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Influence of soil properties on silver fir (*Abies alba* Mill.) growth in the Dinaric Mountains



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ABSTRACT

Tree growth can be influenced by a wide variety of complex interacting factors. The contribution of soil to site productivity is confounded by the interactions between other site factors and silviculture. The contribution of soil properties to the growth of silver fir (*Abies alba* Mill.) was studied in the Dinaric Mountains, which are characterised by abundant sinkholes and limestone outcrops, resulting in diverse micro topography and different soil development at small spatial scales. Basal area increment and height growth data were estimated based on stem analysis of dominant silver fir trees ($n = 65$) on a $50 \text{ m} \times 50 \text{ m}$ sampling grid, and competition intensity was determined. The soil development around each tree was defined using morphological properties of the genetic horizons based on soil probing ($n = 65 \times 12$). In the study area, the chemical and physical soil characteristics (based on 21 soil profiles) were favourable for plant growth. Soil parameters e.g. soil depth, thickness of genetic soil horizons, share of soil types around each tree and soil associations were the factors controlling tree growth. Tree age and competition intensity were also influential factors in the case of height and radial tree growth respectively. Positive effects on height and radial growth were confirmed also for available water capacity of soil and location of tree in slope position (in the sinkhole, out of the sinkhole). The decrease in specific basal area increment with increasing competition intensity was most evident for trees growing on leached soils. The coefficient of determination and the statistical significance of the relationship between height growth and soil association over the last 100 years emphasised the cumulative effect of the soil condition on tree height growth.

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1. Introduction

While tree growth can be influenced by a wide variety of complex interacting factors, it is widely accepted that climate, soil conditions and competition for resources determine species composition and tree growth (Assmann, 1970). In both forest ecology (Coomes and Allen, 2007) and sustainable forest management (Pretzsch, 2009), an understanding of the variation in tree growth is important. Interactions between tree growth, climate and soil conditions (site characteristics) are usually expressed using a height–age site index (the mean height of the 100 largest-diameter trees per hectare at a given age). Site index presents a measurable surrogate of site productivity and can be used to determine site productivity with respect to, for example, wood production. Numerous studies have focused on predicting site productivity from climate, geologic, topographic and soil factors (Wang, 1995;

Ung et al., 2001; Palahí et al., 2004; Seynave et al., 2005; Jensen et al., 2008) or used indicator plants for site quality assessment and classification (La Roi et al., 1988; Strong et al., 1991; Bergès et al., 2006).

The contribution of soil to site productivity is confounded by the interactions between other site factors and silviculture, which influences the competition between trees (Schoenholtz et al., 2000). However, in contrast to the site index concept, individual tree growth models (Monserud, 1975; Wykoff et al., 1982; Pukkala, 1989; Monserud and Sterba, 1996; Pretzsch et al., 2002) can successfully account for unique competition situations and site characteristics (Hasenauer, 2006). In the determination of site index, forest stands should be pure, even-aged and fully stocked, with homogenous soil conditions (Sturtevant and Seagle, 2004; Hasenauer, 2006). Individual tree growth models, however, use individual trees as the basic unit for simulating tree growth. This allows flexibility in the forest management of uneven-aged and mixed species forests and in studying the soil–growth relationship in forest ecosystems growing on heterogeneous sites.

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Many studies have focused on how the growth of individual trees responds to different competition intensities (Mailly et al., 2003; Coomes and Allen, 2007; Stadt et al., 2007; Puettmann et al., 2009); however, less attention has been given to the effect of short-range soil variability on tree growth (Meredieu et al., 1996). Several studies have investigated the variation in forest soil properties at very detailed spatial scales (Phillips and Marion, 2005; Scharenbroch and Bockheim, 2007) and revealed that soil variability can be high, even over short distances and in small areas. Nevertheless, on many occasions, site characteristics, including soil properties, have been assumed to be homogenous in space (Fajardo and McIntire, 2007).

