Isparta University of Applied Sciences

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Determination of biomass and carbon storage amounts in pure and mixed natural black pine (*Pinus nigra* subsp. *pallasiana*) stands: The case of Samsun

Ergün Kahveci[a,*], Ömer Kara[b]

Abstract: In this study, the effects of different canopy closures and slopes on aboveground, soil, and belowground biomass (B) and carbon (C) storage in pure black pine (*Pinus nigra* subsp. *pallasiana*), mixed black pine - Scots pine (*Pinus sylvestris*), and black pine-Turkey oak (*Quercus cerris*) natural stands were investigated. The study was conducted in 88 sample areas selected using a selective sampling method within the boundaries of Atakum (Ada) and the Boğaziçi Forest Management Directorate in Samsun Province. Samples were taken for the aboveground, soil, and belowground components of these areas. The mean tree method was used to estimate tree C storage, while multiple variance analyses were applied to evaluate differences in B and C stocks. According to the obtained findings, average aboveground tree B in pure black pine, mixed black pine - Scots pine, and black pine - Turkey oak stands were 63.61 t/ha, 67.41 t/ha, and 86.51 t/ha, respectively; total vegetative mass was 102.97 t/ha, 101.43 t/ha, and 127.84 t/ha, respectively; aboveground tree C was calculated as 28.93 t/ha, 30.45 t/ha, and 36.49 t/ha, respectively. Similarly, total plant C amounts were 46.07 t/ha, 47.85 t/ha, and 53.08 t/ha; soil organic carbon (SOC) values were 119.42 t/ha, 103.07 t/ha, and 100.88 t/ha. While land slope had no significant effect on B and C storage, B and C storage varied with canopy closure. Additionally, it was found that stand structure, rather than soil properties, was a key determinant of C storage.
Keywords: Samsun, Black pine, Pure and mixed natural stands, Aboveground and belowground biomass, Carbon storage

Saf ve karışık doğal karaçam (*Pinus nigra* subsp. *pallasiana*) meşcerelerinde biyokütle ve karbon depolama miktarlarının belirlenmesi: Samsun örneği

Özet: Bu çalışmada; saf karaçam (*Pinus nigra* subsp. *pallasiana*), karışık karaçam-sarıçam (*Pinus sylvestris)* ve karaçam-meşe (*Quercus cerris)* doğal meşcerelerinin toprak üstü, toprak ve toprak altı biyokütle (B) ve karbon (C) depolama miktarları üzerine farklı kapalılık ve eğim etkisi araştırılmıştır. Çalışma, Samsun İli Atakum (Ada) ve Boğaziçi Orman İşletme Şefliği sınırları içinde, seçme örnekleme yöntemiyle belirlenen 88 örnek alanda gerçekleştirilmiştir. Bu alanlarda toprak üstü, toprak ve toprak altı bileşenlerine yönelik örnekler alınmıştır. Ağaçlara ait C depolama miktarlarının tahmininde orta ağaç yöntemi, biyokütle ve karbon stoklarındaki farklılıkların değerlendirilmesinde ise çoklu varyans analizleri kullanılmıştır. Elde edilen bulgulara göre, saf karaçam, karaçam - sarıçam ve karaçam - meşe karışık meşcerelerinde ortalama toprak üstü ağaç biyokütlesi sırasıyla 63.61 t/ha, 67.41 t/ha ve 86.51 t/ha; toplam bitkisel kütle 102.97 t/ha, 101.43 t/ha ve 127.84 t/ha; toprak üstü ağaç karbonu 28.93 t/ha, 30.45 t/ha ve 36.49 t/ha olarak hesaplanmıştır. Aynı şekilde, toplam bitkisel karbon miktarları 46.07 t/ha, 47.85 t/ha ve 53.08 t/ha; toprak organik karbon değerleri ise 119.42 t/ha, 103.07 t/ha ve 100.88 t/ha'dır. Arazi eğiminin B ve C depolama üzerinde anlamlı etkisi bulunmazken, B ve C depolamanın kapalılığa göre farklılık gösterdiği tespit edilmiştir. Ayrıca, C depolama üzerinde toprak özelliklerinden çok meşcere yapısının belirleyici olduğu ortaya konmuştur.
Anahtar kelimeler: Samsun, Karaçam, Saf ve karışık doğal meşcereler, Toprak üstü ve toprak altı biyokütle, Karbon depolama

1. Introduction

The primary driver of climate change is the continuous increase in atmospheric greenhouse gas concentrations since 1750, primarily due to human activities (Stocker et al., 2013). As of 2019, atmospheric CO_2 levels had reached approximately 410 parts per million, higher than at any time in at least the past 2 million years, and this increase is attributed with high confidence to human activities (Intergovernmental Panel on Climate Change, 2023). In this context, reducing greenhouse gas emissions and enhancing long-term carbon (C) storage in terrestrial systems are essential strategies for mitigating climate change. Forest ecosystems play a vital role by sequestering terrestrial C and removing CO_2 from the atmosphere (Zeydanlı et al., 2010). Under the Paris Agreement, Türkiye's updated Nationally Determined Contribution (NDC) aims to reduce greenhouse gas emissions by 41% by 2030 relative to the business-as-usual scenario, highlighting the critical role of the Land Use, Land-Use Change, and Forestry (LULUCF) sector (Türkiye Cumhuriyeti, 2023, 2024). Within this framework, sustainable management and protection of forests remain central to national climate policy (Asan et al., 2005).

[a] Tokat Gaziosmanpasa University, Niksar Vocational School, Department of Forestry, Tokat, Türkiye
[b] Karadeniz Technical University, Faculty of Forestry, Department of Forest Engineering, Trabzon, Türkiye
[*] **Corresponding author** (İletişim yazarı): ergun.kahveci@gop.edu.tr
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Forest ecosystems cover approximately 30% of the Earth's surface and account for a substantial proportion of terrestrial gross organic matter production (Güner and Makineci, 2017). Forest biomass (B) contains a significant fraction of terrestrial C, while soils store a substantial portion of belowground carbon (BGC) (Dixon et al., 1994; Mukul et al., 2020). Accurately quantifying the C stored in tree components such as stems, branches, bark, leaves, and roots, as well as in litter, deadwood, and soil, is necessary for C trading, national greenhouse gas inventories, and sustainable forest management (Page et al., 2002; Tolunay et al., 2017). Although a range of methods, from direct harvest to remote sensing, have been applied to estimate B and C stocks, site-specific data remain essential for precise reporting (Alemdağ, 1981; Lu & Batistella, 2005).

Within this ecological and policy context, *P. nigra* (black pine) forests hold particular strategic importance in Türkiye. *P. nigra* constitutes approximately 18% of the country's total forest area, making it the second most widespread conifer species after *Pinus brutia* Ten. Its relatively high drought tolerance and broad ecological amplitude have led to its identification as a key species in climate change adaptation strategies in southern Europe and Türkiye. Furthermore, it is expected to maintain ecological relevance under future climate conditions, including high-emission scenarios such as SSP5-8.5 (Lindner et al., 2010; Intergovernmental Panel on Climate Change, 2023). Accurate quantification of B and C stocks in both pure and mixed *P. nigra* stands is therefore essential for informing mitigation-oriented and adaptation-oriented forest management strategies.

To better understand this adaptation potential, this study examines the structural dynamics of stand composition. One of the primary objectives is to compare the B and C stocks in pure and mixed forest stands. The higher productivity and C storage potential often observed in mixed stands are frequently attributed to ecological mechanisms such as niche complementarity and facilitation, in which coexisting species utilize light, water, and nutrient resources more efficiently (Loreau and Hector, 2001). In mixed stands composed of light-demanding conifers, such as *P. nigra*, and deciduous species with deeper rooting systems, such as *Q. cerris*, differences in crown architecture and root distribution can enhance aboveground light interception and belowground resource acquisition. This complementary resource use can result in stand densities and productivity levels exceeding those observed in pure stands (Pretzsch and Biber, 2016; Pretzsch et al., 2017).

Despite these theoretical benefits, quantitative evidence on the specific interactions between *P. nigra* and *Q. cerris* remains limited, particularly in the transitional zones of the Black Sea region. Unlike more extensively studied mixtures such as pine-beech or spruce-fir, the association of drought-tolerant *P. nigra* with the deciduous species *Q. cerris* may present a distinct form of functional complementarity. Moreover, national forest C inventories in Türkiye often rely on coefficients derived from pure stands or ecological regions that differ from mixed *P. nigra* ecosystems, which can introduce biases when applied to structurally complex forests (Asan et al., 2005; Öztürk, 2022). Therefore, obtaining site-specific B and C data under varying canopy closure and topographic conditions is essential to reduce uncertainty and fill gaps in the national literature.

