

Height growth of *Quercus petraea* coppices: Effects of tree type, stand management, and site conditions – A case study from the Czech lowlands

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Abstract: This study examines height growth and its driving factors in stools and standard trees, the two key structural components of coppice-with-standards stands. We focused on sessile oak [*Quercus petraea* agg. (Matt.) Liebl.] stands over 90 years old at two contrasting sites near Brno (South Moravian Region, Czech Republic): one actively managed and one left unmanaged for more than 40 years as a strict nature reserve. Tree heights were analysed using two-factor analysis of variance (ANOVA) with post hoc tests and multinomial logistic regression. A total of 1 239 trees were measured (584 stools and 655 standards). Standard trees were the tallest on average (21.8 m), significantly exceeding all the stool categories, whereas managed triple-stem stools were the shortest (15.97 m). Across all categories, unmanaged stands generally reached greater heights than managed stands did, except for standard trees. The forest type, exposure and slope had significant effects on height class probabilities, whereas elevation was important only for smaller trees. Overall, the results demonstrate that both the tree type and site conditions strongly influence height growth in *Q. petraea* coppice-with-standards stands, with management history leaving a clear biological legacy in the present-day stand structure.

Keywords: environmental factors; managed vs unmanaged coppice-with-standard; sessile oak; standard tree; stem growth; stool

Historically, coppice-with-standards management, along with coppice cultivation, was a typical practice in the suburban area of Brno (South Moravian Region, Czech Republic). The area, located at lower to mid-elevations with a maximum altitude of approximately 380 m a.s.l., is dominated by broadleaved forests and has been shaped and maintained by anthropogenic activities for centuries (Kirby, Watkins 2015; Kirby et al. 2017). Man-

agement practices favoured oak, particularly sessile oak [*Quercus petraea* agg. (Matt.) Liebl.], because of its valuable properties for fuel, charcoal, timber products, and economic utilisation. Traditional practices, including forest grazing and coppice management, strongly promoted oaks and reduced the proportion of otherwise competitive European beech (Strandberg et al. 2005; Vandekerkhove et al. 2016).

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Q. petraea agg. has a broad ecological niche, showing relative tolerance to soil type and nutrient availability. It can occur not only on poor, stony, sandy, clayey, or calcareous soils (Nicolescu et al. 2025), typically on mildly acidic to neutral soils (pH 4.4–7.3) (Timbal, Aussenac 1996), but also occasionally on highly acidic soils (pH 2.5–3.5) (Nicolescu et al. 2025). The species does not tolerate high or fluctuating groundwater levels or waterlogged areas and favours warm, sunny, south- or southwest-facing slopes, where summer heat stimulates rapid growth. It has drought resistance and a high tolerance to dry conditions because of its ability to access deep soil water (Černý et al. 2024) and xeromorphic leaf traits (e.g. thicker cuticles, sunken stomata, dense pubescence, and reduced leaf area).

Coppice management has been widespread in lowland European forests for centuries (Rackham 1980; Bridge et al. 1986). This system has involved the repeated harvesting of shoots emerging from stumps and surrounding areas at short intervals, ensuring a steady supply of fuelwood. Coppice renewal was often combined with the cultivation of standard trees grown from seed, which were left to mature and provide construction timber and sawlogs. This practice is commonly described as coppice-with-standards (Müllerová et al. 2014). In such forests, long-lived standard trees form a prominent canopy above a short-rotation understorey. The density of standard trees varied considerably across sites and periods (Rackham 1980; Szabó 2010), and although other tree species occurred, oaks clearly predominated among the standard trees (Rackham 1980).

Forests managed in this way experienced more frequent disturbances than high forests did because of the shorter rotation periods. Clearings increase sunlight availability, affecting microclimatic conditions (soil temperature and moisture), evapotranspiration, and nutrient availability. Understorey growth temporarily accelerated following harvests (Haneca et al. 2005) until canopy closure was reestablished (Buckley 1992). These cyclical changes also influence the growth dynamics of standard trees (Altman et al. 2013; Müllerová et al. 2014, 2015; Matula et al. 2019).

In Central Europe, coppice rotation cycles changed from approximately 7 years in the medieval period to 30–40 years by the 20th century (Szabó 2010; Müllerová et al. 2014). In the latter half of the 20th century, the widespread use of fossil fu-

els contributed to a shift towards modern forestry practices, predominantly based on seed-origin high forests. Coppice management largely disappeared across Europe, including the Czech Republic (Haneca et al. 2009; Müllerová et al. 2014, 2016). Remnants of this practice can still be observed in present-day forests as decaying stools and mature standard trees. Like other landscapes shaped by traditional management, many coppice-derived stands are now recognised for their high conservation value (Rackham 1980; Sjölund, Jump 2013; Roleček, Řepka 2020; Bridge et al. 1986; Slach et al. 2021).

