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Forstwesen**Analyzing Population Diversity of Common Hornbeam (*Carpinus betulus* L.)
in Native Habitats in Türkiye: A Focus on Leaf Characteristics****Analyse der Populationsvielfalt der Gemeinen Hainbuche (*Carpinus betulus* L.)
in natürlichen Lebensräumen der Türkei: Ein Fokus auf Blattmerkmale**Fahrettin Atar^{1*}, Ebru Atar¹, Deniz Güney¹, İbrahim Turna¹**Keywords:** Plasticity, adaptation, diversity, elevation, Common hornbeam**Schlüsselbegriffe:** Plastizität, Anpassung, Vielfalt, Höhenlage, Gemeine Hainbuche**Abstract**

The primary aim of this investigation was to examine the morphological diversity of leaves in naturally occurring populations of common hornbeam (*Carpinus betulus* L.) in Türkiye. Twelve common hornbeam populations, distributed over four distinct watersheds in the Eastern Black Sea Region, were sampled from three altitude levels, ranging from sea level to 1200 meters. Nine morphological characteristics of the leaves were analyzed biometrically. We found a high degree of phenotypic heterogeneity both within and among the investigated populations. The eco-geographic principle's classification of populations was disclosed. Altitude appeared to be the primary factor influencing variation in the majority of leaf attributes from the Camlıhemşin, Çaykara, and Espiye watersheds. Compared to trees at lower altitude, trees at higher altitudes were characterized by smaller leaves. The populations in the Trabzon-Maçka watershed, however, did not show this trend. Largest leaves were observed for trees from the Trabzon-Maçka watershed region at the second altitude level. Overall, our findings support the notion that the Eastern Black Sea area is a hotspot of biodiversity and that the intricate evolutionary process leading to leaf morphological variability may be a consequence of adaptation and plasticity.

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Zusammenfassung

Das Ziel dieser Arbeit ist, die morphologische Vielfalt von Blättern in natürlich vorkommenden Populationen der Gemeinen Hainbuche (*Carpinus betulus* L.) in der Türkei zu untersuchen. Zwölf Populationen der Gemeinen Hainbuche, die sich über vier verschiedene Einzugsgebiete in der östlichen Schwarzmeerregion verteilen, wurden innerhalb drei Höhenstufen zwischen Meereshöhe und 1200 Meter Seehöhe beprobt. Neun morphologische Merkmale der Blätter wurden biometrisch analysiert. Es wurde ein hoher Grad der phänotypischen Heterogenität sowohl innerhalb als auch zwischen den untersuchten Populationen festgestellt. Darüber hinaus wurde die Klassifizierung der Populationen nach dem ökogeografischen Prinzip aufgedeckt. Die Höhenlage war der primäre Faktor, der die Variation der meisten untersuchten Blattmerkmale in den Einzugsgebieten Camlihemşin, Çaykara und Espiye signifikant beeinflusste. Im Vergleich zu Bäumen auf niedrigerer Seehöhe zeichneten sich Bäume in höheren Lagen durch kleinere Blätter aus. Die Populationen im Einzugsgebiet Trabzon-Maçka zeigten diesen Trend nicht. Die größten Blätter in dieser Region wurden in der zweiten Höhenstufe beobachtet. Insgesamt weisen unsere Ergebnisse darauf hin, dass die östliche Schwarzmeerregion ein Hotspot für Biodiversität ist und der komplexe evolutionäre Prozess, der zur morphologischen Variabilität der Blätter führt, eine Folge von Anpassung und Plastizität ist.

1 Introduction

Plant adaptability and vitality features (reproduction, seeding, and growth) are affected by both biotic and abiotic influences in varied ecosystems (Matesanz *et al.* 2010; Varol *et al.* 2022). Changes in ecological variables, whether spatial or temporal, can impact the morphological features of plants (Herrera and Bazaga 2013; Koç *et al.* 2024; Özel *et al.* 2024). The development and adaptation of plant anatomical, physiological, and morphological characteristics are significantly influenced by the limitations associated with these variables. These limitations play a crucial role in shaping the diverse traits observed among plant populations (Nascimbene and Marini 2015). The eco-geographic principle's classification refers to the categorization of populations based on the geographic and ecological characteristics of their habitats. This principle considers factors such as altitude, latitude, climate, and soil types, which influence the phenotypic traits and genetic diversity within and among plant populations. Understanding these relationships helps in elucidating the adaptive mechanisms of species to different environmental conditions (Tekin *et al.* 2022).

The soil, temperature, and precipitation patterns of an ecosystem are all significantly influenced by altitude (Körner 2007; Dogan *et al.* 2023). The life history properties of plants and their evolutionary reactions could be influenced by a variety of climatic factors, encompassing variables such as rainfall, temperature and light (Leingärtner

et al. 2014; Sevik *et al.* 2017; Ertürk *et al.* 2024). Species dwelling at higher altitudes exhibit morphological and physiological distinctions from those at lower altitudes, leading to differentiated characteristics based on the elevation changes (Körner 1999). Some researchers have reported that the morphological and anatomical characteristics of plants are influenced by altitude (Cordell *et al.* 1998; Özbucak *et al.* 2013). This situation indicates the adaptation ability of plants to factors such as water and nutrient deficiencies, temperature changes, etc. (Vitousek 1982; Aragon *et al.* 2012).