There are many different chemical, physical and biological soil parameters. Among these, the following indicators of forest soil quality have often been used: organic matter and the C/N ratio (e.g., Edmonds and Chappell, 1994; Lavoie et al., 2007; Laubhann et al., 2009), soil texture (e.g., Bravo and Montero, 2001; Jennifer and Gower, 2006; Martin and Gower, 2006), nutrient status (e.g., Wang, 1995; Wang and Klinka, 1996; Pinto et al., 2008), cation exchange capacity (Jokela et al., 1988; Bravo and Montero, 2001), pH value (e.g., Pinto et al., 2008; Viet et al., 2013) and humus forms (e.g., Kölli, 2002; Bergès et al., 2005; Ponge and Chevalier, 2006). However, the applicability of these properties is often limited by the cost and time needed for the assessment (Schoenholtz et al., 2000). Frequently, especially in dry areas and in forests growing on shallow soils, water stored in the soil can be the overriding soil quality parameter (Katzensteiner, 2000; Witty et al., 2003; Vilhar et al., 2005).

Silver fir growth in relation to different environmental factors had already been studied in the past. Becker (1982) showed that silver fir stand productivity is positively related to rainfall, negatively related to temperature and poorly correlated with site nutritional quality. This was also reported by Pinto et al. (2007) for the radial growth. Lebourgeois (2007), Lebourgeois et al. (2010) reported about sensitivity of shade tolerant silver fir species to frost and drought. Nitrogen supply (expressed as C/N ratio) was correlated with radial growth only at the beginning of the 20th century while the positive effect of nitrogen is disappearing today due to eutrophication during 20th century. However, (Pinto et al., 2008) found nutritional resources as the factor determining silver fir site index. This study also revealed that radial growth of silver fir is not determined by the site's level of exchangeable bases (Pinto et al., 2007). Piskernik (1985), Pinto et al. (2007) showed that radial growth of silver fir is strongly positively correlated with available soil water. Variables related to water availability showed a positive effect also on height growth (site index), but only when water is a height growth limiting factor (lower precipitation and higher temperature) (Pinto et al., 2008). They also found negative effect of exchangeable aluminium in the B horizon on ring width. Study of growth and yield characteristics of silver fir in Slovenia (Kadunc, 2010) revealed that site index of silver fir is positively correlated with concave topography and east aspect. Significant effect of elevation on silver fir growth has been confirmed by Keller (1978), Pinto et al. (2007, 2008), Kadunc (2010). Silver fir is also very sensitive to SO₂ emissions, resulting in significant reduction of tree ring widths (Elling et al., 2009).

All these studies were carried out in a larger area or on wide ecological amplitude or soil conditions. To better understand the contribution of soil properties to site quality and consequently tree growth, a small spatial scale (16 ha) was selected in our study. Studied area is located in a region of the Dinaric Mountains, with silver fir and European beech as the main tree species. Limestone is the main parent material and, with its specific weathering and landforms, generating the variability in soil development. The soil characteristics of an individual tree were estimated using the concept of a "plant's zone of influence" (Casper et al., 2003), and the site area was reduced to the level of individual trees. This approach allows unique competition and unique soil properties to be assessed.

In our study, we sought to find a cost- and time-effective indicator of forest soil properties for areas with similar environmental conditions, i.e., climate and geology. To achieve this objective, we set the following goals: (1) determine whether the height growth dynamics of trees depend on soil horizon development, (2) examine whether the influence of the soil is cumulative and increases with time and (3) determine whether the effect of the soil is different for different competition intensities and, consequently, consider both the competition and soil in the evaluation of basal area increment.

