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Population-level variations in morphological and physical seed traits of *Quercus cerris* L. in Türkiye

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ABSTRACT: Oaks represent ecologically dominant and evolutionarily dynamic components of temperate forest ecosystems, yet intraspecific variation in reproductive traits remains insufficiently documented for many species. This study aimed to quantify and compare population-level variation in seed morphological and physical traits of *Quercus cerris* L. across different biogeographical regions of Türkiye. Mature seeds were collected from five natural populations located in the Black Sea (Samsun), Central Anatolia (Eskişehir), Aegean (Manisa and Afyonkarahisar), and Marmara (Balıkesir) regions. A total of 500 sound seeds were measured for seed length (SL), seed width (SW), seed shape (SS), seed size (SSi), seed volume (V), thousand-seed weight (TSW), and seed moisture content (SMC). Data were analyzed using one-way ANOVA, Duncan's test, correlation analysis, hierarchical clustering, and principal component analysis (PCA). Significant differences among populations were detected for all investigated traits ($p < 0.05$). Size- and weight-related variables exhibited the strongest inter-population differentiation, whereas SMC showed comparatively lower variation. PCA revealed that the first two principal components explained 98.19% of the total variance, with the primary axis associated mainly with seed size and mass. Western populations (Manisa and Balıkesir) were characterized by larger and heavier seeds, while other populations showed comparatively smaller morphometric values. These findings indicate pronounced intraspecific morphological differentiation in *Q. cerris* and suggest that seed size constitutes a key component of population-level variability. The results provide a scientific basis for seed source selection, conservation planning, and adaptive forest management under heterogeneous environmental conditions.

Keywords: Turkey oak, acorn morphometrics, intraspecific variability, population differentiation

Türkiye'de *Quercus cerris* L. tohumlarinin morfolojik ve fiziksel özelliklerinde populasyon düzeyinde varyasyonlar

ÖZET: Meşeler, ılıman orman ekosistemlerinin ekolojik olarak baskın ve evrimsel açıdan dinamik bileşenlerini temsil etmekle birlikte, birçok türde üreme özelliklerine ilişkin tür içi varyasyon yeterince belgelenmemiştir. Bu çalışma, *Quercus cerris* L. türünde farklı biyocoğrafik bölgelerdeki populasyonlar arasında tohum morfolojik ve fiziksel özelliklerindeki varyasyonu nicel olarak belirlemeyi ve karşılaştırmayı amaçlamıştır. Olgun tohumlar, Karadeniz (Samsun), İç Anadolu (Eskişehir), Ege (Manisa ve Afyonkarahisar) ve Marmara (Balıkesir) bölgelerinde yer alan beş doğal populasyondan toplanmıştır. Toplam 500 sağlam tohumda tohum boyu (SL), tohum eni (SW), tohum şekli (SS), tohum büyüklüğü (SSi), tohum hacmi (V), bin tane ağırlığı (TSW) ve tohum nem içeriği (SMC) ölçülmüştür. Veriler tek yönlü varyans analizi (ANOVA), Duncan testi, korelasyon analizi, hiyerarşik kümeleme ve temel bileşenler analizi (PCA) kullanılarak değerlendirilmiştir. Tüm incelenen özellikler bakımından populasyonlar arasında istatistiksel olarak anlamlı farklılıklar belirlenmiştir ($p < 0,05$). Boyut ve ağırlıkla ilişkili değişkenler (SL, SW, SSi, V ve TSW) populasyonlar arası en güçlü ayrışmayı gösterirken, SMC görece daha düşük varyasyon sergilemiştir. PCA sonuçları, ilk iki temel bileşenin toplam varyansın %98.19'unu açıkladığını ve birincil eksenin esas olarak tohum boyutu ve kütlesi ile ilişkili olduğunu ortaya koymuştur. Batı populasyonları (Manisa ve Balıkesir) daha büyük ve daha ağır tohumlarla karakterize edilirken, diğer populasyonlarda görece daha küçük morfometrik değerler saptanmıştır. Elde edilen bulgular, *Q. cerris*'te belirgin bir tür içi morfolojik farklılaşmaya işaret etmekte ve tohum boyutunun populasyon düzeyindeki varyabilitenin temel bir bileşeni olduğunu göstermektedir. Sonuçlar, tohum kaynağı seçimi, genetik kaynakların korunması ve değişken çevresel koşullar altında uyumlu orman yönetimi uygulamaları için bilimsel bir temel sunmaktadır.

