DIRECT AND INDIRECT DRIVERS OF ABOVEGROUND BIOMASS IN THE FOREST ECOSYSTEMS OF THE HINDUKUSH HIMALAYA

ULLAH, A.[1] – ZEB, A.[1,2*] – AHMAD, S.[1] – KHAN, K.[1]

[1]*Department of Forestry, Shaheed BB University, Sheringal Dir (Upper), 18050, Khyber Pakhtunkhwa, Pakistan*

[2]*Department of Renewable Resources, University of Alberta, 751 General Services Building, Edmonton, AB, T6G 2H1, Canada*

[*]*Corresponding author*
e-mail: zeb@ualberta.ca

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Abstract. We quantified the effects of tree structure and environmental drivers on aboveground biomass (AGB) in Hindu Kush Himalayan forests using data from 225 plots and SEM-based analyses. The path analysis explained 78% of AGB variation ($R^2 = 0.78$), identifying direct and indirect effects. Diameter at breast height (DBH) was the strongest direct predictor of AGB ($\beta = 0.59$, $p < 0.000$), followed by soil available nitrogen ($\beta = 0.21$, $p < 0.000$) and elevation ($\beta = 0.16$, $p < 0.000$). Temperature had a significant negative direct effect ($\beta = -0.12$, $p < 0.00$), and precipitation had a significant positive direct effect ($\beta = 0.12$, $p < 0.00$). The significant role of soil available nitrogen was found to be indirectly mediated by its strong positive effect on DBH ($\beta = 0.68$, $p < 0.001$) and tree height ($\beta = 0.25$, $p < 0.000$), dominant predictors of biomass. Elevation influenced AGB indirectly by enhancing tree height ($\beta = 0.22$, $p < 0.01$) and DBH ($\beta = 0.14$, $p < 0.001$), both of which exerted strong positive effects on biomass. Overall, AGB is driven primarily by tree size, with edaphic and climatic conditions acting as critical secondary controls on tree growth.
Keywords: *aboveground biomass, DBH, soil available nitrogen, elevation, temperature, SEM*

Introduction

Forests are essential for maintaining biodiversity, regulating the global climate, and driving carbon dynamics. They absorb nearly 30% of anthropogenic CO_2 emissions annually, making them one of the largest terrestrial carbon sinks (Ciais et al., 2013; Friedlingstein et al., 2020). This capacity relies on both above-ground biomass (AGB) and below-ground biomass (BGB), which store carbon over decadal to centennial timescales. Although belowground biomass (BGB), comprising roots and associated soil biota, plays a critical role in long-term carbon stabilization, aboveground biomass (AGB)—including stems, branches, and foliage—represents the most dynamic and readily observable component of the forest carbon pool. Together, these biomass pools are closely related to bio-geochemical cycling and ecosystem function (Luo et al., 2023; Hu et al., 2025).

Understanding the ecological and environmental drivers of biomass has become increasingly urgent amid habitat loss, climate change, and unsustainable resource use (Arodudu et al., 2020; Altman et al., 2024). Beyond species identity, structural traits such as tree height, canopy architecture, and diameter at breast height (DBH) strongly influence biomass accumulation by mediating resource capture and competitive dynamics (Feldpausch et al., 2012; Hunter et al., 2013). Abiotic gradients, especially elevation, further shape forest structure by modifying soil fertility, temperature, and moisture

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regimes. These structural environmental interactions are under growing pressure from climate change. Rising temperatures, altered precipitation patterns, and nitrogen constraints are reshaping carbon allocation strategies, often reducing aboveground productivity through increased drought stress, vapor pressure deficits, and shifts in nutrient use efficiency.

Recent ecosystem studies highlight the complex interplay between climate, elevation, and soil nutrients in shaping forest productivity (Ma et al., 2017; Karim et al., 2023). Elevation is a master variable that coordinates temperature, precipitation, and soil processes, thus indirectly regulating biomass through effects on structural traits (Haq et al., 2024). Meta-analyses in China show strong indirect controls of elevation in plant allometry, often through altered leaf nitrogen and shifts toward higher BGB fractions in cooler, nutrient-limited environments (Gong et al., 2023; Zhang et al., 2024). Climate factors such as mean annual temperature (MAT) and mean annual precipitation (MAP) also act through direct and indirect pathways. Although warming may initially improve photosynthesis, it frequently intensifies water stress and respiratory losses, suppressing AGB and favoring root allocation (Ma et al., 2023). Similarly, precipitation extremes increase tree mortality and destabilize top carbon stocks (George-Chacón et al., 2022; Peters et al., 2023).

The availability of nutrients further modifies these dynamics. Nitrogen-rich soils improve tree functional diversity, carbon storage, and aboveground growth through niche complementarity and improved resource use, particularly when expressed via structural variability in DBH and tree height (Chen et al., 2023b, 2024). The structural traits themselves are active mediators of biomass rather than passive indicators. Variation in AGB between biomes has been associated with maximum community height, stem density, and size inequality (Chen et al., 2022, 2023a). DBH, in particular, exhibits close links to growth sensitivity, with its relationship to MAT and precipitation often being species-specific and inversely related to height growth (Anderson-Teixeira et al., 2022; Sheng et al., 2023). Greater structural complexity generally improves productivity through improved light capture and resource partitioning, but these benefits can be undermined by climatic extremes that erode structural advantages (Ma et al., 2023; Dupont-Leduc et al., 2024.

