Ann. For. Res. 67(2): 151-166, 2024
https://doi.org/10.15287/afr.2024.3885

ANNALS OF FOREST RESEARCH
www.afrjournal.org

Exploring the association between adaptive and growth traits and within-individual genetic diversity in common beech (*Fagus sylvatica*)

Mihnea Ioan Cezar Ciocîrlan[1,2]✉, Elena Ciocîrlan[1], Gheorghe Raul Radu[2], Dănuț Chira[2], Oliver Gailing[1,3], Costel Vînătoru[4], Ourania Grigoriadou-Zormpa[3], Boban Vucetic[3], Katharina Birgit Budde[5], Sergiu Florea[1], Mihai-Daniel Niță[1], Alexandru Lucian Curtu[1]

Ciocîrlan M.I.C., Ciocîrlan E., Radu R.G., Chira D., Gailing O., Vînătoru C., Grigoriadou-Zormpa O., Vucetic B., Budde K.B., Florea S., Niță M.D., Curtu A.L., 2024. Exploring the association between adaptive and growth traits and within-individual genetic diversity in common beech (*Fagus sylvatica*). Ann. For. Res. 67(2): 151-166.

Abstract Common beech (*Fagus sylvatica* L.) is one of Europe's most widespread forest tree species. In the actual context of climate change, this species has responded through its self-regulation mechanisms, proving a high plasticity. It is important to explore the specific mechanisms driving its response to climate change, taking into account silvicultural, phenological, and genetic perspectives and their interaction. Here, we tested for association between adaptive and growth traits and within-individual genetic diversity measured as individual heterozygosity (proportion of heterozygous loci per sampled individual), based on six genomic microsatellite markers (gSSRs, genomic simple sequence repeats) and six expressed sequence tag microsatellites (EST-SSRs) for 55 beech trees. We evaluated the spring and autumn phenology of beech trees sampled along an altitudinal gradient (560 - 1150 m) and the architectural traits using a non-destructive terrestrial laser scanning method (TLS). The effect of stand density at the onset of the growing season was evaluated by quantifying the competition through the *Hegyi* index. The onset of bud burst and senescence, as well as the length of the growing season, varied significantly and inversely proportionally with the altitudinal gradient. There was a difference of 14 days between the individuals located at the extremities of the altitudinal gradient in the onset of bud burst, 15 days in the onset of senescence, and 30 days in the length of the growing season. We obtained a very significant and positive correlation between altitude and bud burst and a very significant but negative one between altitude and the length of the growing season. An increase in tree competition directly implied a decrease in DBH and crown dimensions, especially by neighbours closer than 4 m. Stem's slenderness significantly increased with higher competition. Our results revealed a positive relationship between individual heterozygosity and the length of the growing season, as well as with the trunk volume and DBH. Higher individual heterozygosity was associated with a longer growing season, and a precocious onset of bud burst in beech. Higher heterozygosity was also associated with considerably higher total tree biomass. The genetic diversity was inversely proportional to stem forking. TLS shows great potential in extracting beech tree biomass indicators, but we still recommend using the conventional method as a complementary method for data validation, although it is time-consuming.

Keywords: common beech, heterozygosity, microsatellites, phenology, competition, slenderness, terrestrial scanning, 3D tree shape, architectural traits.

Addresses: [1]Faculty of Silviculture and Forest Engineering, "Transilvania" University of Brasov, Brasov, Romania | [2]Brasov Research Station, National Institute for Research and Development in Forestry "Marin Drăcea", Brasov, Romania | [3]Department of Forest Genetics and Forest Tree Breeding, Büsgen-Institute, Georg-August University of Göttingen, Göttingen, Germany | [4]Plant Genetic Resources Bank for Vegetables, Floriculture, Aromatic, and Medicinal Plants Buzău, Buzău, Romania | [5]Department of Forest Genetic Resources, Northwest German Forest Research Institute, Hann, Münden, Germany.

✉ **Corresponding Author:** Mihnea Ioan Cezar Ciocîrlan (mihnea.ciocirlan@icas.ro).

Manuscript: received September 28, 2024; revised December 4, 2024; accepted December 4, 2024.

Introduction

Common beech is one of Europe's most important and widespread forest tree species (Houston et al. 2016). It is known to be drought-sensitive and to have a highly competitive potential (Leuschner 2020). Due to the high plasticity capability that this species manifests through its self-regulation mechanisms (Ciocîrlan et al. 2022), it becomes an alternative for many coniferous monocultures as a general forest policy in Europe aims to reintroduce broadleaf tree species (Geßler et al. 2007).

In the actual context of climate change, forest management implies a better understanding of the responses of this species to variable environmental conditions (Kutnar et al. 2021) and invasive biotic agents (cryptogamic agents, invertebrates, etc.) (Chira et al. 2022, Ciceu et al. 2024). The genetic variation is responsible for determining the adaptability of trees to their environment (Müller-Starck et al. 1992). In the context of climate changes, common beech underwent a genotypic specialization, leading to different locally adapted races and ecotypes (Božič et al. 2013).

Phenology is considered a critical adaptive feature (McKown et al. 2018); it is relatively easy to observe and directly impacts a species' distribution range, survival rate, and reproductive performance (Chuine 2010). Bud burst timing and leaf senescence can be associated with susceptibility to pathogens in forest trees (van Asch et al. 2007, Krokene et al. 2011, McKinney et al. 2011). Leaf phenology is a bioindicator that is highly sensitive to temperature variation. The onset of bud burst, the period of every phenophase, and the onset of senescence (yellowing and falling of the leaves) are triggered by specific thermal thresholds (Badeck et al. 2004). The timing of bud burst in trees is an important adaptive trait with many implications for forest management (Casmey et al. 2022).

Phenology monitoring of common beech was performed both at the level of nurseries between different provenances (Nielsen & Jørgensen 2003), in climate-controlled chambers (Fu et al. 2019), and in common gardens (Besliu et al. 2024). Phenology monitoring performed along an altitudinal transect revealed that the onset of bud burst, senescence, and the length of the growing season varied inversely proportionally to the elevational gradient (Ciocîrlan et al. 2024). An individual can adapt to various site conditions, exhibiting different phenological behaviors in high and low altitudes, thus directly determining the length of their growing season (Menamo et al. 2021).

Tree growth and architecture depend on many factors, especially site conditions (Tomșa et al. 2021) and genetic makeup (Chéné et al. 2012). Each branch responds to the micro-environmental conditions (Abegg et al. 2021). Growth is an important fitness trait in forest trees, as the growth rate positively correlates with individual reproductive success (e.g., Avanzi et al. 2020) and is often used as a predictor for survival (Bigler & Bugmann 2004). In common beech, growth rate and bud burst timing are heritable traits (Gauzere et al. 2016). However, in natural settings and uneven-aged trees, growth traits such as height and DBH might instead reflect microenvironmental variation and tree age.

Terrestrial laser scanning (TLS) methods have already demonstrated potential for application in forests. In the early 2000s, it was introduced to take basic measurements of tree height and diameter (Hopkinson et al. 2004); a few years later, the application of this method led to the estimation of entire aboveground biomass (Calders et al. 2015). Nowadays, TLS can describe and characterize woody tree structures by assessing in situ 3D models of forests (Calders et al. 2020), and TLS devices are essential tools for Forest Inventories (Coșofreț et al. 2018, Torralba et al. 2022, Molina-Valero et al. 2022) and ecology and biodiversity studies (Valbuena et al. 2020, Dănilă 2021a, Dănilă 2021b).

TLS methods can successfully estimate an extensive range of forest structural indices (Pascu et al. 2019). Apostol et al. (2018)

revealed that TLS methods are as accurate as conventional ones in extracting the values of the tree's diameter. Still, they recommend the latter for extracting tree height values. In the following years, TLS methods were improved. Capalb et al. (2023) stated that the data obtained from the point clouds recorded by TLS can be successfully used to determine both the diameter and the height of the trees in even-aged and relatively even-aged spruce stands; however, reporting certain limitations in the case of small individuals. The use of TLS revealed differences in the crown structure of common beech between mixed and pure stands. More precisely, the crowns of individuals in mixed stands are wider and lower reaching than those in pure ones (Barbeito et al. 2017).

Phenotypic traits are controlled by the interactions between the genotype and the environment (Li et al. 2017, Bian et al. 2022). Heterozygosity is one of the most important characteristics that can influence the growth rate of forest trees (Mitton et al. 1980). Previous studies have shown that low individual heterozygosity, for example, due to mating of related individuals or genetic drift in small populations, can cause a reduction in fitness (reviewed in Leimu et al. 2006).

