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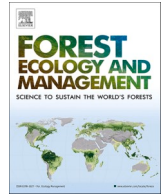
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# Decadal forest mensuration cycle significantly underestimates net primary production in dense young beech stands

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## ABSTRACT

The early development of naturally regenerated forest stands is highly dynamic and includes rapid shifts in productivity and mortality. To characterise the growth dynamics in the initial decades, we assessed aboveground biomass stocks ( $S_{ab}$ ), aboveground biomass productivity ( $DP_{ab}$ ), and aboveground biomass mortality ( $DM_{ab}$ ) in five naturally regenerated European beech stands located in the Inner Western Carpathians. We developed allometric models for aboveground biomass compartments based on a sample of 262 trees. We also established five circular sampling plots within each stand and, for 15 years, carried out annual measurements of stem diameter at the base and height for all trees within the sampling plots. We then utilised the allometric models to calculate annual biomass accumulation in aboveground biomass compartments on an area basis. Our findings show that, despite the declining contribution of foliage to the total aboveground stock, about a quarter of annual net primary production in young beech stands enters the dead biomass pool due to leaf fall and tree mortality. The growth dynamics and biomass allocation patterns of young beech forests necessitate the development of specific allometric models to describe their growth and carbon capture processes.

## 1. Introduction

European beech (*Fagus sylvatica* L.) is a broadleaved tree species widely distributed across Europe, from Sicily in the south to Scandinavia in the north (De Rigo et al., 2016). Its range extends longitudinally from the Cantabrian Mountains in the west to the Carpathians and Balkan Mountains in the east (Saltré et al., 2015). In the Western Carpathians, European beech is the most prevalent tree species, commonly found in pure monocultures or mixed stands alongside Norway spruce (*Picea abies* (L.) Karst.) and silver fir (*Abies alba* Mill.). The Carpathians boast highly productive beech forests, emphasising the suitability of the species for the region. Future projections indicate that beech may further expand its presence in the area, potentially outcompeting tree species locally more vulnerable to climate change, such as spruce (Lindner et al., 2010; Hlásny et al., 2014; Kunca et al., 2019). Consequently, the ecological (Černecký et al., 2020) and economic (Kožuch and Banáš, 2020) importance of beech in Central Europe is expected to increase as the European climate continues to change.

The prominence of beech in Slovakia is already on the rise; the share of beech in the total forest stock increased from 30.3 % to 34.6 %

between 2000 and 2020. European beech stands 0–20 years of age currently cover nearly 133,000 ha and account for 35.7 % of the total forest area in this age class, indicating the potential for future dominance of the timber stock in the country (Moravčík et al., 2021). The National Forest Inventory data also supports this trend, with beech comprising approximately 40 % of all trees with a diameter at breast height below 7 cm (Šebeň et al., 2017). The expansion of beech cover was driven, at least in part, by an increasing reliance on natural regeneration as a component of prescribed forest management. Economic and environmental factors motivate this shift away from planting by hand. Natural regeneration does not incur additional costs, making it economically attractive, while it aligns with the principles of close-to-nature forest management (Barna et al., 2011). The successful natural regeneration of beech in the area has been documented extensively, highlighting its ability to tolerate varying levels of shade and open conditions (Feldmann et al., 2020; Jaloviar et al., 2020). European beech is also adaptable to a wide range of soil types and tolerates varying pH levels, except in extremely acidic conditions (Walthert et al., 2013).

The key distinction between naturally regenerated and planted forests lies in the tree density of the youngest cohorts. When beech

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seedlings are planted, they are typically established at a density of 2–3 thousand individuals per hectare (Repáč et al., 2017). However, a dense carpet of hundreds of thousands of individuals can cover the same area in the case of a successful beech mast. For example, Šebeň et al. (2017) observed 520 thousand seedlings per hectare in a 4-year-old naturally regenerated beech stand growing in full sunlight without the cover of a mature stand. The growth dynamics of planted and natural stands thus differ significantly during the initial stages of growth, driven by the availability of crown space as a proxy resource (Holgén and Hånell, 2000). In planted forests, intense competition for light is delayed until canopy closure occurs, but it begins right from the start in dense, naturally regenerated stands. Small seedlings strive to grow and expand their crowns, while less competitive individuals are outcompeted by more vigorous neighbours (Fuentes et al., 2010), resulting in a substantial reduction in tree numbers during the early stages of stand growth.

Given the long life span of most tree species, forest mensuration data are typically gathered every 10 + years and are suitable for describing stand development throughout the harvest cycle (Kershaw Jr et al., 2016). However, although common in most of Europe at 10 years or similar intervals (Gschwantner et al., 2022), these periodic observations are unlikely to capture the rapid dynamics of the early stages of forest growth. There is a gap in understanding how intense competition impacts stand productivity and tree survival during the initial growth phase (Axer et al., 2021). While older stands with much larger biomass stocks attract research attention (e.g., Le Goff and Ottorini, 2022), it is essential to recognise that young forests exhibit different biomass allocation patterns compared to older stands (Konôpka et al., 2016) and experience far higher mortality rates (Larson et al., 2015). These factors shape the development of the emerging forest and determine the composition and density of the mature stand that will eventually emerge. In a young forest, growth and mortality processes coincide and overlap each growing season, rendering estimates of cumulative biomass production and mortality based on the typical 10-year observation period meaningless. Since young trees have different biomass allocation patterns than mature trees, challenging the direct application of biomass allometric models typically developed for older stands (West and West, 2009; Pajtk et al., 2018).

This study is motivated by several factors, including the lack of understanding of dynamics in very dense stands and the need for specific allometric models to inform forest management practice. A growing body of literature discusses the role of forests in the global carbon cycle and their potential contribution to climate change mitigation (Favero et al., 2020). Climate change models long predicted an increase in the frequency and severity of weather conditions and events that may accelerate forest decline (Bréda and Peiffer, 2014), and there is already evidence of such a shift (García-Duro et al., 2021). For instance, the current large-scale Norway spruce dieback in Czechia and neighbouring regions serves as a relevant example where such diebacks contribute to the expansion of land covered by young forests (Čermák et al., 2021; Krejza et al., 2021), including those dominated by beech. Consequently, there is a need to describe the growth dynamics of young, dense forests accurately. The objectives of this paper were, therefore, (i) to develop aboveground allometric models for young naturally regenerated European beech, (ii) to utilise these models to describe the productivity and biomass accumulation in five beech forests during an early decade of growth, and (iii) to estimate the impact of intense competition on the transfer of biomass from live to dead pool.