The most significant organs of plants that vary in size, color, and shape are their leaves (Li *et al.* 2019). The capacity of a leaf to modify its morphology and physiology in response to environmental changes is known as phenotypic plasticity, and it is caused by contrasting environments (Schlichting 1986; Sultan 2000). Zotz *et al.* (2011) state that many plants undergo sudden and significant modifications in leaf morphology as a response to external influences. These plants are able to adapt to a changing environment due to the plasticity of their leaf morphology (Wells and Pigliucci 2000). Elevation has a significant impact on leaf morphology and physiology within a species (Körner 1999). With an increase in leaf surface area, plants exhibit a proportional increase in photosynthesis, transpiration, and respiration (Özen and Onay 2013). Therefore, it can be stated that the morphological characteristics of leaves are associated with the growth of plants. Moreover, specific leaf area (SLA), identified as an informative trait (Wright *et al.* 2004; Poorter *et al.* 2009), serves as an indicator for ecophysiological traits such as stress tolerance, leaf longevity, and growth rate (Weiher *et al.* 1999; Wright and Westoby 2002). A higher SLA signifies a reduction in leaf thickness, diminished leaf density, or a combination of the two (Scheepens *et al.* 2010). Poorter *et al.* (2009) highlighted the strong correlation between SLA and factors such as water availability, temperature and irradiance.

Leaf morphological characters such as length, width, and area generally exhibit a negative correlation with an increase in altitude (Körner *et al.* 1986). Paridari *et al.* (2013) observed that trees at higher elevations tend to have smaller leaf laminas compared to those at lower altitudes. In tropical highlands, as altitude increases, leaf mass per area (LMA) increases, while leaf size often decreases (Grubb 1977; Körner 1989). Therefore, studies investigating the relationships between altitude and plant morphology provide valuable insights into ecological research. (Paridari *et al.* 2013). Various outcomes have emerged in studies on plant morphometrics (Poljak *et al.* 2018; Adamidis *et al.* 2021). Morphological variability may be significantly impacted by variations in a number of variables, including temperature, light, precipitation, slope, depth of soil, and relative humidity. Forest trees commonly display adaptations to various environmental conditions (Savolainen *et al.* 2007). Additionally, genotype, environment, and their interactions all influence the phenotype of a tree (Falconer and Mackay 1996; Cobanoglu *et al.* 2023; Yigit *et al.* 2023). Moreover, morphological traits within a single tree can differ greatly, particularly in big trees (Hagemeyer and Leuschner 2019). Additionally, morphological variability can be influenced by the kind of forest community, soil acidity and habitat, management type (Poljak *et al.* 2022), and other factors (Adamidis *et al.* 2021).

Including different taxon delimitations (Mac-Key 1988; Sękiewicz *et al.* 2016), population variability (Douaihy *et al.* 2012; Poljak *et al.* 2018), morphological seed involution variation (Boratyński *et al.* 2007; Atar 2022), physiological and morphological seed characterization (Drvodelić *et al.* 2015; Atar *et al.* 2017; Atar *et al.* 2020), cultivar characterization and selection (Ertan 2007; Poljak *et al.* 2016), and variation of macro- and micromorphological leaves (Bednorz 2006; Paridari *et al.* 2013; Amer *et al.* 2016; Güney *et al.* 2016; Aykut *et al.* 2017), morphological knowledge remains crucial in numerous domains within the field of plant science (Poljak *et al.* 2015; Atar and Turna 2018). Additionally, morphological characterization remains the formal process for cultivar registration and protection (Pereira-Lorenzo *et al.* 1996). Furthermore, the evolutionary adaptability of plants to various environments may be predicted using morphological plasticity (Nicotra *et al.* 2010).

The *Carpinus* genus, belonging to the Betulaceae family, comprises approximately 40 species indigenous to the Northern Hemisphere, ranging from Europe to eastern Asia, extending south to the Himalayas, and found in North and Central America (Krüssmann 1984; Furlow 1990; Hillier 1991; Suszka *et al.* 1996). In Türkiye, the oriental hornbeam (*Carpinus orientalis* Mill.) and common hornbeam (*Carpinus betulus* L.) species are naturally distributed. The common hornbeam is found in the Black Sea Region, which constitutes the entire Europe-Siberia floral area in Türkiye. Additionally, it locally spreads in the Amanos Mountains. The general geographical distribution of the common hornbeam includes all of Europe, Türkiye, the Caucasus, and Iran. It typically forms mixed forests with beech, chestnut, oak, and alder and occasionally occurs in pure stands (Yalırık 1982; Anşın and Özkan 2006). The common hornbeam extends in the Black Sea forests from sea level up to an elevation of 1200–1300 m.

