resulting Q-matrix demonstrated clear assignment of most individuals to one of three distinct genetic clusters, while a subset of accessions displayed varying degrees of admixture, indicating shared ancestry or recent gene flow. A dendrogram constructed using the aligned Q-matrix further supported the STRUCTURE results, revealing three well-separated clusters with patterns consistent with the inferred genetic structure (Fig. 5c). Similarly, PCA based on SSR allele data mirrored the STRUCTURE groupings, with the first two principal components distinguishing the major clusters and positioning admixed individuals between them

(Fig. 5d). Cluster 1 comprised 150 *C. annuum* and two accessions of *C. baccatum* and one *C. chinense*. Cluster 2 included 157 *C. annuum* accessions along with one accession each of *C. baccatum*, *C. chacoense*, *C. frutescens*, *C. galapagoense*, and two of *C. chinense*, whereas cluster 3 was solely of 157 *C. annuum* accessions (Table S4).

Discussion

Qualitative trait variation between and across varietal groups

The comprehensive evaluation of morphological traits in the UGA-Capsi-Core pepper collection provides

critical insights into the genetic diversity and trait variability underlying this important horticultural crop. The morphological characterization of pepper accessions revealed significant insights into the genetic diversity and phenotypic variations within the studied germplasm, with important implications for pepper breeding and diversity assessment. The significant variation in plant growth habit aligns with previous studies demonstrating the importance of architectural diversity in pepper breeding (Tripodi and Greco 2018; Solomon et al. 2019), suggesting potential for developing cultivars with optimized plant structures that can enhance yield and resource efficiency and for adapting varieties to different cultivation systems. The highly significant association in fruit positioning represents a critical finding with substantial breeding implications, as highlighted by Moreira et al. (2018), who emphasized the role of fruit placement in harvesting efficiency and mechanization potential. The considerable genetic diversity observed in fruit positioning could thus be exploited for developing cultivars tailored to different agricultural systems and harvesting technologies, directly influencing yield and market preferences. The marginally significant fruit color association suggests subtle genetic variations, opening avenues for further investigation into color-related genetic diversity; although the variation was limited, it may still be relevant for breeding programs targeting varieties with specific color characteristics for market differentiation or nutritional value, since fruit color is often linked to phytonutrient content. By contrast, the non-significant variation in leaf shape indicates limited differentiation for this trait among the studied accessions under the evaluated field conditions, rather than strong discriminatory power for diversity analysis. This observation is consistent with Dias et al. (2013), who reported that while morphological and molecular variability are evident in *Capsicum*, certain anatomical features exhibit relative stability. Such stability may reflect functional constraints on leaf architecture or the influence of shared breeding history, rather than definitive evolutionary conservation. Overall, the observed variations, particularly in plant growth habit and fruit positioning, provide valuable resources for targeted breeding programs, reinforcing the importance of comprehensive germplasm characterization in the development of resilient and productive pepper cultivars.

Quantitative trait variation, multivariate insights between and across varietal groups

The morphological characterization of pepper accessions revealed significant phenotypic diversity, offering critical insights into the genetic richness of the UGA-Capsi-Core collection. Variation across traits such as germination, plant vigor, plant height, and number of lobes reflects both genetic differentiation and environmental influence, consistent with earlier findings on *Capsicum* diversity and breeding potential (Tripodi and Greco 2018; Solomon et al. 2019). The presence of substantial variability in plant architecture suggests opportunities for tailoring growth habits to improve yield and adaptability under diverse cultivation systems. Fruit positioning, highlighted in other studies as a key determinant of harvest efficiency and mechanization (Moreira et al. 2018), further underscores the importance of structural diversity in pepper improvement. While fruit color showed only marginal variation, suggesting a conserved trait, this still aligns with previous observations that color diversity may offer opportunities for nutritional enhancement and consumer preference (Dias et al. 2013). Leaf shape similarly exhibited little variability, indicating a conserved morphological trait across accessions, as reported in earlier studies (Dias et al. 2013). Collectively, these patterns highlight the need for targeted trait-based selection in breeding programs.

