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Height-based biomass models differ for naturally regenerated and planted young trees

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ABSTRACT

This study investigated biomass allocation in young stands of European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.) across 31 forest sites in the Western Carpathians, Slovakia. A total of 541 trees aged 2–10 years, originating from natural regeneration and planting, were destructively sampled to quantify biomass in four components: foliage, branches, stems, and roots. Generalized non-linear least squares (GNLS) models with a weighing variance function outperformed log-transformed seemingly unrelated regression (SUR) models in terms of accuracy and robustness, especially for foliage and branch biomass. When using height as the predictor, SUR models tended to underestimate biomass in planted beech, leading to notable underprediction of aboveground and total biomass. Biomass allocation patterns varied significantly by species and regeneration origin. Using a non-linear system of equations and component ratio modelling, we found out that planted spruce displayed low variability and a consistent dominance of needle biomass, while naturally regenerated beech showed greater variability and a higher proportion of stem biomass, reflecting stronger competition-driven vertical growth. Interspecific differences in total biomass were more pronounced when using tree height, with spruce generally exhibiting greater biomass than beech at equivalent heights. Overall, stem base diameter marginally outperformed tree height as a predictor of biomass. However, tree height-based models showed strong performance and are particularly suitable for integration with remote sensing applications. These findings can directly support forest managers and modellers in comparing regeneration methods and biomass estimation approaches for early-stage stand development, carbon accounting, and remote sensing calibration.

1. Introduction

There is a global drive toward forest establishment as part of climate change mitigation strategies. Large-scale tree planting has become a cornerstone of many national and international efforts to achieve Net Zero carbon targets (Burke et al., 2023). This approach, often executed through systematic planting of trees in degraded or deforested areas, not only contributes to carbon sequestration but also enhances biodiversity and contributes to other ecosystem services (Pérez-Silos et al., 2021). At the same time, biodiversity conservation and nature restoration initiatives generate growing interest in using natural regeneration as a forest establishment mechanism (Chazdon et al., 2020). Both approaches—planting and natural regeneration—offer distinct benefits. Planting

allows for controlled, rapid establishment of forest cover and can be tailored to meet specific management objectives (Sloan et al., 2019). In contrast, natural regeneration tends to produce forests with a greater variety of species and structural complexity, which can be advantageous for long-term ecosystem health and adaptability (Chazdon et al., 2020). A critical aspect underpinning both strategies with respect to climate change mitigation goals is the need for precise and reliable measurement of biomass accumulation and carbon sequestration.

Research shows that young trees established through natural regeneration develop differently from planted trees, necessitating distinct biomass prediction models (Staples et al., 2020). In the early stages of growth, tree development, and biomass accumulation are strongly affected by competition for resources (Carnevale and

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Montagnini, 2002; Kremer and Bauhus, 2020). In naturally regenerated forests, intense competition dominates, with densities sometimes reaching several hundred thousand individuals per hectare (Konôpka et al., 2024). In contrast, planted forests are established at much lower densities, around 3,000 to 6,000 trees-ha⁻¹, postponing competitive pressure until later stages of development. The differences in density impact individual growth rates and influence how biomass is allocated among stems, branches, foliage, and roots as trees grow (Konôpka et al., 2010; Poorter et al., 2012). Since competition for space shapes tree architecture, biomass models designed for planted trees may not directly apply to naturally regenerated stands. Accurate carbon accounting and effective forest management may thus need biomass prediction models that account for the unique growing conditions of each stand type. With mechanisms such as carbon farming and carbon trading increasingly being used to generate funding for forest establishment (Gifford, 2020), their economic and regulatory viability hinges on accurate reporting.

The literature is replete with studies presenting biomass models for young or small trees, particularly in plantations (Annighöfer et al., 2022; Blujdea et al., 2012; Johansson, 2007; Specht and West, 2003). These studies often rely on diameter at breast height (DBH) as the primary predictor variable because it is relatively easy to measure and correlates well with biomass in more mature trees (Temesgen et al., 2015). However, for very young trees, DBH is not suitable as young trees have not yet developed a substantial trunk girth at the standardised height of 1.3 m or may not have reached this height at all (Pajtkík et al., 2008). In young trees, DBH measurements can thus be either unavailable or too small to provide reliable estimates. This presents a significant limitation: models that rely solely on DBH may fail to capture early growth dynamics. During the initial stages of development, other tree dimensions—such as diameter at base, overall tree height, or even crown dimensions—can offer more meaningful insights into biomass accumulation (Goodman et al., 2014; Niklas, 1995). Because biomass allocation of young trees differs markedly from that of older individuals, the reliance on models for mature trees based on DBH can lead to systematic underestimation or overestimation of biomass in young stands, particularly when these models are extrapolated outside their intended age range (Weiskittel et al., 2015).

Recent advances in near-field remote sensing technology, particularly the emergence of low-cost unmanned aerial vehicles (UAVs) equipped with LiDAR sensors, have revolutionised forest monitoring (Næsset, 2011; Saarela et al., 2020; Zhao et al., 2018). UAV-mounted LiDAR provides large-scale, cost-effective three-dimensional representations of forest canopy. Although it cannot measure tree diameter, LiDAR generates reliable measurements of tree height (Kwak et al., 2007), a parameter also directly correlating with biomass accumulation and forest productivity. The high spatial resolution of LiDAR datasets allows for the differentiation of individual trees in dense stands (Holmgren et al., 2008), even in heterogeneous natural regeneration settings (Hill et al., 2017). Such detailed information is invaluable for forest managers and researchers aiming to understand forest dynamics and carbon sequestration processes, particularly on a large scale. To fully utilize these technological advancements, it is critical that biomass prediction models adapt to use tree height as the primary predictor variable (Xu et al., 2021). Integrating height-based biomass models with remote sensing data would enable direct, large-scale estimation of biomass and carbon stocks.

The primary objective of this study is to develop height-diameter allometric models tailored to young spruce (*Picea abies* (L.) Karst.) and beech (*Fagus sylvatica* L.) trees growing in naturally regenerated and planted forest stands. Following that, we aim to develop biomass components models (foliage, branches, stem, and roots) using diameter at base and height as predictors. Shifting the focus from traditional diameter-based to height-based models would allow us to link remote sensing data to biomass and carbon accumulation estimates. If successful, such models may enhance our ability to monitor and report forest carbon stocks in newly established stands, thereby supporting

climate change mitigation efforts. The final objective is to quantify the relationship between the predictors (diameter at base and height) and the relative proportion of biomass components under different regeneration types. We therefore hypothesize that the type of regeneration (natural, planted) influences the height-to-diameter at base relationship in young European beech and Norway spruce trees.