The aims of this study were to:

- (1) assess how the morphological variability of some common hornbeam leaf traits varies with altitude;
- (2) identify leaf variations within and between populations of the species; and
- (3) reveal how the morphological plasticity of the leaf traits varies with eco-geographic factors.

2 Materials and Methods

2.1 Selection of populations and the collection of leaf

Natural populations of common hornbeam were sampled for this study from four distinct watersheds in the Eastern Black Sea Region's forests. Leaf samples of common hornbeam were collected from populations that grew at varying altitudes in the watersheds of Rize-Çamlıhemşin, Trabzon-Çaykara, Trabzon-Maçka, and Giresun-Espiye in Türkiye (Figure 1).



Figure 1: The geographical locations of common hornbeam populations (Caudullo et al. 2017).

Abbildung 1: Die geografischen Standorte von Gemeine-Hainbuche-Populationen (Caudullo et al. 2017).

The research encompassed 12 populations distributed across three distinct altitude zones, reaching up to 1200 meters above sea level (Table 1). Eco-geographic principle's classification was applied by analyzing the morphological traits of the leaves in relation to the altitude and geographic location of the sampled populations. This involved categorizing populations into distinct eco-geographic zones based on their altitude ranges (0-400 m, 400-800 m, 800-1200 m) and comparing the morphological variability within and between these zones. A total of 134 trees were sampled for leaves: 30 from Maçka, 46 from Çaykara, 30 from Çamlıhemşin, and 31 from Espiye. Leaf samples were collected from the outer (light-exposed) section of the tree crowns by climbing each tree, resulting in a total collection of 6850 leaves (50 leaves \times 137 trees). Within the scope of the study, the heights of trees selected from each population vary between 15-20 m and their diameters range from 18-25 cm. The populations were selected from pure stands of hornbeam and mixed stands where hornbeam predominates, with beech, oak, and chestnut also present in the mix.

Table 1: Information on the sites, where populations of common hornbeam were sampled.

Tabelle 1: Informationen der Standorte, auf denen Populationen der Gemeinen Hainbuche untersucht wurden.

Watershed	Population Name	Number of trees sampled	Latitude	Longitude	Altitude (m.a.s.l.)
Çamlıhemşin	ÇH1	9	40°52'46'' - 40°49'52''	39°41'56'' - 39°41'11''	0-400
	ÇH2	12	40°49'31'' - 40°47'32''	39°40'57'' - 39°40'15''	400-800
	ÇH3	9	40°43'42'' - 40°43'19''	39°38'11'' - 39°36'26''	800-1200
Çaykara	Ç1	15	40°48'47'' - 40°45'53''	40°15'30'' - 40°15'08''	0-400
	Ç2	15	40°44'38'' - 40°42'34''	40°14'07'' - 40°12'28''	400-800
	Ç3	16	40°41'54'' - 40°41'36''	40°13'15'' - 40°11'52''	800-1200
Maçka	M1	13	41°08'39'' - 41°04'39''	41°00'26'' - 41°01'27''	0-400
	M2	11	41°03'42'' - 41°03'15''	41°00'39'' - 41°01'11''	400-800
	M3	6	40°59'35'' - 40°58'57''	40°59'06'' - 40°59'05''	800-1200
Espiyе	E1	12	40°55'26'' - 40°52'48''	38°44'10'' - 38°45'45''	0-400
	E2	12	40°50'54'' - 40°48'02''	38°46'28'' - 38°47'45''	400-800
	E3	7	40°47'07'' - 40°45'08''	38°47'25'' - 38°46'35''	800-1200

2.2 Measurements of Leaf Characteristics

In the study, morphological characteristics such as leaf length, leaf width, leaf area, specific leaf area, petiole length, number of leaf veins, leaf vein angle, leaf shape index, and leaf length to petiole length ratio were measured (Table 2). Leaf vein angle has been obtained by measuring 3 different parts of the leaf, including the bottom, middle, and upper parts of the leaf. The ratio of leaf length to the corresponding leaf width was used to calculate the leaf shape index (Jeong *et al.* 2011; Wang and Zhang 2012).

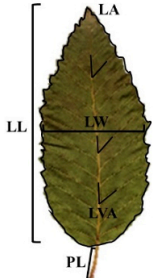
Determination of the specific leaf area: first of all, the area of each leaf was measured. Then the leaves were kept in a drying kiln for 24 hours at 65°C. After that, oven-dry weights were measured by precision scales. After these processes, specific leaf area values were determined by proportioning the dry weight of the leaf area (Kardel *et al.* 2010; Scheepens *et al.* 2010).

Leaf samples were scanned at a resolution of 1200 dpi using a scanner (Hewlett-Packard Scanjet G4010). Subsequently, leaf-related measurements were conducted utilizing the Image Analysis Software (ImageJ). This software has been employed in various scientific studies to analyze variations in leaf characteristics (Bayramzadeh *et al.* 2008; Atar 2022).

Table 2: List of the leaf morphological characteristics studied.

Tabelle 2: Liste der untersuchten blattmorphologischen Merkmale.