## 2. Material and methods

### 2.1. Stand selection

The fieldwork for this study was conducted between 2007 and 2021 in the lower and middle altitudes of the Inner Western Carpathians, Central Slovakia. This region was selected as it represents current and

likely future environmental conditions suitable for European beech and where this species has been increasing its dominance for some time (Barna et al., 2011). To begin, we utilised the National forest stand database (<http://gis.nlcsk.org/igis/>) to identify suitable stands of naturally regenerated European beech. We selected even-aged stands, with a maximum age of 10 years at the time of selection, and growing on a mesotrophic cambisol. We then visited all stands identified from the database to verify their characteristics. We ultimately selected nine young stands that met further criteria verifiable in situ: at least 90 % contribution of beech to stand density, full canopy cover, absence of visible pest or browsing damage, and no history of silvicultural interventions since the regeneration stage. Our fieldwork activities encompassed two main missions: (i) sample aboveground tree parts to establish allometric relationships and (ii) conduct repetitive measurements to estimate biomass stock, biomass production, and tree mortality.

#### 2.1.1. Destructive sampling

The sampling of aboveground tree biomass to construct allometric equations was conducted in three campaigns in August and September of 2010, 2015, and 2020. Each sampling campaign covered three stands, creating a dataset of destructively sampled trees from all nine originally selected stands. The timing of sample collection was chosen to coincide with the period of fully developed foliage. We selected 25–30 individual trees within each sampled stand, resulting in 262 trees harvested (Table 1). Care was taken to avoid damaged, deformed, or atypically shaped trees and trees on the edges of forest stands. Trees representing all bio-sociological positions, including dominant, co-dominant, intermediate, and suppressed, were included in the sample. Severely suppressed individuals showing initial symptoms of crown dieback were excluded.

Each selected tree was felled, and the stem diameter at the base ( $D_0$ ) was measured using a digital calliper (Format IP 67,  $\pm 0.01$  mm). Subsequently, all branches were detached from the stem using secateurs and placed in separate bags. The height of each tree ( $\pm 1.0$  cm) was determined as the length of the now branch-free stem using a tape measure. All collected samples were transported to the laboratory, where the foliage was manually separated from the branches. The aboveground tree biomass compartments, including the stem, branches, and leaves, were dried in a large-capacity oven at 95 °C. The stems were dried for 120 h, branches for 72 h, and foliage for 48 h to ensure constant weight was reached, we used laboratory oven Memmert UN750 (Mettler GmbH + Co. KG, Germany). The dried tree components were then weighed with an accuracy of 0.05 g (RADWAG WLT 3/6/X scale), allowing the determination of component biomass at the individual tree level.

#### 2.1.2. Annual tree observations

Data collection describing tree growth and vigour spanned 15 years, starting from autumn 2007 and concluding in autumn 2021. In autumn 2007, five circular sampling plots were established within each of the selected stands, ensuring a minimum distance of 20 m between them and avoiding stand edges. The diameter of the sampling plots was between 1.6 and 3.0 m, modus was exactly 2.0 m, and each plot contained around 10 individual beech trees on average at the end of the observation. Each tree within the plot was labelled with a metallic marker for identification. Stem diameter at base ( $D_0$ ) was measured using a digital calliper as above. At the same time, tree height was determined using a measuring pole for trees up to 4 m ( $\pm 5$  cm) or a hypsometer for trees exceeding the 4-meter threshold (Vertex 5 Haglöf,  $\pm 0.01$  m). All measurements were carried out in late autumn, after the annual expansion of girth and height had ceased but before leaf fall. Trees that died within the current year were recorded to track tree mortality. No recruitment into the canopy or establishment of new trees within the sampling plots was observed in any of the stands due to intense competition during the period of observation from 2007 to 2021.

Annual measurements were started in all nine selected stands.

**Table 1**

Size and weight of 260 European beech sample trees destructively sampled to develop allometric equations for aboveground biomass and its components.

Characteristics	Mean	SD	Median	Min	Max	25. p	75. p	Skewness
Diameter D <sub>0</sub> (mm)	23.4	22.3	15.21	4.2	129.0	10.4	27.2	2.543
Tree height (m)	2.54	2.81	1.48	0.24	13.05	0.83	3.00	2.174
Stem with bark (kg)	1.023	3.474	0.040	0.0009	26.743	0.014	0.284	4.941
Branches (kg)	0.231	1.090	0.012	0.0001	13.880	0.004	0.087	9.762
Foliage (kg)	0.066	0.209	0.012	0.0005	2.472	0.005	0.048	8.385
Aboveground (kg)	1.158	4.154	0.066	0.0015	43.095	0.024	0.434	6.533

However, as the study progressed, the number of stands observed gradually decreased from nine to five (Table 2), as some fell afoul of our criteria to observe stands free from human intervention and reasonably undamaged. One stand suffered severe damage from snow, another experienced bark browsing by red deer (*Cervus elaphus* L.), and two stands were thinned due to a misunderstanding with the local forester, leading to their progressive elimination from the study. This paper reports only on measurements conducted in the five undamaged stands.

## 2.2. Data processing and modelling

### 2.2.1. Aboveground biomass models

We developed allometric relationships for three distinct tree components: foliage, branches, and stem over bark, as well as for the total aboveground tree biomass. Diameter, height, and their combination were utilised as predictors in constructing these models. The model development and comparison process followed the methodology outlined in Pajtk et al. (2008), models incorporating diameter (D<sub>0</sub>) and height (H) as predictor variables demonstrated the best performance. Consequently, we exclusively utilised equations with these two predictors in subsequent biomass calculations. The general equation for the models is as follows

$$Y = b_0 \cdot X_1^{b_1} \cdot X_2^{b_2} \cdot X_3^{b_3} \dots X_n^{b_n} \cdot \theta \quad (1)$$

where  $Y$  is the dependent variable,  $X_1 - X_n$  are independent variables,  $b_0 - b_n$  are model coefficients and  $\theta$  represents the multiplicative error term. We did not log-transform this function to obtain its linear form following (Pajtk et al., 2018).

