

Morphological Variation in Cone and Needle Characteristics of Black Pine (*Pinus nigra* J.F. Arnold) Under Different Topographic Conditions

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Potential global warming impact makes it important to study the morphological response of plants under stress conditions. The ability of trees to survive and adapt to possible scenarios can be understood in detail thanks to this awareness. This study investigated the variation in needle and cone morphology of black pine trees growing in different altitudes and aspects (slope surface) within the Western Black Sea region of Türkiye. The research material consisted of 1560 needle and 1560 cone samples from 78 destructively sampled adult black pines growing in six forest stands of varying altitude and aspect. Altitude and aspect were found to be significant in influencing all investigated morphological characteristics including needle length (nl), needle width (nw), needle thickness (nt), sheath length (sl), cone length (cl), cone width (cw), and cw/cl ratio. The most obvious variation between morphological features was found in the cw as a function of altitude, with cones becoming wider as altitude increased. In addition, the morphological diversity of needles and cones due to aspect effect is more common at lower altitudes where there is a greater water deficit. Morphological variation was found to be higher in south-facing slopes where water stress is higher.

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INTRODUCTION

Natural resource management alternatives need to be identified and precautions taken, particularly in the light of the experience of global climate change, which has been felt in recent years and is likely to continue (Berseth and Letourneau 2025). It is therefore necessary to understand the morphological adaptations and growth responses of tree species under changing topographic and climatic conditions (Biricik *et al.* 2021a; İzmir *et al.* 2024). Determining the optimal topographic conditions for tree species of high ecological and economic importance, especially those commonly used in afforestation studies, is essential for natural resource management (Seki 2023). Considering that Türkiye has a heterogeneous structure in terms of topographic and climatic features (Ekim and Güner 2000), it is inevitable that there will be local morphological variations for primary tree species (Turna *et al.* 2006; Ergül Bozkurt *et al.* 2021; Yildirim and Turna 2021). Particularly in the context of global climate change, the protection and use of local populations of black pine species with high genetic and phenotypic variation, and the

ability to adapt to different climatic conditions is important (Linares and Tíscar 2010; Çengel *et al.* 2012; Vacek *et al.* 2023).

There are significant relationships between topographic features and wood anatomy (Biricik *et al.* 2021b), radial growth (Doğan and Köse 2019; Bolat 2025), floristic variation (Kavgacı *et al.* 2013), reserve accumulation (Santini *et al.* 2019), and sapling morphology (Seki 2023) of black pine. The ecosystems of the black pine have been negatively affected by climate change (Martín-Benito *et al.* 2008; Janssen *et al.* 2018) and, as with all ecosystems, appear to be affected by possible climate scenarios. To be ready for these possible scenarios, attention should be paid to the studies investigating the relationships between topographic features and black pine morphology. It is of great importance to understand the morphological adaptations of trees, especially in the face of decreasing precipitation, increasing drought and water stress due to global warming. Analyzing how trees morphologically adapt to changing environmental and topographical conditions is an important strategy formulation for the expected climate scenarios (Buraczyk *et al.* 2022; Laaribya *et al.* 2024).

Black pine (*Pinus nigra* J. F. Arnold) is one of the most important tree species in Europe, both ecologically and commercially (Giovannelli *et al.* 2017; Raptis *et al.* 2021). This species has a very wide distribution, including Europe, Asia Minor, and North Africa, thanks to its elastic ecological adaptation to different habitats (Raptis *et al.* 2018; Vacek *et al.* 2023; Bolat 2025). It is also an important tree species that has the potential to grow outside its natural range and is planted in a wide variety of habitats (Misir and Misir 2007). This species is suitable for afforesting steep slopes at risk of erosion, for creating ecosystems on abandoned agricultural land and in areas in need of reclamation, such as mining areas (Misir *et al.* 2007; Vacek *et al.* 2021; Vacek *et al.* 2023). It is also seen as a potential alternative to existing conifer species in Central Europe, if the summer drought scenarios are realized (Thiel *et al.* 2012). Black pine is also the second most widespread conifer species in Türkiye after *Pinus brutia* Ten. Black pine, which occupies about 18% of the total forest area (4.2 million ha) in Türkiye (GDF 2021), can form pure and mixed forests at altitudes between 400 and 2100 m (Coode and Cullen 1965). Its resistance to a wide range of ecological conditions makes it one of the most favoured tree species for reforestation and rehabilitation projects in the country (Öner and Eren 2008; Atalay and Efe 2010; Ayan *et al.* 2017; Bilir 2021). This study investigated the effects of altitude and aspect on needle and cone morphology in black pine stands distributed in Karabük, located in the Western Black Sea region of Türkiye.

EXPERIMENTAL

Study Area and Data Collection

This study was conducted in Karabük (Dikmen), in the Western Black Sea region of Türkiye. The study area is located in the A4 square grid according to the Davis grid system (1965 to 1985) and is within the European-Siberian phytogeographic region. The average annual temperature in Karabük is 13.3 °C and the average annual rainfall is 548.7 mm, according to climate data for the period 1991 to 2020. Approximately 74% of Karabük is covered by forest, and its forests occupy an important place among the country's forests, both ecologically and commercially (GDF 2023). The most common tree species in the study area is black pine (*Pinus nigra* J.F. Arnold). In addition to pure black pine stands, there are also mixed stands of black pine with Scots pine (*Pinus sylvestris* L.), Calabrian

pine (*Pinus brutia* Ten.), oak (*Quercus* spp.), Kazdagi fir (*Abies nordmanniana* subsp. *equi-trojani*), and oriental beech (*Fagus orientalis* Lipsky.) in the study area.