Building on this biological legacy, the present study specifically compares managed and unmanaged coppice-with-standards stands, aiming to clarify how management continuity versus abandonment influences tree height development and stand structure.

The novelty of this study lies in providing the first robust, empirically documented evidence that in overaged coppice-with-standards stands, sprouts are indeed shorter than standard trees. Although this relationship may appear intuitive, it has not been formally demonstrated or published in peer-reviewed literature. Consequently, this study addresses a significant research gap in the understanding of structural dynamics in overaged coppice-with-standards stands.

Research questions. The aim of this study is to compare the heights (height strata) of key components in coppice-with-standards stands, namely, old stools and mature standard trees of *Q. petraea* agg., within a region historically managed using this system. A further objective is to assess the influences of selected environmental and management factors on the height growth of *Q. petraea* agg. across the chosen sites. Two contrasting sites were selected for this purpose: one under ongoing forestry management and the other unmanaged for approximately 40 years as part of a forest reserve, although both were historically managed as coppice-with-standards stands.

The study specifically addresses the following questions:

- (i) Do managed and unmanaged coppice-with-standards stands differ in the height development of stools and standard trees? Which factors significantly influence the height growth of stools and standard trees?
- (ii) Are there differences in height among stools with one, two and three and more stems?

MATERIAL AND METHODS

Study site. This study compares coppice-with-standards forests at two sites near Brno (South Moravian Region, Czech Republic): the Masaryk Forest School Enterprise Křtiny ('ŠLP') and the Bosonožský Hájek Nature Reserve ('BH').

The ŠLP site (49°14'46.8"N, 16°36'03.6"E; 46.7 ha) lies within forests managed by Mendel University in Brno. Historically managed as coppice-with-standards until about 1950, it has been systematically restored to this system since 2013. The stands are dominated by *Quercus petraea* agg., accompanied by *Tilia cordata* and *Carpinus betulus*, with a relatively low stocking density (50–80%). ŠLP represents the managed variant.

The BH site (49°11'24.3"N 16°29'53.7"E; 46.6 ha) is a Natura 2000 protected area with long-term absence of forestry interventions (approx. 40 years). The forest structure still reflects former coppice-with-standards management but now shows higher stocking density (80–100%) and gap formation due to natural mortality. Dominant species composition is similar to ŠLP. BH represents the unmanaged variant.

Both sites lie in the Brno Highlands (Hercynian subprovince) at elevations of 300–350 m a.s.l., in the moderately warm to warm climatic zone (mean annual temperature 9.2–10.2 °C; precipita-

tion 390–650 mm). Potential natural vegetation at both sites corresponds to acidophilous oak and oak–hornbeam forests (*Melampyro nemorosi–Carpinetum*). Their contrasting management regimes provide a suitable framework for evaluating tree height development and structural differentiation in overaged coppice-with-standards stands (Figure 1). A detailed characterisation of the natural habitat types of both sites is provided in Table 1.

Field survey. During the spring of 2024, overmatured stands of both research sites showing visible signs of age-related decline (up to 25% at BH and up to 5% at ŠLP) were selected for further survey. Although these stands are classified as coppice-with-standards, the over-maturity led to a reduction of age-related differences in tree dimensions between the standards and the stools. The selected area of both study sites was walked in detail, and every accessible tree was visually inspected to determine whether it represented a standard tree or a stool. Stools were further classified as single-stem, double-stem, or triple-stem (three or more stems). To be classified as a standard tree, an individual had to possess a straight, upright trunk with no basal features indicating previous multistep growth (e.g. cut marks from prior removal of shoots during historical stem selection in stools). Compared with surrounding individuals, standard trees generally exhibit thicker trunks

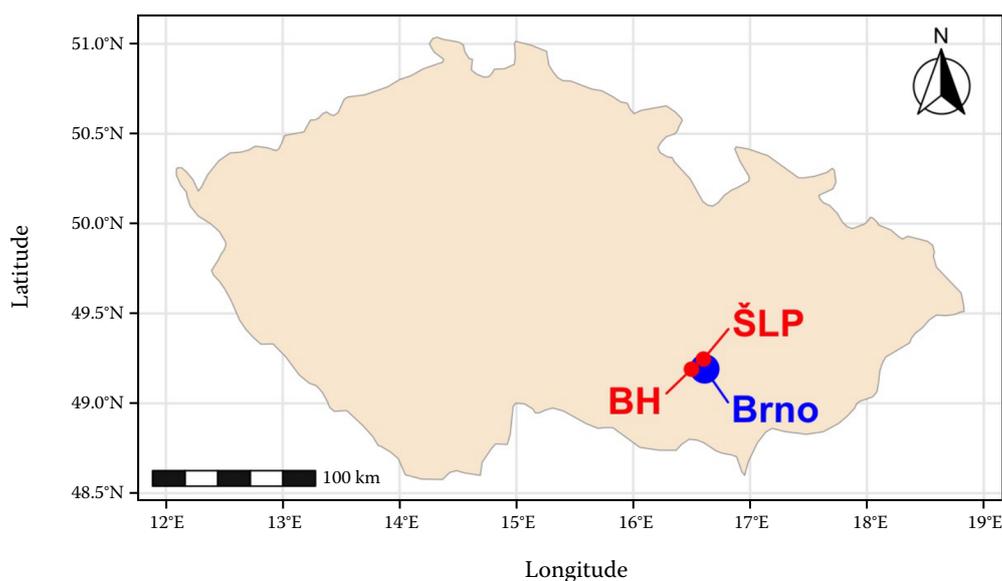


Figure 1. Locations of the analysed BH and ŠLP coppice-with-standards sites near the city of Brno (South Moravian Region, Czech Republic)