2. Materials and methods

2.1. Stand selection and tree measurements

In 2020, we selected 31 forest stands across the Western Carpathians, focusing on moderately fertile sites (Table S1). The dataset included 16 stands of European beech, seven originating from natural regeneration and nine established by planting, and 15 stands of Norway spruce, with seven naturally regenerated and eight planted. Stand selection was based on the following criteria: (a) each stand consisted of nearly 100% beech or spruce, with negligible presence of other tree species, (b) all trees within a given stand originated either entirely from natural regeneration or were planted, (c) selected trees were not visibly damaged (e.g., browsing by game), and (d) stand age ranged from 2 to 10 years, with age for planted stands counted from the time of planting and for naturally regenerated from the harvest of previous stands. Between 2021 and 2024, whole-tree sampling was conducted at selected sites during the second half of the growing season to capture maximum foliage biomass. Firstly, we pre-selected 100 trees distributed in a semi-uniform manner across the regenerated stand to capture variation in stand conditions (e.g., trees located near the edge of the adjacent mature stand and those in the stand centre away from shading) and to avoid spatial clustering. Tree heights were measured, and individuals were evenly assigned to four crown classes (overtopped, intermediate, codominant, and dominant), ensuring coverage of nearly the entire height range. From this pool, at least five representative trees were selected from each subgroup, including only individuals with healthy crowns and no visible signs of damage, to minimize potential bias in subsequent model estimations. In total, we sampled 290 beech and 246 spruce trees, for a combined total of 536 individuals (Table 1).

Trees were carefully excavated to recover the complete belowground system, including all roots with a diameter greater than 2 mm. For each tree, d_0 and h were recorded with a precision of ± 0.01 mm and ± 0.1 cm, respectively. The belowground parts (hereinafter referred to as roots) were separated from the aboveground parts at the soil surface level. All biomass components were packed in labelled paper bags and transported to the laboratory. In the lab, branches were removed from the stems. For beech, leaves were manually separated from branches to obtain four biomass components: leaves, branches, stems, and roots. In spruce, needles were separated after 5–6 weeks of drying in a well-ventilated room, once they could be removed by shaking the branches. Each biomass component, foliage, branches, stems, and roots, was then oven-dried at 105 °C for approximately one week and weighed using a laboratory scale (PCE-BSH 6000, PCE Instruments, UK, precision ± 0.1 g). The resulting dry mass data were used for subsequent biomass modelling.

2.2. Height-diameter at stem base relationships estimation

The relationship between stem base diameter and tree height was analyzed using a generalized non-linear model (Eq. 1), incorporating a power weighting function to account for heteroscedasticity, following the approach of Pinheiro et al. (2023). Furthermore, to assess the differences in the relationship between species and type of regeneration, the categorical variables were transformed to binary variables:

$$h = (\alpha_{00} + \alpha_{01} \times \text{species} + \alpha_{02} \times \text{regen}) \times d_0^{(\alpha_{10} + \alpha_{11} \times \text{species} + \alpha_{12} \times \text{regen})} + \varepsilon \quad (1)$$

Table 1Descriptive statistics of d_0 and h for all trees sampled in this study. Regen: regeneration type, S.D.: standard deviation, CV: coefficient of variation, d_0 : diameter at base.

Species	Regen.	No. of sampled trees	d_0 (mm)				Height (m)			
			Mean	Min–Max	S.D.	CV	Mean	Min–Max	S.D.	CV
European beech	Natural	170	14.50	4.20–68.50	8.67	0.60	1.25	0.24–5.40	0.81	0.65
	Planted	120	29.05	2.40–73.20	19.06	0.66	1.77	0.12–5.09	1.14	0.64
Norway spruce	Natural	145	23.15	1.55–97.70	22.30	0.96	1.29	0.11–5.30	1.17	0.91
	Planted	101	49.64	4.65–135.25	29.24	0.59	2.32	0.27–5.56	1.27	0.55

where h is the modelled tree height (m), d_0 is the diameter at stem base (mm), and categorical predictors represent species (beech = 0, spruce = 1) and regeneration type (planted = 0, natural = 1). Parameters α_{00} and α_{10} define the baseline of the curve, while coefficients α_{01} and α_{02} account for species and α_{11} and α_{12} for regeneration effects on the multiplicative constant and exponent, respectively and ε denotes the random error. The underlying heteroscedasticity was modelled using a variance power function with d_0 as predictor (Eq. 3).

Differences in height–diameter relationships between species and regeneration types were tested using t -tests ($\alpha = 0.05$). Nonsignificant coefficients were interpreted as indicating no statistical difference between species or regeneration types. The 95% confidence intervals for model predictions were calculated using the “delta” method (Miguez, 2023; van der Vaart and Wellner, 1996).

2.3. Biomass components estimation using generalized non-linear models (GNLS)

The relationships between predictor variables (diameter at base and height) and biomass component fractions were first modelled using GNLS (Eq. 2). GNLS was chosen to account for heteroscedasticity in residuals by incorporating the variance structure function (Eq. 3a) in the form of a power function using d_0 as a predictor. Parameter λ was then further used to calculate the weights of residuals w_{mj} for each biomass component separately (Eq. 3b).

$$\widehat{BC}_i = \beta_0 \times P_i^{\beta_1} + \varepsilon_i \quad (2)$$

where \widehat{BC} -hat is the biomass component to be estimated, P is the predictor variable (d_0 or h), β_0 and β_1 are the model parameters, and ε is the random error. The variance function and the weights of residuals w_m were calculated as Eqs. 3a and 3b:

$$\text{var}(\varepsilon_i) = \sigma^2 \times d_{0i}^\lambda \quad (3a)$$

$$w_{mj} = 1/d_{0j}^\lambda \quad (3b)$$

For both predictors (diameter at base and height), we used d_0 as the variance function variable, as some models did not converge when using h .