This study investigated the effects of altitude and aspect on the needle and cone morphology of black pine in the Dikmen Forest Chiefdom within the boundaries of the Karabük Forest Enterprise. To this end, forest stands at different altitudes and with different aspects were identified and sampled within the study area. In determining the stands to be sampled, care was taken to select stands from three different altitude groups and two different aspect groups within each altitude group. As a result, a total of 6 different stands were sampled from the southern and northern aspects of each of the 700 to 900 m, 900 to 1100 m, and 1100 to 1300 m altitude groups. A total of 78 sample trees were destructively sampled to examine needles and cones, 10 to 15 trees from each sample stand. Care was taken to ensure that the sample trees selected were healthy, average in diameter and height for the stand, and representative of the stand. Care was also taken to ensure that the competitive status of the sample trees within the stand was close to each other. Figure 1 illustrates the location of the study area within the country and sample trees within the Dikmen Forest Chiefdom.

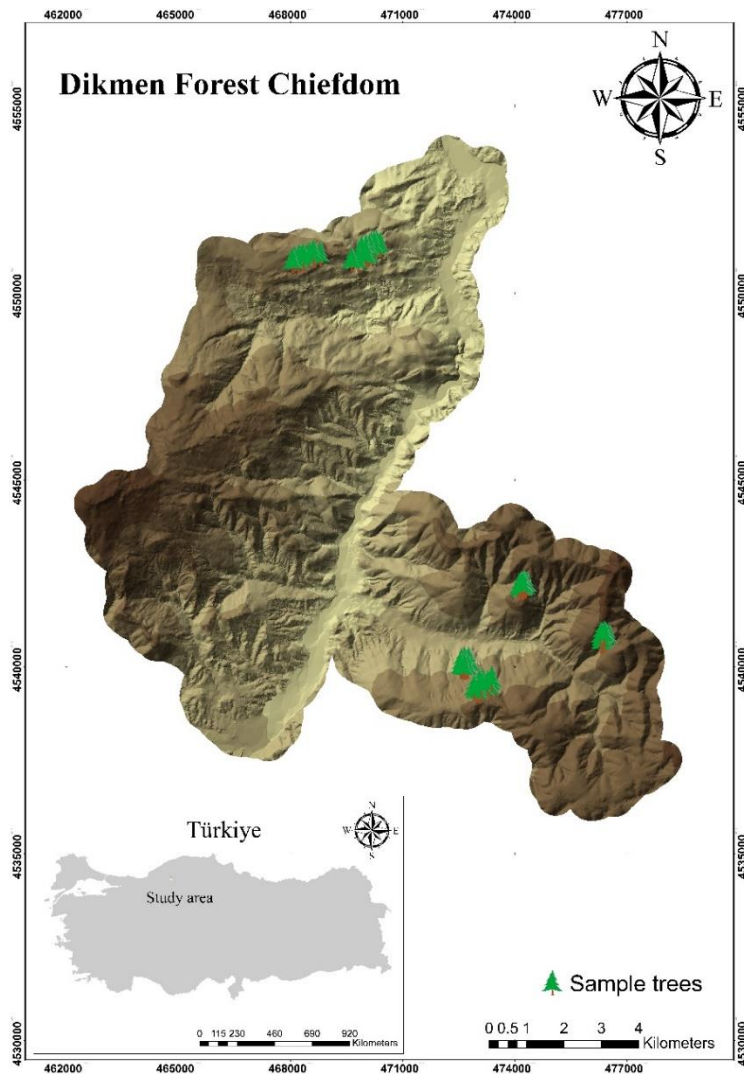


Fig. 1. Location of the study area within the country and distribution of sample trees within the study area

The first step was to measure and record the diameter at breast height (dbh) and total height (h) of each felled tree, and then to collect needle and cone samples. A total of 20 needle and 20 cone samples were taken from the crown of each sample tree. Needles with no visible insect and/or fungi damage were sampled from well grown shoots and cones were sampled from last year's crop at the top of the crown. Needle length (nl), needle width (nw), needle thickness (nt), sheath length (sl), cone length (cl), and cone width (cw) were then measured on needle and cone samples. All measurements were taken using a digital caliper (Insize digital caliper) with an accuracy of 0.01 mm. In addition, the cw/cl ratio, an indicator of cone shape, was calculated for each cone sample.

Evaluation and Statistical Analysis

Descriptive statistics including minimum, maximum, mean, and standard deviation were calculated for the needle and cone characteristics for each population and for the overall. Graphs were then created using the violin plot to see the differences in data structure between populations, their distribution, and frequency within the population. Violin plot, which is similar to box plot, provides more detailed information about the data. They are also useful for a more detailed analysis of the separation between populations on the same scale but with different colors.

