

Structural traits and carbon storage potential of tree and pole vegetation in three land-use types in Ngargoyoso, Central Java, Indonesia

ULFI HANUM¹, WINDA SAGITA ARMADHAN¹, ZAHRA HANUN¹, ZHALZABILLA SHAF¹,
SESILIA RETNO AYU NINGTYAS¹, ALYA AFRA INAS NUR¹, MUHAMMAD INDRAWAN¹, SUNARTO¹,
SUGIYARTO², AHMAD DWI SETYAWAN^{1,3,✉}

¹Department of Environmental Science, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia. Tel./fax.: +62-271-663375, ✉email: volatileoils@gmail.com

²Department of Biology, Faculty of Mathematics and Natural Sciences, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

³Biodiversity Research Group, Universitas Sebelas Maret. Jl. Ir. Sutami 36A, Surakarta 57126, Central Java, Indonesia

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Abstract. Hanum U, Armadhan WS, Hanun Z, Shafa Z, Ningtyas SRA, Nur AAI, Indrawan M, Sunarto, Sugiyarto, Setyawan AD. 2025. Structural traits and carbon storage potential of tree and pole vegetation in three land-use types in Ngargoyoso, Central Java, Indonesia. *Cell Biol Dev* 9: 37-53. Understanding the relationship between plant structural characteristics and carbon storage is not just essential for ecological management and climate mitigation, but also highly relevant and applicable. This study investigates how Aboveground Biomass (AGB) and carbon stock correlate with the structural traits of tree and pole vegetation across three land-use types: pine forest, agroforestry, and rubber plantation in Ngargoyoso Sub-district, Central Java, Indonesia. Field sampling was conducted using 90 plots divided equally across the sites, with vegetation categorized into trees (DBH>20 cm) and poles (DBH 10-20 cm). Non-destructive measurements of diameter at breast height (DBH) and tree height were used to estimate biomass through species-specific allometric equations. Carbon stock was then calculated using a standardized conversion factor (0.47×AGB). The results show that agroforestry systems exhibit the highest total carbon stock (82.46 MgC/ha), followed by rubber forest (81.41 MgC/ha) and pine forest (66.29 MgC/ha). Variations in carbon accumulation are strongly influenced by vegetation composition, structural diversity, and DBH distribution. The predominance of fast-growing, nitrogen-fixing species such as *Leucaena leucocephala* in agroforestry contributed to higher biomass accumulation. These findings emphasize the practical implications of this study, highlighting the importance of structural traits such as DBH and height, which reflect physiological growth status and are key determinants in carbon storage capacity across different vegetation types.

Keywords: Aboveground biomass, agroforestry, carbon stock, DBH, structural traits, tropical forest physiology

INTRODUCTION

The continuous increase of greenhouse gas concentrations in the atmosphere, particularly carbon dioxide (CO₂), is the primary driver of global climate change and warming (Dewa and Sejati 2019). Forest ecosystems play a critical role in mitigating these changes through carbon sequestration, a process where atmospheric carbon is absorbed and stored in plant biomass via photosynthesis. In this context, trees function not only as carbon sinks but also as living indicators of how structural and physiological traits affect carbon accumulation across different vegetation systems (Ferrini et al. 2020; Qiu et al. 2020).

Photosynthesis is the primary physiological mechanism by which plants convert atmospheric CO₂ into organic compounds. The products of this process are stored as biomass, predominantly in the stem, branches, and leaves. Among these, the stem particularly in tree-level vegetation accounts for the largest portion of Aboveground Biomass (AGB), which is directly proportional to carbon stock (SNI 2011). The size and volume of the stem are strongly influenced by morphological traits, such as stem diameter and height, which are outcomes of both genetic growth potential and environmental adaptation. This implies that

diameter at breast height (DBH) and total plant height are not merely biometric data but physiological proxies of cumulative growth and carbon assimilation capacity (Diana et al. 2022).

The anatomical and physiological traits of plant species, such as the density and distribution of stomata, vascular cambium activity, wood density, and growth form, also influence their capacity to accumulate biomass. Plants with a high stomatal density exhibit greater carbon fixation potential (Praseti et al. 2018). Similarly, species that develop large-diameter stems and higher wood density generally possess greater biomass and carbon stock per unit area. As a result, species composition and structural diversity significantly affect the overall carbon sequestration potential of a given vegetation system (Ambarwati et al. 2019).

In the Indonesian context, forest degradation and land-use change have dramatically altered the country's carbon budget. Indonesia ranks among the top global emitters of carbon, primarily due to forest clearing, fires, and unsustainable land conversion (Syah 2017; Han et al. 2019). Despite this, the country also holds great potential for climate mitigation through the rehabilitation and sustainable management of forests. Approaches such as agroforestry—integrating trees with crops and/or livestock have been

promoted as nature-based solutions that combine ecological restoration with socio-economic benefits (Alinus et al. 2017).

Ngargoyoso Sub-district, located on the diverse slopes of Mount Lawu in Central Java, presents a rich and varied landscape of vegetation systems. These include pine forests, rubber plantations, and agroforestry areas, each with its own uniqueness (BPS 2021; Sanjaya and Kumiawan 2021). Each land-use type demonstrates different levels of structural complexity and species richness. The largely homogenous pine (*Pinus merkusii*) and rubber (*Hevea brasiliensis*) stand in contrast with the diverse agroforestry systems that incorporate a mix of plantation crops with indigenous forest species such as *Leucaena leucocephala*, *Tectona grandis*, and *Swietenia mahagoni* (Bachtiar and Resti 2017; Minarno 2022).

Previous studies in Ngargoyoso, Karanganyar, Indonesia have highlighted that carbon stock varies greatly between these systems due to differences in species composition, DBH range, stand density, and vertical stratification (Utami et al. 2020; Wijayanto and Prasetyo 2021). Minarno (2022) reported that the carbon stock in Ngargoyoso ranged from 0.80 to 9,018.41 tons/ha, depending on vegetation type and sampling location. This indicates a strong need for a more structured evaluation focusing on the physiological and structural underpinnings of carbon storage.

Moreover, despite general knowledge of forest carbon dynamics, limited studies have explicitly quantified how structural plant traits contribute to AGB and carbon accumulation in mixed systems like agroforestry compared

to monocultures. The use of species-specific allometric equations that consider DBH and height provides a more accurate and biologically grounded method to estimate biomass and carbon stock (Banaticla 2003; Chave et al. 2005; Siregar 2007).

This study aims to estimate the aboveground biomass and carbon stock of tree and pole vegetation in three different land-use types in Ngargoyoso Sub-district pine forest, agroforestry, and rubber plantation. It emphasizes the role of structural plant traits such as DBH, plant height, and species composition in carbon accumulation. These findings will not only contribute to a better understanding of carbon dynamics across land-use gradients but also offer practical insights into how plant structural characteristics can inform forest management and carbon monitoring strategies from a physiological perspective.

MATERIALS AND METHODS

Study area

This study was conducted in Ngargoyoso Sub-district, Karanganyar District, Central Java, Indonesia, located on the western slope of Mount Lawu (elevation: 673-1,079 m asl). The area is characterized by a tropical montane climate with moderate to high rainfall and supports diverse vegetation systems, including pine forest, agroforestry, and rubber plantation (Figure 1).

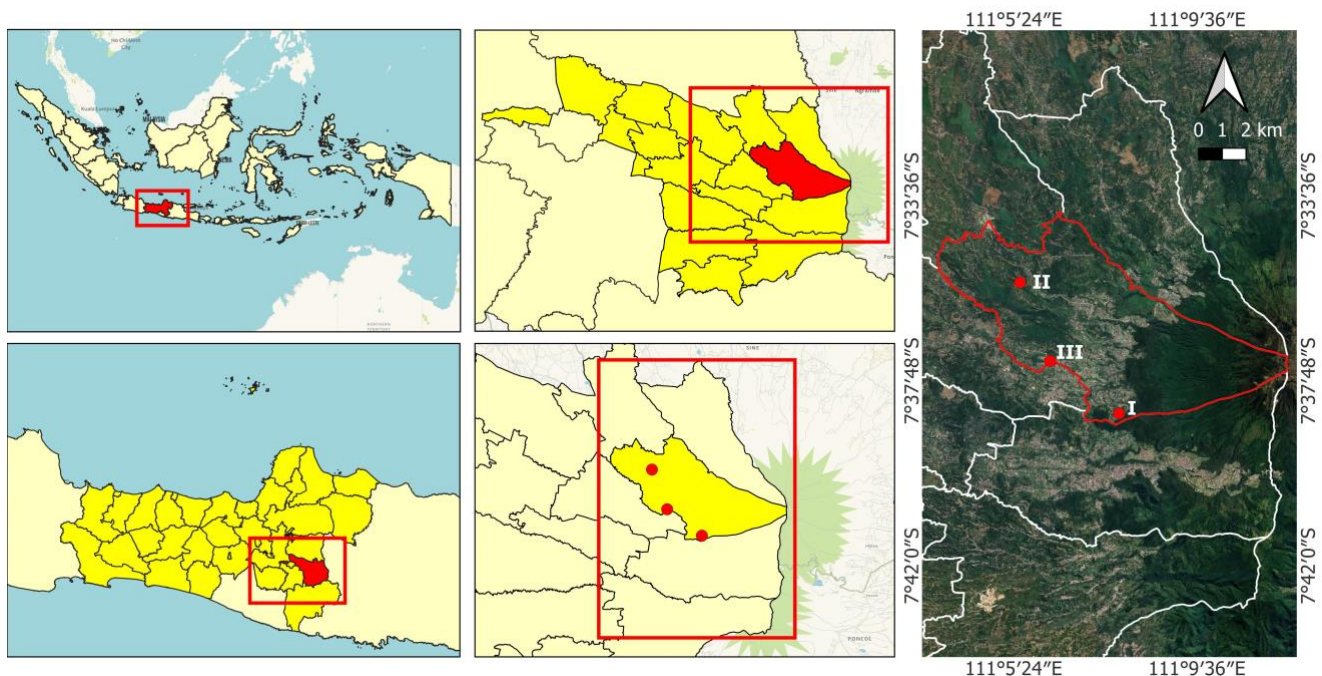


Figure 1. Map of research location in Ngargoyoso Sub-district, Karanganyar District, Central Java, Indonesia. I: Pine forest, II: Agroforestry area; III: Rubber plantation

Three land-use types were selected to represent different vegetation structures and management intensities. Three distinct land-use types were selected to represent different vegetation compositions and structural complexities namely (i) Pine forest (Site I): Located in Berjo Village (1,079 m asl; -7.6418137, 111.1301613), dominated by *Pinus merkusii*, with a uniform canopy structure, used primarily for timber and resin production; (ii) Agroforestry area (Site II): Situated in Surodadi Village (676 m asl; -7.5930470, 111.0922240), characterized by high species richness and vertical stratification, combining timber (*Tectona grandis*, *S. mahagoni*), legumes (*L. leucocephala*), and fruit trees (*Mangifera indica*, *Durio zibethinus*); (iii) Rubber plantation (Site III): Located in Puntukrejo (673 m asl; -7.6223074, 111.1038714), dominated by *Hevea brasiliensis* in monoculture stands with limited inclusion of other species. These sites represent a structural and functional gradient from homogeneous monocultures to diverse, mixed-use systems, offering an ideal framework to examine the influence of vegetation traits on aboveground biomass and carbon storage.