This study was conducted in natural stands of pure black pine, mixed black pine - Scots pine, and black pine-Turkey oak within the boundaries of the Atakum and Boğaziçi Forest Management Directorates of Samsun province in the Central Black Sea Region. Three primary C pools were analyzed: aboveground biomass (AGB), belowground biomass (BGB), and soil C. The effects of stand structure, canopy closure, and slope on C stocks were also investigated. By explicitly linking stand structure, canopy closure, and topographic conditions to multiple C pools, this study aims to quantify C storage in these mixed ecosystems, provide region-specific data to Turkey's forest C inventory, and support silvicultural decision-making while strengthening national greenhouse gas inventory assessments.

2. Materials and methods

2.1. Study area and site characteristics

The material of this study consists of a 1583 ha area (comprising 585 ha of *P. nigra*, 403 ha of *P. nigra - P. sylvestris*, and 595 ha of *P. nigra - Q. cerris*) within the boundaries of the Atakum and Boğaziçi Forest Management Directorates in Samsun Province. The study area is located between 41°16′14″-41°16′58″ N latitude and 36°07′16″-36°07′39″ E longitude. Although the region ranges from sea level to 1,388 m in elevation, sampling was conducted on south-facing slopes at elevations between 450 and 850 m (Figure 1).

The climate of the study area is defined as "B2 B'1 r a'" and "B3 B'1 r a'" according to the Thornthwaite (1948) method and is classified as 'Humid, mesothermal, water-deficient, near-maritime climate'. Regarding phytogeography, the area is situated within the Euro-Siberian (Euxin-Colchic) flora region of the Holarctic zone, specifically within the A6 square according to Davis's (1965-1988) grid system. The dominant tree species are beech (*Fagus orientalis* Lipsky), red pine (*P. brutia*), black pine (*P. nigra*), Scots pine (*P. sylvestris*), hornbeam (*Carpinus betulus* L.), sessile oak (*Q. petraea*), and Turkey oak (*Q. cerris*) (Orman Genel Müdürlüğü, 2020). The geological structure of the region comprises sedimentary, volcanic, and lava rocks from the Eocene, Cretaceous, and Neogene periods, with alluvial deposits present in the delta plains (Hekimoğlu et al., 2007; Orman Genel Müdürlüğü, 2010). The research area is generally located in the fourth site class and has a low growth environment.

2.2. Stand structure, canopy closure, slope classes, and plot selection

A total of 88 sample plots were identified in the field, and samples were collected from these plots according to different canopy closure classes (41-70% and 71-100%) and slope classes (17-36% and 36-58%). Slope was classified into two broad categories primarily due to the limited availability of suitable stands across other slope gradients within the study area; this grouping was necessary to ensure balanced replication and adequate statistical power. We acknowledge that this coarse classification may mask finer topographic gradients. Consequently, relationships between slope and B and C stocks should be interpreted as broad categorical differences rather than continuous slope-response functions. Topography is widely recognized as an essential driver of forest structure and ecosystem functioning at the landscape scale (Jucker et al., 2018).

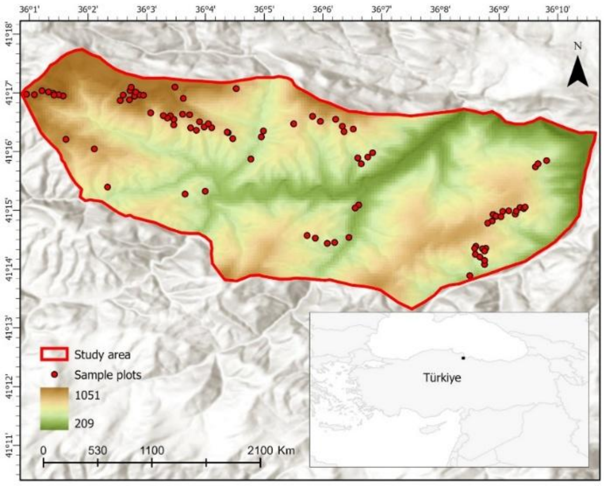


Figure 1. Location of the study area and distribution of the sample plot

Within the scope of the study, a total of 88 sample plots were selected from black pine stands and mixed natural stands, of which black pine is the dominant species. The sampling design was based on developmental stages and species composition, with an explicit focus on the b stage (young developmental stage; diameter 8-19.9 cm) and the c stage (mature developmental stage; diameter 20-35.9 cm). These stands consist of pure black pine, mixed black pine-Scots pine, and mixed black pine-Turkey oak stands. Each stand structure was selected from areas representing canopy closure classes 2 (41-70%) and 3 (71-100%). All sample plots were located within the same elevation range (450-850 m) and on south-facing slopes.

Degraded areas, roadsides, and artificial afforestations were excluded from the sample. In each sample plot, trees of healthy, single-stemmed, crown-intact, and non-stressed individuals were selected and felled, with selection based on factors such as stand structure, canopy cover, slope, and aspect.

In addition, stand structure, canopy closure, and slope classes (moderately steep: 17-36%; steep: 36-58%) were considered the main criteria for plot selection. In this context, stem, branch, foliage, and bark samples were taken from 82 sample trees. The stems were divided into 2-meter sections, diameter measurements were taken, and a 3-5 cm thick cross-section was cut from each sample tree. Branches and leaves were weighed separately, and their fresh weights were recorded.

2.3. Biomass sampling and estimation methods

2.3.1. Aboveground biomass

In total, 82 sample trees were felled in 49 sample areas. Stem sections, as well as branch and foliage samples, were collected from each sample tree. In addition, median diameter measurements were taken for 2576 trees, and height and age measurements were recorded for 440 trees.

This study employed the median tree method (Saraçoğlu, 2002) to estimate AGB and aboveground carbon (AGC) content at the stand level. In this method, a representative 'median tree' is identified for each sample area based on diameter distribution. The biomass of this tree is calculated, and the resulting value is then scaled to a per-hectare basis by multiplying it by the number of trees within the sample plot.

The median tree method was preferred because it provides a practical and cost-effective approach for estimating tree B and C stocks under field conditions characterized by limited accessibility, steep slopes, and heterogeneous stand structures, where exhaustive destructive sampling is complex. This method has been widely applied in forest B studies and has yielded reliable estimates in relatively homogeneous stands (Cairns et al., 1997; Saraçoğlu, 2002). However, its representativeness may decrease in highly heterogeneous stands with multimodal diameter and height distributions; therefore, the resulting B and C estimates should be interpreted as area-level approximations rather than exact stand totals (Cairns et al., 1997). Future studies integrating plot-level destructive sampling or remote sensing approaches could further refine these estimates.

Each stem section was dried at 65 ± 3 °C for 96 hours, and its moisture content was determined by comparing the oven-dry weight with the fresh weight. Stem volume was calculated using the sectional method, and total fresh and dry weights were obtained. Branch and foliage samples were dried under the same conditions, and total branch and foliage B was calculated by extrapolating sample weights to the whole tree. Bark B was determined by dividing bark fresh volume by bark cross-sectional volume and multiplying by the corresponding fresh and dry weight ratios (Tüfekçioğlu et al., 2002).

2.3.2. Ground vegetation, litter, and deadwood

During the fieldwork, 352 litter, 88 ground vegetation, and 88 deadwood samples were collected. Ground vegetation sampling was carried out in 1 x 1 m quadrats. All ground vegetation was cut and its fresh weight determined; the samples were then dried in the laboratory. Litter samples were taken in 25 x 25 cm quadrats at each sampling site and collected without distinction between decay and humus. A total of 352 samples were baked at 65±3°C for 48 hours to calculate litter B:

$$LLB(t\ ha^{-1}) = \sum \frac{m.10^4}{0.0625x10^6} \tag{1}$$

Where *LLB* is the litter biomass per hectare (t/ha), *m* is the oven-dry litter mass (g), *0.0625* is the area of the litter cage (m²), 10^6 is the conversion factor from grams to tonnes, and 10^4 is the conversion factor from square meters to hectares.