2. Methods

2.1. Study area

This study was conducted in the Dinaric Mountains in south-west Slovenia (lon. 14°26'E, lat. 45°35'N, 850 m a.s.l.). The karst geology of the site is characterised by abundant sinkholes and limestone outcrops, resulting in diverse micro topography. The soils, predominantly Litosols, Leptosols, Cambisols and Luvisols, are derived from the limestone parent material, and the soil depth can vary between 0 and 300 cm or more, depending on the micro topographic position. Precipitation is evenly distributed throughout the year, with a mean annual precipitation of 2150 mm (source: www.meteo.si). The mean temperature averages 6.5 °C, and late spring and early autumn frosts are common (FMP, 2004). The prevalent plant community is dinaric silver fir – European beech forest (*Omphalodo-Fagetum*). The main tree species are silver fir (*Abies alba* Mill.), Norway spruce (*Picea abies* Karst.) and European beech (*Fagus sylvatica* L.). Sycamore (*Acer pseudoplatanus* L.) and Elm (*Ulmus glabra* Huds.) are also present. The tree species composition (Table 1) is a result of acceleration of silver fir until 1964, when forest management strategies changed to become more natural-based (Gašperšič, 1967). Most of the stands are managed using a selection (single-tree or group) or irregular shelterwood system, which leads to considerable within-stand variation in tree age and structure.

2.2. Experimental design

2.2.1. Plot establishment

Dominant silver fir trees were located by establishing circular sampling plots on a 50 m × 50 m sampling grid (Fig. 1). Trees with a diameter at breast height (DBH) larger than 10 cm were mea-

Table 1
Summary information and interval estimates at a 95% confidence level for 65 sampling plots.

Tree species Units	DBH cm	Stand density Stems ha ⁻¹	Stand basal area m ² ha ⁻¹	Stand volume m ³ ha ⁻¹
<i>Abies alba</i>	45.9 ± 14.1	206.7 ± 13.8	33.4 ± 2.0	548.7 ± 37.3
<i>Picea abies</i>	34.7 ± 3.3	6.7 ± 3.3	0.7 ± 0.3	12.3 ± 6.2
<i>Fagus sylvatica</i>	23.3 ± 23.2	145.2 ± 22.8	5.4 ± 0.9	67.3 ± 13.2
<i>Acer pseudoplatanus</i>	40.1 ± 2.8	7.2 ± 2.7	0.9 ± 0.3	12.9 ± 4.4
<i>Ulmus glabra</i>	31.2 ± 0.8	1.2 ± 0.8	0.1 ± 0.1	1.2 ± 0.8
Total	38.2 ± 24.1	367.1 ± 23.7	40.5 ± 2.0	642.4 ± 32.2

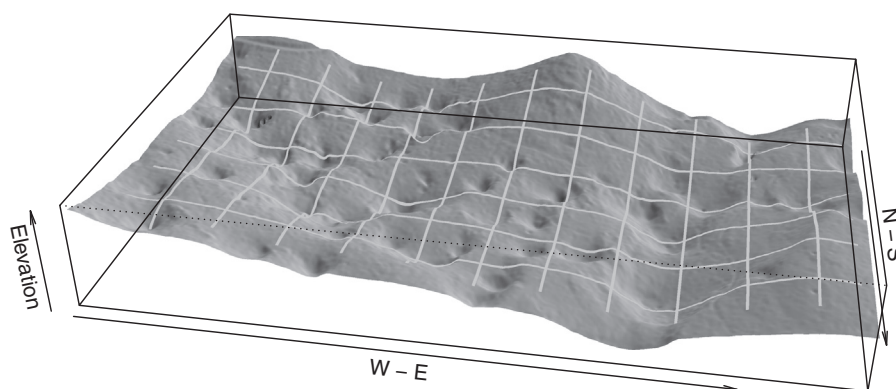


Fig. 1. LiDAR-based digital elevation model of the study area (16 ha). Grey lines indicate a 50 m × 50 m sampling grid from which dominant silver fir trees were selected and soil properties were estimated for studying soil–growth relationships. Elevation ranges from 820 to 880 m a.s.l.

sured in each 500 m² sample plot. In each plot, the following data were recorded for each sample tree: species, DBH, distance and azimuth from the plot centre. Trees were then ordered according to decreasing DBH, based on dominant height definition (the average height of the 100 largest-diameter trees per hectare at the time of measurement). Every third tree (mean dominant height) was selected for detailed stem analysis; a total of 65 trees were harvested.

The stem of each tree was then divided into 15–20 sections (depending on the tree height). The base of each section was sampled at heights of 0.15 m (stump) and 1.3 m (DBH) and at 4.1-m intervals to a diameter of 30 cm. The tree top, at a diameter below 30 cm, was divided into 1-m sections. Disks were removed (a total of 992) from the base of each section to conduct detailed stem analysis on each subject tree.

