

# Tree and stand growth differ among soil classes in semi-natural forests in central Europe

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## ABSTRACT

We determined the size of differences in stand and tree growth in semi-natural forests with respect to 16 reference soil groups. The forest area of Slovenia (11.8 thousand km<sup>2</sup>) was used as the study area, and reference soil units were derived from the national soil map at a 1:25,000 scale consisting of 10,781 polygons with an average size of 117.95 ha. Stand growth was defined as periodic stand basal area increment, while the growth of Norway spruce, silver fir, Scots pine, European beech and sessile oak trees was estimated by the periodic diameter increment of 238,349 dominant trees on 67,061 permanent sampling plots. A linear fixed-effects model and linear mixed-effect models were used for studying stand and tree growth in different site, stand and tree conditions. The soil unit was the dummy variable with Dystric Cambisols set as the reference category. Soil contributed 4.3 % to the explained variability of basal area increment and 4–27 % to the explained variability of the diameter increment of the five tree species. Soil was a stronger driver of stand and tree growth than climate or topography. Stand and tree species production rate on soil units was in the interval of –28 % to +5 % and –47 % to +14 % of that on the reference soil unit, respectively. Stand growth was the highest on Eutric Gleysols and the lowest on Histosols, and tree species generally exhibited the highest and the lowest growth rates on different soil units. We suggest that soil should be considered in growth models and studied interrelatedly with climatic, site and stand variables.

## 1. Introduction

The growth patterns of trees and forest stands depend on complex interactions between environmental, stand and tree factors (Pretzsch, 2010). Environmental factors include climate, topography, soil, geology and vegetation. Most studies on tree and stand growth have focused on the impact of stand variables, including the density, mixture and heterogeneity of forest stands, and recently also on climatic variables. Topographic factors, such as slope, aspect and elevation, have also quite often been included in growth models. However, soil characteristics and soil types have rarely been accounted for in tree growth modelling. Soils are a crucial factor in the productivity of forests (Binkley, 2013); the natural fertility of forest soil depends on many soil characteristics, including organic matter content, clay content, clay mineralogy, the presence of weatherable minerals, pH, base saturation and biological activity. Forest soils differ in their productive potentials and can range from porous, well-aerated soils with excellent nutrient-supplying and

-retaining capacities to shallow young soils which are poor in properties which control vegetation productivity. Quantifying the impact of soil on forest productivity is challenging, and the impact remains largely unknown.

Two main approaches to studying the impact of soil on tree and stand growth can be distinguished. The first approach is focused on the impact of specific soil variables, such as soil moisture, soil nutrient content and availability, soil texture and other soil properties such as humus characteristics (e.g. humus type, pH value, C and N content), on the growth patterns of individual trees or forest habitats (e.g. Scharnweber et al., 2013; Kobal et al., 2015; Lévesque et al., 2016; Calvaruso et al., 2017). Due to the demanding and precise field measurements, such studies are usually done on a relatively small spatial scale. A relatively small number of trees are observed, and dendrochronological methods are often applied to analyse tree growth patterns. However, if soil variables are derived from soil maps or assessed in the field by rapid determination methods, the spatial scale of the investigation and the sample size

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can be larger. Studying multiple interactions between soil, climate and other variables is challenging (Aertsen et al., 2012) since the growth response of a tree species under various environmental factors may be specific for a soil class (Seltmann et al. 2021).

The second and less frequent approach to studying the soil-forest productivity relationship is to classify soils and study tree and stand growth by soil classes. Depending on the aim of the growth studies, soil may be classified in different ways, based on either single (e.g. texture, depth, moisture, nutrients) or multiple properties. Soil taxonomic systems classify soils according to morphologic, genetic, chemical, physical and biological properties (IUSS Working Group WRB, 2015). Soil classes are a result of specific soil forming factors and processes (Bockheim and Gennadiyev, 2000). Growth studies accounting for soil classes are characterized by large samples of trees and stands and larger spatial scales. Data from national forest inventories are often applied, and terrestrial measurements of trees and stands can be combined using satellite images or lidar data. Such growth studies have not only examined tree growth but also stand growth and site productivity (van Sundert et al., 2018) with respect to soil classes (e.g. Brandl et al., 2014). The accuracy of tree measurements is usually lower than that in the first type of growth studies, but this is compensated by a much larger sample of trees.

In forest growth modelling, a soil class can be used as an explanatory variable since it represents a typical complex of soil properties. The impact of soil classes on tree growth has been studied either by basal area (Monserud and Sterba, 1996; Vospernik, 2021) or diameter increment (e.g. Toledo et al., 2011); in both cases the diameter of trees is measured 1.3 m above the ground (dbh, diameter at breast height). The increment of trees is usually calculated based on consecutive measurements in a period of several years. The growth of dominant trees, usually defined as the 100 largest trees per hectare, is much less impacted by stand conditions than that of understorey trees. Therefore, the growth models of dominant trees have been used for estimating forest site productivity (Pretzsch, 2010) and have been integrated in forest stand simulators (Rosset et al., 2013). Stand growth is often measured by stand basal area or stand volume increment. Stand basal area increment (BAI) is the sum of the basal area increments of trees above a certain threshold size (e.g.  $\text{dbh} \geq 10$  cm). Contrary to BAI, stand volume increment may be subjected to greater error since stand volume is calculated based on three measured parameters, namely dbh, height and form, of which the last two are difficult to obtain accurately.

Information from soil maps is highly relevant for ecological forestry since soil represents one of the three bases besides climate and geomorphology for describing forest sites (Simon et al., 2020). Soil maps have been elaborated at different spatial scales by using various mapping procedures. Soil maps at a regional scale indicate contrasting soil properties in the forest area; therefore, a different response of trees and stands growing on different soil types is expected. Different soil classification systems are used across countries. For comparing the results of forest growth studies, it is important that soil classification applied at the country level is transcribed to international soil groups. Harmonized soil classification systems (e.g. FAO-UNESCO, 1974; FAO, 1988; Soil Atlas of Europe, 2005; IUSS Working Group WRB, 2015) are therefore of great importance for communication at the international level. The World Reference Base (WBR) is a comprehensive classification system characterized by two levels of soil units: 32 reference soil groups (RSG) and RSG combined with a set of principal and supplementary qualifiers (IUSS Working Group WRB, 2015). Although the system has been broadly accepted at the international level, there are almost no studies quantifying the growth rates of forest stands and trees on reference soil groups.

Forest management activities can alter the characteristics of forest soil (Augusto et al., 2002; Binkley, 2013). Management activities impact the state of forest stands, which has a strong influence on soil moisture, interception and evapotranspiration; the temperature regime at the surface of soils; and nutrient availability. In addition, harvesting may

cause soil compaction. In some forest areas fertilizing with N and P is practiced to compensate for leaching soil supplies (Binkley, 1990). In contrast, the impact of close-to-nature forestry on forest soil (Hukić et al., 2021) and other components of the forest ecosystem is assumed to be lower compared to that of industrial forest management. Close-to-nature forestry is based on the natural regeneration of tree species, applies silvicultural systems that mimic natural stand dynamics, and prohibits the use of fertilizers and pesticides (Bončina, 2011; Schütz, 2011). After harvesting, a significant part of trees (i.e. all branches, tops of the stems, leaves) remains in forests, increasing the amount of organic matter in forest soil and positively influencing soil conditions (Grigal and Vance, 2000). Slovenia is one of the rare European countries in which clearcutting is prohibited by law, which has resulted in relatively well-preserved semi-natural forests. This, together with the availability of a large dataset on tree growth, presents an opportunity to study tree and stand growth in well-preserved semi-natural forests with respect to soil units and other stand and site variables.

Therefore, our main objectives were 1) to determine the significance of soil classes for explaining tree and stand growth in different sites and stands and 2) to test for differences in the growth rate of five main tree species (Norway spruce, silver fir, Scots pine, European beech and sessile oak) and forest stands growing on different soils. The influence of soil on tree and stand growth has seldom been investigated based on a large-scale data. This is one of the rare attempts to quantify the importance of soil units for tree and stand growth at the regional spatial scale. We presumed that stand parameters are the main driver of tree and forest growth, while the relative influence of climate, soil and topography remains unknown. We expected significant differences in tree and stand growth among soil units. Our intention was to determine the size of differences in stand and tree growth with respect to reference soil groups (hereafter soil units). We assumed that the main tree species in semi-natural forests reach their growth optimum on different soil units.

