



Evaluation of *Phaseolus* and *Vigna* species in the Mediterranean climate: a morphological and chemical analysis

Miguel Brilhante¹ · Federico Richter · Maria M. Romeiras² · Pedro Talhinhos¹

Received: 10 July 2024 / Accepted: 5 May 2025 / Published online: 30 June 2025
© The Author(s) 2025

Abstract Understanding the adaptability and nutritional potential of cultivated bean species to specific climates is essential for sustainable agriculture and food security. This study investigates the performance of African bean landraces (including *Phaseolus coccineus*, *Phaseolus lunatus*, *Phaseolus vulgaris*, and *Vigna unguiculata*) in Mediterranean climates through detailed morphological and mineral content analyses. Using internationally defined descriptors, our assessment of morphological characters revealed significant variability among accessions, with production yields indicating acceptable adaptability. For instance, the *Phaseolus* spp. accessions PL12ST and PL17ST, and the *Vigna unguiculata* accessions

VU07BE and VU18MP, exhibited the highest seed production yield and seed size, efficiently converting vegetative growth into reproductive growth. The coefficient of variation (CV) values for morphological traits, which are crucial for selecting and developing cultivars to enhance agronomic performance, ranged significantly. Mineral profile analysis highlighted significant differences among accessions, with PV21SO and VU06MO displaying higher mineral contents. Furthermore, a comparison with sub-Saharan Africa (SSA)-grown accessions revealed that mineral contents were generally higher in SSA-grown samples. Hence, this study offers valuable insights into the adaptability of these crops to the Mediterranean climate, which can enhance productivity through targeted breeding programmes to improve yield potential and nutritional value.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10722-025-02474-0>.

M. Brilhante · F. Richter · M. M. Romeiras (✉) · P. Talhinhos
Linking Landscape, Environment, Agriculture and Food (LEAF), Instituto Superior de Agronomia (ISA), Universidade de Lisboa, Tapada da Ajuda, 1340-017 Lisbon, Portugal
e-mail: mmromeiras@isa.ulisboa.pt

M. Brilhante
e-mail: mbrilhante@isa.ulisboa.pt

F. Richter
e-mail: federico.richter1@gmail.com

P. Talhinhos
e-mail: ptalhinhos@isa.ulisboa.pt

M. M. Romeiras · P. Talhinhos
Associate Laboratory TERRA, Instituto Superior de Agronomia (ISA), Universidade de Lisboa, Tapada da Ajuda, 1340-017 Lisbon, Portugal
e-mail: ptalhinhos@isa.ulisboa.pt

M. M. Romeiras
Centre for Ecology, Evolution and Environmental Changes (CE3C) and Change–Global Change and Sustainability Institute, Faculdade de Ciências, Universidade de Lisboa, 1749-016 Lisbon, Portugal

Keywords Fabaceae · Morphologic traits · Micronutrients · Plant genetic resources · Phenotypic variation · Pulses

Introduction

Fabaceae is one of the largest and most economically important plant families worldwide, boasting 770 genera and over 19,500 recognised species (Azani et al. 2017; Christenhusz and Byng 2016). Second only to Poaceae in economic importance, Fabaceae species are cultivated across a wide range of agro-climate tropical and temperate zones (Yahara et al. 2013; FAO 2016). In Sub-Saharan Africa (SSA), grain legumes (or pulses) play an important role as a source of food for humans, fodder, and as natural nitrogen fixers, improving soil fertility (Odendo et al. 2011; Vidigal et al. 2019). These legumes, both native and introduced, provide not only protein, minerals, vitamins, dietary fibres, and energy but also represent a significant income source for smallholder farmers (Brilhante et al. 2021; Catarino et al. 2021).

The genera *Phaseolus* and *Vigna* stand out among the grain legumes, encompassing the most widely cultivated and consumed species in SSA and worldwide (Rawal and Navarro 2019). The *Phaseolus* genus includes 89 species, primarily native to the Neotropics (Delgado-Salinas et al. 2006). Despite this diversity, only five species have undergone domestication: *P. acutifolius* A.Gray (tepary bean), *P. coccineus* L. (runner bean), *P. ×dumosus* Macfad. (year-long bean), *P. lunatus* (lima bean), and *P. vulgaris* L. (common bean) (Gepts 2001; Bitocchi et al. 2013). *Phaseolus vulgaris*, the most studied and economically significant species of the genus (Guerra-García et al. 2017), is an annual, self-pollinated herbaceous plant characterised by a low crossing frequency (Burle et al. 2010). It was independently domesticated about 8000 years ago in Mexico and South America, originating from two genetically distinct wild gene pools, the Andean and Mesoamerican (Frascarelli et al. 2025). These gene pools differ in seed size, seed shape, growth habits, and stress adaptation (Musango et al. 2016; Lei et al. 2020). Introduced to Europe and subsequently Africa by Portuguese and Spanish traders before the colonial era (Greenway 1945; Wortmann and Allen 1994), *P. vulgaris* became a globally cultivated crop across tropical and temperate zones,

contributing to food and security with its high protein content (21–25%), and significant levels of essential minerals, vitamins, and dietary fibres (Gioia et al. 2019). The species exhibits considerable diversity, with over 40 recognised races and thousands of landraces adapted to local farming systems and marginal environments (Blair et al. 2010). *Phaseolus lunatus*, also an annual herbaceous plant, originates from the region between Mexico and Peru and shares a dual domestication pattern with *P. vulgaris*, encompassing Mesoamerican and Andean gene pools (Gutiérrez Salgado et al. 1995; Bitocchi et al. 2017). Cultivated for both fresh and dry seeds, it is valued for its large seed size, creamy texture, delicate flavour and nutritional composition, containing approximately 25% of protein (Granito et al. 2007; López-Alcocer et al. 2016). Although less distributed than *P. vulgaris*, *P. lunatus* demonstrates resilience to abiotic and biotic stresses and has gained interest for its potential in climate-resilient agriculture (e.g., Soares et al. 2025). It includes landraces adapted to both humid lowlands and temperate zones (Bitocchi et al. 2017) and is cultivated across Latin America, Africa, and the Mediterranean region (Martínez-Nieto et al. 2020). *Phaseolus coccineus* is a perennial climbing plant native from Mexico to Nicaragua (POWO 2024). Unlike the predominantly autogamous (self-pollinated) *P. vulgaris* and *P. lunatus*, *P. coccineus* is primarily allogamous (outcrossing) (Santalla et al. 2004). It tolerates colder climates, preferring wetter climates at higher altitudes (Guerra-García et al. 2017). Originally domesticated in Mexico and Guatemala, it is now also cultivated and consumed in Africa and Europe (e.g., Arriagada et al. 2021; Spataro et al. 2011), with both immature pods and seeds being consumed (e.g., Kimani et al. 2019). Additionally, the species holds ornamental value due to its bright red flowers and climbing habit (Schwember et al. 2017). *P. coccineus* germplasm collections reveal considerable phenotypic plasticity, including adaptation to photoperiod and frost resistance, characters being explored for interspecific hybridisation with *P. vulgaris* to enhance abiotic stress tolerance (Rodino et al. 2007). Less studied but of increasing interest, *P. acutifolius* and *P. ×dumosus* offer important drought and heat tolerance characters, making them relevant for breeding under climate change scenarios (Broughton et al. 2003; Parker and Vallejos 2019).

The genus *Vigna* includes approximately 105 globally recognised species adapted to diverse climates, ranging from rainforests to arid savannas (Mackinder et al. 2001; POWO 2024), with two centres of origin in Asia and Africa (Maxted et al. 2004). Despite its species richness, few species have been domesticated (Tomooka et al. 2014), among which *V. radiata* (L.) Wilczek (mung bean), *V. mungo* (L.) Hepper (urd bean), *V. unguiculata* (L.) Walp. (cowpea), *V. angularis* (Willd.) Ohwi and Ohashi (azuki bean), *V. subterranea* (L.) Verdc. (Bambara groundnut), *V. aconitifolia* (Jacq.) Maréchal (moth bean), and *V. umbellata* (Thunb.) Ohwi and Ohashi (rice bean) (e.g., Harouna et al. 2020) are particularly noteworthy. Among *Vigna* species, *V. unguiculata* (cowpea) is the most widely cultivated and commercialised native African legume (Singh et al. 1997; Timko and Singh 2008). The African origin of cultivated cowpea is supported by its high genetic variability and archaeological evidence of Neolithic domestication (Maréchal 1978). It subsequently spread to other regions, with historical evidence indicating its cultivation by the Greeks and Romans (Tosti and Negri 2005). Adapted to hot and semi-arid environments, cowpea is a self-pollinated species thriving in low rainfall regions (Singh 2020). Its adaptability, coupled with its nutritional values (e.g., 18–35% protein, vitamins, and minerals) and drought resilience, explains its importance in the traditional farming systems in SSA, where 80% of continental production is concentrated in the dry savanna and Sahelian zones (Animasaun et al. 2015). Traditionally, cowpea is integrated into crop rotations to improve soil fertility and serves as both a primary protein source and as fodder (Alemu et al. 2016).

Centuries of *Phaseolus* and *Vigna* cultivation in Africa have led to the development of numerous indigenous landraces with marked phenotypic and genotypic diversity, particularly in flower and seed characteristics. This diversity reflects adaptation to varying farming practices, soil, and climatic conditions, enhancing their resilience to environmental stresses and making them promising candidates for cultivation in Mediterranean climates, where water scarcity and temperature fluctuations challenge to agricultural productivity.

This study aimed to evaluate the agronomic performance and adaptability of 44 accessions of grain legumes (i.e., *Phaseolus coccineus*, *P. lunatus*, *P. vulgaris*, and *Vigna unguiculata*) commonly cultivated

in SSA under Mediterranean climate conditions. Specifically, we aimed to (1) characterise the morphology of the accessions based on internationally established agronomic characters; (2) assess the seed content of 11 minerals; (3) compare results with available data from same accession cultivated in their environment of origin; and (4) provide experimental evidence regarding the adaptability of these important plant genetic resources to Mediterranean climate.

Methodology

Plant material

A total of 44 accessions (Table 1) belonging to two plant genera and collected from different origins (i.e., collected in Angola [21], Cabo Verde [10], Cameroon [1], and Mozambique [12]) between 2018 and 2019 were selected for this study. The material included 26 *Phaseolus* spp. accessions (i.e., 20 *P. vulgaris*, five *P. lunatus*, and one *P. coccineus*) and 18 *Vigna unguiculata* accessions.

Field experiments

The field experiments were conducted between March and October 2021 at the Instituto Superior de Agronomia, Lisboa, Portugal (coordinates: 38.707107, −9.18181; altitude: 60 m). Each accession was sown in a separate 1 m³ pot filled with sandy soil from the Setúbal Peninsula, with 16 replicates of each accession (sowing date: April 08). The meteorological information was gathered daily from the weather station next to the field. The soil water balances were calculated as described by Allen et al. (1998). The plants were irrigated when the soil water content reached a pre-set threshold. This threshold was theoretically determined following the FAO guidelines (Allen et al. 1998) for dry-grain legumes. This set the critical level when the soil water content was less than 45% of the water between the field capacity and the wilting point.