Despite advances in biomass modeling, the mechanisms by which elevation, climate, and soil nutrients shape AGB through functional traits remain unresolved adequately, especially in topographically complex and climatically sensitive regions such as the Himalayas. Most prior studies have either overlooked the mediating role of traits, such as DBH and tree height, or examined environmental drivers in isolation, thus limiting their predictive power under future climate scenarios.

Here, we integrate multiple drivers within a unified framework to disentangle direct and indirect pathways influencing AGB. Using structural equation modeling (SEM), we evaluate how elevation, temperature, precipitation, and soil available nitrogen regulate biomass via functional traits in mountainous forests. By applying both unified and habitat-specific models, we aim to capture both generalizable patterns and localized responses across ecological gradients. This study focuses on the following two objectives:

1. To quantify the relative contributions of structural variables (DBH, tree height), climatic variables (temperature, precipitation), edaphic variables (soil available nitrogen), and topographic variables (elevation) in determining AGB in forest ecosystems of the Hindu Kush Himalayas.

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2. To disentangle the direct and indirect pathways through which environmental drivers influence AGB via tree structural traits, using unified and habitat-specific structural equation modeling (SEM).

This study advances biomass research in three key ways. First, it explicitly integrates structural traits into models of biomass regulation, treating DBH and tree height as mediators rather than static predictors. Second, it disentangles direct from indirect pathways, clarifying how soil available nitrogen and elevation shape biomass primarily through structural growth. Third, by focusing on Himalayan forest ecosystems- where steep gradients amplify environmental effects it provides rare traits-based insights into carbon storage under climate change. Together, these contributions strengthen the theoretical understanding of biomass allocation patterns and inform management strategies to maintain carbon sinks in vulnerable montane forests.

Research methodology

Study site

This investigation was conducted in the Malakand Division (MKD) of Pakistan's Khyber Pakhtunkhwa Province, a region that encompasses subtropical, moist, and dry temperate ecological zones. The division includes the districts of Swat, Chitral, Lower Dir, and Upper Dir. Its geographical coordinates extend from 72◦0′0″E longitude to 35◦29′59.99″N latitude, with a significant elevational gradient ranging from 450m to 7782m (*Figure 1*). The climate in the study area changes from subtropical to temperate. The mean annual temperatures range from 6◦C to 40◦C, while the annual precipitation levels range between 500 mm and 1600 mm. 3 Forest cover is a prominent feature, occupying roughly 27% of the total land area, which corresponds to approximately 0.8 million ha. This region hosts a diverse range of forests, such as subtropical broad-leaved, semi-evergreen, subtropical chir pine, moist temperate, dry temperate, and alpine forests (*Table 1*). These ecosystems exhibit substantial ecological and structural diversity, supporting a mixture of evergreen and broad-leaved species (Ali and Qaiser, 1993-2020 continued).

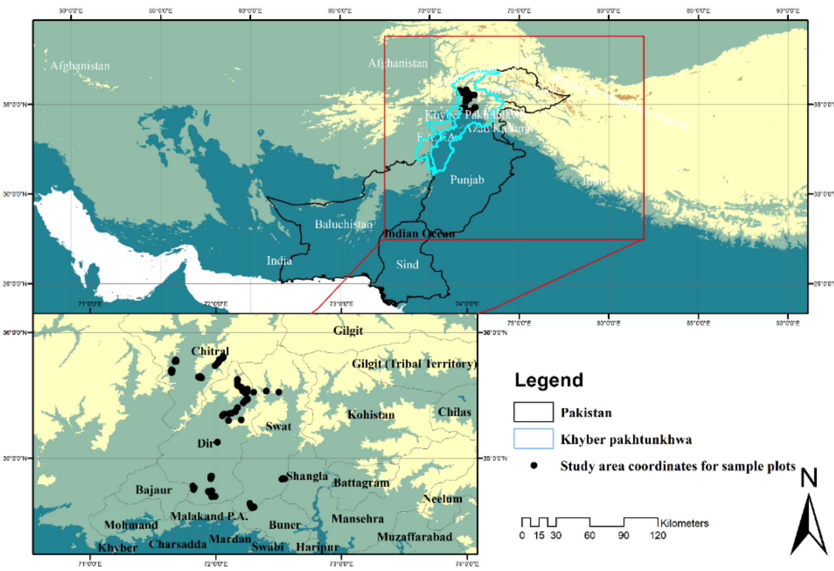

Figure 1. *Study area map*

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Table 1. *Altitude, slope, climate, dominant tree species, ecological roles, and major challenges of forest types in the Hindukush Himalayan region*

Forest Type	Altitude (mean)	Slope (%)	Climate	Dominant tree Species	Ecological Role	Challenges
Dry Temperate Forests	2539.3 m	64.3	Cold, low rainfall	*Cedrus deodara, Pinus wallichiana, Quercus ilex, Pinus gerardiana*	Watershed management, erosion control, habitat for wildlife	Overgrazing, harsh climate, deforestation
Moist Temperate Forests	2236.6 m	44.5	Cold, high rainfall	*Cedrus deodara Pinus wallichiana Abies pindrow Picea smithiana Quercus ilex*	Rich biodiversity, water regulation, carbon sink	Deforestation, climate change
Subtropical Forests	1273.4 m	50.57	Warm, subtropical	*Pinus wallichiana Pinus roxburghii Olea ferruginea Quercus ilex Eucalyptus camaldulensis*	Soil stabilization, economic resource (resin), biodiversity	Forest fires, overharvesting, land conversion