BH – Bosonožský Hájek Nature Reserve; ŠLP – Masaryk Forest School Enterprise Křtiny

Table 1. Characteristics of natural habitats by site

Natural habitat (EEA 2006; Chytrý 2013; Chytrý et al. 2010) Description	Site	
	BH	ŠLP
	area share (%)	
L 3.1 – Hercynian oak–hornbeam forests Forests dominated by <i>Carpinus betulus</i> , <i>Quercus petraea</i> agg., and <i>Q. robur</i> , with admixture of <i>Tilia cordata</i> . The shrub layer includes understorey trees and <i>Corylus avellana</i> .	81	73
L 7.1 – dry acidophilous oak forests Open oak forests dominated by <i>Quercus petraea</i> with <i>Betula pendula</i> and <i>Pinus sylvestris</i> in the tree and shrub layers.	18	14
L 6.5B – acidophilous thermophilous oak forests without <i>Genista pilosa</i> Open forests dominated by <i>Q. petraea</i> . Lower tree layer may include <i>Carpinus betulus</i> . The shrub layer is poorly developed, mostly consisting of smaller oaks.	–	13
T 4.2 – mesophilous herbaceous margins Margins and gaps at the edges of oak–hornbeam forests.	1	–
Total	100	100

BH – Bosonožský Hájek Nature Reserve; ŠLP – Masaryk Forest School Enterprise Křtiny

and branches. If a tree showed features of a standard tree but displayed a cut mark at the trunk base, it was classified as a single-stem stool. For each selected stool or standard tree, the geographic coordinates, forest type (sft), habitat type (sft_agg), slope (slope), exposure (exposure), altitude and tree height were collected. Tree heights were measured using the Arboreal Tree Height mobile application (<https://arboreal.se/en/tree-height>) with an accuracy of 0.1 m. Height measurements were taken using an iPhone 14 Pro (Apple Inc., USA) equipped with a LiDAR sensor.

The numbers of *Q. petraea* agg. individuals analysed by site and management type are presented in Table 2. A total of 1 239 trees were measured in the field, including 247 individuals at the BH site and 992 at the ŠLP site.

Although the number of sampled trees differs between the two sites, this imbalance does not bias the

analysis because the relative proportions of the three categories are similar across sites. As a result, the design is proportionally balanced, ensuring that the effects of site and category are not confounded.

Data analysis. Statistical analyses were conducted at two levels: (i) comparison of individual tree heights using two-factor analysis of variance (ANOVA) with multiple comparisons, and (ii) assessment of the influence of selected factors on the heights of *Q. petraea* agg. individuals using multinomial logistic regression.

Two-factor ANOVA with multiple comparisons (comparison of tree heights). This method compares tree heights (height) between two grouping factors: management status (manag_status: managed vs unmanaged) and tree type (object_detail: standard tree; stools: single-stem, double-stem, triple-stem). Prior to applying ANOVA, the data were tested for compliance with its mandatory

Table 2. The numbers of *Q. petraea* agg. individuals by site and forest management type

Site	Standard trees (coppice-with-standards) (pcs)	Coppice (stools)			Total (pcs)
		single-stem (pcs)	double-stem (pcs)	triple-stem (pcs)	
BH (unmanaged)	62	91	68	26	247
ŠLP (managed)	593	185	171	43	992
Total (pcs)	655	276	239	69	1 239

BH – Bosonožský Hájek Nature Reserve; ŠLP – Masaryk Forest School Enterprise Křtiny; pcs – pieces

assumptions, specifically the normality of residuals and the homogeneity of variances across groups. Multiple comparisons were performed using Tukey's honestly significant difference (HSD) test, and the output provides a table with the corresponding *P*-values.

Multinomial logistic regression (influence of factors on tree height). Due to the large number of trees measured and the often dense, heterogeneous canopy conditions, individual height measurements were not always unambiguous. To reduce the influence of individual measurement uncertainty, tree heights were transformed into four height classes: Q1 (low) – the shortest 25% of trees, Q2 (medium–low) – the next 25%, Q3 (medium–high) – the following 25%, and Q4 (high) – the tallest 25%.