2.4. Biomass components estimation by fitting seemingly unrelated regression (SUR)

While weighted non-linear regression is a widely used method for estimating biomass component parameters without transforming the original data, it does not fully account for the principle of additivity. This is important because the error structures of individual biomass components are inherently correlated. Therefore, we applied a natural log (ln–ln) transformation to both the predictor and response variables to reduce heteroscedasticity and linearize the relationships (Eq. 4). This enabled the use of SUR, which was performed using the R package “systemfit” (Henningsen and Hamann, 2007). The general system of equations was defined as Eq. 4:

$$\ln(\widehat{BC}_{\text{leaves}}) = \ln(\gamma_{0\text{leaves}}) + \gamma_{1\text{leaves}} \times \ln(P) + \ln(\varepsilon_i)$$

$$\begin{aligned} \ln(\widehat{BC}_{\text{branches}}) &= \ln(\gamma_{0\text{branches}}) + \gamma_{1\text{branches}} \times \ln(P) + \ln(\varepsilon_i) \ln(\widehat{BC}_{\text{stem}}) \\ &= \ln(\gamma_{0\text{stem}}) + \gamma_{1\text{stem}} \times \ln(P) + \ln(\varepsilon_i) \end{aligned}$$

$$\ln(\widehat{BC}_{\text{roots}}) = \ln(\gamma_{0\text{roots}}) + \gamma_{1\text{roots}} \times \ln(P) + \ln(\varepsilon_i) \quad (4)$$

where \widehat{BC}_x represents the biomass component, P is the predictor (diameter at base or height), γ_0 and γ_1 are regression coefficients, and ε_i is a random error. To correct for bias introduced by the log transformation, a correction factor (CF; Eq. 5) according to (Baskerville, 1972) was applied during back-transformation:

$$CF_i = \sigma_i^2 / 2 \quad (5)$$

where σ^2 is the sample variance of the logarithmic equation (Paresol, 1999), thus the biomass components were predicted as Eq. 6:

$$\widehat{BC}_i = e^{(\ln(\widehat{BC}_i) + CF_i)} \quad (6)$$

Total biomass was then calculated as Eqs. 7 and 8:

$$\widehat{\text{Total}} = \widehat{BC}_{\text{leaves}} + \widehat{BC}_{\text{branches}} + \widehat{BC}_{\text{stem}} + \widehat{BC}_{\text{roots}} \quad (7)$$

$$\widehat{\text{ABG}} = \widehat{BC}_{\text{leaves}} + \widehat{BC}_{\text{branches}} + \widehat{BC}_{\text{stem}} \quad (8)$$

where Total represents whole tree biomass, and ABG stands for above-ground biomass only.

To evaluate the performance of the GNLS and SUR models, root mean square error (RMSE) values for each biomass component equation were compared (Eqs. 9a and 9b), and predicted values from both approaches were plotted for visual inspection of discrepancies. Both GNLS and SUR were evaluated on different scales, with log-log transformed data for SUR and weighted residuals for GNLS. Thus, a normalized root mean square error (NRMSE) was used to compare the two different approaches used (Eqs. 10a and 10b).

$$\text{RMSE}_{\text{gnls}_m} = \sqrt{\frac{1}{n-k} \sum_{j=1}^n (\widehat{BC}_{mj} - \widehat{BC}_{mj})^2 \times w_{mj}} \quad (9a)$$

$$\text{RMSE}_{\text{sur}_m} = \sqrt{\frac{1}{n-k} \sum_{j=1}^n (\ln(\widehat{BC}_j) - \ln(\widehat{BC}_j))^2} \quad (9b)$$

where \widehat{BC}_j is the observed biomass component dry weight, \widehat{BC}_j -hat is the predicted value, n is the number of observations, k is the number of parameters being estimated, and m represents the m -th biomass component. The RMSE was evaluated for each biomass component separately.

The NRMSE was calculated using the normalisation by the mean of the predicted m -th biomass component as Eqs. 10a and 10b:

$$\text{NRMSE}_{\text{gnls}_m} = \frac{\text{RMSE}_{\text{gnls}_m}}{\widehat{BC}_m} \quad (10a)$$

$$\text{NRMSE}_{\text{sur}_m} = \frac{\text{RMSE}_{\text{sur}_m}}{\ln(\text{BC}_m)} \quad (10b)$$

2.5. Biomass components partitioning

To investigate differences in biomass allocation along the tree height gradient, we calculated the proportion of each biomass component relative to total biomass. This component-wise partitioning enabled the identification of potential shifts in growth strategy or resource allocation across tree development stages. The component ratio method (Jenkins et al., 2003) (Eq. 11) and non-linear equations (Eq. 12) were used for partitioning. As no heteroscedasticity and low error-structure correlations between biomass component ratios were observed during pre-analysis, ordinary least square parametrization (OLS) was used to estimate the relationships between the biomass component ratios BC_{ratio} and predictors P (d_0 and h). The models' performance was further compared using the RMSE. The general equation for separate biomass components is shown in Eq. 11:

$$\text{BC}_{\text{ratio}} = \frac{\text{BC}}{\text{Total}} \quad (11)$$

where BC is the biomass component's dry weight (foliage, branches, stem, and roots) and Total represents the total biomass dry weight.

$$\widehat{\text{BC}}_{\text{ratio}} = \theta_0 \times P^{\theta_1} + \varepsilon \quad (12)$$

where θ_0 and θ_1 are regression parameters to be estimated using the same method as Eq. 12.

All statistical analyses were conducted using R Statistical Software v4.3.1 (R Core Team, 2013). The “nlme” package (Pinheiro et al., 2023) was used for height–diameter and GNLS biomass components model development. The “systemfit” package (Henningsson and Hamann, 2007) was used for estimation of the ln-transformed (Section 2.4) and non-linear systems of equations. The “nlraa” package (Miguez, 2023) was used to calculate the 95% confidence intervals of GNLS model predictions using the “delta” method.