### 2.2.2. Model implementation on a stand level

We used our location-specific allometric relations to calculate several descriptors of stand productivity on an area basis. For this purpose, data from 11 repetitive stand measurements were implemented, we have arbitrarily chosen the period between the years of 2010 and 2020. Stock of aboveground biomass (S<sub>ab</sub>) was calculated as the sum of biomass of individual tree components of all living trees in a specific year. Net primary productivity (NPP) was defined as the new aboveground biomass produced by living trees in a given year (ANPP, e.g. Gower et al., 1996). The concept of decennial productivity of aboveground biomass (DP<sub>ab</sub>) in this study builds on annual net primary productivity established as the difference in living biomass between the current and previous year (Waring et al., 1998). The DP<sub>ab</sub> represents the sum of annual NPP estimates over 10 years. Decennial productivity of

woody aboveground biomass (DP<sub>wab</sub>) was calculated as DP<sub>ab</sub>, but includes only the annual accumulation of woody biomass over bark in stems and branches. Decennial mortality of aboveground biomass (DM<sub>ab</sub>) was calculated as the sum of woody biomass of trees which have died in each year over 10 years. Finally, the decennial increment of woody aboveground biomass (DCI<sub>wab</sub>) is defined as biomass increment over 10 years. This is one of the key productivity indicators used in commercial forestry and is calculated as the difference between living woody biomass stock in year  $x$  and year  $x-10$ . DCI<sub>wab</sub>, therefore, cannot capture the productivity of trees that have died during the observation period due to competition or pest and pathogen pressure.

### 2.2.3. Regressions model fitting

Data describing tree and stand development were used to generate regression models that best describe observed trends. A range of models was tested in each instance, the best-fitting model was chosen on the basis of AIC. Statistica 13 (Tibco Soft) was used to fit regression models, for each dataset, we selected a range of models capable of capturing the process under investigation, ranging from simple linear models to quadratic one-phase decay equations.

## 3. Results

Destructively sampled beech saplings exhibited a diameter range of 4.2 to 129 mm (D<sub>0</sub>), and a height range of 0.25 to 13.05 m (Table 1). We pooled all data from destructive sampling to Fig. 1. construct allometric models suitable for beech forests originating from natural regeneration. We found relatively conservative relationships between D<sub>0</sub>, H, and the biomass of all sampled components (Table 3 and Fig. 2). Diameter (D<sub>0</sub>) was a slightly better predictor of tree biomass than height, and incorporating both predictors into a single model led to a small improvement in model performance (Table 3). Among the different biomass components, stem biomass was predicted with the highest accuracy, while equations for foliage biomass were the least accurate across all model combinations.

Juvenile trees are known for rapid changes in the proportion of standing biomass allocated to different pools. Our beech stands had similar dynamics; the relative contribution of foliage biomass shifted from over 50 % to less than 5 % in stands ranging between 5 and 25 years old (Fig. 3). This rapid change in tree biomass allocation is particularly pronounced in trees with D<sub>0</sub> up to 50 mm. Beyond this threshold, the rate of change slows down, and the ratios of biomass compartments stabilise.

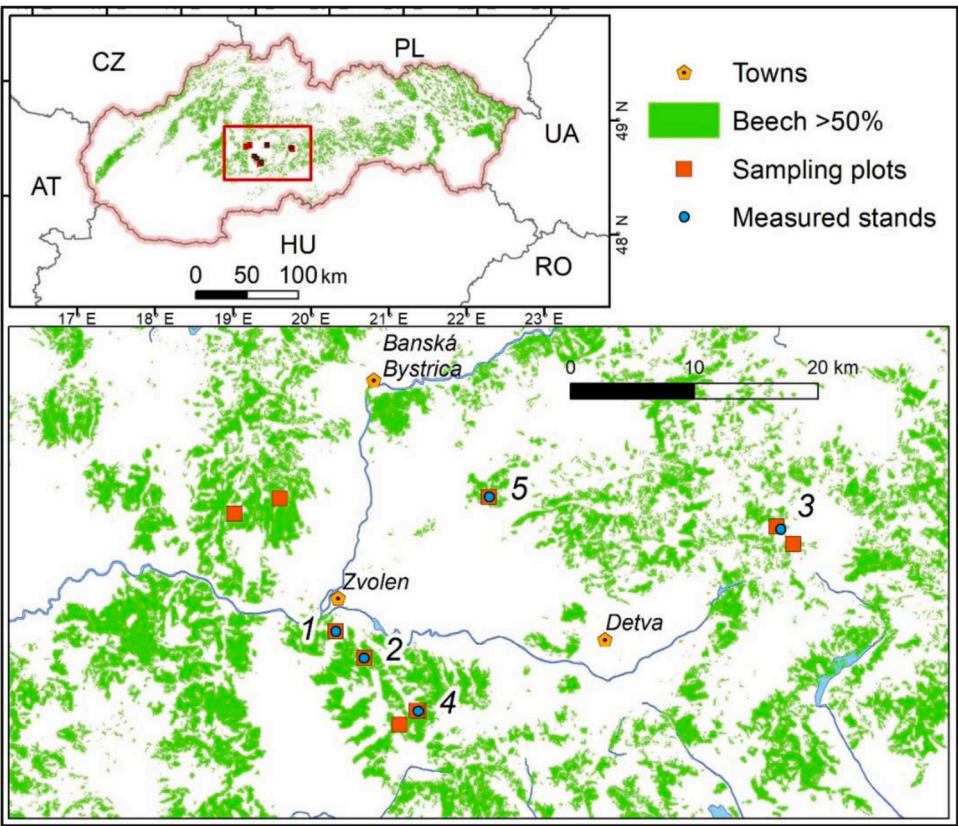
Rapid changes at the stand level characterise the early growth stages

**Table 2**

Location and stand description of five European beech stands used to observe stand development between 2008 and 2021. Stand density uncertainty expressed as standard deviation among sub-plots within a stand.