Sampling design

Vegetation sampling employed a stratified design across three land-use types: pine forest, agroforestry, and rubber plantation. Each site was subdivided into two vegetation strata based on stem diameter: (i) Tree stratum: Individuals with DBH > 20 cm, (ii) Pole stratum: Individuals with DBH 10–20 cm. For each stratum, 15 plots were established per site, resulting in a total of 90 sampling plots (3 sites × 2 strata × 15 plots). Plot sizes were: (i) 20 × 20 m (400 m²) for the tree stratum, (ii) 10 × 10 m (100 m²) for the pole stratum

Plot locations were selected randomly within representative areas of each land-use type and georeferenced using GPS. Within each plot, all woody individuals meeting the DBH criteria were inventoried. For each individual, the following were recorded: species identity, DBH (via stem circumference), and estimated total height.

Species identification was conducted using local names and verified through botanical references or expert consultation. This stratification allowed the analysis of biomass contribution across developmental stages and structural layers, facilitating comparison within and between land-use types in terms of regeneration, productivity, and carbon storage potential.

Measurement of structural parameters

The assessment of vegetation structure was based on two key biometric indicators: diameter at breast height (DBH) and total plant height, both of which are widely recognized as reliable proxies for plant growth and aboveground biomass accumulation. DBH was measured at 1.3 meters above ground level using a diameter tape. For individuals with irregular stem forms such as buttresses or basal swellings the measurement was taken above the deformity where the stem resumed a cylindrical shape. DBH values were obtained by dividing the measured stem circumference by π (3.14), following the standard forestry formula. Total plant height was estimated for representative individuals in each plot using a hypsometer or visual estimation, particularly for tall species such as *P. merkusii*, *T. grandis*, and *S. mahagoni*. These height measurements complemented DBH data and were used in allometric equations that required both parameters. Species identification was conducted in the field using vernacular names provided by local informants and confirmed through taxonomic references. Each individual was subsequently categorized into one of two structural strata pole (DBH 10–20 cm) or tree (DBH > 20 cm) to reflect different stages of ontogenetic development. This stratification facilitated the evaluation of growth patterns, carbon input from younger vegetation, and the contribution of mature individuals to the total biomass pool. Together, DBH and height data provided a comprehensive picture of stand structure, enabling accurate estimation of biomass and carbon stock across different land-use types.

Table 1. Estimation of aboveground biomass (AGB) using species-specific allometric equations

Species	Allometric equation (AGB in kg)	Reference
<i>Pinus merkusii</i> Jungh. & de Vriese	$AGB = 0.0936 \times D^{2.4323}$	Siregar 2007
<i>Leucaena leucocephala</i> (Lam.) de Wit	$AGB = 0.206 \times D^{2.305}$	Banaticla 2003
<i>Acacia auriculiformis</i> A.Cunn. ex Benth	$AGB = 0.077 \times D^{0.90}$	Arupa 2014
<i>Swietenia mahagoni</i> (L.) Jacq.	$AGB = 0.290091 \times D^{2.3}$	Hendri 2001
<i>Albizia chinensis</i> (Osbeck) Merr.	$AGB = 0.0272 \times D^{2.831}$	Ketterings et al. 2001
<i>Cocos nucifera</i> L.	$AGB = 4.5 + 7.7 \times H^1$	Hairiah et al. 2001
<i>Artocarpus heterophyllus</i> Lam.	$AGB = 0.1792 \times D^{2.25112}$	Samsu 2019
<i>Gmelina arborea</i> Roxb.	$AGB = 0.153 \times D^{2.217}$	Banaticla 2003
<i>Hevea brasiliensis</i> Muell Arg.	$AGB = 0.11 \times 0.63 \times D^{2.62}$	Ketterings et al. 2001
<i>Mangifera indica</i> L.	$AGB = -2.43 + 0.154 \times D + 0.193 \times H^2$	Chavan et al. 2012
<i>Averrhoa bilimbi</i> L.	$AGB = 0.3699 \times D^{1.9374}$	Ilyas 2013
<i>Hibiscus tiliaceus</i> L.	$AGB = 0.168 \times 0.47 \times D^{2.47}$	Chave et al. 2005
Other species (branched trees)	$AGB = 0.11 \times \rho \times D^2 + 0.62$	Ketterings et al. 2001

Note: D: diameter at breast height (cm); H: total tree height (m); ρ : wood density (g/cm³); AGB: aboveground biomass (kg); ¹For *Cocos nucifera*, the equation represents composite biomass: 4.5 (trunk) + 7.7 (fronds) + H (crown), as per Hairiah et al. 2001; ²Equation for *Mangifera indica* is valid only for trees with D ≥ 10 cm and H ≥ 5 m to avoid negative estimates, based on calibration range in Chavan et al. 2012

Biomass estimation

Aboveground biomass (AGB) was estimated non-destructively using species-specific allometric equations that relate measurable structural traits primarily DBH and height to biomass accumulation. These equations typically follow the form $AGB = a \times D^b$ or $a \times D^b \times H^c$, where D is diameter at breast height (cm), H is total height (m), and a , b , and c are species-specific constants derived empirically. A set of allometric models was selected based on species identity and growth form, as summarized in Table 1, drawing from previously validated equations for tropical species (e.g., Banaticla 2003; Chave et al. 2005; Siregar 2007). For species lacking specific models, generalized equations based on wood density or branching type were applied. The calculated biomass of each individual was aggregated at the plot level and extrapolated to a per-hectare basis (MgB/ha), enabling comparison across sites and structural strata. This approach ensures ecological accuracy while capturing functional differences in biomass allocation driven by vegetation structure and composition.

Carbon stock calculation

The aboveground carbon stock was derived from the estimated biomass values using a standardized conversion factor of 0.47, which reflects the average proportion of carbon in dry plant biomass. This coefficient, endorsed by the Indonesian National Standard (SNI 7724:2011) and consistent with IPCC guidelines, assumes that 47% of dry biomass consists of organic carbon bound in structural compounds such as cellulose and lignin. For each sampled individual, the calculated biomass (in mg/ha) was multiplied by 0.47 to obtain its carbon equivalent. Carbon values were computed separately for each stratum tree and pole and then aggregated to generate the total aboveground carbon stock per land-use type. This approach allows for the integration of species- and size-specific biomass variation into landscape-level carbon accounting. The use of a fixed conversion factor ensures comparability across sites, while still capturing structural differences in carbon accumulation that result from variations in DBH, height, wood density, and vegetation composition. By linking structural traits to functional outcomes, this method provides ecologically meaningful insights into the role of vegetation systems in carbon sequestration.

Data analysis

Data analysis focused on quantifying and comparing Aboveground Biomass (AGB) and carbon stock across different land-use types and structural strata. For each plot, individual AGB values derived from allometric equations were summed and converted to a per-hectare basis. Carbon stock was then calculated using the standard factor ($0.47 \times AGB$). These values were averaged for the tree and pole strata separately, allowing for stratified comparisons that reflect differences in structural development and regenerative status. Site-level totals were obtained by aggregating values from both strata. Visual representations were employed to illustrate variation across land uses, including stacked bar charts that displayed the relative

contribution of trees and poles to total biomass and carbon stock. Additionally, DBH class distributions were plotted to assess population structure and regeneration dynamics. Rather than applying inferential statistics, the analysis emphasized descriptive comparisons, highlighting how variations in species composition, stem diameter, and canopy layering shape the carbon storage potential of each system. This approach aligns with the study's objective to link structural traits with ecological function and provides a framework for interpreting the role of vegetation architecture in long-term carbon dynamics.

RESULTS AND DISCUSSION

Species composition and site characteristics

Vegetation composition and structure differed markedly among the three land-use types in Ngargoyoso pine forest, agroforestry system, and rubber plantation. A total of 32 occurrences of species were recorded across both tree (DBH > 20 cm) and pole (DBH 10-20 cm) strata, representing 25 unique species after accounting for overlaps between strata. Several species, such as *L. leucocephala* and *S. mahagoni*, were present in both strata, indicating active regeneration and demographic continuity across growth stages. These variations reflect differences in land management practices and species selection, which in turn shape the ecological functions related to aboveground biomass accumulation. Structural traits such as stem diameter and plant height played a significant role in determining the carbon stock potential at each site, underscoring the importance of both floristic diversity and vertical stratification in vegetation-based carbon storage.

The pine forest, although dominated by *P. merkusii*, did not exhibit the lowest species richness among the three land-use types. In fact, the rubber plantation recorded the lowest species richness, with only four species identified, despite having a higher total number of individuals. In the pine forest, the tree stratum was densely populated with mature *P. merkusii* individuals, whereas the pole stratum was sparsely populated, with limited regeneration. This lack of vertical stratification and reduced undergrowth diversity is characteristic of monoculture systems, where dense canopies and allelopathic litter inhibit seedling establishment. Consequently, the pine forest presents a static biomass structure, limited ecological resilience, and constrained potential for long-term carbon accumulation.

In contrast, the agroforestry system supported the highest species richness and structural complexity. It combined timber species such as *T. grandis* and *S. mahagoni* with nitrogen-fixing legumes like *L. leucocephala* and fruit-bearing trees such as *D. zibethinus* and *M. indica*. The pole stratum was well-populated, indicating active regeneration and layered canopy development. This multi-strata configuration allows for efficient resource use, improved soil fertility, and continuous carbon input across different growth stages.