Multivariate Analysis of Variance (MANOVA) and Tukey HSD test, a *post-hoc* multiple comparison test, were used to test for differences in needle and cone characteristics between forest stands with different topography. A significance level of 0.05 was used to test for differences in the mean needle and cone characteristics between groups. Principal component analysis (PCA) was also used to investigate needle and cone characteristics of topographically different stands. All the analyses mentioned in this section have been carried out using the R software (version 4.1.2, R Core Team).

RESULTS AND DISCUSSION

Information on the 78 destructively sampled trees in the sampled stands with diverse topographical characteristics is presented in Table 1. The mean dbh values of the felled trees were approximately 28.3 to 32.0 cm and the mean h values were approximately 12.0 to 17.7 m. It can be seen that the sampled trees in each of the stand group are of a similar size in terms of dbh and h.

Table 1. Distribution and Characteristics of the Sample Trees

Sampled Stand Code	Altitude	Aspect	Number of Sample Trees	Descriptive Statistics (Mean $\pm$ SD)	
				dbh (cm)	h (m)
1N	700 to 900 m (the lowest altitude)	North	15	28.7 $\pm$ 3.9	14.1 $\pm$ 1.8
1S		South	15	28.3 $\pm$ 5.2	12.0 $\pm$ 2.0
2N	900 to 1100 m (the moderate altitude)	North	13	31.4 $\pm$ 2.6	17.5 $\pm$ 2.3
2S		South	10	31.0 $\pm$ 2.5	17.7 $\pm$ 1.9
3N	1100 to 1300 m (the highest altitude)	North	15	31.5 $\pm$ 5.2	14.9 $\pm$ 1.6
3S		South	10	32.0 $\pm$ 4.9	16.8 $\pm$ 0.9

Detailed descriptive statistics for measurements on 1560 needles and 1560 cones from 78 sample trees are presented in Table 2. Throughout the study area, nl ranged between 75.18 to 176.51 mm (mean = 125.35 mm), nw ranged between 0.85 to 2.10 mm (mean = 1.47 mm), nt ranged between 0.29 to 1.24 mm (mean = 0.79 mm), sl ranged between 10.50 to 31.48 mm (mean = 17.34 mm), cl ranged between 36.39 to 85.74 mm (mean = 57.14 mm), cw ranged between 17.93 to 37.41 mm (mean = 27.27 mm), and the cw/cl ratio ranged between 0.27 to 0.82 (mean = 0.48).

When the mean values of the morphological characteristics associated with the needles were examined, the longest needles (130.84 mm) were found in the 2S, while the shortest needles (121.94 mm) were found in the 3N. The needles with the highest width value (1.56 mm) were measured in the 1N, and the needles with the lowest width value (1.36 mm) were measured in the 1S. The thickest needles (0.93 mm) were found in the 1N, while thinnest needles (0.74 mm) were found in the 3N. Regarding the values of the sl, which is another morphological characteristic of the needles, the longest (17.59 mm) were found in the 3S, and the shortest (16.72 mm) in the 1S. The longest cones (59.84 mm) were obtained in the 1S, while the shortest cones (55.75 mm) were obtained in the 1N. The cone widths with the longest value (28.98 mm) were obtained in the 3S, and the thinnest cones (25.99 mm) were obtained in the 1N. The highest cw/cl ratio (0.51) was found in both the 3N and 3S, and the lowest value (0.44) was found in the 1S.

The data structure related to the needle and cone characteristics in the populations is visualized with violin plots in Figs. 2 and 3, respectively. Figure 2 shows that the stands (2N, 2S) with the lowest intra-population variation in needle characteristics are found in the moderate altitude (900 to 1100 m). It can also be seen that the aspect effect is quite high in the lowest altitude (700 to 900 m). The sl, nw, and nt characteristics have the highest range at the highest altitude (1100 to 1300 m). It is obvious that the needle characteristics, especially in 1N, have a unique structure compared to other stands. As shown in Fig. 3, the cones expand with increasing altitude. It can be seen that only the data structures of the cone characteristics at the lowest altitude differ between the aspects.

Table 2. Detailed Descriptive Statistics for Needle and Cone Samples

Sampled Stands/ Needle and Cone Features	Number of Sample	Minimum	Maximum	Mean	Standard Deviation
1N (700 to 900 m - North)					
nl (mm)	300	83.24	176.51	122.14	22.10
nw (mm)		1.09	2.10	1.56	0.19
nt (mm)		0.51	1.24	0.93	0.12
sl (mm)		10.76	26.89	16.76	2.54
cl (mm)		36.39	77.62	55.75	7.49
cw (mm)		17.93	34.48	25.99	3.68
cw/cl ratio		0.27	0.82	0.47	0.06
1S (700 to 900 m - South)					
nl (mm)	300	100.04	158.60	123.29	9.15
nw (mm)		0.85	1.84	1.36	0.20
nt (mm)		0.37	0.98	0.76	0.12
sl (mm)		11.53	26.73	17.30	2.32
cl (mm)		43.30	85.74	59.84	7.43
cw (mm)		20.35	33.87	26.28	2.17
cw/cl ratio		0.33	0.63	0.44	0.05

