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Original Article

Effects of Species Diversity on the Aboveground Biomass of *Acacia mangium* in a Mixed-Species Forest Stand in Thach That, Hanoi

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Abstract: Mixed-species plantations are considered as a pathway to sustainable forest management due to potential gains in productivity and ecosystem services compared with monocultures. Evidence on the relationship between species diversity and biomass in tropical plantations - particularly for crops such as *Acacia mangium* (*A. mangium*) - remains limited. This study tests the hypothesis that aboveground biomass (AGB) of *A. mangium* increases with forest species diversity. Data were collected in a 1-ha Marteloscope plot in Thach That (Hanoi), comprising 916 trees from 14 species. AGB was estimated using species-specific allometric equations; species diversity was characterized using the Shannon, Simpson, Berger–Parker, and evenness indices. Regression analyses employed three model forms (additive, exponential, and multiplicative) and were evaluated with AIC, BIC, R^2, and MSE. The exponential model provided the best representation of the relationships among variables. Notably, the effects of species diversity on biomass were nonlinear and heterogeneous, depending on model specification, some diversity indices tended to show negative associations with individual-tree biomass. The study underscores the importance of model-form selection when analyzing the diversity–biomass relationships and suggests expanding the Marteloscope network and integrating remote-sensing data to enable upscaling and to support evidence-based management of mixed-species plantations.

Keywords: Mixed plantation, Marteloscope, tree diversity, aboveground biomass, diversity–productivity relationship.

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1. Introduction

Forest biomass plays a crucial role in sequestering atmospheric carbon through the photosynthetic activity of plants, whereby carbon is fixed and stored in leaves, stems, branches, and roots, thus contributing to the regulation of the natural carbon cycle and the reduction of atmospheric CO_2 concentrations, which are among the main drivers of global warming and the greenhouse effect [1]. The protection and development of forests, particularly the enhancement of forest biomass, therefore have not only ecological significance but also provide an important contribution to climate change mitigation.

In Vietnam, most plantation forests are currently monocultures established with a single tree species to simplify management and maintenance, but recent trends are shifting toward mixed-species plantations in which two or more species grow together within the same stand [2]. This model aims to utilize resources such as space, light, and nutrients more efficiently, thereby potentially improving productivity and enhancing the ecological stability of plantations.

Over the past two decades, numerous studies examining the relationship between species diversity and ecosystem functioning have particularly emphasized the link between productivity and species richness [3, 4]. This relationship can be explained by the complementarity effect in resource utilization, whereby different tree species in mixed stands can exploit water, nutrients, and light in mutually supportive ways [5]. Essentially, each species has specific requirements or distinct mechanisms of resource uptake, enabling them to coexist and use resources more efficiently than monocultures. The interaction between biodiversity and the carbon cycle is considered a critical factor in mitigating the damages and losses caused by climate change, while also buffering against fluctuations in natural ecosystems [6, 7].

Numerous studies over the past two decades have documented a strong positive relationship between tree species richness and forest productivity (e.g., basal area growth, biomass accumulation, or volume increment) across diverse forest types worldwide. In the U.S. Pacific Northwest, greater species richness in conifer stands was associated with higher net basal area growth, largely driven by increased tree recruitment [8]. Large-scale forest inventories in the United States and Germany similarly showed that more diverse stands consistently produced greater wood volume per hectare across regions and forest types [9]. In subtropical China, a large-scale BEF experiment demonstrated that species-rich mixtures more than doubled aboveground carbon compared with average monocultures, with functional and phylogenetic diversity further amplifying productivity gains [4].

Tree species diversity in production forests has also been shown to positively influence multiple ecosystem services. For example, Gamfeldt et al. (2013) demonstrated that mixed-species forests containing five tree species can produce up to 50% more biomass than monocultures. Moreover, the negative effects of biodiversity loss on forest productivity further highlight the superior potential of mixed-species stands compared to monocultures [11]. However, some studies have reported neutral or even negative relationships between aboveground biomass and species diversity [13-15].