The rubber plantation presented an intermediate pattern, with *H. brasiliensis* as the dominant species, accompanied by scattered individuals of *S. mahagoni*. While this system

was more structurally diverse than the pine forest, it still lacked the species richness and vertical complexity observed in agroforestry. The vegetation profile reflects a production-oriented system, where species selection is driven primarily by economic value particularly latex production rather than ecological function.

These distinctions are reflected in Table 2, which shows higher total biomass and carbon stock in the agroforestry site, particularly within the pole stratum. The results affirm that vegetation composition and structural diversity are central to optimizing carbon storage and should be integral to sustainable land use and climate mitigation strategies.

Dominance of vegetation in each land-use type

Vegetation dominance across the three land-use systems pine forest, agroforestry area, and rubber plantation was shaped by plantation design, species composition, and specific management objectives. As shown in Table 2, the tree stratum consistently contributed the majority of aboveground biomass (AGB) and carbon stock at all sites, reflecting the structural maturity of dominant canopy species. Figure 2 illustrates this trend, where the three layers visually dominate the stacked bars while the contribution of the pole stratum varies. This variation reveals differences in regeneration dynamics and vertical complexity, with profound implications for long-term carbon sequestration and ecosystem resilience, underscoring the importance of this research.

In the pine forest, *Pinus merkusii* was the predominant species, forming a nearly homogeneous stand with large-diameter trees and a dense canopy. These characteristics restricted light availability in the understory, resulting in minimal regeneration and poor pole development. The pole stratum contributed only 3.99 MgB/ha of biomass and 1.87 MgC/ha of carbon—less than 4% of the tree layer's total indicating a sharply skewed structure. Such imbalance is typical of monoculture pine systems, where shade-intolerant secondary species are unable to establish. While these stands can accumulate substantial biomass in mature individuals, they lack vertical diversity and regenerative capacity, reducing their ecological resilience and long-term adaptability.

In contrast, the agroforestry system exhibited a more balanced vertical profile, with significant contributions from both tree and pole strata. Tree biomass reached 125.13 MgB/ha, while pole biomass was the highest among all sites at 50.29 MgB/ha. This structure reflects active regeneration, age diversity, and multi-layered canopy development. Species like *L. leucocephala*, *G. gnemon*, and *T. grandis* were present across strata, supporting ongoing biomass input and ecological succession. The resulting vertical integration enhances resilience, nutrient cycling, and carbon assimilation, establishing agroforestry as a functionally superior system.

The rubber plantation, dominated by *H. brasiliensis*, recorded the highest tree biomass (131.41 mgB/ha) and a moderate contribution from the pole layer (41.80 mgB/ha). The presence of *S. mahagoni* in both strata contributed to limited structural diversity within an otherwise monocultural

system. Though less heterogeneous than agroforestry, this configuration still supports modest vertical layering and under-canopy productivity.

Overall, vegetation dominance patterns across land uses reveal that systems with species diversity and well-developed strata, such as agroforestry, achieve superior carbon storage and ecological function. These findings highlight the value of structural complexity in shaping long-term carbon dynamics and land-use sustainability.

Ecological implications of vegetation composition

Variations in species composition among the three land-use types pine forest, agroforestry, and rubber plantation have notable ecological consequences, particularly in terms of biodiversity, structural complexity, and carbon storage potential. This study demonstrates that agroforestry systems, which host a more diverse assemblage of species and a balanced distribution between tree and pole strata, deliver more dynamic and resilient ecological functions than monoculture systems. The resilience of agroforestry systems, even in the face of environmental challenges, should reassure us of their potential to sustain our ecosystems. These compositional differences are reflected not only in the diversity of species but also in the ability of each system to support multi-layered canopies and sustain long-term carbon accumulation.

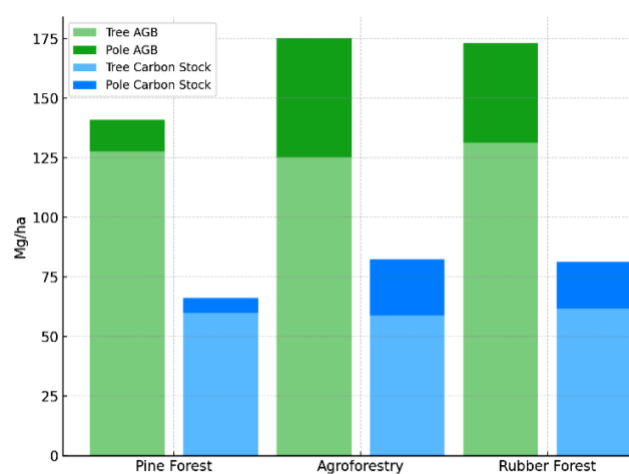


Figure 2. Stacked aboveground biomass and carbon stock by forest

Table 2. Aboveground biomass and carbon stock - tree and pole category (all sites)

Site	Stratum	AGB (MgB/ha)	Carbon stock (MgC/ha)
Pine forest	Tree	127.61	59.95
Pine forest	Pole	3.99	1.87
Agroforestry	Tree	125.13	58.83
Agroforestry	Pole	50.29	23.63
Rubber forest	Tree	131.41	61.76
Rubber forest	Pole	41.80	19.65

As indicated in Table 2, the agroforestry area exhibited the highest combined aboveground biomass and carbon stock, largely due to the strong contribution from the tree stratum (183.96 mgB/ha), with the pole stratum (73.92 mgB/ha) also contributing significantly. This structure reflects a productive overstory coexisting with an actively regenerating understory, resulting in a vertically integrated and ecologically functional system. The coexistence of timber, fruit, and leguminous species promotes niche differentiation, optimizes light capture across canopy layers, and enhances microclimatic buffering factors that collectively improve ecosystem productivity and carbon sequestration (Chave et al. 2005; Ferrini et al. 2020). The presence of nitrogen-fixing plants such as *L. leucocephala* further supports soil fertility and understory development, reinforcing the long-term sustainability of the agroforestry system.

In contrast, the pine forest, although dominated by large trees, lacked species diversity and vertical stratification. Its understory was sparse, resulting in minimal ecological layering and reduced habitat heterogeneity. This system's homogeneity limits its capacity to support broader ecosystem services and increases its vulnerability to pests, climatic stress, and ecological disruption (Han et al. 2019). The rubber plantation, while exhibiting slightly higher diversity than the pine forest with four recorded species and a pole stratum biomass of 40.63 MgB/ha still fell short of agroforestry in both structural richness and regenerative layering. In comparison, the agroforestry site contained 29 species across both strata, with the pole layer alone contributing 73.92 MgB/ha of biomass, indicating a more robust regenerative profile. These differences underscore the superior vertical integration and compositional heterogeneity of agroforestry systems.

Vegetation composition also affects litter quality, soil nutrient cycling, and faunal interactions. In agroforestry systems, the mix of leguminous shrubs, hardwoods, and fruit trees not only sustains high carbon inputs but also supports biodiversity through pollination and seed dispersal networks. The balanced biomass contributions from tree and pole strata enhance structural stability, which may buffer carbon storage under environmental fluctuations (Figure 2).

Ultimately, the ecological integrity and carbon performance of a land-use system are closely linked to its vegetative composition. Diverse, multi-functional systems like agroforestry provide greater long-term benefits by integrating productive and ecological functions within a single landscape framework (Ambarwati et al. 2019; Ferrini et al. 2020).

Aboveground biomass and carbon stock by land-use type

Pine forest

The pine forest site, characterized by a monocultural stand of *P. merkusii*, demonstrated a relatively high accumulation of aboveground biomass primarily concentrated in the tree stratum. As presented in Table 2, tree biomass in this site reached 127.61 MgB/ha, corresponding to a carbon

stock of 59.95 MgC/ha. In contrast, the pole stratum contributed only 13.44 MgB/ha (or 6.32 MgC/ha), accounting for less than 10% of the total biomass (Figure 2).

The dominance of the tree stratum is consistent with the plantation's structure, where uniform canopy height, wide spacing, and absence of understory cultivation limit regeneration and pole development. This pattern reflects typical characteristics of conifer-based monocultures in tropical uplands, which tend to produce high per-individual biomass due to rapid trunk expansion but support relatively low structural heterogeneity (Han et al. 2019).

While the total AGB of 141.05 MgB/ha and carbon stock of 66.27 MgC/ha are moderately high, they are lower than those observed in agroforestry and rubber plantation systems (Table 3, Figure 3). This suggests that despite the high biomass per tree, the uniform structure and low undergrowth density limit total site productivity. Similar observations were reported by Ambarwati et al. (2019), where monoculture pine plantations had lower total carbon stock than mixed-species stands of similar age due to their reduced vertical complexity and canopy layering.

Moreover, the limited pole contribution indicates weak regeneration or shade intolerance of young individuals under dense pine canopies. Pine litter, known for its high lignin and resin content, may also inhibit seedling growth and soil microbial activity, thereby reducing below-canopy productivity (Ferrini et al. 2020). This ecological limitation not only affects biomass dynamics but also poses long-term sustainability concerns under climate variability.

Table 3. Comparison of total aboveground biomass and carbon stock per site

Site	Total AGB (MgB/ha)	Total carbon stock (MgC/ha)
Pine forest	141.05	66.29
Agroforestry	175.42	82.46
Rubber forest	173.21	81.41

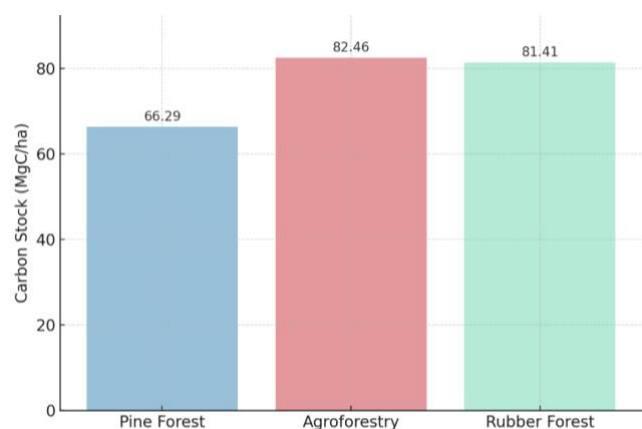


Figure 3. Total carbon stock in each land use type

In terms of carbon sequestration, *P. merkusii* is recognized for its rapid early-stage growth and wood density, contributing effectively to short- to medium-term carbon storage (Siregar 2007). However, the lack of species diversity and multi-age structure in pine forests is a significant constraint, reducing their long-term stability and adaptive capacity. This emphasizes the need for more diverse systems like agroforestry, which can offer more sustained carbon storage. Therefore, while pine forests contribute to immediate biomass accumulation, their ecological and physiological contributions to sustained carbon storage are relatively constrained when compared to more heterogeneous systems like agroforestry.

