

Is neglecting soil variables in tree growth studies justified? Lessons from modelling the growth of three oak species

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ABSTRACT

We analysed differences in growth among *Quercus petraea*, *Q. robur*, and *Q. cerris* in natural forests across 16 reference soil groups. The study encompassed the forested area of Slovenia (11.8 thousand km²), with soil information derived from the national soil map at a scale of 1:25,000. Oak growth was evaluated using periodic basal area increment data from 52,333 trees measured on 17,733 permanent sample plots. The effects of site, stand, and individual tree characteristics on growth were examined using linear mixed-effects models. Soil unit was included as a dummy variable. Soil contributed 16.3, 11.2, and 14.0% to the explained variability in basal area increment of *Q. petraea*, *Q. robur*, and *Q. cerris*, respectively. The difference between the highest and the lowest mean basal area increment across soil units for *Q. petraea*, *Q. robur*, and *Q. cerris* amounted to 70, 39, and 29% of their mean basal area increment, respectively. The three oak species reached the highest and lowest growth rates on different soil units. *Q. petraea* performed best on Dystric and Eutric Planosols, *Q. robur* on Eutric and Dystric Gleysols, and *Q. cerris* on Haplic Luvisols. This study demonstrates that soil-related factors represent an important component of growth modelling and should be evaluated alongside tree, stand, site and climatic variables.

1. Introduction

Individual tree growth models are usually developed using tree, stand, and environmental explanatory variables. Soil, together with climate, topography, geology, and vegetation, is a key environmental factor. In recent decades, many growth studies have emphasized the impact of climate variables, often in interaction with stand attributes (e.g. mixture, density, heterogeneity). By contrast, soil variables have seldom been included in growth studies, even more rarely than topographic variables (e.g. elevation, aspect, slope), despite the fact that they are crucial for forest productivity (Binkley, 2013). Although soil characteristics can strongly modulate growth responses to changing climatic conditions, they are often omitted from multivariate studies of climate change impacts on tree and stand growth (Chakraborty et al., 2019; Harvey et al., 2020; Shi et al., 2024). The labour-intensive measurement of soil characteristics is probably the main reason for the frequent omission of soil variables in tree growth studies.

Two main types of studies on the impact of soil on tree growth can be distinguished (Bončina et al., 2023). The first type is characterized by detailed field measurements of soil properties and associated tree

growth response, typically conducted over limited areas and with relatively small sample sizes (e.g. Aertsen et al., 2012; Scharnweber et al., 2013; Kobal et al., 2015; Lévesque et al., 2016; Calvaruso et al., 2017; Selmann et al., 2021). The second type, also applied in this study, evaluates the impact of soil classes on tree and stand growth. Several approaches to soil classification exist, relying on one or more soil characteristics. Individual soil classes reflect the influence of specific soil-forming factors and processes (Bockheim and Gennadiyev, 2000). In regional-scale growth studies, soil class is typically included as an explanatory variable alongside other site descriptors, using large datasets derived from forest inventories. Permanent sample plots with repeated tree measurements at 10-year intervals are commonly used in such analyses (Schelhaas et al., 2018; Selmann et al., 2021; Bončina et al., 2023).

Soil characteristics can influence the distribution of tree species, their competitiveness, and growth processes. The natural fertility of forest soils is governed by a combination of physical, chemical, and biological properties, including organic matter content, clay content and mineralogical composition, the presence of weatherable minerals, soil reaction, base saturation, and biological activity. As a result, forest soils

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differ substantially in productive potential, ranging from deep, porous, well-aerated soils with high capacities for nutrient supply and retention to shallow, weakly developed soils with limited ability to sustain vegetation productivity. Despite their importance, the contribution of soil properties to tree growth and overall forest productivity remains difficult to quantify and is still not fully understood. Although soil variables are included in some growth studies, they are often represented in a simplified manner, most commonly through soil classes that integrate multiple soil characteristics. Consequently, other drivers, particularly climate, tend to receive greater emphasis, raising the question of whether the relative neglect of soil variables in tree growth studies is justified. The effects of soil classes on basal area increment have commonly been analysed using basal area increment (Monserud and Sterba, 1996; Vospernik, 2021) or diameter increment (e.g. Toledo et al., 2011), with tree diameter conventionally measured at 1.3 m above ground level (DBH, diameter at breast height).

Growth responses to various soil factors can differ significantly between tree species. In Europe, most soil–growth studies have focused on European beech, Norway spruce, and silver fir (Alavi, 2002; Kobal et al., 2015; Yeste et al., 2021). Far fewer studies have examined other tree species, with oaks being a typical example. Oak species often occur as components in forests dominated by spruce and/or beech or fir, and less frequently as the dominant species in specific forest site types. More than 500 oak species are recognized globally (Long et al., 2021). In Europe, more than 20 native oak species are reported (Flies, 1993; Löf, 2024; Lyubanova et al., 2024), of which pedunculate oak (*Q. robur*) and sessile oak (*Q. petraea*) are the most widespread (Eaton et al., 2016). These species are common in the temperate zone (deciduous mixed forests), whereas other oak species, such as downy oak (*Q. pubescens*) and Turkey oak (*Q. cerris*), are more frequent in the (sub-)Mediterranean region and/or in warmer parts (e.g. southern Europe) of temperate forests (Pasta et al., 2016; Lados et al., 2024). Across Europe, oaks have been identified as climate-resilient species, implying that their populations are likely to persist or expand under future climatic conditions (Hanewinkel et al., 2013; Dyderski et al., 2025; Popa and Popa, 2026). However, local declines have also been reported. For instance, *Q. robur* is highly sensitive to drought stress associated with increasing temperatures and altered precipitation regimes. Key vulnerabilities include reduced water availability, extreme heat, and diseases (Nechita and Camarero, 2025). For *Q. cerris*, substantial declines in thermophilic deciduous oak forests have also been reported in parts of its geographical distribution due to the impacts of climate change (Conte et al., 2025).

Information from soil maps is relevant for ecological forestry (Simon et al., 2020). Differences in natural tree species composition and the growth patterns of stands and tree species are expected between soil units (Sellan et al., 2019; Bončina et al., 2023). The competitiveness of tree species and stand dynamics can differ markedly between forest stands established on different soil units (Coates, 2013; Guo et al., 2017). Soil classification systems are based on a combination of morphological, genetic, chemical, physical, and biological soil attributes (IUSS Working Group WRB, 2015).

Soil units are commonly used as criteria for the classification of forest types, as site productivity and species-specific site indices may differ substantially among them (Skovsgaard and Vancly, 2013; Bončina et al., 2021). However, soil classification systems differ across countries, which complicates comparisons among regions. Internationally harmonized frameworks, such as the FAO–UNESCO system and the World Reference Base for Soil Resources (WRB), facilitate cross-regional communication and comparability (FAO–UNESCO, 1974; FAO, 1988; Soil Atlas of Europe, 2005; IUSS Working Group WRB, 2015). The WRB currently defines 32 reference soil groups (RSGs, hereafter referred to as soil units), characterized by combinations of principal and supplementary qualifiers. However, few studies have modelled tree growth across reference soil groups under varying stand conditions at regional scales (but see Kostić et al., 2021a, 2021b), and this gap is particularly pronounced for less frequently studied yet regionally important species

such as *Quercus robur* at its southeastern distribution margin. Studies evaluating the influence of soil on oak growth at regional spatial scales therefore remain limited. We assume that the importance of soil factors in growth studies has been underestimated, partly due to the assumption that soil variables explain only a minor proportion of growth variability in tree growth models.