In Vietnam, research on the relationship between tree species diversity and forest productivity remains limited, particularly for widely cultivated species such as *Acacia mangium* (*A. mangium*). This study provides a scientific basis for the development of sustainable plantation models, thereby enhancing socio-economic efficiency, protecting the environment, and contributing to sustainable development at both local and national scales.

2. Materials and Methods

2.1. Study Site

The research focused on assessing the influence of tree species diversity on the biomass of *A. mangium* within a Marteloscope permanent sample plot established in a mixed-species plantation forest without any silvicultural management interventions. The study site is located in Thach That commune, within the Hoa Lac Campus of Vietnam National University, Hanoi - approximately 40 km west of the city center. The elevation of the study area ranges from 150 to 300 m above sea level, and the terrain is gently dissected with multiple sloping surfaces.

One Marteloscope permanent sample plot was established under the framework of the BioEcon Project (https://bioecon.eu/), following the installation protocol of the BioEcon Project [15]. The Martelocospe encompasses an area of 1 hectare and is subdivided into a grid of 16 quadrats (Figure 1). Within each quadrats, spatial coordinates (x, y), total tree height (Ht), and diameter at breast height (dbh) at 1.3 m above ground level were recorded for all trees with dbh greater than 5 cm. Species identification was conducted in the field using an expert-based approach, with taxonomic verification conducted by forest ecology and botany specialists. All field measurements were conducted in 2021.

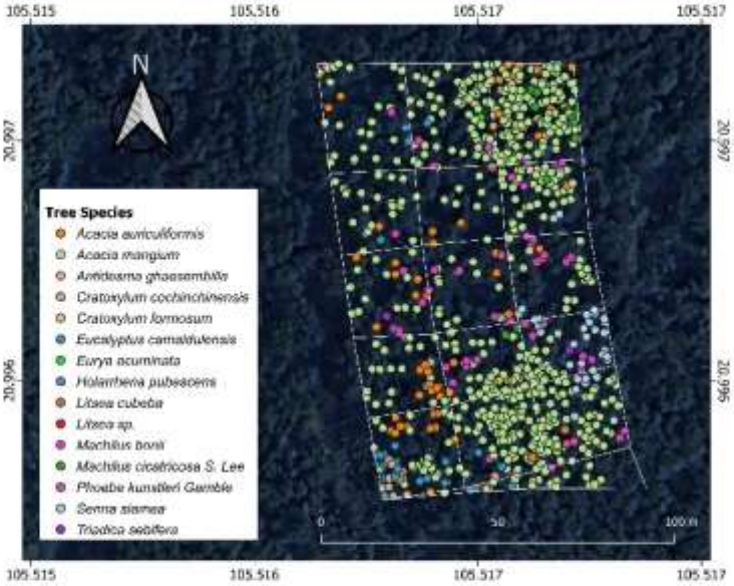

Figure 1. Study area (20°59′48.11″N, 105°30′59.78″E).

A total of 916 individual trees were recorded within the Marteloscope and 14 species were identified, namely *Acacia mangium*, *Acacia auriculiformis*, *Antidesma ghaesembilla*, *Cratoxylum cochinchinense*, *Cratoxylum formosum*, *Eucalyptus camaldulensis*, *Eurya acuminata*, *Holarrhena pubescens*, *Litsea cubeba*, *Litsea* sp., *Machilus bonii*, *Machilus cicatricosa* S. Lee, *Phoebe kunstleri* Gamble, *Senna siamea*, and *Triadica sebifera*.

Aboveground tree biomass (AGB) was estimated using allometric equations incorporating variables including dbh and h. Previous studies have demonstrated that combining both diameter and height improves the accuracy of biomass estimation [16]. A three-step strategy guided the selection of appropriate allometric equations: i) Priority was given to equations developed for the same tree species under environmental conditions comparable to those of the study area; ii) Next, preference was given to equations constructed for ecological regions that encompass the study area; and iii) When species- or region-specific allometric equations were unavailable, equations developed for forest types with comparable ecological characteristics in the study area were applied. The precision of biomass estimation depends strongly on the quality and ecological relevance of the selected allometric equations. Biomass values in this study were therefore calculated using the equations listed in Table 1. Only species for which species-specific allometric equations were available are listed individually in Table 1. For the remaining species, biomass was calculated using allometric models developed for ecologically and morphologically similar functional groups when species-level equations were not available.