Acronyms	Morphological characters (unit of measurement)
LL	Leaf length (cm)
LW	Leaf width (cm)
LA	Leaf area (cm ²)
SLA	Specific leaf area (cm ² g ⁻¹)
PL	Petiole length (cm)
V	Number of leaf veins
LVA	Leaf vein angle (°)
LSI	Leaf shape index
LL/LP	leaf length to petiole length ratio



2.3 Statistical analysis

Descriptive statistical parameters were computed for each population to assess the extent of variation in each characteristic. Analysis of variance (ANOVA) was employed to identify whether there were statistically significant differences in terms of measured morphological characters both among populations and within populations. Using principal component analysis, hierarchical cluster analysis, K-means clustering method and discriminant analysis, the overall population diversity of leaf morphological characteristics was investigated. Pearson's correlation coefficient was utilized to assess the correlation between pairs of morphological characteristics and altitude. The morphological plasticity index (PI) was calculated following the formula from Cepak (1995): $PI = (X_{max} - X_{min}) / X_{max}$; where X_{min} and X_{max} are the minimum and maximum mean value measurement of each morphological characteristics. The morphological plasticity index takes values between 0 and 1. The statistical package programs "R v.3.4.3" and "Windows SPSS Software 23.0" were used to analyze the data.

3 Results

The summary of the results from the descriptive statistical analysis (including arithmetic means and coefficients of variation), analysis of variance, and Duncan tests for the leaf traits in the sampled populations is presented in Table 3. It was determined that the values of leaf length, leaf width, and leaf area decrease with an increase in elevation in populations from each watershed. Generally, the highest values were detected at lower altitudes. However, in the Mačka watershed, an exception was observed where the leaf width did not show a significant decrease with increasing altitude,

and in some cases, even showed slightly higher values at mid-altitudes (400-800 m) compared to the lowest altitude (0-400 m). In contrast, SLA and petiole length values increased with altitude in each population. The number of leaf veins and vein angle, however, did not exhibit a systematic change associated with elevation. For the morphological characteristics under study, the overall coefficients of variation varied from 11.1% (V) to 34.7% (LL/PL). Higher altitude populations showed the least amount of morphological variation for the bulk of the leaf characteristics that were studied.

Table 3: The results of analysis of variance, Duncan test and descriptive statistics concerning the values of leaf characteristics among populations. For abbreviations please see Table 1 and 2.

Tabelle 3: Ergebnisse der Varianzanalyse, des Duncan-Tests und der deskriptiven Statistiken bezüglich der Werte von Blattmerkmalen zwischen den Populationen. Für Abkürzungen siehe Tabelle 1 und 2.

Leaf Characters	Statistical parameters	Populations												Overall Mean	p-value
		CH1*	CH2	CH3	C1	C2	C3	M1	M2	M3	E1	E2	E3		
LL (cm)	Mean	8.50	7.81	8.04	8.31	8.00	7.52	7.79	8.19	7.65	7.56	7.35	7.08	7.83	0.000
	CV(%)	14.2	17.2	16.6	14.4	17.9	15.7	17.4	13.1	20.4	20.9	21.5	20.8	18.0	
	Dun.T.	a	de	c	ab	cd	fg	de	bc	ef	fg	g	h		
LW (cm)	Mean	4.18	3.75	4.25	4.26	4.01	4.00	4.14	4.33	4.04	4.14	3.97	3.94	4.08	0.000
	CV(%)	18.1	18.9	16.0	13.8	15.2	17.2	16.6	14.9	13.8	32.6	19.7	22.9	19.3	
	Dun.T.	b	e	ab	ab	cd	d	bc	a	cd	bc	d	d		
LA (cm ²)	Mean	25.57	21.29	25.04	25.42	23.50	22.29	23.47	24.62	22.13	22.27	21.57	20.98	23.22	0.000
	CV(%)	29.8	33.4	29.5	24.3	30.5	29.5	30.8	32.3	41.7	38.2	38.9	40.4	33.1	
	Dun.T.	a	d	a	a	bc	cd	bc	ab	d	cd	d	d		
SLA(cm ² g ⁻¹)	Mean	145.16	133.00	161.54	145.01	155.38	166.36	155.93	156.40	143.09	141.53	153.89	148.52	151.03	0.000
	CV(%)	24.0	23.7	21.5	19.1	23.5	22.6	18.5	18.4	28.2	21.4	22.5	21.6	22.8	
	Dun.T.	de	f	ab	de	c	a	c	bc	de	e	c	d		
PL (cm)	Mean	1.37	1.32	1.39	1.28	1.37	1.38	1.25	1.35	1.33	1.29	1.42	1.26	1.34	0.000
	CV(%)	22.8	23.4	21.6	24.8	23.7	22.2	23.9	22.4	24.1	25.2	32.4	27.6	24.9	
	Dun.T.	abc	cd	ab	de	abc	abc	e	bc	bcd	de	a	e		
V	Mean	12.85	13.58	12.52	13.34	12.98	13.24	13.83	13.24	13.01	12.39	13.73	13.85	13.21	0.000
	CV(%)	13.2	10.0	9.2	10.0	11.3	8.8	10.0	8.9	9.0	15.6	10.0	8.8	11.1	
	Dun.T.	d	b	e	c	d	a	c	e	a	ab	a			
LVA (°)	Mean	36.85	36.22	36.65	36.31	35.46	38.10	37.30	36.89	36.40	36.55	36.92	37.55	36.75	0.000
	CV(%)	16.9	15.0	13.3	15.7	13.4	11.0	14.4	10.4	11.0	14.4	15.7	15.6	14.2	
	Dun.T.	bcd	de	bcd	de	e	a	abc	bcd	cd	cd	bcd	ab		
LSI	Mean	2.06	2.0	1.90	1.96	2.00	1.89	1.90	1.91	1.89	1.88	1.85	1.83	1.94	0.000
	CV(%)	12.1	11.5	10.2	12.8	12.9	10.4	13.8	10.9	13.7	15.1	11.2	15.0	13.1	
	Dun.T.	b	a	d	c	c	d	d	d	d	de	de	ef	f	
LL/PL	Mean	6.61	6.33	5.93	6.84	6.09	5.78	6.53	6.55	5.98	6.04	5.56	6.00	6.19	0.000
	CV(%)	39.1	45.4	17.7	27.9	27.7	38.1	30.8	47.0	33.5	19.5	36.1	33.4	34.7	
	Dun.T.	ab	bc	d	a	cd	de	ab	ab	cd	cd	e	cd		