Measurement of tree structural attributes

This study used data collected from 225 randomly selected sampling plots, comprising 100 plots from each of the three major forest types. To adequately represent spatial heterogeneity, the sampling plots were systematically distributed within each forest type. A horizontal distance of approximately 1 km was maintained between successive plots, while an altitudinal separation of 500 m was applied to ensure coverage across elevational gradients. This sampling strategy was designed to capture spatial variability and encompass a wide range of microhabitats and environmental conditions, thus enhancing the ecological representativeness of the data set. Each plot was established with dimensions of 20 × 20 m, following standard protocols for forest inventory studies. Within each plot, detailed tree-level attributes were recorded. These included the diameter at breast height (DBH), the total height of the tree, the age of the stand, and the composition of the species. All woody stems with a DBH greater than 1 cm were measured to ensure the inclusion of mature trees and juvenile individuals. The DBH was measured at 1.3 m above ground level using a diameter tape, while the tree height was assessed with a hypsometer or clinometer, depending on field conditions. The age of the stand was determined through the increment coring of the dominant trees or, where feasible, through local knowledge and forest management records.

Soil sampling and analysis

Within each 20 × 20 m plot, soil samples were collected from three 1 × 1 m subplots at a depth of 0 to 15 cm using a soil auger and composited per plot. The samples were air-dried, ground, and sieved (2 mm) before analysis. Organic matter was determined by the Walkley–Black dichromate oxidation method (Walkley and Black, 1934). The available nitrogen was estimated using the alkaline $KMnO_4$ method (Subbiah and Asija, 1956), while the available phosphorus was measured using the Olsen method (Olsen et al., 1954). The available potassium was extracted with 1 M ammonium acetate and quantified by flame photometry. Total phosphorus and potassium were determined after wet acid digestion, using spectrophotometry and flame photometry, respectively. These analyses

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provided an assessment of soil fertility in relation to vegetation composition and degradation status.

Climatic data

First, the geographical coordinates (latitude and longitude) and elevation of each plot were recorded using a handheld Global Positioning System (GPS). Climatic variables were initially compiled to characterize the environmental conditions of the study sites. These included mean annual temperature (MAT, °C), growing degree days (number of days > 5 °C), cloud cover (%), mean annual precipitation (MAP, mm year^{-1}), wet day frequency (days), and potential evapotranspiration (PET, mm year^{-1}). Climatic data, including MAT and MAP, were obtained from the WorldClim Global Climate Database (Version 1.4, 30 arc-second resolution; available at www.worldclim.org). The aridity index, calculated as MAP/PET, was derived from the Global Database for Aridity and PET (30 arc-second resolution; available at www.cgiar-csi.org/data). We recognize that the use of gridded climatic data at 30 arc-second resolution may not fully represent plot-level microclimatic conditions, especially in rugged terrain. Nevertheless, such datasets are commonly applied in mountain ecology to characterize regional climatic controls on forest structure, and their use is appropriate for examining broad climatic influences rather than local microclimatic effects (Gardner et al., 2019; Ding et al., 2021; Stewart et al., 2022).

These variables were selected because they represent key climatic controls on forest structure and functioning. Temperature and precipitation directly influence vegetation growth and biomass accumulation, while growing degree days reflect thermal suitability for plant development. Cloud cover and wet day frequency describe moisture-related atmospheric conditions, and PET together with the aridity index represents integrated water–energy balance. For the final Structural Equation Modeling (SEM) analysis, only mean annual temperature and mean annual precipitation were included, as these variables are widely recognized as the primary climatic drivers of forest biomass at regional scales and allow a parsimonious representation of climate–biomass relationships. The remaining climatic variables were therefore used only for site characterization and were not incorporated into the final SEM framework.

Aboveground biomass estimation

The biomass above ground (AGB) in t ha^{-1} was estimated using a two-step procedure. First, stem biomass (t ha^{-1}) was calculated from stem volume and basic wood density. The total AGB was then obtained by applying a biomass expansion factor (BEF), as recommended in the literature (Adnan et al., 2014).

Stem volume estimation

Following the established literature on forest mensuration for the calculation of the stem volume (m^3 ha^{-1}), we used species-specific or general allometric models that link the diameter of the tree at breast height (DBH) and the total height (H) to the volume (Canadas-Lopez et al., 2025). However, for trees where no species-specific equation was available, we used the generic volume formula (*Eq. 1*).

$$V = a + b \cdot (DBH)^2 \cdot H \quad \text{(Eq.1)}$$

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where *V* is the volume of the stem (m^3), *DBH* is the diameter at breast height (cm), *H* is the height of the tree (m), and *a*, *b* are the model coefficients obtained from local area published allometric relationships. The volume per hectare was obtained by adding the volumes of individual trees and taking it up to the hectare level.

Stem biomass and AGB calculation

Stem biomass was calculated by multiplying the estimated stem volume by basic wood density (BWD) (*Eq. 2*) (Adnan et al., 2014), all BWD values and their sources are listed in *Supplementary Table S1*.

$$Stem\ biomass\ (tha^{-1)} = \frac{V(m^3ha^{-1})xBWD(kgm^{-3})}{1000} \quad \text{(Eq.2)}$$

The total aboveground biomass was then estimated as (Eq. 3)

$$AGB(tha^{-1}) = Stem\ biomass(tha^{-1})xBEF \quad \text{(Eq.3)}$$

We adopted a BEF value of 1.51, consistent with averages reported in the literature for tropical and subtropical forests (Adnan et al., 2014; on Climate Change, 2006).