Deadwood samples were collected from 1 x 1 m areas, selecting only those with a diameter greater than 2.5 cm. These materials, collected from 88 sample areas, were dried at the same temperature and for the same time, and B values per hectare were calculated.

2.3.3. Belowground biomass

A total of 352 root samples were collected using steel pipes with a diameter of 6.4 cm and a length of 30 cm (Tufekcioglu et al., 2003; Böhm, 2012). Mixing with the litter was prevented when inserting the steel pipes. In the laboratory, the roots were washed and separated into three diameter categories: 0-2 mm (fine roots), 2-5 mm (small roots), and 5-10 mm (coarse roots). They were then dried at 65°C and weighed. Root biomass (RB) was calculated using the following formula:

$$RB(t\ ha^{-1}) = \sum \frac{300.m}{V.10^6.10^4} \quad (2)$$

Where RB is the root biomass per hectare (t/ha), m is the oven-dry root mass obtained from the soil core (g), V is the volume of the soil cylinder (0.964608 L), 10^6 is the conversion factor from grams to tons, and 10^4 is the conversion factor from square meters to hectares.

2.4. Organic carbon content and carbon stock calculations

Soil pits were opened down to the bedrock depth, and both volume and bag samples were collected from five depth intervals: 0-10 cm, 10-30 cm, 30-50 cm, 50-80 cm, and 80-100 cm (Kantarcı, 2000; Türüdü, 2004). Soil samples were air dried, crushed in a mortar, passed through a 0.5 mm sieve, and prepared for laboratory analysis.

In addition to soil samples, organic carbon (OC) content was determined for the main components of the vegetative mass, including stem, bark, branches, leaves, roots, ground vegetation, deadwood, and litter. All plant material samples were ground to a fine powder, and 0.10 g subsamples were prepared for chemical analysis. OC concentrations in both soil and vegetative samples were determined using the Walkley-Black wet digestion method (Walkley and Black, 1934; Gülçur, 1974). A correction factor of 1.30 was applied in this method, assuming that approximately 77% of OC is oxidized during digestion, as commonly adopted in soil C studies (Walkley and Black, 1934; Gülçur, 1974). Organic C (%) was calculated using the following equation:

$$Organic\ C\% = [(N_1 \times A) - (N_2 \times B)] \times 0.003 \times 200 \times f_1 \quad (3)$$

Where N_1 is the actual normality of potassium dichromate ($K_2Cr_2O_7$) solution, A is the volume of potassium dichromate solution used (mL), N_2 is the actual normality of iron sulphate ($FeSO_4.7H_2O$) solution, B is the volume of iron sulfate solution used in titration (mL), 0.003 is the equivalent weight of C, 200 is the conversion factor for 100 g of soil or litter, and f_1 is the correction factor (100/77 = 1.30).

Following the determination of OC concentrations, soil organic carbon stocks (SOCS, t/ha) were calculated for each depth interval using the bulk density (BD) values of the corresponding soil horizons according to the equation:

$$SOCS = SOC\% \times BD \times d \times 10 \quad (4)$$

Where $SOC\%$ is the OC concentration (%), BD is the bulk density (g/cm^3), and d is the soil depth (m), and 10 is the conversion factor to express the stock in t/ha. A stoniness correction factor was not applied due to inconsistent field data availability; therefore, the reported values represent C stocks for the fine-earth fraction only.

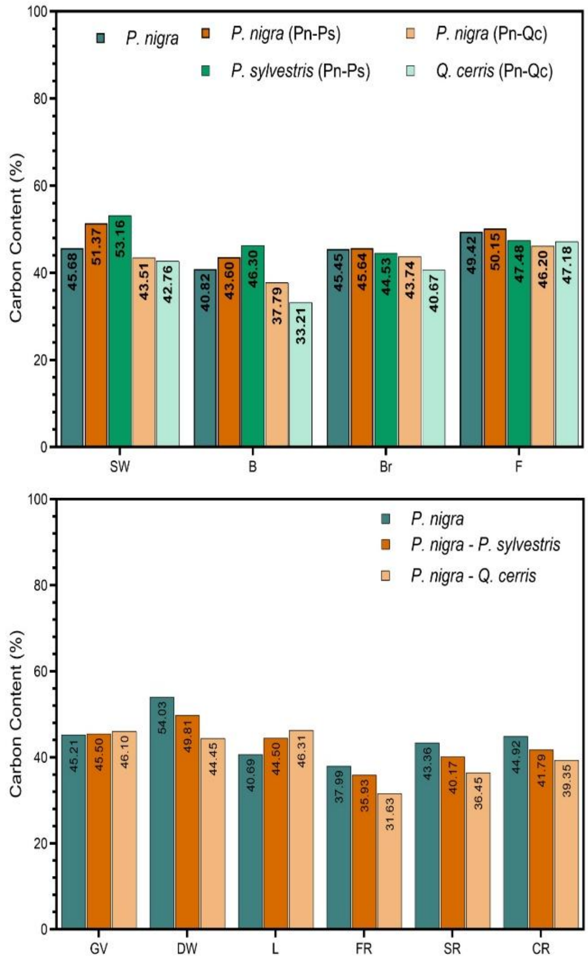
2.5. Statistical analyses

The SPSS (2013) package program was used to analyze the collected data. First, the data were tested for normal distribution and homogeneity of variances, which are basic assumptions for Multiple Analysis of Variance (MANOVA). Preliminary tests confirmed that the data were normally distributed and the variances were homogeneous. This ensured that MANOVA yielded reliable results. Differences in B and C storage potential among stand structures were analyzed using MANOVA under these assumptions. Duncan's multiple-comparison test was used to identify the sources of significant differences.

3. Results and discussion

3.1. Carbon contents of plant mass components

The C concentrations (%) in plant B components varied significantly with both species and stand structure (Figure 2). Coniferous species generally exhibit higher lignin contents, resulting in elevated C concentrations compared to those of deciduous species (Lamlom and Savidge, 2003; Thomas and Malczewski, 2007). In the present study, woody tissues (stem wood and branches) contained higher C concentrations than foliage, litter, or ground vegetation. This pattern supports the view that the higher lignin content of woody tissues enhances their capacity to store C (Bert and Danjon, 2006). Additionally, wood density has been reported as a significant factor influencing C concentration, particularly in coniferous species (Thomas and Malczewski, 2007).



Pn: *Pinus nigra*, Pn-Ps: *Pinus nigra - Pinus sylvestris*, Pn-Qc: *Pinus nigra - Quercus cerris,* SW: stem wood, B: bark, Br: branch, F: foliage, GV: ground vegetation, DW: deadwood, L: litter, FR: fine root, SR: small root, CR: coarse root

Figure 2. Carbon content in plant mass

In mixed *P. nigra* - *P. sylvestris* stands, stem wood C concentration reached its highest value at 53.16%, which is broadly consistent with values reported for *P. sylvestris* in earlier studies (Laiho and Laine, 1997; Tolunay, 2009) and with recent findings for *P. nigra* in Turkey, including studies conducted in the Sündiken Mountains (Çömez et al., 2025). Pure *P. nigra* stands exhibited a stem C concentration of 45.68%, comparable to the values reported by Öztürk (2022). In contrast, lower stem C concentrations observed in mixed *P. nigra* - *Q. cerris* stands reflect the influence of oak species, indicating that species composition is a key determinant of C concentration.

Bark C concentration exhibited an opposite trend. In mixed *P. nigra* - *P. sylvestris* stands, bark C concentration was 43.60%, whereas it decreased to 33.21% in mixed *P. nigra* - *Q. cerris* stands. These differences are primarily attributed to species-specific chemical characteristics, particularly variations in lignin proportion (Bert and Danjon, 2006). The relatively higher bark C concentrations in Scots pine mixtures are consistent with previous findings reported for conifer-dominated stands (Laiho and Laine, 1997; Tolunay, 2009; Çömez, 2010).

Branch C concentration was 45.45% for *P. nigra* and 44.53% for *P. sylvestris*, in general agreement with the findings of Öztürk (2022). Higher branch C concentrations reported for *P. nigra* in some studies may be associated with differences in site conditions or genetic variability (Güner and Çömez, 2017). Foliage C concentration was higher in Scots pine mixtures, with a value of 47.48% for *P. sylvestris*, although slightly lower than values reported elsewhere in Turkey. In oak-containing mixtures, foliage C concentrations were lower, consistent with the generally lower C concentrations observed in deciduous leaves (Makineci et al., 2011). These variations highlight the influence of species-specific traits and interspecific interactions on C accumulation.