The multinomial logistic regression model estimates the probability of each target category (e.g. Q2, Q3, and Q4) relative to a chosen reference category (e.g. Q1). Model outputs are expressed as logarithms of the odds ratios for each predictor–category combination. These ratios indicate how the probability of a tree belonging to a given height category changes with a one-unit change in the predictor relative to the reference category (Q1).

The model includes four height categories ($k = 4$), resulting in three equations that compare Q2, Q3, and Q4 with the reference category Q1. The general formula for a single equation is shown in Equation (1) below:

$$\ln \frac{P(Y_i = k)}{P(Y_i = l)} = \beta_{k0} + \beta_{k1}X_{i1} + \beta_{k2}X_{i2} + \dots + \beta_{kp}X_{ip} \quad (1)$$

where:

- | | |
|---|---|
| $\frac{P(Y_i = k)}{P(Y_i = l)}$ | – the odds ratio, which represents how much more likely an observation is to belong to category k than to the reference category; |
| β_{k0} | – the intercept for the equation comparing category k to the reference, representing the log-odds when all the predictors are zero; |
| $\beta_{k1}, \beta_{k2}, \dots, \beta_{kp}$ | – regression coefficients for predictors, where indicates how the log-odds change with a one-unit increase in the predictor; |
| $X_{x1}, X_{x2}, \dots, X_{xp}$ | – the predictor values for the i -th observation. |

In the R environment, the multinomial logistic regression model was implemented according to Equation (2):

```
model_multinom <- multinom (height_cat-
  egory ~ altitude + sft + sft_agg + exposure      (2)
  + manag_status + object_detail + slope,
  data = data_categorised)
```

where:

- | | |
|-----------------|--|
| height_category | – height class (Q1–Q4); |
| altitude | – elevation of the tree base (m a.s.l.); |
| sft | – forest site type (2B, 2C, 2D, 2H, 2S); |
| sft_agg | – habitat type based on sft (rich/dry); |
| exposure | – cardinal exposure; |
| manag_status | – management status of the site (managed/unmanaged); |
| object_detail | – tree type (standard tree; stool: single-stem, double-stem, triple-stem); |
| slope | – slope presence (yes/no; threshold = 15°). |

Two-factor ANOVA and multinomial logistic regression analyses were conducted using R (Version 4.5.1; R Core Team 2025). Tukey's HSD test for multiple comparisons was performed using the 'agricolae' package (de Mendiburu 2023), and multinomial logistic regression was executed using the 'nnet' package (Venables et al. 2003).

RESULTS

Comparison of tree heights by management status, tree type, and their interaction. A comparison of tree heights is presented in Table 3. The results indicate that differences in mean tree heights according to management status (manag_status) are statistically significant, although their effect is smaller than that of tree type (object_detail). Differences in mean heights among tree types (e.g. standard tree vs double-stem stool) are highly significant, indicating that tree type strongly influences height.

The interaction effect between management status (manag_status) and tree type (object_detail) is also highly significant, suggesting that the effect of management status on tree height varies depending on the type of tree.

Multiple pairwise comparisons of the tree height groups are presented in Figure 2 and Table S1 in the Electronic Supplementary Material (ESM).

Table 3. Comparison of tree heights by management status, tree type, and their interaction – results of the two-factor ANOVA

Source of variation	Df	Sum of squares (Sum Sq)	Mean square (Mean Sq)	F-value	P-value	Significance
Management (manag_status)	1	61	61.2	5.944	0.0149	*
Tree type (object_detail)	3	3 586	1 195.2	116.022	< 2e-16	***
Interaction	3	408	136.1	13.209	1.72e-08	***
Residuals	1 231	12 682	10.3	–	–	–
Total	1 238	16 737	–	–	–	–

*significance level 5% (0.05); ***significance level 0.1% (0.001); ANOVA – analysis of variance; Df – degrees of freedom

The following conclusions can be drawn:

- **Effect of tree type.** The tallest average heights were observed for standard trees (standard_tree) in managed stands, with a mean height of 21.80 m. This group is significantly different from all other categories, as indicated by a unique letter assignment (a).
- **Effect of management.** The mean heights also differed significantly according to the management status. In most cases (except for standard trees), compared with their counterparts in managed stands, trees in unmanaged stands presented higher mean heights. For example, the mean height of unmanaged single-stem stools (19.64 m) is significantly greater than that of managed single-stem stools (18.08 m).
- **Statistically indistinguishable groups.** Some groups did not differ significantly from each other. The unmanaged:standard_tree, unma-

- naged:double_stem, and unmanaged:single_stem groups share the letter (b), indicating no significant differences in mean heights. Similarly, the unmanaged:triple_stem and managed:double_stem groups do not differ significantly from each other or from the managed:single_stem group, as shown by the shared letters (cd).
 - **Lowest mean height.** The lowest mean height was recorded for managed:triple_stem stools (15.97 m), which differed significantly from those of all the other groups except for the unmanaged:triple_stem and managed:double_stem groups. This is reflected by the unique letter (d).
- Overall, tree type (object_detail) and management status (manag_status) play key roles in determining tree height, with the tallest average heights observed in managed standard trees, whereas trees in unmanaged stands exhibit a more homogeneous height distribution.