This study focuses on developing growth models for three primary European oak species across temperate and sub-Mediterranean regions. Specifically, we aim to (i) assess the significance of different drivers of tree growth, including tree-, stand-, site-, and climate-related variables, and (ii) evaluate the effect of soil classes on growth patterns within each species. To this end, we investigated the basal area growth of three oak species (*Q. petraea*, *Q. robur*, and *Q. cerris*) across a range of soil classes while accounting for the simultaneous effects of tree-, stand-, site-, and climate-related variables. Previous research indicates that soil can influence the growth of major European tree species (Norway spruce, European beech, Scots pine, silver fir and sessile oak) in diverse ways (Bončina et al., 2023). We expect significant differences in the growth of these oak species among soil classes. Given interspecific differences in ecological niches, we further hypothesize that the examined species attain their growth optima on different soil units.

2. Materials and methods

2.1. Study area

The research was conducted across Slovenia's forests, which extend over an area of about 11.8 thousand km². Continental and Alpine climates prevail, while a sub-Mediterranean climate is present in the coastal area. Carbonate rocks represent the largest share of lithological groups (54.6%), with clastic sediments accounting for 36.0% and metamorphic rocks for 4.2% (Buser and Komac, 2010). Among the factors controlling soil formation, parent material plays a dominant role, with topography having a secondary influence, whereas climate acts as a broader, overarching factor (Vrščaj et al., 2017).

The interaction of diverse topography and climatic influences from the Mediterranean, Alpine, and Pannonian regions results in highly heterogeneous growth conditions. Forest vegetation extends from coastal areas to the timberline at approximately 1500–1700 m a.s.l. Beech-dominated forest types account for about 70% of the total forest area (Bončina, 2012), whereas other forest types with a substantial presence of oak species, including lowland, riparian, and thermophilous broadleaved forests, cover a smaller proportion.

Oak species have a broad ecological amplitude (Wang et al., 2025; Nicolescu et al., 2025). Among the three oak species, *Q. petraea* occurs across the largest proportion of the study area (Table 1) and is found, on average, at higher elevations with higher average annual precipitation. The main characteristics of the three oak species in the study area are as follows (Fig. 1; Table 1; Table S1):

- *Q. petraea* occupies the largest area, mainly in the colline and sub-montane vegetation belts. It grows on a wide range of substrates, from limestone and dolomite to siliceous and sandy rocks, and therefore occurs on a variety of soil units (Table S1), including Anthrosol (ATa), Dystric, Eutric, and Chromic Cambisols (CMc, CMD, CMe, CMx), Eutric Fluvisols (FLe), Dystric and Eutric Gleysols (GLd, GLe), Dystric, Eutric, Mollic, and Rendzic Leptosols (LPd, LPe, LPm, LPk), Haplic Luvisols (LVh), and Dystric and Eutric Planosols (PLd, PLe), which are characterized by either relatively high or very low pH. It can occur as a substantial component during certain successional stages on sites with potential vegetation of beech forests (Bončina et al., 2021). *Q. petraea* sites on carbonate bedrock (Dinaric and sub-Mediterranean regions) are characterized by relatively high rockiness. In contrast, sites on acidophilous soil units usually lack surface rockiness. *Q. petraea* usually occurs as a minor tree species in mixed, mainly broadleaved stands; in the temperate zone it is mainly

Table 1

Ecological characteristics of forest stands dominated by three oak species in the study area (data source: SFS, 2014). Data are presented as means (min-max).

	<i>Q. petraea</i>	<i>Q. robur</i>	<i>Q. cerris</i>
Area of forest stands in which the oak species is present (ha; % of total forest area)	201,498 (24.32)	23,089 (2.79)	35,988 (4.34)
Elevation (m a.s.l.)	421 (60–1264)	241 (81–953)	483 (59–1019)
Mean annual temperature (°C)	8.8 (3.0–13.0)	9.4 (5.0–11.0)	8.9 (3.0–13.0)
Precipitation (mm)	1523 (850–2900)	1377 (1050–2300)	1474 (850–2900)
Inclination (°)	17 (0–55)	5 (0–43)	16 (0–54)
Prevailing soil units	CMd, CMe, CMx	CMd, GLd, LVh	CMx, CMe, CMd
Rockiness (%)	9 (0–100)	3 (0–43)	22 (0–100)
Soil depth (cm)	74 (3–429)	89 (25–121)	67 (10–230)
Site productivity (SP) (m ³)	1.9 (1.1–2.8)	2.0 (1.3–2.7)	1.8 (1.1–2.7)
Average volume of stands in which the observed oak species is present (m ³ ha ⁻¹)	282	276	242
Proportion of observed oak species (%) in total stand volume	5.34	0.75	0.74

associated with *Fagus sylvatica* and *Carpinus betulus*, while on acidic soils it also co-occurs with conifers (e.g. *Picea abies*, *Abies alba*, *Pinus sylvestris*). On thermophilous sites and during certain successional stages, it occurs together with many broadleaved tree species. It

rarely dominates stand volume or forms pure forest stands (Bončina et al., 2021).

- *Q. robur* occurs at lower elevations, in lowlands, or even in moist areas with occasional or periodic flooding. It is common on Chromic Cambisols (CMd, CMe, CMx), Fluvisols (FLd), Dystric and Eutric Gleysols (GLd, GLe), Dystric, Eutric, and Rendzic Leptosols (LPd, LPk), Haplic Luvisols (LVh), and Dystric and Eutric Planosols (PLd, PLk), where it can dominate forest stand composition. These sites are generally warmer than those of *Q. petraea* (Table 1).
- *Q. cerris* is widely distributed in Slovenia. It is more common in the sub-Mediterranean region but also occurs on warm sites in the sub-montane vegetation belt. It is also tolerant of drier conditions, including drought. It can occur as a successional species on sites whose potential vegetation is thermophilous beech forest. (See Fig. 1)

Due to the predominance of close-to-nature forestry, forests are generally well preserved. In oak-dominated stands, the irregular shelterwood system prevails, while the regular shelterwood system is applied less frequently. Selection systems and coppice with standards are rare. These management approaches result in fine-scale mosaics of various stand structures.

2.2. Data

Forest inventory data provided the primary data source (SFS, 2014). Inventories record all trees with a diameter at breast height (DBH) of at least 10 cm on circular permanent sample plots (PSPs) of 500 m². These plots are arranged in sampling grids measuring 250 × 250 m and 250 ×