Site number	Name of site	Geographical unit	WGS coordinates		Altitude (m a.s.l.)	Stand age in 2010 (years)	Stand density in 2010 (trees .100 m <sup>-2</sup> )
			North °	East °			
1	Pustý Hrad	Stiavnicke Mts.	48.5521	19.1253	464	5	4596 ± 2153
2	Kralova	Javorie	48.5341	19.1583	514	6	2293 ± 789
3	Vrchslatina	Slovak Ore Mts.	48.6492	19.6034	978	7	1358 ± 213
4	Sekier	Javorie	48.4986	19.2216	661	10	482 ± 153
5	Hrochot	Polana	48.6576	19.2821	588	13	1256 ± 418





**Fig. 1.** Location of European beech sampling plots (destructive sampling) and measured stands (annual tree size measurements). The areas show forest stands with the proportion of European beech over 50 %.

**Table 3**  
Parameterisation of allometric equations based on diameter ( $D_0$ ) and tree height ( $H$ ) in young European beech, where  $b_0$ ,  $b_1$  and  $b_2$  are regression coefficients; S.E. is standard error; P is p-value;  $R^2$  is coefficient of determination and MSE is mean square error,  $\lambda$  is logarithmic transformation bias and S.D. is standard deviation of the correction factor.

s	Tree component	$b_0$	S.E.	P	$b_1$	S.E.	P	$b_2$	S.E.	P	$R^2$	MSE	$\lambda$	S.D.	AICc
$D_0$	Stem over bark	-11.352	0.099	<0.001	3.030	0.034	<0.001				0.969	0.153	1.079	0.445	-396
	Branches	-12.697	0.141	<0.001	3.033	0.048	<0.001				0.939	0.292	1.136	0.561	-205
	Foliage	-10.231	0.145	<0.001	2.137	0.049	<0.001				0.879	0.309	1.148	0.577	-904
	Aboveground	-10.519	0.088	<0.001	2.904	0.030	<0.001				0.973	0.114	1.057	0.360	-5.16
$H$	Stem over bark	-3.877	0.040	<0.001	2.382	0.039	<0.001				0.934	0.324	1.172	0.692	-39.2
	Branches	-5.158	0.066	<0.001	2.246	0.066	<0.001				0.819	0.866	1.505	1.677	-707
	Foliage	-4.885	0.062	<0.001	1.514	0.061	<0.001				0.702	0.759	1.417	1.282	-1451
	Aboveground	-3.332	0.046	<0.001	2.216	0.046	<0.001				0.902	0.417	1.229	0.881	-15.23
$D_0$ and $H$	Stem over bark	-8.690	0.129	<0.001	1.934	0.051	<0.001	0.948	0.041	<0.001	0.990	0.050	1.024	0.220	-623
	Branches	-12.212	0.313	<0.001	2.833	0.125	<0.001	0.171	0.099	0.085	0.940	0.289	1.134	0.554	-802
	Foliage	-11.212	0.317	<0.001	2.541	0.126	<0.001	-0.367	0.100	<0.001	0.884	0.296	1.142	0.571	-1497
	Aboveground	-8.789	0.156	<0.001	2.192	0.062	<0.001	0.612	0.049	<0.001	0.983	0.072	1.035	0.270	-17.05

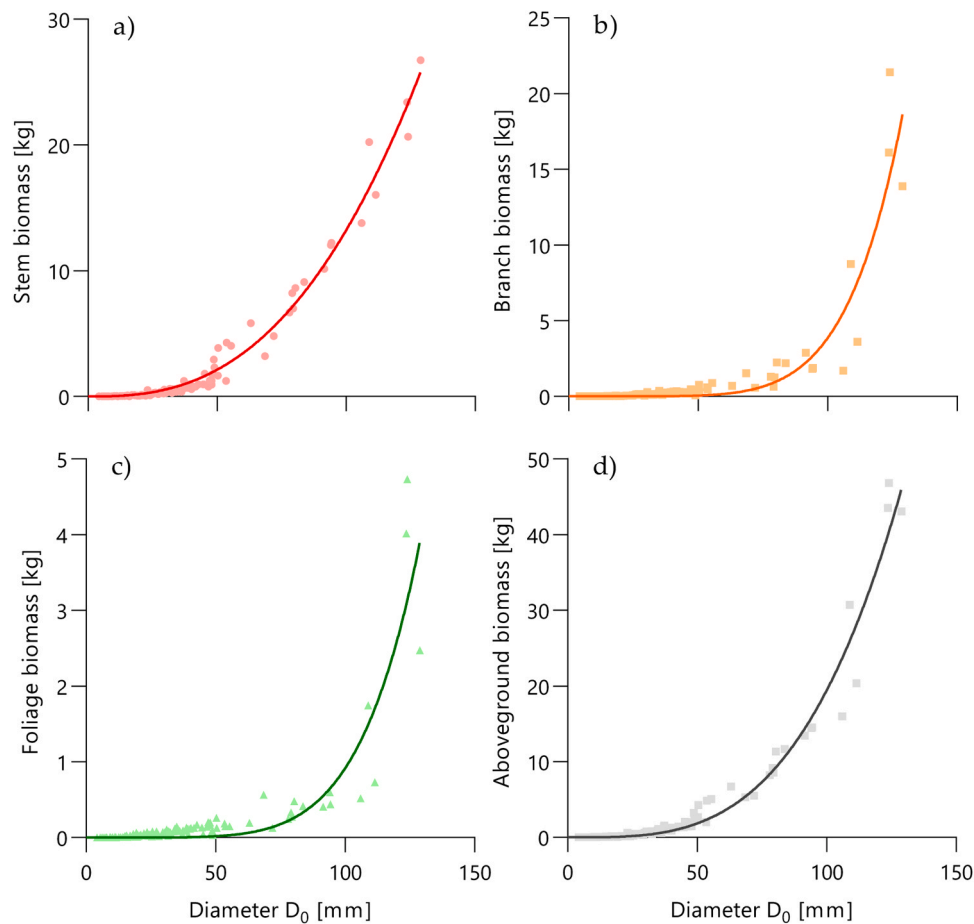
of beech. The extremely high tree density in naturally regenerated stands leads to intense competitive pressure, resulting in a sharp decline in tree numbers (Fig. 4). In our stands, a one-phase decay curve fitted the aggregate data best, indicating a reduction from 420 to 36 thousand trees per hectare between 5 and 20 years of age.