## 2. Materials and methods

### 2.1. Study area

The forest area of Slovenia (11.8 thousand  $\text{km}^2$ ) was used as the study area. The climate in Slovenia is a combination of a continental climate in the northeast, an alpine climate in the high mountain regions and a sub-Mediterranean climate in the coastal region, with geographical variations mainly due to diverse topographic conditions and the influence of the Mediterranean Sea, the Alps and the Pannonian Plain. Mean annual temperature is 9.2 °C, and mean annual precipitation is 1426 mm. The most important lithological groups are carbonate rocks (54.6 %), clastic sediments (36.0 %) and metamorphic rocks 4.2 % (Buser and Komac, 2010). Rendzinas, and Dystric and Eutric brown soils are the most common soil types in the forest area (Vidic et al., 2015). The parent material is considered as the most important of the soil formation factors, followed by topography, while climate is a more general factor (Vrščaj et al., 2017). Forests are distributed from the seashore to the timberline at approximately 1500–1700 m above sea level. Beech forests cover 70 % of the total forest area. Other forest types, such as lowland forests, riverine forests, coniferous forests and thermophilus broadleaved forests, occupy a smaller part of the whole area. Due to the close-to-nature forestry practiced in the last 70 years, forests are well preserved. The predominant management systems (i.e. the irregular shelterwood system and single tree and group selection systems) have contributed to small-scale even-aged and uneven-aged forest stands. The mean growing stock amounts to 304  $\text{m}^3 \text{ha}^{-1}$ . In total, more than 70 tree species have been registered in forest inventories; however, European beech (*Fagus sylvatica*, 33 %) and Norway spruce (*Picea abies*, 30 %) dominate, followed by silver fir (*Abies alba*, 7 %), sessile oak (*Quercus petraea*, 5 %) and Scots pine (*Pinus sylvestris*, 4 %). The large proportion of Norway spruce is a result of the fact that it was favoured by forest management in previous centuries.

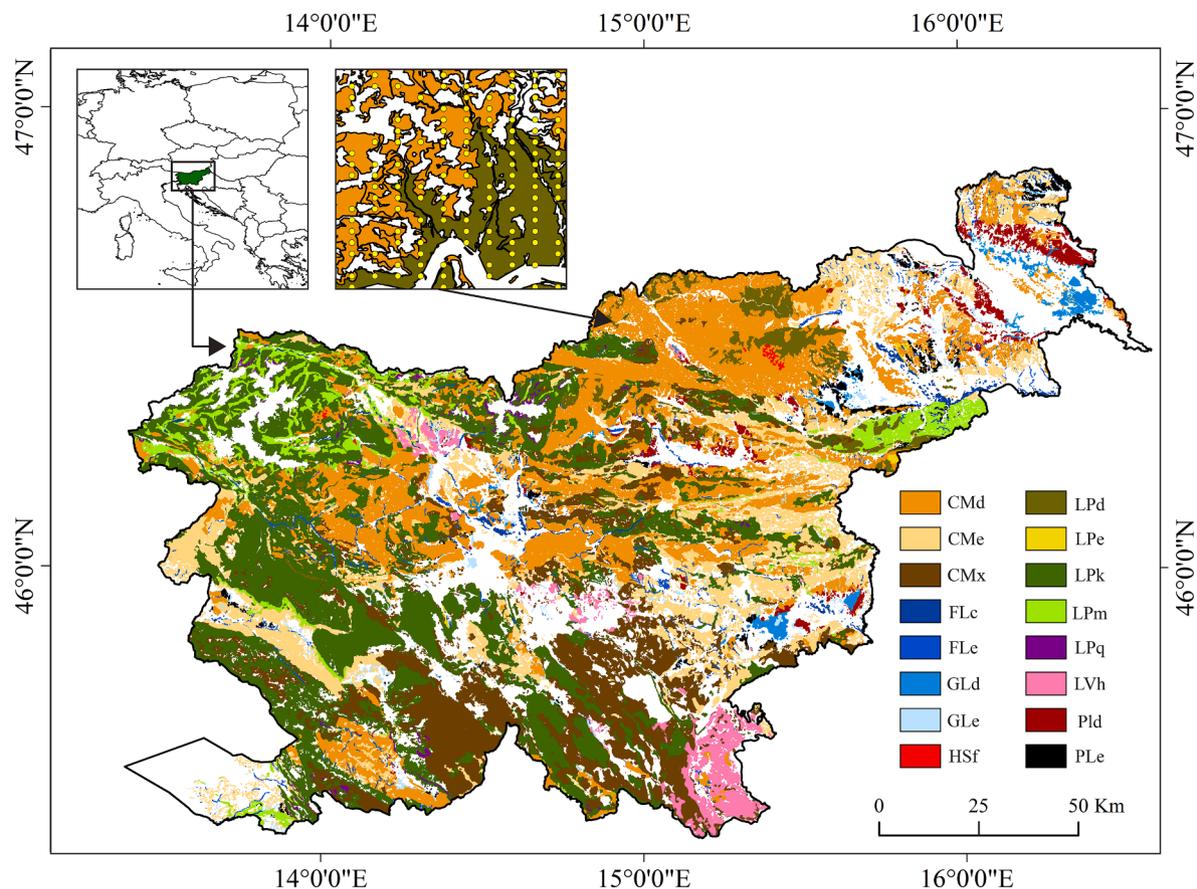


Fig. 1. Map of soil units in the forest area of Slovenia included in the analyses (based on MAFF, 2007) with a detail showing the intersection of soil units and the network of permanent sampling plots (SFS, 2014).

## 2.2. Data

The primary data source was forest inventory data (SFS, 2014). In forest inventories, all trees with a diameter at breast height (dbh)  $\geq 10$  cm are called every ten years on circular permanent sampling plots (PSP) (500 m<sup>2</sup> each) distributed on sampling grids of 250 m  $\times$  250 m and 250 m  $\times$  500 m. Plots were measured twice in moving cycles with approximately-one tenth of the area measured each year. The first measurements were conducted in the period 1992–2004 and re-measurement followed in the period 2002–2014.

Stand growth was defined as periodic stand basal area increment (BAI). BAI was calculated as the difference between the stand basal area of living trees in the second and first inventory. Harvested and dead trees were disregarded, while ingrown trees ( $\geq 10$  cm dbh) were accounted for in the calculation. We analysed stand growth on 72,380 PSPs with a total of 282,217 trees (Appendix A).

Tree growth was defined as the periodic diameter increment of a tree (DI) and calculated as the difference between two consecutive measurements of dbh in a 10 year period. We analysed the tree growth of the five tree species with the highest abundance in the study area: Norway spruce, silver fir, Scots pine, European beech and sessile oak, hereafter spruce, fir, pine, beech and oak, respectively. Tree growth was analysed only for dominant trees, which were defined as the largest 100 trees per hectare at the second measurement. We analysed tree growth on 67,061 PSPs with a total 238,349 trees (Appendix A).

Soil units (SOIL) were derived from the national soil map at a 1:25,000 scale (MAFF, 2007). The soil map is the result of an intensive soil survey in the period 1960–1990 and digitization in the period 1997–1999 (Vidic et al., 2015; Vrščaj et al., 2017), first by the Yugoslav Soil Information System and later (1995–2000) by the Slovenian Soil

Information System using the Slovenian Soil Classification. The legend was translated in accordance with the revised legend of the Soil Map of the World FAO 1988/ISRIC 1997 (Vidic et al., 2015). The soil map is a vector layer with 10,781 polygons with an average size of 117.95 ha, of which 10,008 lie in or intersect forest area. These mapping units were delineated such that they may contain up to three pedosystematic units, which spatially intertwine and cannot be delineated, but their proportions inside of the polygons are given. Based on the predominant pedosystematic unit, the basic mapping units were aggregated mainly by reclassification into 63 pedocartographic units (Vidic et al., 2015) and into 25 FAO soil units (FAO-UNESCO, 1988; IUSS Working Group WRB, 2015), of which 16 were used in our study (Fig. 1). Cambisols and Leptosols prevail, which is also the case on the global level (Soil Atlas of Europe, 2005). The soil units are described by the predominant pedocartographic units with their typical horizons, texture and parent materials. The criterium for including a soil unit into the analyses was a minimum number of 20 PSPs available for the soil unit (Appendix A).

Topographic variables were derived from a digital elevation model with a 12.5 m resolution (GURS, 2014), while climatic variables were derived from long-term climate records in the period 1971–2000 (SEA, 2021) and downscaled from the original 1 km<sup>2</sup> resolution to the PSPs using the nearest neighbour method.