Table 1. Allometric Equations adopted for biomass calculation

Species	Allometric equation	R^2	Expected value of error (%)
Acacia auriculiformis [17]	$AGB = -2.1737 + 0.5109(0.1911\ dbh^{1.9710}\ h^{0.5391})$	0.95	
Acacia mangium [18]	$AGB = e^{-1.073+2.081\,ln(dbh)}$	0.97	
Eucalyptus camaldulensis [19]	$AGB = 0.035(\ dbh^2\ h)^{0.953}$	0.982	
Litsea sp. [20]	$AGB = 0.0547\ dbh^{2.4451}\ h^{0.6131}$		-0.5614
Other species *[21]*	$AGB = e^{-3.1141+0.9719\,ln(dbh^2\ h)}$	0.97	
AGB: Aboveground tree biomass (kg), dbh: diameter at breast height (cm); h: total height (m)			

2.2. Species Diversity and Stand Structure

A set of biodiversity indices was applied to quantify species diversity, relative dominance, and evenness in species distribution within the forest stand. The indices included Simpson's Diversity Index, Shannon's Diversity Index, the Berger–Parker Index, and the Evenness Index.

Simpson's Diversity is a dominance-weighted measure that emphasizes the abundance of the most common species rather than total species richness. The index represents the probability that two individuals randomly selected from a community belong to different species. This index value range from 0 to 1. Higher values indicate greater diversity, whereas values close to 0 indicate low diversity and strong dominance by a few species. Simpson's index is calculated as follows [22]:

$$1 - D = 1 - \frac{\sum_{i=1}^{R} n_i(n_i - 1)}{N(N-1)}$$

where:

- n_i is number of individuals of species i;
- N is total number of individuals of all species;
- R is total number of species.

Shannon's Diversity Index measures diversity by accounting for both species richness and the relative abundance of each species. The index reflects how evenly individuals are distributed across the species present in the community. The value of the index ranges from 0 to $ln(S)$. The index increases with a higher number of species and a more even distribution of individuals. Shannon's index was calculated as follows [23]:

$$H' = -\sum_{p_i}^{s} p_i \ln(p_i)$$

where:

- S is total number of species;
- $p_i = n_i/N$ as relative abundance of species i;
- R is total number of species.

The Berger–Parker Index [24] quantifies species dominance by focusing on the relative abundance of the most common species. The index is given by:

$$D = \frac{N_{max}}{N}$$

where:

- N_{max} is the number of individuals in the most abundant species;

- N is the total number of individuals in the stand;

- A higher index value reflects stronger dominance by a single species and lower overall diversity. The reciprocal $(1/D)$ is sometimes used to illustrate increasing diversity as dominance declines.

The Evenness Index [25] measures the degree to which individuals are evenly distributed among the species within a community. The index is calculated based on the Shannon diversity value and expresses how close the observed diversity is to the maximum possible diversity under a perfectly even distribution. Values range from 0 to 1, where values closer to 1 indicate a more uniform distribution of individuals among species, whereas lower values suggest dominance by one or a few species. The index is computed as:

$$E = \frac{H'}{ln\,S}$$

where:

- H$'$ is the number derived from the Shannon index;

- S is total number of species.

To complement species diversity metrics, additional stand structural variables at quadrats-level were also quantified for use as explanatory factors. Basal area and tree density were selected due to their relevance to stand structure, growing space, and competition dynamics.

Basal area (Gi) was defined as the cross-sectional area of a tree stem at breast height (1.3 m) and calculated as: $G_i = \pi \times \left(\frac{DBH_i}{2}\right)^2$. Plot-level basal area (G) were reported as m² per quadrat and, when required for comparability across stands, were expressed on a per-hectare basis through area standardization.