2.2.2. Collection of the soil samples and description of the soil properties

Prior to harvesting the selected silver firs, detailed soil probing was performed around each tree. Soils were probed 12 times (every 30° clockwise) at different distances from the stem, with respect to tree dimension (Schenk and Jackson, 2002; Brunner et al., 2004; Göttlicher et al., 2008). In total, 780 soil probes were collected at distances between 4 and 8 m from the stem. The eluvial E and illuvial B_t horizons were identified based on a comparison of texture, structure and colour with the above and below horizons. The cambic B_w horizons were characterised by colour differentiation from the

A and E horizons (FAO, 2006). The soil development stages (profile O–C, Leptosol – profile O–A–C, Cambisol – profile O–A–B_w–C, Luvisol – profile O–A–E–B_t–C; Table 2) were defined using the morphological properties of the genetic horizons. The content of rock fragments were estimated in the field using strike tests with a metal rod. To analyse the effect of topography on tree growth, we classified the landforms around each selected tree according to the FAO (2006) classification of slope positions in undulating and mountainous terrain. Trees located in lower slope and bottom of sinkholes were classified into one group (in the sinkhole), other trees were grouped together (out of the sinkhole).

In addition, information about soil chemical and physical properties was obtained. Based on the results of the soil probing conducted around each selected silver fir tree, 21 typical soil profiles representing different soil profile development (pedogenetic soil types) were excavated. To describe the soil profile locations and evaluate the morphological and physical conditions of the soil samples, we followed the FAO methodology (FAO, 2006; IUSS Working Group WRB, 2006). Soil samples were collected from each soil genetic horizon.

2.2.3. Measurement of the competition intensity

The measurements used to determine the competition intensity were collected after cutting and removing the disks from the selected dominant silver fir trees. Circular plots with radii of 25.23 m (area = 2000 m²) were established, with the stump of each sample silver fir in the centre of a plot. Within each plot, the DBH of

Table 2

Chemical properties of the soil horizons. Twenty-one soil profiles were classified into three soil development stages (SDS) with respect to the properties of the soil horizons. Averages and ranges (in brackets) are presented.

SDS Units	Horizon	Thickness cm	pH	C _{org} %	N _{tot} %	C _{org} /N _{tot}	CEC cmol ₍₊₎ kg ⁻¹	BS %
Leptosols (n = 5)	O _l	2.8 (1.0–4.0)	–	50.7 (47.5–52.0)	1.2 (1.1–1.3)	41.9 (38.6–47.6)	–	–
	O _f	1.4 (1.0–2.0)	5.3 (4.8–5.9)	45.5 (33.9–51.3)	1.4 (1.2–1.7)	32.9 (28.2–41.8)	–	–
	O _h	4.7 (3.0–6.0)	4.9 (3.9–5.7)	39.1 (23.5–49.6)	1.7 (1.0–2.3)	23.6 (21.9–24.6)	–	–
	A	16.2 (3.0–40.0)	6.5 (6.2–6.9)	15.9 (7.7–20.0)	1.0 (0.5–1.0)	18.6 (16.3–23.3)	137.0 (67.6–219.8)	99.9 (99.8 – 100.0)
Cambisols (n = 9)	O _l	2.9 (1.0–7.0)	–	48.2 (43.4–50.8)	1.2 (1.1–1.4)	40.4 (33.5–46.1)	–	–
	O _f	1.4 (1.0–2.0)	5.2 (4.9–5.9)	40.1 (32.6–45.6)	1.3 (1.0–1.7)	31.3 (25.1–37.0)	–	–
	O _h	7.0 (4.0–12.0)	5.3 (4.0–6.3)	24.2 (21.4–26.2)	1.3 (1.2–1.4)	18.1 (16.8–19.1)	–	–
	A	10.6 (2.0–37.0)	6.5 (4.7–6.9)	11.2 (8.6–13.3)	0.7 (0.5–0.8)	16.6 (13.6–20.6)	73.0 (26.8–108.5)	99.9 (99.8 – 100.0)
	B _w	33.4 (2.0–76.5)	6.9 (4.6–7.1)	3.6 (0.5–6.3)	0.3 (0.1–0.5)	12.5 (5.4–17.9)	53.8 (13.1–84.3)	99.1 (96.0–99.1)
Luvisols (n = 7)	O _l	1.6 (1.0–2.0)	–	49.1 (47.5–50.4)	1.2 (1.1–1.3)	40.3 (36.5–43.6)	–	–
	O _f	1.0 (1.0–1.0)	5.2 (4.8–5.4)	41.4 (36.7–48.4)	1.3 (1.2–1.4)	30.7 (27.2–34.2)	–	–
	A	5.6 (2.0–16.0)	4.7 (4.4–5.1)	10.1 (6.2–15.2)	0.6 (0.4–0.8)	18.2 (16.2–21.1)	32.1 (19.2–42.6)	93.7 (88.6–98.7)
	E	21.1 (7.0–38.0)	4.9 (3.9–5.4)	2.7 (1.3–5.4)	0.2 (0.1–0.3)	16.6 (14.3–18.0)	14.8 (3.7–27.2)	69.1 (21.4–98.8)
	B _t	46.9 (13.0–117.0)	6.8 (4.2–7.3)	1.1 (0.5–2.4)	0.1 (0.1–0.2)	12.0 (6.7–17.0)	31.9 (18.7–43.3)	94.1 (74.9–99.8)