2N (900 to 1100 m - North)					
nl (mm)	260	102.04	156.01	127.94	16.02
nw (mm)		1.05	1.89	1.48	0.15
nt (mm)		0.45	0.99	0.75	0.09
sl (mm)		14.06	22.30	17.56	1.37
cl (mm)		41.46	76.73	56.29	6.80
cw (mm)		20.91	36.03	27.14	3.08
cw/cl ratio		0.37	0.66	0.49	0.06
2S (900 to 1100 m - South)					
nl (mm)	200	103.45	156.11	130.84	16.24
nw (mm)		1.06	1.89	1.49	0.15
nt (mm)		0.56	0.99	0.75	0.08
sl (mm)		14.03	22.25	17.50	1.34
cl (mm)		46.08	76.73	56.72	6.02
cw (mm)		20.97	36.10	27.70	3.17
cw/cl ratio		0.37	0.66	0.49	0.06
3N (1100 to 1300 m - North)					
nl (mm)	300	75.18	155.57	121.94	19.78
nw (mm)		0.96	2.08	1.45	0.24
nt (mm)		0.29	1.04	0.74	0.13
sl (mm)		10.50	31.48	17.52	3.53
cl (mm)		39.21	76.23	56.50	6.78
cw (mm)		19.28	37.19	28.22	3.17
cw/cl ratio		0.31	0.74	0.51	0.07
3S (1100 to 1300 m - South)					
nl (mm)	200	100.78	155.68	129.47	14.48
nw (mm)		1.03	2.09	1.52	0.23
nt (mm)		0.29	1.05	0.76	0.13
sl (mm)		10.50	30.69	17.59	3.69
cl (mm)		41.46	76.35	57.63	5.96
cw (mm)		21.62	37.41	28.98	2.98
cw/cl ratio		0.37	0.74	0.51	0.07
Overall					
nl (mm)		75.18	176.51	125.35	17.32
nw (mm)		0.85	2.10	1.47	0.21
nt (mm)		0.29	1.24	0.79	0.13
sl (mm)	1560	10.50	31.48	17.34	2.65
cl (mm)		36.39	85.74	57.14	7.00
cw (mm)		17.93	37.41	27.27	3.24
cw/cl ratio		0.27	0.82	0.48	0.07

Where nl is needle length, nw is needle width, nt is needle thickness, sl is sheath length, cl is cone length and cw is cone width

All the morphological characteristics of the needles and cones were significantly different between the sampled stands at different altitudes and aspects (MANOVA, $p < 0.05$). Black pines growing in the lowest altitude, regardless of aspect, and in 3N have the shortest needles. While no effect ($p > 0.05$) of aspect on nl was observed in the low altitude stands (700 to 900 m and 900 to 1100 m), a significant ($p < 0.05$) effect of aspect on nl was observed in the highest altitude (1100 to 1300 m). In this altitude, the needles of the black pines were shorter in the north than in the south.

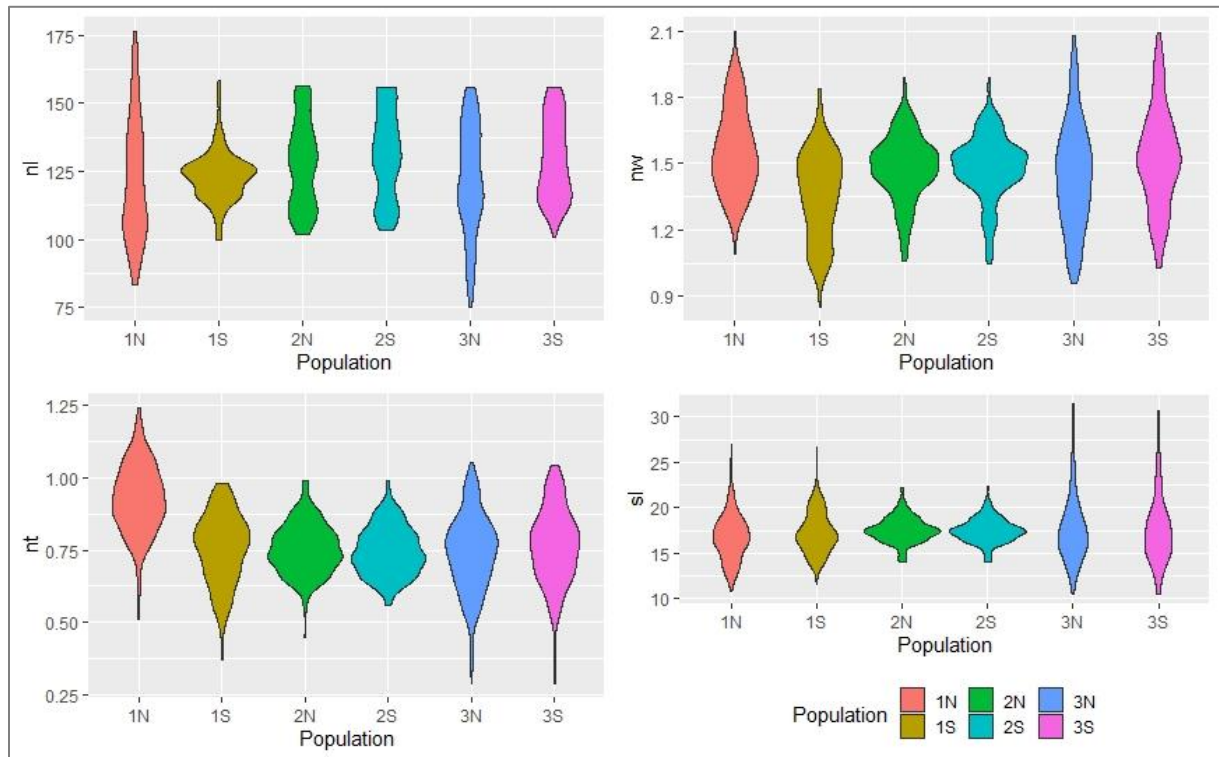


Fig. 2. Boxplots diagram of the needle characteristics with differences between populations