3. Results

3.1. Height–diameter at base allometric equation

The height-to-diameter at base relationship for young European beech and Norway spruce indicates that planted Norway spruce exhibits the lowest height for a given basal diameter, followed by naturally regenerated Norway spruce and planted European beech (Fig. 1). European beech from natural regeneration attains the greatest height for the same basal diameter. The GNLS models show statistically significant differences ($p < 0.05$) with respect to both species and regeneration

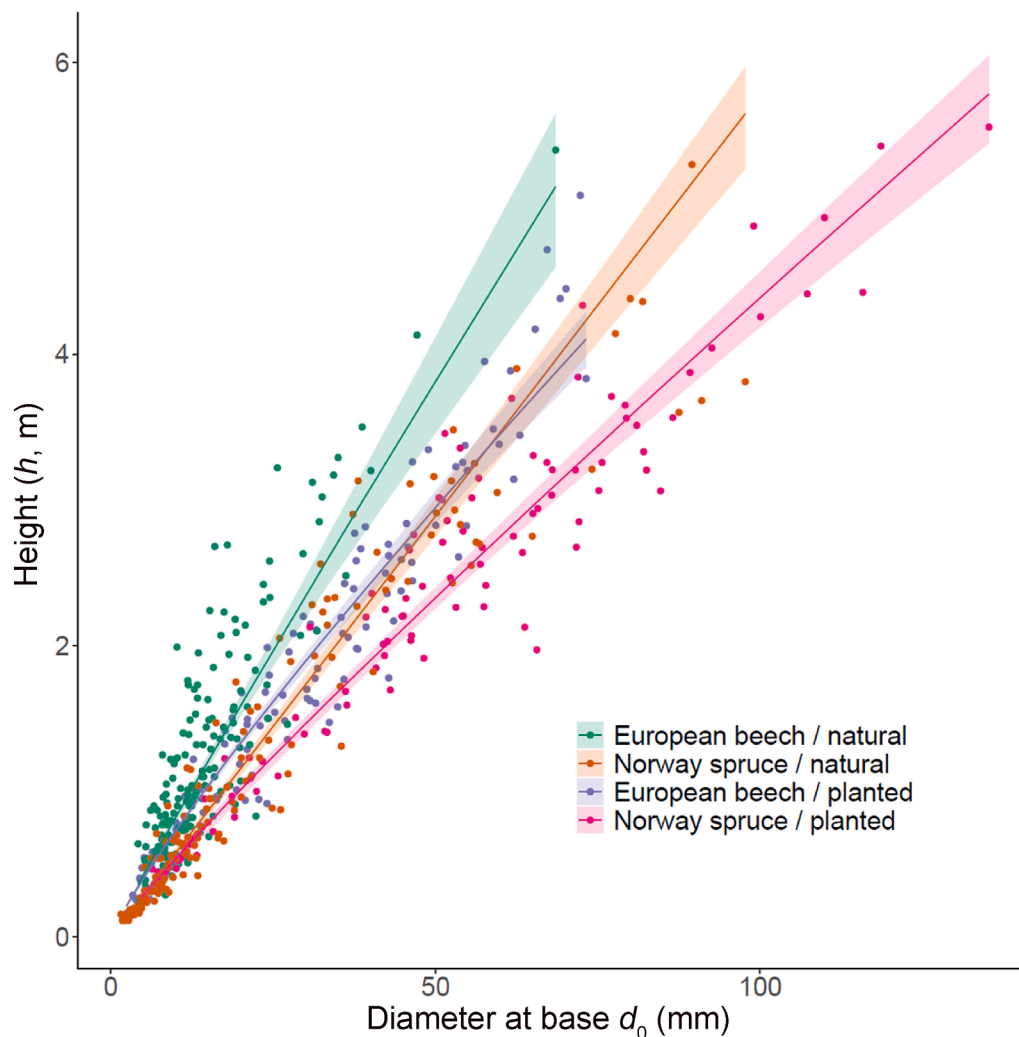


Fig. 1. Height–diameter at base models predictions of European beech and Norway spruce from natural and planted regeneration. The bands represent 95% confidence intervals.

origin (Table 2). Specifically, only the parameter α_{02} , representing the partial exponent for species, was not significantly different from zero. The parameter α_{11} , representing the partial exponent for regeneration origin, had a p -value of approximately 0.06, indicating only a slight deviation from statistical significance.

3.2. Biomass components modelling with consideration of heteroscedasticity and the additivity principle

The analysis showed that the regression parameters (β for GNLS, γ for SUR) were broadly similar across both modelling approaches. However, models using d_0 as a predictor consistently outperformed those using h in terms of predictive accuracy when using RMSE (Tables 2 and 3). The only instances where tree height was a better predictor were roots and foliage in planted Norway spruce and stems in naturally regenerated European beech. In general, the GNLS models performed better when predicting the aboveground biomass components (stem, branches, and foliage) rather than roots (Table 3). The SUR method performed the best for the stem component (Tables 3–5). This was further supported by preliminary correlation analysis between the biomass components and predictor variables (Fig. S1). Correlation coefficients were the highest for spruce from natural regeneration ($r \sim 0.9$) and the lowest for beech from planted regeneration ($r \sim 0.6$).

When comparing model predictions, we observed only minor differences between the GNLS and SUR methods in most cases. The residual plots (Figs. S2 and S3) suggest a correct assessment of heteroscedasticity by both methods. Across all species and regeneration types, the GNLS method yielded consistently lower NRMSE values (ranging from 0.0001 to 0.05) compared to the SUR method (NRMSE > 0.03), regardless of the predictor used (Tables 3 and 4). These findings suggest that GNLS, when combined with appropriate weighting to address heteroscedasticity, offers greater accuracy in component-wise biomass estimation. While not mathematically additive, it provides more accurate estimates than the ln-ln transformed system of linear equations and does so without requiring additional data manipulation. When d_0 is used as the predictor (Fig. 2, left), a global model appears adequate for capturing biomass patterns in both natural and planted regeneration.

However, and this is important when considering the use of remotely sensed predictors, when h is used, distinct differences between regeneration types emerge. As shown in Fig. 2, right, biomass allocation diverges markedly. This trend is consistent across all biomass components, and model coefficients differ substantially when using h as the predictor (Tables 3 and 4).

3.3. Biomass components partitioning

Juvenile trees undergo rapid changes in form and physiology during early development. Fig. 3 illustrates the allocation of biomass across four main components, foliage, branches, stem, and roots, across the observed diameter at base and height range. We observed the greatest dynamics of biomass component partitioning in European beech. In planted regeneration, the proportion of branches increased from less than 10% in individuals with a basal diameter (d_0) below 1 cm to more

Table 2

Height–diameter at base model parameter estimates. Statistically significant estimates are highlighted in grey. df: degrees of freedom, RSE: residual standard error.

