

Morphological seed diversity and viability of Moroccan cowpea landraces (*Vigna unguiculata* L. Walp.) conserved by farmers

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Abstract: Cowpea (*Vigna unguiculata* (L.) Walp.) is an important food crop, renowned for its nutritional quality and resilience to harsh climatic conditions. In Morocco, this legume remains a marginal crop, which threatens the conservation of its local genetic resources. In this context, the present study aimed to evaluate germination capacity, assess morphological diversity, and examine patterns of variation and correlations between these traits in nineteen traditional cowpea populations collected across Morocco, using seven germination parameters and twelve morphological traits. Results revealed significant variability within and between populations for both germination and seed morphological traits. Most populations exhibited high germination capacity and rapid germination rates, indicating an almost complete absence of dormancy. Seed morphological traits showed substantial intra- and inter-population variability, reflecting high phenotypic richness. Principal component analysis (PCA) identified four distinct population clusters, suggesting that the spatial structuring results from a combined effect of differentiation in morphological and germination traits, further influenced by geographical connectivity. Overall, these findings highlight the remarkable richness of Morocco's local cowpea genetic resources, offering valuable insights for conservation and breeding programs to support food security and sustainable agriculture.

Keywords: *Vigna unguiculata* (L.) Walp., landraces, variability, morphological trait, germination performance.

Introduction

Cowpea (*Vigna unguiculata* (L.) Walp.) is a diploid, herbaceous, predominantly self-pollinating annual species, classified under the Fabaceae family (Leguminosae) (Boukar et al. 2018; Padulosi and Ng 1997). It is considered one of humans' earliest domesticated leguminous crops (Osipitan et al. 2021). Cowpea is considered an important multi-purpose food legume cultivated for both dry seed and for its edible aerial parts, such as young leaves, immature pods, and green seeds, which serve as important sources of nutrients for human consumption (Carvalho et al. 2022; Faye et al. 2024). Furthermore, its fodder and shells provide a high-quality feed resource for livestock, especially during fattening periods (Abdou 2022). In addition to its

nutritional qualities, cowpea thereby could be a more suitable crop in current environmental changing scenario, since it is broadly adapted to grown under high temperatures and drought (Carvalho et al. 2017a), and it also performs well even in soils with low fertility due to its distinctive ability to fix atmospheric nitrogen through its root nodules (Mndzebele et al. 2020; Lazard et al. 2023). Its multi-functionality and resilience make this legume a viable and economically attractive crop for grain traders and smallholders, placing it in the category of valuable crops for subsistence agriculture (Amenga et al. 2025; Sylla et al. 2023; Sissoko et al. 2022).

Cowpea's center of origin is believed to be in Africa, from where it spread to various regions across the globe, including Latin America and Southeast Asia (Edeh and Igberi 2012; Belete and Mulugeta 2022). Currently, cowpea is widely cultivated in many developing countries in tropical and subtropical regions, as well as in some temperate zones, such as the Mediterranean area (Dagnon et al. 2021). In Morocco, cowpea is known by the vernacular names "*fûl gnâwa*" (literally "Guinea bean"), "*loubia*", or "*bonnette*". It holds a small area but prominent place in the traditional Moroccan agriculture, particularly within the oases south of the Atlas Mountains. It was introduced from sub-Saharan Africa through trans-Saharan human and trade flows. It is traditionally cultivated alongside other food crops and is also used in traditional medicine. Cowpea has long been valued because of its drought resistance and nutrition, and in regions like Fez, Marrakech, and the oases, its seeds are especially appreciated for their cosmetic, medicinal, and culinary properties (Bryssine 1962; Bellakhdar 1997).

Regarding the current state of legume genetic resources in Morocco, cowpea cultivation is considered as one of the minor to marginal crops corresponding to other legumes such as beans, vetches, grass pea, and fenugreek (El Fatehi et al. 2014). And, it is most commonly grown in association with spring cereals, which are usually sorghum and corn, following intercropping practices that are widespread in the traditional agro-ecosystems of the Rif Mountains (Demongeot et al. 2024; Cobelli et al. 2025). Despite their current marginal status, cowpea landraces, along with other endangered legumes and cereals, have been preserved to a large extent by the resilience of traditional agroecosystems and the continued engagement of farmers in seed selection and exchange. These practices have played a fundamental role in maintaining local genetic resources and ensuring the persistence of valuable agrobiodiversity across generations (Hmimsa and Ater 2008; El Fatehi and Ater 2017; El Fatehi et al. 2021).

Previous research conducted worldwide has predominantly focused on assessing the agronomic performance under diverse cultivation systems (Gerrano et al., 2022; Aliyu et al., 2023; Doumbia et al., 2024; Mkhonta et al., 2025), as well as on molecular and genomic approaches aimed at the genetic improvement and characterization of germplasm (Ongom et al., 2024; Gumede et al., 2022; Lo et al., 2018; Wu et al., 2024). In parallel, several studies have explored the germination dynamics and physiological responses of improved or introduced cowpea varieties under controlled or stress-inducing conditions (Widajati et al., 2023; Ravelombola et al., 2017; Carvalho et al., 2019; Afonso et al., 2025). However, despite the considerable global progress in cowpea research, little attention has been devoted to exploring local germplasm in Morocco. Only a few investigations have reported the persistence of this crop in traditional agroecosystems and its role in maintaining local agrobiodiversity (Hmimsa et al., 2008; El Fatehi et al., 2014; Demongeot et al., 2024; Cobelli et al., 2025). Nevertheless, these studies did not provide a detailed assessment of its germinative behavior, seed morphological diversity, or the extent of variability within and between populations.

In light of this gap, and to provide essential information for the conservation, valorization and genetic improvement programs of neglected cowpea germplasm in Morocco, while ensuring food and nutritional security in regions exposed to climatic instability and contributing to the long-term sustainability of traditional Moroccan agroecosystems, a study was conducted to assess the extent of phenotypic diversity and germinative performance among a collection of traditional cowpea populations conserved by farmers. A combined approach using both qualitative and quantitative descriptors was employed to (1) evaluate the germination capacity

and potential of these landraces under controlled conditions, (2) characterize their seed morphological variability, and (3) explore patterns of variation as well as potential correlations between seed morphology and germinative behavior in the studied populations.

Materials and Methods

Plant material

As part of the preliminary investigation into several local markets, the areas of occurrence and persistence of traditional cowpea (*Vigna unguiculata* L. Walp.) cultivation in Morocco, a field surveys were conducted across 48 weekly markets (*souks*). Based on the information gathered, and taking into account the limited aspect of cowpea cultivation and seed availability, a sampling campaign was carried out between March and May 2021. Seed collection was obtained from local farmers selling their own harvested seeds, originating from their nearby fields. The seeds corresponded to the 2020 harvest, were stored in bags under traditional conditions, and were often treated with salt to protect seeds during storage. Overall, 19 traditional cowpea populations were assembled from ten cultivation areas: eight sites in the Tangier–Tetouan–Al Hoceima region and two sites in the Casablanca–Settat region (Fig. 1, Table 1). In the laboratory, the identity of all collected seeds was verified and confirmed as belonging to the *Vigna unguiculata* species (Fig. 2). These populations were subsequently used for germination and morphological analyses to assess the farmer-maintained genetic diversity of cowpea in Morocco.