Deleterious mutations (i.e., mainly recessive mutations with adverse fitness effects) are (partly) masked in heterozygous individuals. Therefore, trees with low individual heterozygosity might show lower fitness than highly heterozygous individuals. Few loci in specific genes with significant effects (local effect) or many loci with small deleterious effects distributed across the genome (general effect) could cause such heterozygosity-fitness correlations (reviewed in Hansson et al. 2002, Szulkin et al. 2010). The combination of several putatively neutral genetic markers, such as microsatellites, can be used as a proxy for the level of genome-wide individual heterozygosity (Forstmeier et al. 2012).

Silvicultural interventions reduce the density of a stand implicitly of competition (Kirk & Berrill 2016). The competition of an individual with the surrounding trees varies, depending on the species, the size, and shape of the crown (Barbeito et al. 2017), as well as its access to resources (Fichtner et al. 2012). The competition affects seedlings (Palaghianu 2009), as well as juvenile and mature trees (Duduman et al. 2010). Crown shape and size are plastic traits and important for obtaining light, which is a limiting factor for growth (Penanhoat et al. 2024), and trees respond to the competition pressure by adjusting the crown position to increase the light interception intake (Longuetaud et al. 2013).

In this paper, we aimed to assess the variation of common beech phenological traits along an altitudinal transect in the South-Eastern Carpathians and quantify the effects of competition, micro-environment, and individual heterozygosity on phenology (bud burst and leaf senescence) and tree architecture (DBH, tree and trunk heights, total volume, and forking).

Materials and Methods

Study sites

The study was performed in the south-eastern Carpathian Mountains, along an altitudinal transect with four study sites (Figure 1), which overlapped with beech's natural range in the Brasov area. Beech forms mixed stands with deciduous trees (*Acer pseudoplatanus*, *Carpinus betulus*, etc.) and conifers (*Picea*

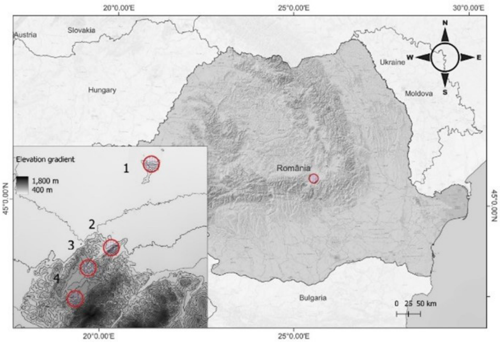

Figure 1 Geographic location of the analysed beech populations in the south-eastern Carpathians Mountains (QGis 2024).

abies and *Abies alba*). Fifty-five common beech individuals aged 80-120 years, located at a 25 m minimum distance from each other and on north-facing slopes, were selected at elevations between 560 and 1150 m (Table 1).

Table 1 Geographic coordinates of the four common beech study sites and sample size.

Site	Coordinates	Altitude (m)	No. of sampled trees
Lempes	45.725833 N 25.653889 E	560-650	26
Tampa	45.636667 N 25.591111 E	650-750	5
Solomon	45.617778 N 25.559722 E	800-1000	11
P. Lupului	45.584444 N 25.544444 E	1000-1150	13

Phenological data

Phenological observations were performed using the methodology proposed by Vitasse et al. (2009). Every individual's phenological stage was evaluated twice a week during the spring and autumn of 2023. A particular phenological stage was assigned to a tree if 50% of the buds or leaves from the upper third of the crown reached this stage (Table 2).

Table 2 Phenological stages of bud development and leaf unfolding.

Code	0	1	2	3
Phenological stage in the field				
Phenological stage	Dormant winter bud	Bud swollen	Bud burst	At least one leaf unfolding

The start of the growing season was associated with bud burst (the third phenological stage from Table 2). The onset of senescence was considered when 50% of the leaves from the upper third of the tree's crown started to turn yellow (Čufar et al. 2012, Schieber et al. 2017). The length of the growing season was calculated as the period between the start of the growing season and senescence (Drobyshev et al. 2010).

Genetic data

DNA was isolated from the 55 adult beech tree buds (Table 1) with the DNeasy Plant Mini Kit (Qiagen, Hilden, Germany). The bud samples were collected in September-October 2020. Samples were genotyped at six nuclear microsatellites (Simple Sequence Repeats, SSRs) (Asuka et al. 2004, Pastorelli et al. 2003, Vornam et al. 2004) and six gene-based Expressed Sequence Tag (EST)-SSRs (Kubisiak et al. 2009, Burger et al. 2018) (Table S1). Genotyping and marker analysis for a larger number of individuals, including 55 adult trees from this study, have been described by Grigoriadou Zormpa et al. (2024). Individual heterozygosity was calculated as the number of heterozygous markers divided by the total number of markers analysed per individual.

Competition intensity

The competition intensity of the target trees was quantified using the *Hegyi* index (Hegyi 1974). The variables used in the index calculation were the diameter of all the neighbouring trees, with at least 7 cm of DBH (diameter at breast height), and the distance between them and the target tree, within a radius of 15 m (Formula 1).

$$(z) = \sum_{i=1}^{n} \frac{D_i}{D_j} \times \frac{1}{Dis_{ij}} \qquad (1)$$

where: *j* – target tree; *i* – competitor tree within a radius of 15 m around each *j*; D – DBH (cm); D*is* – the distance between *j* and *i* (m).

Forking

Forking was evaluated according to the TreeBreeDex protocol (Ducci et al. 2012) shown in Supplementary Figure S1. Each individual was assigned a score depending on the absence or presence of forking and their number and position on the stem.

Slenderness coefficient

The slenderness coefficient (SLC) was calculated as the ratio between the total height of a tree and its diameter measured at the breast height (1.30 m) (Wang et al. 1998), according to the formula 2. Both tree architecture indicators were quantified in the same measure units (meters).

$$SLC = \frac{H}{DBH} \quad (2)$$

where: *SLC* - slenderness coefficient; *H* – the total height of the tree (m); *DBH* – diameter measured at 1.30 m (cm).

Tree architecture

The architectural characteristics of the sampled trees were evaluated using a non-destructive terrestrial laser scanning (TLS) method. A GeoSLAM Horizon Mobile Scanner was employed to capture detailed 3D representations of each tree's structure. The scanning procedure involved walking around each target tree to obtain a comprehensive point cloud, carefully minimizing occlusions caused by neighboring trees and the operator's angle to ensure complete coverage of the tree architecture.

After completing the scans, the raw point clouds were downloaded for further processing using CloudCompare software. The following steps were undertaken to prepare the data for analysis:

- Separation of Vegetation and Ground Points: The Cloth Simulation Filtering (CSF) plugin was utilized to distinguish vegetation points from ground points. This step ensured the separation of the tree structures from terrain features.
- Manual Segmentation of Target Trees: The segment tool in CloudCompare was used to extract the point clouds corresponding to each target tree manually. This ensured that only the points related to the individual trees of interest were included in the analysis.
- Noise Filtering: A noise filter was applied to remove erroneous points from reflections during the scanning process. This step enhanced the accuracy of reconstructing small branches, which is essential for detailed architectural analysis (Figure 2).

The processed point clouds were then imported into TreeQSM (Tree Quantitative Structure Models), implemented in MATLAB (Toh et al. 1999), to extract quantitative architectural traits of the trees. TreeQSM reconstructs tree structures by fitting cylinders

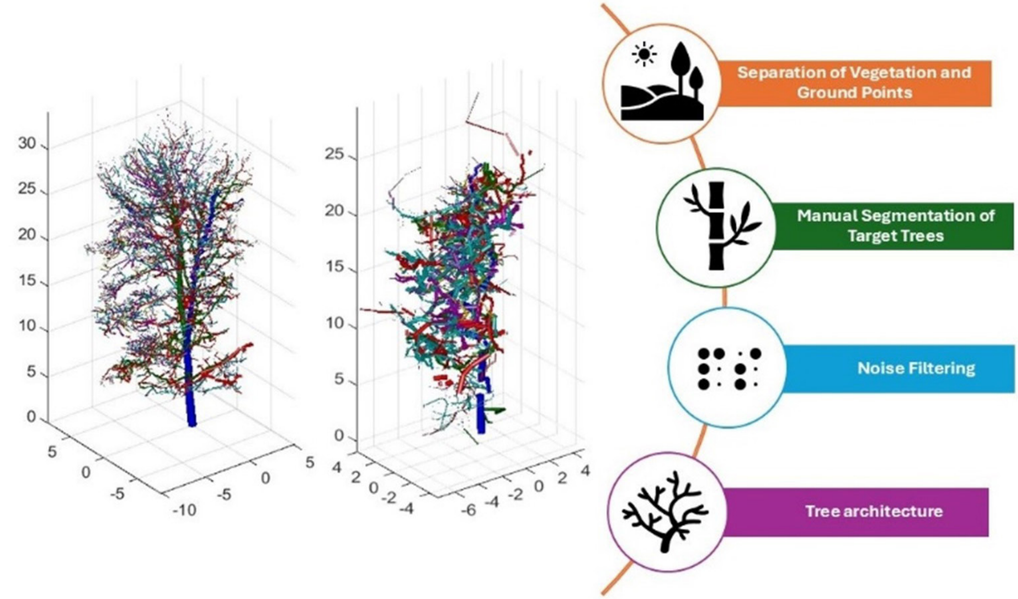

Figure 2 Segmentation and noise filtering (validated and unvalidated cases).