Anahtar Kelimeler: Saçlı meşe, palamut morfometrisi, tür içi varyasyon, populasyon ayrışması

INTRODUCTION

The genus *Quercus* represents one of the most ecologically dominant and taxonomically diverse components of temperate forests in the Northern Hemisphere. With more than 500 species worldwide, the genus exhibits its highest diversification in the Sierra Madre Occidental of Mexico and in East and Southeast Asia (Govaerts et al., 1998; Denk et al., 2017). Approximately 250 species occur in the Americas and about 125 in Asia and Malaysia, while Europe, North Africa, and Macaronesia harbor fewer but ecologically significant taxa (Govaerts et al., 1998). Türkiye, with 18 naturally distributed oak species, constitutes an important diversity center for the genus (Yaltırık, 1984). The wide morphological and genetic variability observed in oaks is closely related to weak reproductive barriers among species, which facilitate frequent hybridization and the formation of mosaic-like mixed populations (Bacilieri et al., 1995; Manos et al., 1999; Samuel, 1999). While this evolutionary flexibility enhances adaptive potential, it also generates complex patterns of variation that complicate taxonomic delimitation. Owing to their deep root systems, substantial litter production, and strong influence on nutrient cycling and soil fertility, oaks are often regarded as ecosystem engineers playing a central role in forest structure and biodiversity maintenance (Crow, 1988; McShea and Healy, 2002; Johnson et al., 2019). In Europe, Anatolia, and the Caucasus, oak species form the structural backbone of many forest ecosystems, and their phylogenetic and morphological diversity provides key insights into paleoclimatic history and forest evolution (Denk and Grimm, 2010; Mölder et al., 2019).

Plant reproductive processes, seed formation, growth dynamics, and adaptive capacity are shaped by both biotic and abiotic factors within ecosystems (Abiem et al., 2023; Chamard et al., 2024). Ecological variability across spatial and temporal scales may lead to substantial differences in morphological traits (Herrera and Bazaga, 2011; Abdusalam and Li, 2018). Environmental factors such as temperature, light, precipitation, slope, soil depth, and relative humidity have been shown to directly influence morphometric characteristics (Khatri et al., 2023; Fan et al., 2024). Although forest trees generally exhibit considerable adaptive capacity (Ravn et al., 2022), phenotypic expression reflects complex genotype × environment interactions (Kremer et al., 2025). Consequently, phenotypic diversity within and among populations emerges as the outcome of multidimensional environmental constraints (Ievinsh, 2006; Soheili et al., 2023).

Morphological data therefore play a fundamental role in plant sciences. They are widely used in taxonomic delimitation (Testé et al., 2022; Martínez-Domínguez et al., 2024), in assessing intra- and inter-population variability (Poljak et al., 2018; Peña et al., 2025), and in the characterization of seeds and reproductive structures (Atar et al., 2020; Avşar, 2020; Yılmaz and Yılmaz, 2021; Atar, 2022; Han et al., 2025). Leaf macro- and micromorphological analyses likewise contribute to understanding phenotypic differentiation (Güney et al., 2016; Gafenco et al., 2024). Furthermore, morphological descriptors remain among the most reliable criteria in varietal identification and registration processes, underpinning conservation and selection programs (Poljak et al., 2016). In this respect, morphological diversity constitutes an indispensable component of both evolutionary research and applied forestry, contributing to the identification of adaptive processes and the conservation of plant genetic resources (Poljak et al., 2015; Atar and Turna, 2018; Wu et al., 2023).

In recent decades, interest in broadleaf tree species has increased considerably across Europe and Türkiye (Huss and Kahveci, 2009). This trend reflects not only the ecological and aesthetic advantages of broadleaf species but also their relatively high photosynthetic efficiency and growth performance under changing climatic conditions (Varol et al., 2022; Zeren Çetin et al., 2025a; Çetin etl al., 2026). The demand for high-quality hardwood timber further enhances their economic value (Blanchet et al., 2025). The success of afforestation and artificial forest establishment depends strongly on the use of genetically high-quality seeds and seedlings (Gregorio et al., 2017). Selection of superior genetic material ensures improved survival, enhanced growth, and greater resilience to environmental stressors (Raya et al., 2025). Accordingly, conservation and sustainable management of genetic diversity represent fundamental pillars of long-term forest ecosystem stability (Güney et al., 2019; Sevik et al., 2021).

Among European and West Asian oaks, *Quercus cerris* L. (Turkey oak) occupies a broad ecological range. In Türkiye, it occurs in most regions except the northeastern and eastern highlands, extending from sea level to elevations of approximately 1500–1900 m (Yaltırık, 1984). The species can reach 35-40 m in height and 1.5-2.0 m in diameter and holds economic significance due to its durable wood and ecological importance as a key wildlife food source (de Rigo et al., 2016). Nevertheless, recent reports indicate declines in oak populations across Europe, associated with climate change, pest outbreaks, and pathogenic fungi (Thomas et al., 2002; Keča et al., 2016). These pressures emphasize the importance of understanding intraspecific variability as a basis for conservation and adaptive forest management. Genetic diversity within forest tree species is a critical determinant of resistance to diseases and adaptation to changing environmental conditions (Sevik et al., 2012, 2017; Güney et al., 2022). Comparative evaluation of populations across different habitats provides an effective approach to detecting such diversity (Chmura and Rozkowski, 2002).