## 2.3. Explanatory variables and their selection

We created a set of 17 and 18 potential explanatory variables for BAI and DI modelling, respectively (Table 1). To reduce multicollinearity, we eliminated one of the variables in the pairs for which the Pearson correlation coefficient was greater than 0.6. Elevation (ELE) was eliminated due to high correlation with the mean amount of precipitation

**Table 1**

List of variables included in the models with their mean values and standard deviations (data from permanent sampling plots (SFS, 2014)).

Variables	Abbreviation	Mean	SD	Min-Max	Model*
<b>Dependent</b>					
Periodic increment of stand basal area (m <sup>2</sup> ha <sup>-1</sup> 10y <sup>-1</sup> )	BAI	7.43	3.76	0.00–36.97	1
Periodic diameter increment (cm 10y <sup>-1</sup> )	DI	4.05	2.46	0.00–19.00	2
<b>Tree</b>					
Initial diameter at breast height (cm)	D	40.96	10.81	10.00–120.00	2
<b>Stand</b>					
Basal area (m <sup>2</sup> ha <sup>-1</sup> )	BA	29.04	12.44	0.77–98.89	1, 2
Quadratic mean diameter (cm)	QMD	26.91	7.90	10.00–82.45	1, 2
Proportion of conifers in total stand basal area	PCON	0.45	0.38	0.00–1.00	1, 2
Gini index of tree diameters	GINI	0.31	0.09	0.00–0.89	1, 2
Shannon index of tree species	SHAN	0.71	0.43	0.00–2.28	1, 2
<b>Site</b>					
Soil units (dummy)	SOIL	–	–	0–1	1, 2
Inclination (°)	INCL	18.21	10.44	0.00–60.00	1, 2
Elevation (m a.s.l.)	ELE	679	312	28–1709	MC
Eastness index (1 = east; –1 = west exposed plot)	EAST	0.01	0.38	–0.77–0.55	1, 2
Northness index (1 = north; –1 = south exposed plot)	NORTH	0.28	0.39	–0.35–1.00	1, 2
Rockiness (%)	ROCK	19.52	23.61	0.00–100.00	1, 2
<b>Climate</b>					
Mean annual temperature (°C)	MAT	7.94	1.72	3.02–13.01	1, 2
Mean annual precipitation (mm)	MAP	1696	430	850–3600	1, 2
Maximum temperature (°C)	TMAX	12.83	2.01	5.04–18.50	MC
Minimum temperature (°C)	TMIN	3.61	1.61	–1.03–9.02	MC
Max temperature of warmest month (°C)	BIO5	23.10	2.35	18.01–28.02	MC
Min temperature of coldest month (°C)	BIO6	–4.20	1.43	–9.51–1.52	MC

\*1, BAI model; 2, DI model; MC, multicollinearity.

(MAP) and mean annual temperature (MAT); the Pearson correlation coefficient amounted to 0.72 and –0.90, respectively. Four climate variables (TMAX, TMIN, BIO5 and BIO6) were eliminated due to high correlation with MAT.

For modelling BAI, five stand, five site and two climate variables were included. Stand basal area (BA) and the number of trees per hectare (N) are an indication of competition pressure in a stand. Quadratic mean diameter (QMD) indicates the developmental stage. The structural diversity of forest stands was described by the Gini coefficient (GINI). GINI ranges from 0 to 1. A higher value indicates uneven-sized stand structure, while values near 0 indicate even-sized stand structure. Tree species mixture was estimated by the Shannon index (SHAN) and by the proportion of conifers in the total stand basal area (PCON). SHAN was calculated based on the proportion of tree species in the total stand basal area. PCON was included in the analyses since the production of conifers is usually larger than that of broadleaves. All stand variables were calculated using the data from PSPs at the beginning of the inventory interval. Four topographic variables were included in the analyses. Inclination (INCL) and rockiness (ROCK) describe the variability of topographic conditions and indicate the extremity of the site. ROCK was taken from the forest inventory database (SFS, 2014); it was visually assessed as the proportion of the area covered by stones and rocks. Rockiness is often applied to describe growth conditions and potentially more vulnerable forests (Bončina et al., 2021). We included two aspect variables in the analyses: eastness and the northness. These variables are often used in forest growth studies (e.g. Mina et al., 2018) because they are easy to calculate. To control for the heterogeneity of climate (SEA, 2021), long-term temperature and precipitation averages were included. For modelling DI we used the same plot-level variables that were used for BAI modelling. Among the tree-level variables, the initial diameter of a tree at the first measurement (D) was used as a proxy for tree size. Additionally, its square (D<sup>2</sup>) was used to account for the possible non-linear relationship between DI and D (Table 1).

Soil was included as a dummy variable. Dystric Cambisols were set as the reference category as this soil unit represents 26 % of the study area. Soil units (SOIL, n = 16, Table 2) differ in typical soil horizons, pH value, parent material and texture. Soil characteristics within a soil unit may vary; however, the differences are expected to be smaller than those between soil units.

## 2.4. Modelling procedure

For modelling BAI, we used a linear fixed-effects model in the *lmer* function in the lme4 R package (Bates et al., 2015) (eq. (1)),

$$BAI_i = \beta_0 + \beta_1 x_{1i} + \beta_2 x_{2i} \dots \beta_n x_{ni} + \varepsilon_i \quad (1)$$

where  $BAI_i$  is the periodic stand basal area increment on plot  $i$ ,  $\beta_0 \dots \beta_n$  are the function parameters and  $\varepsilon_i$  is a random error term.

For modelling DI, a linear mixed-effect model was applied using the *lmer* function in the lme4 R package (Bates et al., 2015) (eq. (2)). Since trees were nested within PSPs, we included sample plots as a random effect. This allowed us to vary the intercepts in the regression equations by PSPs while keeping the variability of the slopes constant. The form of a linear mixed-effect model is as follows:

$$DI_{ij} = \beta_1 x_{1ij} + \beta_2 x_{2ij} \dots \beta_n x_{nij} + b_{1i} z_{1ij} + b_{2i} z_{2ij} \dots b_{in} z_{nij} + \varepsilon_{ij} \quad (2)$$

where  $DI_{ij}$  is the periodic diameter increment of a tree  $j$  on PSP  $i$ ,  $\beta_1 \dots \beta_n$  are the fixed effect coefficients,  $x_{1ij} \dots x_{nij}$  are the fixed effect variables (predictors) and their transformations when applicable for tree  $j$  on PSP  $i$ ,  $b_{1i} \dots b_{in}$  are the random effect coefficients which are assumed to be multivariate normally distributed,  $z_{1ij} \dots z_{nij}$  are the random effect variables, and  $\varepsilon_{ij}$  is the error for tree  $j$  on PSP  $i$  where each PSP's error is assumed to be multivariate normally distributed. The model parameters were estimated with the Maximum Likelihood Estimation (MLE) method (Myung, 2003). Post-Hoc pairwise comparison of slopes for soil units (SOIL) was performed with the Scheffe test to correct significance for all possible contrasts and to account for inequality of group size using the function *emmeans* from the emmeans R package (v1.7.3; Lenth, 2022). The effect size was determined with Cohen's  $d$  using the function *eff\_size()* in the emmeans R package (v1.7.3; Lenth, 2022).

The fit of the BAI model was evaluated with the coefficient of determination ( $R^2$ ), root mean square error (RMSE), log likelihood of the model (logLik) and the Akaike information criterion (AIC). The fit of the DI models was evaluated with the proportion of variance explained by both the fixed and random factors ( $R^2_{cond}$ ), the proportion of variance explained by the fixed factors alone ( $R^2_{marg}$ ), the PSP variance as a percentage of the total variance, i.e. the intraclass correlation (ICC), RMSE, AIC and the estimated standard deviation of the errors (Sigma).

**Table 2**

List of 16 soil units included in the analyses with basic characteristics. A maximum of three pedocartographic units (PCUs) for a soil unit are presented (after Vidic et al., 2015).