Agroforestry area

Among the three land-use types examined, the agroforestry site exhibited the highest structural complexity and species richness, which was clearly reflected in its aboveground biomass and carbon storage capacity. As reported in Table 2, the tree stratum contributed 125.13 MgB/ha of biomass and 58.83 MgC/ha of carbon. Notably, the pole stratum yielded 50.29 MgB/ha and 23.63 MgC/ha, making it the most productive understory layer among all studied sites. These values indicate active regeneration and continuous biomass input, highlighting the site's dynamic growth profile and ecological functionality.

The total aboveground biomass and carbon stock at the agroforestry site reached 175.42 MgB/ha and 82.46 MgC/ha, respectively, outperforming both the pine and rubber plantations (Table 3). This elevated accumulation is attributed to the vertically layered structure and diverse species composition specific to the agroforestry system. Within this site, timber species such as *T. grandis*, fast-growing nitrogen-fixing trees like *L. leucocephala*, and fruit trees including *D. zibethinus* and *M. indica* coexisted, creating a mosaic of ecological niches. This botanical diversity supports various growth forms and promotes vertical resource partitioning, thereby enhancing overall system productivity.

The significant biomass contribution of the pole stratum in agroforestry, as shown in Figure 2, indicates active regeneration and ongoing structural renewal. This vertical stratification enhances light interception and spatial resource efficiency, thereby supporting higher net primary productivity (Chave et al. 2005; Ferrini et al. 2020). Moreover, the presence of nitrogen-fixing species such as *L. leucocephala* contributes indirectly to biomass accumulation by enriching soil nutrient levels and promoting the growth of adjacent vegetation (Qiu et al. 2020; Diana et al. 2022).

The distribution of individuals across DBH classes (Figure 3) confirms the presence of a balanced age structure and steady regeneration. Individuals were recorded across all diameter ranges, supporting sustained growth and ecological resilience. This distribution enhances the system's capacity to withstand environmental disturbances such as drought, pests, or selective harvesting (Ambarwati et al. 2019).

In summary, agroforestry effectively integrates productive land use with ecosystem services such as carbon sequestration and biodiversity support. Its high carbon

stock, spread across both juvenile and mature strata, demonstrates its potential as a sustainable landscape model and a key strategy for climate change mitigation.

Rubber plantation

The rubber plantation, dominated by *H. brasiliensis*, exhibited the highest total tree biomass among the three land-use systems analyzed. According to Table 2, the tree stratum accounted for 131.41 MgB/ha of aboveground biomass and 61.76 MgC/ha of carbon stock, indicating the strong contribution of mature individuals. The pole stratum also played a meaningful role, contributing 41.80 MgB/ha and 19.65 MgC/ha, which reflects moderate levels of regeneration and a degree of vertical stratification. These figures suggest that while the system remains largely monocultural, it exhibits more structural layering than typically observed in production-focused plantations.

Overall, the site's total aboveground biomass and carbon stock amounted to 173.21 MgB/ha and 81.41 MgC/ha, respectively (Table 3), placing it between the more diverse agroforestry system and the structurally simplified pine forest in terms of carbon storage potential. The high tree biomass corresponds with the mature age of the stand, where most individuals surpass 30 cm in DBH and exhibit uniform stem development. This structural consistency aligns with standard monoculture management for latex harvesting, where stand age and planting density are tightly controlled (Siregar 2007). Nevertheless, the existence of pole-sized individuals implies opportunities for natural regeneration or underplanting.

Visualized in Figure 2, the pole stratum's contribution was greater than in the pine forest, suggesting limited but notable vertical complexity. This may be attributed to the presence of shade or intercrop species such as *S. mahagoni* and *M. indica*, which introduce additional layers and modest ecological benefits. Despite the relatively low species richness, this structural enhancement improves the system's ecological functionality compared to a pure monoculture.

Figure 4 shows a bimodal DBH distribution, with peaks in the 21-30 cm and 31-40 cm classes. This likely results from interplanting or canopy openings that enable light penetration and understory growth. However, the benefits of such a structure are limited by the plantation's simplified species composition and management intensity, which constrain resilience and multifunctionality (Ambarwati et al. 2019; Ferrini et al. 2020). While *H. brasiliensis* provides effective medium-term carbon storage, long-term sustainability may depend on strategies like enrichment planting and the integration of multi-strata vegetation to enhance biodiversity and ecosystem services.

Summary of biomass and carbon stock by stratum

Biomass distribution across tree and pole strata

Stratifying aboveground biomass and carbon stock into tree and pole layers provides valuable insights into the structural maturity and regenerative potential of various land-use types. As shown in Table 2, the tree stratum consistently held the majority of AGB across all sites, indicating the critical role of mature canopy trees in carbon

accumulation. However, the varying contribution of the pole stratum across land uses reveals important differences in age structure, vegetation dynamics, and succession stages. This stratified perspective not only reflects the current biomass profile but also signals each system's capacity to sustain long-term carbon storage.

In the pine forest, biomass distribution was heavily skewed toward the tree layer, which contributed 127.61 mgB/ha, around 90.5% of the site's total AGB. The pole stratum added just 13.44 MgB/ha, highlighting poor regeneration and limited vertical complexity. This pattern, visible in Figure 2, is typical of even-aged monocultures like *P. merkusii*, where dense canopies and allelopathic litter inhibit light penetration and understory establishment (Han et al. 2019). The lack of a robust pole layer indicates reduced ecological succession and poses challenges for future carbon continuity without active management intervention.

In comparison, the agroforestry system displayed a more balanced vertical structure, with 125.13 MgB/ha in the tree layer and 50.29 MgB/ha in the pole stratum, or 28.7% of total AGB. This distribution suggests active recruitment, diverse age classes, and multi-species participation. The presence of fast-growing, nitrogen-fixing species like *L. leucocephala* in the pole layer supports rapid canopy renewal and consistent carbon input from younger cohorts (Qiu et al. 2020; Diana et al. 2022). Such complexity enhances the system's ecological resilience and long-term carbon sequestration potential.

The rubber plantation presented an intermediate scenario. While dominated by *H. brasiliensis*, the inclusion of secondary species like *S. mahagoni* resulted in moderate pole development. Tree biomass reached 131.41 mgB/ha, with 41.80 MgB/ha from the pole stratum, indicating some regeneration and layering, albeit less dynamic than agroforestry. This structure reflects a system with modest potential for enrichment and structural improvement (Ambarwati et al. 2019).

Overall, vertical biomass partitioning serves as a functional indicator of ecological health and carbon sustainability. Agroforestry, with its balanced stratification,

exemplifies effective carbon management, whereas systems with limited pole development may face declining resilience and productivity over time (Ferrini et al. 2020).

Contribution of pole stratum to carbon continuity

Although mature trees contribute the majority of current aboveground biomass (AGB), the pole stratum—comprising individuals with diameters at breast height (DBH) between 10-20 cm—plays a crucial role in sustaining carbon stocks over time. As illustrated in Tables 4-6, the pole stratum's biomass contribution varies considerably across land-use types. However, its ecological significance surpasses its numeric share, as it reflects regeneration dynamics, successional progression, and long-term productivity. A well-established pole layer functions as a continuous input source for future canopy biomass, ensuring carbon accumulation persists even as mature trees decline.

In the agroforestry system, the pole stratum contributed 50.29 mgB/ha, or roughly 29% of the site's total AGB, indicating robust regeneration and age diversity. This substantial figure is supported by the presence of fast-growing and multipurpose species such as *L. leucocephala* and *G. gnemon*, which promote rapid biomass accumulation during early growth stages. These species not only enrich the structural diversity but also enhance system resilience by buffering biomass loss from tree harvest or mortality. Such a turnover mechanism supports sustained carbon flux and aligns with ecological models emphasizing functional redundancy and continuity (Chave et al. 2005).

As depicted in Figure 2, the pole layer in agroforestry makes a visually evident and meaningful contribution to total biomass. Trees with varying growth rates and wood densities coexist, supporting complementary roles in carbon dynamics (Diana et al. 2022). In stark contrast, the pine forest exhibited a poorly developed pole stratum, contributing only 13.44 MgB/ha, less than 10% of the total AGB. This structural gap reflects low recruitment and minimal understory activity, increasing the forest's vulnerability to stagnation and long-term decline (Ferrini et al. 2020).

Table 4. Aboveground biomass and carbon stock of pine forest in the tree and pole category

Categories	Family	Local name	Scientific name	Σ individuals	AGB (MgB/ha)	Carbon stock (MgC/ha)
Tree	Pinaceae	Pinus	<i>Pinus merkusii</i> Jungh. & de Vriese	106	124.73	58.62
	Fabaceae	Lamtoro	<i>Leucaena leucocephala</i> (Lam.) de Wit	1	2.20	1.03
	Meliaceae	Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	4	0.68	0.32
Pole	Fabaceae	Akasia	<i>Acacia auriculiformis</i> A.Cunn. ex Benth.	1	0.01	0.004
	Pinaceae	Pinus	<i>Pinus merkusii</i> Jungh. & de Vriese	5	3.99	1.87
	Theaceae	Puspa	<i>Schima wallichii</i> (DC.) Korth.	3	2.67	1.25
	Fabaceae	Lamtoro	<i>Leucaena leucocephala</i> (Lam.) de Wit	2	1.14	0.54
	Moraceae	Ara	<i>Ficus carica</i> L.	4	1.35	0.64
	Myrtaceae	Pucuk Merah	<i>Syzygium paniculatum</i> Gaertn.	1	0.57	0.27
	Sapindaceae	Rambutan	<i>Nephelium lappaceum</i> L.	2	1.42	0.67
	Meliaceae	Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	9	2.29	1.07

Table 5. Aboveground biomass and carbon stocks of agroforestry areas: tree and pole category