Statistical analysis

A suite of statistical approaches was applied to investigate the relationships between above-ground biomass (AGB), soil nitrogen availability, elevation, species diversity, habitat type, and degradation gradients. The pairwise associations between predictor and response variables were first explored using bivariate analyzes. The correlations between the explanatory variables were then examined using correlation matrices and multicollinearity was evaluated using variance inflation factors (VIF). To assess complex interdependencies, structural equation modeling (SEM) was conducted in R version 4.4.1 (R Core Team, 2024) using RStudio version 2024.12.0 (Posit team, 2024). SEM enabled the simultaneous estimation of direct and indirect pathways among the study variables, providing a framework to test the hypothesized causal relationships. The specification of the model was informed by ecological theory and previous empirical evidence. The suitability of the model was evaluated using multiple fit statistics, including the chi-square test (χ^2), root mean square error of the approximation root (RMSEA), the comparative fit index (CFI) and the Tucker-Lewis index (TLI). Model refinement was guided by inspection of modification indices and standardized residuals to achieve an optimal representation of the data.

Result

Bivariate analysis

A bivariate analysis revealed that the structural characteristics of the trees were the main drivers of the aboveground biomass. The height of the tree ($R^2 = 0.553$, $p < 0.001$) and the diameter at breast height (DBH; $R^2 = 0.514$, $p < 0.001$) were the strongest predictors (*Figure 2*). Weak but significant positive relationships with precipitation ($R^2 = 0.137$, $p = 0.001$), soil available nitrogen ($R^2 = 0.076$, $p = 0.017$) and temperature ($R^2 = 0.054$, $p = 0.045$) were also detected. No significant relationship was found between

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biomass and elevation (R^2 = 0.001, p = 0.828). Together, these results highlight the importance of tree morphology over environmental factors for biomass estimation (*Figure 2*).

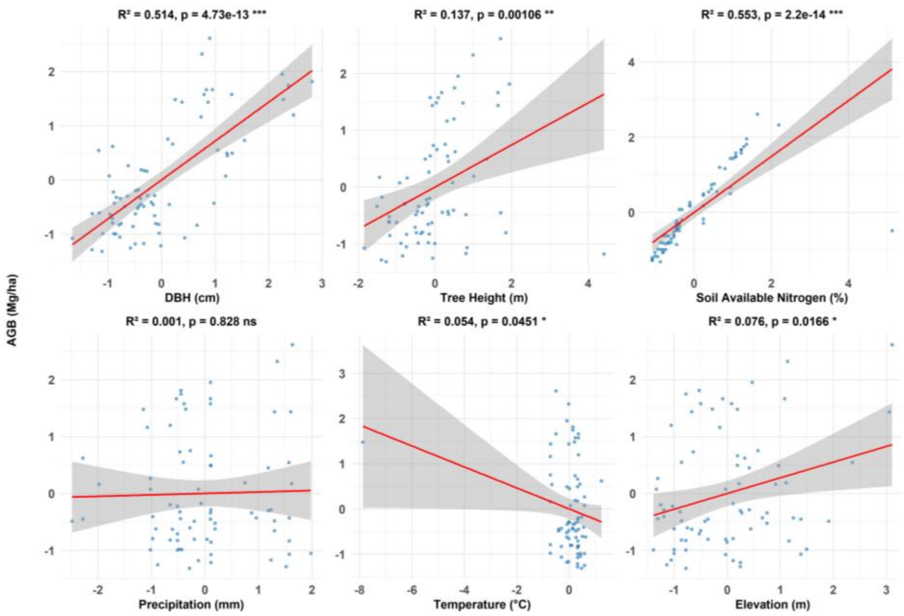

Figure 2. *R^2 and p-values for bivariate associations between biomass and ecological predictors. Tree height and soil available nitrogen have minor but significant effects, whereas DBH exhibits the strongest correlation*

A Pearson correlation analysis was performed to assess multicollinearity between predictor variables (*Figure 3*). Significant correlations ($p < 0.05$) were observed between DBH and soil available nitrogen (r = 0.54) and between DBH and tree height (r = 0.37), while other relationships were weak or non-significant.

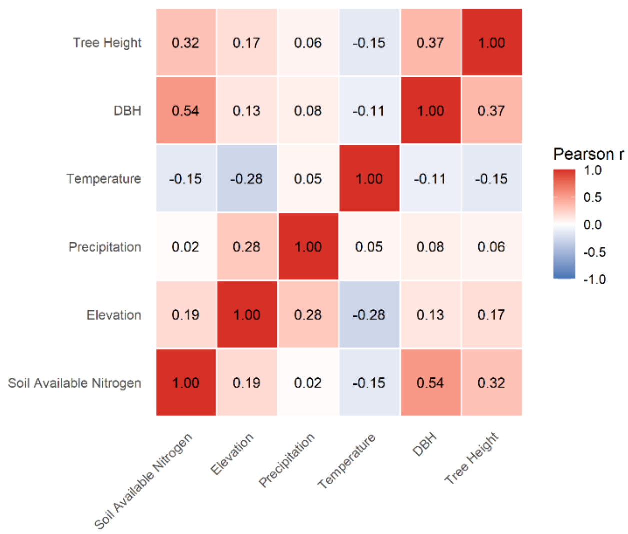

Figure 3. *Ecological predictors' Pearson correlation matrix (values range from-0.28 to 0.54). Soil available nitrogen and DBH have the strongest positive correlation (r =0.54), whereas temperature has negative correlations with elevation (r =-0.28) and other variables*