Parameter	Estimate	Std. error	p -value
α_{00}	0.099215	0.00523	<0.001
α_{01}	−0.03357	0.006749	<0.001
α_{02}	−0.00744	0.006594	0.2597
α_{10}	0.867331	0.016321	<0.001
α_{11}	0.045866	0.02465	0.0633
α_{12}	0.085047	0.027952	0.0025

df = 530, RSE = 0.0275.

Table 3
Biomass components models parameters using GNLS. All parameters were estimated with $p < 0.001$.

Species	Regeneration	Component	d_0				h				RMSE	NRMSE		
			β_0 (SE)	β_1 (SE)	λ	df	RMSE	NRMSE	β_0 (SE)	β_1 (SE)			λ	df
European beech	Natural	Foliage	0.0283 (0.0052)	2.3394 (0.0675)	2.0177	168	0.1864	0.0096	5.3737 (0.3483)	1.5573 (0.1359)	2.3898	168	0.2572	0.0133
		Branches	0.0037 (0.0008)	3.0172 (0.0806)	2.8046	168	0.0374	0.0018	2.9711 (0.1979)	2.1432 (0.1446)	3.1676	168	0.0368	0.0018
		Stem	0.0604 (0.0114)	2.3389 (0.0712)	2.4169	168	0.4598	0.0071	11.7474 (0.8588)	1.6716 (0.1452)	2.9912	168	0.3220	0.0050
	Planted	Roots	0.0203 (0.0034)	2.8283 (0.06)	2.1305	168	0.7634	0.0188	11.5234 (0.4916)	2.3365 (0.0855)	2.1800	168	2.1224	0.0521
		Foliage	0.0055 (0.0007)	2.7935 (0.0372)	2.6933	118	0.0827	0.0007	8.448 (0.4133)	3.0871 (0.0578)	2.6057	118	0.1379	0.0012
		Branches	0.0008 (0.0002)	3.4633 (0.0643)	3.4290	118	0.0303	0.0001	7.9309 (0.6442)	3.8875 (0.0922)	3.1828	118	0.1566	0.0006
Norway spruce	Natural	Stem	0.0466 (0.0062)	2.4212 (0.0399)	2.5957	118	0.5749	0.0012	26.8222 (1.561)	2.7227 (0.0678)	2.5497	118	1.6278	0.0035
		Roots	0.0195 (0.0019)	2.7886 (0.0282)	2.2594	118	1.7415	0.0066	29.2264 (1.3213)	3.1905 (0.0504)	2.2599	118	3.4993	0.0134
		Foliage	0.1005 (0.009)	2.239 (0.0296)	2.1170	143	3.5078	0.0165	42.5504 (2.5009)	2.258 (0.0702)	2.0553	143	9.5801	0.0452
	Planted	Branches	0.0523 (0.0057)	2.3334 (0.034)	2.1148	143	2.1093	0.0132	29.0501 (1.5999)	2.3988 (0.0666)	2.1819	143	3.0479	0.0191
		Stem	0.0776 (0.0048)	2.1703 (0.0237)	2.4771	143	0.8307	0.0034	25.6085 (1.615)	2.0637 (0.067)	2.2632	143	2.3322	0.0098
		Roots	0.0451 (0.0032)	2.4795 (0.025)	2.2996	143	0.7034	0.0062	39.0679 (1.4635)	2.5218 (0.046)	2.0965	143	3.1237	0.0266
European beech	Natural	Foliage	0.0398 (0.005)	2.5253 (0.035)	2.6205	99	3.0002	0.0029	62.5267 (3.0543)	2.6495 (0.0536)	2.6817	99	3.9051	0.0038
		Branches	0.0156 (0.0015)	2.6563 (0.0288)	2.8982	99	0.4706	0.0007	34.7131 (1.895)	2.7667 (0.0606)	2.8300	99	1.2647	0.0018
		Stem	0.0598 (0.0106)	2.2905 (0.0463)	2.6926	99	0.9187	0.0011	50.802 (2.2145)	2.2994 (0.0496)	2.3567	99	3.3301	0.0039
	Planted	Roots	0.0357 (0.0033)	2.4972 (0.027)	2.1604	99	7.5033	0.0118	53.1536 (2.3956)	2.6753 (0.0443)	2.4812	99	4.1292	0.0065

SE: standard error, df: degrees of freedom.

SE: standard error, df: degrees of freedom.

Table 4
Biomass components model parameters derived from the SUR method. The RMSE and NRMSE were calculated from log-transformed values to not reintroduce the heteroscedasticity. All parameters were estimated with $p < 0.001$.