to the point cloud data, allowing for the estimation of various tree characteristics. For the TreeQSM analysis, the following input parameters for the number of point divisions (nPD) were used:

- nPD1 = 2: Defines the number of point divisions in the first pass of the algorithm.
- nPD2Min = 3 and nPD2Max = 2: Set the minimum and maximum number of point divisions in the second pass, refining the model for smaller branches (improved resolution).

The extracted tree characteristics included total volume, trunk volume, branch volume, tree height, trunk height, branch length, number of branches, maximum branch order, diameter at breast height (DBH), and crown diameters (average and maximum), as detailed in Table 3.

Table 3 Tree characteristics.

Tree characteristics	Formula/ Method	Reference
Total Volume	The sum of all cylinder volumes (m^3)	TreeQSM
Trunk Volume	Volume of the stem (m^3)	TreeQSM
Branch Volume	The volume of all the branches (m^3)	TreeQSM
Tree Height (H)	The distance between the base and the top of the highest branch of the tree (m)	TreeQSM
Trunk Height	The distance between the base and the top of the highest first-order branch of the tree (m)	TreeQSM
Branch Length	The sum of the length of all the branches (m)	TreeQSM
Number of Branches	The sum of all the branches (pcs.)	TreeQSM
Max Branch Order	Maximum branching order	TreeQSM
DBHqsm (DBH)	Diameter at breast height in m, the diameter of the cylinder	TreeQSM
Crown Diameter (Average)	The projection reduced to the horizon of the crown, the average value of two perpendicular directions, in m	TreeQSM
Crown Diameter (Maximum)	The projection reduced to the horizon of the crown, the maximum value of two perpendicular directions, in m	TreeQSM

Statistical analyses

The normality of the phenological data set was verified using the *Shapiro-Wilk* test. Further, depending on the p-value, the parametric test of the analysis of the variance, *ANOVA* ($p<0.05$), and the non-parametric *Kruskal-Wallis* ($p<0.05$) test were applied to compare the phenological traits of the beech trees from the 4 study sites (unequal in number of individuals). The post hoc *Dunn* test was used to evaluate the phenological diversity and test for differences between study sites.

Limit values of the significant correlation coefficients (for 53 degrees of freedom) are: * ($p < 0.05$) - $r > 0.289$, ** ($p < 0.01$) $r > 0.375$, and *** ($p < 0.001$) - $r > 0.469$.

The RStudio (R Version 4.2.2.) was used to extract R^2 and p-values for all tree characteristics after TreeQSM analyses.

The RStudio interface was also used to correlate phenological, genetic, and architectural characteristics (Pearson correlation, $\alpha = 0.05$), through the “rcorr” function (the “corrplot” R package). This function provided a visual correlation matrix to detect patterns among variables and test the null hypothesis that the true correlation coefficient *r* equals 0. The results were graphically displayed using the “ggplot2” package in a correlation matrix form.

Results

Phenology monitoring

Initially, the normality of the data set was tested through the *Shapiro-Wilk* test, related to the phenological stages (bud burst and end of the growing season) and the length of the growing season. Significant differences from normality were observed for bud burst (in all four sites) and 50% yellowed leaves (Lempes and Tampa) ($p<0.05$), but not for the length of the growing season (in any site) ($p>0.05$) (Table 4).

Table 4 Normality test (*Shapiro-Wilk*) for the two phenological stages and the length of the growing season.

Phenological indicators	Lempes	Tampa	Solomon	P. Lupului
Bud burst	8.78 x 10^{-5}	0.000131	0.00141	0.01203
50% yellowed leaves	0.006317	0.04595	**0.1234**	**0.1881**
Length of the growing season	**0.05157**	**0.314**	**0.4894**	**0.4492**

The populations' diversity during the spring phenology monitoring in beech was significant ($p<0.05$, *Kruskal-Wallis* non-parametric test), with the start of the growing season occurring according to the altitudinal gradient (inversely proportional relationship). There is a difference of 14 days between the individuals located at the extremities of the altitudinal gradient in the onset of bud burst (based on mean values). Intra-population variation was also significant in the study sites, and there was considerable precocity and lateness compared to the average (Figure 3).

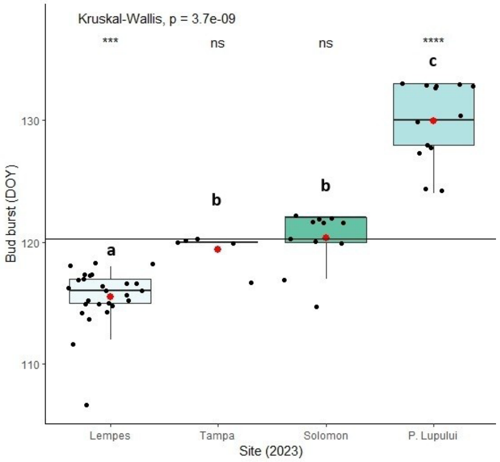

Figure 3 Intra- and interpopulation variation in common beech for the start of the growing season in 2023 (**** - $p \leq 0.0001$, *** - $p \leq 0.001$, and ns - $p > 0.05$) (a, b, and c letters were used to show homogeneous groups).

The phenological evaluation of beech along this altitudinal gradient revealed populations' diversity between study sites, except for Tampa and Solomon ($p = 0.3827$/ $p > 0.05$) (Table 5).

Table 5 The interpopulation variation between four study sites on bud burst phenological stage in beech.

Study sites	Lempes	Tampa	Solomon
Tampa	0.0192	x	x
Solomon	0.0006	**0.3827**	x
P. Lupului	0.0001	0.0149	0.0083

The interpopulation variation during the autumn phenology monitoring in beech was significant ($p<0.05$ *Kruskal-Wallis* test), the start of the senescence was associated with the altitudinal gradient (direct proportional relationship). There is a difference of 15 days between the individuals located at the extremities of the altitudinal gradient in the onset of senescence. Intra-population variation was also significant, with considerable precocity and lateness compared to the average (Figure 4).

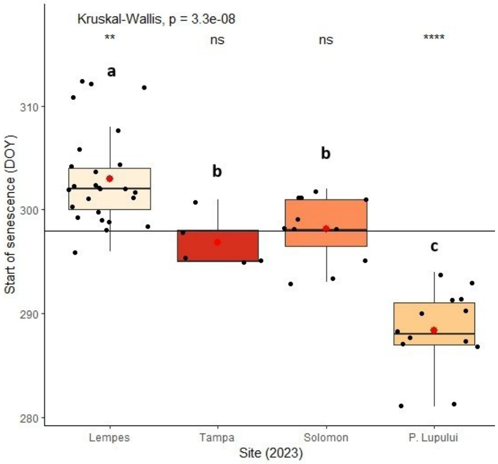

Figure 4 Intra- and interpopulation variation in common beech for the start of senescence in 2023 (a, b, and c letters were used to show homogeneous groups based on significant pairwise differences).

The phenological evaluation of beech along this altitudinal gradient revealed populations' diversity between study sites in obtaining leaf senescence, except for Tampa and Solomon ($p=0.3129$/ $p>0.05$) (Table 6).

Table 6 The interpopulation variation between four study sites in leaf senescence in common beech. .

Study sites	Lempes	Tampa	Solomon
Tampa	0.0111	x	x
Solomon	0.0089	**0.3129**	x
P. Lupului	0.0001	0.0364	0.0016

The populations' diversity for the length of the growing season in beech was significant ($p<0.05$, ANOVA test), and the length of the growing season declined with increasing altitude. There is a difference of 30 days between the individuals located at the extremities of the altitudinal gradient in the length of the growing season. Intra-population variation was also significant (Figure 5).