Seed Germination

For the germination test, undamaged seeds from the 19 populations were evaluated. Each population included three replicates arranged in a randomized complete block design, with 30 seeds per replicate. Before germination, seeds were surface-sterilized in 1% sodium hypochlorite for 5 minutes and rinsed thoroughly with distilled water. Seeds were then placed on two layers of filter paper moistened with distilled water in Petri dishes. The dishes were incubated in a germination chamber at 25 ± 2 °C for 10 days under dark conditions, and the filter paper was kept moist throughout the experiment by adding distilled water as needed. Germination progress was recorded daily and repeated at the same time each day. As defined by Mis et al. (2022), a seed was considered to have germinated when the radicle emerged by at least 2 mm. To better understand and interpret the germination dynamics recorded during this experiment, the calculation of the germination parameters was crucial to understand and enhance this very critical stage of plant development, as it has a direct impact on seedling establishment and crop productivity (Makhaye et al. 2021). Based on daily observations, seven germination parameters were calculated using the equations proposed by El Fatehi et al. (2014) for precocity (PR) and germination duration (DG), and by Lozano-Isla et al. (2019) for germination percentage (GRP), mean germination time (MGT), mean germination rate (MGR), synchronization index (SYN), and uncertainty index (UNC). These parameters are detailed as follows:

- Precocity (PR (days)): Number of days required to observe the first germinated seed.

$$PR = t_{\text{first}}$$

- Germination duration (DG (days)): Total number of days between the first and the last observed germination.

$$DG = t_{\text{last}} - t_{\text{first}}$$

• Germination percentage (GRP (%)): Percentage of seeds that successfully germinated out of the total number of seeds sown.

$$GRP (\%) = \left(\frac{\sum_{i=1}^k n_i}{N} \right) \times 100$$

• Mean germination time (MGT, days): Average time required for germination, taking into account the number of seeds germinated each day.

$$MGT = \left(\frac{\sum_{i=1}^k n_i t_i}{\sum_{i=1}^k n_i} \right)$$

• Mean germination rate (MGR, day⁻¹): Average speed of germination, expressed as the reciprocal of the mean germination time (MGT).

$$MGR = \frac{1}{MGT} = \left(\frac{\sum_{i=1}^k n_i}{\sum_{i=1}^k n_i t_i} \right)$$

• Synchronization index (SYN): Measures the degree of uniformity of germination among seeds.

$$SYN = \frac{\sum c_{n_{1,2}}}{N'}$$

$$\text{Being: } c_{n_{1,2}} = \frac{n_i(n_i-1)}{2} \quad \text{and} \quad N' = \frac{\sum n_i(\sum n_i-1)}{2}$$

• Uncertainty index (UNC (bits)): Quantifies the uncertainty related to the temporal distribution of germination frequency, based on the Shannon index.

$$UNC = - \sum_{i=1}^k f_i \log_2 f_i$$

$$\text{Being } f_i = \frac{n_i}{\sum_{i=1}^k n_i}$$

where:

t_{first} : the day the first seed germinates.

t_{last} : the day of the last germination

n_i : number of seeds germinated at the i^{th} observation time

N : total number of seeds in each experimental unit.

k : last day of germination evaluation.

t_i : time (in days) from the start of the experiment to the i^{th} observation.

$c_{n_{1,2}}$: number of possible seed pairs germinating simultaneously, calculated as: $c_{n_{1,2}} = \frac{n_i(n_i-1)}{2}$.

N' : total number of possible pairs of seeds in the experimental unit, calculated as: $N' = \frac{\sum n_i(\sum n_i-1)}{2}$.

f_i : relative germination frequency, calculated as: $f_i = \frac{n_i}{\sum_{i=1}^k n_i}$.

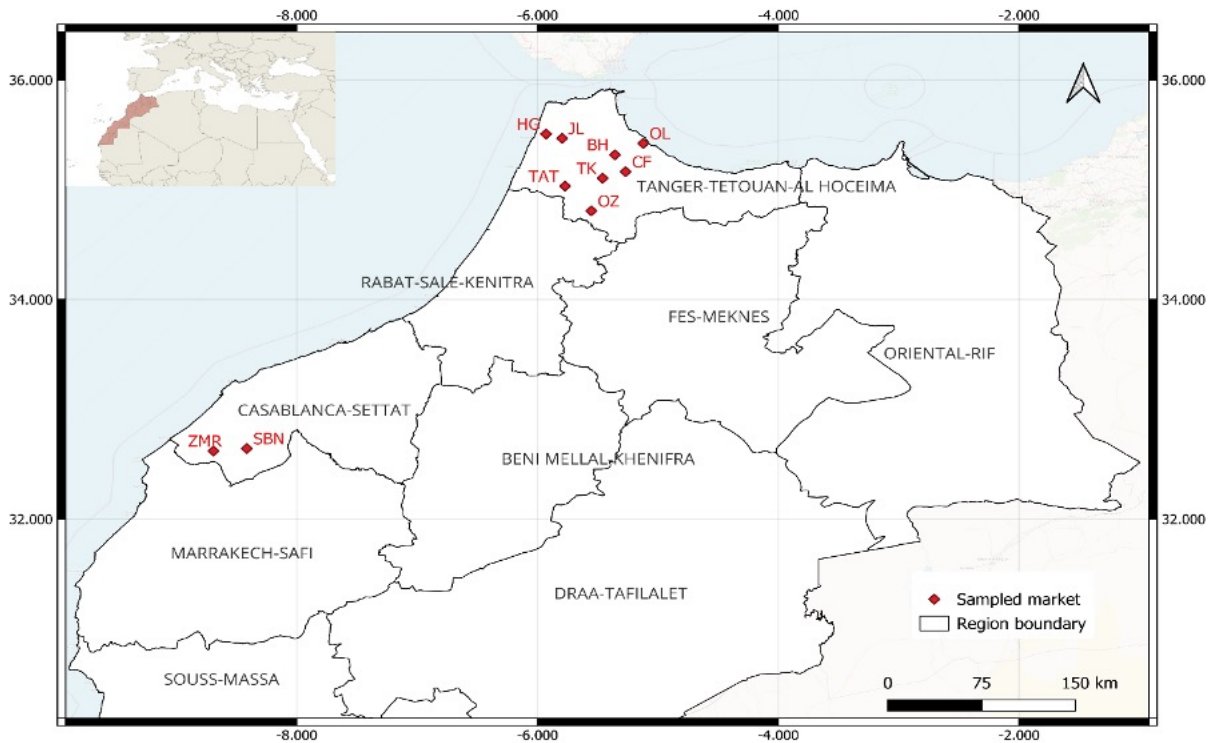


Figure 1. Elevation map of Morocco with sampling locations marked. Site abbreviations correspond to the following localities: OL: Oued Laou (OL1, OL2), BH: Beni Hassan (BH1–BH4), JL: Jbel Lahbib, TK: Tanakoub (TK1–TK3), CF: Chefchaouen (CF1, CF2), OZ: Ouazzane (OZ1–OZ3), TAT = Tatoft, HG: Had Gharbia, ZMR: Zemmamra, and SBN: Sidi Bennour. Insertion Map of part of the Mediterranean showing the position of Morocco (red colored area)