Species	Regeneration	Component	d_0		h					d_f				
			$\ln(\gamma_0)$ (SE)	γ_1 (SE)	CF	df	RMSE	NRM SE	$\ln(\gamma_0)$ (SE)	γ_1 (SE)	CF	df	RMSE	NRM SE
European beech	Natural	Foliage	-3.7502 (0.1828)	2.3745 (0.0706)	0.1036	168	0.4553	0.0935	2.2057 (0.0582)	1.7117 (0.0985)	0.2866	168	0.7571	0.1555
		Branches	-5.9825 (0.218)	3.1173 (0.0842)	0.1475	168	0.5431	0.1059	1.833 (0.0689)	2.3237 (0.1166)	0.4014	168	0.8959	0.1747
		Stem	-4.034 (0.1641)	2.8519 (0.0634)	0.0835	168	0.4088	0.0596	3.1079 (0.0434)	2.302 (0.0733)	0.1589	168	0.5637	0.0821
	Planted	Roots	-2.9598 (0.179)	2.3608 (0.0692)	0.0995	168	0.4460	0.0815	2.9641 (0.0606)	1.6513 (0.1025)	0.3101	168	0.7876	0.1439
		Foliage	-5.2637 (0.1172)	2.7799 (0.0367)	0.0631	118	0.3552	0.0787	2.3739 (0.0478)	2.9422 (0.0544)	0.1213	118	0.4925	0.1091
		Branches	-7.4611 (0.1491)	3.5836 (0.0467)	0.1021	118	0.4519	0.0881	2.3998 (0.0791)	3.7421 (0.09)	0.3313	118	0.8140	0.1587
Norway spruce	Natural	Stem	-3.9404 (0.0781)	2.7817 (0.0245)	0.0280	118	0.2367	0.0418	3.7036 (0.0426)	2.9393 (0.0485)	0.0962	118	0.4387	0.0774
		Roots	-3.1061 (0.1091)	2.4156 (0.0342)	0.0547	118	0.3308	0.0667	3.5382 (0.0521)	2.531 (0.0593)	0.1438	118	0.5363	0.1081
		Foliage	-2.5732 (0.1005)	2.31 (0.0353)	0.0928	143	0.4309	0.1384	4.0925 (0.06)	2.1996 (0.0566)	0.2486	143	0.7051	0.2265
	Planted	Branches	-3.4553 (0.0988)	2.4806 (0.0347)	0.0897	143	0.4236	0.1419	3.7065 (0.0574)	2.3785 (0.0541)	0.2271	143	0.6739	0.2257
		Stem	-3.1041 (0.0682)	2.4631 (0.0239)	0.0427	143	0.2923	0.0995	4.0151 (0.0363)	2.3955 (0.0342)	0.0909	143	0.4264	0.1451
		Roots	-2.4677 (0.0717)	2.117 (0.0252)	0.0473	143	0.3075	0.0943	3.6388 (0.0538)	2.006 (0.0507)	0.1995	143	0.6317	0.1937
		Foliage	-3.1638 (0.1487)	2.4937 (0.0397)	0.0507	99	0.3185	0.0405	4.3111 (0.0576)	2.6419 (0.0594)	0.0986	99	0.4440	0.0565
		Branches	-4.0247 (0.1389)	2.6071 (0.0371)	0.0442	99	0.2974	0.0401	3.7957 (0.061)	2.753 (0.0629)	0.1105	99	0.4701	0.0633
		Stem	-3.3197 (0.1127)	2.4859 (0.0301)	0.0291	99	0.2414	0.0334	4.115 (0.0349)	2.6607 (0.0359)	0.0361	99	0.2688	0.0372
		Roots	-2.8563 (0.1492)	2.2891 (0.0399)	0.0511	99	0.3196	0.0451	4.0049 (0.0552)	2.4258 (0.0569)	0.0905	99	0.4253	0.0600

SE: standard error, CF: correction factor, df: degrees of freedom.

than 25% in individuals with d_0 around 75 mm or approximately 5 m in height. Conversely, the root component ratio decreased from more than 60% to less than 20% in individuals of the same dimensions. In naturally regenerated beech, the pattern of change was similar but less pronounced.

Norway spruce from planted regeneration exhibited relatively stable biomass partitioning; however, in smaller individuals with $d_0 < 75$ mm and height < 3 m, the proportion of roots gradually decreased and was replaced by branches, although the difference was less than 5%. Overall, the stem comprised approximately 40% of total biomass in European beech, regardless of regeneration origin, while in Norway spruce it accounted for about 30%–35% (Fig. 3). Furthermore, Norway spruce showed a higher proportion of foliage (~30%) compared with European beech (~10%).

4. Discussion

Our study suggests that young forest stands established through natural regeneration differ fundamentally from those established by planting in biomass allocation strategies. These differences, observed here in Norway spruce and European beech, are primarily driven by variation in initial stand density and the resulting intensity of competition for light and other resources (Li et al., 2022; Wertz et al., 2020). Naturally regenerated stands often reach extremely high densities (Svoboda et al., 2010), sometimes reaching several hundred thousand stems per hectare (Konôpka et al., 2024), creating strong competition that favours vertical growth. These findings are also supported by our dataset (Table S1), where some plots reached more than 200,000 seedlings per hectare. However, these values are derived from small sampling plots and therefore may not represent the entire stand, but rather localized conditions. As a result, trees in these stands tend to be taller for a given diameter at base (d_0) compared to their planted counterparts (Coomes and Allen, 2007; Vospernik and Sterba, 2015). These architectural differences, driven by early competitive pressure, significantly influence overall biomass distribution and support our hypothesis that regeneration strategy should be explicitly considered in allometric modelling.

Diameter and height are widely used when constructing the models to estimate the biomass of both European beech and Norway spruce across Europe (Bartelink, 1997; Bolte et al., 2004; Cienciala et al., 2005; Johansson, 1999; Wirth et al., 2004), however, only a small portion is focused on allometric models for early growth individuals (Dutcă et al., 2018). The comparison of the model's coefficients is often not possible, as the models for mature trees use diameter at 1.3 m (DBH) or a combination of diameter and height in their estimation. Our study presents unique results considering different regeneration for small individuals.

Differences in competitive environments also shape how biomass is partitioned among tree components. In high-density, naturally regenerated stands, both species showed stronger allocation to the stem as trees increased in height, a pattern particularly pronounced in beech. This likely reflects a growth strategy prioritizing structural support. In contrast, trees in planted stands, where competition is initially limited, invest relatively more in acquisitive components, such as foliage and branches. For spruce, needle biomass remained the dominant component in planted trees across the height range, while naturally regenerated spruce trees shifted biomass investment toward the stem. These findings align with earlier observations in over-dense beech stands in Slovakia, where stem biomass became increasingly dominant over a 10-year period at the expense of foliage and branches (Konôpka et al., 2010, 2024). Importantly, these dynamics underscore the limitations of applying biomass models developed for mature trees to young stands. Mature trees typically allocate the majority of their biomass to the stem and coarse roots (Krejza et al., 2017), but in juveniles, allocation is far more variable, with proportionally more biomass invested in leaves and fine roots during establishment (Helmisaari et al., 2002; Wirth et al., 2004). Our findings highlight the need for biomass models tailored

Table 5
Biomass components ratios models estimation using the non-linear system of equations. SE: standard error, df: degrees of freedom.