Ground vegetation C concentrations were generally consistent with values reported in the literature and tended to be higher in stands dominated by conifer species compared to oak-containing mixtures. This pattern may be related to more favorable light and temperature conditions that promote understory development (Abdallah and Chaieb, 2012). Conversely, increased canopy closure limits light availability in the understory, suppressing ground vegetation growth and reducing its C concentration (Muukkonen and Mäkipää, 2006).

Deadwood C concentrations were relatively high. During decomposition, low-C compounds are preferentially lost, while lignin-rich and C-dense components are retained in deadwood and litter (Harmon et al., 1986; Sandström et al., 2007). Forest management practices, including wood harvesting and residue removal, can reduce deadwood quantities and associated C stocks (Çömez, 2010; Verkerk et al., 2011). Consistent with previous studies, deadwood C concentration was generally higher in conifer-dominated stands, likely due to differences in species composition, litter inputs, and slower decomposition rates (Schulp et al., 2008; Sevgi et al., 2011). Deadwood C may also vary depending on management intensity and disturbance history (Tunç, 2019).

BGC concentrations, including fine, small, and coarse roots, were generally low. This pattern likely reflects the allocation of root B to deeper soil layers, where C is less represented in surface-based measurements (Sarıyıldız et al., 2005). In addition, soil physical properties such as moisture regime and aeration influence root B distribution and C concentration (Çepel, 1996), while parent material may further affect BGC dynamics (Sevim, 1961).

Overall, stand structure and species composition emerged as key determinants of C concentration in plant B components. The relatively low stand density in the study area may have limited C accumulation in woody B, resulting in slightly lower C concentrations than those reported in some comparable studies.

3.2. Changes in biomass and carbon based on components, slope and canopy cover

Land slope, canopy cover, and stand structure collectively influenced the distribution of forest B components across the studied stands (Table 1). Aboveground tree B reached its maximum value (94.28 t/ha) in mixed *P. nigra* - *P. sylvestris* stands located on moderately steep slopes under canopy closure class 3. Stem wood B also peaked under these structural and topographic conditions, consistent with research demonstrating that canopy density and stand complexity promote allocation to long-lived woody tissues by enhancing light interception and C assimilation (Poorter et al., 2012; Cudjoe et al., 2025).

Bark B was highest in mixed *P. nigra* - *Q. cerris* stands, likely associated with species-level variation in bark traits and allocation strategies. Traits such as bark thickness and chemical composition influence B fractions, particularly in mixed-species stands where niche complementarity and functional diversity are greater (Forrester, 2013; Pretzsch and Schütze, 2016). Branch and foliage B similarly peaked in mixed stands, illustrating how species interactions and canopy layering can enhance lateral crown development and B distribution (Pretzsch, 2014; Forrester et al., 2018).

Deadwood B varied markedly among stand types, with the highest accumulation in mixed *P. nigra* - *Q. cerris* stands, and lower levels in pure *P. nigra* stands. This pattern aligns with global findings that mixed forests often support greater dead organic matter due to varied mortality patterns and structural complexity, which influence debris fall and retention (Harmon et al., 2020; Samariks et al., 2025). BGB also differed across stand types, with fine- and coarse-root B peaking in mixed stands under moderately steep slopes and higher canopy closure, reflecting adaptive allocation to structural stability and resource capture on variable terrain (Freschet et al., 2021; Schnabel et al., 2025).

C content showed pronounced variation across canopy closure classes, slope categories, and stand structures, indicating strong structural control over C distribution among B components (Table 2). Patterns in C allocation generally paralleled B trends, but the magnitude of C variation among components reflects differences in tissue turnover and residence time, which are shaped by both biotic and abiotic factors (Lal, 2005; Zhou et al., 2025).

Table 1. Variation of biomass amounts with slope and canopy cover according to stand structure

Slope	Components (B t/ha)	Canopy closure: 2			Canopy closure: 3		
		Pn	Pn - Ps	Pn - Qc	Pn	Pn - Ps	Pn - Qc
17 - 36 %	B_{SW}	34.55±8.92[(1)] 25.88-47.05[(2)]	25.36±6.11 20.91-34.28	52.55±22.51 31.09-83.34	49.82±18.65 26.03-64.70	56.48±12.02 39.77-71.43	55.48±25.98 32.10-82.47
	B_B	4.04±1.00 3.09-5.12	3.02±0.57 2.17-3.38	7.29±1.78 4.67-8.68	6.23±1.44 4.43-7.52	5.52±0.79 4.61-6.38	9.54±2.63 7.57-13.18
	B_S	38.59±9.77 28.97-52.17	28.38±6.17 24.20-37.53	59.84±23.47 35.76-91.27	56.12±20.09 30.46-72.21	61.99±12.50 44.38-77.80	65.02±28.41 39.74-95.65
	B_{Br}	10.56±4.86 4.49-14.77	14.71±7.93 9.02-26.05	18.35±13.55 5.24-34.28	10.73±5.38 6.03-18.15	13.19±4.79 9.03-20.03	20.93±13.66 11.91-40.84
	B_F	4.57±1.85 2.99-6.87	4.56±2.13 2.59-7.56	6.49±3.90 2.26-11.58	4.74±3.91 1.15-9.08	6.52±3.72 3.12-12.56	8.33±5.98 4.48-17.22
	B_{AGT}	53.71±14.71 40.74-73.81	47.65±8.60 37.38-57.81	84.68±29.87 43.26-107.42	71.59±27.76 39.82-97.19	81.71±19.48 58.60-110.39	94.28±45.50 58.03-153.71
	B_{GV}	0.31±0.14 0.16-0.55	0.34±0.18 0.13-0.68	0.29±0.10 0.17-0.43	0.19±0.10 0.09-0.43	0.35±0.14 0.14-0.49	0.24±0.17 0.09-0.59
	B_{DW}	4.21±0.73 3.44-5.60	3.22±0.69 2.02-3.94	3.46±1.03 2.54-5.22	4.35±1.11 2.89-6.78	3.67±1.08 2.37-5.22	3.44±0.84 2.56-4.99
	B_L	15.29±4.81 9.29-21.88	11.45±4.37 5.40-18.02	12.13±4.98 6.93-20.53	13.92±2.25 10.63-17.63	11.18±4.51 5.50-18.61	12.66±4.86 5.32-19.15
	B_{FR}	9.70±3.27 6.52-16.24	8.21±3.30 5.20-14.70	9.93±9.15 5.59-32.31	7.85±2.31 5.23-12.22	10.13±5.22 5.56-21.62	12.83±9.97 4.42-34.10
	B_{SR}	2.52±0.83 1.32-3.77	1.96±0.10 0.77-3.36	1.66±0.75 0.75-2.73	2.44±0.98 1.49-4.06	2.02±0.86 0.94-3.18	2.87±1.18 1.53-4.40
	B_{CR}	12.16±9.57 2.49-28.52	9.04±11.78 2.08-37.41	8.94±10.55 1.74-32.13	7.67±4.55 0.59-15.13	6.67±4.28 1.91-13.99	18.54±17.14 3.49-47.27
36 - 58%	B_{SW}	34.98±15.94 26.03-58.84	25.01±7.21 19.51-34.88	34.45±4.48 29.21-38.75	44.94±8.91 34.95-55.24	60.82±5.73 55.77-68.39	62.16±22.54 42.22-87.01
	B_B	4.67±3.13 2.83-9.35	2.86±0.59 2.21-3.64	5.58±1.69 3.45-7.19	6.07±1.38 4.03-7.01	7.09±2.09 4.19-9.07	8.34±1.38 6.81-9.79
	B_S	39.65±19.07 28.86-68.19	27.87±7.38 21.97-37.64	40.03±5.69 32.66-45.95	51.01±10.02 38.98-62.26	67.91±7.42 61.24-77.46	70.49±23.77 49.79-96.18
	B_{Br}	11.72±3.68 7.54-16.26	11.52±3.62 7.96-16.03	14.30±6.55 7.81-22.06	17.84±6.52 10.47-26.29	18.83±10.09 8.88-32.87	27.69±10.89 17.98-37.34
	B_F	3.89±1.71 2.57-6.25	4.31±1.03 3.45-5.74	5.54±4.15 1.99-10.51	5.02±0.97 3.76-5.90	6.27±2.44 3.37-9.22	9.127±6.63 3.09-18.57
	B_{AGT}	55.27±15.69 44.76-78.43	43.69±10.82 34.75-59.41	59.77±9.79 48.84-70.35	73.87±13.65 61.40-87.14	93.00±12.04 75.14-100.98	107.31±39.62 70.86-151.65
	B_{GV}	0.25±0.82 0.18-0.43	0.39±0.30 0.34-0.42	0.43±0.19 0.23-0.81	0.28±0.22 0.12-0.83	0.21±0.10 0.08-0.35	0.27±0.10 0.14-0.39
	B_{DW}	4.54±0.65 3.78-5.53	4.59±1.41 2.75-6.24	4.16±1.35 2.85-6.75	5.33±1.62 3.98-9.16	3.28±1.06 1.97-5.01	3.92±1.14 2.84-6.43
	B_L	13.75±2.92 10.30-18.43	12.28±4.71 7.87-21.37	10.14±2.17 6.63-12.66	12.55±3.83 8.91-20.80	13.92±1.32 2.84-6.43	11.54±2.28 9.70-15.69
	B_{FR}	10.78±3.65 5.47-15.72	9.56±3.14 4.71-14.07	11.18±6.04 3.68-21.65	9.77±3.96 5.93-17.15	6.86±1.64 4.74-9.17	10.74±7.22 4.69-24.97
	B_{SR}	2.77±1.16 1.01-4.36	2.90±1.10 1.44-4.63	2.38±0.90 0.99-4.04	2.43±0.95 1.56-4.40	1.88±0.77 0.77-2.63	2.66±1.62 1.32-5.55
	B_{CR}	7.54±7.11 1.73-21.12	13.47±8.88 4.49-26.22	9.34±4.51 2.85-16.20	7.65±4.84 4.01-15.64	8.67±5.48 3.19-16.27	11.85±7.86 3.66-22.69