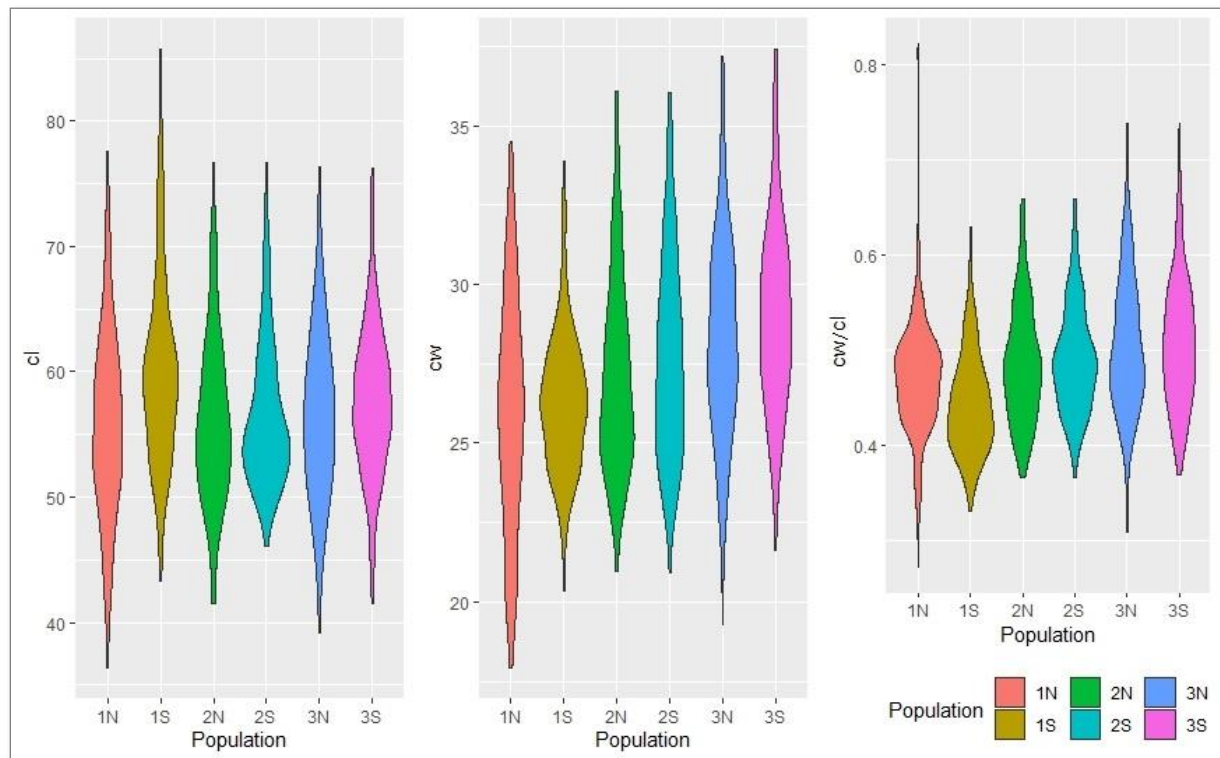


Fig. 3. Boxplots diagram of the cone characteristics with differences between populations

The highest *nw* values were obtained at 700 to 900 m north-facing and 1100 to 1300 m south-facing. The lowest *nw* values were recorded at an altitude of 700 to 900 m on the southern side. There was no aspect effect on the *nw* only in the group of 900 to 1100 m altitude group ($p > 0.05$). Except for the 700 to 900 m north aspect, *nt* values were not different in all groups ($p > 0.05$). The thickest needles, significantly different from the other groups ($p < 0.05$), were observed in the 700 to 900 m north-facing stand. The shortest sheaths were found in the lowest altitude group (700 to 900 m), especially in the north-facing stand in this altitude. In addition, it was found that there was no significant difference ($p > 0.05$) in the *sl* values between the other altitude and aspect groups.