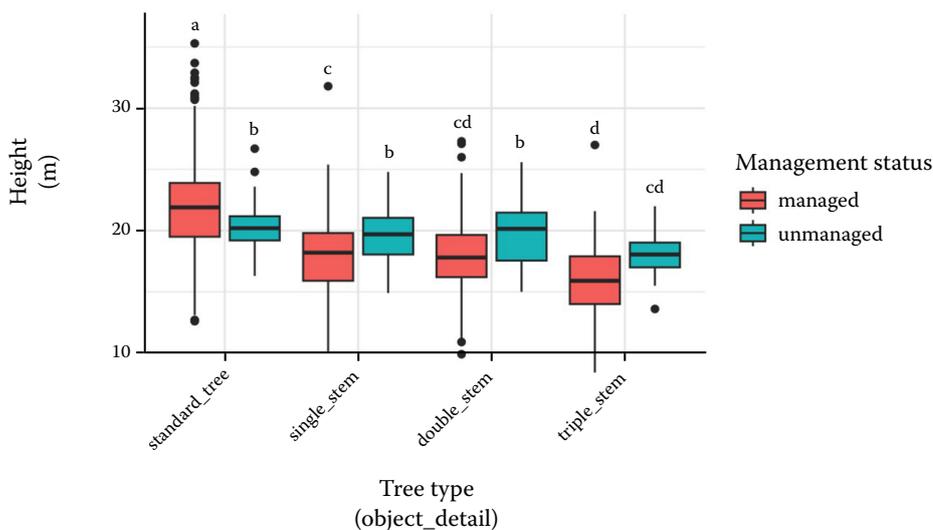


Figure 2. Comparison of tree heights according to management status and tree type based on multiple pair comparisons – Tukey's honestly significant difference (HSD) test

Effects of explanatory factors on tree height.

To assess the influence of selected factors on the heights of *Q. petraea* agg. individuals, the height dataset was divided into four quartiles corresponding to the height categories (see Table S2 in the ESM). Each category contains approximately the same number of trees, with the lowest height category (Q1) including trees 8.4–17.6 m tall and the highest category (Q4) including trees 22.6–35.3 m tall.

The multinomial logistic regression model achieved a residual deviance of 2 657.331, an Akaike information criterion (AIC) of 2 741.331 and a variance explained by the model (Nagelkerke R-squared) of 0.2905. A detailed overview of the model results is provided in Tables 4–6. Analysis of statistically significant predictors ($P < 0.05$) revealed the following conclusions:

- **Altitude.** The relationship with altitude is statistically significant for categories Q2 and Q3. The coefficient for Q2 is positive, indicating that increasing altitude increases the likelihood of a tree being classified in Q2 rather than Q1. The trend for Q3 is weaker. The coefficient for Q4 is not statistically significant ($P > 0.05$).
- **Forest site type (sft).** The forest site type 2D (enriched beech-oak forest) has a strong positive effect on all categories (Q2, Q3, and Q4) relative

to Q1. This effect is strongest for the tallest managed trees (Q4), as indicated by the highest coefficient and lowest p-value (Figures S1 and S2 in the ESM).

- **Habitat type (sft_agg).** The habitat type sft_agg rich has a strong positive effect on Q4, demonstrating that richer sites significantly increase the likelihood of a tree reaching the highest height category (Figure S3 in the ESM).
- **Exposure.** Compared with the reference exposures, south- and west-facing exposures show statistically significant and strongly negative coefficients for all categories (Q2, Q3, and Q4), indicating that these exposures substantially reduce the probability of trees reaching higher height categories (Figures S4–S7 in the ESM).
- **Management (manag_status).** The coefficients for unmanaged stands are significant for Q2 and Q3, suggesting that trees in areas left to natural development (BH, forest reserve) have a higher probability of being in medium height categories (Figure S8 in the ESM).
- **Tree type (object_detail).** Single-stem, double-stem, and triple-stem stools exhibit strongly negative coefficients across all height categories, which is consistent with expectations, as these trees are generally shorter than the reference standard_tree. The negative effect is strongest

Table 4. Coefficients of the multinomial logistic regression model for height category Q2 (medium–low)