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The importance of biomass estimation is underscored by the relative contributions of different variables, with DBH emerging as the strongest predictor, accounting for 48.8% of the variance (*Figure 4*). Soil available nitrogen is the second most influential factor (17.7%), highlighting the role of nutrients availability. Elevation contributes moderately (13.3%), likely due to its indirect influence on the composition of the species and the microclimatic conditions. In comparison, temperature (10.3%) and precipitation (10%) show smaller but comparable effects, suggesting that climatic factors play a secondary role in relation to structural and edaphic drivers (*Figure 4*).

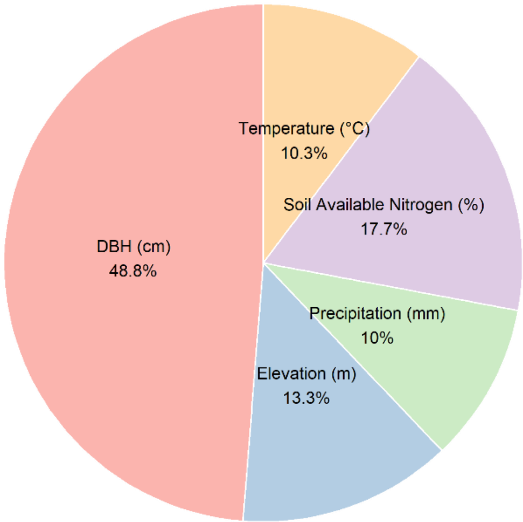

Figure 4. *predictors' relative contributions to biomass variation*

Multiple regression analysis revealed a clear hierarchy of direct effects on aboveground biomass (AGB) (*Figure 5*). Tree diameter at breast height (DBH) was the strongest positive predictor ($\beta = 0.59$, $p < 0.001$), followed by soil available nitrogen ($\beta = 0.21$, $p < 0.001$). Elevation also exhibited a significant positive effect ($\beta = 0.16$, $p < 0.001$), while the mean annual temperature had significants negative relationshipn with AGB ($\beta = -0.12$, $p < 0.01$). Annual precipitation exerted a significant positive direct effect in the multivariate model ($\beta = 0.12$, $p < 0.001$) (*Figure 5*).

The structural equation model showed an excellent fit: (χ^2 (3) = 7.19, p = 0.066; CFI = 0.992, TLI = 0.959, SRMR = 0.025, RMSEA = 0.084). The path analysis explained 78% of the variance in biomass ($R^2 = 0.78$), providing mechanistic information on the regression results (*Figure 6*). The significant role of soil available nitrogen was found to be direct ($\beta = 0.21$, $p < 0.001$) and indirect through DBH ($\beta = 0.68$, $p < 0.001$), which was the dominant predictor of biomass (*Figure 6*). Indirectly, elevation affects biomass through its positive effects on tree height ($\beta = 0.22$, $p < 0.01$) and DBH ($\beta = 0.14$, $p < 0.001$), which in turn have strong direct positive impacts on biomass (*Figure 6*). Precipitation exerted a direct positive effect on biomass ($\beta = 0.12$, $p < 0.01$), indicating that moisture availability directly improves forest productivity. However, temperature had a significant negative effect on biomass ($\beta = -0.12$, $p < 0.01$), but did not significantly influence tree height (*Figure 6*). Together, these results highlight the indirect pathways through which soil available nitrogen, precipitation, and elevation regulate aboveground biomass.

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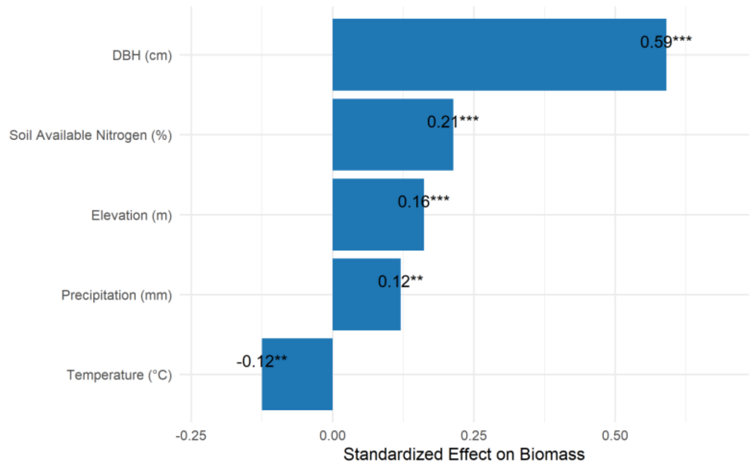

Figure 5. *Standardized regression coefficients of biomass predictors (β) with significance levels. Temperature has a significant negative effect, whereas DBH has the strongest positive effect. Elevation and soil available nitrogen show intermediate beneficial effects. Note: * P < 0.05, ** P < 0.01, *** P < 0.001*