Table 3. MANOVA and Tukey HSD Results on Needle and Cone Characteristics in Sample Stands

Sampled stands	<i>nl</i> (mm)	<i>nw</i> (mm)	<i>nt</i> (mm)	<i>sl</i> (mm)	<i>cl</i> (mm)	<i>cw</i> (mm)	<i>cw/cl</i> ratio
	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD	Mean $\pm$ SD
1N (700 to 900 m - North)	122.14 $\pm$ 22.10 A	1.56 $\pm$ 0.19 D	0.93 $\pm$ 0.12 B	16.76 $\pm$ 2.54 A	55.75 $\pm$ 7.49 A	25.99 $\pm$ 3.68 A	0.47 $\pm$ 0.06 B
1S (700 to 900 m - South)	123.29 $\pm$ 9.15 A	1.36 $\pm$ 0.20 A	0.76 $\pm$ 0.12 A	17.30 $\pm$ 2.32 AB	59.84 $\pm$ 7.43 C	26.28 $\pm$ 2.17 A	0.44 $\pm$ 0.05 A
2N (900 to 1100 m - North)	127.94 $\pm$ 16.02 B	1.48 $\pm$ 0.15 BC	0.75 $\pm$ 0.09 A	17.56 $\pm$ 1.37 B	56.29 $\pm$ 6.80 AB	27.14 $\pm$ 3.08 B	0.49 $\pm$ 0.06 C
2S (900 to 1100 m - South)	130.84 $\pm$ 16.24 B	1.49 $\pm$ 0.15 BC	0.75 $\pm$ 0.08 A	17.50 $\pm$ 1.34 B	56.72 $\pm$ 6.02 AB	27.70 $\pm$ 3.17 BC	0.49 $\pm$ 0.06 CD
3N (1100 to 1300 m - North)	121.94 $\pm$ 19.78 A	1.45 $\pm$ 0.24 B	0.74 $\pm$ 0.13 A	17.52 $\pm$ 3.53 B	56.50 $\pm$ 6.78 AB	28.22 $\pm$ 3.17 CD	0.51 $\pm$ 0.07 DE
3S (1100 to 1300 m - South)	129.47 $\pm$ 14.48 B	1.52 $\pm$ 0.23 CD	0.76 $\pm$ 0.13 A	17.59 $\pm$ 3.69 B	57.63 $\pm$ 5.96 B	28.98 $\pm$ 2.98 D	0.51 $\pm$ 0.07 E

Note: Mean and SD are arithmetic mean and standard deviation, respectively. Superscript letters of A, B, C, D, and E are homogeneous subsets of *post-hoc* test results ($p < 0.05$)

The longest cones were obtained in the 700 to 900 m south-facing stand. In general, black pine cones growing in southern stands were found to be longer than those in northern stands at all altitudes. However, the aspect effect in the altitude groups was only found to be significant ($p < 0.05$) in the lowest altitude group (700 to 900 m). One of the morphological characteristics that shows a clear difference between the different altitude groups is the *cw* value. The cones appear to widen with altitude. However, when the altitude groups were examined within themselves, no aspect effect on *cw* was observed. The *cw/cl* ratio also increased significantly with altitude ($p < 0.05$). The stand with the lowest ratio was 700 to 900 m south facing, followed by 700 to 900 m north facing. The aspect had no effect on this ratio when other altitude groups were considered in isolation. Among the altitude groups, the 900 to 1100 m group was the only one where the aspect had no effect on the morphological characteristics of needles and cones.