Previous studies on *Q. cerris* have primarily focused on seedling characteristics and nursery techniques (Tüfekçi et al., 2016; Toprak et al., 2017; Bilgin, 2019; Deligöz and Gençer, 2021; Quaranta et al., 2022; Bayar, 2025), drought tolerance (Deligöz and Bayar, 2017, 2018), silvicultural practices (Danielewicz et al., 2014; Bobinac et al., 2019; Meşe et al., 2023; Sönmez and Gencal, 2023; Taşdemir and Yıldızbakan, 2023), and limited aspects of seed and leaf morphology (Bakis and Babaç, 2014; Uslu and Bakış, 2014; Yücedağ, 2024). However, comprehensive assessments of inter-population variation in seed morphological traits remain scarce.

Seed morphology constitutes a fundamental reproductive trait influencing dispersal capacity, germination performance, early seedling establishment, and ultimately population dynamics. Variations in seed size and shape among populations may reflect adaptive differentiation driven by environmental heterogeneity and underlying genetic structure. Despite the ecological breadth of *Q. cerris*, knowledge regarding inter-population variation in its seed morphological traits remains limited. We hypothesize that significant differences exist among geographically distinct populations in terms of seed morphometric characteristics, reflecting patterns of intraspecific diversity and potential ecological differentiation. Accordingly, this study aims to quantify and compare seed morphological traits across populations in order to enhance our understanding of intraspecific variability and to provide a scientific basis for conservation planning, seed transfer strategies, and sustainable forest management practices.

MATERIAL AND METHOD

Selection of populations and the collection of seed

In this study, seeds of *Q. cerris* collected from natural populations representing different biogeographical and climatic regions of Türkiye were used as plant material. The populations were located in the Black Sea (Samsun), Central Anatolia (Eskişehir), Aegean (Manisa and Afyonkarahisar), and Marmara (Balıkesir) regions (Figure 1, Table 1). Seeds from the Balıkesir population were obtained from the seed collection stand numbered TTS-817, those from the Manisa population from TTS-326, and those from the Afyonkarahisar population from TTS-2813. Seeds from the Samsun and Eskişehir populations were collected from pure and natural stands within the respective provinces, selecting phenotypically healthy and superior mother trees. Seed collection was carried out during October–November 2025, corresponding to the optimal seed maturation period for *Q. cerris*. Approximately 20 trees were sampled per population, and care was taken to maintain sufficient spatial distance among sampled trees in order to minimize the probability of relatedness among individuals.

Long-term climatic data (1991–2020) for the studied populations were obtained from the official records of the Turkish State Meteorological Service (MGM). Mean annual temperature among populations ranged from 11.5°C to 17.1°C, while total annual precipitation varied between 346.0 mm and 729.7 mm, indicating substantial climatic heterogeneity across the sampling sites (Table 1).