Tree density per hectare (N) was determined by multiplying the number of trees recorded within the plot (n) by the expansion factor, calculated as the ratio of one hectare to the quadrat area (A): $N = n \times \frac{10000}{A}$

2.3. Data Analysis: Model Selection and Evaluation

To reduce the influence of multicollinearity during model construction, a correlation matrix of the explanatory variables was examined in Rstudio [26]. Only variable pairs with a Pearson correlation coefficient between −0.5 and 0.5 were allowed to appear together in the same model. This pre-filtering step ensured statistical robustness and prevented redundant predictors from being combined in downstream analyses.

Table 2. General model forms

Model type	Model structure
Additive	$AGB = \beta_0 + \sum_{i=1}^{n} \beta_i X_i + \varepsilon$ (Eq.1)
Exponential	$AGB = e^{\beta_0 + \sum_{i=1}^{n} \beta_i X_i} + \varepsilon$ (Eq.2)
Multiplicative	$AGB = \beta_0 {X_1}^{\beta_1} \ldots {X_n}^{\beta_n} + \varepsilon$ (Eq.3)

The effects of stand structure and species diversity on the AGB of *A. mangium* were evaluated using three general model forms including i) additive model; ii) exponential model; and iii) multiplicative model (Table 2). The additive form captures linear and independent effects of stand or diversity variables. The exponential form reflects nonlinear biomass responses, where small shifts in predictors can lead to disproportionate changes in growth. The multiplicative form represents interaction-driven dynamics, allowing combined effects of predictors to emerge. These formulations were chosen to account for linear, nonlinear and interaction-based relationships between stand attributes and AGB, while retaining ecological interpretability. Across all model forms, β_i denotes the estimated coefficient of explainator X_i, and ε represents the residual error.

All three model forms were independently fitted using all possible combinations of explanatory variables, including single-, two-, and three-explainator configurations. These combinations reflected both structural attributes and diversity indices, analysed individually and jointly to facilitate comparative assessment across different ecological dimensions. Log-transformations were applied to Eq.2 and Eq.3 to improve linearity, stabilise variance, and satisfy regression assumptions. A complete list of the tested model equations and variable combinations is provided in Supplementary 1.

The statistical significance of individual predictors was assessed using p-values (Pr(>|t|)), derived from the Student's t-distribution. Lower p-values indicated stronger evidence that the corresponding coefficients contributed meaningfully to the variance in AGB. A threshold of $p < 0.05$ was used to identify statistically significant effects.

Model performance was evaluated using four indicators: Akaike's Information Criterion (AIC), Bayesian Information Criterion (BIC), the coefficient of determination (R^2), and mean square error (MSE). AIC was used as the primary selection criterion because it balances goodness-of-fit and model parsimony by penalising unnecessary parameters, thereby reducing the risk of overfitting. R^2 was considered supportive but not decisive, as it often increases with additional predictors regardless of their contribution. BIC was used as a secondary indicator due to its stronger penalty on model complexity, and MSE complemented the evaluation by reflecting predictive accuracy. The model with the lowest AIC value was retained as the best-performing option, with the remaining criteria used for confirmation.

3. Results

3.1. Stand Diversity

The Marteloscope stored a total AGB of 119,520.64 kg, equivalent to 119.52 tons (Table 4). *A. mangium* was the dominant species in the Marteloscope, accounting for 68.45% of all recorded trees (627 individuals), followed by *Acacia auriculiformis* with 61 individuals, representing 6.66% of the total (Supplementary 2).

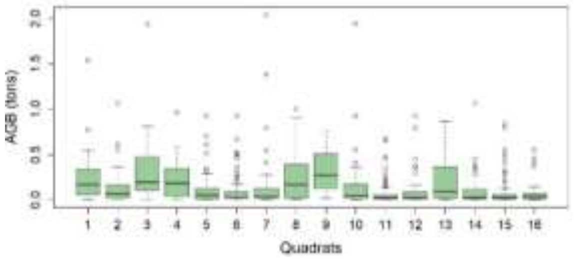

Figure 2. Aboveground biomass across quadrats.

The distribution of AGB varied across the sixteen quadrats (Figure 2). Although most quadrats exhibited relatively low median values, the degree of dispersion and the occurrence of outliers differed clearly. Quadrats 3, 4, 8, 9, and 13 showed higher median AGB and wider interquartile ranges, indicating the presence of larger trees or greater structural heterogeneity. Several outliers in these quadrats exceeded 1.0 tons, reflecting trees with disproportionately high biomass.