Morphological characterisation

The morphological characterisation was performed throughout the life cycle of each accession according to the internationally recognised descriptors of

Table 1 List of 44 *Phaseolus* and *Vigna* accessions analysed

Accessions	Species	Origin	
		Country	City
PV01CU	<i>Phaseolus vulgaris</i>	Angola	Cunene
PV02CU	<i>Phaseolus vulgaris</i>	Angola	Cunene
PV03CU	<i>Phaseolus vulgaris</i>	Angola	Cunene
PV04CU	<i>Phaseolus vulgaris</i>	Angola	Cunene
PV05HI	<i>Phaseolus vulgaris</i>	Angola	Huíla
PV06MA	<i>Phaseolus vulgaris</i>	Angola	Malange
PV07MA	<i>Phaseolus vulgaris</i>	Angola	Malange
PC08MA	<i>Phaseolus coccineus</i>	Angola	Malange
PV09MA	<i>Phaseolus vulgaris</i>	Angola	Malange
PV10MA	<i>Phaseolus vulgaris</i>	Angola	Malange
PV11ST	<i>Phaseolus vulgaris</i>	Cabo Verde	Santiago
PL12ST	<i>Phaseolus lunatus</i>	Cabo Verde	Santiago
PL13ST	<i>Phaseolus lunatus</i>	Cabo Verde	Santiago
PV14ST	<i>Phaseolus vulgaris</i>	Cabo Verde	Santiago
PL15ST	<i>Phaseolus lunatus</i>	Cabo Verde	Santiago
PL16ST	<i>Phaseolus lunatus</i>	Cabo Verde	Santiago
PL17ST	<i>Phaseolus lunatus</i>	Cabo Verde	Santiago
PV18MP	<i>Phaseolus vulgaris</i>	Mozambique	Maputo
PV19MP	<i>Phaseolus vulgaris</i>	Mozambique	Maputo
PV20SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
PV21SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
PV22SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
PV23SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
PV24SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala

Table 1 (continued)

Accessions	Species	Origin	
		Country	City
PV25SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
PV26SO	<i>Phaseolus vulgaris</i>	Mozambique	Sofala
VU01MA	<i>Vigna unguiculata</i>	Angola	Malange
VU02MA	<i>Vigna unguiculata</i>	Angola	Malange
VU03HI	<i>Vigna unguiculata</i>	Angola	Huíla
VU04NA	<i>Vigna unguiculata</i>	Angola	Namibe
VU05CC	<i>Vigna unguiculata</i>	Angola	Cuando Cubango
VU06MO	<i>Vigna unguiculata</i>	Angola	Moxico
VU07BE	<i>Vigna unguiculata</i>	Angola	Benguela
VU08BI	<i>Vigna unguiculata</i>	Angola	Bié
VU09UI	<i>Vigna unguiculata</i>	Angola	Uíge
VU10CN	<i>Vigna unguiculata</i>	Angola	Cuanza Norte
VU11LU	<i>Vigna unguiculata</i>	Angola	Luanda
VU12ST	<i>Vigna unguiculata</i>	Cabo Verde	Santiago
VU13ST	<i>Vigna unguiculata</i>	Cabo Verde	Santiago
VU14ST	<i>Vigna unguiculata</i>	Cabo Verde	Santiago
VU15CA	<i>Vigna unguiculata</i>	Cameroon	Unknown
VU16MP	<i>Vigna unguiculata</i>	Mozambique	Maputo
VU17SO	<i>Vigna unguiculata</i>	Mozambique	Sofala
VU18MP	<i>Vigna unguiculata</i>	Mozambique	Maputo

Phaseolus vulgaris (IPGRI 2001) and *Vigna unguiculata* (Bioversity International 2007). For 23 *Phaseolus* spp. accessions (Table 2), 24 quantitative and 31 qualitative characters were evaluated; for 15 *Vigna unguiculata* accessions (Table 3), 23 quantitative and 24 qualitative characters were assessed. Each morphological character was recorded as the mean value

Table 2 List of quantitative and qualitative morphological characters assessed for *Phaseolus* spp. and respective unit of measurement and coding key

Characters	Acronym	Unit of measurement/coding key
<i>Quantitative</i>		
Leaflet length	LL	mm
Hypocotyl length	HL	mm
Days to maturity	DTM	count
Plant height	PH	cm
Stem diameter	SD	mm
Node no. at main stem	NNMS	count
Node no. at harvest	NNH	count
Days to flowering	DTF	count
Flower buds per inflorescence	FBPI	count
Racemes per plant	RPP	count
Inflorescence length	IL	mm
Pedicle length	PEL	mm
Duration of flowering	DOF	days
Pod length	POL	mm
Pod width	PW	mm
Locules per pod	LPP	count
Pod beak length	PBL	mm
Pods per plant	PPP	count
Total no. of harvested seeds	TNHS	count
Total seed weight	WTHS	g
Ten seeds weight	WTS	g
Seed length	SL	mm
Seed height	SH	mm
Seed width	SW	mm
<i>Qualitative</i>		
Plant type	PT	1–6 (determinate bush to indeterminate, aggressive climber)
Hypocotyl pigmentation	HP	(1) purple, (2) green
Emerging cotyledon colour	ECC	1–5 (purple to very pale green)
Leaf colour anthocyanin	LCA	(0) absent, (1) present
Leaf colour chlorophyll	LCC	(3) pale, (5) medium, (7) dark
Leaf shape	LS	(1) triangular, (2) quadrangular, (3) round
Leaf persistence	LP	(3) dropped, (5) intermediate, (7) persistent
Flower bud size	FBS	(3) small, (5) medium, (7) large
Bracteole shape	SHOB	(3) lanceolate, (5) intermediate, (7) ovate
Bracteole size	SOB	(3) small, (5) medium, (7) large
Bracteole/Calyx length	BCLR	(3) $\leq$ calyx, (5) 1/3 longer, (7) 2 $\times$ calyx
Calyx/Bracteole colour	BCC	(1) green, (2) pale violet, (3) dark purple
Wing opening	WO	(3) closed, (5) moderately diverging, (7) widely diverging
Style protrusion	SP	(0) not protruding, (1) protruding
Pod position	POP	1–4 (base to top or mixed)
Pod cross-section	PCS	1–4 (very flat to figure-8)
Pod curvature	PC	(3) straight, (5) slightly curved, (7) curved, (9) recurving
Pod wall fibre	PWF	(3) contracting, (5) leathery, (7) shattering
Pod beak position	PBP	(1) marginal, (2) non-marginal

Table 2 (continued)

Characters	Acronym	Unit of measurement/coding key
Pod beak orientation	PBO	(3) upward, (5) straight, (7) downward
Standard colour	COS	1–9 (white to purple)
Wing colour	COW	1–9 (white to purple)
Immature pod colour	PCI	1–11 (dark purple to pale yellow to white)
Mature pod colour	PCAPM	1–6 (dark purple to green)
Dry pod colour	DPC	same as PCI
Seed coat patterns	SCP	0–10 (absent to hilum-specific)
Seed coat darker colour	SCDC	1–14 (black to purple)
Seed coat lighter colour	SCLC	same as SCDC
Seed brilliance	BOS	(3) matt, (5) medium, (7) shiny
Seed shape	SDSH	(1) (round to truncate fastigiate)
Apparent seed veining	ASV	(0) absent, (1) present

of ten replicates per accession, following the method described by Talhinhos et al. (2006).

Mineral composition

The mineral contents of the seeds of 18 *Phaseolus* spp. and 10 *Vigna* accessions were determined using inductively coupled plasma optical emission spectrometry (ICP-OES) and included Na, K, Ca, Mg, P, S, Fe, Cu, Zn, Mn, and B. Using a stainless-steel grinder (Kunft coffee mill), the seeds were processed into a powder. A portion of 0.3 g from each sample was weighed (wet weight) and dried in an oven at 105 °C for 24 h and placed in a desiccator with silica gel spheres. After drying, the seeds were weighed again to obtain the dry weight and, consequently, the moisture content. The dried samples were digested in digestion tubes for 90 min at 105 °C using a solution of nitric acid and hydrochloric acid (1:3, v/v). After 24 h was added 1 mL of hydrogen peroxide was added, and the tubes were placed in a digester with a heating cycle to 95 °C that lasted 1 h and remained at 95 °C for another hour. After removal from the digester, the samples were cooled and transferred to a 25 mL volumetric flask, and the volume was adjusted with distilled water. The quantification of minerals was made by ICP-AES (Inductively coupled plasma atomic emission spectroscopy, Thermo Scientific iCAP 7200, Cambridge, UK). Appropriate standards were prepared from a stock solution (100 mg/L) containing the analysed elements (SCP Science, PlasmaQual S22). The concentration of each mineral

was determined using calibration curves at five distinct concentrations. All the measurements were carried out in triplicate, and the results were obtained in mg/L and converted into mg per kg of wet weight (ww) according to the following expression:

$$\text{mg/kgww} = L \times \frac{50}{P}$$

where L is the obtained value in mg/L and P is the sample wet weight in g; 50 mL is the total volume of the analysed solution.

The mineral contents of the *Phaseolus* spp. and *Vigna unguiculata* accessions grown in a Mediterranean climate were compared with those obtained for the same accessions grown in their environment of origin. For this purpose, data from 26 accessions (i.e., 16 *Phaseolus vulgaris* and 10 *Vigna unguiculata*) grown in Africa were retrieved from Catarino et al. (2021).

Data analysis

The data were processed and analysed using the R programme version 4.2.3 (R Core Team 2023). All morphological and mineral content data are presented as mean values. Descriptive statistics were calculated for each accession, morphological quantitative character and mineral content. The normality and homogeneity of variances were examined through Shapiro-Wilks (*shapiro.test* function) and Bartlett (*bartlett.test* function) tests, respectively. The data for both morphological characters and mineral content did not

Table 3 List of quantitative and qualitative morphological characters assessed for *Vigna unguiculata* and respective unit of measurement

Characters	Acronym	Units
<i>Quantitative</i>		
Terminal leaflet length	TLL	cm
Terminal leaflet width	TLW	cm
Stipule length	SL	mm
Stipule width	SW	mm
No. of main branches	NMB	count
No. of nodes in the main stem	NNMS	count
Days to flowering	DTF	count
Days to 1st mature pod	DTFMP	count
Pod length	PL	cm
No. of locules per pod	NLPP	count
Duration of flowering	DOF	count
Standart length	STL	mm
Calyx lobe length	CLL	mm
Peduncle length	PDL	mm
No. of pods per peduncle	NPPP	count
No. of pods per plant	NPPPL	count
Pod width	PW	mm
No.of seeds per pod	NSPP	count
No. of total harvested seeds	NTHS	count
Ten seeds weight	WHS	g
Seed length	SLE	mm
Seed width	SWI	mm
Seed thickness	ST	mm
<i>Qualitative</i>		
Plant pigmentation	PP	0–9 (none to solid)
Terminal leaflet shape	TLS	1–4 (globose to hastate)
Plant hairiness	PH	(3) glabrescent, (5) appressed hairs, (7) pubescent to hirsute
Leaf colour	LC	(3) pale, (5) intermediate, (7) dark green
Leaf texture	LT	1–3 (coriaceous to membranous)
Growth habit	GH	1–7 (erect to climbing)
Growth pattern	GP	(1) determinate, (2) indeterminate
Twinning tendency	TWT	(0) none, (3) slight, (5) intermediate, (7) pronounced
Plant vigour	PV	(3) non-vigorous, (5) intermediate, (7) vigorous
Raceme position	RP	1–3 (above to throughout canopy)
Pod attachment to peduncle	PATP	(3) pendant, (5) 30–90°, (7) erect
Immature pod pigmentation	IPP	0–5 (none to uniformly pigmented)
Pod curvature	PC	(0) straight, (3) slightly curved, (5) curved, (7) coiled
Flowering pigment pattern	FPP	0–5 (not pigmented to completely pigmented)
Flower colour	FC	1–3 (white to mauve-pink)
Pod wall thickness	PWT	(3) thin, (5) intermediate, (7) thick
Seed shape	SSH	1–5 (kidney to rhomboid)
Testa texture	TT	(1) smooth, (3) smooth to rough, (5) rough
Eye pattern	EP	0–9 (absent to full coverage)
Eye colour	EC	0–9 (white to mottled)

Table 3 (continued)

Characters	Acronym	Units
Seed crowding	SC	0–7 (not to extremely crowded)
Leaf marking	LM	(0) absent, (1) present
Splitting of testa	SOT	(0) absent, (1) present
Attachment of testa	AOT	(0) not firm, (1) firm

follow a normal distribution, and the variance was not homogeneous.