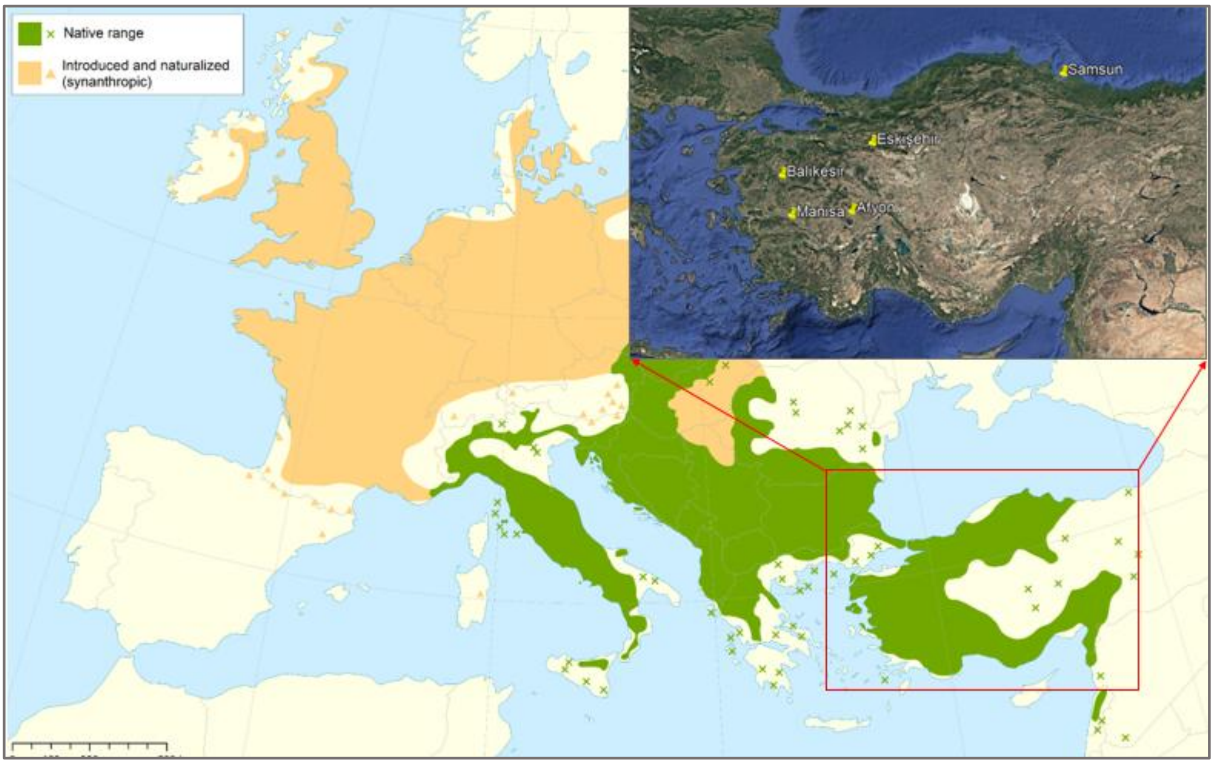

Figure 1. Geographical distribution of the studied *Quercus cerris* populations (Caudullo et al. 2017)

Table 1. Geographic origin and climatic conditions of the studied populations

Population Number	Population Name	°N	°E	Altitude (m a.s.l.)	T (°C)	P (mm)
P1	Balıkesir	39°14'25''	28°02'23''	530	14.7	524.2
P2	Manisa	38°20'45''	28°19'43''	850	17.1	724.6
P3	Afyon	38°25'47''	30°02'27''	1000	11.7	451.4
P4	Eskişehir	39°55'53''	30°39'44''	1330	11.5	346.0
P5	Samsun	41°15'44''	36°22'05''	140	15.0	729.7

T is the mean annual temperature; *P* is the total annual rainfall

Measurements of Seed Characteristics

Prior to morphological measurements, seeds were subjected to the flotation method to distinguish sound and fully filled seeds from empty or damaged ones. To evaluate variation in seed size and shape among populations, measurements were conducted on mature, fully developed, and healthy seeds. Seed dimensions for each population were determined using a digital caliper with a precision of 0.01 mm. In total, 500 seeds were measured, with 100 seeds sampled from each population. The following parameters were recorded or derived.

Seed length (SL, cm): measured as the maximum linear distance from the basal point to the apical tip of the seed.

Seed width (SW, cm): defined as the greatest transverse diameter of the seed, taken perpendicular to the longitudinal axis at its widest section.

Seed shape (SS): calculated as the ratio of seed length to seed width (SL/SW), indicating the degree of elongation or roundness (Kara et al, 2013).

Seed size (SSi): calculated as the arithmetic mean of seed length (SL) and seed width (SW), expressed as (SL + SW)/2, representing the overall dimensional magnitude of the seed (Semiz, 2016).

Seed volume (V, mm^3): calculated using the geometric model $V = (\pi/6) \times SW^2 \times (SL - SW/2) + (\pi/12) \times SW^3$, where SL represents seed length and SW represents seed width, providing an estimate of three-dimensional seed volume based on an ellipsoidal approximation (Semiz, 2016).

Thousand-seed weight (TSW, g): Eight replicates of 100 seeds were randomly selected and weighed using a precision balance. The thousand-seed weight (TSW) was calculated according to the procedure described by the International Seed Testing Association (ISTA, 1996), based on the mean weight of 100 seeds.

Seed moisture content (SMC): determined gravimetrically as the percentage of water loss relative to fresh seed weight, calculated using the equation $SMC (\%) = [(FW - DW) / FW] \times 100$, where FW represents fresh weight and DW represents oven-dry weight after drying to constant mass, indicating the water content of seeds at the time of measurement.

The coefficient of variation (CV) of seed traits was also assessed among populations. The CV was calculated using the equation $CV (\%) = (\sigma / \mu) \times 100$, where σ represents the standard deviation and μ denotes the mean value.