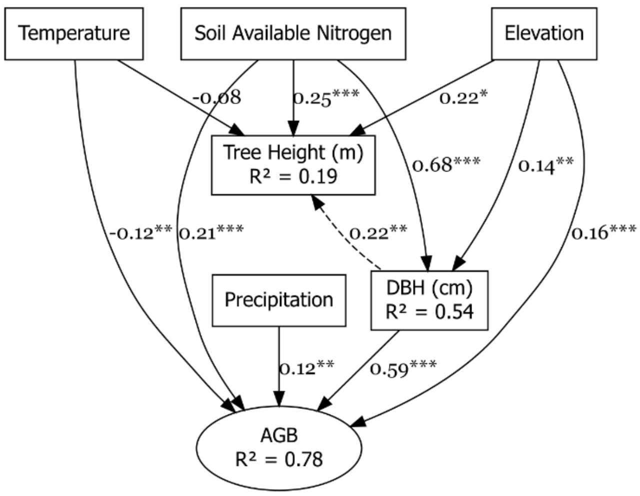

Figure 6. *Structural Equation Model (SEM) displays the aboveground biomass's direct and indirect drivers. Note: Standardized path coefficients are shown by arrows; dashed lines show marginal effects, and solid lines show important paths, * P < 0.05, ** P < 0.001*

It is also worth mentioning that all measured soil nutrients (total nitrogen, phosphorus, and potassium) were initially included in the analysis. However, during model evaluation, only soil available nitrogen showed a statistically significant effect in the final SEM.

To further confirm the mediating effect of available nitrogen on AGB, *Figure 7* illustrates the decomposition of total effects obtained from the structural equation model (SEM). Among the predictors, soil available nitrogen exhibited the strongest total effect on biomass (0.614), primarily through indirect pathways (0.399). DBH also showed a strong positive direct effect (0.591) on biomass. Elevation had a moderate total effect (0.245) with both direct and indirect contributions, while Precipitation showed a smaller direct influence (0.121). In contrast, Temperature had a weak negative direct effect (-0.125) on biomass.

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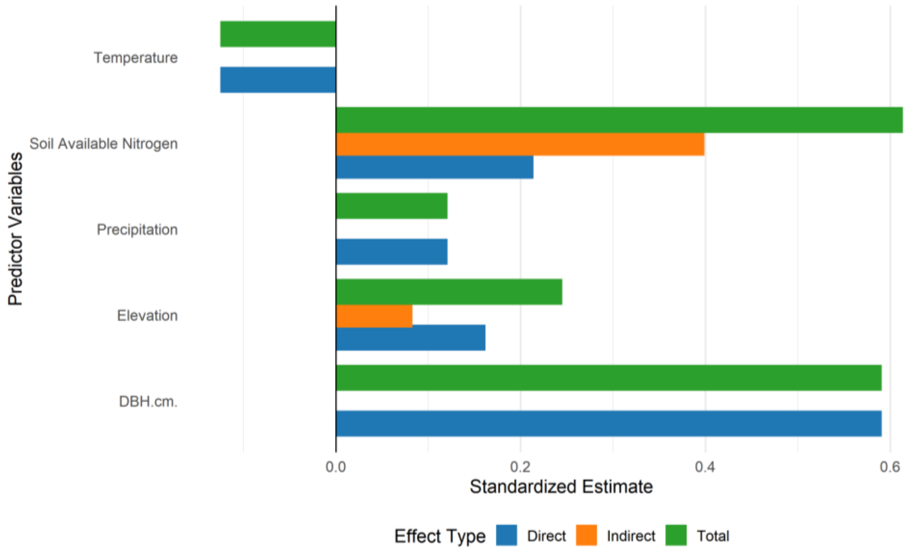

Figure 7. *Summary of standardized direct, indirect, and total effects from the structural equation model showing the relative influence of biotic (DBH) and abiotic (elevation, precipitation, soil available nitrogen, and temperature) factors on AGB*

Discussion

This study provides a comprehensive evaluation of the drivers of aboveground biomass (AGB) in forest ecosystems, showing that biotic structural traits exert stronger and more consistent effects than abiotic environmental factors. Across analyses, DBH (Diameter at Breast Height) was consistently identified as the dominant predictor of AGB, while soil available nitrogen, elevation, temperature, and precipitation played secondary or indirect roles. These findings highlight the importance of disentangling direct from indirect pathways when assessing biomass dynamics and provide insights into how forest structure mediates ecosystem productivity.

DBH emerged as the strongest and most reliable predictor of AGB, with standardized path coefficients of β = 0.50- 0.59, which explain more than half of the variance ($R^2 \approx 0.55$). This result is consistent with allometric research and remote sensing applications, where DBH alone explains 69–90% of biomass variation (Jha, 2020; Yang et al., 2022). Its integration into forest inventories and large-scale biomass models further supports its central role (Somogyi et al., 2007; Temesgen et al., 2015; Fu et al., 2018). Interestingly, while DBH remained a strong driver across ecosystems, its influence was slightly reduced in subtropical forests, where trees are generally denser and shorter. This variation probably reflects differences in growth strategies and resource allocation. However, the consistent predictive strength of DBH in all models emphasizes its robustness as a proxy for structural biomass. The height of the tree showed a weak direct association with biomass ($R^2 \approx 0.05$) but a moderate indirect effect in SEM (β ≈ 0.22). This suggests that height reflects cumulative growth conditions and functions more as a mediator than as a primary driver (Molto et al., 2013; Hunter et al., 2013). Its influence arises from interactions with DBH and soil available nitrogen, as taller trees effectively compete for light and allocate resources to vertical growth. Elevation and nitrogen promoted tree height in our models, reinforcing its role as a structural outcome of environmental and nutrient conditions. Habitat-specific SEMs confirmed consistent but

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modest contributions across ecosystems, with stronger effects in dry temperate forests, where vertical growth is critical for light capture.