Regarding the multivariate analyses with morphological data, firstly, due to the presence of missing values, all accessions and characters with more than 30% missing values were removed. The remaining missing values were then replaced using average imputation with the *naMeanSubst* function from the *MorphoTools2* package (Šlenker et al. 2022). The multivariate analysis was carried out for 19 accessions of *Phaseolus* spp. and 9 accessions of *Vigna unguiculata*, respectively. The characters for multivariate analysis were selected based on the Spearman correlation coefficients (*rcorr* function of Hmisc package; Harrell 2024). Variables with correlation coefficients greater than 0.80 were considered redundant, and one of them was removed. The normalised transformation of the morphological data (mean=0 and standard deviation=1) was carried out before performing the multivariate analysis. The cluster analysis was carried out based on the agglomerative hierarchical method using Euclidean distances and the ward.D method (*hclust* function) to produce a dendrogram. To choose the optimum number of clusters, the *silhouette* function of the *cluster* package was used (Maechler et al. 2023). Moreover, a principal component analysis (PCA) was performed (*prcomp* function), and the eigenvectors and eigenvalues were projected with the *ggplot* function of the *ggplot2* package (Wickham 2016).

The mineral contents across the accessions were compared using a univariate analysis method. The Kruskal–Wallis test at 5% significance was used to perform the test of means because the mineral content data did not follow a normal distribution and the variance was not homogeneous (*kruskal.test* function). As for morphological data, a multivariate analysis was done for mineral content data after standardisation (mean=0 and standard deviation=1). Firstly, based on Euclidean distances and the average method, a

cluster analysis through a heatmap (the *Heatmap* function of the *ComplexHeatmap* package; Gu et al. 2016) was performed to detect patterns of variation across accessions and minerals. Secondly, a principal component analysis (PCA) was performed as described above. Spearman correlations were carried out to ascertain the relationships between mineral content and quantitative morphological characters for *Phaseolus* spp. and *Vigna unguiculata* accessions. Comparisons between the mineral contents of the accessions grown in the Mediterranean and those grown in their environment of origin at SSA were made using the Kruskal–Wallis test at a 5% significance level; the results were presented in boxplot form to understand the variation in mineral contents between samples.

Results

Morphological characterisation

Phaseolus genus

A total of 26 *Phaseolus* spp. accessions were sown in this trial; however, two accessions (PV22SO and PV26SO) did not germinate, and one (PV19MP) did not yield morphological data. Three *Phaseolus lunatus* accessions from Cabo Verde (PL13ST, PL15ST, and PL16ST) germinated in April. They initially had stunted growth until the summer solstice, but then began to grow vigorously as the days became shorter, until flowering. Morphological analyses were performed on the remaining 23 accessions (Table S1). Descriptive statistics for 24 quantitative characters are summarised in Table 4, revealing substantial variability among accessions. Among the characters with higher variability, the following stood out (CV > 100%): Plant height (PH) varied greatly, from 15 cm (PV20SO) to 200 cm (PL17ST), with *P.*

Table 4 Descriptive statistics for quantitative morphological characters of 23 *Phaseolus* spp. accessions

Character ¹	N ²	Average ³	Std. Dev. ⁴	Minimum	Maximum	CV (%) ⁵
LL	21	73.6	10.5	50.0	88.5	14.3
HL	13	1.9	0.5	0.6	2.5	26.7
DTM	13	74.9	5.2	68.0	83.0	7.0
PH	22	39.8	43.2	15.0	200.0	108.5
SD	22	5.6	1.7	3.5	10.0	30.6
NNMS	19	4.6	3.3	2.0	18.0	72.7
NNH	21	5.0	3.8	2.0	20.0	75.7
DTF	21	51.5	56.2	20.0	210.0	109.1
FBPI	20	4.9	4.7	2.0	20.0	96.6
RPP	21	8.2	5.6	4.0	30.0	67.4
IL	19	54.7	48.9	25.0	200.0	89.3
PEL	19	14.9	27.3	4.0	130.0	183.4
DOF	17	32.5	16.3	8.0	69.0	50.2
POL	21	104.1	17.2	67.3	130.0	16.5
PW	21	16.7	13.6	8.0	58.0	81.5
LPP	20	4.3	1.0	2.5	6.0	22.3
PBL	21	12.2	5.1	3.0	20.0	41.6
PPP	18	12.4	26.2	2.0	120.0	211.8
TNHS	17	142.3	80.7	34.0	348.0	56.7
WTHS	17	43.4	29.4	9.5	127.1	67.8
WTS	18	3.1	0.9	1.7	5.4	30
SL	18	13.5	1.7	10.5	16.1	12.7
SH	18	7.3	1.2	6.2	11.4	16.7
SW	18	5.1	0.6	3.7	5.9	12.0

¹The full name and respective description of qualitative morphological characters for *Phaseolus* spp. are presented in Supplementary Table S2

²N, number of observations

³When considering the accessions or species, no significant differences were detected between the average values of the morphological characters according to the Kruskal–Wallis test at a 5% confidence level

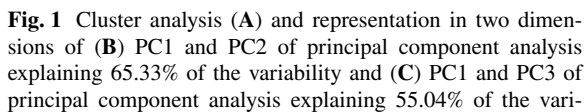
⁴Std. Dev., Standard Deviation

⁵CV (%), coefficient of variation

lunatus accessions (e.g., PL12ST, PL17ST) standing out for their vigorous growth and greater biomass. Days to flowering (DTF) varied from 20 days (PV24SO, PV25SO) to 210 days (PL13ST, PL15ST), suggesting a broad range of phenological behaviours. Pods per plant (PPP) ranged from 2 (PV18MP) to 120 (PL17ST).

Spearman's correlation analysis ($p \leq 0.05$; Table S2) highlighted several significant positive correlations among morphological characters. PH correlated positively with stem diameter (SD; 0.47), node number at the main stem (NNMS; 0.53), node number at harvest (NNH; 0.56), racemes per plant (RPP; 0.65), and seed-related characters, namely total number of harvested seeds (TNHS; 0.64) and weight of total harvested seeds (WTHS; 0.57), indicating a strong relationship between vegetative growth and reproductive yield. Similar trends were observed for SD and pod width (PW; 0.70) and between RPP and duration of flowering (DOF; 0.56).

Cluster analysis using Euclidean distances (cophenetic correlation of 0.94) separated the accessions into two main clusters (Fig. 1A). Cluster I grouped accessions characterised by longer leaflets, thicker stems, longer flowering times, longer pods and pod beaks, a higher number of locules per pod, and broader seeds. Cluster II consisted of *P. lunatus* accessions (PL12ST and PL17ST) distinguished by taller plants with more racemes per plant, nodes at the main stem and harvest, longer inflorescences and pedicels, more flower buds per inflorescence, longer times to flowering, more and wider pods, and heavier seeds. Principal component analysis (PCA) confirmed the clustering (Fig. 1B and C), with the first three components explaining 77.95% of the total variations. PC1 (42.42%) was mainly influenced by architectural characters (e.g., stem diameter, number of nodes, inflorescence length and pedicel length), PC2 (22.91%) by pod traits, and PC3 (12.62%) by flowering and seed characters.



ability of the 19 *Phaseolus* spp. accessions according to 19 morphological characters in a space defined by the vectors and their values

Eighteen *Vigna unguiculata* accessions were sown in this trial, of which three did not germinate (VU10CN, VU13ST, and VU15CA). All accessions started growing vigorously at the beginning of summer, and most of the plants started flowering later than the *Phaseolus* spp. accessions, typically after July. Morphological analyses were performed on the remaining 15 accessions (Table S4). Descriptive statistics for 23 quantitative characters are provided in Table 5, displaying varied levels of phenotypic diversity. Among the characters with higher variability, the following stood out (CV > 50%): clayx lobe length (CLL) varied from 3.0 mm (VU06MO and VU18MP) to 18.0 mm (VU16MP), the number of pods per plant (NPPPL) ranged from 4 (VU12ST) to 25 (VU04NA), and the total number of harvested seeds (NTHS) from 49 (VU16MP) to 1126 (VU04NA). Spearman's correlation analysis ($p \leq 0.05$; Table S5) revealed significant

Table 5 Descriptive statistics for quantitative morphological characters of 15 *Vigna unguiculata* accessions

Character ¹	N ²	Average ³	Std. Dev. ⁴	Minimum	Maximum	CV (%) ⁵
TLL	15	8.1	1.0	6.2	9.9	12.2
TLW	15	4.6	1.0	3.1	6.0	20.6
SL	15	10.9	1.5	7.0	14.0	14.2
SW	15	4.3	1.0	3.0	7.0	23.3
NMB	15	3.2	0.9	2.0	5.0	28.4
NNMS	15	7.6	1.6	5.0	11.0	20.8
DTF	8	75.3	10.9	64.0	102.0	14.5
DTFMP	7	96.4	8.0	77.0	101.0	8.3
PL	8	17.4	1.2	15.8	20.0	7.1
NLPP	8	15.5	1.4	12.0	17.0	9.1
DOF	6	7.0	1.6	5.0	10.0	23.3
STL	6	19.0	3.3	15.0	24.0	17.2
CLL	5	6.6	5.8	3.0	18.0	87.1
PDL	6	14.0	2.3	11.0	17.0	16.5
NPPP	7	2.1	0.4	2.0	3.0	16.3
NPPPL	3	14.0	7.8	4.0	23.0	55.6
PW	8	10.4	1.4	8.0	12.0	13.6
NSPP	9	12.5	3.6	6.7	16.3	28.3
NTHS	9	475.0	329.3	49.0	1126.0	69.3
WHS	10	1.5	0.4	0.9	2.0	24.5
SLE	10	8.4	0.8	6.9	9.9	9.6
SWI	10	6.7	0.7	5.7	8.0	11.0
ST	10	4.8	0.5	4.1	6.0	10.4

¹The full name and respective description of qualitative morphological characters for *Vigna unguiculata* are presented in Supplementary Table S3

²N, number of observations

³When considering the accessions, no significant differences were detected between the average values of the morphological characters according to the Kruskal–Wallis test at a 5% confidence level

⁴Std. Dev., Standard Deviation

⁵CV (%), coefficient of variation

relationships among morphological characters. Pod width (PW) was positively correlated with pod length (PL; 0.71); NTHS with number of seeds per pod (NSPP; 0.80); seed width (SWI) with terminal leaflet width (TLW; 0.72), weight of ten harvested seeds (WHS; 0.67), and seed length (SLE; 0.88).

Cluster analysis based on Euclidean distances grouped the accessions into two main clusters (cophenetic correlation=0.54) (Fig. 2A). Cluster I comprised three accessions associated with larger leaf sizes, longer pod development periods, and higher pod dimensions. Cluster II included accessions with higher reproductive outputs, presented by the higher number of nodes, pods and seeds. PCA supported the cluster analysis (Fig. 2A and B), with the first three components explaining 65.59% of the total variation. The biplots of PC1 vs. PC2 and PC1 vs. PC3 showed clear separation between clusters, accounting for 50.74% and 42.24% of the total variation, respectively. PC1 (27.39%) was mainly influenced by pod and seed traits, PC2 (23.35%) by leaf dimensions and flowering characters, and PC3 (14.85%) by

architectural characters like the number of branches and nodes.