Statistical analysis

The data were analyzed using the statistical software packages R (v.3.4.3) and IBM SPSS Statistics (v.26.0). For each population, descriptive statistics were calculated to quantify the magnitude of variation in the examined traits. Prior to performing ANOVA, the assumptions of homogeneity of variances and normality were tested using Levene's test and the Kolmogorov–Smirnov test, respectively. All evaluated morphological traits satisfied these assumptions, confirming the suitability of parametric analyses. One-way analysis of variance (ANOVA) was then conducted to determine whether significant differences existed among populations for the measured morphological parameters. When significant differences were detected ($p < 0.05$), Duncan's multiple range test was applied to classify populations into statistically homogeneous groups. Multivariate analyses, including principal component analysis (PCA), hierarchical cluster analysis, K-means clustering, and discriminant analysis, were performed to explore overall patterns of population differentiation based on seed morphological characteristics. Relationships among morphological traits were further examined using Pearson's correlation coefficient.

RESULTS

Descriptive statistics (mean, minimum, and maximum values), coefficients of variation (CV%), and the results of the one-way ANOVA for the seed morphological traits are presented in Table 3.

Table 3. Analysis of variance and descriptive summaries of leaf trait values across populations

Seed Traits	Statistical parameters	Populations					Overall Mean	*p*-value
		Balıkesir	Manisa	Afyon	Eskişehir	Samsun		
SL (cm)	Mean	3.83	4.20	3.52	3.26	3.33	3.63	0.000
	Min.	2.75	3.35	2.75	2.80	2.52	2.52	
	Max.	4.70	4.76	4.20	3.75	4.47	4.76	
	CV(%)	10.11	5.77	9.83	7.34	8.79	12.76	
SW (cm)	Mean	2.04	2.06	1.78	1.71	1.78	1.88	0.000
	Min.	1.60	1.55	1.25	1.41	1.46	1.25	
	Max.	2.80	2.99	2.19	2.13	2.39	2.99	
	CV(%)	10.00	8.87	13.09	9.19	11.31	13.10	
SS	Mean	1.89	2.04	2.00	1.91	1.88	1.95	0.000
	Min.	1.21	1.59	1.52	1.57	1.40	1.21	
	Max.	2.50	2.46	2.42	2.24	2.28	2.50	
	CV(%)	12.79	6.14	8.49	7.25	9.45	9.57	
SSi	Mean	2.94	3.14	2.65	2.49	2.56	2.75	0.000
	Min.	2.30	2.53	2.04	2.14	2.07	2.04	
	Max.	3.35	3.88	3.14	2.94	3.31	3.88	
	CV(%)	7.75	6.28	10.34	7.22	8.57	11.96	
V (cm^3)	Mean	8.44	9.51	6.03	5.09	5.67	6.95	0.000
	Min.	4.09	4.79	2.46	2.98	3.20	2.46	
	Max.	14.98	22.27	9.97	8.90	10.97	22.27	
	CV(%)	23.10	23.09	33.05	24.26	29.83	36.20	
TSW (g)	Mean	10672	11528	6976	6584	7908	8734	0.000
	Min.	9990	11000	6100	5940	6840	5940	
	Max.	11220	13040	8020	7440	9000	13040	
	CV(%)	4.22	7.00	10.15	9.42	11.07	24.38	
SMC (%)	Mean	40.77	39.79	36.79	40.95	41.23	39.91	0.026
	Min.	29.08	37.56	33.55	40.01	38.02	29.08	
	Max.	44.77	41.97	38.66	41.86	45.63	45.63	
	CV(%)	15.23	4.00	4.96	1.67	7.42	8.92	

As presented in Table 3, mean seed length (SL) ranged from 3.26 cm (Eskişehir) to 4.20 cm (Manisa), with Balıkesir (3.83 cm), Samsun (3.63 cm), and Afyon (3.52 cm) showing intermediate values. Similarly, seed width (SW) varied between 1.71 cm (Eskişehir) and 2.06 cm (Manisa), while seed shape (SS) and seed size (SSi) followed a comparable trend, with Manisa and Balıkesir generally exhibiting higher mean values compared to Eskişehir and Afyon populations. Seed volume (V) showed considerable variation, with the highest mean value recorded in Manisa (9.51 cm^3) and the lowest in Eskişehir (5.09 cm^3). Thousand seed weight (TSW) also differed markedly among populations, ranging from 6,584 g (Eskişehir) to 11,528 g (Manisa). In contrast, seed moisture content (SMC) displayed relatively narrower differences among populations, with mean values varying between 36.79% (Afyon) and 41.23% (Samsun).

The coefficient of variation (CV%) values indicated moderate to high variability depending on the trait. Seed volume exhibited the highest intra-population variability (up to 33.05% in Afyon), followed by thousand seed weight and seed size-related traits, whereas seed length and width showed comparatively lower variation levels. Moisture content presented relatively stable variability across populations. One-way ANOVA results revealed statistically significant differences among populations for all investigated traits ($p < 0.05$). The highly significant p-values ($p = 0.000$) for SL, SW, SS, SSi, V, and TSW indicate strong inter-population differentiation in seed morphometric characteristics. Although SMC also showed significant differences (*p* = 0.026), the magnitude of variation was comparatively lower. Overall, the findings demonstrate pronounced inter-population variability in seed morphology, particularly in size- and weight-related traits.