Soil units <sup>1</sup> (SOIL)	Abbr. <sup>1</sup>	Forest area <sup>4</sup> (%)	Organic matter <sup>3</sup> (%) mean/sd	Depth <sup>3</sup> (cm) mean/sd	ID of PCU <sup>2</sup>	PCU name <sup>2</sup>	Horizons <sup>2</sup>	pH <sup>2</sup>	Parent material <sup>2</sup>	Texture <sup>2</sup>
Dystric Cambisols	CMD	22.64	8.9/3.8	70/12	28	Dystric brown soils on shaly claystones and sandstones	A-Bv-C	3.5–5	shaly claystones and sandstones (permocarboniferous)	SiL
					32	Dystric brown soils on noncalcareous flysch and decalcified marlstone	A-Bv-C	4.5–5.5	non-calcareous and low calcareous flysch and decalcified marlstone	SiCL-SiC
					30	Dystric brown soils on pyroclastic rocks	A-Bv-C	4–5	pyroclastic rocks (tuff, tuffite)	SiL-SaL
Eutric Cambisols	CMe	10.93	8.1/4.0	80/17	16	Eutric brown soils on mixed carbonate and non-carbonate rocks	A-Bv-C	5–6.5	different carbonate and basic rocks	SiL-CL
					22	Eutric brown soils on marlstone	A-Bv-C	5.5–7	marlstone	SiC-SiCL
					23	Eutric brown soils, typic and calcaric on flysch	A-Bv-C, A-Bca-C	5.5–8	Eocen flysh	SiCL-SiC
Chromic Cambisols	CMx	15.26	9.2/3.8	67/14	37	Brown soils on limestone and dolomite	A-Brz-C-R, A-E-B <sub>t</sub> -C	5.5–6.5	limestone and dolomite	SiCL-SiC-CL
Calcaric Fluvisols	FLc	0.31	4.5/3.4	73/15	49	Undeveloped soil on alluvial deposits	I-II-C	5.5–7.5	river deposits	LSa-SaL
					50	Alluvial soils, eutric, calcaric	A <sub>1</sub> -A <sub>2</sub> -A <sub>3</sub> -C, A <sub>1</sub> -A <sub>2</sub> -Ago-C	7–8	Silt-loamy alluvium	L-SiL
Eutric Fluvisols	FLe	0.42	4.7/3.7 4.5/0.9	97/17	53	Gleyic alluvial soils, eutric	A <sub>1</sub> -A <sub>2</sub> -Go-C	6.5–7.5	loam clayey alluvium	L-SiL
Dystric Gleysols	GLd	0.72	6.5/3.6	71/24	51	Alluvial soils, eutric	A <sub>1</sub> -A <sub>2</sub> -A <sub>3</sub> -C	6.5–7.5	loamy and silt-loamy deposits	SiL-L
					57	Hypogley, eutric	A-Go-Gr	5–6.5	Pleistocene clay and loam	SiCL-SiC
Eutric Gleysols	GLe	0.38	5.9/3.1	92/19	58	Hypogley, dystric	A-Go-Gr	4–5	Pleistocene clay and loam	SiL-SiCL
Fibric Histosols	HSf	0.05	5.8/3.5	47/12	57	Hipogley, eutric	A-Go-Gr	5–6.5	Pleistocene clay and loam	SiCL-SiC
Dystric Leptosols	LPd	2.88	7.3/4.0	54/13	62	Ombic peat soils	H <sub>1</sub> -H <sub>2</sub> -H <sub>3</sub>	4–5	peat	–
Eutric Leptosols	LPe	0.13	5.5/3.5	61/15	11	Ranker, dystric	Ah-C	4–5	non-carbonate rocks	SiL
Rendzic Leptosols	LPk	30.19	8.3/4.3	42/14	10	Eutric ranker	Ah-C	5–6	non-carbonate rocks	CL
					4	Rendzinas on limestone and dolomite	Ah-R	5.5–7	limestone and dolomite	SiL
Mollic Leptosols	LPm	3.83	7.5/3.7	42/14	5	Rendzinas and brown soil on limestone and dolomite	Ah-C, A-Brz-C	5.5–7	limestone and dolomite	SiL, SiCL, Si C
					8	Rendzinas on moraines and talus deposits	A-C	5.5–7.5	carbonate moraines and talus	SiL-SaL
					6	Rendzinas on soft carbonate rocks	Ah-C	6–7.5	marlstone, flysch, lototamnian limestone	SiL
Lithic Leptosols	LPq	0.27	1.6/3.4	45/13	1	Lithosol	(A)-R	7–8	marlstone and flysch	–
Haplic Luvisols	LVh	2.41	10.0/3.9	139/16	42	Leached soil on limestone and dolomite, acric	A-E-Bt-C	3.5–4.2	limestone	SiL-SiCL
					44	Leached soils on siliceous substrate	A-E-Bt-C	4.5–5.5	Pliocene deposits, siliceous substrate	SiL-C
					43	Leached soils on conglomerate	A-E-Bt-C, A-E-Bt-Bg-C	4–5	Pliocene deposits, siliceous substrate conglomerate	SiL-SiCL
Dystric Planosols	PLd	1.36	6.1/3.3	61/19	56	Pseudogley on slope and plain, dystric	A-g-Bg-C	4–5	Pleistocene and Pliocene deposits	SiL-SiCL
Eutric Planosols	PLe	0.76	5.2/2.7	63/23	55	Pseudogley on slope and plain, eutric	A-g-Bg-C	5–6.5	Pleistocene and Pliocene deposits	SiL-SiCL

<sup>1</sup> Names and abbreviations after the pedological map (1:25,000) (MAFF, 2007).<sup>2</sup> After Vidic et al., 2015.<sup>3</sup> Calculated based on the representative soil profiles (MAFF, 2007).<sup>4</sup> Based on the intersection of pedological map (MAFF, 2007) and forest map (SFS, 2014); 7.46% of the total forest area not included in the analyses.

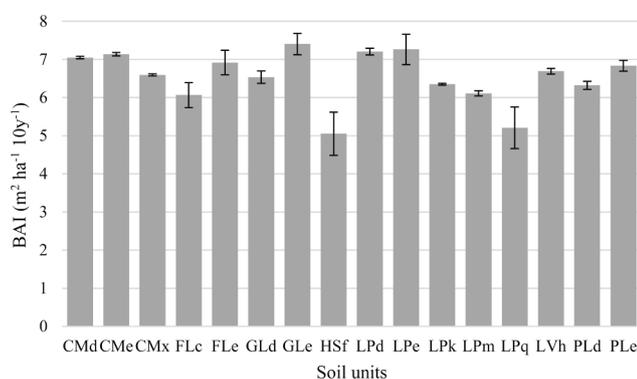
- not available.

**Table 3**

Results of fitting the linear mixed effect model for periodic stand basal area increment (significant coefficients at  $P < 0.05$  are in bold).

	Estimate	Std. Error	P value	<sup>1</sup> Relative decrease in R <sup>2</sup> (%)
(Intercept)	<b>4.3140</b>	0.032	0.000	
QMD	<b>-0.0952</b>	0.001	0.000	26.92
QMD <sup>2</sup>	<b>0.0010</b>	0.000	0.000	10.38
PCON	<b>0.4836</b>	0.006	0.000	33.88
BA	<b>0.0115</b>	0.000	0.000	21.00
GINI	<b>-0.1030</b>	0.024	0.000	0.11
SHAN	<b>0.0116</b>	0.005	0.028	
INCL	<b>-0.0039</b>	0.000	0.000	1.70
ROCK	-0.0001	0.000	0.467	0.00
MAP	<b>-0.0001</b>	0.000	0.000	1.61
MAT	<b>-0.0048</b>	0.002	0.006	0.04
SOIL				4.32
CMe	<b>0.0167</b>	0.008	0.040	
CMx	<b>-0.0871</b>	0.007	0.000	
FLc	<b>-0.1922</b>	0.052	0.000	
FLe	-0.0245	0.040	0.541	
GLd	<b>-0.0984</b>	0.026	0.000	
GLe	0.0661	0.039	0.093	
HSf	<b>-0.4073</b>	0.076	0.000	
LPd	<b>0.0295</b>	0.013	0.021	
LPe	0.0402	0.057	0.478	
LPk	<b>-0.1354</b>	0.007	0.000	
LPm	<b>-0.1833</b>	0.012	0.000	
LPq	<b>-0.3729</b>	0.099	0.000	
LVh	<b>-0.0684</b>	0.013	0.000	
PLd	<b>-0.1405</b>	0.019	0.000	
PLe	-0.0406	0.023	0.079	
R <sup>2</sup>	0.2748			
RMSE	0.5694			
AIC	123,944			
logLik	-61,945			

<sup>1</sup> Relative decrease in R<sup>2</sup> if this variable is omitted from the model and fitted again.