Quantitative analyses reinforced these observations, with ANOVA confirming significant differences for most traits, particularly germination, plant vigor, plant height, and number of lobes, while days to maturity and flowering exhibited greater stability across groups. Similar findings of trait-specific variability have been reported in Ethiopian and West African peppers (Agyare et al. 2016; Anani et al. 2024), and in European and South American collections (Constantino et al. 2020). Genetic variance components further emphasized this pattern: high heritability estimates were observed for number of lobes, indicating strong genetic control and its utility for selection, whereas lodging and main stem height showed low heritability, pointing to stronger environmental influence. The distinction between traits with high genotypic coefficient of variation (e.g., lobes) and those with low variation (e.g., flowering time, maturity) suggests differential breeding potential, consistent with reports

that heritability and genetic advance vary widely across *Capsicum* traits (McLeod et al. 2023). These findings collectively demonstrate that while some traits offer strong potential for direct selection, others may require integrated approaches to achieve improvement.

Multivariate approaches provided additional clarity on trait interactions and population structure. PCA highlighted plant architecture (height, main stem height, vigor, lobes) as the primary drivers of variation, while phenological traits (flowering and maturity) explained additional axes of divergence. Similar trait loadings have been reported in Ethiopian landraces (Solomon et al. 2019), Balkan germplasm (Nankar et al. 2020; Todorova et al. 2024), and Indian bell peppers (Sood et al. 2024), where stature and phenology consistently emerged as determinants of population structure. The overlapping distribution of varietal groups in PCA space mirrors results from European and South American panels (Bozokalfa et al. 2009; González-Pérez et al. 2014; Taranto et al. 2016), reflecting shared ancestry and adaptation rather than distinct separation. Correlation analysis further clarified inter-trait relationships: plant height and main stem height showed the strongest positive association, confirming their interdependence (Ahmed et al. 2014), while germination was moderately associated with vigor, supporting the link between seed quality and early establishment (Demir and Ellis 1992; Pessoa et al. 2015). In contrast, reproductive traits such as flowering and maturity were largely independent of vegetative growth, consistent with the genetic decoupling of developmental timing reported in peppers and other crops (Helsen et al. 2020; Maple et al. 2024). Weak negative correlations between lobes and vigor or height echo earlier reports on trade-offs in resource allocation (Mediavilla et al. 2001). Together, these findings emphasize the complex yet structured nature of phenotypic diversity in *Capsicum*, underscoring the value of combining univariate and multivariate approaches to guide selection in breeding programs.

Diversity study based on SSR marker lined to *Phytophthora capsici*

The SSR marker set employed in this study demonstrated outstanding polymorphism and allelic diversity across the *Capsicum* germplasm, with an average of 12.83 alleles per locus and PIC values frequently exceeding 0.85. These values surpass those reported

in comparable studies. For instance, Buso et al. (2016) identified a maximum of 11 alleles per locus and a highest PIC of 0.83 across highly informative SSR markers evaluated for cross-species transferability—markers which were already considered superior in their class. Likewise, Minamiyama et al. (2006) reported average allele counts of approximately 2.9 and a mean PIC of 0.46 in a linkage mapping population, underscoring the limited diversity in cultivated lines. Motbaynor et al. (2022), examining Ethiopian landraces, observed modest genetic variation, with average PIC values of 0.52 and allele numbers around 4.2. In contrast, the present dataset revealed loci such as EPMS342 and GPMS117 exhibiting 24 and 21 alleles, respectively, with PIC values up to 0.917, demonstrating not only superior marker performance but also rich underlying genetic variability. Collectively, these comparisons affirm the utility and informativeness of the SSR panel used in this study, making it highly suited for fine-scale diversity studies, population structure inference, and pre-breeding in *Capsicum annum*.

The identification of three genetically distinct clusters among 473 *Capsicum* accessions reflects substantial population structure within the collection. Interestingly, while all three clusters were dominated by *C. annum*, clusters 1 and 2 also included accessions from other species (*C. baccatum*, *C. chacoense*, *C. chinense*, *C. frutescens*, and *C. galapagoense*), suggesting that interspecific gene flow or historical introgression, shared ancestral polymorphism and admixture have contributed to the observed clustering patterns. In particular, the distribution of the three *C. baccatum* accessions across two clusters is likely influenced by these evolutionary processes as well as the limited number of accessions representing this species, rather than strict species-level differentiation. This finding aligns with earlier reports that *Capsicum* species, despite varying levels of reproductive isolation, often exchange genetic material when maintained in genebanks or breeding programs (Buso et al. 2016; Nankar et al. 2020). The presence of non-*annuum* accessions within mixed clusters also supports the idea that taxonomic boundaries based on morphology may not fully reflect underlying genomic relationships (Minamiyama et al. 2006). These observations reinforce the need for molecular data when designing core sets, identifying heterotic groups, or conducting genome-wide association studies (GWAS), particularly in collections that include closely related species or hybrids.