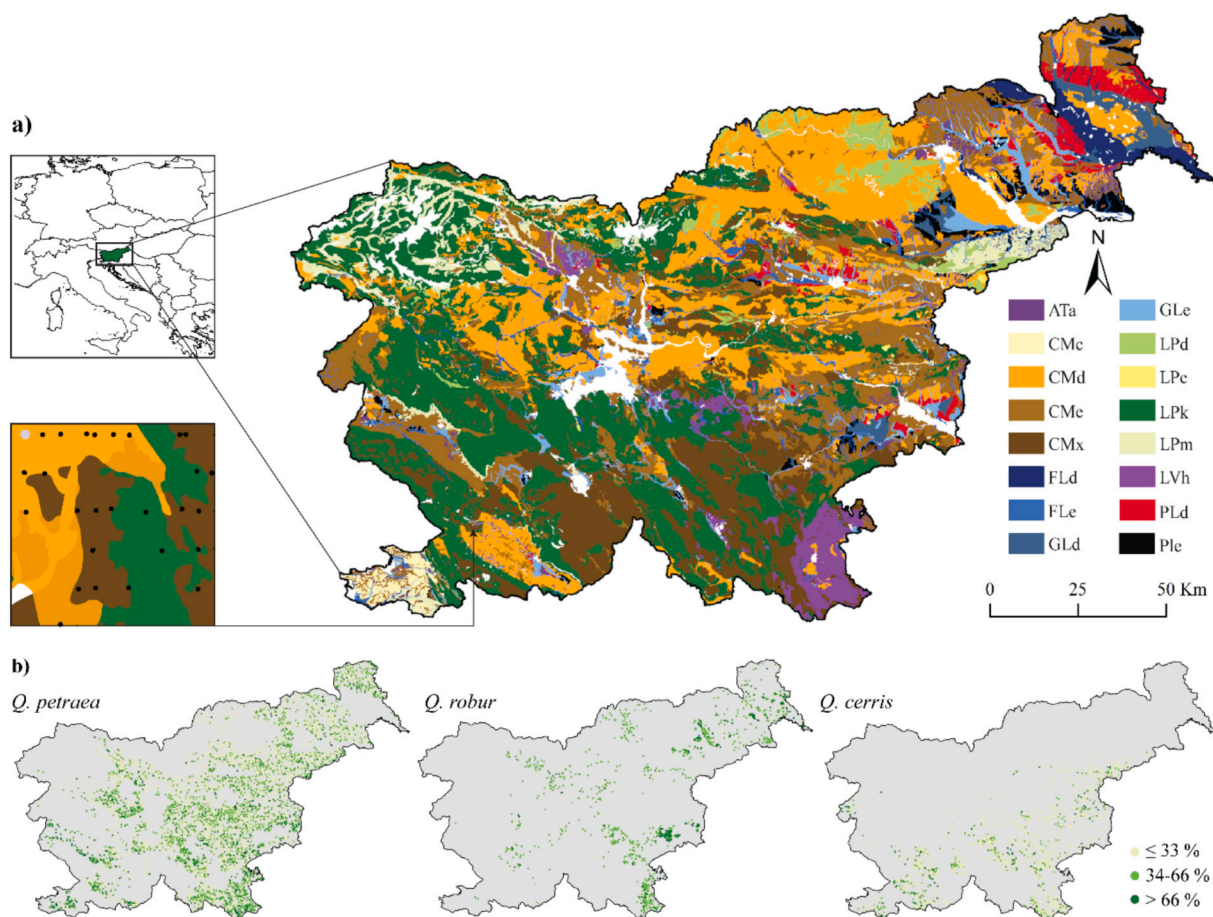


Fig. 1. Study area: (a) location of Slovenia in Europe and distribution of soil units in forested areas (after MAFF, 2007), with permanent sample plots shown in the inset (SFS, 2014); (b) distribution of three oak species.

500 m and are remeasured at 10-year intervals. Data collection followed a rotating system, with roughly one tenth of the total area surveyed annually. Initial measurements were carried out between 1992 and 2004, while subsequent remeasurements took place from 2002 to 2014. The plot centre is marked with a geodetic stake or a 30 cm long iron rod inserted into the ground. Measured trees are marked with a small horizontal notch in the bark.

Tree growth was defined as the periodic basal area increment of a tree (BAI) and was calculated as the difference between two consecutive DBH measurements over a 10-year period. We analysed the growth of three oak species based on data for 52,333 oak trees (Table S1).

Soil data were compiled from the national soil map at a scale of 1:25,000 (MAFF, 2007). Soil depth values (S_DEPTH) were derived from field-based soil profile descriptions collected during the original soil surveys and subsequently summarized at the soil-unit level. This dataset originates from systematic soil surveys carried out between 1960 and 1990 and was later digitized after 1995 (Vidic et al., 2015; Vrščaj et al., 2017) in accordance with the Slovenian Soil Classification. To ensure international comparability, the original legend was adapted to match the revised FAO Soil Map of the World (FAO, 1988; ISRIC, 1997; Vidic et al., 2015). The final vector soil layer (Bončina et al., 2023) consists of 10,781 spatial units with an average area of 117.95 ha, the majority of which (10,008 units) are fully or partially covered by forest.

Each soil polygon represents a composite mapping unit that may include up to three pedosystematic units whose spatial separation is not possible; nevertheless, their relative contributions within individual polygons are documented. Based on the dominant pedosystematic characteristics, the composite units were consolidated into 63 pedo-cartographic units (Vidic et al., 2015). These were later harmonized with international classification systems and grouped into 25 FAO soil units following FAO (1988) and IUSS Working Group WRB (2015), of which 16 were considered in this study (Fig. 1; Table S2). The resulting soil units are defined by characteristic horizon development, texture, and parent material associated with the dominant pedo-cartographic unit (Table S2). Terrain-related variables were extracted from a digital elevation model with a spatial resolution of 12.5 m (GURS, 2014). Climate predictors were derived from long-term climatic averages for the period 1971–2000 (SEA, 2021) and spatially transferred from the original 1 km² grid to the permanent sample plots using the nearest-neighbour approach.

2.3. Explanatory variables and their selection

Based on earlier studies (Bončina et al., 2023; Bončina et al., 2025), candidate predictors were selected for modelling the basal area increment (BAI) of the three oak species (Table 2). The model included two tree-level, four stand-level, six site-level, and seven climatic variables. Tree size was represented by initial DBH and its squared term to address potential non-linear relationships with BAI. Tree-level competition was quantified using BAL, defined as the basal area of trees larger than the subject tree on the plot, whereas stand basal area (BA) and its square root described stand-level competition intensity. Quadratic mean diameter (QMD), derived from individual-tree DBH values, was used as a stand-level indicator of stand age, while species composition was expressed by the proportions of oak species (PQ) and conifers (PCON). Stand variables were calculated from PSP data at the beginning of the inventory period.

Topographic variability was captured using four site variables, including inclination (INCL) and rockiness (ROCK). Rockiness was obtained from forest inventory records (SFS, 2014) and visually assessed as surface stone cover, a commonly applied indicator of site limitation and forest vulnerability (Bončina et al., 2021). We used the volume of a reference tree with a DBH of 45 cm as an indicator of site productivity (SP) (Trifković et al., 2022; Trifković et al., 2023; Bončina et al., 2026). This parameter, derived from adapted one-parameter tree volume functions, is routinely used by the Forest Service for timber volume estimation (Kušar, 2007). Because trees with a DBH of 45 cm differ in height among sites, SP values ranged from 1.10 to 2.91 m³, reflecting differences in site-specific growth potential among sites (Bončina et al., 2021). Climatic heterogeneity was addressed by incorporating long-term mean temperature and precipitation variables (SEA, 2021). Although several interactions were tested, only the MAT:MAP interaction was retained, as it was both statistically significant and biologically meaningful.

Two soil variables were used: soil depth (S_DEPTH) and soil unit (SOIL). Soil depth (S_DEPTH) was defined as the distance from the surface to the underlying parent material. SOIL was included as a dummy variable. Dystric Cambisols were set as the reference category as they are present in the sample for all three oak species. Soil units (SOIL, $n = 16$, Table 2) differ in typical soil horizons, pH value, parent material, and texture. Although soil properties may vary within individual soil units, this variability is expected to be lower than that observed between different soil units. A soil unit was considered in the analyses when at

Table 2

Variables included in the models, along with their mean values and standard deviations calculated across all three oak species, derived from permanent sample plot data (SFS, 2014): number of plots, $n = 17,733$; number of trees analysed, $n = 52,333$. For details see Table S1.