[(1)]: mean ± standard deviation, [(2)]: minimum-maximum values, 2: (41-70%), 3: (71-100%), Pn: *Pinus nigra*, Pn-Ps: *Pinus nigra* - *Pinus sylvestris*, Pn-Qc: *Pinus nigra* - *Quercus cerris*, B_{SW}: stem wood biomass, B_B: bark biomass, B_S: stem biomass, B_{Br}: branch biomass, B_F: foliage biomass, B_{AGT}: aboveground tree biomass, B_{GV}: ground vegetation biomass, B_{DW}: deadwood biomass, B_L: litter biomass, B_{FR}: fine root biomass, B_{SR}: small root biomass, B_{CR}: coarse root biomass

AGC storage was highest in stem wood under closed-canopy conditions, underscoring the dominant role of canopy closure in regulating C accumulation in persistent woody tissues. This is supported by global synthesis studies showing that denser canopies and higher leaf area indices correlate with elevated AGC stocks across temperate forests (Forrester, 2013; Cudjoe et al., 2025). Bark, branch, and foliage C contents were more strongly influenced by stand structure, with mixed stands, especially those with deciduous species, exhibiting higher values, likely due to greater functional diversity and complementary nutrient use (Pretzsch, 2014).

Deadwood C content varied significantly with stand structure and slope, reflecting interactive effects of mechanical stress, species-specific decay rates, and microclimate, which collectively shape the formation and persistence of coarse woody debris (Seidl et al., 2017; Samariks et al., 2025). In contrast, BGC did not vary as markedly among structural categories, indicating that longer-term processes and abiotic constraints moderate soil and root C pools (Jandl et al., 2007).

Table 2. Variations in carbon content with slope and canopy closure structure according to stand structure

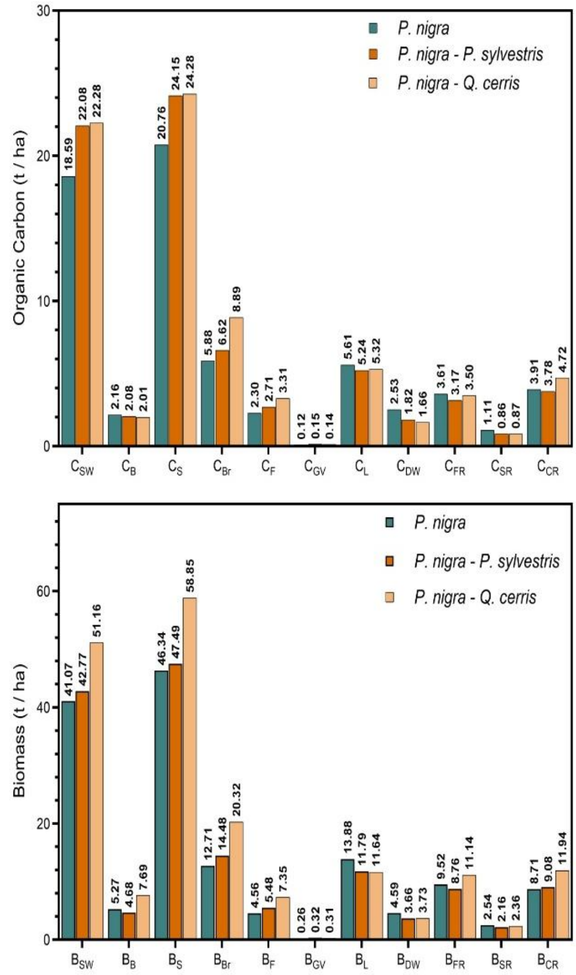
Slope	Components (C t/ha)	Canopy closure: 2			Canopy closure: 3		
		Pn	Pn - Ps	Pn - Qc	Pn	Pn - Ps	Pn - Qc
17 - 36%	C_{SW}	14.81±4.39[(1)]	13.13±2.83	21.77±8.77	21.95±8.07	28.40±4.89	23.67±10.37
		10.25-20.72[(2)]	11.08-17.19	13.35-33.72	11.17-29.450	20.79-33.76	14.12-32.88
	C_B	1.54±0.32	1.31±0.26	1.83±0.41	2.61±0.50	2.41±0.32	2.44±0.30
		1.24-1.86	0.93-1.49	1.29-2.25	1.92-3.04	2.02-2.75	2.13-2.79
	C_S	16.35±4.67	14.44±2.86	23.59±8.86	24.56±8.55	30.81±5.10	26.11±10.67
		11.53-22.58	12.58-18.63	14.64-35.48	13.09-32.34	22.81-36.49	16.24-35.67
	C_{Br}	4.92±2.13	6.65±3.51	9.26±8.38	5.55±3.23	6.26±2.41	9.91±6.58
		1.81-6.33	4.13-11.61	2.31-20.45	2.17-9.89	4.20-9.87	5.25-19.60
	C_F	2.44±1.12	2.06±0.98	2.85±1.67	2.50±2.13	3.08±1.57	4.29±2.51
		1.41-3.87	1.27-3.43	1.01-5.00	0.52-4.38	1.37-5.49	2.46-8.00
	C_{AGT}	23.71±6.42	23.15±3.94	35.71±13.50	32.61±12.49	40.15±8.13	40.32±17.88
		18.20-32.72	18.14-27.61	17.96-49,81	18.38-43.79	29.76-51.85	26.02-63.27
	C_{GV}	0.15±0.89	0.16±0.10	0.14±0.05	0.08±0.04	0.16±0.06	0.11±0.06
		0.066-0.34	0.06-0.35	0.07-0.21	0.04-0.16	0.07-0.23	0.05-0.24
	C_{DW}	2.16±0.44	1.57±0.29	2.06±0.69	2.37±1.02	1.84±0.57	1.53±0.20
		1.57-2.96	1.02-1.89	1.06-3.18	1.47-4.74	1.05-2.65	1.23-1.82
	C_L	6.05±2.04	4.97±1.85	5.33±2.17	5.76±0.97	4.85±1.72	5.47±1.98
		3.47-9.30	2.02-7.95	2.87-9.19	3.98-7.03	2.73-7.65	2.88-8.06
	C_{FR}	3.71±1.11	3.00±1.24	3.07±2.89	3.13±0.84	3.58±1.91	4.28±3.44
		2.67-5.78	1.76-5.50	1.18-10.13	1.90-4.53	2.07-7.94	1.62-11.79
	C_{SR}	1.09±0.40	0.80±0.37	0.62±0.28	1.12±0.45	0.83±0.36	1.04±0.43
		0.53-1.73	0.32-1.27	0.27-0.99	0.64-1.68	0.37-1.33	0.61-1.52
	C_{CR}	5.54±4.30	3.80±4.95	3.48±4.05	3.56±2.09	2.84±1.87	7.33±6.50
		1.08-13.05	0.91-15.73	0.65-12.36	0.28-6.92	0.85-6.23	1.25-18.03
36 - 58%	C_{SW}	15.62±7.60	13.32±3.81	14.92±2.58	21.99±3.54	31.87±2.30	28.74±12.50
		11.23-27.00	9.86-17.81	12.29-17.40	17.20-25.55	29.73-35.12	17.28-41.59
	C_B	1.86±1.19	1.26±0.34	1.40±0.60	2.63±0.79	3.23±1.01	2.36±0.83
		1.19-3.63	0.95-1.74	0.60-2.06	1.49-3.23	1.76-4.07	1.54-3.17
	C_S	17.48±8.79	14.58±4.02	16.32±2.80	24.63±4.16	35.10±2.89	31.10±13.30
		12.42-30.63	10.80-19.05	12.89-18.95	18.69-28.25	32.91-39.19	18.81-44.56
	C_{Br}	4.93±3.33	5.15±1.70	6.31±2.18	8.13±3.49	8.53±4.93	10.08±4.27
		2.62-9.80	3.75-7.53	4.21-8.43	5.02-13.08	4.27-15.65	4.33-13.41
	C_F	1.75±0.69	2.21±0.58	2.10±1.16	2.49±0.62	3.38±1.38	4.02±2.81
		1.17-2.61	1.49-2.84	0.93-3.17	1.73-3.33	1.64-4.82	1.40-7.82
	C_{AGT}	24.16±7.97	21.94±5.61	24.73±3.72	35.25±5.30	47.01±5.07	45.19±19.50
		17.41-34.79	16.41-29.42	21.16-29.91	28.53-40.78	40.99-52.62	24.54-65.79
	C_{GV}	0.11±0.03	0.18±0.19	0.19±0.08	0.14±0.13	0.09±0.04	0.12±0.04
		0.07-0.18	0.16-0.21	0.11-0.34	0.05-0.47	0.04-0.18	0.06-0.18
	C_{DW}	2.30±0.41	2.29±0.65	1.98±0.70	3.29±1.25	1.63±0.59	1.62±0.40
		1.77-2.89	1.52-3.18	1.05-2.81	1.81-6.00	1.06-2.63	1.02-2.07
	C_L	5.65±1.43	5.69±2.41	4.84±1.27	4.99±0.99	5.66±2.81	5.70±0.88
		3.48-8.10	3.55-10.28	3.19-6.75	3.89-6.57	3.12-9.64	4.78-7.08
	C_{FR}	3.86±1.33	3.53±1.28	3.26±1.71	3.75±2.01	2.46±0.89	3.431±2.02
		1.93-6.45	1.78-5.52	1.09-6.17	2.01-7.97	1.35-1.01	1.740-7.39
	C_{SR}	1.18±0.54	1.09±0.37	0.84±0.30	1.04±0.42	0.75±0.32	1.02±0.73
		0.40-1.95	0.51-1.60	0.33-1.38	0.67-1.92	0.27-1.01	0.48-2.37
	C_{CR}	3.28±3.00	5.59±3.79	3.65±1.72	3.31±2.31	3.47±2.32	4.80±3.43
		0.65-8.66	1.91-11.31	1.10-5.66	1.58-7.33	1.31-7.13	1.37-9.62