Qualitative character analysis (Table S6) further highlighted the diversity among *Vigna unguiculata* accessions. Most accessions displayed moderate to intermediate plant pigmentation (PP), glabrescent plant hairiness (PH), intermediate green leaf colour (LC) and leaf texture (LT), and no leaf marking (LM). The predominant terminal leaflet shape (TLS) was sub-hastate, and growth habit (GH) ranged from erect to intermediate, with an even distribution between determinate and indeterminate growth patterns (GP). Most accessions showed no twining tendency (TWT) and were non-vigorous in plant vigour (PV), while raceme position (RP) was mostly located in the upper canopy. Immature pod pigmentation (IPP) showed variations, with green sutures on pigmented valves, absence of pigmentation, and specific pigmented patterns in a few genotypes. Pod curvature (PC) was mostly slightly curved, with a few straight and fully curved pods. Flower pigmentation (FPP) was primarily completely pigmented, with violet (FC)

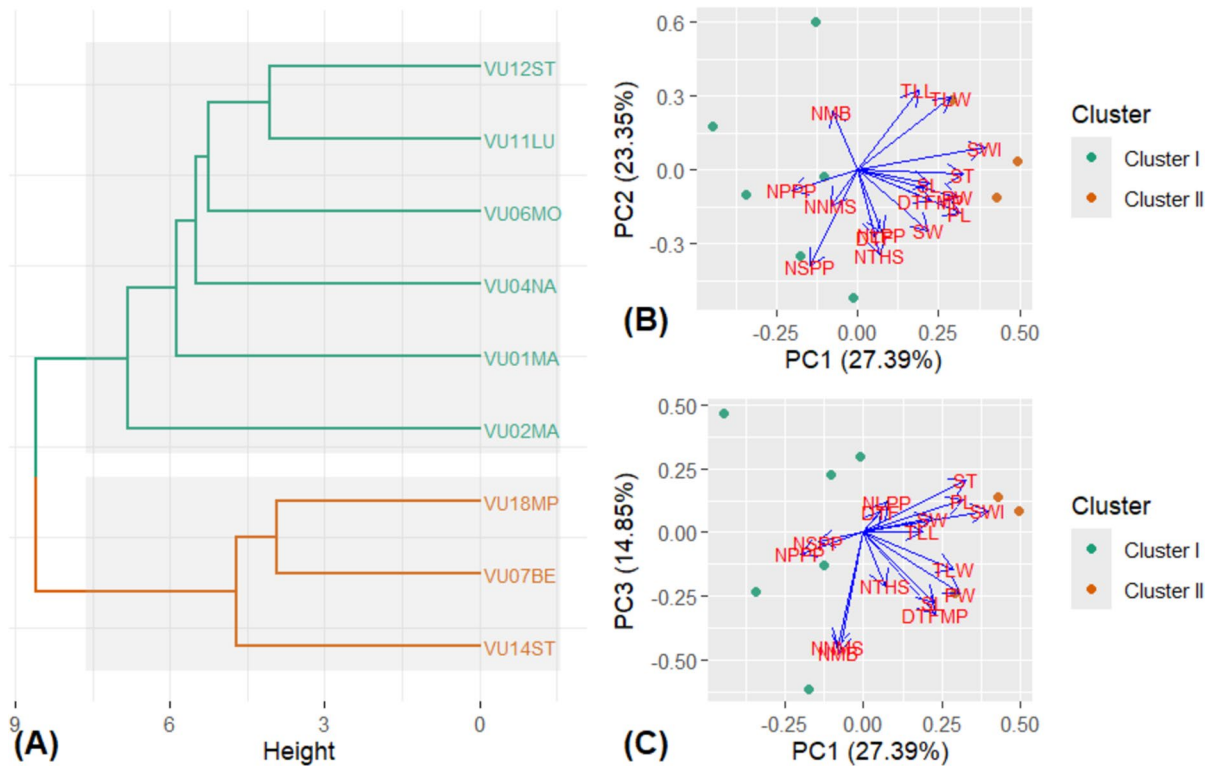


Fig. 2 Cluster analysis (A) and representation in two dimensions of (B) PC1 and PC2 of principal component analysis explaining 50.74% of the variability and (C) PC1 and PC3 of principal component analysis explaining 42.24% of the vari-

ability of the nine *Vigna unguiculata* accessions according to morphological characters in a space defined by the vectors and own values

flowers being the most common, followed by white and mauve-pink. Pod wall thickness (PWT) was mostly intermediate, and seed shapes were predominantly ovoid (SSH), with smooth testa texture (TT) and narrow or Watson eye patterns (EP). Eye colours (EC) were typically brown or tan brown, with occasional blue-black mottles or absent eyes. Seeds were mainly semi-crowded (SC), and the testa was either firmly or loosely attached (AOT), with no splitting of the testa (SOT) observed.

Mineral profiles

The mineral profile was analysed in 28 samples of *Phaseolus vulgaris* (16), *P. lunatus* (one), *P. coccineus* (one), and *Vigna unguiculata* (10), covering 11 essential minerals: sodium (Na), potassium (K), calcium (Ca), magnesium (Mg), phosphorus (P), sulphur (S), iron (Fe), copper (Cu), zinc (Zn), manganese (Mn), and boron (B) (Table S7). Overall, the

genus *Phaseolus* exhibited higher K, Ca, P, S, Fe, and Cu levels, while *Vigna unguiculata* was richer in Na, Mg, Zn, Mn, and B. Among species (Table 6), *P. coccineus* had the highest Ca and K contents. *P. lunatus* was richest in Mn and Fe, and *P. vulgaris* in Cu, P, and S. Conversely, *V. unguiculata* displayed the highest B, Mg, Na, and Zn contents. Mineral variability was generally higher in the accession of *Phaseolus* than *Vigna*, except for B, Mn, Na, and Zn, where *Vigna* showed slightly higher standard deviations (Table S7). Among the accessions, the following results are worth mentioning: *Phaseolus vulgaris* PV09MA exhibited the highest K content (16,092.0 mg/kg ww), while PV24SO had the greatest Ca content (2093.8 mg/kg ww). PV07MA showed the highest Mg level (1932.9 mg/kg ww), and PV11ST stood out for both P (5516.6 mg/kg ww) and Zn (42.8 mg/kg ww) contents. PV10MA had the highest S level (3147.9 mg/kg ww), and PV21SO exhibited the highest Fe concentration (239.9 mg/kg ww).

Table 6 Average values (in mg/kg ww), standard deviations, and homogeneous groups for mineral content according to the four species under study

Minerals	<i>Phaseolus coccineus</i>	<i>Phaseolus lunatus</i>	<i>Phaseolus vulgaris</i>	<i>Vigna unguiculata</i>
Na	14.1 ± 3.7 bc	8.9 ± 2.8 c	17.3 ± 6.6 b	61.7 ± 18.2 a
K	14,882.0 ± 173.6 a	14,313.8 ± 182.3 a	14,633.4 ± 975.2 a	13,135.1 ± 657.2 b
Ca	2082.7 ± 36.5 a	664.5 ± 14.3 c	1646.9 ± 349.9 b	750.6 ± 68.3 c
Mg	1603.4 ± 23.4 ab	1476.2 ± 19.3 b	1603.6 ± 176.9 b	1701.2 ± 111.3 a
P	4457.0 ± 37.4 a	2977.3 ± 23.8 c	4823.2 ± 439.7 a	3929.3 ± 395.5 b
S	2565.2 ± 48.9 ab	2077.5 ± 7.7 b	2749.2 ± 304.8 a	2515.2 ± 188.7 b
Fe	90.8 ± 0.4 bc	154.6 ± 0.9 a	129.8 ± 42.3 ab	88.1 ± 33.9 c
Cu	8.4 ± 0.2 b	6.9 ± 0.1 c	10.1 ± 0.9 a	7.4 ± 0.7 bc
Zn	29.8 ± 0.1 c	35.0 ± 0.3 bc	36.2 ± 3.8 b	42.3 ± 5.0 a
Mn	10.5 ± 0.1 b	15.6 ± 0.1 a	10.7 ± 1.1 b	13.8 ± 1.8 a
B	9.6 ± 0.1 c	12.1 ± 0.1 b	9.6 ± 0.7 c	15.4 ± 2.2 a

Homogeneous groups: accessions sharing one or more letters for each mineral are not statistically different according to the Kruskal–Wallis test ($p < 0.05$)

Mn was most abundant in PL17ST (15.6 mg/kg ww). In *Vigna unguiculata*, VU04NA had the highest Na content (88.1 mg/kg ww), while PV18MP recorded the highest K value (14,132.0 mg/kg ww). VU06MO stood out for its elevated Mg (1963.8 mg/kg ww), P (4590.1 mg/kg ww), and Zn (48.8 mg/kg ww) concentrations. The highest Mn content was recorded in VU16MP (15.6 mg/kg ww), and B was most abundant in VU11LU (19.6 mg/kg ww) (Table S7).

A heatmap combined with hierarchical clustering (Fig. 3) distinguished two main groups. Cluster 1, composed of all *Vigna unguiculata* accessions and one *Phaseolus lunatus* accession, was defined by cluster B, which displayed the highest levels of B, Mg, Mn, Na, and Zn. Cluster 2, grouped all *Phaseolus vulgaris* accessions and one *Phaseolus coccineus* accession, was defined by cluster A, which has the highest levels of Ca, Cu, Fe, K, P, and S. The heatmap presented reveals a clear distinction between the two bean genera, excepting *Phaseolus lunatus*, which presents a mineral profile closer to *Vigna unguiculata*. PCA (Fig. 4) further supported this separation. The biplots of PC1 vs. PC2 (Fig. 4A) and PC1 vs. PC3 (Fig. 4B) showed a clear separation of two clusters of accessions representing the genera *Phaseolus* and *Vigna* and accounting for 70.95% and 59.21% of the total variation, respectively. PC1, accounting for 50.06% of the variability, was mainly influenced by B, Ca, Cu, K and Na. PC2 (20.89%) was mainly influenced by Mg, P, and S and PC3 (9.15%) by Mn and Fe. Altogether, the first three axes of the PCA accounted for 80.11% of the total variability.

Spearman's correlation analysis between quantitative morphological characters and mineral contents

(Fig. 5) revealed significant positive and negative correlations ($p \leq 0.05$) in both *Phaseolus* spp. and *Vigna unguiculata*. For instance, in *Phaseolus* spp., Na correlated negatively with PH (−0.62) and TNHS (−0.81) and positively with SL (0.55). Ca was positively associated with vegetative characters such as PH (0.77) and NNMS (0.51), while Mg and Zn showed strong negative correlations with seed dimensions, i.e., SH (−0.83, −0.71). In *Vigna unguiculata*, K was strongly positively correlated with TLW (0.96) and seed characters, i.e., SLE (0.67) and SWI (0.80), while Na showed positive correlations with NNMS (0.69). Cu, Mn, and Zn were negatively associated with developmental timing characters (e.g., days to flowering) in both genera.

Comparisons between Mediterranean- and sub-Saharan Africa (SSA)-grown accessions revealed significant mineral differences (Fig. 6 and Table S8). Mediterranean-grown *Phaseolus vulgaris* accessions had higher average B, Ca, Cu, Fe, K, P, S, and Zn contents, while the SSA accessions were richer in Mg, Mn, and Na (Fig. 6A). Mediterranean-grown *Vigna unguiculata* accessions presented average higher B, Cu, Fe, K, S, and Zn contents, while the SSA accessions were higher in Ca, Mg, Mn, Na, and P (Fig. 6B). However, at the individual accession level, exceptions were detected. For instance, the SSA-grown *Phaseolus vulgaris* accessions showed higher mineral contents, except for Na. Also, some Mediterranean-grown *P. vulgaris* accessions had lower Ca or Mg contents compared to SSA accessions (Table S6). The SSA-grown *Vigna unguiculata*