Biomass equations developed through the destructive sampling of trees outside our permanent observation plots were then applied to all trees repeatedly measured within the plots. Throughout the period from 2010 to 2020, all stands grew rapidly. Table 4 provides the initial and final aboveground biomass stock ( $S_{ab}$ ) for each stand. Over the decade,  $S_{ab}$  increased 2.7 (Kralova) to 3.3 (Sekier) -fold in the least and most productive stands, respectively. Living biomass corresponds to growth from 48.23 t ha<sup>-1</sup> to 135.94 t ha<sup>-1</sup> in Kralova and from 75.66 t ha<sup>-1</sup> to 255.04 t ha<sup>-1</sup> in Sekier.

Decennial change in woody biomass typically called the decennial

increment ( $DCI_{wab}$ ), increased by 132.18 t ha<sup>-1</sup> between 2010 and 2020, on average. However, the commonly used method of  $DCI_{wab}$  calculation considers only live trees and does not account for the productivity of trees that died during this period. To capture the total woody production over the decade, we considered the decennial production ( $DP_{wab}$ ), which averaged 176.34 t ha<sup>-1</sup>. This indicates that the decadal mensuration commonly used in commercial forestry practice does not capture approximately a quarter of the woody growth in young naturally regenerated stands.

Tracking stand productivity annually allowed us to calculate the flux of woody biomass from living to the dead pool and compare the inter-annual dynamics of biomass production and loss. Fig. 5 shows the annual variation of stem, branch and foliage productivity, clearly illustrating a much larger variation in productivity than mortality. While stand productivity is likely affected by interannual changes in weather



**Fig. 2.** Biomass model fits for (a) stem biomass ( $B_s$ ,  $R^2=0.97$ ,  $AICc=-396.8$ ), (b) branch biomass ( $B_b$ ,  $R^2=0.94$ ,  $AICc=-205.0$ ), (c) foliage biomass ( $B_f$ ,  $R^2=0.88$ ,  $AICc=-904.6$ ) and aboveground biomass ( $B_{ab}$ ,  $R^2=0.98$ ,  $AICc=-5.165$ ) in young European beech trees using stem diameter at base  $D_0$  as the predictor variable.

patterns across the five stands (exponential growth model  $R^2 = 0.46$ ), tree mortality is much more varied over the decade ( $R^2 = 0.29$ ). Finally, the contribution of foliage to  $S_{ab}$  slowly declined between 2010 (6.2–12.3 %) and 2020 (4.9–5.9 %). Interestingly, the variance of the proportion of foliage to total aboveground biomass between stands was much higher in 2010 ( $9.5 \pm 2.63$  %) than in 2020 ( $5.15 \pm 0.93$  %).