**Fig. 2.** Production rate of forest stands on soil units, expressed by periodic stand basal area increment (mean values with s.e. are shown; other factors are fixed at the average value).

### 3. Results

#### 3.1. The impact of soil on stand growth

The BAI model explained 27 % of total BAI variability (Table 3). Soil contributed 4.3 % to the explained BAI variability, which is more than that contributed by the topographic and climatic variables. The highest stand production was registered on Eutric Gleysols, and the lowest on Histosols (Fig. 2). In comparison to the reference Dystric Cambisols, the production rate on soil units was in the interval of -28 % to +5 % of that on the reference soil unit. Pairwise post hoc analyses (Table 4) showed no statistically significant differences within Gleysols and Planosols, but significant differences within Cambisols (CMx vs CMd and CMe) and

**Table 4**

Cohen's d values for pairs of soil units with significant differences in BAI at  $P < 0.05$ .

	CMd	Cme	CMx	Gle	HSf	LPd	LPm
CMx	0.153	0.182					
HSf	0.715	0.744		0.831			
LPd			-0.204		-0.767		
LPk	0.237	0.267	0.085			0.289	
LPm	0.322	0.351	0.169	0.438		0.374	
LVh	0.120	0.149				0.172	-0.202
PLd	0.726	0.276				0.298	
PLe							-0.250

Leptosols (Calcareous vs Dystric Leptosols).

Stand variables contributed most (91 %) to the explained variability of BAI. QMD was the strongest individual predictor followed by PCON and BA. The production rate of forest stands increased non-linearly with increasing quadratic mean diameter (QMD) and increased linearly with stand density (BA), proportion of conifers in the forest stand (PCON) and tree species diversity (SHAN), while all other factors had a negative effect on BAI. Tree species diversity and the tree size heterogeneity (GINI) of forest stands explained a negligible part of stand productivity.

#### 3.2. The impact of soil on tree growth

Soil explained more variability in tree growth than that in stand growth; the contribution of SOIL to the total explained DI variability ranged from 4 to 27 % (Table 5). SOIL was the most important predictor of oak growth and the least important for beech, for which the contribution of SOIL was equal to that of mean annual temperature and mean annual precipitation.

The growth of tree species varied between soil units (Fig. 3). Compared to the growth of trees on the reference soil unit (CMd), growth was more than 14 % higher (see oak on Eutric Gleysols) and 47 % lower (see pine on Fibric Histosols).

Fig. 3 shows that tree species reach their maximum diameter growth on different soil units: spruce performs best on Eutric Gleysols, fir on Haplic Luvisols, pine on Dystric Leptosols, beech on Haplic Luvisols and Eutric Planosols, and oak on Eutric Gleysols. Post hoc analysis (Table 6) showed a limited number of significant differences in the growth of a species between soil units. Statistically differing soil units are often specific for single tree species as follows:

- Spruce: Growth on Fibric Histosols differs significantly from that on most other soil units. A similar pattern was observed for Rendzic and Mollic Leptosols. Significant differences were also found within Leptosols (LPd vs LPk and LPm).
- Fir: Growth on Chromic Cambisols differs significantly from that on other Cambisols. A similar pattern was observed for Leptosols (LPd vs LPk and LPm).
- Pine: Significant differences between Dystric and Eutric Cambisols are specific for pine only. Growth on Rendzic and Mollic Leptosols differs significantly from that on Dystric Cambisols and Dystric Leptosols.
- Beech: Growth is partially similar to that of fir; growth on Chromic Cambisols differs significantly from that on other Cambisols. Rendzic and Mollic Leptosols differ significantly from most other soil units. Growth on dystric pseudogley (PLd) is slower in comparison to Eutric Cambisols and Luvisols, while growth on sites with leached soils (LVh) is faster in comparison to that on Chromic Cambisols.
- Oak: Growth on Eutric Planosols differs significantly from that on most other soil units. Similar to pine, a significant difference was registered in Cambisols (CMd vs CMe). Growth on Rendzic Leptosols is significantly lower in comparison to many other soil units. Sites on Chromic Leptosols are significantly less productive in comparison to sites on Dystric Leptosols and Planosols.

**Table 5**Results of fitting the linear mixed effect model for the diameter increment of dominant trees (significant coefficients at  $P < 0.05$  are in bold).

	Coefficients					<sup>1</sup> Relative decrease in R <sup>2</sup> (%)				
	Spruce	Fir	Pine	Beech	Oak	Spruce	Fir	Pine	Beech	Oak
(Intercept)	<b>2.4600</b>	<b>2.8390</b>	<b>2.3760</b>	<b>2.0220</b>	<b>1.8560</b>					
D	<b>-0.0069</b>	-0.0007	<b>-0.0404</b>	<b>0.0087</b>	<b>0.0107</b>	0.00	0.00	6.81	1.28	1.40
D <sup>2</sup>	<b>0.0001</b>	0.0000	<b>0.0005</b>	<b>0.0000</b>	<b>0.0000</b>	0.00	0.00	5.11	0.00	0.00
BA	<b>-0.0118</b>	<b>-0.0154</b>	<b>-0.0092</b>	<b>-0.0140</b>	<b>-0.0073</b>	56.19	50.00	27.60	56.47	19.39
PCON	<b>0.3411</b>	<b>0.3590</b>	<b>0.3526</b>	<b>0.3350</b>	<b>0.1345</b>	11.60	10.98	13.97	14.08	3.27
QMD	<b>-0.0100</b>	<b>-0.0029</b>	<b>-0.0176</b>	<b>-0.0026</b>	<b>-0.0054</b>	7.73	0.00	14.31	0.00	0.70
GINI	<b>0.2207</b>	<b>0.4986</b>	<b>-0.2868</b>	<b>0.1327</b>	<b>0.0179</b>	2.58	4.88	0.00	1.28	0.00
SHAN	-0.0130	<b>0.1153</b>	-0.0233	<b>0.1250</b>	<b>0.1142</b>	0.00	1.22	0.00	7.68	9.35
INCL	<b>-0.0066</b>	<b>-0.0079</b>	<b>-0.0059</b>	<b>-0.0050</b>	<b>-0.0063</b>	11.60	8.54	8.52	6.40	13.32
ROCK	<b>0.0006</b>	<b>-0.0004</b>	0.0011	<b>-0.0010</b>	<b>-0.0029</b>	0.00	0.00	0.00	1.28	6.54
MAP	<b>0.0000</b>	<b>-0.0002</b>	<b>0.0002</b>	<b>-0.0001</b>	<b>-0.0003</b>	0.00	7.32	5.11	3.84	16.59
MAT	<b>0.0190</b>	<b>0.0137</b>	<b>0.0296</b>	<b>0.0339</b>	<b>0.0252</b>	2.58	0.00	3.41	3.84	2.80
SOIL						7.73	17.07	15.16	3.84	26.64
CMe	-0.0022	<b>-0.0807</b>	<b>-0.1334</b>	0.0157	-0.0075					
CMx	-0.0062	<b>-0.3098</b>	-0.0366	<b>-0.0430</b>	<b>-0.1578</b>					
FLc	<b>-0.2214</b>		<b>-0.4007</b>							
FLe	-0.0753			-0.0355	0.0932					
GLd	-0.0383				0.0994					
GLe	<b>0.1501</b>		0.0296		0.1154					
HSf	<b>-0.4456</b>									
LPd	-0.0277	<b>-0.0743</b>	0.0750	0.0183	0.0392					
LPe	-0.0359			0.0450						
LPk	<b>-0.1065</b>	<b>-0.3084</b>	<b>-0.1586</b>	<b>-0.0792</b>	<b>-0.2181</b>					
LPm	<b>-0.1578</b>	<b>-0.3305</b>	<b>-0.2065</b>	<b>-0.0755</b>	<b>-0.0763</b>					
LVh	0.0353	0.0575	-0.0104	<b>0.0747</b>	<b>-0.0622</b>					
PLd	<b>-0.0922</b>	-0.1913	-0.0276	<b>-0.1106</b>	<b>0.0707</b>					
PLe	-0.0455		<b>-0.1020</b>	0.0608	<b>0.1715</b>					
R <sup>2</sup> cond	0.4212	0.3974	0.3487	0.3663	0.3421					
R <sup>2</sup> marg	0.1264	0.1473	0.1070	0.1300	0.0954					
ICC	0.3375	0.2933	0.2700	0.2721	0.2733					
RMSE	0.4341	0.5041	0.5161	0.5000	0.5624					
AIC	14,780	59,044	30,882	14,890	36,637					
Sigma	0.4870	0.5640	0.5722	0.5000	0.5620					

<sup>1</sup> Relative decrease in R<sup>2</sup> if this variable is omitted from the model and fitted again.