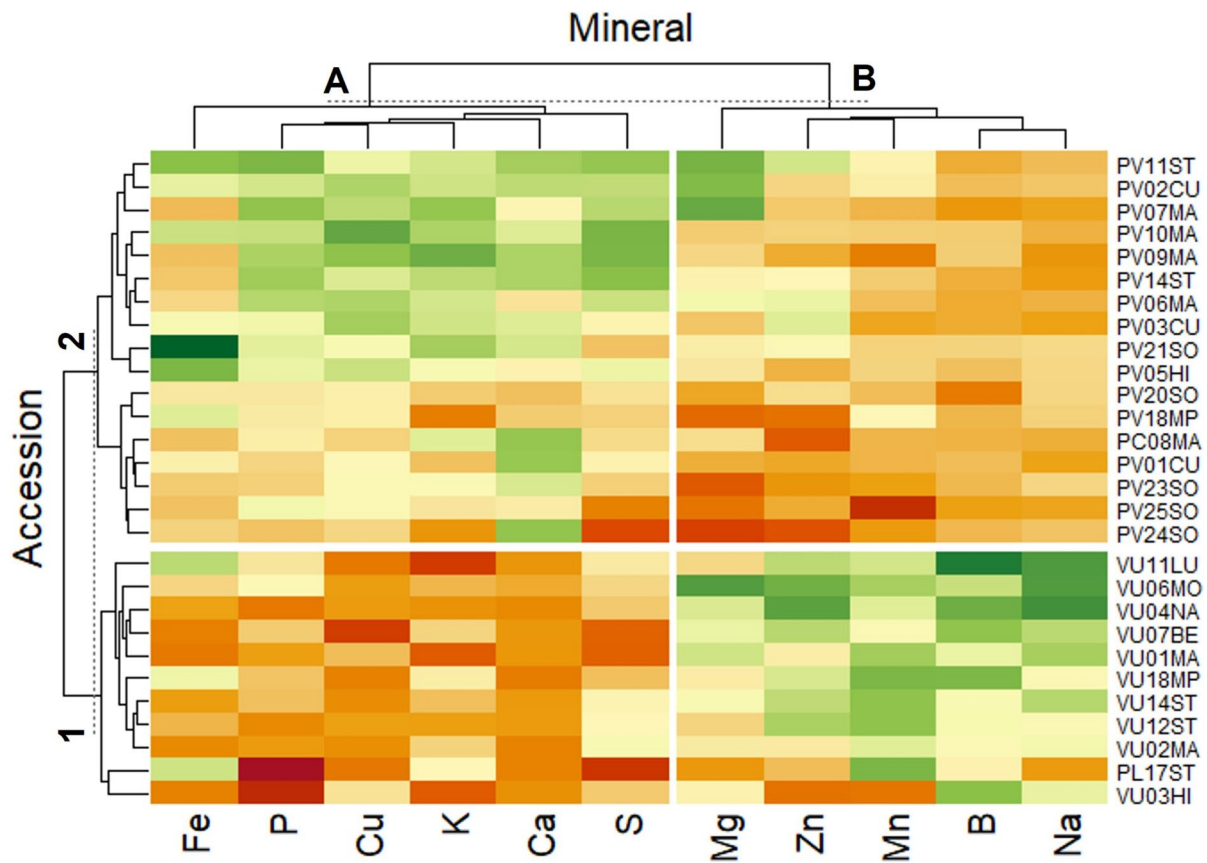
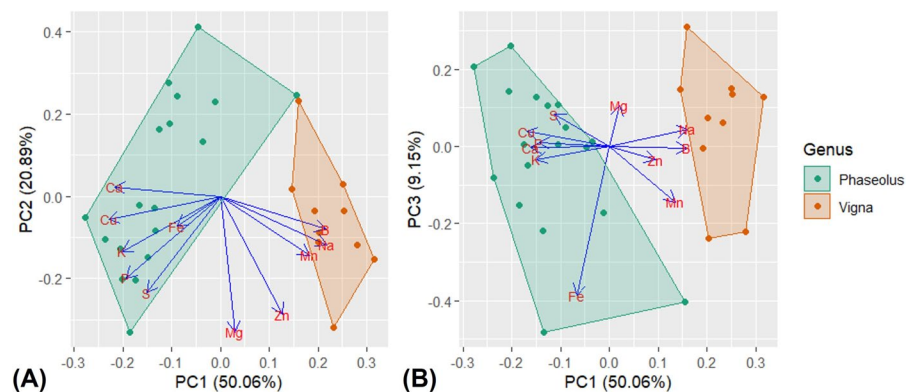


Fig. 3 Heatmap of the 28 bean accessions obtained from the contents of 11 mineral constituents. Brown to pale yellow and green boxes indicate high to low values, respectively

Fig. 4 Representation in two dimensions of **A** PC1 and PC2 of principal component analysis explaining 70.95% of the variability and **B** PC1 and PC3 of principal component analysis explaining 59.21% of the variability of the 28 bean accessions in a space defined by the vectors and their values



accessions showed higher mineral contents, except for K, Zn, and Mn. Also, some Mediterranean-grown

V. unguiculata accessions had lower Ca, P, Fe, Cu or B contents compared to SSA accessions (Table S8).

Fig. 5 Spearman correlation between quantitative morphological characters and mineral contents for **A** *Phaseolus* spp. and **B** *Vigna unguiculata*. Red and blue boxes indicate negative and positive correlation coefficients, respectively. Empty coloured boxes present significant correlations ($p \leq 0.05$) while the non-significant correlations are marked by “X”

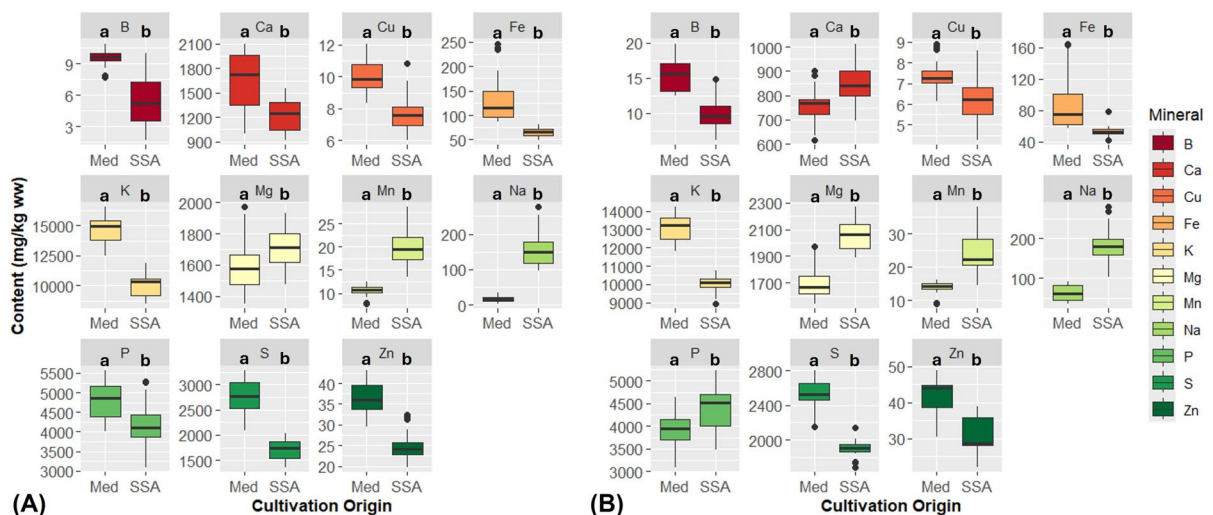
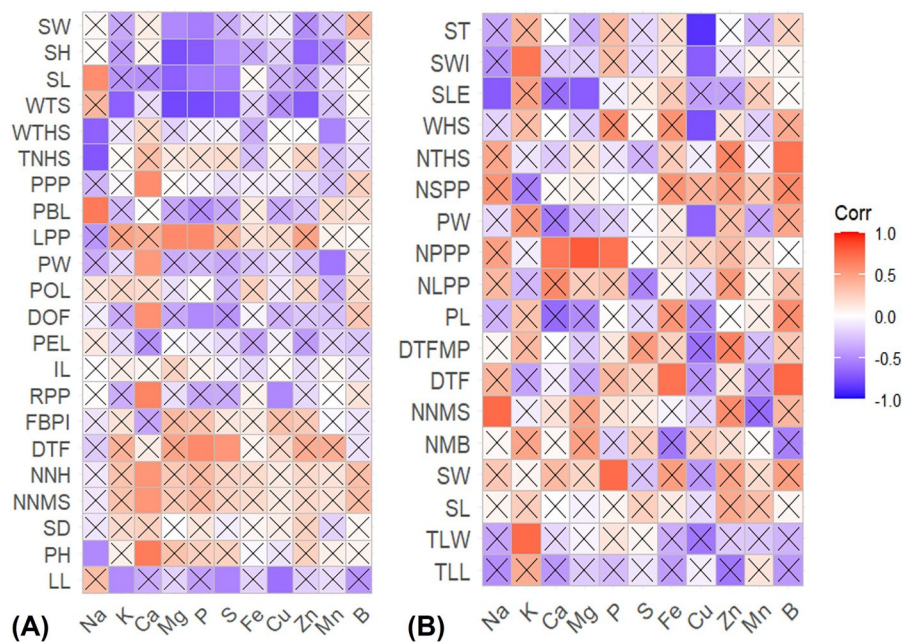


Fig. 6 Variation of 11 mineral contents (mg/kg ww) in **A** *Phaseolus vulgaris* and **B** *Vigna unguiculata* according to the cultivation origin (i.e., Mediterranean and Sub-Saharan Africa). The box represents the 25th, 50th (median), and 75th percentiles, while the whiskers represent the 10th and 90th percentiles with minimum and maximum observations. The dots represent the outliers. Cultivation origins sharing the same letters present no significant differences based on the Kruskal–Wallis test at 5% of confidence

Discussion

Morphological characterisation

The *Phaseolus* spp. and *Vigna unguiculata* accessions exhibited significant morphological variability,

reflecting a broad genetic diversity and potential for adaptation to Mediterranean climate conditions. This variability has practical implications, as it supports their potential for breeding programs targeting improved resilience and productivity under Mediterranean and similar climates. Previous research

also described a great diversity among *Phaseolus* (e.g., Arteaga et al. 2019; Jan et al. 2021; Delfini et al. 2021) and *Vigna* (e.g., Mafakheri et al. 2017; Menssen et al. 2017; Catarino et al. 2021) morphological characters both in Africa and Europe.

The studied accessions showed acceptable adaptability, validated by the obtained yield data. In this sense, *Phaseolus* spp. averaged a total yield of 43.4 g/m², with the *P. vulgaris* accessions PL12ST (127.1 g/m²), PV01CU (91.4 g/m²), and PV25SO (86.8 g/m²) achieving the highest production values. With a better performance, *Vigna unguiculata* yielded 68.9 g/m², with VU18MP (127.8 g/m²) and VU04MA (112.6 g/m²) leading. These yields align with or exceed those reported previously for *Phaseolus vulgaris* (Peláez et al. 2022) under identical growing conditions in field experiments. Moreover, these results indicate that under controlled irrigation, Mediterranean conditions can sustain or even enhance pulse productivity compared to traditional rainfed African systems.

The coefficient of variation (CV) was employed to assess the relative variability of quantitative morphological characters. Our results revealed high CV values in *Phaseolus* spp. accessions, particularly for PH, DTF, PPP, and PEL. In *Vigna unguiculata*, moderate variability (CV < 90%) indicated more stable phenotypes, yet characters like CLL and NTHS still offer breeding potential. The characters with the highest variability were primarily linked to plant yield (e.g., PPP and NTHS), suggesting a broad genetic base that can be exploited in breeding programs to improve yield and climate resilience (Arteaga et al. 2019).

Growth habits in *Phaseolus* spp. accessions were predominantly indeterminate, featuring mostly erect branches, which is consistent with wild and semi-domesticated genotypes (Kwak et al. 2012). Similar results have been reported for *Phaseolus coccineus* (Sicard et al. 2005; Arriagada et al. 2021), *P. lunatus* (Silva et al. 2024), and *P. vulgaris* (Sicard et al. 2005) cultivated in Europe. Most of the *Vigna unguiculata* accessions also exhibited indeterminate growth and a twining tendency, aligning with prior research (e.g., Nuryati et al. 2024; Souza et al. 2024). The determinate growth habit, associated with domestication and enhanced agronomic performance (Smartt 1990; Boote et al. 2003), was only observed in specific *V. unguiculata* accessions (VU01MA, VU12ST, VU14ST, and VU18MP), which displayed fewer nodes on the main stem (NNMS) and fewer days to

flowering (DTF). As suggested by Guilengue et al. (2019), breeding programmes should prioritise determinate growth forms to enhance production in the main stem and primary branches, while considering optimal soil and climate conditions, especially during summer droughts.

The *Phaseolus lunatus* accessions (PL13ST, PL15ST, and PL16ST) from Cabo Verde and all the *Vigna unguiculata* accessions responded remarkably to decreasing day lengths, growing vigorously and flowering after the summer solstice. This sensitivity to photoperiod, characteristic of short-day plants (Bastow and Dean 2002), suggests that day length reduction is a prerequisite for the start of flowering in these accessions. Furthermore, day length manipulation could be exploited to optimise flowering time and yield under Mediterranean conditions.