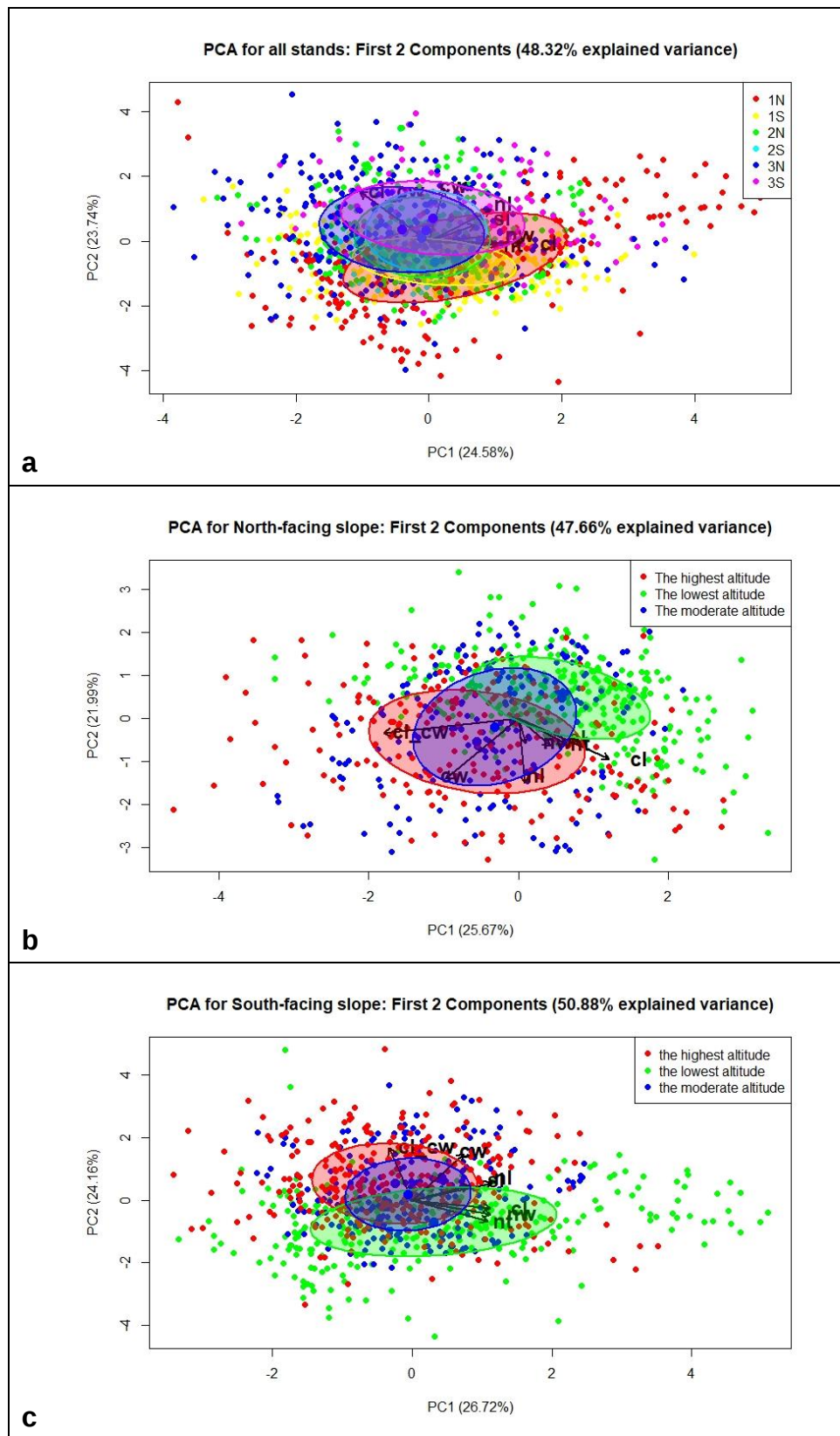


Fig. 4. PCA results for all stands (a), north-facing stands (b), and south-facing stands (c)

This means that the morphological characteristics of black pines growing on different aspects at 900 to 1100 m had no statistically significant differences ($p > 0.05$). In particular, needle and cone morphological differences due to aspect differences were more common at lower altitudes. Morphological differentiation of black pine cones is more pronounced for cw, where there is clear widening of the cone with altitude. Black pines growing at lower altitudes have narrower cones than those growing at higher altitudes.

The results of the PCA analysis are visualized in Fig. 4. The first two components explain 48.32% (PC1: 24.58%, PC2: 23.74%) of the total variance in the combined dataset, 47.66% (PC1: 25.67%, PC2: 21.99%) in north-facing stands, and 50.88% (PC1: 26.72%, PC2: 24.16%) in south-facing stands. As a result of the PCA analysis performed using the same seven morphological characteristics, the explained variance is higher in south-facing stands (50.88%) than in north-facing stands (47.66%). This shows that morphological differentiation with altitude is greater in south-facing stands than on northern slopes. For three different comparisons, it can be seen that cone morphological characteristics, including cw and cw/cl, are the main variables distinguishing individuals at the lowest altitude from those at higher altitudes. Furthermore, the PCA analysis shows that about 50% of the variance in morphological characteristics is explained by altitude and aspect alone. This shows that there may be other ecological factors influencing morphological characteristics that were not investigated in this study.

Conifer morphological traits are known to vary adaptively with geographic and climatic variables (Ji *et al.* 2011). The effects of topographical factors, habitat characteristics, and climatic conditions on the morphology, anatomy, and growth characteristics of many tree species have found an important place in forestry research. Topography has a direct effect on factors, such as the site productivity (Duyar and Makineci 2016; Seki and Sakici 2024), plant morphology (Bozkurt *et al.* 2021; Atar 2022; Özdikmenli *et al.* 2024), tree and sapling growth (Doğan and Köse 2019; Keleş 2020; Bolat 2025), floristic variation (Kavgacı *et al.* 2013), and the diversity of anatomical characteristics (Biricik *et al.* 2021b; Yıldız and Keleş 2022). This study found significant effects of topographic features including altitude and aspect on the needle and cone morphology of mature black pines. Further, significant relationships were also found between all of the investigated morphological characteristics and both altitude and aspect. This is because the growing season, rainfall, solar radiation, and the availability of water are all correlated with these topographical factors.

Conifer needles generally respond to drought conditions because of water stress (le Provost *et al.* 2013). For example, needles of *Picea abies* (L.) Karst. in Southeast Europe (Popović *et al.* 2022) and *Pinus cembroides* in the Davis Mountains of west Texas (Poulos and Berlyn 2007) were found longer in rainy high altitudes without water stress. It is also possible that studies conducted between tree morphology and topographic features may yield different results. Because the ecological requirements of each tree species are different, the relationship between the altitude range from which the samples are taken and the optimal altitude of which the species growth, the climatic characteristics in the years in which the plants are sampled, *etc.* factors can affect the results of such studies. For example, a study by Ergül Bozkurt *et al.* (2021) found that Scots pine needles shortened with altitude, in contrast to this study. Additionally, a negative correlation was found between altitude and needle length of *P. roxburghii* Sarg. in the North-West Himalayan region (Tiwari *et al.* 2013), *P. yunnanensis* in southwestern China (Xu *et al.* 2016), *P. nigra* in Montenegro (Korol *et al.* 2022) and (*P. pinaster* Ait.) in Morocco (Wahid *et al.* 2006).