Duncan's multiple range test results are presented in Table 4. The populations were separated into 3 groups for SW and 4 groups for SL, V, and TSW, indicating substantial inter-population differentiation in size- and weight-related traits. SSi showed the highest differentiation with 5 distinct groups. In contrast, SS and SMC exhibited only 2 groups, suggesting comparatively lower variability among populations for this trait.

Table 4. Results of Duncan's Test

Pop	SW	SL	SS	SSi	V	TSW	SMC
Balıkesir	a	b	b	b	b	b	a
Manisa	a	a	a	a	a	a	a
Afyon	b	c	a	c	c	d	b
Eskişehir	c	d	b	e	d	d	a
Samsun	b	d	b	d	c	c	a
GN	3	4	2	5	4	4	2

GN: Number of group

The results of hierarchical clustering (Ward method) and Pearson correlation analysis are presented in Figure 2. Prior to clustering, discriminant analysis indicated that the populations were significantly separated into two main groups. Accordingly, Manisa and Balıkesir formed the first group, whereas Samsun, Eskişehir, and Afyon constituted the second group. The hierarchical clustering dendrogram supported this separation pattern, clearly distinguishing these two population clusters based on seed morphological traits. This grouping suggests a consistent morphometric differentiation between western populations (Manisa and Balıkesir) and the remaining populations.

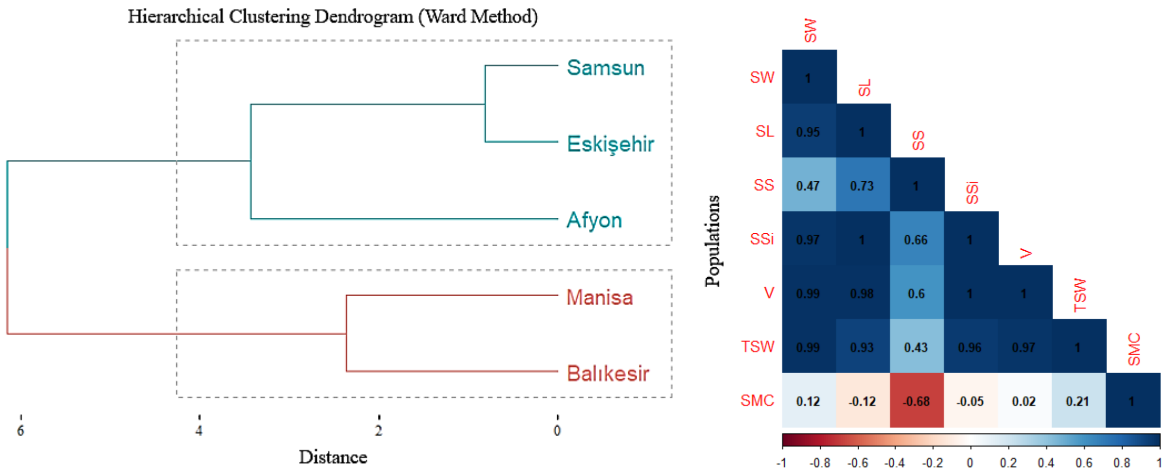

Figure 2. Hierarchical clustering (Ward method) and Pearson correlation matrix of seed morphological traits in *Quercus cerris* populations.

The Pearson correlation matrix revealed strong positive relationships among several seed traits. Notably, TSW showed very strong correlations with SW ($R^2 = 0.99$), SL ($R^2 = 0.93$), and V ($R^2 = 0.97$), indicating that seed weight is closely associated with dimensional and volumetric characteristics. Similarly, SL was strongly correlated with SW ($R^2 = 0.95$), and SS exhibited a strong relationship with SL ($R^2 = 0.73$). These high R^2 values (>0.70) demonstrate that seed size–related traits are highly interdependent. In contrast, SMC displayed weak correlations with most morphological parameters, suggesting that moisture content varies relatively independently from structural seed traits (Figure 2). Overall, the correlation analysis confirms that seed dimensional and weight-related characteristics form a strongly integrated trait complex.