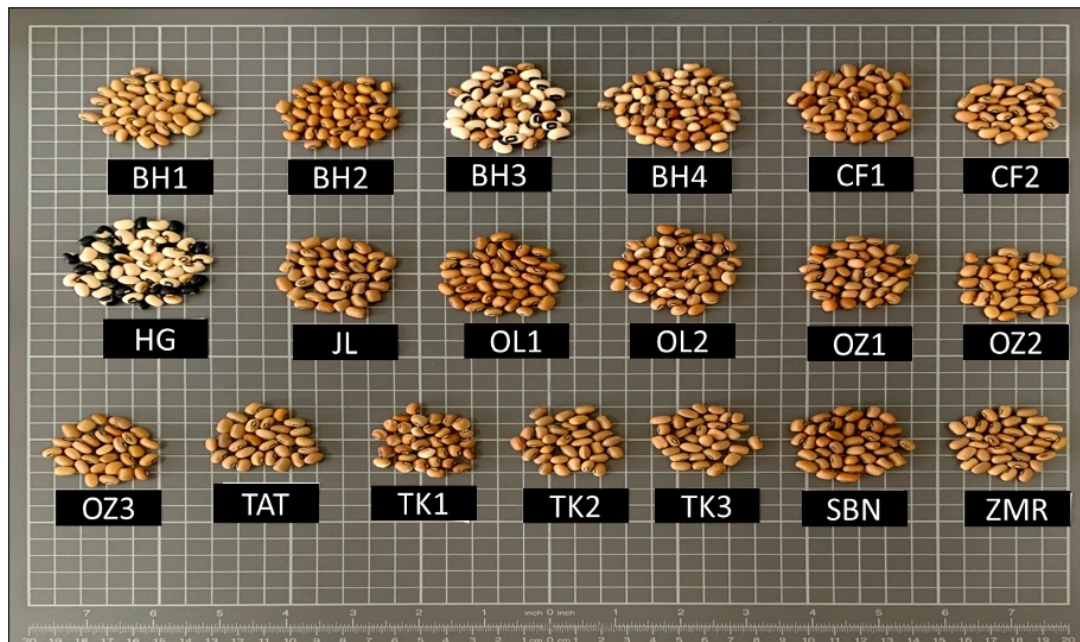


Figure 2. Seed morphology diversity among 19 populations, illustrating the variation in seed qualitative traits (seed shape, seed color, seed color aspect, eye pattern, eye color, and testa texture).

Seed Morphological Characterization

The morphological characterization of the collected populations was assessed using a representative sample of 90 seeds per population, arranged in three replicates of 30 randomly selected seeds each. Seeds of *Vigna unguiculata* (L.) Walp. were characterized based on both qualitative and quantitative traits, following a descriptor list (IBPGR, 1983). Five qualitative traits were visually assessed, including seed shape (SPS), eye color (ECL) eye pattern (EPT), seed texture (STX), and testa splitting (SPT). In addition, the uniformity of seed coat color (SCM) and seed coat color (SCC), was assessed according to Al-Saady et al. (2018). Quantitative characterization involved five traits. The three major seed measurements, length (L), width (W), and thickness (TH), were measured using a digital calliper with a precision of 10^{-2} mm. Furthermore, one seed weight (OSW) and a hundred seed weight (HSW), with three repetitions, were determined using an electronic balance with a precision of 10^{-4} g.

Statistical analysis

All statistical analyses were performed using R software version 4.3.1 (R core Team 2023). Germination parameters were estimated using the GerminaR package (Lozano-Isla et al., 2019), with a focus on a subset of parameters (germination percentage (GRP), mean germination time (MGT), mean germination rate (MGR), synchronization index (SYN), and uncertainty index (UNC)), while precocity (PR) and germination duration (DG) were calculated separately following El Fatehi et al. (2014). The data obtained from both quantitative traits and germination parameters were subjected to standard descriptive statistics (mean, standard deviation (SD), and coefficient of variation (CV%)), using the dplyr package (Wickham et al. 2023). Statistical intra- and inter-population comparisons were performed using one-way analysis of variance (ANOVA), and means were compared using the Student–Newman–Keuls (SNK) test at a 0.05 significance level when differences were found to be significant, employing the multcomp (Hothorn et al. 2008) and agricolae (Mendiburu and Yaseen 2020) R packages. Principal component analysis (PCA) was carried out using the FactoMineR package (Lê et al., 2008) to simplify the quantitative traits and germination parameters, as well as represent the interaction among the studied populations.

Results

Seed germination

The results of analysis of variance (ANOVA) revealed a highly significant variation for the majority of the parameters studied, except for germination percentage (GRP (%)) and synchronization index (SYN) (Table 1). The results indicate that the main differences among populations are related to the time taken to germinate. The coefficient of variation highlighted substantial variability, exceeding 22% for all parameters, except for germination percentage (GRP (%)), which exhibited lower variability (5.23%) (Table 1). The comparison of population means using the SNK test at the 5% significance level revealed distinct groupings for each germination parameter. Mean germination time (MGT (Number of day)) differentiated the populations into five groups, followed by mean germination rate (MGR (Number of day⁻¹)) with four groups. Germination duration (DG (Number of day)) and uncertainty index (UNC (bit)) formed three groups each, while germination percentage (GRP (%)) and precocity (PR (Number of day)) were classified into two groups. Synchronization index (SYN), however, did not make differentiations between populations, forming a single group (Table 1).