Most of the included tree, stand and climatic variables had a significant effect ( $P < 0.05$ ). However, the effects of SHAN, GINI and D were significant for some but not all of the studied species (Table 5). A notable result is that the impact of several factors on DI was of the opposite direction. For instance, MAP positively influenced the growth of spruce and pine but negatively influenced the growth of the other three tree species. The slopes of the impacts of tree, stand and site variables differed noticeably; the same was true for their contribution to the total explained variance. BA contributed most to the explained variability of DI (19–56 %), and the effect of BA was negative for all tree species.

## 4. Discussion

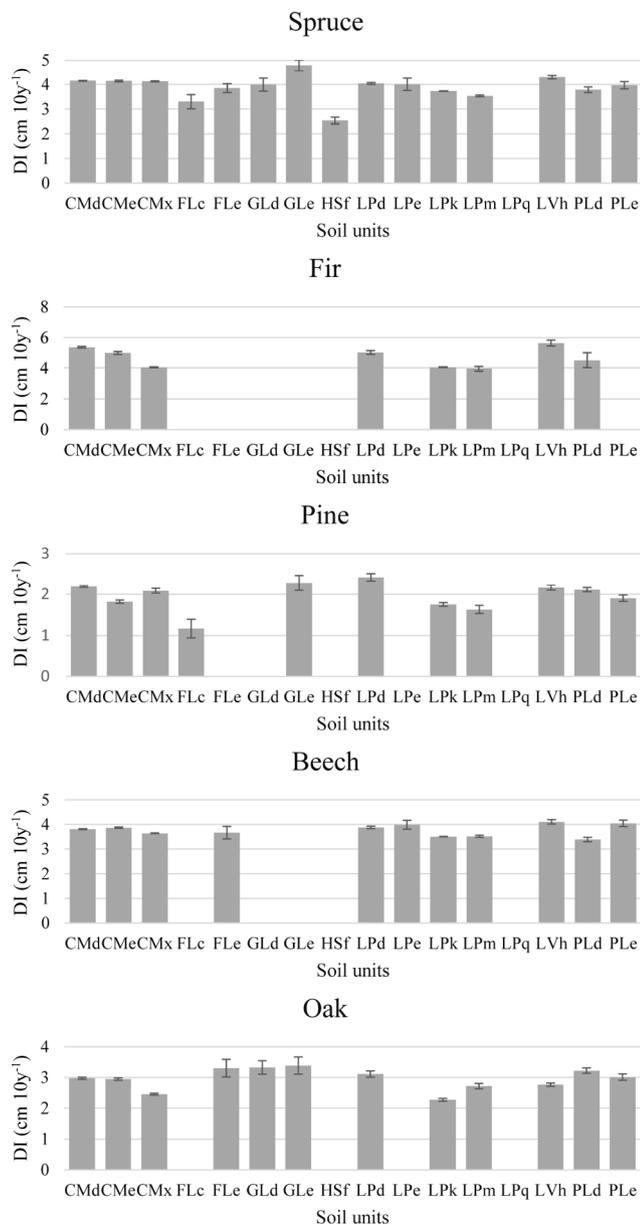
### 4.1. The effect of soil on stand and tree growth

We analysed the impact of soil and other environmental factors on tree and stand growth on more than one million ha of forests. On such a large scale, soil classification into soil units with an approximate size of 118 ha proved detailed enough for quantifying the effect of soil on stand and tree growth. However, more detailed quantification of the impact of soil is needed in the small-scale investigations. The effects of soil in our models should be understood as manifestations of the main effects of soil. Although the growth of trees and stand productivity are expected to change due to climate change (e.g. Albert and Schmidt, 2010), the basic question of how influential soil is for the growth of trees and stands remains relevant. Our stand growth model explained 27 % of BAI variability, while tree growth models explained 34 to 42 % of DI variability. As expected, stand factors were the strongest determinant of growth rate at the stand and tree level. They contributed approximately 90 % to the total explained variability of growth at the stand level, while their

contributions to the explained variability of tree growth were smaller, amounting to 78, 67, 56, 80 and 33 % for spruce, fir, pine, beech and oak, respectively.

Soil was a stronger driver of stand growth than climate or topography. The greater impact of soil in comparison to climate has recently been reported for tree species distribution in temperate forests (Walthert and Meier, 2017). Our finding is contrary to the results of some other studies; for instance, Toledo et al. (2011) found climate to be a stronger driver of tree and stand growth rates in tropical lowland forests than soil. The smaller impact of climate can be explained in three ways. It is likely that the climatic effects that generally govern the production rates of zonal vegetation have been modified by human impact, such as the promotion of conifers, littering or past silvicultural systems applied, which were more intense on some soil units (Bončina et al., 2021). The parent material and topography vary greatly across the forest area, noticeably influencing soil properties and growth conditions. In many sites they override the effect of climate, which is especially evident in areas with azonal forest vegetation. Third, despite the climatic diversity of Slovenia, the differences in climatic extremes are probably too small to be the primary determinant of stand growth.

However, caution is needed in interpreting soil classes as an independent ecological factor. Temperate forest soils reflect seasonal variability in temperature and precipitation as well as many impacts from the aboveground vegetation under which soils develop (Adams et al., 2019). Tree species composition can influence soil properties and the amount of organic material, which can alter soil pH and the rate of organic matter decomposition. The depth of rooting and the resulting allocation differences in aboveground and belowground organic matter also contribute to differences in soil properties (Augusto et al., 2002). Soil properties may also arise as a result of forest management and



**Fig. 3.** Periodic diameter increment of five tree species on 16 soil units (mean values with s.e. are shown; other factors are fixed at the average value).

should therefore not be considered as a factor entirely independent from stand conditions, climate or management. The soil classification we used shows the main differences in soil characteristics between broad soil classes. It is therefore inappropriate for studies on the scale of an individual stand or tree cohort.

The study showed significant differences in stand growth between soil units. Eutric Gleysols, Dystric and Eutric Cambisols, and Dystric and Eutric Leptosols were associated with the largest stand growth rates, while Fibric Histosols and Lithic Leptosols were identified as soils with the lowest growth rates. In the study area, Histosols can be found on high-elevation peats and are characterized by a thick organic soil horizon and a lack of major nutrients, which are washed away. This leads to the lowest growth rate of all soil units and the dominance of spruce (and mountain pine *Pinus mugo* L.). Lithic Leptosols are, in contrast, very shallow, giving trees only very limited chances for developing a large enough rooting system to efficiently absorb water and nutrients, resulting in a low growth rate. Our results on stand growth are generally in line with natural soil fertility levels for reference soil groups (Soil

Atlas of Europe, 2005), where Fluvisols and Gleysols were ranked with a high level, Luvisols and Histosols with a moderate level, and Planosols with a low level; other soil units from our study are not mentioned in the ranking list. However, in our study the productivity of Planosols was relatively higher than that in the ranking list, while the productivity of Histosols was lower.

There were significant differences in stand production within the same group of soil units, the most noticeable being within Leptosols, among which soil depth might have a decisive role. Stand growth on shallow Leptosols on carbonate substrate (Rendzic and Mollic Leptosols) was found to be significantly lower than that on deeper Leptosols on carbonate (LPe) or non-carbonate bedrock (LPd). Similarly, in the group of Cambisols, growth on Chromic Cambisols was significantly lower in comparison to that on Dystric and Eutric Cambisols. In a detailed study of local site type variability and stand productivity in beech forests on three soil units, Kirchen et al. (2017) found that soil water capacity, annual tree transpiration and aboveground biomass production increased in this order: Rendzic Leptosols < Eutric Cambisols < Dystric Cambisols. The soil unit was found as the major driver of stand growth, primarily through its soil water holding capacity. It seems that the amount of water taken up by the roots and transpired from the canopy is the main driver of stand productivity in beech forests in the temperate region (Kirchen et al. 2017).