Correlation analysis is crucial to understand the interactions between morphological characters of agronomic importance, providing valuable insights for breeding strategies for a crop (Owusu et al. 2021). This approach enables the indirect selection of complex, quantitatively inherited characters influenced by genetic effects, such as yield (Mazid et al. 2013). In this study, several positive and significant correlations were identified among morphological characters for *Phaseolus* spp. and *Vigna unguiculata*, particularly those related to yield components. In *Phaseolus* spp., WTHS was positively correlated with FBPI, TNHS, and PH, with the latter appearing as the character most frequently correlated with other characters. These findings are consistent with former research, namely Yeken et al. (2019), which stated positive correlations between plant height and characters such as days to flowering, days to maturity, number of pods per plant, seeds per pod, seed width, and thousand seed weight. Similarly, Delfini et al. (2021) reported positive correlations between total seed weight per plant and the total number of pods per plant, the number of locules per pod and the number of seeds per pod. For *V. unguiculata*, significant correlations were limited to seed characters, namely WHS with SWI and ST. Therefore, no significant correlations were detected between vegetative and reproductive characters. This contrasts with findings from Aliyu et al. (2021) and Owusu et al. (2021), who reported positive correlations between seed weight and several vegetative characters such as the number of branches at flowering, days to flowering, plant height,

and number of pods per plant. Overall, the correlations observed in this study suggest that selection for improved yield in *Phaseolus* spp. may benefit from focusing on characters such as plant height, whereas in *V. unguiculata*, selection based on seed morphological characters could be more effective.

Several accessions, namely PL12ST and PL17ST for *Phaseolus* spp. and VU07BE, VU14ST, and VU18ST for *V. unguiculata*, exhibited the best performance in converting vegetative growth into seed production. However, accessions such as PV01CU, PV03CU, PC08MA, PV14ST, PV25SO, and VU04NA, despite showing a high number of harvested seeds, had smaller and lighter seeds, which translated into a lower yield. The multivariate analysis (Figs. 1 and 2) corroborated the phenotypic diversity, clustering the 19 *Phaseolus* spp. and the 9 *Vigna unguiculata* accessions into two main groups according to vegetative and reproductive characters.

Mineral profiles

The mineral analysis revealed significant differences between bean species, with each taxon presenting unique mineral profiles: *Phaseolus coccineus* (Ca and K), *P. lunatus* (Fe and Mn), *P. vulgaris* (Cu, P, and S) and *Vigna unguiculata* (B, Mg, Na, and Zn). These findings have nutritional implications, particularly for addressing micronutrient deficiencies such as iron and zinc, which remain a global public health concern (Maares and Haase 2016; Muriuki et al. 2020). In this sense, *P. lunatus* (154.6 mg/kg ww) and *P. vulgaris* (129.8 mg/kg ww) showed Fe contents surpassing those reported by several investigations in Africa (Brilhante et al. 2021; Guterres et al. 2022) and the Mediterranean region (e.g., Pinheiro et al. 2010; Celmeli et al. 2018). It should be noted that the accession PV21SO of *P. vulgaris* showed the highest value in this study (239.9 mg/kg ww), suggesting that this accession could contribute to biofortification initiatives. Similarly, *Vigna unguiculata* accessions presented the higher Zn contents (42.2 mg/kg ww) compared to those of *Phaseolus* spp., with a maximum of 47.7 mg/kg ww in the accession VU06MO, aligning with results from African (Boukar et al. 2011; Brilhante et al. 2021) and Mediterranean research (Di Bella et al. 2016; Gerrano et al. 2018). This reinforces their value for nutritional improvement programs targeting zinc-deficient populations.

When comparing mineral profiles between Africa and the Mediterranean-grown accessions, significant differences were detected, agreeing with the findings of Murube et al. (2021) for *P. vulgaris* with European and American-grown accessions. Also, Di Bella et al. (2016) reported significant differences between *P. vulgaris* and *V. unguiculata* African- and Mediterranean-grown accessions, describing higher mineral contents in Africa. Several factors influence the mineral contents in seeds, including soil type and fertility (Sperotto et al. 2014), genetic diversity (Maziya-Dixon et al. 2000; Zacharias et al. 2012), post-harvest handling and storage conditions of the seeds, as well as the maturity of the plant at the time of harvest (Shewfelt 1990; Yeken et al. 2023). In addition, despite previous research suggesting seed coat colour can influence mineral content (e.g., Guterres et al. 2012; Tiwari and Singh 2012; Zhong et al. 2018), no clear pattern was detected in our study.

In this study, we found that phenotypic variability is correlated with mineral content variability. Significant positive and negative correlations were observed between mineral content and several morphological characters associated with reproductive development and, as such, associated with the yield and performance of *Phaseolus* spp. and *Vigna unguiculata*. In *Phaseolus* spp., negative correlations were found between Na content and TNHS and WTHS, probably suggesting a trade-off between salt accumulation and reproductive success. Negative correlations between Mg and several morphological characters were also found, such as with WTS, SL and SH, as described by Ribeiro et al. (2021). Unlike former research (Yeken et al. 2019; Murube et al. 2021), we observed a negative correlation between Cu and LL, a vegetative character, indicating species- or environment-specific mineral dynamics. In *Vigna unguiculata*, Ca positively correlated with NLPP, highlighting its role in reproductive success. This contrasts with some previous research (Lazaridi et al. 2016) but supports the effect of Ca as an important factor in flower and pod development (Mbuma et al. 2022). Cogent with findings from several investigations on pulses (Pinheiro et al. 2010; Celmeli et al. 2018; Murube et al. 2021), our study also did not find significant correlations between Fe and morphological characters.

Conclusion

This study demonstrated the adaptability and agronomic potential of African bean accessions (*Phaseolus coccineus*, *P. lunatus*, *P. vulgaris*, and *Vigna unguiculata*) to Mediterranean climatic conditions through detailed morphological and mineral characterisation. The morphological assessment revealed significant variability among accessions, particularly in characters associated with yield and growth habitat, offering information for targeted selection and breeding. Accessions such as PL12ST and PL17ST (*P. lunatus*) and VU07BE and VU18ST (*V. unguiculata*) exhibited higher performance in converting vegetative growth into seed production. Moreover, the presence of indeterminate growth habitat was predominant, although some *V. unguiculata* accessions exhibited determinate growth, suggesting useful material for breeding programs aimed at Mediterranean environments. Mineral analysis supported the high nutritional value of these beans, with distinct profiles: *P. coccineus* exhibited high Ca and K contents, *P. vulgaris* showed elevated Cu, P, and S contents, *P. lunatus* demonstrated higher Fe and Mn contents, and *V. unguiculata* was richer in B, Mg, Na, and Zn. Variations in mineral profiles were detected not only between species but also among accessions, highlighting the influence of both growing environment and genotype. Correlation analyses revealed associations between morphological characters and mineral contents, providing a better understanding of the characters linked to performance and nutritional quality under Mediterranean conditions. The results confirm the potential of the evaluated African bean accessions both for cultivation and for use in breeding programs aimed at improving yield and nutritional quality in Mediterranean climates.

Author contributions Conceptualization: P.T.; Field experiments: P.T. and F.R.; Formal data analysis: M.B.; Writing—original draft preparation: M.B.; Writing—review and editing: M.B., F.R., M.M.R. and P.T.; Supervision: P.T. All authors have read and agreed to the published version of the manuscript.

Funding Open access funding provided by FCTIFCCN (b-on). This research was supported by Fundação para a Ciência e Tecnologia (FCT) and the research unit UIDB/04129/2020 (LEAF) funded by Portuguese National Funds through FCT,

Portugal. M.B. was supported by an FCT scholarship (UI/BD/151188/2021).

Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

References

- Alemu M, Asfaw Z, Woldu Z, Fenta BA, Medvecky B (2016) Cowpea (*Vigna unguiculata* (L.) Walp.) (Fabaceae) landrace diversity in Northern Ethiopia. *Int J Biodivers Conserv* 8:297–309. <https://doi.org/10.5897/ijbc2016.0946>
- Aliyu OM, Tihamiyu AO, Usman M, Abdulkareem YF (2021) Variance components, correlation and path analyses in cowpea (*Vigna unguiculata* L., Walp). *J Crop Sci Biotechnol* 25:173–182. <https://doi.org/10.1007/s12892-021-00121-5>
- Allen RG, Pereira LS, Raes D, Smith M (1998) Crop evapotranspiration. *FAO irrigation and drainage paper* 56:60–64. <https://www.fao.org/3/x0490e/x0490e00.htm>
- Animasaun DA, Oyediji S, Mustapha OT, Azeez MA (2015) Genetic variability study among ten cultivars of cowpea (*Vigna unguiculata* L. Walp) using morpho-agronomic traits and nutritional composition. *J Agric Sci* 10:119–130. <https://doi.org/10.4038/jas.v10i2.8057>
- Arriagada O, Schwember AR, Greve MJ, Urban MO, Cabeza RA, Carrasco B (2021) Morphological and molecular characterization of selected Chilean runner bean (*Phaseolus coccineus* L.) genotypes shows moderate agronomic and genetic variability. *Plants* 10:1688. <https://doi.org/10.3390/plants10081688>
- Arteaga S, Yabor L, Torres J, Solbes E, Muñoz E, Díez MJ, Vicente O, Boscaiu M (2019) Morphological and agronomic characterization of Spanish landraces of *Phaseolus vulgaris* L. *Agriculture* 9:149. <https://doi.org/10.3390/agriculture9070149>