The analysis of variance revealed significant differences ($P < 0.01$) both within and between populations across all measured morphological characters. Groups formed by populations for each morphological character were identified using the Duncan test. Accordingly, LL, V, and LA resulted in 10, 6, and 5 groups, respectively. Furthermore, there were 8 groups among populations for SLA and PL and 7 groups for LW, LVA, LSI, and LL/PL (Table 3).

The averages of populations located at the same altitude zones were taken to determine the variations in the measured characters across three altitude zones. The mean values, standard deviations, minimum and maximum values of first altitude

(mean of CH1, C1, M1, E1 populations), second altitude (mean of CH2, C2, M2, E2 populations) and third altitude (mean of CH3, C3, M3, E3 populations) are presented in Figure 2. It has been observed that LL, LW, LA, LSI, and LL/PL values decrease with increasing altitude. On the contrary, SLA and PL values increased with altitude. No significant variation related to elevation was noted in the V and LVA values. The level of significance for all morphological characters measured across different altitudes was determined to be $P < 0.001$. Additionally, based on the Duncan test results, each altitude formed a separate group for LL, SLA, LVA, LSI, and LL/PL characters. For LW, LA, PL, and V characters, two distinct groups were identified among altitudes.

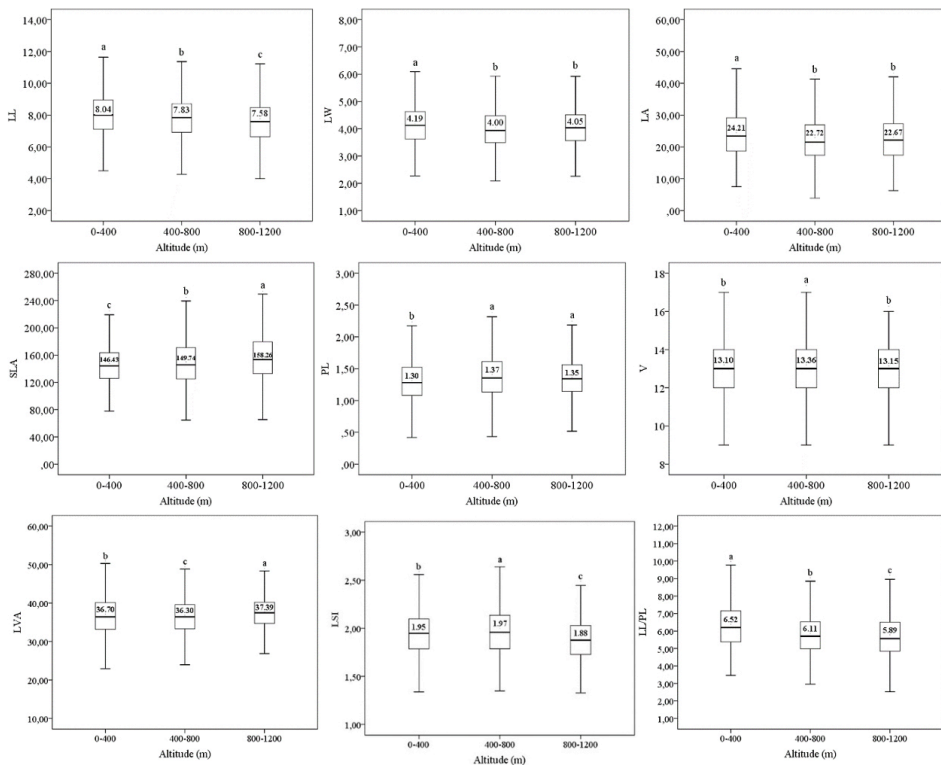


Figure 2: Variation of morphological characteristics of common hornbeam leaves depending on altitudes.