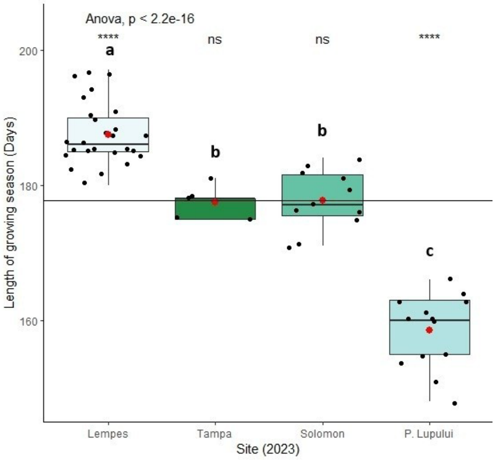

Figure 5 Intra- and interpopulation variation in common beech for the length of the growing season in 2023 (a, b, and c letters were used to show homogeneous groups based on significant pairwise differences).

The phenological evaluation of beech along this altitudinal gradient revealed populations' diversity between study sites in the length of the growing season, except for Tampa and Solomon (p=0.4211/ p>0.05) (Table 7).

Table 7 Interpopulation variation between four study sites in the length of the growing season in beech.

Study sites	Lempes	Tampa	Solomon
Tampa	0.0037	x	x
Solomon	0.0004	**0.4211**	x
P. Lupului	0.0001	0.0470	0.0079

Hegyi competition index distribution of the competitor trees

The competition indices of the competitor trees are influenced by the distance between the subject and competitor trees (Figure 6). As the distance between the two increases, the values of the Hegyi competition index decrease, and there is an inversely proportional relationship between the two (according to the 6th order polynomial function: $y = 3E\text{-}06x^6 - 0{,}0002x^5 + 0{,}0042x^4 - 0{,}0489x^3 + 0{,}309x^2 - 1{,}0275x + 1{,}5836$). It is observed that the competitive effect exerted by neighbours located at a distance above 4 m from the target individual decreases.

Besides the distance, the diameter of the competitor trees influences the values of the competition index directly proportional; the higher it is, the higher the impact of the competitor.

Trunk and crown shape variability of the sampled individuals

A total of 55 individuals of common beech structures were segmented from scans. The total volume of the trees chosen was 509.85 m^3. It was built from 123.92 m^3 of trunk volume (24.3%) and 385.92 m^3 of branch volume (75.7%) (Table 8).

Effects of competition on crown and stem characteristics (*Hegyi index*)

A positive but low *Pearson* coefficient was obtained between the competition index and bud burst (r = 0.08), along with the forking of the stem (r = 0.13), and a negative one with

Table 8 Trunk and crown characteristics of the selected individuals.

Study sites	Lempes		Tampa		Solomon		P. Lupului	
Statistical indicator	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Total volume (m^3)	9.13	10.05	23.72	11.45	5.52	4.34	6.55	6.33
Trunk volume (m^3)	2.51	1.82	4.07	2.15	0.93	0.68	2.05	1.94
Tree height (m)	33.73	3.64	33.65	5.00	27.56	4.51	25.40	7.62
Trunk length (m)	33.33	5.46	33.21	13.12	26.72	8.07	25.82	8.12
DBH (m)	0.41	0.15	0.51	0.15	0.28	0.13	0.38	0.18
Branch volume (m^3)	6.62	8.64	1.96	9.60	4.59	3.98	4.49	4.88
Branch length (m)	909.04	746.16	2328.60	830.92	1636.10	1204.28	1199.21	1139.86
Number of branches (pcs.)	3705.54	2355.10	6881.40	1553.37	9941.55	7557.45	6477.08	6346.78
Maximum branch order	5.88	1.18	8.20	1.30	7.00	1.61	6.69	1.32
Crown diameter (m, average)	7.96	3.14	12.36	2.31	8.50	2.76	7.63	3.05
Crown diameter (m, maximum value)	10.29	3.63	15.70	3.03	11.38	3.76	9.88	3.61

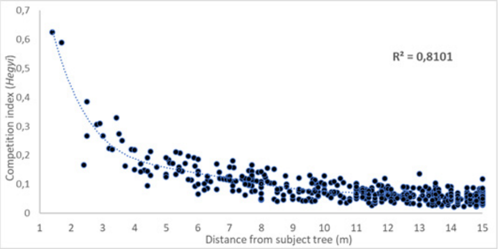

Figure 6 Competition index values according to Hegyi (1974) for competitor trees (*i*) of sampled dominant target trees (*j*).

the length of the growing season (r = -0.09) (Table 9). Negative but distinctly significant values were obtained between the competition index and the total volume of the trees (r = -0.38), trunk volume (r = -0.39), tree height (r = -0.38), and diameter at breast height (DBH) (r = -0.39). Negative but significant values were obtained between the competition index and branch volume (r = -0.36), trunk length (r = -0.34), branch length (r = -0.30), and crown diameter (average value) (r = -0.34). The results revealed that an individual with high competition will grow slenderer (r = 0.32).

Table 9 Effects of competition Hegyi index on crown and stem architectures.

Correlation between competition and…	*Pearson* correlation value
Bud burst	0.08
The length of the growing season	-0.09
Slenderness	**0.32***
Forking	0.13
Total volume	**-0.38****
Trunk volume	**-0.39****
Branch volume	**-0.36***
Tree height	**-0.38****
Trunk length	**-0.34***
Branch length	**-0.30***
Number of branches	-0.12
Maximum branch order	-0.16
DBH	**-0.39****
Crown Diameter (Average)	**-0.34***

Note: * - r > 0.289, ** - r > 0.375, and *** - r > 0.469

Effects of slenderness on crown and stem characteristics

A significant and positive correlation (r = 0.32) was obtained between the slenderness coefficient and the *Hegyi* competition index, revealing that an individual with high competition will grow slenderer (Table 10). Highly significant and negative correlations were obtained between slenderness and trunk volume (r = -0.62), branch volume (r = -0.47), branch length (r = -0.41), and crown diameter (r = -0.58). Tree height, DBH, and total volume were excluded from correlation with slenderness due to their calculation formula.

Table 10 Effects of competition slenderness on crown and stem architectures.

Correlation between slenderness and..	*Pearson* correlation value
Bud burst	-0.23
The length of the growing season	0.24
Forking	0.24
Hegyi index	**0.32***
Heterozygosity	-0.16
Trunk volume	**-0.62*****
Branch volume	**-0.47*****
Trunk length	-0.10
Branch length	-0.41**
Number of branches	-0.14
Maximum branch order	-0.26
Crown diameter (average)	**-0.58*****

Note: * - r > 0.289, ** - r > 0.375, and *** - r > 0.469

Correlations between crown and stem characteristics

Negative and relatively insignificant values were obtained between the forking of the stem and the other crown characteristics, except DBH and Crown Diameter (average value) (Supplementary Figure S2). The highest values of the Pearson correlation coefficient were obtained between the total volume of the tree and the branch volume (r = 0.99), the trunk volume and DBH (r = 0.93), and the Crown diameter (average) and the crown diameter (maximum value) (r = 0.90). The total tree volume was found to be highly correlated with most other stem and crown characteristics: the trunk volume (r = 0.81), the branch volume (r = 0.99), the tree height (r = 0.45), the branch length (r = 0.71), maximum branch order (r = 0.52), DBH (r = 0.78), the Crown diameter (average) (r = 0.82) and the crown diameter (maximum value) (r = 0.71).

Effects of altitude on bud burst, length of the growing season, crown and stem architectures

The influence of altitude on the start of the growing season (bud burst), as well as on its length, is confirmed by a high Pearson correlation coefficient value of r = 0.90 and r = -0.91, respectively (Table 11). It signifies a very significant and inversely proportional correlation between altitude and the length of the growing season, with an increase in altitude leading to a shorter vegetation season. A very significant correlation was also obtained in the case of tree height (r = -0.61), where the increase in altitude negatively influenced the height of the trees. Significant correlations were obtained between altitude and forking (r = 0.41), as well as trunk length (r = -0.44). A non-significant but negative correlation exists between altitude and individual heterozygosity of the sampled beech trees (r = -0.23).

Table 11 Effects of altitude on the length of the growing season, individual heterozygosity, *Hegyi* competition index, forking, and other crown and stem architectures.