- Azani N, Babineau M, Bailey CD, Banks H, Barbosa AR, Pinto RB, Boatwright JS, Borges LM, Brown GK, Bruneau A, Candido E, Cardoso D, Chung KF, Clark RP, Conceição AS, Crisp M, Cubas P, Delgado-Salinas A, Dexter KG, Doyle JJ, Duminil J, Egan AN, Estrella M, Falcão MJ, Filatov DA, Fortuna-Perez AP, Fortunato RH, Gagnon E, Gasson P, Rando JG, Tozzi AMGA, Gunn B, Harris D, Haston E, Hawkins JA, Herendeen PS, Hughes CE, Iganci JRV, Javadi F, Kanu SA, Kazempour-Osaloo S, Kite GC, Klitgaard BB, Kochanowski FJ, Koenen EMJ, Kovar L, Lavin M, Roux M, Lewis GP, Lima HC, López-Roberts MC, Mackinder B, Maia VH, Malécot V, Mansano VF, Marazzi B, Mattapha S, Miller JT, Mitsuyuki C, Moura T, Murphy DJ, Nageswara Rao M, Nevado B, Neves D, Ojeda DI, Pennington RT, Prado DE, Prenner G, Queiroz LP, Ramos G, Filardi FLR, Ribeiro PG, Rico-Arce ML, Sanderson MJ, Santos-Silva J, São-Mateus WMB, Silva MJS, Simon MF, Sinou C, Snak C, Souza ER, Sprent J, Steele KP, Steier JE, Steeves R, Stirton CH, Tagane S, Torke BM, Toyama H, Cruz DT, Vatanparast M, Wieringa JJ, Wink M, Wojciechowski MF, Yahara T, Yi T, Zimmerman E (2017) A new subfamily classification of the Leguminosae based on a taxonomically comprehensive phylogeny: the legume phylogeny working group (LPWG). *Taxon* 66:44–77. <https://doi.org/10.12705/661.3>
- Bastow R, Dean C (2002) The molecular basis of photoperiodism. *Dev Cell* 3:461–462. [https://doi.org/10.1016/s1534-5807\(02\)00296-4](https://doi.org/10.1016/s1534-5807(02)00296-4)
- Bioversity International (2007) Descritores para Feijão frade ou caupi (*Vigna unguiculata* (L.) Walp.). <https://hdl.handle.net/10568/104074>. Accessed 01 Mar 2021
- Bitocchi E, Bellucci E, Giardini A, Rau D, Rodriguez M, Biagetti E, Santilocchi R, Zeuli PS, Gioia T, Logozzo G, Attene G, Nanni L, Papa R (2013) Molecular analysis of the parallel domestication of the common bean (*Phaseolus vulgaris*) in mesoamerica and the andes. *New Phytol* 197(1):300–313. <https://doi.org/10.1111/j.1469-8137.2012.04377.x>
- Bitocchi E, Rau D, Bellucci E, Rodriguez M, Murgia ML, Gioia T, Santo D, Nanni L, Attene G, Papa R (2017) Beans (*Phaseolus* spp.) as a model for understanding crop evolution. *Front Plant Sci* 8:722. <https://doi.org/10.3389/fpls.2017.00722>
- Blair MW, González LF, Kimani PM, Butare L (2010) Genetic diversity, inter-gene pool introgression and nutritional quality of common beans (*Phaseolus vulgaris* L.) from Central Africa. *Theor Appl Genet* 121:237–248. <https://doi.org/10.1007/s00122-010-1305-x>
- Boote KJ, Jones JW, Batchelor WD, Nafziger ED, Myers O (2003) Genetic coefficients in the CROPGRO-soybean model. *Agron J* 95:32–51. <https://doi.org/10.2134/agronj2003.3200>
- Boukar O, Massawe F, Muranaka S, Franco J, Maziya-Dixon B, Singh B, Fatokun C (2011) Evaluation of cowpea germplasm lines for protein and mineral concentrations in grains. *Plant Genet Resour* 9:515–522. <https://doi.org/10.1017/s1479262111000815>
- Brilhante M, Varela E, Essoh AP, Fortes A, Duarte MC, Monteiro F, Ferreira V, Correia AM, Duarte MP, Romeiras MM (2021) Tackling food insecurity in Cabo Verde Islands: the nutritional, agricultural and environmental values of the legume species. *Foods* 10:206. <https://doi.org/10.3390/foods10020206>
- Broughton WJ, Hernández G, Blair M, Beebe S, Gepts P, Vanderleyden J (2003) Beans (*Phaseolus* spp.)—model food legumes. *Plant Soil* 252:55–128. <https://doi.org/10.1023/A:1024146710611>
- Burle ML, Fonseca JR, Kami JA, Gepts P (2010) Microsatellite diversity and genetic structure among common bean (*Phaseolus vulgaris* L.) landraces in Brazil, a secondary center of diversity. *Theor Appl Genet* 121:801–813. <https://doi.org/10.1007/s00122-010-1350-5>
- Catarino S, Brilhante M, Essoh AP, Charrua AB, Rangel J, Roxo G, Varela E, Moldão M, Ribeiro-Barros A, Bandeira S, Moura M, Talhinhos P, Romeiras MM (2021) Exploring physicochemical and cytogenomic diversity of African cowpea and common bean. *Sci Rep* 11:12838. <https://doi.org/10.1038/s41598-021-91929-2>
- Celmeli T, Sari H, Canci H, Sari D, Adak A, Eker T, Tokar C (2018) The nutritional content of common bean (*Phaseolus vulgaris* L.) landraces in comparison to modern varieties. *Agronomy* 8:166. <https://doi.org/10.3390/agronomy8090166>
- Christenhusz MJM, Byng JW (2016) The number of known plants species in the world and its annual increase. *Phytotaxa* 261:201. <https://doi.org/10.11646/phytotaxa.261.3.1>
- Delfini J, Moda-Cirino V, Neto JDS, Zeffa DM, Nogueira AF, Ribeiro LAB, Ruas PM, Gepts P, Gonçalves LSA (2021) Genome-wide association study identifies genomic regions for important morpho-agronomic traits in mesoamerican common bean. *Front in Plant Sci* 12:748829. <https://doi.org/10.3389/fpls.2021.748829>
- Delgado-Salinas A, Bibler R, Lavin M (2006) Phylogeny of the genus *Phaseolus* (Leguminosae): a recent diversification in an ancient landscape. *Syst Bot* 31:779–791. <https://doi.org/10.1600/036364406779695960>
- Di Bella G, Naccari C, Bua GD, Rastrelli L, Lo Turco V, Potorti DG (2016) Mineral composition of some varieties of beans from Mediterranean and Tropical areas. *Int J Food Sci Nut* 67:239–248. <https://doi.org/10.3109/09637486.2016.1153610>
- FAO (2016) The International Year of Pulses. Rome: Food and Agricultural Organizations of the United Nations. <https://www.fao.org/pulses-2016/en>. Accessed 08 May 2024
- Frascarelli G, Galise TR, D'Agostino N, Cafasso D, Cozzolino S, Cortinovis G, Sparvoli F, Bellucci E, Di Vitori V, Nanni L, Pieri A, Rossato M, Vicenzi L, Benazzo A, Delledone M, Bitocchi E (2025) The evolutionary history of the common bean (*Phaseolus vulgaris*) revealed by chloroplast and nuclear genomes analysis. *Theor Appl Genet* 138:47. <https://doi.org/10.1007/s00122-025-04832-z>
- Gepts P (2001) *Phaseolus vulgaris* (Bean). In: Brenner S, Miller JH (eds) *Encyclopedia of Genetics*. Academic Press, London, pp 1444–1445
- Gerrano AS, Van Rensburg WSJ, Venter SL, Shargie NG, Amelework BA, Shimelis HA, Labuschagne MT (2018) Selection of cowpea genotypes based on grain mineral and total protein content. *Acta Agr Scand B-Soil Pl Sci* 69:155–166. <https://doi.org/10.1080/09064710.2018.1520290>

- Gioia T, Logozzo G, Marzario S, Zeuli PS, Gepts P (2019) Evolution of SSR diversity from wild types to U.S. advanced cultivars in the Andean and Mesoamerican domestications of common bean (*Phaseolus vulgaris*). PLoS ONE 14:e0211342. <https://doi.org/10.1371/journal.pone.0211342>
- Granito M, Brito Y, Torres A (2007) Chemical composition, antioxidant capacity and functionality of raw and processed *Phaseolus lunatus*. J Sci Food Agric 87:2801–2809. <https://doi.org/10.1002/jsfa.2926>
- Greenway PJ (1945) Origins of some east African food plants: Part V. East Afr Agr J Kenya, Tanganyika, Uganda and Zanzibar 11:56–63. <https://doi.org/10.1080/03670074.1945.11664470>
- Gu Z, Eils R, Schlesner M (2016) Complex heatmaps reveal patterns and correlations in multidimensional genomic data. Bioinformatics 32:2847–2849. <https://doi.org/10.1093/bioinformatics/btw313>
- Guerra-García A, Suárez-Atilano M, Mastretta-Yanes A, Delgado-Salinas A, Piñero D (2017) Domestication genomics of the open-pollinated scarlet runner bean (*Phaseolus coccineus* L.). Front Plant Sci 8:1891. <https://doi.org/10.3389/fpls.2017.01891>
- Guilengue N, Alves S, Talhinhos P, Neves-Martins J (2019) Genetic and genomic diversity in a Tarwi (*Lupinus mutabilis* Sweet) germplasm collection and adaptability to Mediterranean climate conditions. Agronomy 10:21. <https://doi.org/10.3390/agronomy10010021>
- Guterres L, Duarte MC, Catarino S, Roxo G, Barnabé J, Sebastiana M, Monteiro F, Romeiras MM (2022) Diversity of legumes in the cashew agroforestry system in east Timor (Southeast Asia). Foods 11:3503. <https://doi.org/10.3390/foods11213503>
- Gutiérrez Salgado A, Gepts P, Debouck DG (1995) Evidence for two gene pools of the Lima bean, *Phaseolus lunatus* L., in the Americas. Genet Resour Crop Evol 42:15–28. <https://doi.org/10.1007/BF02310680>
- Harrell FE (2024) Hmisc: harrell miscellaneous. V 5.1-2. <https://CRAN.R-project.org/package=Hmisc>
- Harouna DV, Venkataramana PB, Matemu AO, Ndakidemi PA (2020) Agro-morphological exploration of some unexplored wild *Vigna* legumes for domestication. Agronomy 10:111. <https://doi.org/10.3390/agronomy10010111>
- IPGRI (2001) Descriptores para *Phaseolus vulgaris*. International Plant Genetic Resources Institute. <https://hdl.handle.net/10568/72699>. Accessed 01 Mar 2021
- Jan S, Rather IA, Sofi PA, Wani MA, Sheikh FA, Bhat MA, Mir RR (2021) Characterization of common bean (*Phaseolus vulgaris* L.) germplasm for morphological and seed nutrient traits from Western Himalayas. Legum Sci 3:e86. <https://doi.org/10.1002/leg3.86>
- Kimani PM, Njau S, Mulanya M, Narla RD (2019) Breeding runner bean for short-day adaptation, grain yield, and disease resistance in eastern Africa. Food Energy Secur 8:e171. <https://doi.org/10.1002/fes3.171>
- Kwak M, Toro O, Debouck DG, Gepts P (2012) Multiple origins of the determinate growth habit in domesticated common bean (*Phaseolus vulgaris*). Ann Bot 110:1573–1580. <https://doi.org/10.1093/aob/mcs207>
- Lazaridi E, Ntatsi G, Savvas D, Bebeli PJ (2016) Diversity in cowpea (*Vigna unguiculata* (L.) Walp.) local populations from Greece. Genet Resour Crop Evol 64:1529–1551. <https://doi.org/10.1007/s10722-016-0452-6>
- Lei L, Wang L, Wang S, Wu J (2020) Marker-trait association analysis of seed traits in accessions of common bean (*Phaseolus vulgaris* L.) in China. Front Genet 11:698. <https://doi.org/10.3389/fgene.2020.00698>
- López-Alcocer JJ, Lépiz-Ildefonso R, González-Eguiarte DR, Rodríguez-Macías R, López-Alcocer E (2016) Morphological variability of wild *Phaseolus lunatus* L. from the western region of México. Rev Fitotec Mex 39:49–58
- Maarens M, Haase H (2016) Zinc and immunity: an essential interrelation. Arch Biochem Biophys 611:58–65. <https://doi.org/10.1016/j.abb.2016.03.022>
- Mackinder B, Pasquet R, Polhill R, Verdcourt B (2001) Flora zambesiaca, vol 3 Part 5. Royal Botanic Gardens, Kew
- Maechler M, Rousseeuw P, Struyf A, Hubert M., Hornik K (2023) cluster: Cluster Analysis Basics and Extensions V 2.1.6. <https://CRAN.R-project.org/package=cluster>
- Mafakheri K, Bihanta MR, Abbasi AR (2017) Assessment of genetic diversity in cowpea (*Vigna unguiculata* L.) germplasm using morphological and molecular characterisation. Cogent Food Agri 3:1327092. <https://doi.org/10.1080/23311932.2017.1327092>
- Maréchal R (1978) Etude taxonomique d'un groupe complexe d'espèces des genres *Phaseolus* et *Vigna* (Papilionaceae) sur la base de données morphologiques et polliniques, traitées par l'analyse informatique. Boissiera 28:1–273
- Martínez-Nieto MI, Estrelles E, Prieto-Mossi J, Prieto-Mossi J, Roselló J, Soriano P (2020) Resilience capacity assessment of the traditional lima bean (*Phaseolus lunatus* L.) landraces facing climate change. Agronomy 10:758. <https://doi.org/10.3390/agronomy10060758>
- Maxted N, Mabuza-Diamini P, Moss H, Padulosi S, Jarvis A, Guarino L (2004) An ecogeographic study African *Vigna*. Systematic and ecogeographic studies of crop Genepools 11. International Plant Genetic Resources Institute, Rome
- Maziya-Dixon B, Kling JG, Menkir A, Dixon A (2000) Genetic variation in total carotene, iron, and zinc contents of maize and cassava genotypes. Food Nut Bull 21:419–422. <https://doi.org/10.1177/156482650002100415>
- Mazid RMY, Hanafi MM, Rahim HA, Shabanimofrad M, Latif MA (2013) Agro-morphological characterization and assessment of variability, heritability, genetic advance and divergence in bacterial blight resistant rice genotypes. S Afr J Bot 86:15–22. <https://doi.org/10.1016/j.sajb.2013.01.004>
- Mbumba NW, Gerrano AS, Lebaka N, Labuschagne M (2022) Interrelationship between grain yield components and nutritional quality traits in cowpea genotypes. S Afr J Bot 150:34–43. <https://doi.org/10.1016/j.sajb.2022.07.006>
- Menssen M, Linde M, Omondi EO, Abukutsa-Onyango M, Dinssa FF, Winkelmann T (2017) Genetic and morphological diversity of cowpea (*Vigna unguiculata* (L.) Walp.) entries from East Africa. Sci Hortic 226:268–276. <https://doi.org/10.1016/j.scienta.2017.08.003>
- Muriuki JM, Mentzer AJ, Webb EL, Morovat A, Kimita W, Ndungu FM, Macharia AW, Crane RJ, Berkley JA, Lule SA, Cutland C, Sirima SB, Diarra A, Tiono AB, Bejon P, Madhi SA, Hill AVS, Prentice AM, Suchdev PS, Elliott AM, Williams TN, Atkinsos SH (2020) Estimating the