Soil available nitrogen appeared as the second most influential driver of AGB, although its effect was mainly indirect. While the direct association between nitrogen and AGB was weak, the SEM revealed strong positive pathways through DBH ($\beta \approx 0.25$) and tree height ($r \approx 0.32$), indicating that nitrogen enhances AGB primarily by promoting tree growth rather than biomass accumulation directly. This is consistent with findings from other studies that nitrogen availability promote stem thickening and height growth in mature forests and augments tree responses to increased CO_2 in nutrient-limited ecosystems (Fisk et al., 2002; Norby et al., 2010; Yang et al., 2025). Physiologically, nitrogen stimulates photosynthetic capacity, leaf area development, and xylem formation, thereby indirectly increasing biomass through its influence on tree structural attributes. The model further discovered strong ecological context dependence in nitrogen effects. Nitrogen exerted its strongest effect in moist temperate forests, where cooler and wetter conditions promote microbial activity, organic matter decomposition, and sustained nitrogen mineralization, collectively improving soil structure and root development (Singh et al., 2023; Ogunbode et al., 2025). These environments support high biomass and diverse plant assemblages characteristic of Himalayan moist temperate forests. In contrast, nitrogen effects were weaker in subtropical and dry temperate forests, where higher mineralization rates, lower soil fertility, and moisture constraints reduce long-term nutrient restraint. In such systems, even modest changes in nutrient availability may affect plant density and species composition, but their effects on biomass accumulation remain limited over short temporal scales (Tian et al., 2017; Muhammad et al., 2025). Together, these findings highlight nitrogen as a universally important growth regulator, while representing that its influence to forest biomass is strongly mediated by habitat-specific soil and climatic conditions.

Elevation had a modest direct effect on biomass ($\beta \approx 0.12$), but its primary contribution was indirect through DBH ($\beta \approx 0.68$) and tree height ($\beta \approx 0.22$). These findings align with previous studies indicating that elevation influences forest biomass mainly indirectly, by shaping environmental heterogeneity such as soil development, microclimatic conditions, and species composition. These factors regulate biomass production by strongly affecting tree structural attributes, particularly DBH and tree height (Cabrera and Duivenvoorden, 2020; Zhang et al., 2024). Overall, elevation acts as a contextual driver that constrains or facilitates tree growth through temperature, moisture availability, soil properties, and growing-season length, rather than exerting a direct control on biomass (Körner, 2007; Malhi et al., 2010). The strong indirect pathway through DBH highlight that tree growth is especially sensitive to elevational gradients, showing changes in resource availability and competitive dynamics along mountain slopes (Girardin et al., 2014). The weaker indirect effect through tree height can show cumulative climatic and mechanical restraints on vertical growth at higher elevations, including low temperatures, high wind, and reduced hydraulic efficiency (Körner, 2021). In general, these results underscore the importance of elevation as a context-specific driver that shapes forest biomass indirectly by influencing tree architecture and growth processes. Lower temperatures and altered water availability at higher elevations are known to affect nutrient cycling and structural growth (Jump et al., 2009; Sundqvist et al., 2013). In our models, the influence of elevation was stronger in moist and dry temperate forests, while subtropical forests showed weaker responses, reflecting region-specific interactions with soil and climate. In

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general, elevation appears less as a direct determinant of biomass and more as a structural driver that shapes the size-related traits that ultimately regulate productivity.

Climatic variables exerted relatively weak direct effects, but played a context-dependent role in SEM. Temperature negatively affected biomass ($\beta \approx -0.12$) and tree height, consistent with studies showing that warming reduces productivity through thermal stress and increased evapotranspiration in temperate forests (Peng and Dang, 2003; Ali et al., 2020). Precipitation had a weak but positive effect on biomass ($\beta \approx 0.12$), likely through improved nutrient and water availability. Global observations similarly suggest that precipitation enhances growth in water-limited systems, although its effect is highly variable (Lie et al., 2018; Ma et al., 2023). Temperature exhibited a negative effect on AGB and tree height, aligning with recent evidence that warming and associated increases in vapor pressure deficit and drought stress can decrease tree growth and cut productivity in temperate and montane forests (Yuan et al., 2025). Rising temperatures can increase evapotranspiration, aggravate water deficits, and limit physiological performance, especially in drought-intolerant species and moisture-limited environments, thus constraining biomass accumulation (Lundgren et al., 2025). These findings align with broader evidence that thermal stress under current climate change can reduce forest carbon uptake and structural development, particularly where water availability is limiting. Precipitation had a weak but positive effect on biomass, likely reflecting improved water and nutrient availability that supports growth processes under moisture-limited conditions. Recent studies indicate that seasonal precipitation and soil moisture dynamics regulate tree growth responses to climate variation in montane forest systems, with wetter conditions generally supporting higher growth rates and productivity (Chanda et al., 2024). Although the magnitude may be modest in our SEM, the positive association is consistent with the role of water availability in preserving drought stress and enabling nutrient cycling in forest ecosystems under changing climate.