Regarding germination percentage (GRP (%)), the overall mean was $98.60\% \pm 5.15$. Notably, sixteen populations achieved a germination percentage of 100%, while the lowest values were recorded for population TK3 ($96.67\% \pm 5.77$), population HG ($90\% \pm 10$), and population OL2 ($86.67\% \pm 15.28$) (Table 1, Fig. 3). As for precocity (PR (Number of day))

values ranged from 1 to 2 days (1.23 ± 0.24 days), with a significant variation of 27.92%. Germination duration (DG (Number of days)) ranged from 1 to 4 days (2.63 ± 0.64 days). The OL1 population exhibited the shortest germination duration (1.67 ± 0.58 days), whereas populations TK1 and TK2 recorded the longest (3.67 ± 0.58 days each) (Table 1, Fig. 3). In terms of mean germination time (MGT (Number of days)), the mean across populations was (1.96 ± 0.49 days). The ZMR population showed the longest mean (2.73 ± 0.15 days), while OL1 population showed the shortest mean (1.37 ± 0.32 days). In contrast, the mean germination rate (MGR (Number of day⁻¹)) expressed the highest value in OL1 (0.76 ± 0.21 day⁻¹) and the lowest value in the ZMR population (0.37 ± 0.02 day⁻¹), with an overall mean of (0.54 ± 0.14 day⁻¹). For the uncertainty index (UNC (bit)) and synchronization index (SYN), the overall mean was (1.08 ± 0.37 bit) and (0.50 ± 0.15), respectively. The highest uncertainty index (UNC (bit)) value was recorded in population TK1 (1.73 ± 0.32 bit), whereas the highest synchronization index (SYN) was observed in OL1 (0.66 ± 0.29). Conversely, the lowest uncertainty index (UNC (bit)) was found in OL1 (0.66 ± 0.57 bit), and the lowest synchronization index (SYN) in TK1 (0.30 ± 0.08) (Table 1).

Table 1: Analysis of Variance of germination seed parameters among 19 *Vigna unguiculata* L. Populations.

POPULATION	GRP (%)	PR (day)	DG (day)	MGT (day)	MGR (day ⁻¹)	UNC (bit)	SYN
OL1	100 ^a	1.00 ± 0.00^b	1.67 ± 0.58^c	1.37 ± 0.32^c	0.76 ± 0.21^a	0.66 ± 0.57^c	0.66 ± 0.29^a
OL2	86.67 ± 15.28^b	1.67 ± 0.58^b	2.67 ± 0.58^b	2.18 ± 0.67^c	0.50 ± 0.19^d	0.98 ± 0.01^c	0.49 ± 0.01^a
BH1	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.43 ± 0.12^c	0.70 ± 0.06^b	0.96 ± 0.07^c	0.51 ± 0.05^a
BH2	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.50 ± 0.20^c	0.67 ± 0.09^c	0.92 ± 0.07^c	0.54 ± 0.05^a
BH3	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.63 ± 0.15^c	0.62 ± 0.06^d	0.90 ± 0.15^c	0.55 ± 0.10^a
BH4	100 ^a	1.33 ± 0.58^b	3.00 ± 0.00^b	2.03 ± 0.38^c	0.50 ± 0.10^d	1.15 ± 0.37^c	0.49 ± 0.16^a
TK1	100 ^a	1.00 ± 0.00^b	3.67 ± 0.58^a	2.30 ± 0.56^d	0.45 ± 0.12^d	1.73 ± 0.32^a	0.30 ± 0.08^a
TK2	100 ^a	1.33 ± 0.58^b	3.67 ± 0.58^a	2.60 ± 0.36^a	0.39 ± 0.06^d	1.73 ± 0.32^a	0.32 ± 0.04^a
TK3	96.67 ± 5.77^a	1.00 ± 0.00^b	2.33 ± 0.58^c	1.92 ± 0.37^c	0.53 ± 0.10^d	1.62 ± 0.20^b	0.57 ± 0.22^a
CF1	100 ^a	1.67 ± 0.58^{ab}	3.00 ± 0.00^b	2.27 ± 0.15^d	0.44 ± 0.03^d	0.93 ± 0.45^c	0.57 ± 0.22^a
CF2	100 ^a	1.00 ± 0.00^b	3.00 ± 0.00^b	2.00 ± 0.20^c	0.50 ± 0.05^d	1.47 ± 0.09^c	0.57 ± 0.22^a
OZ1	100 ^a	1.00 ± 0.00^b	3.00 ± 0.00^b	1.73 ± 0.32^c	0.59 ± 0.10^d	1.36 ± 0.21^c	0.41 ± 0.10^a
OZ2	100 ^a	1.00 ± 0.00^b	3.00 ± 0.00^b	1.90 ± 0.10^c	0.53 ± 0.03^d	1.35 ± 0.18^c	0.43 ± 0.09^a
OZ3	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.73 ± 0.15^c	0.58 ± 0.05^d	0.77 ± 0.27^c	0.63 ± 0.16^a
TAT	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.43 ± 0.32^c	0.72 ± 0.15^b	0.78 ± 0.09^c	0.63 ± 0.06^a
JL	100 ^a	1.00 ± 0.00^b	2.00 ± 0.00^c	1.60 ± 0.10^c	0.63 ± 0.04^d	0.95 ± 0.06^c	0.52 ± 0.04^a
HG	90 ± 10^b	1.33 ± 0.58^{ab}	3.00 ± 0.00^b	2.40 ± 0.19^c	0.42 ± 0.03^d	1.30 ± 0.29^c	0.41 ± 0.09^a
ZMR	100 ^a	2.00 ± 0.00^a	3.00 ± 0.00^b	2.73 ± 0.15^a	0.37 ± 0.02^d	0.77 ± 0.27^c	0.63 ± 0.16^a
SBN	100 ^a	2.00 ± 0.00^a	3.00 ± 0.00^b	2.57 ± 0.21^b	0.39 ± 0.03^d	0.90 ± 0.15^c	0.55 ± 0.10^a
OVERALL MEAN \pm SD	98.60 ± 5.15	1.23 ± 0.24	2.63 ± 0.64	1.96 ± 0.49	0.54 ± 0.14	1.08 ± 0.37	0.50 ± 0.15
MIN	70.00	1	1	1.00	0.34	0.00	0.26
MAX	100.00	2	4	2.90	1.00	1.92	1.00
CV (%)	5.23	27.92	22.21	24.92	25.97	34.83	29.77
F	2.17 *	4.24 ***	12.62 ***	5.89***	4.64 ***	3.89 ***	1.96*

Values are presented as mean \pm standard deviation (SD) for each population. Overall mean \pm SD represents the mean across all populations, minimum (Min), maximum (Max), coefficient of variation (CV %), the Student–Newman–Keuls test at $\alpha = 5\%$ (SNK groups), and F-value indicating significant differences among populations (NS: not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Populations: OL = Oued Laou (OL1, OL2); BH = Beni Hassan (BH1–BH4); JL = Jbel Lahbib; TK = Tanakoub (TK1–TK3); CF = Chefchaouen (CF1, CF2); OZ = Ouazzane (OZ1–OZ3); TAT = Tatofit; HG = Had Gharbia; ZMR = Zemmamra; SBN = Sidi Bennour. Parameters: GRP = germination percentage; PR = precocity; DG = germination duration; MGT = mean germination time; MGR = mean germination rate; UNC = uncertainty index; SYN = synchronization index.