Species	Regeneration	Component	d_0						h					
			θ_0	θ_1	SE (θ_0)	SE(θ_1)	df	RMSE	θ_0	θ_1	SE (θ_0)	SE (θ_1)	df	RMSE
European beech	Natural	Foliage	0.1026	0.0183	0.0071	0.0216	168	0.0261	0.1568	−0.2715	0.0015	0.0158	168	0.0417
		Branches	0.0330	0.5173	0.0026	0.0213	168	0.0473	0.1136	0.2712	0.0014	0.0196	168	0.0450
		Stem	0.3462	0.0477	0.0070	0.0062	168	0.0578	0.3815	0.2951	0.0015	0.0062	168	0.0804
		Roots	0.7940	−0.3142	0.0141	0.0066	168	0.0595	0.3338	−0.3060	0.0015	0.0078	168	0.0765
	Planted	Foliage	0.3161	−0.2799	0.0098	0.0127	118	0.0442	0.1075	0.0307	0.0023	0.0246	118	0.0260
		Branches	0.0413	0.4001	0.0017	0.0148	118	0.0421	0.1399	0.5129	0.0031	0.0228	118	0.0526
		Stem	0.2295	0.2091	0.0030	0.0048	118	0.0985	0.3930	0.0631	0.0025	0.0072	118	0.0565
		Roots	0.6279	−0.2509	0.0099	0.0064	118	0.0887	0.3353	−0.3305	0.0024	0.0074	118	0.0582
Norway spruce	Natural	Foliage	0.3477	−0.0437	0.0024	0.0025	143	0.0670	0.3052	−0.0568	0.0009	0.0026	143	0.0659
		Branches	0.1530	0.1056	0.0019	0.0041	143	0.0505	0.2076	0.1032	0.0009	0.0044	143	0.0506
		Stem	0.1873	0.1412	0.0016	0.0028	143	0.0649	0.2824	0.1695	0.0008	0.0030	143	0.0591
		Roots	0.3781	−0.2303	0.0033	0.0036	143	0.0493	0.1938	−0.2324	0.0009	0.0039	143	0.0467
	Planted	Foliage	0.2883	0.0266	0.0028	0.0026	99	0.0502	0.3134	0.0225	0.0007	0.0022	99	0.0504
		Branches	0.1273	0.1292	0.0021	0.0043	99	0.0370	0.1897	0.1207	0.0007	0.0037	99	0.0383
		Stem	0.2367	0.0326	0.0027	0.0031	99	0.0558	0.2571	0.0579	0.0007	0.0027	99	0.0551
		Roots	0.4519	−0.2139	0.0051	0.0032	99	0.0527	0.2379	−0.2242	0.0006	0.0028	99	0.0530

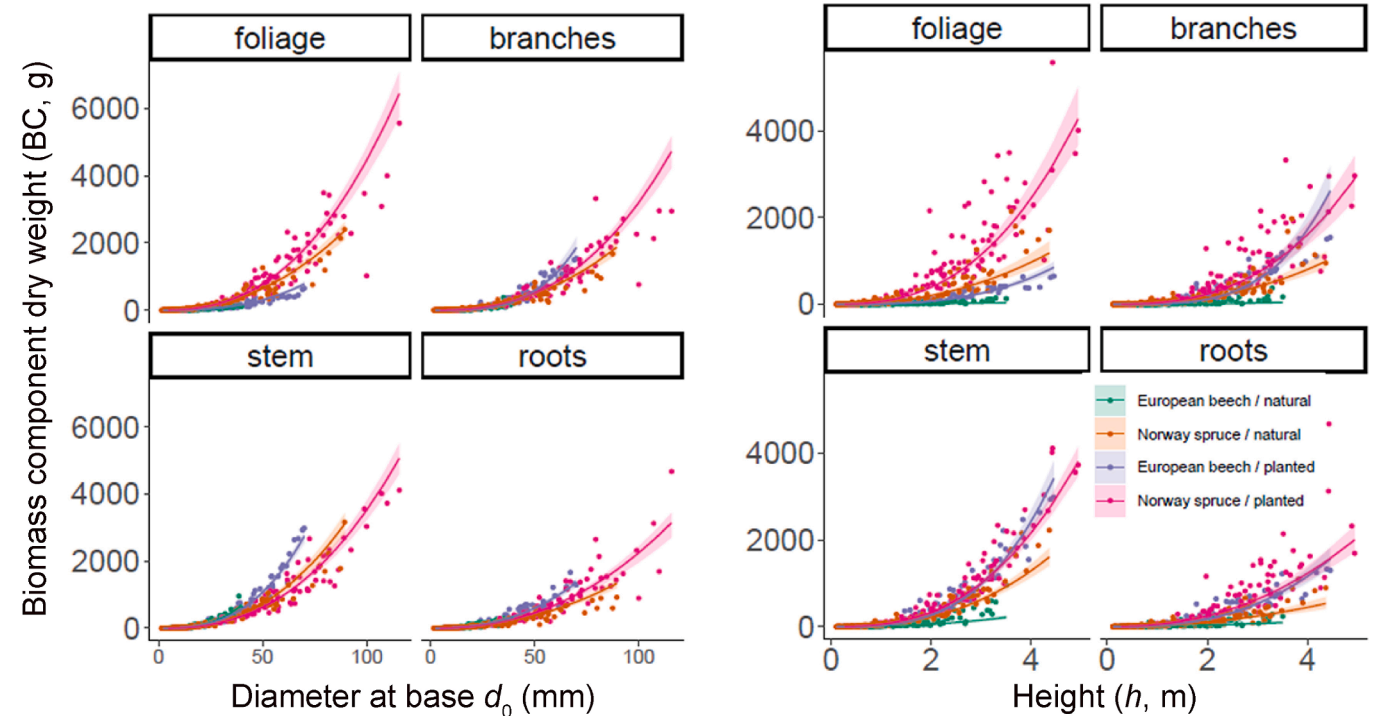


Fig. 2. Biomass component predictions for naturally regenerated and planted Norway spruce and European beech based on d_0 and h , using the weighted GNLS method. Shaded areas indicate 95% confidence intervals around the fitted curves using the “delta” method.

specifically to young trees, reflecting their unique developmental strategies and component-wise allocation shifts. Applying mature-tree models to early developmental stages may lead to significant estimation errors in both forest inventories and ecosystem modelling.

While our analysis showed that diameter at base generally offers slightly greater predictive accuracy for biomass estimation, tree height emerged as a highly practical and informative alternative. In our case, models based on height performed comparably to those using diameter, especially for total biomass. Similar results for different species growing in plantations were also found by [Blujdea et al. \(2012\)](#). More importantly, height-based models might become increasingly useful when considering their compatibility with modern remote sensing technologies. Advances in UAV-based LiDAR and photogrammetry now enable high-resolution, cost-effective, and large-scale acquisition of tree height data across diverse forest landscapes ([Wagner et al., 2024](#)). Our height-based models are particularly well-suited for integration with

UAV-derived data, offering a scalable and efficient approach to biomass estimation in young forests ([Tao et al., 2024](#)). This is especially valuable in contexts where rapid assessment is needed, such as monitoring natural regeneration after disturbance, evaluating afforestation programs, or informing on vegetation development on abandoned land ([Goodbody et al., 2018](#); [Stamatopoulos et al., 2024](#)). As remote sensing becomes increasingly accessible, the operational integration of these data into biomass modelling will likely play a key role in scaling up forest monitoring, particularly in regions undergoing rapid ecological change or reforestation ([Tao et al., 2024](#)). Furthermore, early stand development undergoes increased growth dynamics, especially concerning mortality ([Lutz and Halpern, 2006](#); [Waller et al., 2024](#)). The use of repeated remote sensing data gathering in combination with height-based models could therefore greatly increase the accuracy of biomass quantification.