Principal component analysis revealed that the first two components accounted for the vast majority of the total variance (Table 5). The first two principal components explained 98.19% of the total variation, with PC I accounting for 75.48% and PC II for 22.71%. PC I was strongly and positively associated with SL (0.997), SW (0.967), SS (0.675), SSi (1.000), V (0.994), and TSW (0.951), indicating that this component primarily represents overall seed size and weight dimensions. In contrast, SMC showed a negligible loading on PC I (–0.069). PC II was mainly influenced by SMC (0.975), suggesting that this component reflects variation in moisture content independent of seed size-related traits. Other variables contributed weakly to PC II, with SS showing a moderate negative loading (–0.701). The high eigenvalue of PC I (5.284) further confirms that the major source of variation among populations is associated with seed dimensional and mass-related characteristics, whereas PC II captures moisture-related differentiation. Overall, PCA results indicate that seed size and weight traits constitute the primary axis of morphological variation, while moisture content represents a secondary and largely independent component.

Table 5. Results of the PCA on seed morphological characteristics

Measured Characters	PC – Principal Components	
	PC I	PC II
SL	0.997	0.215
SW	0.967	-0.065
SS	0.675	-0.701
SSi	1.000	0.018
V	0.994	0.098
TSW	0.951	0.296
SMC	-0.069	0.975
Eigen value	5.284	1.590
Variation %	75.48%	22.71%

The PCA biplot (Figure 3) shows the distribution of populations according to the first two principal components. Dim1 (75.5%) represents variation mainly associated with seed size and weight traits. Manisa and Balıkesir are positioned on the negative side of Dim1, corresponding to higher values of SL, SW, SSi, V, and TSW, whereas Afyon, Eskişehir, and Samsun are located toward the positive axis, indicating comparatively lower values for these traits.

Dim2 (22.7%) is largely influenced by SMC, which loads strongly on the positive axis. Samsun is distinctly separated along Dim2, suggesting greater differentiation in moisture content, while Afyon is positioned in the opposite direction and shows some association with SS. Taken together, the PCA indicates that separation among populations is primarily driven by seed dimensional and weight-related variables, with moisture content contributing a secondary source of variation.

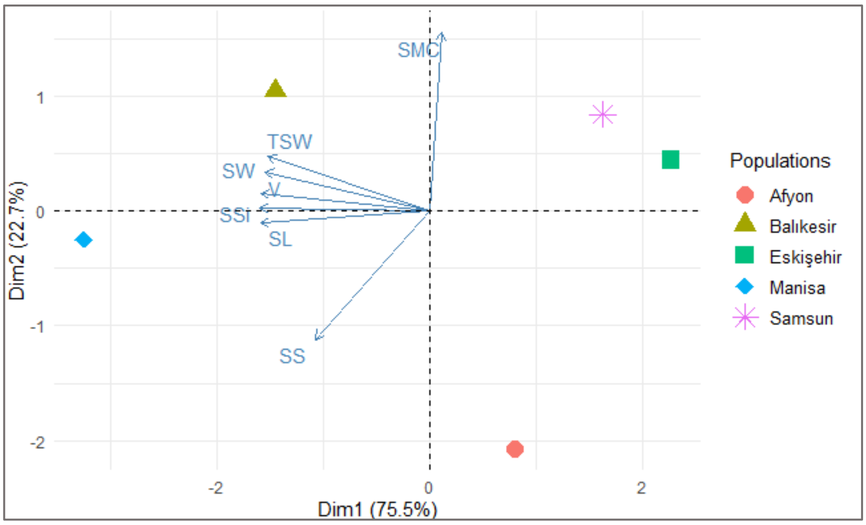

Figure 3. PCA biplot of *Q. cerris* populations based on seed morphological characteristics

DISCUSSION

Numerous factors, some of which are unpredictable, influence plant growth and consequently morphological traits. The primary determinants of plant growth are genetic structure (Kurz et al., 2023) and environmental factors (Tandogan et al., 2023; Özel et al., 2025). Therefore, all factors associated with these components affect plant development and morphological characteristics. For instance, while plant habitus directly influences morphological traits, all factors affecting habitus also impact plant growth and morphology. Plant habitus itself is shaped by the interaction of multiple interrelated factors, including genetic structure (Hrivnak et al., 2024), environmental factors such as climatic (Dogan et al., 2023; Zeren Cetin et al., 2025b) and edaphic conditions (Erdem et al., 2024), as well as stress factors such as drought (Koç et al., 2021), frost (Sevik and Karaca, 2016), UV-B radiation (Çobanoglu and Kulaç, 2024; Ozel et al., 2021), and heavy metals (Kulac et al., 2025). Consequently, many of these factors, both directly and indirectly, influence plant growth and morphological traits (Isinkaralar et al., 2024).

The present study revealed pronounced inter-population differences in acorn morphology in *Q. cerris*, with significant variation in seed length, width, shape index, volume, thousand-seed weight (TSW) and moisture content. Multivariate analyses further demonstrated that size-related variables largely structured the differentiation among populations, indicating that seed morphometry in this species is not randomly distributed but follows a coherent morphological pattern. These findings are consistent with a growing body of evidence suggesting that acorn traits represent both taxonomically informative and ecologically meaningful characters in the genus *Quercus*.