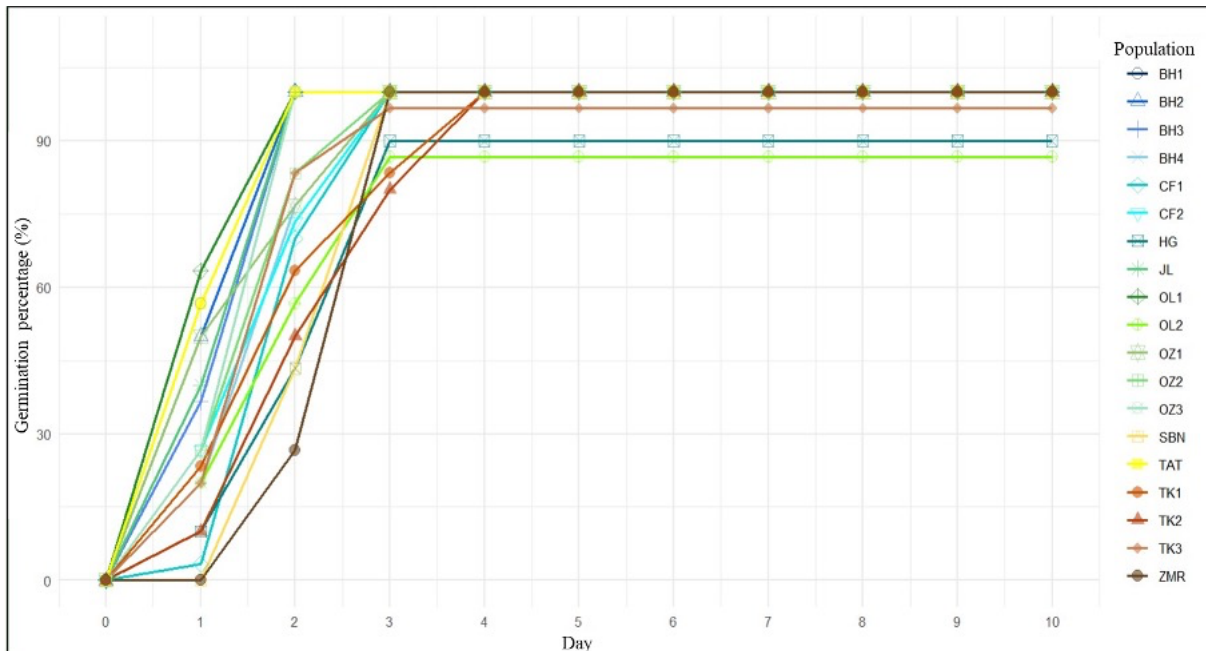


Figure 3. Temporal dynamics of cowpea seed germination: cumulative germination percentage over time across populations.

Seed Morphological Characterization

The analysis of variance (ANOVA) conducted on five quantitative traits across the studied populations revealed highly significant differences ($P < 0.001$) (Table 2), indicating substantial morphological diversity among individuals within these populations. This variation is particularly pronounced for seed weight-related traits, as evidenced by the high F-values ($F = 17.10$ for one-seed weight (OSW) and $F = 12.03$ for hundred-seed weight (HSW)). The Student–Newman–Keuls (SNK) test at the 5% significance level (Table 2) identified distinct groupings of populations based on quantitative seed traits. For seed length (L(mm)), thickness (TH (mm)), and one seed weight (OSW (mg)), populations were divided into six groups. In contrast, five and four groups were identified for seed width (W (mm)) and hundred-seed weight (HSW (mg)), respectively (Table 2).

The HG population recorded the highest mean values for seed length (8.57 ± 1.11 mm), width (6.30 ± 0.48 mm), and thickness (5.23 ± 0.54 mm), whereas the BH3 population had the shortest seeds (7.45 ± 0.66 mm). The OL2 population exhibited the narrowest seeds (5.73 ± 0.26 mm), and the BH4 population had the thinnest seeds (4.52 ± 0.26 mm). For seed weight, the TAT population showed the highest value, while the BH4 population recorded the lowest for both weight-related traits. Mean values for one seed weight (OSW) ranged from (0.13 ± 0.01 mg) to (0.20 ± 0.02 mg), whereas hundred-seed weight (HSW) varied from (12.82 ± 0.54) mg to (19.00 ± 0.16 mg).

Table 2. Analysis of Variance of Morphological Traits among 19 *Vigna unguiculata* L. Populations.

POPULATION	L (MM)	W (MM)	TH (MM)	OSW (G)	HSW (G)
BH1	7.74 ±0.40 ^f	5.90±0.31 ^e	4.76±0.29 ^e	0.15±0.02 ^f	13.98±0.53 ^d
BH2	7.91±0.68 ^f	5.99±0.40 ^e	4.85±0.31 ^e	0.15±0.02 ^f	13.41±0.26 ^d
BH3	7.45±0.66 ^f	6.02±0.36 ^e	4.81±0.33 ^e	0.16±0.03 ^d	16.19±0.63 ^b
BH4	7.56±0.56 ^f	5.80±0.28 ^e	4.52±0.26 ^f	0.13±0.01 ^f	12.82±0.54 ^d
CF1	8.04±0.41 ^d	6.00±0.30 ^e	4.88±0.26 ^e	0.16±0.02 ^c	14.85±0.61 ^c
CF2	7.93±0.62 ^f	5.87±0.39 ^e	5.05±0.33 ^c	0.16±0.02 ^d	15.18±0.20 ^c
HG	8.57±1.11 ^a	6.30±0.48 ^a	5.23±0.54 ^a	0.18±0.04 ^b	18.63±0.21 ^a
JL	7.73 ±0.54 ^f	5.86±0.44 ^e	4.86±0.32 ^e	0.16±0.02 ^c	15.17±0.36 ^c
OL1	7.82±0.42 ^f	5.73±0.26 ^e	4.71±0.37 ^e	0.14±0.02 ^f	13.34±0.72 ^d
OL2	7.52±0.45 ^f	5.90±0.41 ^e	4.76±0.52 ^e	0.15±0.03 ^f	13.94±0.59 ^d
OZ1	8.31±0.45 ^b	6.27±0.34 ^b	4.99±0.31 ^d	0.16±0.02 ^d	13.39±1.31 ^d
OZ2	8.16±0.46 ^c	6.11±0.34 ^d	4.78±0.21 ^e	0.16±0.02 ^d	13.82±0.64 ^d
OZ3	8.22±0.59 ^c	6.27±0.27 ^b	5.15±0.23 ^a	0.16±0.02 ^d	13.83±0.12 ^d
SBN	7.75±0.60 ^f	5.95±0.36 ^e	4.75±0.33 ^e	0.14±0.01 ^f	13.98±1.53 ^d
TAT	8.49±0.58 ^b	6.25±0.43 ^b	5.12±0.35 ^a	0.20±0.02 ^a	19.00±0.16 ^a
TK1	7.77±0.41 ^f	6.23±0.35 ^c	4.99±0.22 ^d	0.16±0.02 ^d	13.28±0.94 ^d
TK2	7.98±0.63 ^e	6.09±0.42 ^d	5.08±0.20 ^b	0.16±0.02 ^d	15.10±0.71 ^c
TK3	7.98±0.46 ^e	6.02±0.33 ^e	4.87±0.24 ^e	0.15±0.02 ^e	13.73±0.09 ^d
ZMR	7.83±0.55 ^f	5.94±0.37 ^e	4.77±0.26 ^e	0.16±0.02 ^d	14.02±0.43 ^d
Overall mean ± SD	7.93±0.65	6.03±0.40	4.89±0.37	0.16±0.03	14.61±1.76
Min	6.24	4.91	3.87	0.10	12.01
Max	10.62	7.40	6.17	0.25	19.11
CV (%)	8.13	6.57	7.47	17.10	12.03
F	8.54 ***	6.71 ***	9.15 ***	12.29 ***	19.12 ***