- burden of iron deficiency among African children. *BMC Med* 18:31. <https://doi.org/10.1186/s12916-020-1502-7>
- Murube E, Beleggia R, Pacetti D, Nartea A, Frascarelli G, Lanzavecchia G, Belluci E, Nanni L, Gioia T, Marciello U, Esposito S, Foresi G, Logozzo G, Frega GN, Bitocchi E, Papa R (2021) Characterization of nutritional quality traits of a common bean germplasm collection. *Foods* 10:1572. <https://doi.org/10.3390/foods10071572>
- Musango R, Kudzu K, Mhungu S, Tibugur H (2016) Phenotypic characterization of common bean (*Phaseolus vulgaris* L.) accessions conserved at the genetic resources and biotechnology institute. *J Biol Env Sci* 8:26–36
- Nuryati N, Soehendi R, Hermanto C, Suyanto S, Krisdiana R, Pardal SJ, Jumakir J, Adie MM, Krisnawati A, Baliadi Y, Abubakar B (2024) Morphological diversity, correlation studies, and multiple-traits selection for yield and yield components of local cowpea varieties. *Open Agri* 9:20220231. <https://doi.org/10.1515/opag-2022-0231>
- Odendo M, Bationo A, Kimani S (2011) Socio-economic contribution of legumes to livelihoods in Sub-Saharan Africa. In: Bationo A, Waswa B, Kihara J, Kimetu J (eds) *Fighting poverty in Sub-Saharan Africa: The multiple roles of legumes in Integrated Soil Fertility Management*. Springer, Netherlands, pp 27–46
- Owusu EY, Karikari B, Kusi F, Haruna M, Amoah RA, Attamah P, Adazebra G, Sie EK, Issahaku M (2021) Genetic variability, heritability and correlation analysis among maturity and yield traits in Cowpea (*Vigna unguiculata* (L) Walp) in Northern Ghana. *Heliyon* 7:e07890. <https://doi.org/10.1016/j.heliyon.2021.e07890>
- Parker TA, Vallejos CE (2019) Tepary bean (*Phaseolus acutifolius*) as a model for climate-resilient legumes. *Front Plant Sci* 10:956. <https://doi.org/10.3389/fpls.2019.00956>
- Peláez D, Aguilar PA, Mercado M, López-Hernández F, Guzmán M, Burbano-Erazo E, Denning-James K, Medina CI, Blair MW, Vega JJ, Cortés AJ (2022) Genotype selection, and seed uniformity and multiplication to ensure common bean (*Phaseolus vulgaris* L.) var. Liborino. *Agronomy* 12:2285. <https://doi.org/10.3390/agronomy12102285>
- Pinheiro C, Baeta JP, Pereira AM, Domingues H, Ricardo CP (2010) Diversity of seed mineral composition of *Phaseolus vulgaris* L. germplasm. *J Food Compos Anal* 23:319–325. <https://doi.org/10.1016/j.jfca.2010.01.005>
- POWO (2024) <http://powo.science.kew.org>. Accessed 10 May 2024
- R Core Team (2023) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rawal V, Navarro D K (2019) The Global Economy of Pulses. FAO. <https://openknowledge.fao.org/server/api/core/bitstreams/2c70eed3-4170-4b0e-963b-995323fe94a1/content> Accessed 9 May 2024
- Ribeiro ND, Santos GGD, Maziero SM, Santos GGD (2021) Genetic diversity and selection of bean landraces and cultivars based on technological and nutritional traits. *J Food Compos Anal* 96:103721. <https://doi.org/10.1016/j.jfca.2020.103721>
- Rodino AP, Lema M, Pérez-Barbeito M, Santalla M, De Ron AM (2007) Assessment of runner bean (*Phaseolus coccineus* L.) germplasm for tolerance to low temperature during early seedling growth. *Euphytica* 155:63–70. <https://doi.org/10.1007/s10681-006-9301-6>
- Santalla M, Monteagudo AB, González AM, De Ron AM (2004) Agronomical and quality traits of runner bean germplasm and implications for breeding. *Euphytica* 135:205–215. <https://doi.org/10.1023/b:euph.0000014912.07993.e7>
- Schwember AR, Carrasco B, Gepts P (2017) Unraveling agronomic and genetic aspects of runner bean (*Phaseolus coccineus* L.). *Field Crop Res* 206:86–94. <https://doi.org/10.1016/j.fcr.2017.02.020>
- Shewfelt RL (1990) Sources of variation in the nutrient content of agricultural commodities from the farm to the consumer. *J Food Quality* 13:37–54. <https://doi.org/10.1111/j.1745-4557.1990.tb00004.x>
- Sicard D, Nanni L, Porfiri O, Bulfon D, Papa R (2005) Genetic diversity of *Phaseolus vulgaris* L. and *P. coccineus* L. landraces in central Italy. *Plant Breeding* 124:464–472. <https://doi.org/10.1111/j.1439-0523.2005.01137.x>
- Silva JM, Araújo JL, Oliveira HCA, Pereira LBS, Sperandio MVL, Corte-Real NM, Ulisses C (2024) Salicylic acid induces acclimation to water deficit in *Phaseolus lunatus* genotypes. *Rev Bras Eng Agr Amb* 28:e279027. <https://doi.org/10.1590/1807-1929/agriambi.v28n4e279027>
- Singh BB, Raj DM, Dashiell KE, Jackai LEN (1997) Advances in cowpea research. International institute of tropical agriculture (IITA) and Japan international research center for agricultural sciences (JIRCAS), Ibadan, Nigeria
- Singh B (2020) Cowpea: the food legume of the 21st century. John Wiley and Sons, Hoboken
- Šlenker M, Koutecký P, Marhold K (2022) MorphoTools2: an R package for multivariate morphometric analysis. *Bioinformatics* 38:2954–2955. <https://doi.org/10.1093/bioinformatics/btac173>
- Smartt J (1990) Grain Legumes: evolution and genetic resources. Cambridge University Press, Cambridge
- Soares VF, Pereira GS, de Oliveira Marques A, Leal Junior GA (2025) *Phaseolus lunatus* landraces from northeast Brazil: genetic diversity and anthracnose resistance. *Genet Resour Crop Evol* 72:2287–2306. <https://doi.org/10.1007/s10722-024-02098-w>
- Souza TMA, Souto LS, Dutra Filho JA, Santos CSA, Silva LS, Peixoto TDC, Sá FVS (2024) Cowpea growth and production under water stress and soil mulching. *Rev Bras Eng Agr Amb* 28:e271643. <https://doi.org/10.1590/1807-1929/agriambi.v28n3e271643>
- Spataro G, Tiranti B, Arcaleni P, Belluci E, Attene G, Papa R, Spagnoletti Zeuli P, Negri V (2011) Genetic diversity and structure of a worldwide collection of *Phaseolus coccineus* L. *Theor Appl Genet* 122:1281–1291. <https://doi.org/10.1007/s00122-011-1530-y>
- Sperotto RA, Ricachenevsky FK, Williams LE, Vasconcelos MW, Menguer PK (2014) From soil to seed: micronutrient movement into and within the plant. *Front Plant Sci* 5:438. <https://doi.org/10.3389/fpls.2014.00438>
- Talhinhas P, Leitão J, Neves-Martins J (2006) Collection of *Lupinus angustifolius* L. germplasm and characterisation of morphological and molecular diversity. *Genet Resour Crop Evol* 53:563–578. <https://doi.org/10.1007/s10722-004-2684-0>

- Timko MP, Singh B (2008) Cowpea, a Multifunctional Legume. In: Moore PH, Ming R (eds) *Genomics of Tropical Crop Plants*. Plant Genetics and Genomics: Crops and Models, vol 1. Springer, New York. https://doi.org/10.1007/978-0-387-71219-2_10
- Tiwari BK, Singh N (2012) *Pulse chemistry and technology*. Royal Society of Chemistry, London
- Tomooka N, Naito K, Kaga A, Sakai H, Isemura T, Ogiso-Tanaka E, Iseki K, Takahashi Y (2014) Evolution, domestication and neo-domestication of the genus *Vigna*. *Plant Genet Resour* 12:S168–S171. <https://doi.org/10.1017/s1479262114000483>
- Tosti N, Negri V (2005) On-going on-farm microevolutionary processes in neighbouring cowpea landraces revealed by molecular markers. *Theor Appl Genet* 110:1275–1283. <https://doi.org/10.1007/s00122-005-1964-1>
- Vidigal P, Romeiras MM, Monteiro F (2019) Crops Diversification and the Role of Orphan Legumes to Improve the Sub-Saharan Africa Farming Systems. In: Hasanuzzaman M, Teixeira Filho MCM, Fujita M, Nogueira TAR (eds) (2020) *Sustainable Crop Production*. IntechOpen <https://doi.org/10.5772/intechopen.88076>
- Wickham H (2016) *Data Analysis*. In: *Use R!* Springer, Cham. https://doi.org/10.1007/978-3-319-24277-4_9
- Wortmann CS, Allen DJ (1994) *African bean production environments: their definition, characteristics and constraints*. Occasional Publication Series 11, CIAT
- Yahara T, Javadi F, Onoda Y, Queiroz LP, Faith DP, Prado DE, Akasaka M, Kadoya T, Ishihama F, Davies S, Slik JWF, Yi T, Ma K, Bin C, Darnaedi D, Pennington RT, Tuda M, Shimada M, Ito M, Egan AN, Buerki S, Raes N, Kajita T, Vatanparast M, Mimura M, Tachida H, Iwasa Y, Smith G, Victor JE, Nkonki T (2013) Global legume diversity assessment: concepts, key indicators, and strategies. *Taxon* 62:249–266. <https://doi.org/10.12705/622.12>
- Yeken MZ, Nadeem MA, Karaköy T, Baloch FS, Çiftçi V (2019) Determination of Turkish common bean germplasm for morpho-agronomic and mineral variations for breeding perspectives in Turkey. *Kahramanmaraş Sütçü İmam Üniversitesi Tarım Ve Doğa Dergisi* 22:38–50. <https://doi.org/10.18016/ksutarimdoga.vi.563740>
- Yeken MZ, Soydemir HE, Kibar H, Çiftçi V (2023) Long-term storage affects on the phenolic, mineral, color and cooking traits of chickpea seed. *J Stored Prod Res* 102:102122. <https://doi.org/10.1016/j.jspr.2023.102122>
- Zacharias J, Leilani A, Jacob D, Miklas PN, Hossain KG (2012) Genetic variability of mineral composition in common bean seed. *Annu Rep Bean Improv Coop* 55:59–60
- Zhong L, Fang Z, Wahlqvist ML, Gangcheng W, Hodgson JM, Johnson SK (2018) Seed coats of pulses as a food ingredient: characterization, processing, and applications. *Trend Food Sci Tech* 80:35–42. <https://doi.org/10.1016/j.tifs.2018.07.021>

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.