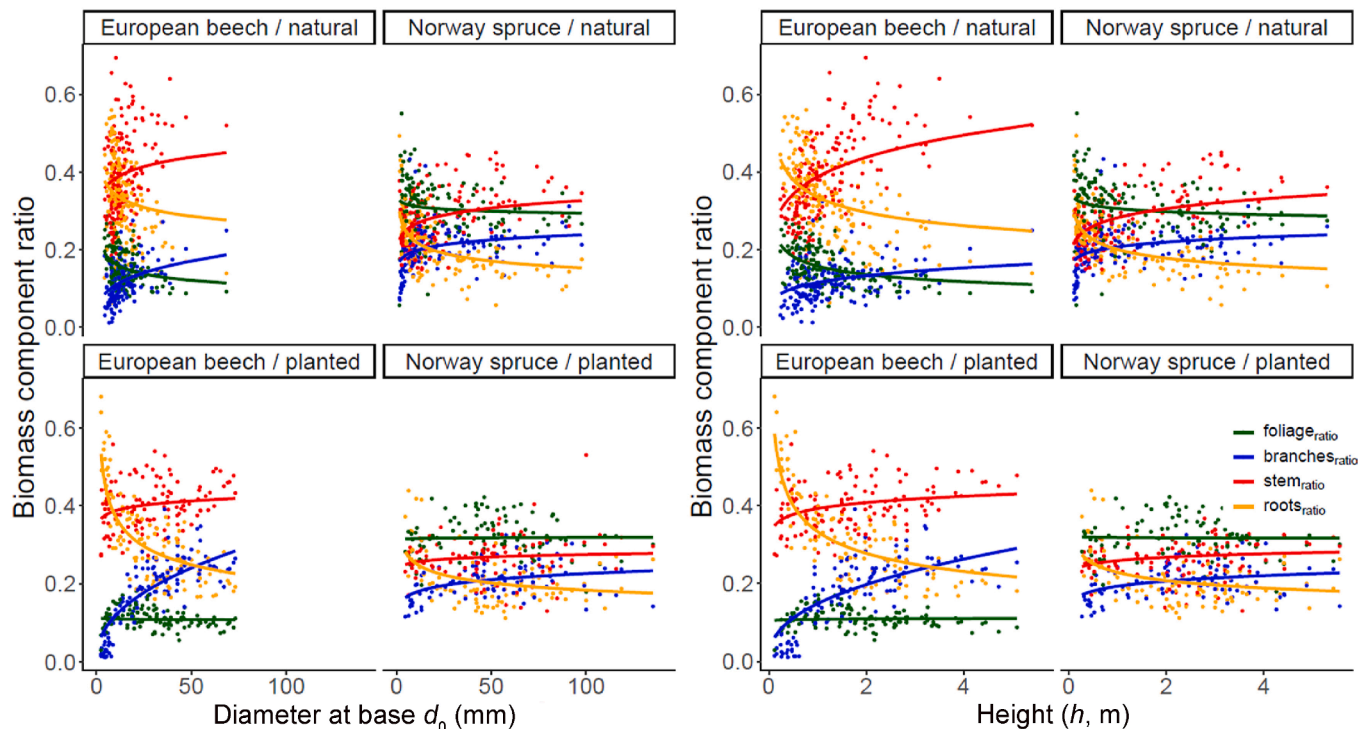


Fig. 3. Proportion of tree components in the total biomass for young European beech and Norway spruce of different origins across the diameter at base and height range.

Despite the good predictive performance of our models, several limitations should be acknowledged. First, our dataset focused primarily on young trees up to approximately 10 years of age. As a result, larger individuals, which contribute disproportionately to stand-level biomass and carbon storage, were underrepresented, as we saw the poorest fit for this cohort. Future research should aim to expand sampling to include a broader range of tree sizes and developmental stages, thereby improving continuity and integration with existing models calibrated for older or larger trees. Second, while our models captured general patterns across sites, they did not explicitly account for environmental variations such as soil properties, microclimate, or site history. Factors like soil moisture, nutrient availability, and climatic stress can influence both growth rates and biomass allocation patterns, potentially affecting model performances across ecological gradients. Furthermore, genetic variability was not assessed in this study, even though it may also have influenced the observed differences in allometry between the studied groups.

5. Conclusions

We show that naturally regenerated trees are taller and show stronger investment in stem biomass compared to their planted counterparts, likely driven by higher stand densities and greater competition. These differences underline the need to account for regeneration type in early biomass modelling. We also show that GNLS models, especially when weighted to accommodate heteroscedasticity, outperform log-transformed linear systems in both accuracy and consistency. Our study strongly suggests that both diameter at base and tree height are suitable predictors of biomass, but argues that tree height offers distinct advantages for operational forest monitoring. The compatibility of height-based models with UAV-derived remote sensing data opens promising opportunities for large-scale, cost-efficient biomass estimation in young forests. Future research could also focus on the usability of general allometric equations for mature trees originating from different regeneration practices.

CRediT authorship contribution statement

Peter Marčiš: Writing – review & editing, Writing – original draft, Methodology, Formal analysis, Data curation, Conceptualization. **Jozef Pajtk:** Writing – original draft, Formal analysis, Conceptualization. **Bohdan Konópka:** Writing – review & editing, Writing – original draft, Investigation, Conceptualization. **Martin Lukac:** Writing – review & editing, Writing – original draft, Methodology, Investigation, Conceptualization.

Use of artificial intelligence

ChatGPT 4o was used to improve the grammar and clarity of text written by the authors. No AI-generated text is presented in this paper.

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Data availability

Data will be made available on request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.fecs.2025.100406>.

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