Values are presented as mean ± standard deviation (SD) for each population. Overall mean ± SD represents the mean across all populations, minimum (Min), maximum (Max), coefficient of variation (CV %), the Student–Newman–Keuls test at $\alpha = 5\%$ (SNK groups), and F-value indicating significant differences among populations (NS: not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$). Populations: OL = Oued Laou (OL1, OL2); BH = Beni Hassan (BH1–BH4); JL = Jbel Lahbib; TK = Tanakoub (TK1–TK3); CF = Chefchaouen (CF1, CF2); OZ = Ouazzane (OZ1–OZ3); TAT = Tatoft; HG = Had Gharbia; ZMR = Zemmamra; SBN = Sidi Bennour. Traits: L= length, W= width, TH= thickness, OSW= one seed weight, HSW= hundred-seed weight

Subsequently, the kidney–rhomboid shape was observed in four populations (TK3, OZ1, OZ2, SBN). Thus, the ovoid shape was recorded in three populations (BH3, BH4, TK1), while the ovoid–globose, rhomboid, kidney–ovoid, and globose shapes were each observed in a single population (OL2, JL, HG, and BH2, respectively), reflecting a nearly equal distribution of these less frequent forms. Concerning seed color, 14 populations exhibited uniformly brown seeds with a self-colored brown eye (Table 3). In contrast, five populations (BH3, BH4, HG, OL2, and TK1) were heterogeneous, showing variability in seed color ranging from brown to beige, except for HG, which displayed seeds with a distinctive, black-mottled seed coat. All beige seeds had brown eyes, except in BH3 and HG, where both brown and black eye colors were observed. Among beige-colored seeds, eye pattern variation was particularly pronounced. Populations OL2 and TK1 exhibited the Holstein group pattern, while population BH4 showed both Holstein group and Kabba group patterns. Population BH3 displayed both small eye and Kabba group patterns. Distinctively, the HG population showed seeds with six different eye

patterns, namely Holstein group - small eye - narrow eye - Kabba group - Watson - Narrow eye (Table 3, Fig. 2). Concerning seed coat texture, the studied populations showed a very heterogeneous texture, ranging from smooth to wrinkled. Smooth seed surfaces were observed in BH4, JL, and OZ2, whereas BH3 and HG had wrinkled seeds. According to the qualitative trait analysis of the seeds, testa splitting was the only non-discriminating trait, as it was absent in all evaluated cowpea populations.

Table 3: Qualitative Morphological Traits of Seeds from Local Cowpea Populations.

POPULATION	SEED SHAPE	SEED COLOR	SEED COLOR ASPECT	EYE PATTERN	EYE COLOR	SPLITTING OF TESTA	TESTA TEXTURE
BH1	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
BH2	Globose	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
BH3	Ovoid	Cream-Brown	Heterogeneous	Small eye-Self-colored-kabba group	Black-Brown	Absent	Wrinkled
BH4	Ovoid	Cream-Brown	Heterogeneous	Holstein-Kabba group-Self-coloured	Brown	Absent	Smooth
CF1	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
CF2	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough to wrinkled
HG	Kidney - Ovoid	Cream-Black	Heterogeneous	Holstein group – Small eye-Kabba group – Watson group – Narrow eye – Self-colored	Black - Brown	Absent	Wrinkled
JL	Rhomboid	Brown	Homogeneous	Self-colored	Brown	Absent	Smooth
OL1	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Smooth to rough
OL2	Ovoid - Globose	Cream-Brown	Heterogeneous	Holstein group-Self-colored	Brown	Absent	Rough to wrinkled
OZ1	Kidney-Rhomboid	Brown	Homogeneous	Self-colored	Brown	Absent	Rough to wrinkled
OZ2	Kidney-Rhomboid	Brown	Homogeneous	Self-colored	Brown	Absent	Smooth
OZ3	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
SBN	Kidney-Rhomboid	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
TAT	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
TK1	Ovoid	Cream-Brown	Heterogeneous	Holstein group-Self-colored	Brown	Absent	Rough to wrinkled
TK2	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Rough
TK3	Kidney-Rhomboid	Brown	Homogeneous	Self-colored	Brown	Absent	Smooth to rough
ZMR	Kidney	Brown	Homogeneous	Self-colored	Brown	Absent	Smooth to rough

OL = Oued Laou (OL1, OL2); BH = Beni Hassan (BH1–BH4); JL = Jbel Lahbib; TK = Tanakoub (TK1–TK3); CF = Chefchaouen (CF1, CF2); OZ = Ouazzane (OZ1–OZ3); TAT = Tatof; HG = Had Gharbia; ZMR = Zemmamra; SBN = Sidi Bennour.

Multivariate analysis

The principal component analysis (PCA) of germination and seed morphological traits in the 19 cowpea populations revealed that the first three principal components together accounted 69.54% of the total variance. The first axis (PC1), which explained 33.76 % of the total variation, was strongly influenced and impacted by seed size traits ((thickness (TH) (20.33), width (W) (17.55), length (L) (16.62), and one seed weight (OSW) (15.89)). The second axis (PC2), contributed 23.85 % of the variance and was associated with germination dynamics (mean germination rate (MGR) (23.87), mean germination time (MGT) (22.57), synchronization index (SYN) (17.03), and uncertainty index (UCN) (16.74)). The third axis (PC3) captured 11.9 % of the variation and was characterized by seed mass and germination performance ((PR) (31.66), germination duration (DG) (25.67), hundred seed weight (HSW) (14.95), and germination percentage (GRP) (8.64)) (Table 4, Table 5).