Abbildung 2: Variation der morphologischen Merkmale von Blättern der gemeinen Hainbuche in Abhängigkeit von der Höhenlage.

The results revealed significant variations in the plasticity index (PI) of each characteristic (Figure 3). Overall, the plasticity index in the 1st altitude zone was generally

low when considering all parameters. LA, PL, SLA, and LL/PL parameters exhibited notably high plasticity indices. The plasticity index of LA was maximal at all three altitudes. In the 1st and 3rd altitudes, V, and in the 2nd altitude, LSI had the minimum plasticity index. In Figure 3, relationships between each morphological characteristic were depicted as a correlation matrix. Accordingly, it was determined that many measured leaf characters have significant correlations with each other at a 95% confidence level.

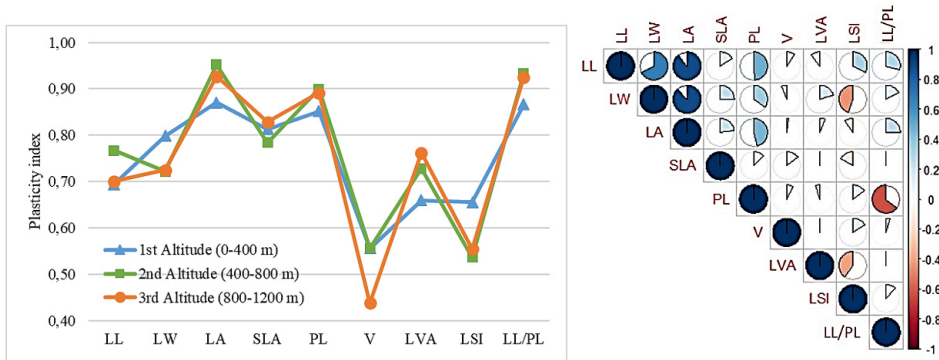


Figure 3: A, Plasticity index depending on altitudes and B, Pearson correlation coefficients between pairs of morphological characters.

Abbildung 3: Plastizitätsindex in Abhängigkeit von den Höhenlagen und Pearson-Korrelationskoeffizienten zwischen Paaren von morphologischen Merkmalen.

Five principal components, elucidating approximately 96.71% of the overall variability, were derived as outlined in Table 4. PC I accounted for only one-third of the total variance (35.40%), followed by the subsequent five PCs (20.06%, 16.18%, 12.55%, and 12.52%, respectively). The majority of leaf-size parameters, including LL, LW, LA, and LL/PL, exhibited the strongest correlations with PC I, aligning with expectations. Conversely, PL demonstrated a negative correlation with PC II, while the only positively correlated variable with PC II was LSI. Additionally, LVA exhibited a high correlation with PC III, V was significantly correlated with PC IV, and the sole variable positively correlated with PC V was SLA.

Table 4: Results of the PCA on morphological characteristics.

Tabelle 4: Ergebnisse der Hauptkomponentenanalyse (PCA) der morphologischen Merkmale.

Measured Characters	PC – Principal Components				
	PC I	PC II	PC III	PC IV	PC V
LL (cm)	0.923				
LW (cm)	0.904				
LA (cm ²)	0.957				
SLA (cm ² g ⁻¹)					0.997
PL (cm)		-0.844			
V				0.993	
LVA (°)			0.989		
LSI		0.944			
LL/PL	0.923				
Eigen value	2.832	1.605	1.294	1.004	1.002
Variation %	35.40%	20.06%	16.18%	12.55%	12.52%

K-means clustering and hierarchical cluster analysis were used to determine the degree of dissimilarity or similarity among the investigated populations (Figure 4). Discriminant analysis was used to evaluate the significance of the groups that emerged from the cluster analysis. Discriminant analysis revealed that splitting into two groups was statistically significant ($P < 0.05$). Accordingly, in terms of all measured leaf characters, the Çaykara-3, Maçka-1, Espiye-2, and Espiye-3 populations were in the same group, and the other populations formed the other group. Although statistically significant separation into two groups was identified, cluster analysis suggests the potential existence of six distinct groups based on leaf characters. The spatial distribution of these six different groups is illustrated in Figure 4. Populations C3 and E2 are grouped together, while M1 and E3 form another distinct group. The remaining populations do not belong to any specific group. As depicted in Figure 4, populations from neighboring basins tend to form clusters with each other.