## 4. Discussion

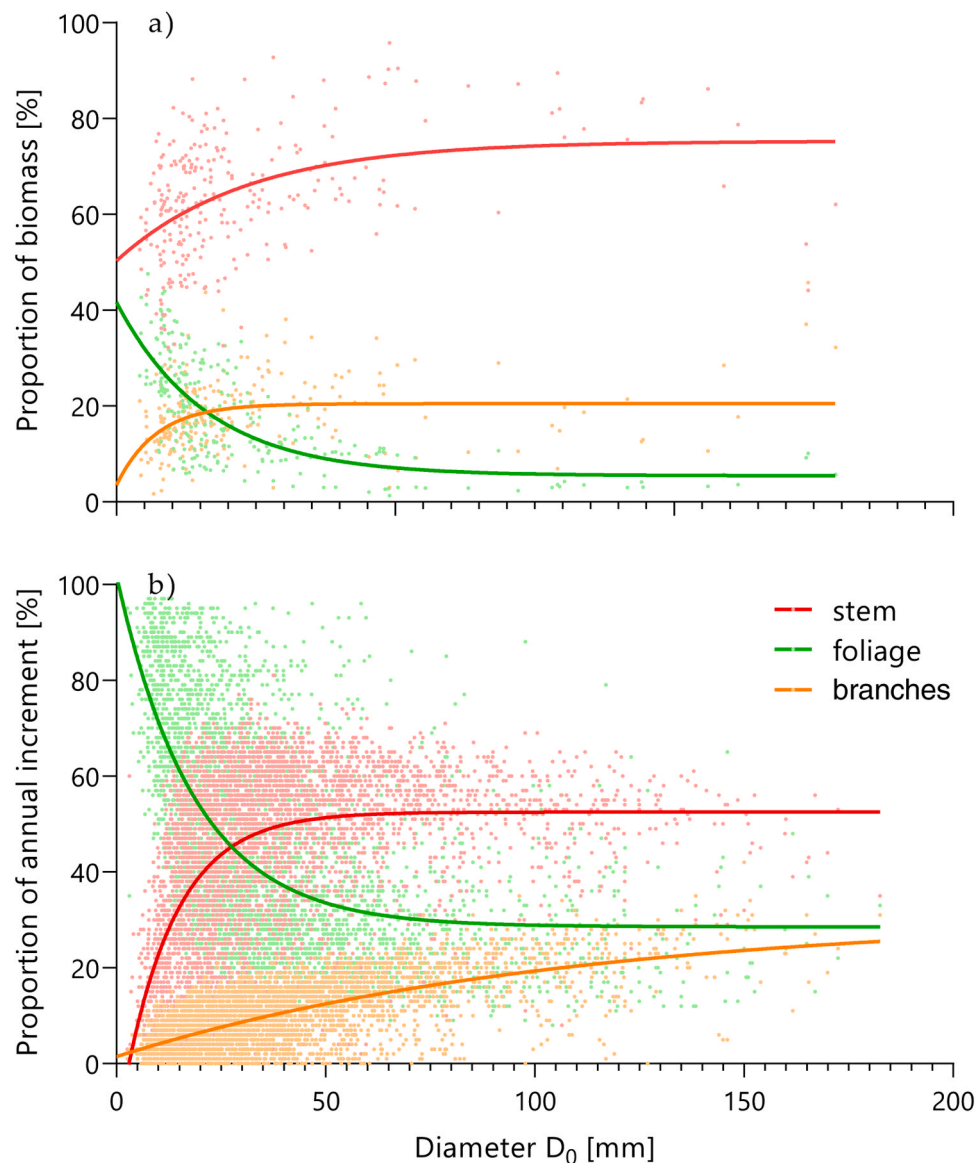
### 4.1. Beech biomass models

In this study, we developed new allometric models for aboveground biomass estimation in young naturally regenerated stands of European beech. These models apply to stands characterised by high density and intense competition without management interventions. Previous allometric models for European beech have predominantly focused on middle-aged or mature trees, with limited coverage of young stands {Dutcă, 2020 #38; Husmann, 2018 #28; Le Goff, 2022 #42; Muukkonen, 2007 #18; Vejpusková, 2015 #14}. We build upon the work of Annighöfer et al. (2016), who provided generic biomass equations for seedlings and saplings of various tree species in Europe. However, their equations predict aboveground biomass as a whole and do not address biomass partitioning into individual components. Similarly, Widagdo et al. (2020) emphasised the need for species-specific biomass allometric equations and biomass partitioning models for planted and natural *Larix gmelinii* trees in northeast China. They highlighted the substantial differences in biomass allocation patterns between trees experiencing varying levels of competition for resources.

We recognise that initial stand density plays a crucial role in forest

growth modelling, and accurately parameterising its relationship with biomass allocation is essential (Dahlhausen et al., 2017). To address this, we have developed separate models for naturally regenerated forests, acknowledging their distinct characteristics and dynamics. Our findings highlight the significant changes in biomass allocation during the initial stages of forest growth, challenging the use of allocation data from older stands where biomass allocation has already approached its final values (Wirth et al., 2004). It is worth noting that the five stands we observed for a decade had different tree densities at the beginning of our observation period. Alongside age, these variations could be influenced by factors such as masting events, early herbivore grazing, ground vegetation, soil conditions, and potential differences in canopy cover during seedling establishment (Barna et al., 2011; Bílek et al., 2014; Vacek, 2017). However, towards the end of the observation window, all stands converged to a similar tree density, suggesting that environmental conditions impose constraints on stand development once a critical tree size is attained (Long and Vacchiano, 2014).

Considering these dynamics and the interplay between initial stand density, biomass allocation, and environmental factors, our models provide valuable insights into the biomass dynamics of young naturally regenerated stands of European beech, contributing to a more comprehensive understanding of forest growth and supporting improved parameterisation in forest growth models. Our findings are consistent with previous research, which suggests that stem diameter is a reliable predictor of aboveground tree component biomass. Adding tree height as a second predictor variable in our models resulted in only a slight improvement in their performance. Typically, tree diameter is the preferred variable for biomass estimation, as it is relatively easier and quicker to measure, particularly in challenging field conditions.



**Fig. 3.** Proportion of total aboveground biomass and increment in three compartments as a function of stem diameter at base  $D_0$  in European beech. Pane (a) shows the contribution of stem ( $R^2=0.19$ ,  $AICc=1274$ ), branch ( $R^2=0.10$ ,  $AICc=1011$ ) and foliage ( $R^2=0.49$ ,  $AICc=1064$ ) to current-year aboveground stock ( $n = 262$ ), while pane (b) shows the contribution of stem ( $R^2=0.30$ ,  $AICc=22735$ ), branch ( $R^2 =0.43$ ,  $AICc=24281$ ) and foliage ( $R^2=0.37$ ,  $AICc=13678$ ) increment to the annual aboveground total ( $n = 4261$ ).

However, it is worth noting that Dutcă et al. (2020) have demonstrated that models using both stem diameter and tree height provide more accurate predictions of tree aboveground biomass at the plot or stand level compared to models based on stem diameter alone. Using diameter and height measurements can enhance the accuracy of biomass estimates, especially when assessing larger-scale forest dynamics.

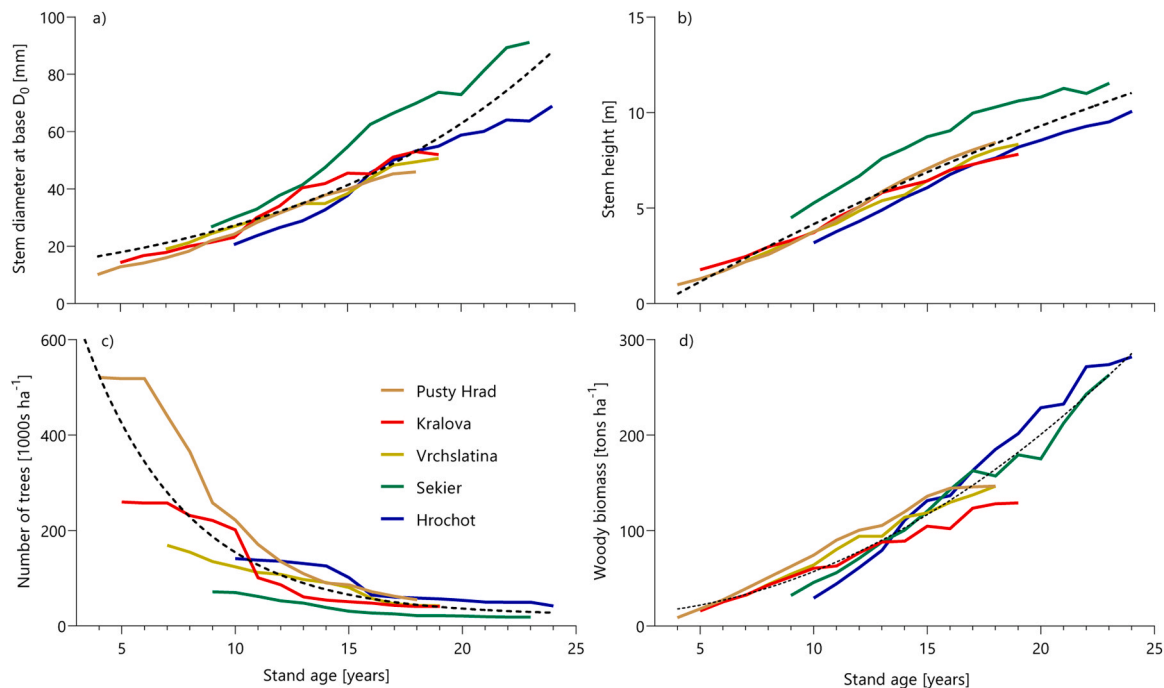
#### 4.2. Beech stand productivity

The historical Czechoslovak yield tables provided information on beech forests starting from 20 years of age, without details on younger stands. According to the tables, a 20-year-old beech forest of yield class, comparable to the five measured in this study, had a density of approximately 40 thousand trees per hectare. Our findings align well with this information, as our best-fit curve (Fig. 4c) indicates a density of 36 thousand trees per hectare at 20 years of age. Applying our allometric models to sampling plot data, we estimated that average annual aboveground net primary productivity (ANPP) ranges between 16 and