Seed size, particularly seed mass, emerged as a central component of population differentiation. This result aligns with previous morphometric investigations showing that acorn length, width and weight are among the most powerful descriptors of variation within and among oak taxa (Bakış & Babaç, 2014). Beyond taxonomic discrimination, seed mass has repeatedly been identified as a functionally critical trait influencing early establishment. In field-based studies of Mediterranean oaks, seed mass explained a substantial proportion of variation in seedling biomass and relative growth rate during the first growing season, whereas environmental factors became more influential in later stages (Pérez-Ramos et al., 2010). The dominance of

TSW and other size-related parameters in the present analysis therefore likely reflects more than structural variation; it may indicate potential differences in early recruitment performance among populations.

The ecological implications of seed size variation are further supported by experimental evidence demonstrating that larger acorns often produce more vigorous seedlings and exhibit greater tolerance to partial predation (García-Hernández et al., 2023). In large-seeded oaks, the loss of cotyledon reserves does not necessarily compromise germination or emergence, suggesting that seed size may function as a tolerance strategy under high predation pressure. From this perspective, the substantial variation observed among *Q. cerris* populations in seed mass could represent an adaptive response to local selective pressures, balancing the trade-off between enhanced seedling performance and increased predation risk.

Climatic influences may also contribute to the observed morphological differentiation. Broad-scale analyses across Chinese oak species have demonstrated that seed traits, including mass, desiccation sensitivity and germination behaviour, are strongly associated with climatic gradients (Xia et al., 2022). Similarly, in *Quercus variabilis*, both seed length and width were positively correlated with temperature and negatively correlated with precipitation variables, whereas the width-to-length ratio remained comparatively stable across geographic gradients (Zhou et al., 2013). In the present study, the relatively stable shape index contrasted with more pronounced variation in absolute size parameters, suggesting that dimensional changes may occur primarily through scaling effects rather than proportional reshaping. Such a pattern is compatible with climate-driven size adjustments while maintaining functional seed geometry.

It is also important to consider the interplay between intrinsic species-specific patterns and environmental plasticity. Morphological investigations across oak taxa have shown that species-level differentiation often exceeds environmentally induced variation, although environmental gradients can still shape trait expression within species (Stephan et al., 2018). The clustering of populations observed here may therefore reflect a combination of underlying genetic differentiation and site-specific ecological conditions. Given the well-documented capacity for introgression and phenotypic plasticity in oaks, morphological divergence at the population level may signal early-stage ecological specialization rather than strict taxonomic separation.

The independence of moisture content from the primary size-related axis suggests that physiological seed traits may respond to different selective pressures than structural dimensions. Studies on desiccation-sensitive oak seeds indicate that moisture-related traits and drying responses are tightly linked to post-dispersal climatic conditions (Xia et al., 2022). Consequently, variation in moisture content among *Q. cerris* populations may reflect local adaptations to differences in autumn temperature regimes or soil moisture availability during dispersal and early germination phases.

Taken together, the results indicate that acorn morphology in *Q. cerris* exhibits structured, ecologically interpretable variation across populations. Seed size appears to function as a pivotal trait linking morphological differentiation with potential performance consequences during early establishment. At the same time, the coexistence of size variation and relative stability in shape metrics suggests that adaptive responses may primarily operate through adjustments in resource provisioning rather than changes in seed geometry. Such patterns are consistent with theoretical expectations that reproductive traits mediate plant responses to environmental heterogeneity and contribute to regeneration niche differentiation.

CONCLUSION

This study demonstrates that acorn morphology in *Q. cerris* exhibits structured and statistically significant variation among populations, primarily driven by size-related traits such as seed length, width and thousand-seed weight. The dominance of these parameters in multivariate analyses suggests that seed size constitutes a central axis of intraspecific differentiation. Given the well-established relationship between seed mass and early seedling performance, the observed morphological divergence likely carries functional implications for regeneration dynamics.

Understanding the drivers of intraspecific seed trait variation is particularly relevant under ongoing climate change, as shifts in temperature and precipitation regimes may alter selective pressures acting on seed size and physiology. If larger seeds confer advantages under increasing drought stress or predation intensity, population-level differences documented here could influence future regeneration dynamics and stand composition. Further experimental evaluation of germination performance and seedling growth under controlled environmental conditions would help clarify the functional consequences of the morphological divergence detected in this study.

AUTHOR CONTRIBUTIONS

Selin Sancı Bayrak: Original idea, study design, material supply and measurements, and manuscript writing. **Fahrettin Atar:** Original idea, study design, data evaluation, manuscript writing. All authors discussed the results and contributed to the final version of the manuscript.

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The authors declare no conflict of interest.

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