	Variables	Abbreviation	Mean	SD	Min-Max	Model*
Dependent	Periodic basal area increment of trees (cm ² 10y ⁻¹)	BAI	163.8	143.1	16.4–1868.2	✓
Tree	Initial diameter at breast height (cm)	DBH	29.9	11.8	10.0–110.0	✓
	Basal area sum of trees larger than the observed tree	BAL	13.1	10.1	0.0–69.6	✓
	Basal area (m ² ha ⁻¹)	BA	29.1	10.6	0.8–102.7	✓
	Quadratic mean diameter (cm)	QMD	24.4	5.9	10.0–66.0	✓
Stand	Proportion of studied oak species in stand volume	PQ	6.8	17.3	0.0–100.0	✓
	Proportion of conifers in total stand basal area	PCON	16.9	24.3	0.0–99.1	NS
	Soil units (dummy)	SOIL	–	–	–	✓
	Site productivity	SP	1.8	0.2	1.1–2.8	NS
Site	Inclination (°)	INCL	15.3	10.4	0.0–55.0	✓
	Elevation (m a.s.l.)	ELE	412.1	160.2	44.0–1264.0	MC
	Rockiness (%)	ROCK	10.2	15.8	0.0–100.0	✓
	Soil depth (cm)	S_DEPTH	73.3	32.5	0.0–429.0	✓
	Mean annual temperature (°C)	MAT	8.8	1.4	3.0–13.0	✓
	Mean annual precipitation (mm)	MAP	1502.7	339.3	850.0–2900.0	✓
Climate	Mean diurnal range (°C)	BIO2	8.9	1.8	0.0–14.0	✓
	Minimum temperature (°C)	TMIN	4.8	1.0	1.0–9.0	MC
	Maximum temperature (°C)	TMAX	13.7	1.7	7.0–18.5	MC
	Max temperature of warmest month (°C)	BIO5	24.1	1.6	18.0–28.0	MC
	Min temperature of coldest month (°C)	BIO6	–3.5	1.1	–9.5–1.5	MC

* ✓, included; NS, non-significant; MC, multicollinearity.

least 20 PSPs were available for that unit.

2.4. Modelling procedure

Modelling of periodic basal area increment (BAI) was conducted using linear mixed-effects models (Eq. 1) implemented in R with the *lmer* function from the *lme4* package (Bates et al., 2015). Given that individual trees were clustered within permanent sample plots (PSPs), we incorporated these plots as random components in our model structure. This specification enabled plot-specific variation in baseline values while maintaining uniform relationships between predictors and response across all locations. Species-specific models were developed separately for *Q. petraea*, *Q. robur*, and *Q. cerris*. The general model structure was:

$$\begin{aligned} \text{BAI}_{ij} = & \beta_0 + \beta_1 \text{DBH}_{ij} + \beta_2 \text{DBH}^2_{ij} + \beta_3 \sqrt{\text{BA}}_i + \beta_4 \text{QMD}_i + \beta_5 \text{BAL}_{ij} + \beta_6 \text{PQ}_i \\ & + \beta_7 \text{INCL}_i + \beta_8 \text{ROCK}_i + \beta_9 \text{S_DEPTH}_i + \beta_{10} \text{MAT}_i + \beta_{11} \text{MAP}_i \\ & + \beta_{12} \text{BIO2}_i + \beta_{13} (\text{MAT} : \text{MAP})_i + \beta_{14} (\text{SOIL})_i + \mu_j + \varepsilon_{ij} \end{aligned}$$

where β_0 is the intercept; $\beta_1 \dots \beta_{14}$ are the model coefficients for tree-level (DBH, DBH², BAL), stand-level ($\sqrt{\text{BA}}$, QMD, PQ), site (INCL, ROCK, S_DEPTH, SOIL), and climate variables (MAT, MAP, BIO2, MAT:MAP); μ_j is the random intercept for the grouping variable permanent sample plot; and ε_{ij} is the model residual at the tree level.

Parameter estimation was performed using maximum likelihood estimation (MLE) (Myung, 2003). To assess differences among soil unit categories (SOIL), post-hoc pairwise comparisons were carried out using the Scheffé procedure, which accounts for multiple testing and unequal sample sizes. These comparisons were implemented with the *emmeans* function from the *emmeans* R package (version 1.7.3; Lenth, 2022). Model performance was assessed using multiple diagnostic metrics, including the coefficient of determination (R^2), root mean square error

(RMSE), log-likelihood (logLik), and the Akaike information criterion (AIC). Both the conditional R^2 (R^2_{cond}), reflecting the total variance explained by fixed and random effects together, and the marginal R^2 (R^2_{marg}), representing variance explained by fixed effects alone, were calculated. The intraclass correlation coefficient (ICC) was estimated to assess the share of total variance attributable to PSP-level clustering. Additional model performance indicators, including RMSE, AIC, and the residual standard deviation (Sigma), were also reported.

3. Results

3.1. The impact of soil on tree growth

Predictors included in the BAI growth models explained 0.39 to 0.44 of the BAI variability (Table 4). The models differed in their sets of predictors. Tree size and basal area were included in all models, whereas other stand variables were retained only in some. A similar pattern was observed for topographic variables. Two climate variables (MAT and MAP) were included in all models, while the remaining climate predictors were retained only for the BAI growth of *Q. robur*. Soil units were significant predictors of the BAI growth of all three oak species.

Most included tree, stand, and climatic variables had a significant effect ($p < 0.05$; Table 3). The slopes of the impacts of tree, stand, and site variables differed noticeably among species, as did their contributions to the explained variance. Diameter at breast height (DBH) and BA accounted for the largest shares of explained variability in BAI (2.4–31.3%), and the effect of BA was negative for all tree species.

Tree size increased BAI; for two species, the relationship was slightly non-linear. For all three oak species, BAI decreased significantly with increasing proportion of the observed species in total stand volume. BAI was lower on sites with shallower soils and on steep, rocky slopes. Climate factors exhibited opposite effects on BAI across species. MAT and MAP increased BAI in *Q. robur* but were negatively associated with

Table 3

Results from fitting a linear mixed-effects model to the basal area increment of three oak tree species, using CMD as the reference soil unit.

	Coefficients			¹ Relative decrease in R^2 (%)		
	<i>Q. petraea</i>	<i>Q. robur</i>	<i>Q. cerris</i>	<i>Q. petraea</i>	<i>Q. robur</i>	<i>Q. cerris</i>
(Intercept)	209.33	−400.48	289.09	–	–	–
DBH	6.06	8.27	6.39	30.05	78.54	21.10
DBH ²	0.03	–	0.02	2.53	–	0.00
$\sqrt{\text{BA}}$	−15.89	−14.71	−30.42	20.22	2.41	31.34
QMD	−1.63	–	–	0.03	–	–
BAL	–	−2.53	0.65	–	0.00	6.14
PQ	−0.41	−0.64	−0.59	14.32	3.01	17.95
INCL	−0.87	–	−0.90	6.46	–	0.63
ROCK	−0.72	–	−0.45	4.49	–	2.99
S_DEPTH	0.18	0.20	0.39	2.53	0.02	3.78
MAT	−5.10	45.18	−7.28	0.56	1.81	0.63
MAP	−0.04	0.23	−0.05	2.53	1.21	1.41
BIO2	–	9.05	–	–	1.21	–
MAT:MAP	–	−0.03	–	–	0.61	–
SOIL	–	–	–	16.29	11.16	14.02
ATa	55.01	–	−55.41	–	–	–
CMc	−55.84	–	18.86	–	–	–
CMe	1.65	−11.88	−34.54	–	–	–
CMx	−23.03	−46.05	–	–	–	–
FLd	–	30.02	–	–	–	–
FLe	13.61	–	–	–	–	–
GLd	26.53	20.62	–	–	–	–
GLe	–	48.62	–	–	–	–
LPd	7.36	−22.37	−7.78	–	–	–
LPe	1.14	–	–	–	–	–
LPm	–	–	−11.64	–	–	–
LPk	−21.24	−44.70	−22.38	–	–	–
LVh	−11.44	−24.59	9.26	–	–	–
PLd	32.76	5.99	–	–	–	–
PLe	31.78	9.56	–	–	–	–

Note: Only statistically significant predictors retained after stepwise selection are shown.