The projection of populations on the factorial plane (PC1–PC2) revealed a structured gradient along the first axis, from the positive to the negative pole. As a result, four major population clusters were distinguished. These groupings are closely related to differentiation in germination and morphological characteristics (Fig. 4), reflecting also a geographical pattern in the distribution of populations sharing similar trait profiles. The first group consists of six populations (BH1, BH2, BH3, BH4, OL1, and JL) that are negatively correlated with the first principal component (PC1). These populations, mainly clustered all the population from the Beni Hassan region, are characterized by high germination performance despite smaller seed size (low values of length (L), width (W), thickness (TH), hundred-seed weight (HSW), and single seed weight (OSW)). The second group includes five populations (CF1, OL2, TK3, SBN, and ZMR), which are negatively correlated with both PC1 and PC2. Although this group is geographically dispersed, it notably includes the populations SBN and ZMR, originating from the Casablanca-Settat region. Seeds in this group are characterized by small size and poor, delayed, and poorly synchronized germination. The third group (CF2, OZ1, OZ2, TK1, and TK2) consists of populations that are positively correlated with PC1 and negatively with PC2. These groups include two populations, each from the Tanakoub and Ouazzane regions, characterized by moderate seed size and germination performance. Finally, the fourth group includes three populations (HG, OZ3, and TAT) that are significantly and positively correlated with PC1. These populations are distinguished by the largest, widest, thickest seeds with high values across all morphological traits. While TAT and OZ3 display rapid and synchronized germination, HG shows slightly delayed and less uniform germination.

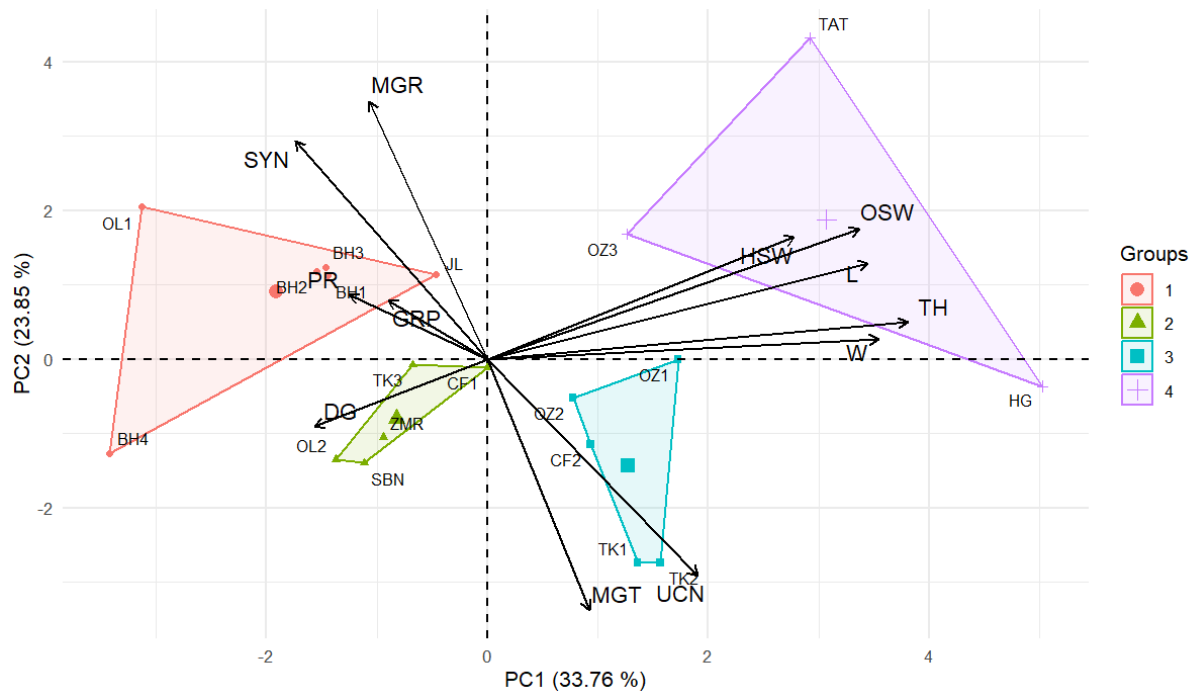


Figure 4. Principal component analysis (PCA) biplot of the studied 19 cowpea populations.

Table 4. Eigenvalues, individual and cumulative percentage of variance explained by the first three principal components (PCs).

Principal Component	PC1	PC2	PC3
Eigenvalues	4.05	2.86	1.43
Explained proportion of variation	33.76	23.85	11.93
Cumulative proportion of variation	33.76	57.61	69.54

Table 5. Trait loadings and contributions of dimensional variations (ctr) explained by the first three Principal Components (PCs).

Variable	PC1.	ctr (PC1)	PC2	ctr (PC2)	PC3	ctr (PC3)
SYN	-0.41	4.22	0.70	17.03	0.18	2.21
UCN	0.45	5.07	-0.69	16.74	-0.18	2.21
GRP	-0.21	1.12	0.19	1.23	-0.35	8.64
MGT	0.22	1.19	-0.80	22.57	0.29	5.75
MGR	-0.26	1.61	0.83	23.87	-0.24	3.97
PR	-0.30	2.18	0.21	1.50	0.67	31.66
DG	-0.37	3.42	-0.22	1.62	0.61	25.67
L	0.82	16.62	0.31	3.32	-0.13	1.21
W	0.84	17.55	0.07	0.15	-0.01	0.01
TH	0.91	20.33	0.12	0.50	0.01	0.00
OSW	0.80	15.89	0.42	6.13	0.23	3.72
HSW	0.66	10.81	0.39	5.35	0.46	14.95

GRP: germination percentage, PR: precocity, DG: germination duration, MGT: mean germination time, MGR: mean germination rate, UNC: uncertainty index, SYN: synchronization index, L: length, W: width, TH: thickness, OSW: one seed weight, HSW: hundred-seed weight.

Discussion

Morocco is considered a key refuge for agricultural biodiversity, thanks to its diversified agroecosystems and the practices of farmers that support and preserve the diversity of cultivated crops (Achtaq et al. 2010; El Fatehi et al. 2021; Toujgani et al. 2022; Hmimsa et al. 2024; Chmarkhi et al. 2024). However, the long and frequent periods of drought observed in recent years have harmed crop growth, geographical distribution, and yields (Kassout et al. 2022). In response to this increasing climatic pressure, landraces are particularly valued for their genetic diversity and ability to resist environmental stresses. They represent an important lever for improving the resilience of agricultural systems and ensuring food security (Lazaridi et al. 2024). Thus, the identification, characterization and evaluation of local crop or plant genetic heritages appear to be priority actions. This study aims to assess the germination and diversity of cowpea seeds sold in various weekly markets across Morocco.