[(1)]: mean ± standard deviation, [(2)]: minimum–maximum values, 2: (41-70%), 3: (71-100%), Pn: *Pinus nigra*, Pn-Ps: *Pinus nigra - Pinus sylvestris*, Pn-Qc: *Pinus nigra - Quercus cerris*. C_{SW}: stem wood carbon, C_B: bark carbon, C_S: stem carbon, C_{Br}: branch carbon, C_F: foliage carbon, C_{AGT}: aboveground tree carbon, C_{GV}: ground vegetation carbon, C_{DW}: deadwood carbon, C_L: litter carbon, C_{FR}: fine root carbon, C_{SR}: small root carbon, C_{CR}: coarse root carbon

Overall, the consistently higher AGB and BGB observed in mixed stands underscore the role of species complementarity and structural diversity in enhancing forest productivity (Forrester, 2013; Warner et al., 2023). At the same time, C storage is strongly regulated by canopy closure and tissue type. These results align with contemporary forest C frameworks that emphasize multidimensional controls on C stocks and highlight the importance of integrating structural, compositional, and site-specific factors when interpreting forest C dynamics (Zhou et al., 2025).

3.3. Biomass and carbon amounts according to stand structures

Stand-level patterns illustrated in Figure 3 demonstrate apparent differences in the allocation of B and C among ecosystem components depending on stand structure. Mixed stands, particularly those including oak species, exhibited greater accumulation of B and C in stems, branches, foliage, and coarse roots. In contrast, pure stands showed a relatively higher proportion of C stored in litter, deadwood, and fine roots. This contrast reflects differences not only in total production but also in the distribution of C among pools with varying residence times.



Pn: *Pinus nigra*, Pn-Ps: *Pinus nigra - Pinus sylvestris*, Pn-Qc: *Pinus nigra - Quercus cerris*

B_{SW}: stem wood biomass, B_{B}: bark biomass, B_{S}: stem biomass, B_{Br}: branch biomass, B_{F}: foliage biomass, B_{GV}: ground vegetation biomass, B_{L}: litter biomass, B_{DW}: deadwood biomass, B_{FR}: fine root biomass, B_{SR}: small root biomass, B_{CR}: coarse root biomass, C_{SW}: stem wood carbon, C_{B}: bark carbon, C_{S}: stem carbon, C_{Br}: branch carbon, C_{F}: foliage carbon, C_{GV}: ground vegetation carbon, C_{L}: litter carbon, C_{DW}: deadwood carbon, C_{FR}: fine root carbon, C_{SR}: small root carbon, C_{CR}: coarse root carbon

Figure 3. Biomass and organic carbon amounts of the plant mass in the stands (t/ha)

In mixed stands containing *Q. cerris*, increased B and C allocation to stem and branch components can be linked to the functional traits of deciduous species, such as higher wood density, wider crown architecture, and more heterogeneous rooting systems. These traits promote greater light capture and resource-use efficiency, thereby enhancing C accumulation in long-lived woody tissues. The observed pattern supports the view that structural and functional complementarity in mixed stands favors C storage in more persistent B pools (Tolunay, 2009; Makineci et al., 2011; Forrester and Bauhus, 2016).

In contrast, pure *P. nigra* stands allocate a larger share of C to litter, deadwood, and fine roots. These components exhibit faster turnover rates and greater sensitivity to decomposition and disturbance processes, leading to more dynamic C cycling. The relatively high deadwood and litter C stocks observed in pure conifer stands are consistent with the high lignin content and slower decomposition of coniferous residues (Harmon et al., 1986; Lamlom and Savidge, 2003; Duboc et al., 2012). Similar distributions have been reported in conifer-dominated forests, where dead organic matter constitutes a substantial fraction of total ecosystem C (Harmon et al., 1990; Palviainen et al., 2004).

Mixed stands, by contrast, tended to exhibit lower accumulation of dead organic matter, which may be attributed to altered microclimatic conditions and improved litter quality resulting from species mixing. The presence of deciduous species modifies litter chemistry and enhances microbial activity, thereby accelerating decomposition and reducing C residence time in litter and deadwood pools. This mechanism has been widely reported in temperate mixed forests and is associated with greater functional diversity of decomposer communities (Berg and McClaugherty, 2008; Sarıyıldız and Küçük, 2008; Prescott and Grayston, 2013).

From a C management perspective, these differences are particularly relevant. Although pure stands may store a considerable proportion of C in short-lived and highly dynamic pools, mixed stands preferentially allocate C to structurally stable and long-lived woody components, such as stem wood and coarse roots. C stored in these components generally exhibits longer residence times and contributes more effectively to long-term C sequestration. This interpretation aligns with global assessments emphasizing that woody B represents the most stable and climatically relevant forest C pool (Fahey et al., 2010; Pan et al., 2011; Intergovernmental Panel on Climate Change, 2022).

Overall, the results indicate that stand structure influences not only the magnitude of B and C stocks but also their internal distribution among functionally distinct pools. Consequently, species composition and stand mixing emerge as critical factors shaping the balance between short-term C cycling and long-term C storage in forest ecosystems.