Correlation between altitude and..	*Pearson* correlation value
Bud burst	**0.90*****
The length of the growing season	**-0.91*****
Heterozygosity	-0.23
Hegyi index	**0.28**
Forking	**0.41****
Total volume	-0.20
Trunk volume	-0.20
Branch volume	-0.19
Tree height	**-0.61*****
Trunk length	**-0.44****
Branch length	0.08
Number of branches	0.24
Maximum branch order	0.20
DBH	-0.17
Crown diameter (average)	-0.10

Note: ** - r > 0.375 and *** - r > 0.469

Effects of heterozygosity on bud burst, length of the growing season, crown and stem architectures

The influence of heterozygosity on the length of the growing season is significant (r = 0.30); a higher individual's heterozygosity contributes to a longer growing season and a precocious onset of bud burst in beech (r = -0.21) (Table 12). Higher heterozygosity was associated with a higher total volume of the tree and its trunk, DBH, the Crown diameter (average), and, inversely proportional but insignificant, with forking.

Table 12 Effects of heterozygosity on the length of the growing season, forking, and other crown and stem architectures.

Correlation between heterozygosity and…	*Pearson* correlation value
Bud burst	**-0.21**
The length of the growing season	**0.30***
Forking	-0.21
Total volume	**0.26**
Trunk volume	**0.35***
Branch volume	0.22
Tree height	0.18
Trunk length	-0.06
Branch length	**0.06**
Number of branches	**-0.16**
Maximum branch order	-0.08
DBH	0.30*
Crown diameter (average)	0.25

Note: * - r > 0.289

Discussion

The onset of bud burst and senescence, as well as the length of the growing season, varied very significantly and inversely proportionally with the altitudinal gradient, confirming similar studies (Anev 2023, Ciocîrlan et al. 2024, Skvareninova et al. 2024). We obtained a very significant and positive correlation between altitude and bud burst (r = 0.90), very similar to the result obtained by Schieber et al. (2013) (r = 0.93). There is a gap of 14 days between the individuals located at the extremities of this elevational gradient, regarding the start of bud burst, 15 days in the onset of senescence, and 30 days in the length of the growing season. These values show the extent of local adaptation of beech trees in the study area and can be of interest to the forest practice. The ecotype selection of beech can contribute to avoiding early or late frosts (Silvestro et al. 2019). Individuals with a longer growing season, which has an early onset of bud burst, can be damaged by early autumn frosts. The selection of phenotypes could be a solution to increase the adaptation of trees in the actual context of climate change.

We also obtained a very significant and negative correlation between altitude and tree height (r = -0.61), similar to the one obtained by Svoboda et al. (2006) (r = -0.51) in Norway spruce. This correlation suggests that the beech trees will reach lower heights with the increase in altitude, not only due to different site conditions that this implies but also to the changes in the composition of the stands in which it is found and their interaction with its new competitors (Sharma et al. 2016), in the present case, Norway spruce and silver fir.

An increase in competition directly implied a decrease in DBH and crown dimensions, confirming the results of Dorji et al. (2019); the higher it is, the more the inhibitory effects are felt by the analysed beech individuals (Ji et al. 2023). Vacek & Lepš (1996) revealed that the strongly suppressed individuals by their neighbours are the most susceptible to environmental stresses. Das et al. (2016) claimed that the suppression exerted by the surrounding trees could cause the death of an individual. In the case of beech, Duduman et al. (2010) found that in natural uneven-aged stands, the radial growth is influenced primarily by the competition exercised by its first seven neighbours. Our results suggest that the effects of competition exerted by the individuals located at a distance above 4 m decrease significantly. The correlation between DBH and crown diameter (average value) is much stronger compared with the one obtained by Svoboda et al. (2006) on Norway spruce (0.27).

The stem's slenderness significantly increased with increasing competition, contrary to the results of Penanhoat et al. (2024) on one-year-old common beech saplings. We obtained negative and significant correlations between individual slenderness and total volume, trunk volume, branch volume, branch length, crown diameter, and DBH, similar to Tomșa et al. (2021) on four European white oak species. Shamaki (2022) obtained similar negative correlations between slenderness and DBH, total volume, and a similar positive correlation with tree height on eucalyptus, gmelina, and teak.

A positive but low *Pearson* coefficient value was obtained between the *Hegyi* competition index and bud burst, along with the forking of the stem, and a negative and low one with the length of the growing season. The beech's forking is lower at higher altitudes, where its competitors, Norway spruce and silver fir, are dominant (several meters taller), and the density of the stand is also lower.

A similar study from Germany (Burkhardt et al. 2020) that combined putatively neutral and potentially adaptive markers to evaluate the effects of heterozygosity on oak tree architectures revealed a significant relationship between branch angle and individual heterozygosity. Tomșa et al. (2021) obtained no significant relationship between individual heterozygosity and other tree-shape characteristics in oak species, similar to Mitton et al. (1981) on blackjack pine and lodgepole pine. Still, Moosavi et al. (2024) showed that English yew individual heterozygosity increased with tree age (indicated by DBH), and the relationship was strongest for late developmental stages (old adult trees). Ledig et al. (1993) stated that more heterozygous Pitch pine individuals exhibit a more significant mean annual growth. Cole et al. (2016) demonstrated that the growth of aspens is strongly influenced by individual heterozygosity, confirming Jelinski's (1993) results.

Our study revealed a significant and positive relationship between individual heterozygosity and the length of the growing season, as well as with the trunk volume and DBH, contrary to the results obtained by Savolainen & Hedrick (1995) on Scots pine. We found a positive but nonsignificant correlation between heterozygosity and the tree's height, similar to Moran et al. (1989) in river oak. The association between individual heterozygosity and growth-related traits such as DBH in our study may indicate a direct relationship between heterozygosity and growth or higher heterozygosity in older than in younger trees (i.e., selection favoring heterozygous individuals). Additional data on tree age are necessary to distinguish between these two options. However, we recommend continuing the research on this topic, using the same methodology but replicating it in other site conditions.

Conclusions

An increase in altitude led to a tardive onset of bud burst and a precocious onset of senescence, directly implying a shorter growing season. The height, forking, and trunk length of beech trees increased in lower elevations.

The influence of a competitor on a target beech is determined by the distance between the two trees (the most significant effects exerted by neighbours below 4 m distance) and the competitor's diameter (inverse proportional relationship). Negative significant correlations were found between the competition index and the tree biomass indicators (total volume, trunk volume, height, stem diameter, branch volume, trunk length, branch length, and crown diameter). A beech tree with high competition will reveal a slenderer growth.

A higher individual's heterozygosity contributed to a longer growing season in common beech. Higher heterozygosity was associated with considerably higher total tree biomass. The genetic diversity was inversely proportional but nonsignificant to stem forking.

TLS demonstrated great potential in extracting beech tree biomass indicators, but we still recommend using the conventional method as a complementary method for data validation, although it is time-consuming.

Compliance with ethical standards

Conflict of interest

The authors declare there is no conflict of interest.

Funding

This research was funded by the Ministry of Research, Innovation, and Digitalisation (MCID), Romania, through the: "Nucleu" Program PN 23090102, 34 PFE/30.12.2021 "Increasing the institutional capacity and performance of INCDS 'Marin Drăcea' in the activity of RDI—CresPerfInst" and the FNR-funded project DroughtMarkers (BMEL, Waldklimafonds, reference number: 2218WK43B4).

Acknowledgments

We want to acknowledge "Transilvania" University from Brasov, "Marin Drăcea" National Institute for Research and Development in Forestry (INCDS), the administration of the National Agency for Natural Protected Areas (ANANP), and RNP Romsilva. We also thank Florentina Chira, Costel Mantale, and Cătălin Grideanu for helping with the fieldwork.

References

Abegg M., Boesch R., Schaepman M. E., Morsdorf F., 2021. Impact of beam diameter and scanning approach on point cloud quality of terrestrial laser scanning in forests. IEEE Transactions on Geoscience and Remote Sensing 59(10): 8153-8167. https://doi.org/10.1109/TGRS.2020.3037763

Anev S., 2023. Altitudinal and latitudinal variation in leaf phenology of European beech (*Fagus sylvatica* L.) in Western Bulgaria. Forestry Ideas 29, 2(66): 245-257.