Predictor	Coefficient	SE	Z-value	P-value
Intercept	–1.677	0.577	–2.907	0.004
Altitude	0.013	0.003	4.504	< 0.001
Sft: 2C – dry beech forest	–1.225	0.302	–4.057	< 0.001
Sft: 2D – enriched beech-oak forest	2.116	0.353	5.987	< 0.001
Sft: 2H – loamy beech forest	0.697	0.487	1.433	0.152
Sft: 2S – fresh beech forest	0.358	0.316	1.134	0.257
Sft_agg: rich	–0.452	0.361	–1.254	0.210
Exposure: north	–0.281	0.381	–0.738	0.461
Exposure: south	–0.984	0.293	–3.361	< 0.001
Exposure: west	–1.548	0.326	–4.748	< 0.001
Manag_status: unmanaged	0.589	0.267	2.207	0.027
Object_detail: single_stem	–1.015	0.245	–4.151	< 0.001
Object_detail: double_stem	–1.202	0.253	–4.753	< 0.001
Object_detail: triple_stem	–2.248	0.403	–5.584	< 0.001
Slope: slope_yes	–0.538	0.214	–2.508	0.012

Bold – P -values less than 0.05; predictors marked in this way are considered statistically significant (significance level $\alpha < 0.05$); SE – standard error; sft – forest type; sft_agg – habitat type; manag_status – management (managed vs unmanaged); object_detail – tree type; slope_yes – presence of slope

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Table 5. Results of the multinomial logistic regression model – coefficients for height category Q3 (medium–high)

Predictor	Coefficient	SE	Z-value	P-value
Intercept	–0.041	0.522	–0.078	0.938
Altitude	0.006	0.003	2.278	0.023
Sft: 2C – dry beech forest	–0.678	0.296	–2.287	0.022
Sft: 2D – enriched beech-oak forest	2.826	0.301	9.375	< 0.001
Sft: 2H – loamy beech forest	1.279	0.489	2.615	0.009
Sft: 2S – fresh beech forest	0.239	0.329	0.726	0.468
Sft_agg: rich	0.637	0.334	1.909	0.056
Exposure: north	–0.514	0.392	–1.310	0.190
Exposure: south	–1.421	0.313	–4.539	< 0.001
Exposure: west	–1.893	0.341	–5.544	< 0.001
Manag_status: unmanaged	1.576	0.285	5.539	< 0.001
Object_detail: single_stem	–1.980	0.267	–7.405	< 0.001
Object_detail: double_stem	–1.821	0.268	–6.804	< 0.001
Object_detail: triple_stem	–3.594	0.483	–7.448	< 0.001
Slope: slope_yes	–0.845	0.230	–3.677	< 0.001

Bold – *P*-values less than 0.05; predictors marked in this way are considered statistically significant (significance level $\alpha < 0.05$); SE – standard error; sft – forest type; sft_agg – habitat type; manag_status – management (managed vs unmanaged); object_detail – tree type; slope_yes – presence of slope

for triple-stem stools, confirming their lowest probability of reaching higher height categories (Figure S9 in the ESM).

– **Slope.** The presence of slope (slope_yes) has a statistically significant negative effect on all categories, indicating that trees located on slopes have

a lower probability of reaching greater heights than those in the reference category Q1 (Figure S10 in the ESM).

Overall, the most influential factors for tree height were forest type (sft 2D – enriched beech-oak forest), exposure (south and west), and tree

Table 6: Results of the multinomial logistic regression model – coefficients for height category Q4 (high)

Predictor	Coefficient	SE	Z-value	P-value
Intercept	1.643	0.528	3.109	0.002
Altitude	–0.001	0.003	–0.328	0.743
Sft: 2C – dry beech forest	–0.323	0.327	–0.986	0.324
Sft: 2D – enriched beech-oak forest	3.877	0.284	13.634	< 0.001
Sft: 2H – loamy beech forest	1.483	0.503	2.948	0.003
Sft: 2S – fresh beech forest	0.261	0.335	0.778	0.436
Sft_agg: rich	1.965	0.330	5.946	< 0.001
Exposure: north	–1.223	0.426	–2.875	0.004
Exposure: south	–1.713	0.359	–4.768	< 0.001
Exposure: west	–2.025	0.375	–5.399	< 0.001
Manag_status: unmanaged	0.360	0.398	0.904	0.366
Object_detail: single_stem	–3.408	0.350	–9.738	< 0.001
Object_detail: double_stem	–3.293	0.350	–9.405	< 0.001
Object_detail: triple_stem	–5.971	1.070	–5.582	< 0.001
Slope: slope_yes	–0.533	0.243	–2.193	0.028

Bold – *P*-values less than 0.05; predictors marked in this way are considered statistically significant (significance level $\alpha < 0.05$); SE – standard error; sft – forest type; sft_agg – habitat type; manag_status – management (managed vs unmanaged); object_detail – tree type; slope_yes – presence of slope

type (object_detail). The altitude was significant for the lower height categories but became negligible for the tallest trees.