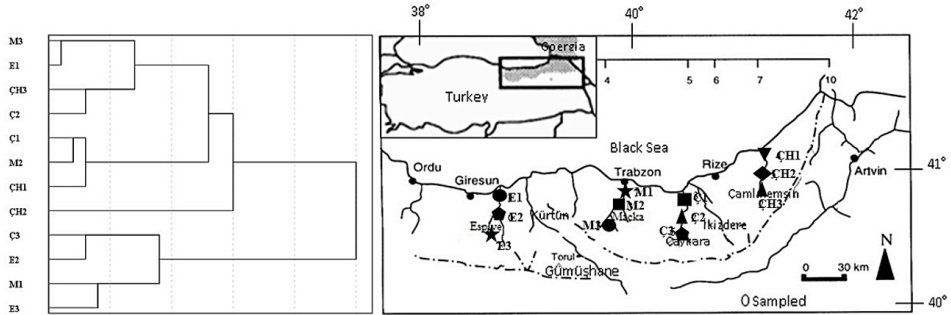


Figure 4: A, Dendrogram and B, map of population groups related to hierarchical cluster analysis.

Abbildung 4: Dendrogramm und Karte der Populationengruppen im Zusammenhang mit der hierarchischen Clusteranalyse.

4 Discussion

High diversity in morphological characteristics was demonstrated by the research done, and variations within and between populations were confirmed for all the parameters that were evaluated. Our findings showed the non-homogeneity of populations concerning leaf characteristics. Variation in most of these characteristics appeared to be related mostly to altitude. Moreover, all measured leaf characteristics provided evidence that the species has evolved plastic strategies based on varying altitudes. Additionally, variations and differences among populations at the same altitude may be due to different gene and genotype frequencies among and within populations. Di Pierro *et al.* (2017) investigated the genetic basis of local adaptation across altitudinal gradients in 18 natural Alpine Norway spruce populations and reported that most of the genetic variability was found within populations, but there was little but significant variation between geographic groups.

The leaf morphological characteristics of the majority of woody plants are influenced by a variety of abiotic variables along environmental gradients. Several studies have reported substantial phenotypic variations as adaptive responses to changes in altitude (Premoli *et al.* 2007; Bresson *et al.* 2011; Varol *et al.* 2022). In our study, it was observed that the leaf length, leaf width, and leaf area values in populations from each watershed decrease with increasing altitude, and generally, the highest values are obtained in populations located at lower altitudes. Atar *et al.* (2014) reported significant differences in the morphological characteristics of *Carpinus orientalis* leaves across three different altitudes. They indicated that leaf width ranged from 2.11 to 2.20 cm, leaf length from 4.24 to 4.38 cm, leaf area from 6.39 to 6.66 cm², and specific leaf area from 157.56 to 170.15 cm² g⁻¹. Paridari *et al.* (2013) obtained similar findings

in their morphometric study on common hornbeam leaves. Their research revealed that trees at higher altitudes exhibited smaller leaf lamina compared to those at lower altitudes. In the study conducted by Atar (2022), 13 morphological characteristics were analyzed in common hornbeam seed involucre, and it was reported that populations exhibit high phenotypic variability both among themselves and within their own groups. Additionally, trees at higher altitudes were characterized by smaller involucre compared to those at lower altitudes. Moreover, a study investigating how altitude affects the biometric characteristics of hornbeam tree indicated important effects of elevation variations on the characteristics under investigation (Kiaei *et al.* 2019). Changes in abiotic factors such as soil moisture, air temperature, and atmospheric CO₂ concentrations along altitude gradients likely lead to strong differential selection, resulting in the local adaptation of *Carpinus betulus* populations (Panek and Waring 1995; Beerling *et al.* 1996; Halbritter *et al.* 2018).

It has been reported for a variety of plant species that as altitude increases, leaf length, width, and area typically decrease. The morphological traits and morphological plasticity changes of 17 populations of *Primula nivalis* at varying elevations were investigated by Abdulsalam and Li (2018). As a result of their study, it was reported that plant height, leaf length and petiole indicated a significant negative correlation with altitude and as the altitude increased, plant height and leaf length decreased. In the study investigating the morphological characters of the mericarp of 24 species in the Selineae tribe, it was stated that the length of mericarp varies from 2.7 to 11.4 mm, while the width of mericarp varies from 1.4 to 9.3 mm (Lee *et al.* 2018). Yousefzadeh *et al.* (2010) observed significant variations in parameters such as leaf width, leaf vein angle, and number of leaf pairs in *Parrotia persica* based on altitude. Moreover, Korner *et al.* (1986) reported that the length, width, and area of leaves often decrease with an increase in altitude. Research on *Alnus incana* conducted by Poljak *et al.* (2018) indicated an inverse relationship between petiole length and leaf blade area values concerning altitude.