Apostol B., Chivulescu S., Ciceu A., Petrila M., Pascu I.S., Apostol E.N., Leca Ș., Lorenț A., Tănase M., Badea O., 2018. Data collection methods for forest inventory: A comparison between an integrated conventional equipment and terrestrial laser scanning. Annals of Forest Research *61*(2): 189-202. https://doi.org/10.15287/afr.2018.1189

Asuka Y., Tani N., Tsumura Y., Tomaru N., 2004. Development and characterization of microsatellite markers for *Fagus crenata* Blume. Molecular Ecology Notes *4*(1):101-103. https://doi.org/10.1046/j.1471-8286.2003.00583.x

Avanzi C., Heer K., Büntgen U., Labriola M., Leonardi S., Opgenoorth L., Piermattei A., Urbinati C., Vendramin G.G. & Piotti A., 2020. Individual reproductive success in Norway spruce natural populations depends on growth rate, age and sensitivity to temperature. Heredity, 124(6): 685-698. https://doi.org/10.1038/s41437-020-0305-0

Badeck F.-W., Bondeau A., Böttcher K., Doktor D., Lucht W., Schaber J., Sitch, S., 2004. Responses of spring phenology to climate change 162(2): 295-309. https://

doi.org/10.1111/j.1469-8137.2004.01059.x

Barbeito I., Dassot M., Bayer D., Collet C., Drössler L., Löf M., del Rio M., Ruiz-Peinado R., Forrester D. I., Bravo-Oviedo A., Pretzsch H., 2017. Terrestrial laser scanning reveals differences in crown structure of *Fagus sylvatica* in mixed vs. pure European forests. Forest Ecology and Management, 405: 381-390. https://doi.org/10.1016/j.foreco.2017.09.043

Besliu E., Curtu A.L., Apostol E.N., Budeanu M., 2024. Using adapted and productive European beech (*Fagus sylvatica* L.) provenances as future solutions for sustainable forest management in Romania. Land, 13(2): 183. https://doi.org/10.3390/land13020183

Bian L., Zhang H., Ge Y., Čepl J., Stejskal J., EL-Kassaby Y.A., 2022. Closing the gap between phenotyping and genotyping: review of advanced, image-based phenotyping technologies in forestry. Annals of Forest Science 79(1): 22. https://doi.org/10.1186/s13595-022-01143-x

Bigler C. & Bugmann H., 2004. Predicting the time of tree death using dendrochronological data. Ecological Applications, 14(3): 902-914. https://doi.org/10.1890/03-5011

Božič G., Ivanković M. & Kutnar, L., 2013. Genetic structure of European beech (*Fagus sylvatica* l.) seed stands from different forest sites of Gorjanci Mountains as revealed by isoenzymes. Sumarski List, 137(1–2): 25-32.

Budde K. B., Hötzel S., Müller M., Samsonidze N., Papageorgiou A. C., Gailing O., 2023. Bidirectional gene flow between *Fagus sylvatica* L. and *F. orientalis* Lipsky despite strong genetic divergence. Forest Ecology and Management 537: 120947. https://doi.org/10.1016/j.foreco.2023.120947

Buiteveld J., Vendramin G. G., Leonardi S., Kamer K., Geburek T., 2007. Genetic diversity and differentiation in European beech (*Fagus sylvatica* L.) stands varying in management history. Forest Ecology and Management 247(1-3): 98-106. https://doi.org/10.1016/j.foreco.2007.04.018

Burger K., Müller M., Gailing O, 2018. Characterization of EST-SSRs for European beech (*Fagus sylvatica* L.) and their transferability to *Fagus orientalis* Lipsky, *Castanea dentata* Bork., and *Quercus rubra* L. Silvae Genetica 67(1): 127-132. https://doi.org/10.2478/sg-2018-0019

Burkardt K., Pettenkofer T., Ammer C., Gailing O., Leinemann L., Seidel D., Vor T., 2021. Influence of heterozygosity and competition on morphological tree characteristics of *Quercus rubra* L.: a new single-tree based approach. New Forests 52(4): 679-695. https://doi.org/10.1007/s11056-020-09814-1

Calders K., Adams J., Armston J., Bartholomeus H., Bauwens S., Bentley L. P., Chave J., Danson F. M., Demol M., Disney M., Gaulton R., Krishna Moorthy S. M., Levick S. R., Saarinen N., Schaaf C., Stovall A., Terryn L., Wilkes P., Verbeeck H., 2020. Terrestrial laser scanning in forest ecology: Expanding the horizon. Remote Sensing of Environment, 251: 112102. https://doi.org/10.1016/j.rse.2020.112102

Calders K., Newnham G., Burt A., Murphy S., Raumonen P., Herold M., Culvenor D., Avitabile V., Disney M., Armston J., Kaasalainen M., 2015. Nondestructive estimates of above-ground biomass using terrestrial laser scanning. Methods in Ecology and Evolution, 6(2): 198-208. https://doi.org/10.1111/2041-210X.12301

Capalb F., Petrila M., Lorenț A., Apostol B., Marcu C., Badea O., 2023. Estimarea volumului la arbori individuali pe baza norilor de puncte obținuți prin scanare cu laser terestru (TLS) - studiu de caz pentru arborete de molid din vestul Carpaților Meridionali. Revista de Silvicultură şi Cinegetică, 28(53): 12-18.

Casmey M., Hamann A., Hacke U. G., 2022. Adaptation of white spruce to climatic risk environments in spring: Implications for assisted migration. Forest Ecology and Management, 525: 120555. https://doi.org/10.1016/j.foreco.2022.120555

Chéné Y., Rousseau D., Lucidarme P., Bertheloot J., Caffier V., Morel P., Belin É., Chapeau-Blondeau F., 2012. On the use of depth camera for 3D phenotyping of entire plants. Computers and Electronics in Agriculture, 82: 122-127. https://doi.org/10.1016/j.compag.2011.12.007

Chira D., Borlea F. G., Chira F., Mantale C., Ciocîrlan M. I. C., Turcu D. O., Cadar N., Trotta V., Camele I., Marcone C., Mang Ș. M., 2022. Selection of Elms Tolerant to Dutch Elm Disease in South-West Romania. Diversity, 14(11): 980. https://doi.org/10.3390/d14110980

Chuine I., 2010. Why does phenology drive species distribution? Philosophical Transactions of the Royal Society B: Biological Sciences, 365(1555): 3149-3160. https://doi.org/10.1098/rstb.2010.0142

Ciceu A., Bălăcenoiu F., de Groot M., Chakraborty D., Avtzis D., Barta M., Blaser S., Bracalini M., Castagneyrol B., Chernova U. A., Çota E., Csóka G., Dautbasic M., Glavendekic M., Gninenko Y. I., Hoch G., Hradil K., Husemann M., Meshkova V., et al., 2024. The ongoing range expansion of the invasive oak lace bug across Europe: current occurrence and potential distribution under climate change. Science of The Total Environment, 949: 174950. https://doi.org/10.1016/J.SCITOTENV.2024.174950

Ciocîrlan M. I. C., Ciocîrlan E., Chira D., Radu G. R., Păcurar V. D., Beșliu E., Zormpa O. G., Gailing O., Curtu A. L., 2024. Large Differences in Bud Burst and Senescence between Low- and High-Altitude European Beech Populations along an Altitudinal Transect in the South-Eastern Carpathians. Forests, 15(3): 468. https://doi.org/10.3390/f15030468

Ciocîrlan M. I. C., Curtu A. L., Radu G. R., 2022. Predicting leaf phenology in forest tree species using UAVs and satellite images: A case study for European beech (*Fagus sylvatica* L.). Remote Sensing, 14(24): 6198. https://doi.org/10.3390/rs14246198

CloudCompare Software. CloudCompare “Unified”

2.13.2. Kharkiv version. Available online: https://www.danielgm.net/cc/ (Accessed on 10.08.2024)

Cole C.T., Stevens M.T., Anderson J.E. et al., 2016. Heterozygosity, gender, and the growth-defense trade-off in quaking aspen. Oecologia 181: 381-390. https://doi.org/10.1007/s00442-016-3577-6

Coșofreț C., Barnoaiea I., Scriban R.E., Dănilă I.C., Duduman M.L., Bouriaud O., 2018. Utilizarea scanerului laser terestru în măsurătorile forestiere: Cerințe metodologice și precauții necesare la aplicarea în practică. Bucovina Forestieră 18(2): 137–153. https://doi.org/10.4316/bf.2018.014

Čufar K., De Luis M., Saz M.A. et al., 2012. Temporal shifts in leaf phenology of beech (*Fagus sylvatica*) depend on elevation. Trees 26: 1091-1100. https://doi.org/10.1007/s00468-012-0686-7

Cvrčková H., Máchová P., Poláková L., Trčková O., 2017. Evaluation of the genetic diversity of selected *Fagus sylvatica* L. populations in the Czech Republic using nuclear microsatellites. Journal of Forest Science 63(2): 53-61. https://doi.org/10.17221/88/2016-JFS

Dănilă I. C., 2021. Use of terrestrial laser scanner in short rotation crops for above-ground woody biomass estimation. Proceedings CYSENI 2021, 24-28 May, Kaunas, Lithuania. https://cyseni.com/wp-content/archives/proceedings/Proceedings_of_CYSENI_2021.pdf