DISCUSSION

Accuracy and limitations of height measurements. In this study, tree heights were measured using the Arboreal Tree Height mobile application. To minimise potential bias, measurements were consistently taken by the same person to ensure methodological uniformity in all studied sites. Furthermore, a phone model iPhone 14 Pro with a LiDAR sensor was used for measurements. This adds significant credibility compared to a standard camera-only phone. The Arboreal Tree Height app produced results with an accuracy of 0.1 m comparable to traditional methods (Haglöf Vertex II) while being significantly faster, with less office processing and more cost-effective (Atcher Soler 2025). On the other hand, it should be mentioned that the height measurements are sensitive to user positioning and stand structure and visibility (Sandim et al. 2023). In our field survey, data were collected in over-aged coppice-with-standards stands, so there were no problems with high stem density and canopy closure. The Arboreal Tree Height app in smartphone-based LiDAR combines scientific accuracy with practical efficiency (Elias et al. 2025; Morocho Toaza et al. 2025) and is perceived as a modern tool in forest inventory. The main factors that potentially affect stem growth in coppices or standard trees include (i) root systems and their (im)balance with the aboveground system; (ii) genetic traits of stems, i.e. genetic differences between stools and standard trees and between stools and standard trees; (iii) competition within and between stools (including standard trees) and related resource availability; and (iv) specific differences in site quality (growth areas).

We consider Salomón et al. (2013) publication to be a comprehensive overview of this subject. There are few such publications, which is why it is the main article we discuss.

Stem and root growth and ageing. Relationships between the stool structures and increases in stem diameter of Pyrenean oak (*Quercus pyrenaica* Willd.) coppices were investigated in central Spain by Salomón et al. (2013). They concluded that stems belonging to larger stools – characterised by greater spatial extents, higher stem densi-

ties, and greater stump root biomass – exhibited lower growth potential than stems from smaller stools did. A similar pattern was observed in our study (Figure 2; Table S1 in the ESM), particularly when the mean heights of triple-stem vs double-stem and single-stem stools were compared. This phenomenon can be partly explained by root ageing, which increases root biomass and exacerbates the imbalance between roots and stems. As a result, root respiration consumes a substantial portion of photosynthetically produced carbohydrates, thereby limiting stem growth (DesRochers, Lieffers 2001; Landhäuser, Lieffers 2002; Corcuera et al. 2006).

The ageing of coppice stands as a potential explanation for low productivity has also been discussed for other oak species, such as holm oak (*Quercus ilex* L.) in southern France (Cartan-Son et al. 1992) and white oak (*Quercus alba* L.), scarlet oak (*Quercus coccinea* Muenchh.), and black oak (*Quercus velutina* Lam.) in eastern North America (Dey, Jensen 2002). Coppicing likely leads to partial root mortality in older stools, with some roots no longer connected.

According to Salomón et al. (2013), standard trees growing within coppices may play important roles in growth and ageing processes. Their large crowns and interconnected root systems with stools could increase resource availability within the coppice (see Competition section below).

This is a potential topic for further research, which the authors intend to pursue in the future.

Genetic traits of stems, i.e. genetic differences between stools and between stools and standard trees. In the study by Salomón et al. (2013), the authors analysed 781 stems obtained from 1 ha of a *Q. pyrenaica* coppice and identified 146 distinct genotypes, indicating a substantial role of clonal regeneration (over 80%). Such heterogeneity suggests, according to the authors, considerable temporal differences in stump regeneration within the stand. Furthermore, comparisons across different stands revealed high variability in clonal structure among stands in the Valsaín area of central Spain. In contrast, in the area located 50 km from Valsaín, six times more genotypes were identified than in Valsaín, resulting in clonal reproduction of only 14% (Valbuena-Carabaña et al. 2008).

In contrast to the commonly held assumptions of low genetic diversity and imbalances between

aboveground and belowground organs in large, overmature coppice stools (clones), often attributed to centuries of coppice management, Salomón et al. (2017) challenge these views on the basis of their study of *Q. pyrenaica* coppices. Their results demonstrated that traditional management did not increase losses in genetic diversity; in contrast, it facilitated the recruitment of new genotypes and the establishment of unevenly aged stands with heterogeneous clonal structures (Salomón et al. 2013, 2017). This represents a prospective area for future investigation that the authors plan to explore.

Competition. Clones with large dimensions lead to greater variability in stem growth, which stimulates intraclonal competition in certain tree species, including oaks (Peterson 1997; Dolezal et al. 2009). In coppices, one would therefore expect stronger competition within stumps than between stumps; however, this was not confirmed by the findings of Salomón et al. (2013) for *Q. pyrenaica* coppices. According to the authors, these results suggest that each stool can exert a similar competitive effect regardless of its clonal identity. This implies that these stools primarily compete for aboveground resources rather than for belowground resources; i.e. competition does not depend on root distribution or clonal structure.

Unilateral or asymmetric competition occurs when larger trees have a disproportionate competitive advantage over smaller ones, typically for resources such as light. In contrast, bilateral or symmetric competition arises when all trees compete with their neighbours, regardless of their size (Weiner 1990). Similarly, Adame et al. (2008a) reported that unilateral competition explains the greater variability in stem growth than bilateral competition does, indicating that in dense coppice stands, light competition may have a stronger effect than competition for belowground resources.