Our study showed that SOIL was a relatively more important explanatory variable in the DI growth models than in the stand growth model. For some tree species SOIL explained even more DI variability than the tree size variables. We found that variation in the growth rate of tree species between soil units is larger than that of stand growth rate. The physiological requirements of tree species for growth, survival and regeneration are substantially different (San-Miguel-Ayanz et al., 2016; Walthert and Meier, 2017) and resulted in a different growth response to site factors in the forest area. A certain tree species can colonise sites with very different soils; it can grow well on some of them, while on the others its growth is reduced. The response of other tree species in the same area can be different or even opposite, which is likely to be a reason for the smaller variation in stand growth rate between soil units in comparison to single tree species growth. The analysed tree species can grow on a broad range of soils (San-Miguel-Ayanz et al., 2016). The interval between the highest and the lowest mean diameter increment on soil units for spruce, fir, pine, beech and oak amounted to 54, 31, 57, 17, and 38 % of the mean diameter increment of tree species, respectively. Although some of the studied tree species reach the highest and the lowest growth rates on the same soil units, this occurs for the majority of tree species on different soil units, which is probably a consequence of different optimal ranges of soil, topographic and climatic parameters between tree species (Abbott et al., 2017). In spite of the many differences in the diameter growth between the tree species on the observed soil units, a common pattern can be recognized: the growth of trees on calcareous Leptosols was low or even the lowest. The ranking list of soil units with respect to the productivity of single species is to a great extent in accordance with the results of Vospernik (2021).

Spruce reached the highest growth rate on Eutric Gleysols, followed by Haplic Luvisols and Cambisols, although these differences were not significant. A high growth rate on Eutric Gleysols was also observed for oak and pine, while beech and fir were not present there. The main disadvantage of Gleysols for plant growth is surface water logging or a high level of underground water. Spruce is often classified as sensitive to a high underground water level (e.g. San-Miguel-Ayanz et al., 2016), while recent findings indicate the remarkable ability of spruce to adapt to waterlogging (Walthert and Meier, 2017). In Slovenia, Gleysols developed mainly as a consequence of high precipitation rather than of a high groundwater level. In most areas, high precipitation causes temporary water logging only, which fits well to the demands of spruce. Seltnann et al. (2021) examined the basal area increment of spruce on three soils (Cambisols, Podzols and water influenced soils) and found the highest increment on sites with Cambisols. Similarly, Monserud and

**Table 6**Cohen's d values for pairs of soil units with significant differences in DI of tree species at  $P < 0.05$ .

a) Spruce								
	CMd	Cme	CMx	Gle	HSf	LPd	LPk	LPm
HSf	0.916	0.910	0.902	1.224				
LPd					-0.859			
LPk	0.219	0.214	0.206		-0.697	0.162		
LPm	0.324	0.320	0.311		-0.591	0.267		
LVh					-0.988		-0.291	-0.397
PLd					-0.726			
Ple					-0.822			
b) Fir								
	CMd	CMe	CMx	LPd	LPk	LPm		
CMx	0.545	0.406						
LPd			-0.417					
LPk	0.547	0.404		0.415				
LPm	0.586	0.443		0.454				
LVh			-0.651		-0.648	-0.688		
c) Pine								
	CMd	FLc	LPd					
CMe	0.233							
FLc	0.700							
LPd		-0.831						
LPk	0.277		0.408					
LPm	0.361		0.492					
d) Beech								
	CMd	CMe	CMx	LPd	LPk	LPm	LVh	
CMx	0.086	0.117						
LPk	0.158	0.189	0.072	0.195				
LPm	0.151	0.182		0.188				
LVh			-0.235		-0.308	-0.300		
PLd		0.252					0.370	
e) Oak								
	CMd	CMe	CMx	LPd	LPk	LPm	LVh	
CMx	0.281	0.268						
LPd			-0.350					
LPk	0.388	0.374		0.458				
PLd			-0.407		-0.514			
Ple	-0.305	-0.319	-0.586		-0.693	-0.441	-0.416	

Šterba (1996) found that spruce grows best on the Eutric Cambisols, Podzols and Eutric Planosols over flysch and worst on Leptosols derived from calcareous bedrock. We found that spruce had a significantly lower growth rate on Rendzic and Mollic Leptosols than that on Dystric Leptosol. Spruce was favoured by forest management in the previous century, which currently results in its higher abundance and larger spatial distribution. A higher level of alteration of forest stands due to favouring Norway spruce significantly increases their susceptibility to natural disturbances (Bončina et al., 2017). Therefore, caution is needed in the interpreting the results on spruce diameter growth since they are based on data for living trees in the observed period, while the different mortality rate of spruce between soil units was neglected.

The maximum growth rate of fir was registered on Luvisols, although differences in growth rate with respect to other soil units were not significant. Haplic Luvisol is among the most productive soil types, with an accumulation of high-activity clays and a high base saturation, which fits well with fir's growth demands (Dobrowolska et al., 2017). Fir is well adapted to moist conditions but very susceptible to extreme water

stress (Walder et al., 2021) and thus exhibits its highest growth rate on soil types with a high-water holding capacity. Fir registered a high growth rate on Eutric and Dystric Cambisols (see also Dinca et al., 2022) and a low growth rate on Chromic Cambisols, even significantly lower in comparison to Dystric Leptosols and Haplic Luvisols, which indicates fir prefers sites with lower pH (Dobrowolska et al., 2017).

Pine is characterized by a large autecological but narrow sinecological amplitude; therefore, it can grow in various sites, but actually its presence is limited to nutrient-poor and dry sites where other tree species (e.g. beech and spruce) are less competitive. On fertile and moist sites, it is outcompeted by other tree species (Bončina et al., 2021). Scots pine is often present in disturbed, pioneer or early-succession stages in sites with other potential forest types, such as beech forests, which was also partly the case in our study. However, there are also vast areas of natural Scots pine forests in Europe. In our study area, the highest growth rate of pine was registered on District Leptosols and Eutric Gleysols. It grows poorly on Rendzic and Mollic Leptosols, and the most poorly on Calcaric Fluvisols. However, due to the high variability of

diameter increment, significant differences in DI were found only for a few pairs of soil units. Obviously, pine reaches maximum growth rates on the same soil types as most other tree species, but despite the same growth conditions, pine exhibits significantly lower DI than other more competitive tree species.

In comparison to the other tree species observed, the variation in beech growth rate between soil units was quite small, and none of the soil units stood out with a very low growth rate. This suggests that beech growth is not particularly sensitive to soil (Walthert et al., 2013). The highest growth rate was observed on Haplic Luvisols and Eutric Planosols, which are both well drained, followed by Leptosols and two Cambisols. In contrast to Kirchen et al. (2017), who studied stand biomass production in beech forests, we did not find significant differences in beech tree growth between Eutric and Dystric Cambisols. However, we found significantly lower growth on Chromic Cambisols. Again, beech growth on Rendzic and Mollic Leptosols was significantly slower in comparison to that on several soil units. The lowest growth rate of beech was found on Dystric Planosols, probably due to the low soil water holding capacity.

Oaks have often been recognized as resistant to climate change and therefore as species which may prosper in the future. The growth rate of oak across the soil units is the most specific; the lowest rate was registered on Rendzic Leptosols and Chromic Cambisols and was only 40 % of that on Gleysols and Eutric Planosols. This is in line with the statement that sessile oak prospers on fertile and moist soils (San-Miguel-Ayanz et al., 2016) as are the latter, while Rendzic Leptosols are characterized by shallow soil with low water holding capacity and nutrient supply. Pairwise analyses showed significant differences in diameter increment mainly for three units (Chromic Cambisols, Dystric Planosols and Rendzic Leptosols) versus several other units.

Tree size has often been recognized as a variable explaining the majority of variance in individual tree growth models (e.g. Monserud and Sterba, 1996; Vospernik, 2021), but it seems this is not the case for dominant trees. In our study, the impact of tree size was negligible, with the exception of pine.

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

Stand factors are the strongest driver of tree and stand growth. The growth rate of forest stands increases with increasing stand density, while the opposite is true for the growth rate of tree species. From an individual tree perspective, stand basal area is a measure of competition for light and other resources negatively affecting the growth rate of dominant trees (Weiskittel et al., 2011). In our study, basal area is the strongest predictor in individual tree growth models, contributing even up to 56 % to the total explained variability of diameter growth. Quadratic mean diameter describes the developmental stage of the stand and the overall crowdedness in the stand (Newton, 2021). In several growth studies the age of the stand or trees is included in the growth models. However, in our study area stands are characterized by long regeneration periods and the considerable impact of mature trees on regeneration growth due to close-to-nature forestry. Therefore, information on stand or tree age is neither relevant nor available. The negative effect of quadratic mean diameter on stand growth is relatively high and non-linear; for a given stand basal area the production is higher in a stand with higher tree number and therefore a lower quadratic mean diameter. The effect of mean quadratic diameter on tree diameter growth is very weak and negative, with the latter being opposite to the results of some studies focused on all trees in a stand (e.g. Trifković et al., 2022). Since we studied only dominant trees, the basal area of overtopping trees (usually marked as BAL) was not included as an indicator of individual tree competition pressure.