3.4. Biomass and carbon differences depending on slope and canopy cover

B and C stocks of vegetation components varied systematically along canopy closure and slope gradients (Table 3). Increasing canopy closure was associated with a pronounced shift in B and C allocation toward overstory components, particularly stem wood and foliage. Under denser canopies, trees tend to invest more in vertical growth and stem development, resulting in greater C accumulation in long-lived woody tissues. This response reflects a structural optimization strategy under light-limited conditions, where competitive pressure favors allocation to persistent aboveground components.

Table 3. Variations of biomass and carbon with slope and canopy closure, according to components

B components and C	CC and SLP classes		n	Mean (t/ha)
B_{SW}	CC	2	24	34.78
		3	25	55.01
C_{SW}		2	24	15.60
		3	25	26.20
B_B		2	24	4.58
		3	25	7.08
C_B		2	24	1.53
		3	25	2.61
B_S		2	24	39.06
		3	25	62.09
C_S		2	24	17.13
		3	25	28.80
C_F		2	24	2.23
		3	25	3.29
B_{GV}		2	24	0.33
		3	25	0.26
C_{GV}		2	24	0.15
		3	25	0.12
B_{DW}	SLP	17-36 %	47	3.72
		36-58 %	41	4.36
C_{DV}		17-36 %	47	1.84
		36-58 %	41	2.23

B: biomass, C: carbon, n: sample size, B_{SW}: stem wood biomass, C_{SW}: stem wood carbon, B_B: bark biomass, C_B: bark carbon, B_S: stem biomass, C_S: stem carbon, B_F: foliage biomass, C_F: foliage carbon, B_{GV}: ground vegetation biomass, C_{GV}: ground vegetation carbon, B_{DW}: deadwood biomass, C_{DW}: deadwood carbon, CC: canopy closure, SLP: slope

In contrast, ground vegetation B and C declined consistently with increasing canopy closure, indicating substantial light limitation beneath closed canopies. Reduced understory development under high canopy closure is a well-documented response in temperate forests and is primarily driven by restricted photosynthetically active radiation reaching the forest floor. Consequently, C allocation shifts away from short-lived understory pools toward the tree layer (Pieper, 1990; Naumburg and DeWald, 1999; Barbier et al., 2008; Depauw et al., 2020). This vertical redistribution highlights the dominant role of canopy structure in controlling the relative contribution of overstory and understory components to total ecosystem C storage.

Slope effects were most evident in dead organic matter pools, particularly deadwood. Deadwood B and C increased with slope steepness, suggesting that steeper terrain enhances mechanical stress factors such as wind exposure, soil instability, and gravitational effects, which collectively increase tree mortality and breakage. In addition, steep slopes often exhibit reduced soil contact and heterogeneous microclimatic conditions, which may slow decomposition and prolong C residence time in deadwood pools. Similar topographic controls on deadwood accumulation have been reported across a range of climatic conditions in forest ecosystems (Tolunay, 1997; Kang et al., 2006; Seidl et al., 2017).

Unlike deadwood, living B components showed a weaker and less consistent response to slope, indicating that topography primarily regulates C storage through its influence on disturbance regimes and decomposition processes rather than through direct effects on tree growth. This distinction suggests that canopy closure is the primary driver of C allocation to living B, whereas slope primarily governs the accumulation and persistence of dead organic matter.

Overall, these findings demonstrate that canopy closure and slope exert complementary but distinct influences on forest C dynamics. Canopy closure predominantly controls C storage in living B by favoring the allocation of C to long-lived woody components. At the same time, slope influences C residence time by regulating the formation and persistence of dead organic matter. Together, these spatial controls underscore the importance of incorporating both stand structural attributes and topographic context into forest C assessments and sustainable management strategies (Tolunay and Çömez, 2008; Vesterdal et al., 2008; Pugh et al., 2020).

3.5. Biomass and carbon assessment with multivariate analysis

Multivariate analysis of variance was used to determine whether B and C contents of aboveground and belowground components differed significantly across stand structure, canopy closure, and slope. The analysis revealed that canopy closure and stand structure were the primary sources of variation across most B and C components, whereas slope exerted a more limited effect (Table 4). To assess the relative importance of these factors, partial eta-squared (η^2) values were calculated for each source of variation. According to commonly accepted thresholds (Cohen, 2013), several canopy closure effects corresponded to large effect sizes, indicating a strong explanatory power of this factor.

Stem wood B and C content varied significantly with canopy closure ($p < 0.001$), with canopy closure explaining a substantial proportion of the observed variance ($\eta^2 = 0.444$). These results statistically confirm that increased canopy closure is associated with greater allocation to stem components, consistent with trends in B accumulation (Vesterdal et al., 2008; Cudjoe et al., 2025). Bark B and C content showed significant responses to both stand structure and canopy closure ($p < 0.001$), reflecting differences among species assemblages in stem-related traits such as bark thickness (Tolunay and Çömez, 2008).

Table 4. Multiple variance analysis results for biomass and carbon amounts

Attribute	Source of variation	Sum of squares	Degrees of freedom	Mean square	F-value	p-value	η^2
B_{SW}	CC	5110.961	1	5110.961	22.634	0.000	0.380
C_{SW}	CC	1348.273	1	1348.273	29.586	0.000	0.444
B_B	SS	84.638	2	42.319	14.695	0.000	0.443
	CC	80.350	1	80.350	27.901	0.000	0.430
C_B	CC	14.295	1	14.295	34.947	0.000	0.486
B_S	CC	6472.993	1	6472.993	24.382	0.000	0.397
C_S	CC	1640.213	1	1640.213	31.908	0.000	0.463
B_{Br}	SS	504.876	2	252.438	3.668	0.035	0.165
C_F	CC	13.739	1	13.739	5.487	0.025	0.129
B_{GV}	CC	0.135	1	0.135	6.484	0.013	0.079
C_{GV}	CC	0.034	1	0.034	6.399	0.013	0.078
B_{DW}	SS	15.512	2	7.756	6.439	0.003	0.145
	SLP	7.518	1	7.518	6.241	0.015	0.076
C_{DW}	SS	12.708	2	6.354	13.911	0.000	0.268
	SLP	2.596	1	2.596	5.684	0.020	0.070

B_{SW}: stem wood biomass, C_{sw}: stem wood carbon, B_B: bark biomass, C_B: bark carbon, B_S: stem biomass, C_S: stem carbon, B_{Br}: branch biomass, C_F: foliage carbon, B_{GV}: ground vegetation biomass, C_{GV}: ground vegetation carbon, B_{DW}: deadwood biomass, C_{DV}: deadwood carbon, CC: canopy closure. SS: stand structure SLP: slope, Significant at $p < 0.05$

Branch B was significantly affected by stand structure (*p = 0.035*), whereas foliage C content responded primarily to canopy closure (*p = 0.025*). These findings indicate that distinct structural drivers regulate different B components; specifically, branching patterns are driven by species-specific crown architecture, while foliage density is limited by light availability (Naumburg and De Wald, 1999; Pretzsch, 2014). Ground vegetation B and C content were significantly influenced only by canopy closure (*p = 0.013*), further supporting the dominant role of canopy structure in controlling understory development through shading (Pieper, 1990; Zhou et al., 2025).

Deadwood B and C content varied significantly with both stand structure and slope (*p < 0.05*). This result highlights the importance of topographic factors in regulating dead organic matter pools, confirming that slope effects on deadwood accumulation are more pronounced due to mechanical stress than on living B components (Kang et al., 2006; Samariks et al., 2025).

As a result, the multivariate analysis confirms that canopy closure is the dominant source of variation across the vast majority of plant components, particularly influencing C storage in stems and foliage. While stand structure influenced variation in specific components such as branches, bark, and deadwood, slope was influential primarily on deadwood. These findings reveal the complex effects of forest structural diversity and ecological location on C dynamics, underscoring the importance of accounting for stand characteristics for effective C management.

3.6. Duncan Test results for biomass and carbon amounts among stand structures

Duncan's multiple-range test revealed statistically significant differences among stand structures for selected B and C components (Table 5). For bark B, the mixed *P. nigra - Q. cerris* stands formed a distinct statistical group, with values significantly higher than those of pure *P. nigra* and mixed *P. nigra - P. sylvestris* stands. This result indicates that species composition plays a measurable role in bark B differentiation, as confirmed by post-hoc comparisons. The distinct grouping of oak mixtures is attributed to species-specific traits, particularly oak's thicker bark structure compared to pine (Tolunay and Çömez, 2008).