Seed Germination

Cowpea seed germination revealed significant differences among the studied parameters, with very high intra- and inter-population variation. The most collected populations exhibit seeds with high germination, characterized by a high germination capacity, exceeding 98%, and early and rapid germination, occurring within 1 to 4 days. Similar results have been reported in previous studies on the same species under controlled germination conditions (Ravelombola

2017; Paiva et al. 2018; Widajati et al. 2023; Afonso et al. 2025), as well as for different varieties of vetch (El Fatehi et al. 2014), beans (Fountain et al. 1990), and peas (Kende et al. 2024). Such high germinability indicates that most seeds retained excellent physiological quality, resulting from intrinsic factors, including seed reserves and the genetic adaptation of the parent plant (Carrera-Castaño et al., 2020), as well as extrinsic factors related to biotic and abiotic environmental conditions (Lamichhane et al., 2018). For mean germination time (MGT), the results revealed significant variation, indicating irregularity in germination speed among the studied populations. This fluctuation may be attributed to the physiological status of the seeds, as older seeds generally exhibit a higher mean germination time (MGT), which slows their ability to germinate and grow efficiently (Mavi et al. 2010). Since the mean germination time (MGT) is defined as the inverse of the mean germination rate (MGR), a negative relationship was observed between the mean germination time (MGT) and the mean germination rate (MGR). A lower mean germination time (MGT) is typically considered a key indicator of seed vigour, reflecting strong seedling emergence performance. This is because higher mean germination rate (MGR) values are directly associated with better seed performance and optimized field emergence. This relationship is critical, as rapid germination enables seeds to more effectively overcome abiotic constraints, as well as biotic pressures such as pathogen attacks (Vleugels et al. 2011; Weston et al. 2000). The uncertainty index and germination synchronization have often been used in conjunction with other parameters to provide an overall assessment of seed performance (Genze et al. 2020). For these indices, the results showed that the populations germinated irregularly and asynchronously. The TK1 population showed a higher uncertainty index and mean germination time, which indicates slower synchrony and mean germination rate. This correlation showed that seeds germinate over a longer period, which may affect the success of seedling establishment.

Seed Morphological Characterization

Morphological diversity across nineteen local Moroccan populations confirmed the presence of substantial variation for the same trait both within and between populations. These observations stand in contrast to the findings of Ghalmi et al. (2010) in Algeria and Morales-Morales et al. (2024) in southeastern Mexico, who reported minimal intra-population variation among local cowpea varieties. In contrast, our results corroborate previous reports from Greece (Lazaridi et al., 2017), Southern European countries (Carvalho et al., 2017b), and Mozambique (Gomes et al., 2021), all of which documented considerable morphological variability both within and across cowpea landraces. The genetic variability observed among the different populations in this study may result from farmer-driven selection practices, which are often based on morphological criteria such as fruit shape and color. Although these selection preferences are subjective, they can introduce genetic variation within landraces, thereby contributing to the observed diversity (Orobiyi et al. 2018; Cebolla et al. 2013). Notable differences were observed in the morphological traits of seeds. When comparing our results with previous studies, we found similarities with the data reported by Gomes et al. (2021) in Mozambique, particularly regarding seed length (7.80 mm), width (6.50 mm), and thickness (4.63 mm). Furthermore, our results are in agreement with those of Gerrano et al. (2019) in South Africa concerning the average weight of a single seed (0.16 g), as well as with Nkoana et al. (2019) for the average weight of 100 seeds (14.61 g). For qualitative traits, substantial phenotypic variability was observed both within and between populations. Regarding seed color, eye pattern, and eye color, the majority of the collected cowpea populations exhibited a homogenized brown coloration with a self-colored eye. However, four populations from the northern region showed considerable variability within the same population. This mixture of seeds could be due to mixing by farmers (Al-Saady et al. 2018), by seed collectors, or by traders. Such heterogeneity is evidence of the potential presence and persistence of this crop in Morocco,

particularly in traditional agroecosystems, especially those in the north, which play the role of genetic resource conservatories (Hmimsa et al. 2008; El Fatehi et al. 2021). The availability and presence of local cowpea populations with high genetic diversity underlines the importance of the cowpea gene pool in Morocco, which is linked to the adaptation of the crop to local conditions over the centuries, as observed in Algeria (Basseddik & Tellah 2021), and may also be due to traditional agricultural practices. This diversity reflects the existence of a local conservation strategy pursued by farmers through continuous cultivation and local seed selection.

Multivariate analysis

The principal component analysis (PCA) revealed a marked structuring of morphological and germinative traits within the different populations studied (Fig. 4). The first axis (PC1) is mainly explained by traits describing seed size. Doumbia et al. (2013) and Molosiwa et al. (2016) also obtained similar results, where seed length, seed width, seed thickness, and seed weight were revealed to be valuable traits in the discrimination of cowpea populations. The second axis (PC2) groups variables associated with germination dynamics. While the third axis (PC3) is influenced by mixed parameters linking seed mass and germination performance. The projection of populations on the factor plane (PC1 – PC2) allowed us to divide the populations into four main groups with a coherent spatial organization, suggesting that the structuring of morphological and germination traits is influenced by the geographical context. This spatial organization is principally attributable to the connectivity of the weekly markets, given their approximation, promoting the exchange of this genetic heritage through the seed circuit between farmers and itinerant traders, which could explain the points of similarity between the different populations studied. The first group, which is characterized by high germinative performance with small seeds, would suggest a local selection that has favored rapid emergence to the detriment of seed size. The second group includes populations with small seeds and low germination potential, which could indicate that these seeds have been exposed to harsh growing conditions during their growth cycle or due to their physiological status. The third group comprises populations with moderate germinative and morphological characteristics. These characteristics could result from the plant's adaptation to variable environments at different development stages, or the complex interaction between genotype and environment (Xue et al. 2021; Bhatt et al. 2025). The fourth group includes populations with heavy, long, large, and thick seeds. These seeds are thought to be more attractive and influence demand on the food markets (Egbadzor et al. 2013).

Conclusion

This study highlights the persistence of cowpea cultivation in Morocco, despite its classification as a marginalized and underutilized legume. Its continued presence in low-input farming systems reflects a local conservation strategy maintained by farmers. Using a combined germination and morphological approach, the results revealed substantial variability observed both within and between the nineteen traditional cowpea populations. Germination performance was remarkable, with high germination capacity and rapid rates, indicating an almost complete absence of dormancy, while seed morphological traits exhibited substantial intra- and inter-population variability, highlighting significant phenotypic richness among the nineteen local populations studied. Principal component analysis (PCA) distinguished four main groups with a coherent spatial arrangement, suggesting that the structuring of morphological and germination traits is influenced by the geographical context. The genetic diversity of traditional Moroccan cowpea offers opportunities for in-situ conservation, improvement of locally adapted varieties, and revitalization of this neglected crop. Promoting these landraces can enhance food

security, support rural livelihoods, and strengthen the sustainability and resilience of Moroccan agroecosystems, particularly if complemented by a more in-depth agro-morphological evaluation to identify the most discriminating traits and populations for local breeding programs.

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