¹ Relative decrease in R^2 if this variable is omitted from the model and fitted again, calculated based on marginal R^2 (R^2_{marg}).

Table 4

Performance metrics of BAI models for three oak species.

	AIC	AICC	BIC	R ² cond.	R ² marg.	ICC	RMSE	Sigma
<i>Q. petraea</i>	504,231	504,231	504,464	0.58	0.39	0.30	85.11	91.50
<i>Q. robur</i>	61,189	61,189	61,331	0.57	0.43	0.25	114.85	125.14
<i>Q. cerris</i>	73,761	73,761	73,895	0.71	0.44	0.48	73.31	74.28

BAI in *Q. petraea* and *Q. cerris*. For *Q. robur* only, BIO2 and the MAT:MAP interaction were significant. Overall, climate variables accounted for a minor share of the explained variance.

In the growth models for the three oak species, SOIL explained a substantial share (11–16%) of the variability in BAI. SOIL was the most important predictor in the *Q. petraea* model and the least important in the *Q. robur* model. Growth varied markedly between soil units (Fig. 3). Relative to growth on the reference soil unit (CMD), growth was about 20% higher (see *Q. petraea* on ATa) and 50% lower (see *Q. petraea* on Calcaric Cambisols, CMc) (Fig. 2).

Fig. 3 indicates that the oak species achieved their highest growth on different soil units: *Q. petraea* performed best on Eutric and Dystric Planosols and ATa, *Q. robur* on Eutric Gleysols and FLd, and *Q. cerris* on Haplic Luvisols. The ratio of the highest to lowest predicted growth rates across soil units, with all other predictors held at their mean values, was 2.42, 1.51, and 1.31 for *Q. petraea*, *Q. robur*, and *Q. cerris*, respectively.

Post-hoc analysis (Fig. 4) showed a limited number of significant differences in tree growth between soil units. Soil units exhibiting significant differences were often species-specific, as follows:

- *Q. petraea*: Growth on CMc, CMe, CMx, LPk, PLd, and PLe differed significantly from that on most other soil units. A similar pattern was observed for Rendzic and Mollic Leptosols. Significant variation

occurred within Cambisols (CMc vs other CM and CMx vs other CM) and Leptosols (LPk vs other LP).

- *Q. robur*: Growth on CMx differed significantly from that observed on most other soil units. Significant differences were found within Cambisols (CMx vs CMD) but not within Gleysols or within Leptosols.
- *Q. cerris*: Significant differences were found between units within Cambisols. Growth on LVh differed significantly from that on CMc and CMx.

4. Discussion

Our results highlight the need to include soil variables in growth studies of tree species. Recent growth studies have focused mainly on other variables, particularly stand mixture and climate variables, while soil variables have often been neglected. Similarly, studies examining climate–growth relationships typically exclude soil variables, despite the potential for soil–climate interactions to influence tree growth.

4.1. The effect of soil on tree growth

Our study demonstrated that soil variables accounted for a substantial share of the explained variability in basal area increment (BAI) of the three oak species, contributing 16.3, 11.2, and 14.0% for *Quercus petraea*, *Q. robur*, and *Q. cerris*, respectively. When combined with other

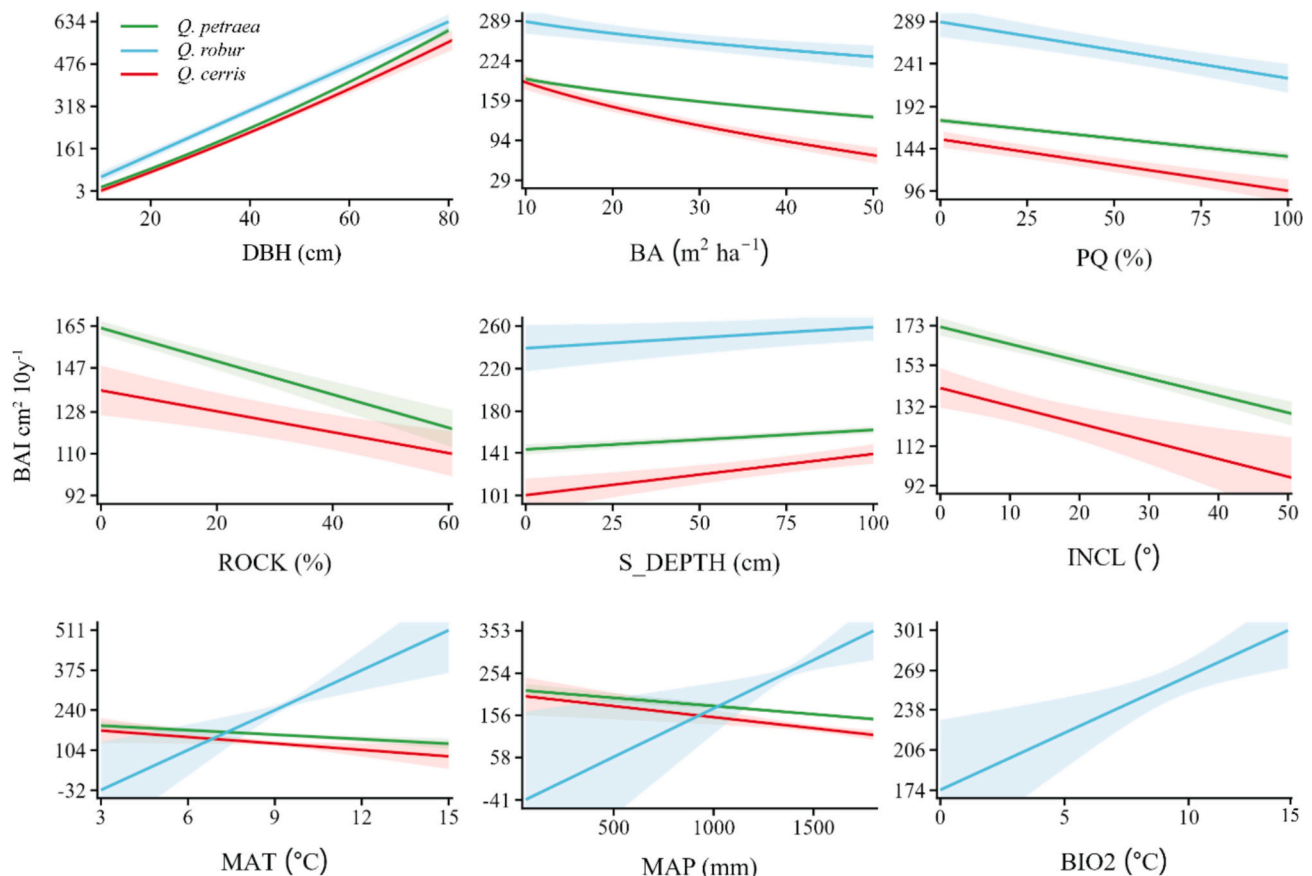


Fig. 2. Growth response of three oak species to selected explanatory tree, site, and environmental variables; shaded areas indicate 95% confidence intervals.