A decrease in *nw* with altitude has been observed for *P. pinaster* Ait. Karst. in Morocco (Wahid *et al.* 2006) and *P. sylvestris* L. populations from the Carpathian region (Köbölkuti *et al.* 2017). In this study, no significant trend was observed between *nw* and altitude. Nature is a dynamic environment, with many different factors at play that are difficult to detect, and significant relationships between morphological features and topographic factors may not always be detected. As in this study, no significant relationship was found between altitude and many morphological characteristics of the *P. brutia* (Ten.) of Crete Island, Greece (Dangasuk and Panetsos 2004).

A positive correlation between *cw* and *cw/cl* ratio of black pine and altitude was found in this study. Moreover, the aspect's effect on the cone morphology was only observed at low altitudes, where the water deficit was high. Similarly, *Pinus canariensis* cones have been reported to be larger at higher altitudes (Gil *et al.* 2002). Similar to this study, significant morphological differences as a function of altitude were found in the study for Scots pine species (Turna and Güney 2009). This study found that Scots pine cones, particularly at lower altitudes, were smaller in both width and *cw/cl* ratio. In contrast, negative correlation between cone characteristics and altitude were found in the study (Singh and Thapliyal 2012) executed for *Pinus wallichiana* in north-western Himalayas. Further, there was no significant relationship between altitude and cone characteristics of *Pinus yunnanensis* in southwestern China (Xu *et al.* 2016).

In this study, needle length and cone dimensions increased especially depending on the altitude. A study by Seki (2023) in Cemaller Forest Chieftdom within Karabük concluded that needle characteristics and stomatal density of black pine saplings were higher at higher altitudes due to less water deficit and high rainfall. In addition, the morphological characteristics of the sapling needles of the rainier year were higher than those of the year with low rainfall. Although the optimal requirements and sensitivities of saplings and mature trees in terms of ecological factors are different, this study and the study of Seki (2023) show that altitude and hence precipitation are important factors for black pines of all ages. Increasing altitude and precipitation have a positive effect on the morphology of black pine needles.

Water stress can cause modifications in needles not only in size but also in other characteristics, such as cuticular wax content, as the results obtained for *Pinus pinaster* (Le Provost *et al.* 2013). Moreover, in the study by Biricik *et al.* (2021b), which examined the differences between the wood elements of black pines grown at different altitudes and under different aspects, it was found that the most optimal growing conditions for black pine are at higher altitudes where there is more rainfall. Likewise, the positive effects of precipitation on the radial growth of black pine have been demonstrated in many studies (Doğan and Köse 2019; İzmir *et al.* 2024; Bolat 2025). Additionally, Biricik (2021a) stated that the most suitable growing conditions for the black pine species are higher altitudes due to the moisture increase. In addition, the study investigating the carrying capacity of stands of the three main pine species in Türkiye found that the most optimal growing conditions for all pine species were in rainy regions (Seki *et al.* 2025).

Trees growing at lower altitudes can have a stressful environment, and even at these sensitive altitudes the effect of aspect can be more pronounced (Popović *et al.* 2022). The results of this study are evidence in favour of this phenomenon. The aspect's effect on all other morphological characteristics was more pronounced at the lowest altitude (700 to 900 m). Possible reasons for this can be interpreted as a higher temperature stress, an excess of water loss, and low humidity conditions on the south-facing slopes. However, the aspect's effect on *cw* was not observed at any altitude.

Therefore, the morphological variation of trees varies depending on the examined location, species, and topographic features. There is a need to increase the number of studies examining morphological adaptations, especially in countries with topographically heterogeneous structures, such as Türkiye, and to better understand the adaptations of species to changing climatic conditions. Although studies investigating the effects of environmental and ecological stress on plant morphology are common, these studies generally focus on above-ground morphological characteristics. Drought is an important environmental stress affecting tree roots, thus the responses and variations of below-ground characteristics under changing climatic and environment conditions should be investigated in future studies.

In addition to morphological adaptations, the diversity and extent of genetic variation in a species also increases the ability of its ecosystem to adapt to changing climatic conditions (Çengel *et al.* 2012). For this reason, it is important to focus on studies that examine genetic variation in primary tree species.

CONCLUSIONS

1. There is considerable variation in the morphological characteristics of black pine needles and cones depending on topographical features such as altitude and aspect. It was concluded that the nl and sl of black pines growing at lower altitudes with less rainfall are generally shorter than compared to those growing in stands at higher altitudes. It is also observed that cone dimensions, especially width and width/length ratio, increase with altitude. The main reason for this morphological variation depending on altitude can be associated with precipitation differences and water stress.
2. It was determined that the aspect effect was not significant at all altitudes and was more noticeable at the lowest altitude.
3. The aspect has an individual effect on the morphology of the needle and the cone of black pine, as well as a complex effect together with the altitude. The effect of the aspect is more visible, especially at lower altitudes where the environmental stress is more severe. The greater variation in morphological characteristics, especially in the south-facing slopes, is evidence of this situation. These sensitive ecosystems at critical altitudes need to be more carefully managed.
4. The study results show that the adaptation and morphological responses of black pine under various conditions are different. The results of this study can also be used to determine optimal habitat conditions for black pine, particularly to increase the success of afforestation studies. Additionally, correlating these morphological responses with expected climate scenarios allows foresters to have meaningful prescriptions for the changing climatic regimes.

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