A similar grouping pattern was observed for branch B, where the highest values were again detected in mixed *P. nigra - Q. cerris* stands, which differed significantly from other stand types. These differences reflect structural contrasts among stand types; specifically, the spreading crown architecture and lateral branching of deciduous species allow for greater canopy space occupation (Alaback, 1984; Pretzsch et al., 2016). Furthermore, recent studies confirm that interspecific competition in pine-oak mixtures stimulates plasticity in crown allometry, leading to increased branch allocation of B (Cudjoe et al., 2025).

Table 5. Duncan test results for biomass and carbon by stand structure

B components and C	Stand structure	n	Mean (t/ha)	Homogeneous groups
B_B	Pn-Ps	17	4.676	a
	Pn	16	5.269	a
	Pn-Qc	16	7.685	b
B_{Br}	Pn	16	12.713	a
	Pn-Ps	17	14.480	ab
	Pn-Qc	16	20.318	b
B_{DW}	Pn-Ps	28	3.655	a
	Pn-Qc	28	3.726	a
	Pn	32	4.590	b
C_{DW}	Pn-Qc	28	1.660	a
	Pn-Ps	28	1.815	a
	Pn	32	2.529	b

Pn: *Pinus nigra*, Pn-Ps: *Pinus nigra - Pinus sylvestris*, Pn-Qc: *Pinus nigra - Quercus cerris*, B: biomass, C: carbon, n: sample size, B_B: bark biomass, B_{Br}: branch biomass, B_{DW}: deadwood biomass, C_{DW}: deadwood carbon, a, ab, and b: indicate different groups (*p < 0.05*)

In contrast, deadwood B and C content were significantly higher in pure *P. nigra* stands, which were placed in a separate statistical group from mixed stands. This finding indicates that pure stands tend to accumulate more dead organic matter. This pattern is consistent with slower lignin decomposition rates in lignin-rich coniferous litter compared to mixed-leaf litter (Makineci, 1999). Additionally, pure stands on steep slopes are more susceptible to physical stress and breakage, contributing to the accumulation of coarse woody debris, a function recently highlighted as a critical C pool in coniferous ecosystems (Kang et al., 2006; Samariks et al., 2025).

Taken together, the Duncan test results demonstrate that stand structure influences B and C storage in a component-specific manner. Mixed stands tend to allocate more B to living structural components such as bark and branches, whereas pure stands exhibit higher accumulation of deadwood and associated C. These results emphasize that species composition affects not only total B but also its partitioning among ecosystem components, a consideration directly relevant to forest management and C assessment (Pretzsch, 2005; Öztürk, 2022).

3.7. Soil organic carbon assessment

Soil organic matter is formed by decomposing plant residues and soil organisms (Çepel, 1995; Kantarcı, 2000). These substances, which are decomposed and transformed into humus, contribute to the accumulation of OC in the soil (Trumbore, 1997; Kramer and Gleixner, 2006). Since approximately 58% of organic matter is composed of C, it constitutes an essential source of C storage (Post et al., 2001). Soil organic matter enhances soil properties, including aggregate stability, aeration, water-holding capacity, temperature regulation, and root development (Brady and Weil, 2017). Forests also have a positive impact on soil structure and biodiversity (Kozlowski, 2002; Vesterdal et al., 2008; Prescott and Grayston, 2013). Soil is the largest active C pool in terrestrial ecosystems, containing approximately 1100-1600 Pg of C. This exceeds living vegetation and the atmosphere (Sundquist, 1993; Lal, 1995). In field data, differences in soil C content depend on the distribution of litter and its subsequent decomposition. Soil C accumulation is influenced by various factors, including texture, moisture, pH, nutrient status, and climate (Jandl et al., 2007).

In Turkish forests, soil organic carbon (SOC) values were reported as 71.6 t/ha for black pine stands (Kantarcı, 1979; Eruz, 1984), 78.0 t/ha for Scots pine (Çepel, 1977; Tolunay, 1992), 82.3 t/ha for oak (Özhan, 1977; Başaran et al., 2008), and 52.6 t/ha for black pine-oak mixed forests (Özkan, 2003; Çelik, 2006). Tolunay and Çömez (2007, 2008) reported average values of 77.1 t/ha for conifers, 80.4 t/ha for deciduous stands, and between 62.2 and 70.8 t/ha in mixed stands. Karatepe (2004) determined the C content to be between 12.8 and 79.1 t/ha in areas with different bedrock types; Babur (2018) reported values of 48.05, 53.34, and 40.77 t/ha in black pine, cedar, and beech stands, respectively. Sarıyıldız et al. (2013) determined values of 79 t C/ha in black pine, 71 °C in fir, 67 °C in beech, and 65 t C/ha in meadows.

The SOC values obtained in this study were generally consistent with the ranges reported in the literature. Slightly higher values were found in some stand structures, while similar or slightly lower values were found in others. Differences may be due to the study area's unique edaphic and topographic conditions, as well as local factors such as stand structure, canopy cover, and slope. The findings suggest that OC in Turkish forest soils exhibits regional and structural variability. Furthermore, a positive relationship was determined between organic matter content and SOC, highlighting the impact of organic matter on C storage. Clayey soils bind C more stably, while stoniness reduces C storage capacity. Stand age, canopy cover, and species mix are critical structural influences (Tolunay and Çömez, 2008).

Statistical analyses revealed that factors such as stand structure, canopy cover, and slope had no significant effect on SOC content ($p > 0.05$). This may be due to the study being conducted in areas with similar edaphic and climatic conditions. However, the lack of a strong and consistent relationship in our dataset suggests that edaphic controls, such as soil texture, clay content, and BD, as well as legacy site factors, exert a dominant influence on SOC at the spatial scale examined. This interpretation aligns with previous studies showing that, while tree species composition and litter quality significantly drive C dynamics in surface organic layers, mineral-soil SOC storage is primarily constrained by soil physical properties, mineral associations, and parent material rather than immediate vegetation characteristics (Jandl et al., 2007; Vesterdal et al., 2008; Schmidt et al., 2011). Furthermore, the high spatial heterogeneity of these soil properties likely masks the effects of stand structure variables. Consequently, forest management strategies focused solely on modifying stand composition may have limited effects on mineral-soil SOC unless accompanied by measures that explicitly address soil physical and edaphic conditions. Despite relatively high AGB, SOC stocks may remain low due to processes such as rapid decomposition, erosion on sloping terrain, and limited stabilization of organic matter through mineral associations. Differences in litter quality and microbial activity can further decouple AGB accumulation from soil C sequestration (Vesterdal et al., 2008; Yuan and Chen, 2012).

This study provides essential data on SOC stocks in natural *P. nigra* stands in Samsun. The findings suggest that regional soil and climate conditions can impact C content, and that SOC remains relatively stable in similar ecosystems. In this context, local-scale soil C data benefits sustainable forestry and soil management.

4. Conclusions

This study investigated the effects of stand structure, canopy cover, and slope on AGB and BGB, as well as AGC storage and BGC, in natural *P. nigra* stands within the borders of Samsun province. The findings revealed that C is distributed heterogeneously among plant components and that structural and environmental factors significantly influence this distribution.

The canopy closure factor resulted in significant differences in the B and C content of stem wood, bark, and ground vegetation components, with generally higher values observed in stands with canopy closure class 3. In contrast, slope had a pronounced effect on deadwood B and C stocks, which increased with steeper slopes. Stand structure comparisons indicated that mixed *P. nigra - Q. cerris* stands exhibited higher B and C accumulation in bark, branch, and root components. SOC also varied with stand structure, with the highest value (119.42 t/ha) observed in pure *P. nigra* stands, highlighting the importance of vegetation structure and soil properties in determining soil C storage.

The results further revealed that species diversity and structural characteristics directly affect C sequestration. In particular, *P. nigra - Q. cerris* stands demonstrated a high potential in terms of AGC and BGC storage capacity, underscoring the relevance of stand structure in forest C dynamics.

Overall, this study demonstrates that forest C stocks are strongly influenced by stand structure, species composition, and canopy characteristics. Mixed stands showed a greater potential for balanced B distribution and C storage than pure stands. These findings highlight the importance of incorporating species diversity and canopy regulation into forest management and climate-oriented policy frameworks.

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