In contrast, quadrats 1, 2, 6, 7, 10, 11, and 16 displayed lower medians, mostly below 0.2 tons, and narrower distributions, suggesting a more uniform stand structure with smaller individuals. The remaining quadrats (5, 12, 14, and 15) occupied an intermediate position, with moderate variability and occasional high-biomass trees. Overall, the pattern indicates that AGB is not evenly distributed throughout the Marteloscope but is instead concentrated in a subset of quadrats where size structure or species composition may enhance biomass accumulation.

The diversity indices also revealed differences among quadrats (Figure 3). The Shannon index ranged from approximately 2.5 to over 4.5, with a median near 4.0, reflecting generally high richness and balanced species representation. The Simpson index showed consistently high diversity (median ≈ 0.97), with only a few quadrats dropping below 0.94.

Evenness values clustered tightly between 0.88 and 0.96, indicating uniform distribution of individuals among species in most quadrats. The Berger–Parker index exhibited greater variation: while most values ranged from 1.3 to 1.6, several quadrats presented higher outliers, suggesting localized dominance by particular species. Collectively, the indices indicate structurally diverse but not uniformly distributed stands, with occasional patches of species dominance.

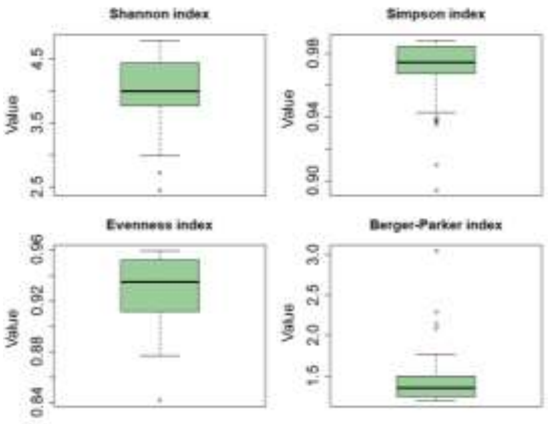

Figure 2. Stand-level diversity indices.

3.2. Model Selection And Evaluation

The correlation matrix (Figure 3) revealed several strongly correlated variable pairs that were avoided in the same model to prevent multicollinearity: G–N, G–Sh, G–Sm, N–Sh, N–Sm, Sh–Sm, Sh–E, and Sm–E. Since the correlation coefficients of these pairs were outside the −0.5 to 0.5 range, the corresponding variables were not combined within any single candidate model. In contrast, weak or negligible correlations such as E–D indicated that these variables could be used together without concern for collinearity.

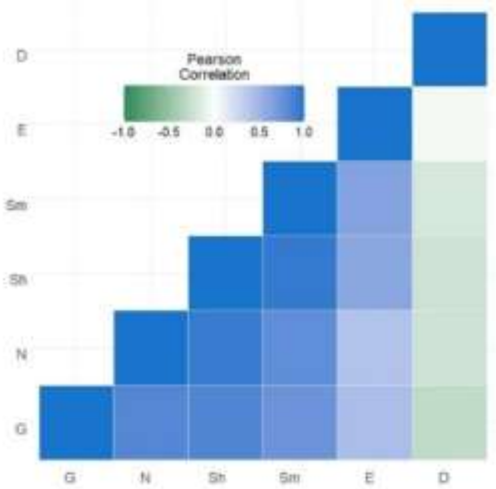

Figure 3. Pearson’s correlation matrix between AGB and input variables.

Only regression models that satisfied the fundamental statistical assumptions, including homogeneity of variance, normality, linearity, and absence of autocorrelation, and demonstrated acceptable goodness of fit were retained for analysis. Across all selected models, representing three groups based on the number of variables (single-, two-, and three-variable regressions), the explanatory power was relatively low ($R^2 < 0.15$), indicating weak predictive strength (Table 3). However low R^2 values are acceptable in this context because the primary aim was not to precisely predict tree-level biomass, but to identify and interpret underlying ecological relationships.