Tree species composition contributed up to 34 % to the total explained variability of stand growth rate. In the same site, the production of conifers usually exceeds that of broadleaves if the production rate is measured by the stand basal area increment or stand volume increment (Pretzsch, 2010), both of which are common in growth and yield science. This is the main reason for the positive effect of conifers on the higher growth rate of forest stands. Individual species growth models also showed that tree growth rate is slightly higher in stands with a higher proportion of conifers. The proportion of conifers contributed 0–14 % to the total explained variability of tree diameter growth. This effect is related to the competition conditions for tree growth, which are assumed to be lower in stands with conifers, likely due to the smaller crowns of conifers in comparison to those of broadleaves of the same diameter (Badoux, 1949). The Shannon index as an additional variable to describe the impact of tree species composition had a weak positive effect on stand growth rate; growth studies have found a positive, negative or insignificant impact of species mixture on tree and stand growth (Forrester and Bauhus 2016; Mina et al., 2018; Pretzsch et al., 2021). The possible explanation for a positive impact is the complementarity effect between tree species, resulting in the more efficient use of growth space in mixed forest stands (Pretzsch and Schütze, 2009). However, this effect depends on tree, stand and site variables (e.g. Huber et al., 2014; Mina et al., 2018).

The impact of structural heterogeneity on growth has been more frequently studied in relation to stand productivity than to the growth of individual trees (e.g. Lei et al. 2009). Several studies (e.g. Dănescu et al., 2016) have found a positive impact of structural heterogeneity on stand growth and have suggested niche complementary as the underlying reason. In our study the Gini coefficient had a weak negative impact on stand growth. The same finding was reported, for instance, by Liang et al. (2007) and Wang et al. (2019), who argued that stand heterogeneity negatively impacts stand growth due to reduced total light interception in the stand. In our study the significant positive effect of stand heterogeneity on diameter growth was determined for spruce, fir and beech, while the effect of stand heterogeneity on pine growth was negative and very weak, but still significant. Several studies have found a different response of tree diameter growth to stand heterogeneity (e.g. Lei et al., 2009; Dănescu et al., 2016; Trifković et al., 2022).

The group of environmental factors in the study included the already discussed soil unit, but also topographic and climatic predictors. Stand growth rate as well as the growth of all tree species observed in our study area was lower on steeper terrain. Inclination markedly contributes to the total explained variability of stand and tree growth rate, at 1.7 and 6.5–13.3 %, respectively. Inclination and other topographic attributes may strongly influence soil attributes (e.g. soil moisture, soil organic carbon and nitrogen content) and thus growth conditions for trees (Wu, 2015). Surface rockiness has rarely been considered in growth studies (e.g. Trifković et al., 2022). In our study the effect of rockiness on stand and tree growth was weak and mostly negative. Pyrke and Kirkpatrick (1994) reported the significant impact of rockiness on the growth rate of Eucalyptus species; in stony soil root development can be hindered, resulting in reduced tree growth. In our study the negative effect of rockiness is more important for oak. The possible reason is the range of sites oak occupies (Bončina et al., 2021); for instance, it grows in sites on carbonate with extremely high rockiness (>70 %), which are inappropriate for beech, but also in highly productive sites on non-carbonate with the complete absence of surface rockiness (Bončina et al., 2021).

Understanding the response of tree species to climatic variables is highly relevant in the context of climate change. In the DI growth models, the impact of temperature was positive in models of all observed tree species, which is in accordance with the broadly accepted statement about the impact of temperature on tree growth (Ryan, 2010). The

impact of precipitation on the growth rate of trees was either negative (fir, beech and oak) or positive (spruce and pine). [Gauli et al. \(2022\)](#) reported that Norway spruce growth can be stimulated mainly by the increase in precipitation in May, June and July. Mean annual precipitation was a stronger predictor of tree growth for fir, pine and especially oak than mean annual temperature. The annual amount of precipitation correlates significantly with elevation (Pearson coefficient = 0.85). The results illustrate that the growth rate of fir, beech and oak decreases along an elevational gradient, while the response of spruce indicates that mid elevations are optimal for its growth, and higher altitudes limit its growth owing to the low average temperatures ([Schelhaas et al., 2018](#)).

#### 4.3. Study limitations

Some limitations of the study need to be mentioned. The conditional and marginal  $R^2$  are not very high. The explained variability amounted to 27 % and 34–42 % for stand and tree growth, respectively. This is still in range with other studies; for instance, [Schelhaas et al. \(2018\)](#) presented diameter increment models for 20 tree species/species groups based on diameter increment observations of over 2.3 million trees. The explained variance ranged from 10 % to 53 % depending on the species. One of the reasons for the low marginal  $R^2$  is the analysis of dominant trees. When all trees were included, the marginal  $R^2$  increased considerably (results not shown). The next limitation is related to the accuracy of the soil map ([Vrščaj et al., 2017](#)). A higher spatial resolution and more accurate delineation of pedocartographic units could considerably improve stand and tree growth models. Another study limitation is the use of 10-year increment data and the influential factors measured at the beginning of the inventory period. Although this is a common approach in growth studies based on national forest inventory data (e.g. [Schelhaas et al., 2018](#); [Trifković et al., 2022](#)), we should be aware that the stand structure may change considerably over a decade, especially due to harvesting or natural disturbances, which were not considered in our study. Another limitation of the study is that we used long-term climatic data. Therefore, extreme weather events (e.g. extreme droughts) and climate anomalies were not directly considered in the study. However, these weaknesses are partly compensated for by a large-data set and site diversity. We showed differences in tree and stand growth among soil classes; however, more studies are needed to understand the complex interactions between soil, climatic and other variables influencing stand and tree growth, which can be specific for a single soil class.

#### 4.4. Conclusion

In the study we quantified the differences among soil classes in stand and tree growth for five common European tree species. In studying the impact of soil on forest productivity, we limited the examination to the stand basal area increment and diameter increment of dominant trees. The study showed that relatively broad soil classes explain a substantial part of the variability of stand and tree growth and are a better predictor of productivity than climate when productivity is studied on a large scale. The determined stand and tree species production rate intervals of –28 % to +5 % and –47 % to +14 % of that on the reference soil unit (Dystric Cambisols), respectively, suggest varying production capacities and a differential future response. The finding that tree species generally exhibited the highest and the lowest growth rates on different soil units should spur forest managers to pay greater attention to soil properties in determining optimal tree species compositions and stand structures, or when transforming altered forests towards near natural compositions. Soil seems to have been neglected when studying the impact of climate change on forest ecosystems. Climate variables should be interrelated with soil and many other tree, stand, site and environmental variables to understand their complex impact on forest ecosystems.

#### Declaration of Competing Interest

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

#### Data availability

The authors do not have permission to share data.

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#### Appendix A

See [Table A1](#).

**Table A1**  
Number of plots and trees for BAI and DI modelling included in the analyses.

Soil Unit	BAI modelling		DI modelling									
			Spruce		Fir		Pine		Beech		Oak	
	Plots	Trees	Plots	Trees	Plots	Trees	Plots	Trees	Plots	Trees	Plots	Trees
CMd	16,605		9,752	26,313	1,850	3,502	3,054	6,892	6,262	14,277	2,922	5,386
CMe	7,410		2,772	6,495	636	1,242	892	1,956	3,748	9,354	1,851	3,470
CMx	16,443		6,202	15,371	4,736	12,058	668	1,424	8,878	23,251	2,014	4,106
FLc	120		28	70			26	62				
FLe	205		82	182					59	115	49	85
GLd	509		53	111							38	92
GLe	215		54	128			39	110			43	81
HSf	57		55	194								
LPd	2,323		1,308	3,531	474	882	169	346	1,121	2,731	232	470
LPe	102		27	76					57	153		
LPk	21,408		10,728	26,772	5,616	11,590	923	1,998	12,333	32,253	856	1,566
LPm	3,089		1,844	4,973	207	306	155	307	1,419	3,417	290	539
LPq	33											
LVh	2,172		728	1,550	142	299	353	843	441	951	800	1,698
PLd	1,035		238	481	27	38	457	1,056	311	643	356	721
PLe	651		172	306			254	606	203	394	247	526

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