A high level of specific leaf area (SLA) indicates a wider ecological niche for a given species and rising production (photosynthesis) (Ishii *et al.* 2018). In our study, SLA and PL values increased in each population with the altitude's rise. Another study conducted in Hawaii, examining the variations in leaf morphology of *Metrosideros polymorpha* species based on environmental factors, also reported similar results. It was observed that as the elevation increases from 70 m to 2350 m, leaf length per area decreases and leaf mass per area increases (Joel *et al.* 1994). Additionally, the increase in leaf mass per area with elevation that it was observed could reflect decreasing nutrient availability with increasing elevation (Vitousek *et al.* 1992). Öztürk *et al.* (2015) analyzed leaf area and leaf area index (LAI) parameters as indicators of leaf development to determine the impact of air and soil temperature on *Carpinus betulus* leaves. The study reported strong positive correlations between air and soil temperatures and leaf area as well as leaf area index. In an extensive investigation of Catalan *Quercus ilex* forests by Ogaya and Peñuelas (2007), increased leaf mass

per area was noted in drier conditions, as well as in sunnier locations with lower air temperatures. Similarly, Kolozsvári *et al.* (2020) evaluated certain morphometric and physiological indices on two woody plant species, *Fagus sylvatica* and *Carpinus betulus*, and characterized their plant behavior in different forest regions, elevations, and light intensities. The study concluded that hornbeam leaves exhibited higher specific leaf weight compared to beech leaves, with the highest value obtained from samples taken from trees growing at forest edges where light intensity was higher than within the forest. Stiegel and Mantilla-Contreras (2018) conducted an experimental study aiming to analyze the environmental effects, including microclimate and soil moisture, prevalent in the upper canopies of forest stands, on leaf traits of juvenile *Fagus sylvatica*, *Acer pseudoplatanus*, and *Carpinus betulus*. Following the treatments, it was observed that the leaves of *Carpinus betulus* exhibited a tendency towards decreased SLA, attributed to the treatment involving warmer and drier microclimates. The average SLA values recorded for *Carpinus betulus* were $155 \text{ cm}^2 \text{ g}^{-1}$. Furthermore, the environmental impact on SLA was found to be more pronounced under conditions of lower soil moisture. Indeed, it has been highlighted that leaves possessing elevated leaf mass per area exhibit a structure that reduces both transpirational water loss and photosynthetic rates (Hultine and Marshall 2000). In another study investigating the variation in SLA of mature *Carpinus betulus* trees in a closed forest, based on leaf position and growth period, it was reported that the SLA values were lowest in the upper part of the crowns, with the highest SLA values obtained in measurements taken in May (Huzulák and Eliáš 1975).

The results revealed significant differences in the plasticity index for each characteristic. LA, PL, SLA, and LL/PL parameters exhibited notably high plasticity indices. In research conducted by Paridari *et al.* (2013) on *Carpinus betulus* species, characteristics such as vein count, tooth count, and stomatal sizes demonstrated minimal plasticity, whereas stomatal density and leaf area exhibited the greatest degree of plasticity. The highest plasticity was found in the leaf-apex length of *Alnus subcordata* by Akbarian *et al.* (2011) and the leaf-petiole length of *Castanea sativa* by Zarafshar *et al.* (2010).

In this study, although the diversity of the examined leaf characteristics in populations investigated in the Çamlıhemşin, Çaykara, and Espiye basins was mostly associated with altitude, this was not the case for populations in the Trabzon-Maçka watershed. In this region, trees at the second altitude exhibited the largest leaf sizes. Atar *et al.* (2014) conducted a study investigating the elevation-dependent variation of certain leaf characteristics in *Carpinus orientalis* in the Trabzon-Maçka basin, which encompasses three elevation zones, similar to our study. Consistent with our study results, this research also found that parameters such as leaf length, leaf area, and specific leaf area exhibited the highest values in populations belonging to the second altitude zone. This situation is likely dependent on habitat variables related to management type and soil characteristics. Common hornbeam forests are managed in two ways: as high forests and as coppice forests. Hornbeam forests are managed as

high forests in the majority of the populations under investigation, and they are usually found in mixed stands with chestnut, beech, and oak. However, the hornbeam trees located in the first altitude zone of the Maçka watershed may be continually cut and regenerated, resembling a coppice management system. Therefore, the lower leaf sizes of trees at the first altitude can be explained by this phenomenon. Poljak *et al.* (2022) reported similar findings, indicating that chestnut stands managed as coppice yield smaller fruits compared to chestnut stands managed as high forests. Furthermore, they highlighted that factors such as soil acidity, habitat type, and forest community type can influence fruit size (Poljak *et al.* 2012). The washing caused by excessive rainfall on the slopes facing north in the Eastern Black Sea region leads to lime removal from the soil. Consequently, the soil exhibits an acidic nature. In addition to the kind of management, habitat modifications, like soil acidity, can significantly affect leaf size in the Maçka watershed.

5 Conclusions

In conclusion, genetic diversity plays a pivotal role in forest ecosystem adaptation and stability overall, especially in the face of environmental stress and inadequate management that pose long-term threats. Therefore, it is essential to delineate the genetic makeup of *C. betulus* and other natural forest resources, particularly to facilitate the implementation of both in-situ and ex-situ conservation efforts. This research highlights the significance of altitude, along with its associated factors like rainfall and temperature, as a key driver of morphological variations in *C. betulus* leaves. Additionally, the leaves of *C. betulus* exhibit heightened adaptive plasticity and stability amidst fluctuating environmental conditions. To comprehensively grasp the altitude adaptation of this species, more extensive studies incorporating ecophysiological characteristics are warranted.

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Conflict of interest

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

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