Table 3. Selected models

Number of explainators	Model structure		R^2	AIC
Single-variable model	$AGB = e^{\left(2.63+46.03\frac{1}{\sqrt{N}}\right)}$	(Eq.4)	0.1219	2055.153
Two-variable model	$AGB = e^{\left(4.78-1.35\times10^{-7}N^2-0.6968\frac{1}{D^2}\right)}$	(Eq.5)	0.0807	2085.893
Three-variable model	$AGB = e^{\left(13.20+6.70\frac{1}{G}-10.71\sqrt{E}+0.73\sqrt{D}\right)}$	(Eq.6)	0.0360	2117.636

Considering single-variable model (Eq.4), the positive coefficient of $1/\sqrt{N}$ indicated that per-tree biomass increases as stand density decreases, reflecting reduced competition for limited resources. This trend is visually reflected in Figure 4, where observed AGB declines with increasing stand density and the model captures the overall trajectory despite substantial variability at low densities. Recent studies confirmed this density–biomass trade-off in both natural and planted forests, where lower density enhances light capture and soil water availability, thereby improving individual growth [27]. Meta-analytical evidence also indicated that trees respond to density stress primarily through changes in crown development rather than organ-level biomass allocation, reinforcing this interpretation [28]. Although the model accounts for only about 12% of AGB variation, its explanatory power is meaningful in demonstrating a consistent ecological mechanism.

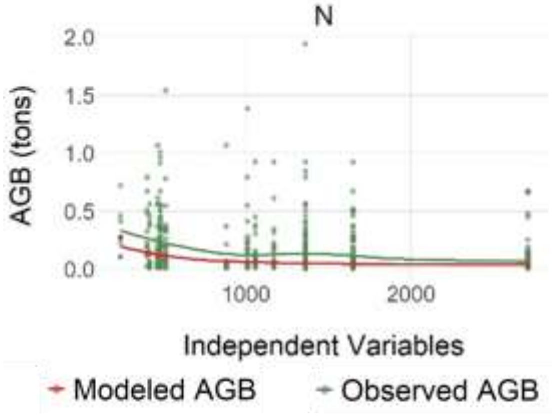

Figure 4. Modeled AGB vs Observed AGB of Eq.4.

The two-variable model (Eq.5) showed that per-tree biomass declines as stand density (N^2) increases and as species dominance intensifies ($1/D^2$), indicating that both competition and reduced diversity limit individual growth. Dense stands restrict access to light, water, and nutrients, while dominance by a few species reduces resource complementarity. Empirical studies have shown that biodiversity can enhance productivity through functional complementarity, although the effect depends on stand conditions [30, 31]. This trend is visible in Figure 5, where modeled values follow the decline in observed AGB despite considerable variability.

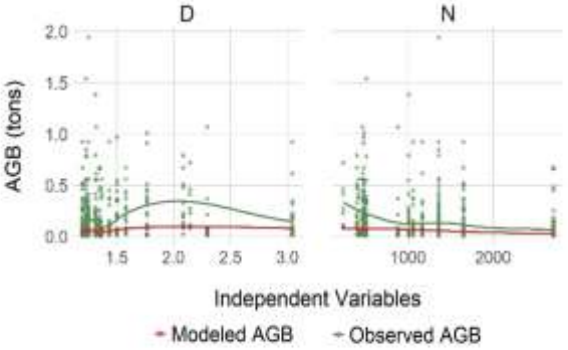

Figure 5. Modeled AGB vs Observed AGB of Eq.5.

The three-variable model (Eq.6) identified stand basal area (1/G), species evenness ($\sqrt{E}$), and dominance ($\sqrt{D}$) as significant predictors of AGB at the individual-tree level. The positive coefficient of 1/G indicates that trees located in quadrats with lower total basal area tend to accumulate more biomass, suggesting that reduced stand packing allows individuals greater access to growing space and below/aboveground resources. In contrast, $\sqrt{E}$ showed a significant negative association with biomass, implying that higher evenness does not necessarily favour individual growth in this plantation system. The coefficient of $\sqrt{D}$ was positive but comparatively small, suggesting that increasing species dominance has a modest but detectable effect on enhancing biomass at the tree level. These patterns are reflected in Figure 6, where modeled values track the observed variation in AGB across gradients of basal area, evenness, and dominance, despite substantial scatter in the field data.