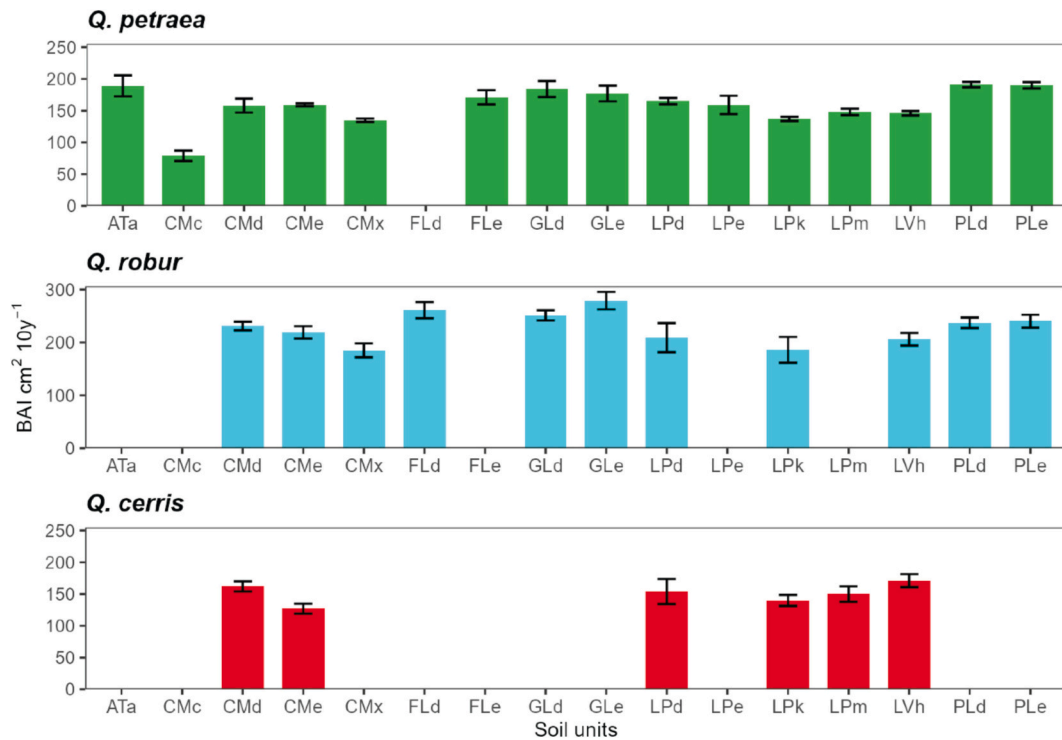


Fig. 3. Periodic basal area increment of three oak species across 16 soil units; error bars indicate 95% confidence intervals.

soil-related (e.g. soil depth) and topographic variables (inclination, rockiness), the explained variability increased to 29.8% for *Q. petraea*, 11.8% for *Q. robur*, and 24.0% for *Q. cerris*. For *Q. petraea* and *Q. cerris*, the influence of soil-related factors was comparable to that of tree size or stand density, highlighting the importance of soil and topographic conditions for oak growth.

Soil variables also appear to be relatively strong predictors of growth for oak species compared with many other tree species. Bončina et al. (2021) demonstrated that soil properties were stronger predictors of growth for sessile oak than for Norway spruce, silver fir, or Scots pine. This pattern may be explained by two main factors. First, *Quercus* species—particularly *Q. petraea* and *Q. cerris*—exhibit a broad ecological amplitude across different substrates and soil types. In contrast, many other tree species (e.g. European beech and sycamore) occupy a wider elevational range than oak species, but their sites are less variable with

respect to soil conditions. Second, tree species differ markedly in their physiological requirements for growth, survival, and regeneration (San-Miguel-Ayán et al., 2016; Walthert and Meier, 2017), resulting in species-specific growth responses to site factors. Overall, our results suggest that oak growth is sensitive to soil conditions.

Tree growth reflects the interaction between soil properties and species-specific traits, with root system architecture and plasticity playing a central role (Kostić et al., 2021a, 2021b; Galindo-Castañeda et al., 2022; Holz et al., 2024). Soil depth, moisture regime, and nutrient availability determine resource supply, while root traits influence how efficiently these resources are exploited. Deep, moist soils enable the development of extensive root systems and support stable uptake of water and nutrients, whereas shallow or skeletal soils restrict root development and limit growth. The pronounced growth differences among soil units observed in this study likely reflect these soil–root

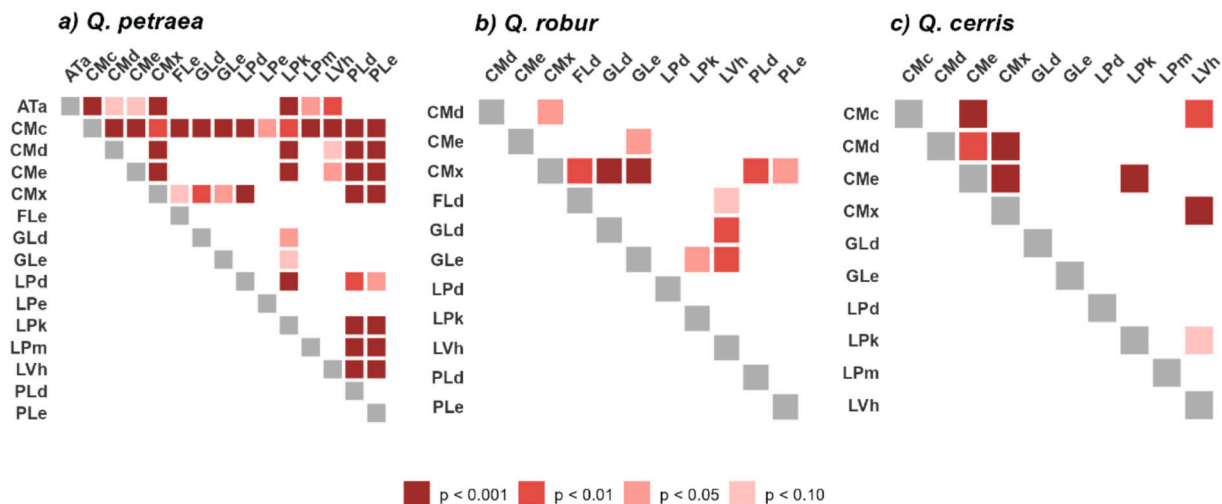


Fig. 4. Significant differences in BAI between pairs of soil units (post-hoc test).

interactions, emphasizing the importance of root plasticity in oak species (Brunner et al., 2015; Trouvé et al., 2015).

All three oak species analysed are capable of growing on a wide range of soils (Eaton et al., 2016; Pasta et al., 2016), yet their growth performance varied considerably among soil units. The difference between the highest and lowest mean BAI, expressed relative to the mean BAI across soil units, amounted to 70% for *Q. petraea*, 39% for *Q. robur*, and 29% for *Q. cerris*. The broader soil gradient occupied by *Q. petraea* likely explains its greater variability in growth response, whereas *Q. robur* is more restricted to lower vegetation belts and a narrower range of soil classes.

Despite species-specific differences, a common pattern emerged: oak growth was consistently lowest on calcareous Leptosols and Chromic Cambisols, which are characterized by shallow profiles, low nutrient availability, and limited water-holding capacity. These findings are consistent with previous studies and underscore the importance of physical and hydrological soil properties in shaping oak productivity (Vospertnik, 2021).