31 tons of dry mass per hectare. Comparing these values with other studies, Campioli et al. (2011) reported ANPP of 12 tons per hectare per year for 31 to 38-year-old European beech stands in North-Eastern France, while Mund et al. (2010) measured approximately 13 tons per hectare per year in a mature beech-dominated forest in central Thuringia, Germany. Zianis and Mencuccini (2005) estimated ANPP in mature unproductive forests of *Fagus moesiaca* in Greece to be between 2 and 16 metric tons per hectare per year. The discrepancy in ANPP values between the mentioned and our study can be attributed to the age of the stands. In our case, all the forests were in the initial stage of rapid expansion, which further emphasises the importance of having specific allometric equations for this age cohort. Stand level ANPP reaches its maximum in young forest stands and then declines as stands mature, as indicated by Gower (2003).

Growth patterns and dynamics in young stands differ significantly from those in older and more mature stands. For example, we observed a decline in foliage mass as a proportion of total aboveground biomass within a 10-year period, decreasing from approximately 10 % to 5 %.





**Fig. 4.** Development indicators in five young European beech stands under 25 years old. Dashed line represents best-fit models for (a) stem diameter at base  $D_0$  (exponential,  $R^2=0.86$ ,  $AICc=292$ ), (b) stem height (polynomial,  $R^2=0.89$ ,  $AICc=-14.9$ ), (c) tree density (one-phase decay,  $R^2=0.79$ ,  $AICc=588$ ) and (d) above-ground woody biomass (exponential,  $R^2=0.95$ ,  $AICc=402$ ).

**Table 4**  
Aboveground biomass stock in 2010 and 2020 in individual tree components and biomass woody aboveground productivity calculated as cumulative annual growth ( $DP_{wab}$ ) or decennial current increment ( $DCI_{wab}$ ) in five European beech stands. All values in tons dry mass per hectare, unless otherwise stated.

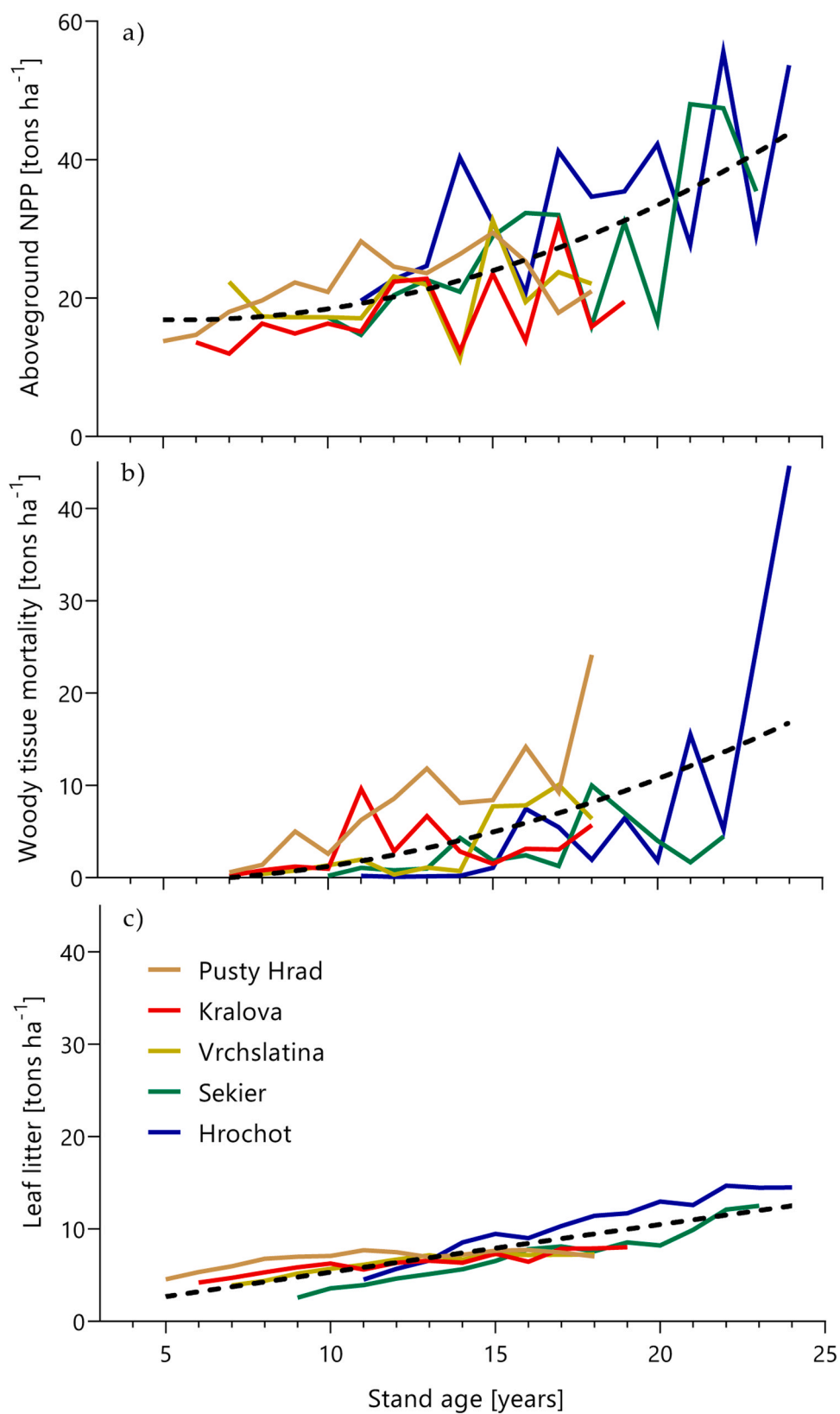
Site		(1) Pusty hrad		(2) Kralova		(3) Vrchslatina		(4) Sekier		(5) Hrochot	
Stock	Year	2010	2020	2010	2020	2010	2020	2010	2020	2010	2020
	Stem	31.14	118.48	33.72	96.94	33.75	116.67	55.41	175.95	62.07	207.10
	Branches	7.84	27.20	9.21	31.11	9.85	29.90	15.62	66.96	17.22	66.72
	Foliage	5.96	7.45	5.30	7.89	5.18	7.52	4.63	12.13	6.60	14.48
	Aboveground	44.94	153.13	48.23	135.94	48.78	154.09	75.66	255.04	85.89	288.30
Productivity	$DP_{wab}$	165.2		121.5		136.5		215.6		242.9	
	$DCI_{wab}$	106.7		85		102.9		171.8		194.5	
	$((DP_{wab}-DCI_{wab})/D_{pwab}) * 100$	35.4 %		30 %		24.6 %		20.3 %		19.9 %	