Categories	Family	Local name	Scientific name	Σ individuals	AGB (MgB/ha)	Carbon Stock (MgC/ha)	
Tree	Fabaceae	Lamtoro	<i>Leucaena leucocephala</i> (Lam.) de Wit	21	28.80	13.54	
	Theaceae	Puspa	<i>Schima wallichii</i> (DC.) Korth.	1	0.63	0.30	
	Meliaceae	Suren	<i>Toona sinensis</i> (A.Juss.) M.Roem	2	3.21	1.51	
	Malvaceae	Durian	<i>Durio zibethinus</i> Murray	10	8.63	4.06	
	Gnetaceae	Melinjo	<i>Gnetum gnemon</i> Linn.	3	5.17	2.43	
	Fabaceae	Petai	<i>Parkia speciosa</i> Hassk	2	4.06	1.91	
	Lamiaceae	Jati	<i>Tectona grandis</i> Linn. F	8	23.83	11.20	
	Meliaceae	Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	5	3.12	1.47	
	Fabaceae	Sengon	<i>Albizia chinensis</i> (Osbeck) Merr.	4	22.52	10.58	
	Myrtaceae	Cengkeh	<i>Syzygium aromaticum</i> L.	1	4.16	1.96	
	Arecaeae	Kelapa	<i>Cocos nucifera</i> L.	5	0.27	0.13	
	Lauraceae	Alpukat	<i>Persea americana</i> P. Mill	2	9.33	4.39	
	Malvaceae	Waru	<i>Hibiscus tiliaceus</i> L.	1	0.48	0.23	
	Moraceae	Ara	<i>Ficus carica</i> L	2	4.79	2.25	
	Lamiaceae	Jati Putih	<i>Gmelina arborea</i> Roxb. ex Sm.	1	0.43	0.20	
	Sapindaceae	Rambutan	<i>Nephelium lappaceum</i> L.	3	5.69	2.67	
	Fabaceae	Akasia	<i>Acacia auriculiformis</i> A. Cunn. ex Benth.	2	0.01	0.00	
	Pole	Fabaceae	Lamtoro	<i>Leucaena leucocephala</i> (Lam.) de Wit	17	25.65	12.05
		Malvaceae	Durian	<i>Durio zibethinus</i> Murray	6	6.77	3.18
		Meliaceae	Suren	<i>Toona sinensis</i> (A.Juss.) M.Roem	1	0.96	0.45
Myrtaceae		Cengkeh	<i>Syzygium aromaticum</i> L.	4	3.95	1.86	
Gnetaceae		Melinjo	<i>Gnetum gnemon</i> Linn.	2	2.22	1.05	
Meliaceae		Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	2	0.58	0.27	
Malvaceae		Waru	<i>Hibiscus tiliaceus</i> L.	1	0.51	0.24	
Fabaceae		Sengon	<i>Albizia chinensis</i> (Osbeck) Merr.	5	2.48	1.16	
Euphorbiaceae		Macaranga	<i>Macaranga</i> Thouars	5	3.58	1.68	
Moraceae		Nangka	<i>Artocarpus heterophyllus</i> Lam.	1	0.36	0.17	
Oxalidaceae		Belimbing wuluh	<i>Averrhoa bilimbi</i> L.	2	1.80	0.85	
Lamiaceae		Jati	<i>Tectona grandis</i> L.f.	1	0.79	0.37	
Myrtaceae		Jambu Bol	<i>Syzygium malaccense</i> (L.) Merr. & L.M.Perry	1	0.34	0.16	
Anacardiaceae		Mangga	<i>Mangifera indica</i> L.	1	0.30	0.14	

Table 6. Aboveground biomass and carbon stocks of rubber plantations: tree and pole category

Categories	Family	Local name	Scientific name	Σ individuals	AGB (MgB/ha)	Carbon Stock (MgC/ha)
Tree	Euphorbiaceae	Karet	<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	159	122.07	57.37
	Meliaceae	Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	6	9.34	4.39
Pole	Euphorbiaceae	Karet	<i>Hevea brasiliensis</i> (Willd. ex A.Juss.) Müll.Arg.	137	40.63	19.10
	Meliaceae	Mahoni	<i>Swietenia mahagoni</i> (L.) Jacq.	4	1.17	0.55

The rubber plantation presented an intermediate pattern, with the pole layer contributing 41.80 MgB/ha or 24% of total AGB. Although dominated by *H. brasiliensis*, the inclusion of shade-tolerant or intercrop species lends moderate vertical layering. However, without sustained recruitment of diverse species, the system risks plateauing in its regenerative capacity (Ambarwati et al. 2019). Ecologically, the pole stratum acts both as a buffer that maintains carbon levels during canopy turnover and as a bridge to future tree biomass. Systems with healthy pole populations are better equipped to recover from disturbance and sustain long-term carbon sequestration. Integrating pole strata into monitoring and management strategies is thus essential for accurately forecasting future carbon dynamics (Poorter et al. 2017; Diana et al. 2022).

Structural efficiency in biomass allocation

Structural efficiency in vegetation systems refers to the ability to convert space and light into aboveground biomass through optimized organization of tree diameters, vertical stratification, and canopy height variability. Efficient systems feature well-developed tree and pole strata, enabling active biomass accumulation across multiple age cohorts. This configuration minimizes competition within stands and supports continuous growth, a dynamic process that enhances both carbon capture and long-term ecological productivity. These structural traits are crucial indicators of how well a system can sustain carbon dynamics over time.

Among the land-use types studied, agroforestry demonstrated the highest level of structural efficiency. As

shown in Table 2, biomass was distributed between the tree (125.13 mgB/ha) and pole (50.29 mgB/ha) strata, indicating effective vertical space utilization. Figure 2 illustrates this balance, with stacked bars revealing a well-stratified canopy composed of overstory, sub-canopy, and regenerating individuals. This multi-tiered structure allows for the efficient light interception, reduced self-shading, and continued regeneration, contributing to long-term carbon accumulation (Poorter et al. 2017; Ferrini et al. 2020).

Diameter distribution in agroforestry (Figure 4) further confirms structural density and demographic diversity. High variability in DBH classes supports stand complexity and correlates with greater crown complementarity and spatial efficiency. The coexistence of fast-growing legumes like *L. leucocephala* and dense-wood species such as *T. grandis* and *S. mahagoni* enables both rapid and sustained carbon storage (Chave et al. 2005; Qiu et al. 2020). These synergies reduce the risk of self-thinning and improve resilience to environmental changes.

In comparison, the pine forest exhibited structural stagnation, with 90.5% of its total AGB (127.61 mgB/ha) concentrated in the tree stratum and only 13.44 MgB/ha contributed by the pole layer, despite the presence of 40 individuals in that category (Table 4). The dominance of *P. merkusii* and the narrow DBH distribution indicate limited functional regeneration and inefficient vertical space utilization (Han et al. 2019). Although poles were present, their low biomass contribution suggests poor structural layering, which compromises redundancy and reduces the forest's carbon buffering capacity.

The rubber plantation showed intermediate efficiency. While tree biomass was dominant (131.41 MgB/ha), the pole layer contributed 41.80 MgB/ha, supported by underplanted species like *S. mahagoni*. Despite moderate vertical layering, limited diameter diversity reduced its ecological adaptability (Ambarwati et al. 2019). Overall, agroforestry systems exemplify structural efficiency by combining species diversity, vertical layering, and regenerative dynamics, making them a model for both carbon productivity and sustainability (Diana et al. 2022).

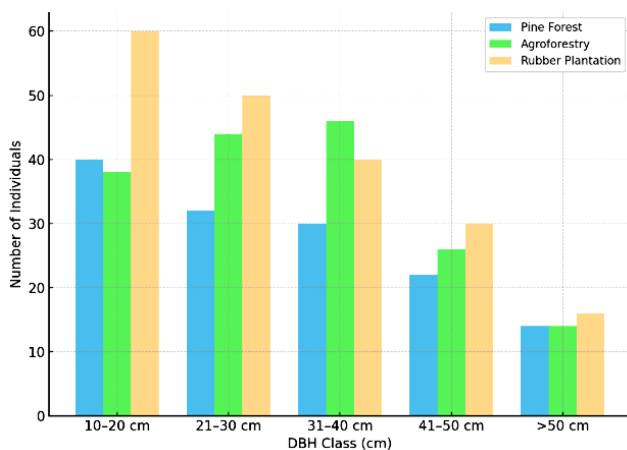


Figure 4. Distribution of DBH class across sites

Management implications of vertical stratification

The vertical stratification of vegetation into tree and pole layers provides essential ecological insights and practical guidance for sustainable land use and forest management. By understanding how aboveground biomass (AGB) and carbon are distributed vertically, land managers can develop more effective strategies to enhance productivity and secure long-term carbon retention. As shown in Table 2, the proportion of biomass within the pole stratum varied notably across land-use types, from just 9.5% in the pine forest to 28.7% in agroforestry. Figure 2 further illustrates these contrasts, underscoring the greater vertical complexity of multi-strata systems. This stratified perspective is crucial for informing carbon monitoring, regeneration planning, and the design of ecosystem service-based incentive schemes.

Incorporating layer-specific data into carbon inventories is essential for capturing the full dynamics of biomass accumulation, particularly in diverse systems like agroforestry. Standard approaches often emphasize mature trees, underrepresenting the pole stratum's contribution to both current biomass and future carbon potential. This study demonstrates that poles can account for up to one-third of AGB, underscoring their ecological and functional significance (Ferrini et al. 2020; Diana et al. 2022). Therefore, carbon assessment protocols especially within frameworks such as REDD+ should adopt stratified reporting to avoid underestimation and better support mitigation strategies (Chave et al. 2005).

The pole stratum also serves as a regenerative buffer that facilitates biomass turnover as older trees senesce or are harvested. In systems where this layer is underdeveloped, such as the pine forest, restoration should prioritize reestablishing pole-sized individuals using practices like enrichment planting, understory release, or gap creation. Selecting fast-growing, mid-canopy and shade-tolerant species can help rebuild vertical complexity and improve future carbon input (Poorter et al. 2017; Ambarwati et al. 2019). These strategies are particularly relevant in degraded sites or aging plantations with limited natural regeneration.

Moreover, vertical stratification provides a foundation for integrating forest management with Payment for Ecosystem Services (PES) and carbon credit initiatives. Agroforestry systems with well-developed strata not only offer high carbon storage but also deliver co-benefits like soil stabilization, habitat provision, and climate regulation. Recognizing the role of the pole layer enhances policy frameworks such as REDD+ benefit-sharing and community forest agreements (Qiu et al. 2020). Lastly, integrating stratification knowledge into training programs can promote more holistic, system-based management approaches, shifting focus from overstory trees to the broader regenerative potential of diverse forest layers.