For *Q. petraea*, the highest productivity was observed on Dystric and Eutric Planosols (PLd and PLc), particularly within a soil pH range of 4.0–6.5, while the lowest growth rates occurred on Calcaric Cambisol (CMc) and Chromic Cambisols (CMx). Growth on these Cambisol units reached only 41% of that observed on Planosols. This difference is likely attributable to the higher water-holding capacity, moderate organic matter content, and favourable texture of Planosols, which enhance nutrient availability and support optimal root development. In contrast, Cambisols tend to have higher pH, stonier or carbonate-rich substrates, and lower water retention, which constrain radial and height growth (Vidic et al., 2015). This pattern aligns with the preference of sessile oak for fertile and moist soils. Rendzic Leptosols (LPk), characterized by shallow soil depth (42(SD = 14) cm) and low water-holding capacity (Table S2; Vidic et al., 2015), also supported relatively low growth, highlighting that soil depth, organic matter content, and water retention strongly influence the growth potential of *Q. petraea*. Pairwise comparisons revealed significant differences in diameter increment between Planosols and several Cambisol units, reflecting the strong influence of soil structure and water dynamics on growth potential. The sensitivity of *Q. petraea* to soil water availability is well documented, with drought-induced reductions in both radial and height growth (Trouvé et al., 2015).

The highest growth rates of *Q. robur* were recorded on Eutric and Dystric Gleysols (GLd, GLe) and on Eutric Fluvisols (FLc), all of which are characterized by deep soils and favourable moisture conditions. These results are consistent with findings from lowland forests in Serbia, where the diameter increment of *Q. robur* on Haplic Gleysols was 49% higher than on Solonchaks soils under otherwise comparable environmental conditions (Kostić et al., 2021a, 2021b). Similar soil-related growth differences have been reported across Central Europe (Bronisz et al., 2012; Tumajer and Tremel, 2016; Skiadarensis et al., 2021), confirming that water availability is a key driver of *Q. robur* productivity and that trees growing on moist soils are generally less vulnerable to oak decline.

For *Q. cerris*, the highest growth rates were observed on Haplic Luvisols (LVh) and Dystric Cambisols (CMD), both moderately acidic, deep soils with favourable water regimes. Although Turkey oak exhibits a broad ecological amplitude (Keresztesi, 1967; Simeone et al., 2019), fertile soils with stable moisture conditions promote higher productivity. Trees growing on deep, nutrient-rich soils such as Cambisols tend to develop larger leaf areas and exhibit more vigorous growth than those on shallow, skeletal soils with limited water retention (Jovanović et al., 2023). Significant growth differences within Cambisols, and higher growth on Haplic Luvisols (LVh) compared to Calcaric and Chromic Cambisols (CMc and CMx), further highlight the importance of soil water availability. Luvisols, with their argic horizons and higher clay content, provide enhanced water-holding capacity and a more stable moisture regime (IUSS Working Group WRB, 2015; IUSS Working Group

WRB, 2022). Observed reductions in radial and height growth under drought conditions confirm the sensitivity of *Q. cerris* to water stress (Trouvé et al., 2015).

Soil properties interact strongly with climatic factors, particularly water availability, to determine oak productivity. Deep, fertile soils with high water-holding capacity can buffer trees against drought and allow continued growth during dry periods, while shallow or nutrient-poor soils can exacerbate water stress (Trouvé et al., 2015; Brunner et al., 2015; Kostić et al., 2021a, 2021b). Soil moisture mediates the effects of precipitation and temperature on radial growth, making it a central factor in species-specific growth responses (Walther and Meier, 2017). These findings underscore that soil is not merely a background factor but a critical driver of oak growth, especially under variable climate conditions, highlighting the importance of including soil × climate interactions in forest management and growth modelling.

Our results clearly demonstrate that soil properties, particularly depth, fertility, and water-holding capacity, are key drivers of oak growth. Given the pronounced interactions between soil, topography, and climate, it is essential to explicitly incorporate soil factors and their linkages with climatic conditions into growth models and forest management planning, as they strongly influence the productivity and resilience of European oaks.

4.2. The effect of other predictors on stand and tree growth

Although tree size often accounts for most of the variation in individual tree growth models (Monserud and Sterba, 1996; Vospertnik, 2021), this effect was not clearly observed in the oak species analysed here.

Tree-related factors represent the most influential drivers of growth for *Q. robur*, while for the other two oak species stand variables are of approximately equal (*Q. petraea*) or even greater importance (*Q. cerris*). The growth of all three oak species increased markedly with increasing tree size. The second tree variable, the basal area of overtopping trees (BAL), was significant for two oak species. In the model for *Q. cerris*, the impact of BAL on growth was unexpectedly positive and is difficult to explain. BAL is commonly used as an indicator of competition, with higher values reflecting increased shading and reduced light availability, which typically lead to decreased radial growth (Gould et al., 2011; Trifković et al., 2022). Nonetheless, similarly counterintuitive findings, including positive BAL effects, have been reported. For example, Briseño Reyes et al. (2020) found that BAL increased diameter increment in *Pinus engelmannii*, *Pinus herrerae*, and *Quercus arizonica* in temperate forests in Mexico, while Bayat et al. (2022) observed positive BAL effects on the growth of *Fagus*, *Carpinus*, and *Quercus* species in natural deciduous forests in Iran. These results indicate that the influence of BAL may depend on species-specific ecological traits and stand conditions and may reflect facilitative interactions or favourable site conditions rather than purely competitive effects. Such results contrast with the commonly assumed negative influence of larger neighbouring trees and highlight the complexity of tree interactions in structurally diverse stands (Pretzsch, 2022).

Stand basal area (BA) is a common proxy for competition for light and other resources and is typically associated with reduced growth rates (Weiskittel et al., 2011). In our study, BA emerged as the most influential stand-level variable in individual tree growth models for *Q. cerris* and *Q. petraea*, accounting for 20.2 and 31.3% of the total explained variance in tree growth, respectively. In contrast, its contribution to explained growth variability in *Q. robur* was considerably smaller.

For all observed oak species, their proportion in total stand volume was the second most important stand-level predictor, contributing from 3.0% (*Q. robur*) to 18% (*Q. cerris*) of total explained growth variability. These results suggest that oak growth benefits from the presence of other species in mixed stands. In general, research on tree growth has found species mixtures to have positive, negative, or non-significant effects

(Forrester and Bauhus, 2016; Pretzsch and Schütze, 2021), depending on factors at the tree, stand, and site levels (e.g. Huber et al., 2014; Mina et al., 2018). In our case, a plausible explanation is that admixture species commonly associated with oaks (e.g. *Carpinus betulus*, *Acer campestre*, *Sorbus* spp., *Fraxinus* spp.) are typically shorter than oak trees of similar DBH, implying lower competition for light. In contrast, admixture with beech may reduce oak growth (Hein and Dhôte, 2006).

The third stand variable, quadratic mean diameter (QMD), explained only a minor share of growth variability and was retained only in some models. QMD provides information on both stand development stage and stand crowdedness (Newton, 2021). Many growth studies include stand or tree age as predictors. In our study, the effect of QMD on basal area growth was significant only for *Q. petraea*, although the effect was weak and negative, which contrasts with some previous findings (e.g. Trifković et al., 2022).

The group of environmental factors in the study included the already discussed soil unit, but also topographic and climatic predictors. The growth of *Q. petraea* and *Q. cerris* was lower on steeper terrain, whereas this pattern was not observed for *Q. robur*, which occurs mainly on flat terrain; consequently, the inclination gradient for *Q. robur* was limited. Inclination (INCL) accounted for a notable share of the explained variability in *Q. petraea* growth (6.5%). Topographic characteristics, including inclination, can markedly impact soil attributes (e.g. soil moisture and organic carbon and nitrogen contents), thereby shaping growth conditions (Wu, 2015).