Together, these findings demonstrate that forest structure, especially DBH and nitrogen-mediated growth, exerts a more reliable influence on biomass than climatic or topographic factors. Temperature and precipitation, though weaker overall, shape biomass indirectly through their effects on structural traits and habitat-specific conditions. Elevation further underscores the importance of indirect ecological pathways, as its strongest contributions were mediated through tree size traits rather than direct biomass accumulation. The use of SEM was crucial in separating these direct and indirect influences, showing that multiple regression alone may obscure the underlying mechanisms. For example, soil available nitrogen's strong role in regression was clarified as primarily indirect through DBH, while precipitation's negligible regression effect masked its positive direct and indirect contributions. This highlights the value of structural modeling in uncovering the complexity of biomass regulation.

By demonstrating the predominance of tree structure over climate or topography in predicting biomass, this study provides actionable insights for carbon accounting and forest management. DBH remains the most robust and scalable parameter for biomass estimation, reinforcing its role in field inventories, remote sensing, and large-scale carbon models. Soil available nitrogen emerges as a critical mediator of structural growth, suggesting that nutrient management may enhance the potential for carbon sequestration in specific ecosystems. In contrast, the negative effects of temperature highlight the risks of a decrease in biomass under climate warming, particularly at higher elevations. Overall, the results support a dual perspective: general models emphasizing structural predictors such as DBH and nitrogen for broad-scale carbon accounting and habitat-

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specific models that incorporate climate and elevation to capture localized responses. This approach strengthens the predictions of how forests will respond to environmental change and helps to target management strategies that sustain productivity and carbon storage under shifting conditions. This study demonstrates that forest biomass is governed primarily by structural traits, with DBH as the strongest and most consistent predictor in all models. Soil available nitrogen further enhances biomass indirectly by promoting tree size, while elevation and climate exert weaker but context-dependent influences. These findings emphasize the importance of distinguishing direct from indirect ecological effects and highlight that structural attributes provide a more reliable basis for biomass estimation, carbon accounting, and forecasting ecosystem responses under environmental change

Conclusion and recommendations

This study provides a nuanced understanding of the drivers of aboveground biomass (AGB) in the Hindu Kush Himalayan forests by employing a multi-model analytical framework. Our integrated approach, which combines multiple regression with path analysis, reveals a clear hierarchy of controls: structural attributes of the tree, specifically DBH and height, act as the primary direct determinants of biomass, while environmental factors such as soil available nitrogen and climate operate predominantly through indirect pathways by modulating tree growth.

The most significant insight from our path model is the mechanistic role of soil available nitrogen. Its substantial total effect on AGB is almost entirely mediated through DBH, positioning it not as a direct driver of carbon storage but as a critical growth catalyst. This clarifies that soil fertility improves forest biomass by allowing for larger tree size rather than through a direct physiological pathway. Similarly, the complex, counteracting pathways of precipitation explain its non-significant net effect in a standard regression model, highlighting how traditional analyses can mask important underlying ecological processes. The persistent direct effect of tree height, independent of DBH, underscores the need to consider multiple dimensions of tree architecture for an accurate estimation of biomass.

Management and conservation implications

Our findings have direct implications for forest management and climate change mitigation strategies.

- Forest carbon management: Practices aimed at improving carbon sequestration should prioritize the protection and growth of large trees, as DBH is the strongest direct correlate of AGB.
- Soil fertility: Management activities that conserve or improve soil available nitrogen can be effective strategies to promote forest growth and carbon storage in the long term, given its strong indirect effect through tree diameter.
- Monitoring: The dominant role of DBH supports its continued use as a robust and practical metric for rapid biomass assessment in forest inventory and carbon monitoring programs in the region.

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APPENDIX

Table S1. *Species-specific basic wood density (BWD) values used for biomass estimation, with regional sources from Pakistan and the Hindukush Himalaya*

Species	Basic Wood Density (BWD) Range (g/cm³)	Primary Reference(s) from Pakistan / Region
Abies pindrow (Silver Fir)	0.40 – 0.45	Ahmed et al. (2011); Forest product reports (Murree Hills)
Cedrus deodara (Deodar)	0.50 – 0.55	Ahmed et al. (2011); Standard Pakistani forestry texts
Eucalyptus camaldulensis (River Red Gum)	0.65 – 0.75	Sheikh (1993); Plantation timber studies (UAF, etc.)
Olea ferruginea (Indian Olive)	0.85 – 0.95	Malik et al. (2014); Silvical studies (Salt Range, Punjab)
Picea smithiana (Morinda Spruce)	0.42 – 0.48	Ahmed et al. (2011)
Pinus gerardiana (Chilgoza Pine)	0.55 – 0.60	Sheikh (1993); Studies from Balochistan/KPK
Pinus roxburghii (Chir Pine)	0.55 – 0.60	Hussain (1991); Timber mechanics studies
Pinus wallichiana (Blue Pine)	0.45 – 0.50	Ahmed et al. (2011)
Quercus ilex (Holly Oak)	0.75 – 0.85	Extrapolated from regional genus data; aligns with Dr. M. Ashraf's work (Peshawar)

Note: *Quercus ilex* lacks a direct, widely published density study from Pakistan. The value is a conservative estimate based on the high density of the *Quercus* genus in similar dry temperate Himalayan forests and is consistent with entries for Pakistani oaks in global wood density databases that cite regional sources

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