Comparison of total biomass and carbon stock across sites

Total aboveground biomass by land-use type

The comparison of total aboveground biomass (AGB) among the three land-use types—agroforestry, rubber

plantation, and pine forest reveals notable differences in structural composition and ecological function. As reported in Table 5, agroforestry recorded the highest total AGB at 175.42 MgB/ha, followed closely by the rubber plantation at 173.21 MgB/ha, while the pine forest trailed behind with 141.05 MgB/ha. These variations are not solely a reflection of the land-use category but rather stem from differences in species diversity, stand structure, and vertical stratification.

The agroforestry system's superior biomass accumulation is closely tied to its heterogeneous composition, which includes a mix of fast-growing legumes and long-lived hardwood species. The presence of *L. leucocephala*, *T. grandis*, and *S. mahagoni* creates a layered canopy structure that maximizes vertical light capture and allows for simultaneous growth across multiple strata. This structural complexity supports higher light-use efficiency and stand productivity (Poorter et al. 2017; Qiu et al. 2020). As shown in Table 2 and Figure 2, the relatively balanced contribution of both tree and pole strata illustrates the efficient spatial organization of biomass in agroforestry.

In the rubber plantation, the total AGB was only slightly lower than that of agroforestry, largely due to the mature age and uniform spacing of *H. brasiliensis*. Interplanted hardwoods like *Swietenia mahagoni* introduced some structural variation, but the biomass remained concentrated in the tree stratum. The system's vertical stratification was less developed, limiting regeneration and understory productivity. Although productive, the plantation exhibits reduced resilience due to limited age diversity and ecological layering (Ambarwati et al. 2019).

The pine forest, dominated by *P. merkusii*, showed the lowest AGB, reflecting its simple, even-aged structure and low wood density. The dense, uniform canopy suppresses understory growth and regeneration, leading to minimal pole development and underutilized vertical space (Han et al. 2019). With biomass concentrated in mature individuals, the system shows signs of stagnation and limited long-term productivity. Overall, these findings suggest that vegetation diversity, structural layering, and species composition are stronger determinants of total biomass than land-use type alone. Agroforestry's combination of regenerative layering and functional diversity makes it a more resilient and sustainable model for carbon accumulation (Chave et al. 2005; Ferrini et al. 2020).

Total carbon stock and sequestration potential

Aboveground carbon stock, derived from biomass (AGB), provides a crucial measure of an ecosystem's capacity to mitigate climate change through carbon sequestration. As presented in Table 6 and illustrated in Figure 3, the agroforestry system recorded the highest carbon stock at 82.46 MgC/ha, followed closely by the rubber plantation with 81.41 MgC/ha. The pine forest exhibited the lowest value at 66.29 MgC/ha. These differences are largely driven by variations in vegetation structure, species diversity, and regeneration dynamics across the three land-use types.

The strong carbon performance of the agroforestry system is closely tied to its rich species composition and vertically stratified structure. The inclusion of fast-growing nitrogen-fixing species such as *L. leucocephala*, high-

density hardwoods like *T. grandis* and *S. mahagoni*, as well as *A. chinensis* the third highest contributor to AGB enhances both short-term accumulation and long-term carbon storage (Chave et al. 2005; Diana et al. 2022). Notably, the pole stratum contributes 28.7% of the total biomass, indicating active recruitment and a strong foundation for future carbon input (Table 5). This dynamic structural profile enables agroforestry systems to sustain consistent carbon levels across developmental stages.

Beyond current stock levels, agroforestry demonstrates high potential for long-term carbon sequestration due to its continuous biomass turnover. The coexistence of various growth stages ensures that as mature trees are harvested or decline, younger individuals continue to contribute to the carbon pool. This contrasts with the pine forest, where most carbon is stored in mature *P. merkusii* trees, and little regeneration occurs, resulting in limited future sequestration capacity (Figure 2). The rigidity of such even-aged monocultures restricts adaptability and reduces resilience to environmental change.

The rubber plantation showed carbon stock levels comparable to agroforestry but lacked equivalent structural diversity; the dominance of *H. brasiliensis*, with minimal support from underplanted hardwoods, limits regeneration, and vertical complexity. While productive in the short term, the system's static structure may not sustain carbon levels in the long run without management interventions (Ambarwati et al. 2019; Ferrini et al. 2020).

Overall, these findings highlight the critical role of structural diversity and regenerative layering in sustaining carbon stocks. Agroforestry's combination of high biomass, dynamic structure, and species functionality makes it a strong candidate for inclusion in REDD+ programs and ecosystem-based carbon strategies (Qiu et al. 2020).

Structural and functional basis of biomass differences

Variations in total aboveground biomass (AGB) and carbon stock across land-use types are shaped more by structural traits than by plantation area or age. Key parameters such as diameter at breast height (DBH), tree height, stand density, and species functional diversity play a central role in biomass accumulation. These structural characteristics interact with physiological functions like photosynthesis and nutrient uptake, influencing how efficiently vegetation captures and stores carbon. Therefore, analyzing these traits provides a meaningful framework for assessing the carbon storage capacity of different land-use systems.

The agroforestry system demonstrated the highest total AGB and carbon stock (Table 3), strongly associated with its diverse DBH distribution and vertically layered canopy structure (Figure 2, Figure 4). Trees were represented across a wide range of diameter classes, indicating ongoing recruitment and demographic diversity. This structural layering allows for efficient vertical light use and spatial partitioning, supporting multiple photosynthetic levels (Poorter et al. 2017). Furthermore, the presence of high wood-density species such as *T. grandis* and *S. mahagoni* enhances the amount of carbon stored per unit volume (Chave et al. 2005).

Functionally, the agroforestry system incorporates a mix of fast-growing pioneers like *L. leucocephala*, fruit trees such as *M. indica*, and durable hardwoods. This mixture promotes complementarity in resource use, growth rate, and development stages, contributing to both rapid biomass gain and long-term storage (Qiu et al. 2020; Diana et al. 2022). As a result, agroforestry exhibits high productivity and resilience.

In contrast, the pine forest, dominated by *P. merkusii*, exhibited narrow DBH distribution and limited understory development (Table 2, Figure 4). Biomass was concentrated in a single canopy layer, indicating structural stagnation and low regenerative capacity. The low wood density of *P. merkusii* further limits carbon storage efficiency, explaining the site's lowest AGB and carbon stock values (Han et al. 2019).

The rubber plantation presented an intermediate scenario with broader DBH classes and modest pole contributions. However, dominated by *H. brasiliensis*, the inclusion of intercropped hardwoods added limited structural variation. However, the system's uniform design and mid-range wood density constrain its overall biomass potential (Ambarwati et al. 2019). Land-use systems with greater structural complexity such as agroforestry demonstrate superior carbon storage capacity. These traits support more efficient ecological processes and highlight the value of diversity and layering in sustainable biomass management (Ferrini et al. 2020).

Implications for land-use strategy and carbon policy

The observed variation in aboveground biomass (AGB) and carbon stock across pine forest, agroforestry, and rubber plantation systems has significant implications for land-use planning, forest rehabilitation, and climate policy development. The structural and functional differences between these systems reveal distinct ecosystem services and strategic values, allowing them to be aligned with specific landscape objectives such as carbon sequestration, biodiversity support, and socio-economic resilience. The findings underscore the urgent need for differentiated approaches based on vegetation structure and ecological performance.

Agroforestry emerged as the most effective carbon sink, with the highest AGB (175.42 MgB/ha) and carbon stock (82.46 MgC/ha), alongside rich species diversity and well-developed vertical stratification (Tables 2-3; Figures 2-3). This system supports simultaneous ecological and livelihood goals, making it ideal for buffer zones, community-managed areas, and transition zones at agricultural frontiers. Its layered structure promotes continuous regeneration and stable carbon accumulation while also delivering timber, fruit, and fuelwood. Such multifunctionality aligns with national climate-smart land-use strategies and international initiatives like REDD+ and Payment for Ecosystem Services (PES) (Diana et al. 2022; Ferrini et al. 2020).

The rubber plantation, although largely monocultural, recorded a high carbon stock (81.41 MgC/ha) due to mature tree stands and moderate contributions from the pole layer. The integration of intercrop species such as *S. mahagoni* has added some structural diversity. As a

transitional land-use model, rubber plantations hold the potential for enrichment through underplanting and species diversification. When supported by reforestation frameworks such as the Bonn Challenge or Forest Landscape Restoration (FLR), they can evolve into more functionally complex systems with enhanced carbon and biodiversity benefits (Ambarwati et al. 2019).

In contrast, the pine forest, dominated by *P. merkusii*, showed the lowest carbon stock (66.29 MgC/ha) and weak regenerative capacity. Its biomass was concentrated in mature trees with limited understory development and pole presence, resulting in structural stagnation. Rehabilitation strategies such as gap enrichment, selective thinning, and underplanting of broadleaf species could improve its resilience and carbon dynamics (Han et al. 2019; Ferrini et al. 2020). These interventions are suitable for REDD+ readiness efforts, particularly in forest enhancement or restoration contexts.

Policy recommendations based on this analysis include prioritizing agroforestry in multi-functional land-use programs, enhancing rubber plantations for carbon and ecological gains, and investing in structural rehabilitation for pine systems. Integrating vertical stratification data into national monitoring protocols would support more accurate assessments of forest carbon and help optimize climate-related land-use strategies.

Distribution of DBH class across vegetation types

Distribution of DBH classes between sites

Diameter at breast height (DBH) class distribution is a key structural indicator that reveals the age structure, regeneration dynamics, and management effects within different land-use systems. As illustrated in Figure 4, DBH patterns varied markedly across the three sites, indicating differences in stand composition and growth-stage representation. These patterns offer insight into each system's capacity for long-term biomass turnover and carbon storage, as well as its ecological resilience and management needs.

In the pine forest, individuals were heavily concentrated in larger DBH classes (≥ 31 cm), with minimal representation in the lower diameter ranges (10-20 cm). This pattern reflects the even-aged, mature character of the *Pinus merkusii* monoculture, which is managed primarily for resin and timber extraction. The lack of young stems and a poorly developed understory indicate minimal natural recruitment, likely due to dense canopy closure and allelopathic effects from pine litter (Han et al. 2019). Without interventions such as underplanting or gap creation, this static structure may limit long-term carbon accumulation and reduce the forest's adaptive capacity.