Surface rockiness has seldom been incorporated in growth studies, with only a few exceptions (Li et al., 2022; Trifković et al., 2022; Bončina et al., 2023). In our study, rockiness negatively impacted the growth of *Q. petraea* and *Q. cerris* and explained 4.5 and 3.0% of BAI variability, respectively. This contribution was much larger than that of climate variables. In soils with high rock content, root development may be impeded, leading to reduced growth (Ceacero et al., 2020). The relatively strong effect of rockiness in the *Q. petraea* model is consistent with the distribution of *Q. petraea* across a broad rockiness gradient. On carbonate substrates, rockiness can exceed 50% of the surface, while highly productive sites on non-carbonate substrates are often characterized by low surface rockiness (Bončina et al., 2021). Soil depth positively influenced the growth of all three oak species; its contribution to the explained variability was highest for *Q. cerris* (3.8%), exceeding the contribution of climatic variables.

Understanding species responses to climatic factors is crucial under changing climate conditions. However, in our study, the contribution of individual climatic variables to the explained growth variability was small (< 3%). We observed contrasting climate–growth relationships among species. Temperature had a positive impact on *Q. robur* growth but a negative impact on *Q. petraea* and *Q. cerris*. Vospernik et al. (2023) reported a positive relationship between oak growth and mean temperature during the growing season in Austria. The negative impact of temperature observed here is not consistent with the prevailing view of temperature–growth relationships (Ryan, 2010). However, a negative impact of temperature on growth in *Q. petraea* and *Q. cerris* may indicate that their realized ecological optima do not occur in the warmest parts of their distributions. In Hungary's dry lowland forests, the radial growth of *Q. petraea* and *Q. cerris* decreased in response to higher temperatures during May and August, affecting both the current and prior years (Mészáros et al., 2022). High temperatures during these periods can constrain radial growth and latewood formation, likely by increasing evapotranspiration and thus exacerbating soil moisture deficits.

We also found contrasting precipitation effects. Radial growth of *Q. robur* was positively influenced by precipitation, consistent with evidence that summer water availability often limits oak growth (e.g. Friedrichs et al., 2009; Rybníček et al., 2015; Netsvetov et al., 2019; Nechita et al., 2019; Sochová et al., 2024). In contrast, *Q. petraea* and *Q. cerris* exhibited negative responses, contrary to most previous findings where precipitation was a key growth-limiting factor (Mészáros et al., 2022). The positive effect of precipitation on *Q. robur* likely

reflects the high annual rainfall in the study area (>1300 mm), which reduces drought stress and allows trees to fully benefit from water availability. Conversely, the negative responses of *Q. petraea* and *Q. cerris* may be linked to species-specific sensitivities to excessive moisture, including reduced root-zone oxygen, increased pathogen susceptibility, or altered nutrient dynamics (Bose et al., 2021; Gauli et al., 2022; Mészáros et al., 2022).

Mean annual precipitation was a stronger predictor of *Q. petraea* growth than mean annual temperature, highlighting the importance of water even in humid environments. The strong positive correlation between precipitation and elevation ($r = 0.85$) provides additional context: while *Q. robur* may benefit from higher moisture at greater elevations, the growth of *Q. petraea* and *Q. cerris* declines, suggesting that precipitation may exceed their optimal range. Overall, these results underscore the importance of species-specific responses, whereby high water availability enhances growth for some oaks but can limit it for others under very wet conditions.

These species-specific patterns are consistent with broader evidence of non-linear and context-dependent precipitation effects. Vospernik (2021) reported a relatively uniform oak growth response to annual precipitation between 400 and 800 mm, followed by a steep increase above 800 mm, indicating threshold responses to water availability. Furthermore, the response of *Q. robur* to climatic variables has been shown to be age-dependent, with young trees reacting differently from older individuals (Rozas, 2003). These findings highlight that generalizing climate–growth relationships across species or age classes can be misleading and emphasize the need to account for species traits, stand conditions, and tree age when interpreting precipitation effects. Caution is warranted when interpreting these results, as the overall contribution of precipitation to explained variability was small, which limits the strength of inference.

In addition to soil properties and stand structural attributes, forest management practices can influence basal area increment (BAI), particularly through long-term effects on stand density, species composition, and organic matter dynamics (e.g. Bončina, 2011; Schütz, 2011;). In the forests included in this study, close-to-nature forestry predominates, with irregular shelterwood systems being most common in oak stands, while regular shelterwood system, selection systems and coppice with standards occur less frequently. Management practices were therefore not explicitly included as predictors in the statistical models but were considered qualitatively when interpreting the results. Consequently, management effects are interpreted indirectly through stand-level structural variables (e.g. basal area, quadratic mean diameter), which integrate the cumulative legacy of past management interventions.

4.3. Limitations of the study

Our models captured a moderate proportion of tree growth variability ($R^2 = 0.39–0.44$), indicating that a considerable share of variation remains unexplained. This level of explanatory power is consistent with previous studies: Schelhaas et al. (2018) reported explained variances between 10 and 53% for diameter increment models of 20 tree species; Bončina et al. (2025) found an R^2 of 0.50 for a basal area increment model of European beech (*Fagus sylvatica*); and in semi-natural forests of Central Europe, Bončina et al. (2023) reported R^2 values ranging from 0.34 for oaks to 0.42 for spruce across different soil classes. These findings suggest that, although not all variability is captured, the performance of our models is comparable to that typically observed in mixed-species and environmentally heterogeneous stands.

An additional limitation relates to the temporal origin of the soil data, which are based on surveys carried out between 1960 and 1990. Although the datasets were subsequently digitized and adapted to the FAO Soil Map of the World to ensure harmonization and international comparability, subsequent developments in soil systematics may introduce some uncertainty in the interpretation of soil unit classifications.

Several factors may contribute to this moderate explanatory power. First, the spatial resolution and generalization of the soil map may limit model accuracy; higher-resolution maps and more precise delineation of pedocartographic units could substantially improve predictions (Dai et al., 2019; Adeniyi and Maerker, 2024).

Second, the use of 10-year increment data, with influential variables measured only at the start of each inventory period, may not fully capture changes in stand structure over time, such as those caused by harvesting or natural disturbances. While this approach is standard practice in research based on national forest inventories (e.g. Schelhaas et al., 2018; Trifković et al., 2022; Trifković et al., 2023), it represents an inherent limitation of long-term growth assessments.

A further constraint is the reliance on long-term climatic averages, which do not explicitly capture extreme weather events or anomalies, such as severe droughts. In addition, because our approach relied on soil classes, some potentially influential soil properties were not included and might have marginally improved model performance. Nonetheless, the extensive dataset and the diversity of study sites help to mitigate these limitations. Despite noticeable differences in growth among soil classes, additional research is necessary to better understand the complex interplay of soil, climate, and other environmental factors, which may also vary within a single soil class.

5. Conclusion

Soil is often neglected in studies of tree growth responses to environmental conditions at broad spatial scales. This study quantified growth differences among soil classes for major European oak species. The main conclusions of the study are as follows:

- The difference between maximum and minimum mean basal area increments among soil units for *Q. petraea*, *Q. robur*, and *Q. cerris* amounted to 70, 39, and 29% of their mean basal area increment, respectively.
- Relatively broad soil classes included in the individual tree growth models for the three oak species contributed 11.2–16.3% of the explained variability in basal area growth.
- The oak species exhibited their highest and lowest growth rates on distinct soil units.
- Soil proved to be a stronger predictor of growth than the climatic variables included in this study.

Given the strong effect of soil on tree growth, the inclusion of soil variables can improve tree growth modelling. To better understand their complex effects, soil variables should be evaluated in combination with other relevant factors at the tree, stand, and site levels.

CRedit authorship contribution statement

Vasilije Trifković: Writing – review & editing, Writing – original draft, Visualization, Validation, Software, Methodology, Formal analysis, Data curation. **Andrej Bončina:** Writing – review & editing, Writing – original draft, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

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Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.catena.2026.110302>.

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