This finding aligns with similar dynamic changes in foliage contribution observed in other tree species, such as *Cunninghamia lanceolata* in China, where the ratio of foliage to total stock stabilised at around 20 years of age (Xiang et al., 2021). The intense competition for canopy space, driven by the rapid expansion of aboveground biomass in our stands, reduced canopy depth. Initially, the foliage covered the entire vertical profile of the trees, but over time, it was reduced to only the upper part of the tree crowns (data not shown). This process of canopy reduction and restructuring has been well documented by Dassot et al. (2015), who observed changes in tree morphology, including a decrease in the relative proportion of live crown to tree height and stagnating crown projection area. Young stands' shorter and narrower crowns accommodate less foliage, which is critical for tree survival at this stage. It is important to note that vertical growth becomes a critical process during this period, sometimes leading to the development of unstable stands. Thus, allometric equations for young trees are essential for constructing forest growth models that can optimise thinning decisions to enhance productivity and ensure stand stability. These equations provide valuable information for accurately estimating biomass allocation and understanding the dynamics of young beech stands. By incorporating allometric equations for young trees recruitment into forest growth models (Petritsch et al., 2007; Irauschek et al., 2021), we can better manage and plan interventions such as thinning, to optimise stand development and

overall productivity.

Our data offer an interesting view of the differences in annual NPP variation between the growth of woody parts (stem and branches) and foliage. As beech is deciduous, annual leaf production is approximately equal to litter fall. While the production of woody parts, which dominates annual NPP from  $D_0$  of about 25 mm, demonstrates significant inter-annual oscillation (Fig. 5a), leaf litter fall shows only minimal inter-annual variability (Fig. 5c). This is likely due to the different lengths of the tissue formation periods, previous studies conducted in Slovakia (Barna et al., 2011) have shown that leaf growth period lasts until the end of June, and is locally known as 'St John's shoots'. However, the diameter increment corresponding to the formation of woody parts lasts until early October (Bošefa et al., 2013). The shorter foliage growth period typically means only a small influence of weather conditions in the current year, as spring is usually characterized by sufficient soil moisture. Conversely, a combination of temperatures and precipitation patterns shapes the annual diameter increment throughout the growing season, which carries a higher risk of drought exposure.

Finally, we found a significant discrepancy between productivity estimates based on annual and decennial observations. The annual observations allowed us to track tree mortality, which contributed to the flux of woody biomass from the living to the dead pool. As a result, the cumulative productivity over the 10 years was higher than the



**Fig. 5.** The development of aboveground net primary production (a,  $R^2 = 0.47$ ,  $AICc=276$ ), woody tissue mortality (b,  $R^2 = 0.29$ ,  $AICc=217$ ) and annual leaf litter production (c,  $R^2 = 0.63$ ,  $AICc=67.7$ ) in five young European beech stands. Dashed lines represent best-fit models, all are exponential equations.

productivity estimated from stocks measured only at the beginning and end of the period. Overall, we estimate that in young beech forests, approximately a quarter of aboveground net primary production (ANPP) is missed when relying solely on the typical forest mensuration cycle carried out every 10 years. This finding is important for understanding carbon sequestration and carbon cycling in forest stands. On an annual basis, approximately 20 % of current woody mass production left the living biomass pool due to tree mortality, and an additional 5–10 % of ANPP was invested in short-lived foliage. During the very early growth stages of naturally regenerated forests, many trees do not survive due to intense competitive pressure. Our study quantifies this process and highlights its importance for biomass and carbon accumulation in European beech forests. To put this into context, latest Slovak forest inventory data estimate the carbon stock in young trees - less than 7 cm DBH – at  $3.8 \pm 1.8$  million tons (Šebeň et al., 2017), thus around 1 million tons of C cycled through the forests every decade could be unreported as a result of decennial inventory. Understanding the dynamics of tree mortality and carbon allocation within different biomass pools is crucial for accurately assessing carbon sequestration rates and overall ecosystem productivity in young forest stands.

## 5. Conclusions

Our study presents new allometric models describing the rapid development of young European beech forests. The observed stands showed rapid growth and intense competition, leading to changes in biomass allocation and canopy structure over the decade-long observation period. Foliage mass declined as a proportion of total aboveground biomass, indicating a shift in resource allocation. We also highlight the discrepancy between estimates of productivity based on annual and decennial observations. The annual observations, which accounted for tree mortality and biomass flux, resulted in higher cumulative productivity over the 10 years compared to estimates based on measurements at the beginning and end of the period. Our research fills the knowledge gap in understanding biomass dynamics and allocation patterns in young beech stands. By providing age-specific allometric models, we enhance the accuracy of biomass and productivity estimates in these forests, shedding light on carbon accumulation and the importance of tree mortality in ecosystem processes.

## CRedit authorship contribution statement

**Bohdan Konopka:** Conceptualization, Funding acquisition, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Jozef Pajtk:** Conceptualization, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Vladimir Seben:** Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. **Martin Lukac:** Conceptualization, Formal analysis, Funding acquisition, Methodology, Writing – original draft, Writing – review & editing.

## Declaration of Competing Interest

The authors do not declare any conflict of interest.

## Data Availability

Data will be made available on request.

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