In contrast, the agroforestry system showed a more evenly distributed DBH profile, with a strong presence of individuals in the 10-30 cm range. This distribution reflects ongoing regeneration and the coexistence of multiple growth forms, from juvenile shrubs to mature canopy trees. The presence of fast-growing and nitrogen-fixing species such as *L. leucocephala* enhances the occupation of lower DBH classes, promoting rapid canopy renewal and vertical complexity (Qiu et al. 2020). Such diversity contributes to

biomass turnover and improves resilience to disturbances, supporting long-term ecosystem stability and productivity (Chave et al. 2005; Ambarwati et al. 2019).

The rubber plantation exhibited a moderate DBH distribution, with peaks in the 21-40 cm classes. While *H. brasiliensis* dominated, the inclusion of species like *S. mahagoni* and *M. indica* introduced some variation. Regeneration was more apparent than in the pine forest but remained less dynamic than in agroforestry. The relatively narrow spread of DBH classes suggests limited structural plasticity, which could constrain the system's long-term ecological flexibility (Ferrini et al. 2020).

Overall, DBH class distribution offers a useful lens for assessing forest succession and regenerative capacity. Agroforestry's continuous diameter representation supports its role as a resilient, carbon-rich system, while monocultures like pine forests may benefit from targeted silvicultural interventions to enhance sustainability (Diana et al. 2022).

Correlation of number of individuals and diameter class

The distribution of individuals across diameter at breast height (DBH) classes provides important insights into forest population structure, regeneration status, and long-term sustainability. As shown in Figure 3, each land-use type displayed a distinct DBH pattern, reflecting differences in species composition, management intensity, and stand development. These structural differences influence how biomass is turned over and how carbon is stored or replenished over time. Therefore, DBH class analysis serves as a valuable indicator of ecosystem function, resilience, and future productivity.

In the pine forest, most individuals were concentrated in intermediate DBH classes, peaking at 31-40 cm, with few trees in the smallest class (10-20 cm). This indicates an even-aged structure likely established through a single planting cycle of *P. merkusii*, which dominates the canopy. The scarcity of younger individuals reflects weak regeneration, likely caused by dense canopy cover that restricts light and by allelopathic litter suppressing seedling growth (Han et al. 2019; Ferrini et al. 2020). Such a skewed structure is common in monocultures and signals low capacity for natural succession and long-term carbon continuity.

Conversely, the agroforestry system exhibited a classic inverse-J distribution, with a high number of individuals in the smallest DBH class, gradually declining across larger classes. This structure reflects continuous recruitment and a healthy, multi-aged population. The presence of fast-growing and nitrogen-fixing species like *L. leucocephala* ensures rapid early-stage biomass input while supporting long-term canopy renewal (Qiu et al. 2020; Diana et al. 2022). These conditions contribute to high resilience and sustained ecosystem productivity, positioning agroforestry as a structurally and functionally superior system.

The rubber plantation showed a relatively uniform DBH distribution, with a concentration in the 21-40 cm range, suggesting a synchronized planting history with limited regeneration. While some pole-sized individuals were present, mainly from interplanted species like *Swietenia mahagoni*, the overall structure lacked the recruitment

dynamics seen in agroforestry. This intermediate profile may support stable short-term carbon storage, but without enhanced diversity or undergrowth development, long-term sustainability could be compromised (Ambarwati et al. 2019).

DBH class patterns reveal key aspects of forest dynamics. Systems with continuous diameter distribution, like agroforestry, offer greater ecological stability and long-term carbon potential. At the same time, monocultures with limited size classes may require active intervention to support regeneration and carbon resilience (Poorter et al. 2017).

Structural contributions to biomass and carbon accumulation

Role of tree vs pole

Stratifying vegetation into tree (DBH>20 cm) and pole (DBH 10-20 cm) categories provides a valuable framework for assessing biomass accumulation across developmental stages. As shown in Table 5, the tree stratum consistently accounted for the majority of aboveground biomass and carbon stock across all land-use types. However, the relative contribution of the pole stratum varied widely among the sites, highlighting differences in structural complexity, regeneration potential, and vegetation dynamics. These stratification patterns offer important insights into the long-term sustainability of biomass and carbon storage in different systems.

In the pine forest, the pole stratum contributed only 13.44 MgB/ha, less than 10% of the total AGB, compared to 127.61 MgB/ha from the tree stratum. This imbalance reflects a structurally stagnant monoculture dominated by *P. merkusii*, where dense canopies, thick needle litter, and limited understory light prevent natural regeneration (Han et al. 2019). The near-absence of young individuals in lower strata indicates a discontinuity in biomass input, raising concerns about long-term carbon decline. Without interventions such as underplanting or thinning, the system is at risk of reduced productivity as mature trees age.

In contrast, the agroforestry system showed a much more balanced structure, with the pole stratum contributing 50.29 MgB/ha, approximately 29% of the total AGB. This robust lower layer reflects active recruitment and species turnover, supported by a diverse mix of fast-growing and nitrogen-fixing species like *L. leucocephala*, *G. gnemon*, and *P. speciosa* (Qiu et al. 2020; Diana et al. 2022). The structural layering enhances resilience and enables carbon continuity, ensuring that future canopy layers are already in development. Such dynamic systems maintain long-term biomass productivity and ecological stability.

The rubber plantation exhibited an intermediate pattern, with 41.80 MgB/ha (24% of total AGB) in the pole layer. While *H. brasiliensis* dominates the canopy, the presence of understorey species like *S. mahagoni* and *M. indica* adds structural depth and modest regeneration. Although more flexible than pine systems, its stratification is still less dynamic than agroforestry (Ambarwati et al. 2019).

Figure 2 visually confirms these differences, emphasizing the pole layer's ecological significance. Serving as both buffer and bridge, the pole stratum stabilizes current carbon

stocks while supporting future canopy development. Its presence is crucial for sustaining biomass continuity and resilience in multi-layered forest landscapes.

Impact of species composition and wood density

Species composition and wood density (ρ) are fundamental factors influencing aboveground biomass and carbon storage potential. Variations in these attributes across different land-use types significantly shape biomass structure and accumulation efficiency, as reflected in Table 5 and Figure 4. Wood density, in particular, is directly correlated with carbon content per unit volume, meaning that ecosystems dominated by high-density species tend to store more carbon over time (Chave et al. 2005). Therefore, both the diversity and functional traits of species present in a system play pivotal roles in determining its carbon sequestration capacity.

The agroforestry system demonstrated the highest AGB (175.42 MgB/ha) and carbon stock (82.46 MgC/ha), supported by its diverse species assemblage. It included fast-growing nitrogen-fixing legumes (*L. leucocephala*), fruit-bearing trees (*D. zibethinus*, *M. indica*), and high-density hardwoods like *T. grandis* and *S. mahagoni*. This combination allows for rapid biomass accumulation in early growth stages while ensuring long-term carbon stability due to the presence of dense, slow-growing species. The functional complementarity between species with differing growth rates and wood densities enhances both temporal and vertical occupation of space, leading to greater ecosystem productivity and resilience (Poorter et al. 2017; Diana et al. 2022).

By contrast, the pine forest, dominated by *Pinus merkusii*, exhibited a lower total AGB (141.05 MgB/ha) and carbon stock (66.29 MgC/ha). Despite some individuals reaching large sizes, the relatively low wood density of this softwood species limits its carbon storage efficiency. Furthermore, the system's structural uniformity and lack of understory diversity reduce the potential for complementary resource use, regeneration, and long-term carbon gain (Siregar 2007; Ferrini et al. 2020).

The rubber plantation presented an intermediate scenario. While *H. brasiliensis* contributes most of the biomass with its moderate wood density, the inclusion of species like *S. mahagoni* in the pole layer enhances density variation and structural heterogeneity. This results in a respectable AGB (173.21 MgB/ha) and carbon stock (81.41 MgC/ha), though still less dynamic than agroforestry in terms of ecological function.

Ultimately, systems with diverse species composition and a range of wood densities, such as agroforestry, offer greater carbon sequestration potential through both rapid initial accumulation and sustained long-term storage. In contrast, low-diversity monocultures lack these synergies, reducing their ecological efficiency under changing environmental conditions.

Stacked AGB and carbon stock per stratum

Figure 2 effectively visualizes the relative contributions of tree and pole strata to total aboveground biomass and carbon stock through stacked bar charts for each land-use

type. These graphics complement the numerical data in Table 2, offering a clear comparison of vertical biomass distribution. By distinguishing the contributions of each stratum, the figure highlights differences in structural complexity, regeneration dynamics, and carbon storage efficiency among systems. This visual approach is particularly helpful in conveying ecological patterns that may not be immediately evident from tabular data alone.

In the pine forest, the chart clearly shows the overwhelming dominance of the tree stratum, with the pole layer forming only a minor component. This top-heavy structure reflects the homogeneity of the *P. merkusii* monoculture, where dense canopy cover and low understory light limit the development of lower vegetation layers. While such stands can accumulate significant biomass early in their growth cycle, the lack of regeneration diminishes long-term carbon sustainability (Han et al. 2019; Ferrini et al. 2020). Over time, this structural limitation reduces resilience as the forest becomes increasingly dependent on aging canopy trees.

The agroforestry system, in contrast, presents a more balanced vertical structure, as seen in the near-proportional stacking of tree and pole biomass in Figure 2. With 125.13 MgB/ha in trees and 50.29 MgB/ha in poles (Table 2), the system supports continuous recruitment and multi-aged stand development. This configuration promotes long-term carbon storage through sustained turnover and supports ecosystem functions such as nutrient cycling and biodiversity conservation (Chave et al. 2005; Qiu et al. 2020). The visual harmony between strata underscores the structural efficiency and ecological value of agroforestry systems.

The rubber plantation falls between the two extremes. Although dominated by *H. brasiliensis* with 131.41 MgB/ha in the tree stratum, the pole layer contributes a notable 41.80 MgB/ha, forming a visible secondary tier in the chart. The presence of shade species like *S. mahagoni* enhances vertical complexity and suggests moderate regenerative activity (Ambarwati et al. 2019). Overall, Figure 2 visually affirms that systems with more evenly stratified biomass, such as agroforestry, tend to be more productive, adaptive, and carbon-efficient.

Physiological interpretation and ecological implications

Relationship between DBH, tree age, plant type, and carbon stock

Diameter at breast height (DBH) is a widely used structural indicator in forest ecology, closely linked to aboveground biomass and carbon stock accumulation. As shown in Table 2 and calculated using the species-specific allometric models in Table 1, DBH is a key variable in estimating tree biomass due to its strong correlation with stem volume and woody tissue density. This non-linear relationship means that larger DBH values often translate into disproportionately higher carbon content, though wood density also plays a significant role (Chave et al. 2005). Evaluating DBH distribution across land-use types thus offers insight into stand development, regeneration dynamics, and carbon sequestration potential.