These findings are complemented by the study of Altman et al. (2013) on the growth of oak standards originating from former high-forest stands in the Děvínský les National Nature Reserve in the Pálava region, Czech Republic. By monitoring the radial growth responses of the standard trees, the authors concluded that growth is influenced by the intensity of competition with the understorey. This competition is temporarily removed or reduced following thinning (coppicing), allowing standard

trees to grow beyond their usual increases. The effect gradually diminishes as the understorey fills the space again. Light competition is negligible if the understorey is too sparse to compete with emergent trees. However, as the coppicing cycle extended over several decades, light competition could have a substantial impact. The same applies to young trees before they reach the canopy layer, which are not yet shaded. The authors further noted that other factors may affect radial growth, such as increased soil nutrient availability following understorey removal and competition for water.

Similar results were reported by Müllerová et al. (2016) regarding the response of standard oak trees from former high-forest stands at five limestone oak–hornbeam sites and acidophilous oak forests in the Český kras Protected Landscape Area, Czech Republic. The authors reported that the greater the number of smaller trees (particularly hornbeams) surrounding the standard trees, the stronger the radial growth response to disturbances, such as coppicing. This suggests that competition from larger trees (i.e. more single-stem stools derived from seeds) reduces the response of the growth of standard trees to coppicing, i.e. the detectability of this change via radial increment.

Consistent findings were also reported by Matula et al. (2019), who reported increased growth of coppice stools with increasing distance from the nearest oak standard tree. The negative effect of standard trees on coppice growth was similarly confirmed by Atwood et al. (2009). Interestingly, however, this negative impact was not greater than the negative effect of competition from neighbouring coppice stools, as noted by Matula et al. (2019). The authors attributed this to the relatively low density of oak standards and their declining health, which may have reduced their competitive strength, as observed for most standard trees following harvest during the conversion to high forest at the Hádecká Planinka research plot near Brno, Czech Republic.

Influence of site on stem growth. Salomón et al. (2013) reported that including different growth areas in the analysis of stem diameter growth in *Q. pyrenaica* coppices substantially improved the performance of their growth model, increasing its explanatory power from 17.5% to 44.4%. According to the authors, this suggests that the variability among the analysed areas

could be attributed to differences in silvicultural interventions and past disturbances such as fires, soil properties, or climatic conditions (Adame et al. 2008b).

We reached similar conclusions in our study, demonstrating the influence of forest type on the probability of height growth for stools and standard trees, including whether the stand was managed or unmanaged (Figures S1 and S2 in the ESM). We also showed that the probability of occurrence of different height categories of individuals in the studied stands varied according to whether they were located on drying or rich sites and whether they were managed or unmanaged (Figure S3 in the ESM). Our results further highlight the importance of aspect. In particular, compared with the reference category, the southern (south exposure) and western (west exposure) aspects substantially reduced the likelihood of trees reaching taller height categories (Figures S4–S7 in the ESM). Elevation (altitude) was found to be significant mainly for the shorter height categories but became negligible for the tallest trees (Figures S8 and S9 in the ESM). Finally, with respect to slope, trees growing on slopes had a lower probability of attaining greater heights (Figure S10 in the ESM).

Site types and local microclimates, including aspect and slope, are critical determinants of oak growth and vitality. On marginal, warm, and dry sites – where these systems were traditionally managed – oaks reach smaller sizes, reflecting natural adaptation to less favourable conditions. Consequently, the heights achieved in abandoned coppices and former high forests largely reflect both historical site selection and the subsequent cessation of management.

Studies conducted on oak coppice underscore the benefits of thinning (forest management) for increasing the growth of standard trees (Ducrey, Toth 1992; Mayor, Rodà 1993; Cañellas et al. 2004; Müllerová et al. 2016). However, as Salomón et al. (2013) caution, thinning in *Q. pyrenaica* coppices should be performed carefully because inconspicuous clonal aggregates can obscure the genetic structure, potentially leading to genotype loss and reduced genetic diversity. On the basis of their study, which identified 146 genotypes per hectare, the authors argue that genotype loss due to thinning would further exacerbate the already low number of distinct genotypes.

CONCLUSION

Our study compared managed vs unmanaged overaged coppice-with-standards stands. The results support an understanding of structural dynamics in overaged coppice systems. Tree type and management status play key roles in determining tree height. The tallest average heights are observed in managed standard trees, whereas trees in unmanaged stands exhibit a more homogeneous height distribution. It is worth noting that our study is the first to confirm these findings.

In light of current discussions and findings on the effective management of lowland forests, we suggest recommendations for the potential reintroduction of coppice forests (not only in the Czech Republic): (i) newly established coppice stands should not be created in areas of currently overmature, dense coppices where this type of management has been practised for centuries, or (ii) existing dense coppices should be allowed to undergo local natural mortality and decay, with regeneration efforts commencing only after these stands have developed into open, well-spaced forests with natural sexual regeneration.

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