Dănilă I., 2021. ForCrops: Estimarea producției supraterane de biomasă lemnoasă din culturile forestiere cu creșteri rapide, prin scanare laser terestră. Bucovina Forestieră 21(2): 245-248. https://doi.org/ 10.4316/bf.2018.014

Das A.J., Stephenson N.L. & Davis K.P., 2016. Why do trees die? Characterizing the drivers of background tree mortality. Ecology, 97: 2616-2627. https://doi.org/10.1002/ecy.1497

Dorji Y., Annighöfer P., Ammer C., Seidel D., 2019. Response of beech (*Fagus sylvatica* L.) trees to competition-new insights from using fractal analysis. Remote Sensing, 11(22): 2656. https://doi.org/10.3390/rs11222656

Drobyshev I., Övergaard R., Saygin I., Niklasson M., Hickler T., Karlsson M., Sykes, M. T., 2010. Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. Forest Ecology and Management, 259(11): 2160-2171. https://doi.org/10.1016/j.foreco.2010.01.037

Ducci F., De Cuyper B., Pâques L.E., Proietti R., Wolf H. (Compilers), 2012. Reference protocols for assessment of trait and reference genotypes to be used as standards in international research projects. Ed. CRA SEL - Arezzo, Italy: p. 82.

Duduman G., Roibu C. C., Duduman M. L., Miron-Onciul M., 2010. The influence of competition and dimensional-spatial characteristics of trees on their radial growth in Old-Growth Slătioara forest, Romania. AES Bioflux, Cluj-Napoca, 2(2): 215-230.

Fichtner A., Sturm K., Rickert C., Härdtle W., Schrautzer J., 2012. Competition response of European beech *Fagus sylvatica* L. varies with tree size and abiotic stress: Minimizing anthropogenic disturbances in forests. Journal of Applied Ecology, 49(6): 1306-1315. https://doi.org/10.1111/j.1365-2664.2012.02196.x

Forstmeier W., Schielzeth H., Mueller J. C., Ellegren H. & Kempenaers B., 2012. Heterozygosity-fitness correlations in zebra finches: Microsatellite markers can be better than their reputation. Molecular Ecology, 21(13): 3237-3249. https://doi.org/10.1111/j.1365-294X.2012.05593.x

Fu Y. H., Piao S., Zhou X., Geng X., Hao F., Vitasse Y., Janssens I. A., 2019. Short photoperiod reduces the temperature sensitivity of leaf-out in saplings of *Fagus sylvatica* but not in horse chestnut. Global Change Biology, 25(5): 1696-1703. https://doi.org/10.1111/gcb.14599

Gauzere J., Klein E. K., Brendel O., Davi H. & Oddou-Muratorio S., 2016. Using partial genotyping to estimate the genetic and maternal determinants of adaptive traits in a progeny trial of *Fagus sylvatica*. Tree Genetics and Genomes, 12: 115. https://doi.org/10.1007/s11295-016-1062-3

Geßler A., Keitel C., Kreuzwieser J., Matyssek R., Seiler W., Rennenberg H., 2007. Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees - Structure and Function 21(1): 1-11. https://doi.org/10.1007/s00468-006-0107-x

Hansson B. & Westerberg L., 2002. On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11(12): 2467-2474. https://doi.org/10.1046/j.1365-294X.2002.01644.x

Hegyi F., 1974. A simulation model for managing jack-pine stands. Fries J (ed) Growth models for tree and stand simulation: International Union of Forestry Research Organizations Working Party S4, Skogshögskolan, Garpenberg, pp 74–90.

Hopkinson C., Chasmer L., Young-Pow C., Treitz P., 2004. Assessing forest metrics with a ground-based scanning LIDAR. Canadian Journal of Forest Research, 34(3): 573-583. https://doi.org/10.1139/x03-225

Houston D.T., de Rigo D., Caudullo G., 2016. *Fagus sylvatica* in Europe: Distribution, habitat, usage and threats. In: San-Miguel-Ayanz J., de Rigo D., Caudullo G., Houston D.T., Mauri A. (eds.). European Atlas of Forest Tree Species. Publication Office of the European Union: Luxembourg, 2016; pp. 94–95.

Jelinski D. E., 1993. Associations between environmental heterogeneity, heterozygosity, and growth rates of *Populus tremuloides* in a Cordilleran Landscape. Arctic and Alpine Research, 25(3): 183–188. https://doi.org/10.1080/00040851.1993.12003002

Ji Y., Zhang P. & Shen H., 2023. Competition intensity affects growing season nutrient dynamics in Korean pine trees and their microhabitat soil in mixed forest. Forest Ecology and Management, 539: 121018. https://

doi.org/10.1016/j.foreco.2023.121018

Kirk C., Berrill J.P., 2016. Second-log branching in multiaged redwood and Douglas-fir: Influence of stand, site, and silviculture. Forests, 7(7): 147. https://doi.org/10.3390/f7070147

Krokene P., Lahr E., Dalen L.S., Skrøppa T. & Solheim H., 2011. Effect of phenology on susceptibility of Norway spruce (*Picea abies*) to fungal pathogens. Plant Pathology, 61(1): 57-62. https://doi.org/10.1111/j.1365-3059.2011.02487.x

Kubisiak T., Carey D., Burdine C., Koch J., 2009. Characterization of ten EST-based polymorphic SSR 2 loci isolated from American beech, *Fagus grandifolia* Ehrh. Permanent Genetic Resources Note Added to Mol Ecol Resour, 9(6): 1460-1466. https://doi.org/10.1111/j.1755-0998.2009.02759.x

Kutnar L., Kermavnar J., Pintar A.M., 2021. Climate change and disturbances will shape future temperate forests in the transition zone between Central and SE Europe. Annals of Forest Research, 64(2): 67-86. https://doi.org/10.15287/afr.2021.2111

Ledig F.T., Guries R.P., Bonefeld B.A., 1983. The Relation of Growth to Heterozygosity in Pitch Pine. Evolution, 37(6): 1227-1238. https://doi.org/10.2307/2408843

Leimu R., Mutikainen P., Koricheva J. & Fischer M., 2006. How general are positive relationships between plant population size, fitness and genetic variation? Journal of Ecology, 94(5): 942-952. https://doi.org/10.1111/j.1365-2745.2006.01150.x

Leuschner C., 2020. Drought response of European beech (*Fagus sylvatica* L.) - A review. Perspectives in Plant Ecology, Evolution and Systematics, 47: 125576. https://doi.org/10.1016/j.ppees.2020.125576

Li Y., Suontama M., Burdon R.D., Dungey H.S., 2017. Genotype by environment interactions in forest tree breeding: review of methodology and perspectives on research and application. Tree Genetics and Genomes, 13(3): 1-18. https://doi.org/10.1007/s11295-017-1144-x

Longuetaud F., Piboule A., Wernsdörfer H., Collet C., 2013. Crown plasticity reduces inter-tree competition in a mixed broadleaved forest. European Journal of Forest Research, 132(4): 621-634. https://doi.org/10.1007/s10342-013-0699-9

McKinney L. v., Nielsen L.R., Hansen J.K. & Kjær E.D., 2011. Presence of natural genetic resistance in *Fraxinus excelsior* (Oleraceae) to *Chalara fraxinea* (Ascomycota): An emerging infectious disease. Heredity, 106(5):788-797. https://doi.org/10.1038/hdy.2010.119

McKown A. D., Klápště J., Guy R. D., El-Kassaby Y. A., Mansfield S. D., 2018. Ecological genomics of variation in bud-break phenology and mechanisms of response to climate warming in *Populus trichocarpa*. New Phytologist, 220(1): 300-316. https://doi.org/10.1111/nph.15273

Menamo T., Kassahun B., Borrell A. K., Jordan D. R., Tao Y., Hunt C., & Mace E., 2021. Genetic diversity of *Ethiopian sorghum* reveals signatures of climatic adaptation. Theoretical and Applied Genetics, 134(2): 731-742. https://doi.org/10.1007/s00122-020-03727-5

Mitton J. B., Knowles P. Sturgeon K. B., Linhart Y. B., Davis M., 1981. Associations between heterozygosity and growth rate variables in three western forest trees. In: Conkle M.T. (tech. coord.) Proceedings of the Symposium on isozymes of North American forest trees and forest insects. USDA For. Serv. Gen. Tech. Rep. PSW-48: 27-34.