In the pine forest, large DBH values were primarily associated with *P. merkusii*, a fast-growing species with tall, slender stems. Although these trees contribute significantly to total biomass due to their size, their softwood characteristics result in lower carbon density per unit volume (Siregar 2007). The narrow DBH distribution and limited presence of smaller stems suggest minimal recruitment, highlighting a structurally stagnant stand dominated by a single cohort. This uniformity reduces both structural resilience and long-term carbon continuity.

By contrast, the agroforestry system exhibited a wide distribution of DBH classes, indicating active regeneration and species turnover. Lower DBH classes included fast-growing pioneers such as *L. leucocephala* and *G. gnemon*, while high-density hardwoods like *T. grandis* and *S. mahagoni* occupied the upper classes. This diversity reflects functional complementarity among species, allowing the system to capture carbon quickly in the early stages while maintaining long-term carbon reserves in slower-growing, dense-wood trees (Poorter et al. 2017; Diana et al. 2022). Such multi-stage development supports greater ecosystem productivity and stability.

In the rubber plantation, *H. brasiliensis* was dominant in the middle DBH classes, offering steady biomass contribution but limited structural variation. While interplanted species such as *S. mahagoni* provide some enrichment, the overall functional diversity is lower than in agroforestry (Ambarwati et al. 2019). As a result, the system performs well in current carbon storage but lacks the regenerative layering needed for long-term sequestration.

These findings emphasize the combined importance of DBH, species identity, and wood density in determining carbon storage. Agroforestry's integration of diverse DBH classes and wood densities explains its superior carbon accumulation, as reflected in Table 3 and Figure 3.

Physiological influences: Stomata, canopy density, and productivity

Structural parameters such as DBH, height, and biomass are physical manifestations of underlying physiological traits, particularly those associated with canopy architecture, stomatal regulation, and photosynthetic capacity. These physiological mechanisms influence how vegetation captures light, regulates water loss, and absorbs nutrients, ultimately shaping aboveground biomass accumulation and carbon storage across different land-use systems. Differences in carbon sequestration performance among the sites studied can be attributed to how effectively each system converts environmental resources into plant biomass through these physiological pathways. Consequently, evaluating structure offers a window into the functional performance of each vegetation type.

Among the three land-use systems, the agroforestry site exhibited the highest total AGB and carbon stock, as supported by Table 3 and Figure 3. This result reflects the system's multi-layered canopy and species diversity, which enhance vertical light distribution and minimize shading redundancy. Trees with varying heights and crown shapes such as *L. leucocephala*, *S. mahagoni*, and *M. indica* optimize the use of solar radiation across the vertical

profile. Such vertical stratification allows for more sustained photosynthesis and biomass accumulation throughout different canopy layers (Poorter et al. 2017; Ferrini et al. 2020).

Physiologically active species in agroforestry, including *L. leucocephala*, *P. speciosa*, and *G. gnemon*, are known for high stomatal density and transpiration rates. These characteristics promote efficient carbon assimilation and nutrient cycling, especially under favorable moisture conditions. Their presence in the pole stratum supports rapid turnover and regeneration, allowing the system to maintain productivity and carbon input across successional stages (Qiu et al. 2020; Diana et al. 2022). This physiological dynamism is key to the resilience of agroforestry under fluctuating environmental conditions.

In contrast, the pine forest dominated by *P. merkusii* is characterized by a closed, coniferous canopy with low stomatal conductance. Although efficient under water-limited conditions, this conservative strategy limits long-term carbon gain and regeneration. The dense needle-leaf canopy also blocks light from reaching lower strata, suppressing understory growth and physiological activity (Han et al. 2019). This explains the low pole biomass and stagnant productivity observed in Table 2 and Figure 2.

The rubber plantation represents an intermediate case, where *H. brasiliensis* shows moderate stomatal behavior and an open crown. While this supports steady carbon assimilation, the plantation lacks the physiological and structural diversity needed for high ecological resilience (Ambarwati et al. 2019). Overall, the synergy of structural complexity and physiological variation in agroforestry provides superior conditions for efficient and sustained carbon sequestration.

Land-use management and carbon sequestration potential

Agroforestry as the highest carbon absorption system

The findings of this study highlight the superior carbon sequestration performance of agroforestry systems, reinforcing their relevance for sustainable land-use planning and climate change mitigation. As indicated in Table 3, the agroforestry area recorded the highest total aboveground biomass (175.42 MgB/ha) and carbon stock (82.46 MgC/ha) among the three land-use types. These values surpass those of the rubber plantation (81.41 MgC/ha) and pine forest (66.29 MgC/ha), with Figure 3 clearly showing agroforestry's dominant position in carbon accumulation. Such outcomes underscore the ecological and functional advantages of structurally diverse vegetation systems.

These results can be directly attributed to the structural and compositional characteristics of agroforestry. The presence of multiple canopy layers, species diversity, and nitrogen-fixing plants such as *L. leucocephala* enhances nutrient cycling, improves soil fertility, and supports continuous biomass input from various growth stages (Qiu et al. 2020; Diana et al. 2022). This diversity of form and function contributes to stable and efficient carbon assimilation, making agroforestry systems more resilient to disturbances such as drought, pests, or harvesting events.

The system's regenerative potential is particularly important for maintaining long-term carbon stocks.

Unlike monocultures, which are typically uniform in age and canopy structure, agroforestry integrates trees, poles, shrubs, and herbaceous species in complementary arrangements. This spatial and functional integration increases light interception, root overlap, and water-use efficiency, resulting in higher total productivity and carbon gain (Chave et al. 2005; Poorter et al. 2017; Ferrini et al. 2020). Agroforestry's heterogeneity also supports biodiversity and enhances ecological resilience, contributing to its multi-functional value.

Beyond carbon storage, agroforestry systems offer co-benefits, including biodiversity conservation, livelihood diversification, and improved soil health. These characteristics make agroforestry a strategic land-use model for community-based forest management and national carbon offset initiatives. As Ambarwati et al. (2019) suggest, well-managed agroforestry systems can rival natural forests in ecological productivity and sustainability.

However, the widespread adoption of agroforestry as a carbon mitigation strategy requires supportive institutions, targeted training, and incentive-based policy frameworks. Integrating agroforestry into climate-smart initiatives such as REDD+ and Payment for Ecosystem Services (PES) could enhance its value within carbon markets and rural development agendas (Diana et al. 2022). From a management perspective, prioritizing agroforestry in landscape restoration programs could yield dual benefits: restoring degraded lands and stabilizing carbon stocks through structurally and functionally complex vegetation systems.

Recommendations for heterogeneous vegetation management

The findings of this study reaffirm the critical role of vegetation heterogeneity, most clearly exemplified in the agroforestry system, as a primary driver of aboveground biomass accumulation and long-term carbon storage. Systems characterized by diverse species compositions, layered vertical structures, and functional complementarity consistently outperform homogeneous plantations in carbon sequestration capacity. The stratified biomass and carbon data presented in Table 2, alongside total site comparisons in Table 3, demonstrate that structurally complex vegetation supports more effective carbon capture. Visual evidence from Figure 2 reinforces this, showing balanced contributions from both tree and pole strata in agroforestry, while monoculture systems like pine forests rely heavily on a single dominant layer. This highlights the importance of designing and managing landscapes with vertical complexity and species interactions in mind.

To maintain and enhance such beneficial heterogeneity, several strategic recommendations can be proposed. First, the integration of mixed-species planting schemes should be encouraged, combining fast-growing pioneers, nitrogen-fixing legumes, and high-density timber species such as *L. leucocephala*, *S. mahagoni*, and *T. grandis*. This combination balances rapid early-stage biomass accumulation with long-term carbon stability. Second, functional layering must be maintained, ensuring that tree, pole, and understory strata remain active. Over-pruning or canopy homogenization

should be avoided, as diverse vertical layers enhance light use efficiency and support natural regeneration processes. Third, the role of the pole stratum must be recognized and protected. As shown in this study, poles contribute significantly to biomass and act as a buffer for future carbon input, yet they are often underrepresented in forest inventories and management practices.

Furthermore, successful system design should be guided by ecological succession, allowing for a gradual transition from early-successional species to structurally and functionally dominant late-successional trees. Management should also be adapted to site-specific landscape contexts, taking into account variables such as slope, soil fertility, and local biodiversity. These factors influence both structural development and carbon dynamics. From a policy perspective, incorporating carbon stock and vegetation structure into land-use regulations can support more informed and targeted investment, especially within REDD+ and climate-smart agriculture initiatives. Finally, agroforestry should be promoted as a leading model for carbon-smart landscapes. Its demonstrated performance in carbon stock, vertical integration, and resilience makes it ideal for rehabilitation efforts, particularly in upland tropical regions. Through these measures, land managers and policymakers can foster multi-functional systems that deliver both ecological restoration and climate mitigation benefits.

In conclusion, this study demonstrated that land-use systems with greater structural and species heterogeneity, particularly agroforestry, are more effective in accumulating aboveground biomass and sequestering carbon than monoculture plantations. Among the three evaluated land-use types in Ngargoyoso Sub-district, agroforestry recorded the highest total biomass (175.42 MgB/ha) and carbon stock (82.46 MgC/ha), followed by rubber plantation and pine forest. This superior performance is attributed to its multi-strata structure, functional species diversity, and balanced contributions from both tree and pole strata. Vegetation characteristics such as DBH, wood density, and vertical stratification were found to be closely associated with physiological processes, including photosynthesis, canopy efficiency, and regeneration potential. Systems dominated by single-aged or softwood species, like *Pinus merkusii*, accumulated less carbon and showed lower regenerative capacity, whereas systems integrating fast-growing pioneers and dense hardwoods showed sustained carbon accumulation and structural renewal. Stacked biomass data and DBH class distributions revealed that pole strata play a critical role in maintaining carbon continuity, especially in heterogeneous systems. Furthermore, species composition influenced not only total biomass but also the ecological resilience and adaptability of the system to long-term environmental change. The findings highlight agroforestry as a promising land-use model for integrated carbon management and biodiversity conservation. Promoting structurally diverse vegetation through informed management strategies can enhance carbon sequestration, ecosystem services, and landscape resilience in tropical upland regions. These insights are essential for shaping effective

climate-smart land-use policies and sustainable forest development programs.

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