The convergence of all three selected models on an exponential functional form is ecologically meaningful. Biomass allocation in trees is inherently nonlinear, shaped by asymmetric competition, allometric scaling, and resource limitation. Exponential and log-linear structures are well established in forest ecology because they capture non-proportional changes in biomass under varying stand densities and species compositions [31]. The persistence of this form across one-, two-, and three-variable models suggests that AGB scales multiplicatively rather than additively with ecological drivers, consistent with self-thinning theory and classical allometric growth laws [32]. Methodologically, this convergence indicates that exponential formulations best balance fit and biological realism, reinforcing their value for modelling biomass–diversity–density relationships in both mixed and plantation forests.

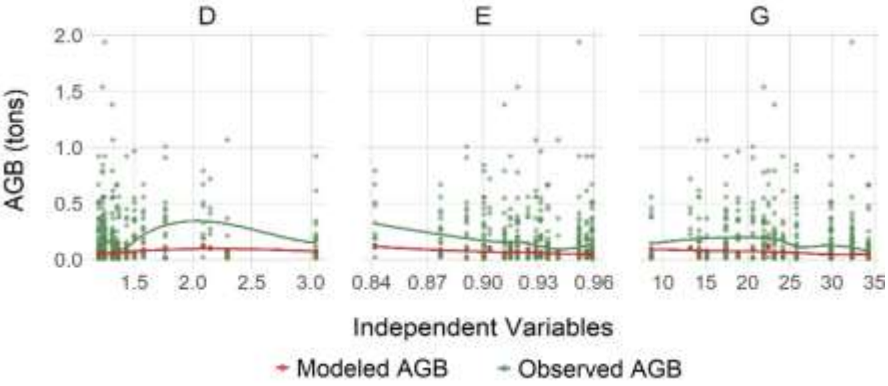

Figure 6. Modeled AGB vs Observed AGB of Eq.6.

Our findings highlight that stand density and basal area are central drivers of individual-tree biomass, suggesting clear silvicultural implications. The positive effects of lower density indicate that thinning to maintain moderate stocking can enhance tree growth by reducing competition for light and soil resources. The negative influence of species evenness and the modest positive role of dominance imply that in this plantation system, productivity is strongly linked to the prevalence of fast-growing species such as *A. mangium*. While monocultures of competitive species may maximise biomass and timber yield, they do so at the cost of reduced diversity, a trade-off that has implications for ecosystem resilience, nutrient cycling, and long-term sustainability. Thus, forest management must balance short-term biomass gains with broader ecosystem services.

At the same time, several limitations should be acknowledged. This study is based on a single plot in northern Vietnam, which constrains the generalisation of results to other sites with different soils, climates, or management histories. The relatively low explanatory power of the models ($R^2 < 0.15$) indicates that other factors, such as soil fertility, water availability, and legacy management practices. likely play important roles in shaping biomass. Moreover, conventional indices like evenness or dominance might not fully capture functional trait diversity that influences competition and growth. Future research should therefore expand to multiple sites, integrate environmental variables and functional traits, and combine ground data with remote sensing approaches (e.g., LiDAR) to improve model accuracy and applicability. In follow-up studies, increment coring will be used to validate stand-age estimates and help disentangle age effects from structural and diversity influences when interpreting AGB patterns.

4. Conclusion

- AGB in Acacia plantations is influenced by stand density and species composition. High density suppresses per-tree growth through competition, while high evenness reduces biomass in functionally similar stands.

- This creates a trade-off: monocultures or low-diversity stands can maximize productivity and carbon storage, but at the expense of biodiversity and resilience.

- From a management perspective, careful thinning and balanced species mixtures are essential to optimize yield, carbon sequestration, and long-term ecosystem stability.

- Future research should extend across plantation types and environments, and include functional trait diversity, to develop sustainable silvicultural strategies that reconcile productivity with biodiversity conservation.

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