Mitton J. B., Pierce B. A., 1980. The distribution of individual heterozygosity in natural populations. Genetics, 95(4): 1043-1054. https://doi.org/10.1093/genetics/95.4.1043

Molina-Valero J.A., Martínez-Calvo A., Ginzo Villamayor M.J., Novo Pérez M.A., Álvarez-González J.G., Montes F., Pérez-Cruzado C., 2022. Operationalizing the use of TLS in forest inventories: The R package FORTLS. Environmental Modelling and Software, 150: 105337. https://doi.org/10.1016/j.envsoft.2022.105337

Moosavi S.J., Budde K.B., Heurich M., et al., 2024. Genetic variation of English yew (*Taxus baccata* L.) in the Bavarian Forest National Park, Germany. European Journal of Forest Research, 143: 1249-1265. https://doi.org/10.1007/s10342-024-01687-9

Moran G.F., Bell J.C., Turnbull J.W., 1989. A cline in genetic diversity in river sheoak *Casuarina cunninghamiana*. Aust. J. Bot. 37: 169-180.

Müller-Starck G., Baradat P., Bergmann F., 1992. Genetic variation within European tree species. New Forests, 6: 23-47. https://doi.org/10.1007/BF00120638

Müller-Starck G., Starke R., 1993. Inheritance of Isoenzymes in European Beech (*Fagus sylvatica* L.). Journal of Heredity, 84(4): 291-296. https://doi.org/10.1093/oxfordjournals.jhered.a111341

Nielsen C. N., Jørgensen F. V., 2003. Phenology and diameter increment in seedlings of European beech (*Fagus sylvatica* L.) as affected by different soil water contents: Variation between and within provenances. Forest Ecology and Management, 174(1–3): 233-249. https://doi.org/10.1016/S0378-1127(02)00042-7

Palaghianu C., 2009. Researches on forests regeneration by informatical tools. Universitatea” Ştefan cel Mare”, Suceava, Romania. PhD Diss. [In Romanian].

Pascu I.S., Dobre A.C., Badea O., Tănase M.A., 2019. Estimating forest stand structure attributes from terrestrial laser scans. Science of the Total Environment, 691: 205-215. https://doi.org/10.1016/j.scitotenv.2019.06.536

Pastorelli R., Smulders M.J.M., Van’T Westende W.P.C., Vosman B., Giannini R., Vettori C., Vendramin G.G., 2003. Characterization of microsatellite markers in *Fagus sylvatica* L. and *Fagus orientalis* Lipsky. Molecular Ecology Notes, 3(1): 76-78. https://doi.org/10.1046/j.1471-8286.2003.00355.x

Penanhoat A., Guerrero Ramirez N., Aubry-Kientz M. et al., 2024. Effect of competition intensity and neighbor identity on architectural traits of *Fagus sylvatica*. Trees, 1-11. https://doi.org/10.1007/s00468-024-02544-3

QGIS. QGIS Project 3.22.6-Białowieża. Available online: https://qgis.org/ (Accessed on 24.06.2024)

R Project for Statistical Computing. R Version 4.2.2. (Released on 31.10.2022). Available online: https://www.r-project.org/ (accessed on 18 August 2024).

Rajendra K. C., Seifert S., Prinz K., Gailing O., Finkeldey R., 2014. Subtle human impacts on neutral genetic diversity and spatial patterns of genetic variation in European beech (*Fagus sylvatica*). Forest Ecology and Management, 319: 138-149. https://doi.org/10.1016/j.foreco.2014.02.003

Savolainen O., Hedrick P., 1995. Heterozygosity and fitness: no association in Scots pine. Genetics 140(2): 755–766. https://doi.org/10.1093/genetics/140.2.755

Schieber B., Janík R., Snopková Z., 2013. Phenology of common beech (*Fagus sylvatica* L.) along the altitudinal gradient in Slovak Republic (Inner Western Carpathians). Journal of Forest Science, 59(4):176-184. https://doi.org/10.17221/82/2012-jfs

Schieber B., Kubov M., Janík R., 2017. Effects of climate warming on vegetative phenology of the common beech *Fagus sylvatica* in a submontane forest of the Western Carpathians: Two-decade analysis. Polish Journal of Ecology, 65(3): 339-351. https://doi.org/10.3161/15052249PJE2017.65.3.003

Shamaki S. B., 2022. Relationships between tree slenderness coefficients and stand characteristics for major plantation-grown species in North-western Nigeria. Journal of Agriculture and Environment, 18(2): 125-134.

Sharma R. P., Vacek Z. & Vacek S., 2016. Modeling individual tree height to diameter ratio for Norway spruce and European beech in Czech Republic. Trees - Structure and Function, 30(6): 1969-1982. https://doi.org/10.1007/s00468-016-1425-2

Silvestro R., Rossi S., Zhang S., Froment I., Huang J. G. & Saracino A., 2019. From phenology to forest management: Ecotypes selection can avoid early or late frosts, but not both. Forest Ecology and Management, 436: 21-26. https://doi.org/10.1016/j.foreco.2019.01.005

Skvareninova J., Sitko R., Vido J., Snopková Z., Skvarenina J., 2024. Phenological response of European beech (*Fagus sylvatica* L.) to climate change in the Western Carpathian climatic-geographical zones. Front. Plant Sci., 15: 1242695. https://doi.org/10.3389/fpls.2024.1242695

Svoboda M., Matějka K., Kopáček J., Žaloudík J., 2006. Estimation of tree biomass of Norway spruce forest in the Plešné Lake catchment, the Bohemian Forest. Biologia (Poland), 61(20): 523-532. https://doi.org/10.2478/s11756-007-0075-7

Szulkin M., Bierne N. & David P., 2010. Heterozygosity-fitness correlations: A time for reappraisal. Evolution, 64(5): 1202-1217. https://doi.org/10.1111/j.1558-5646.2010.00966.x

Toh K. C., Todd M. J., Tütüncü R. H., 1999. SDPT3 - a MATLAB software package for semidefinite programming, version 1.3. Optimization Methods and Software, 11(1-4), 545-581.

Tomșa V. R., Curtu A. L., Niță M. D., 2021. Tree shape variability in a mixed oak forest using terrestrial laser technology: Implications for mating system analysis. Forests, 12(2): 253. https://doi.org/10.3390/f12020253

Torralba J., Carbonell-Rivera J. P., Ruiz L. Á., Crespo-Peremarch P., 2022. Analyzing TLS scan distribution and point density for the estimation of forest stand structural parameters. Forests, 13(12): 2115. https://doi.org/10.3390/f13122115

Vacek S. and Lepš J., 1996. Spatial dynamics of forest decline: the role of neighbouring trees. Journal of Vegetation Science, 7: 789-798. https://doi.org/10.2307/3236457

Valbuena R., O'Connor B., Zellweger F., Simonson W., Vihervaara P., Maltamo M., Silva C. A., Almeida D. R. A., Danks F., Morsdorf F., Chirici G., Lucas R., Coomes D. A., Coops N. C., 2020. Standardizing Ecosystem Morphological Traits from 3D Information Sources. Trends in Ecology and Evolution, 35(8): 656-667. https://doi.org/10.1016/j.tree.2020.03.006

van Asch M., van Tienderen P. H., Holleman L. J. M. & Visser M. E., 2007. Predicting adaptation of phenology in response to climate change, an insect herbivore example. Global Change Biology, 13(8):1596-1604. https://doi.org/10.1111/j.1365-2486.2007.01400.x

Vitasse Y., Delzon S., Dufrêne E., Pontailler J. Y., Louvet J. M., Kremer A., Michalet R., 2009. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? Agricultural and Forest Meteorology 149(5):735-744. https://doi.org/10.1016/j.agrformet.2008.10.019

Vornam B., Decarli N., Gailing O., 2004. Spatial distribution of genetic variation in a natural beech stand (*Fagus sylvatica* L.) based on microsatellite markers. Conservation Genetics 5(4):561-570. https://doi.org/10.1023/B:COGE.0000041025.82917.ac

Wang Y., Titus S.J., LeMay V.M., 1998. Relationships between tree slenderness coefficients and tree or stand characteristics for major species in boreal mixed wood forests. Canadian Journal of Forest Research, 28(8): 1171-1183. https://doi.org/10.1139/x98-092

Zormpa O.G., Budde K.., Wilhelmi S., Vucetic B., Müller M., Gailing O., Ciocîrlan M.I.C., Ciocîrlan E., Curtu A.L., Targem M., Wildhagen H., 2024. Differences in fine-scale spatial genetic structure of European beech populations along elevational gradients. Research Square https://doi.org/10.21203/rs.3.rs-4559673/v1