Beyond diversity assessment, the SSR panel employed here included markers previously linked to *P. capsici* resistance. In our unpublished work, ten representative accessions from this germplasm panel were screened under *P. capsici*-inoculated field conditions, which led to the identification of a highly tolerant genotype, UGA-CAPS-374, along with two moderately tolerant lines (UGA-CAPS-392 and UGA-CAPS-255). Marker–trait association analysis further identified 12 SSR markers (SSR3, HpmsE062, HpmsHsMADS, CAMS089, U196349_CAPS, EPMS331, EPMS376, EPMS418, EPMS480, EPMS501, EPMS404 and GPMS112) significantly associated with resistance. This SSR set was intentionally assembled from published *P. capsici* resistance mapping and validation studies; accordingly, several associated loci (e.g., SSR3, HpmsHsMADS, HpmsE062, CAMS089, and U196349_CAPS) are reported to reside within or be closely linked to the major resistance QTL region on chromosome P5, whereas the remaining loci are retained based on demonstrated resistance linkage/utility in prior studies but lack consistent, explicitly reported physical chromosomal assignments across the literature (and some may represent non-nuclear SSRs). Although minor or isolate-specific resistance QTLs have been reported on chromosome P11, the specific SSR loci underlying those regions are not consistently defined in accessible linkage resources and therefore were not individually assigned here. These loci represent promising candidates for validation and potential deployment in marker-assisted selection (MAS) pipelines. UGA-CAPS-374 is a *C. annuum* conical bell-type accession that consistently showed the lowest disease scores across two replicated inoculated field evaluations (10 plants per replication), with only a single plant mortality observed. This stable tolerance and cultivated background make it a particularly valuable donor for breeding programs targeting *P. capsici* resistance. When considered alongside the population structure analysis presented in this study, these preliminary findings highlight the feasibility of integrating SSR-based diversity characterization with phenotypic screening, thereby accelerating the identification of resistance sources and laying the foundation for targeted breeding strategies in *Capsicum*. These insights set the stage for our subsequent work, which will focus on validating these markers across larger populations and diverse environments.

Conclusion

The combined evaluation of quantitative and qualitative traits provided a comprehensive view of morphological diversity in the UGA-Capsi-Core collection, capturing both measurable growth parameters and distinctive fruit descriptors. This integrative characterization enhances the resolution of diversity patterns and underscores the utility of the germplasm for targeted breeding and selection. Our results highlight the remarkable allelic richness and clear population structure within this diverse *Capsicum* panel, revealed through highly informative SSR markers. The identification of three major genetic clusters, together with markers previously associated with *P. capsici* resistance, demonstrates the dual value of these markers for both diversity assessment and resistance breeding. Looking ahead, comprehensive screening of all accessions under *P. capsici* field pressure, combined with robust marker–trait association analysis, will provide critical insights for identifying resistant sources and uncovering novel resistance genes. Such integration of molecular and phenotypic data will not only accelerate the development of *P. capsici*-resistant cultivars but also broaden and strengthen the genetic base of pepper breeding programs worldwide.

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Author contributions DJ designed and conducted the experiments, analyzed the data, and wrote the manuscript. JMG assisted with laboratory experiments. NT supported plant maintenance and DNA isolation. TM provided horticultural guidance and expertise. MA and MT contributed experimental support and provided expertise in plant pathology. DNL provided collaborative input and resources. ANN conceived and designed the study, supervised the project, and critically revised the manuscript. All authors read and approved the final version of the manuscript.

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Data availability All data generated or analyzed in this study are included in this published manuscript and its supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

Generative AI The authors declare that no Generative AI was used in the creation of this manuscript.

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