each tree stem (≥ 10 cm) was measured (Table 1). We considered the distance-dependent Hegyi competition index (Hegyi, 1974), which requires information about the distances between the subject and competitor trees, in addition to the competitor tree's DBH. Therefore, we also determined the horizontal distances between the silver fir trees and their potential competitors using a Vertex IV (Haglöf Sweden).

2.3. Laboratory work

2.3.1. Laboratory analysis of soil samples

Soil samples were air dried and passed through a 2 mm sieve. The fine earth fraction (< 2 mm) was retained for chemical and physical analyses. The following methods were used: the pH value (pH) was determined in calcium chloride following ISO 10,390 using an automatic pH-meter Metrohm Titrino; organic carbon (C_{org}) and total nitrogen (N_{tot}) contents were determined using dry combustion following ISO 10,694 and/or 13,878 on a Leco CNS-2000; carbonates were determined following ISO 10,693 using a Scheibler calcium-meter; and soil texture was determined following ISO 11,277 using the sedimentary method and pipette according to Köhn. The concentrations of the exchangeable basic cations (sodium, potassium, calcium and magnesium) and the exchangeable acid cations (iron, manganese, aluminium) were determined in a 0.1 mol L^{-1} barium chloride extract of the soil using atomic absorption/emission (Na, K) spectrometry. Free H^+ acidity was determined by measuring the pH of the barium chloride solution before and after extraction. Subsequently, the exchangeable acidity was calculated based on the sum of the acid cations and the free H^+ .

2.3.2. Detailed stem analysis

Stem disks were air dried for a minimum of 3 months before being prepared for tree-ring measurements. From each disk, a block was cut out from the centre, excluding the reaction wood. The bottom surface was sanded with progressively finer grades of sand paper. Tree ring widths were measured in two directions along the block, with a precision of 0.01 mm using ATRICS (Levanič, 2007) and the WinDendro software (Regent Instruments Inc.). Each ring width series was checked, corrected and dated both visually and using the PAST software. A standard arithmetic mean function was used to obtain the individual tree-ring width series.

2.4. Data analysis approach

Available water capacity (AWC), defined as difference between field capacity and permanent wilting point, was calculated per tree level using equation proposed by Teepe et al. (2003) for forest soil (Eq. (1)). AWC was first calculated at soil horizon level for each soil probe:

$$AWC_i = \beta_0 + \beta_1 \cdot BD + \beta_2 \cdot \text{Clay} + \beta_3 \cdot \text{Silt} \quad (1)$$

where BD means soil bulk density, Clay means clay content and Silt means silt content in the soil horizon i . Data were obtained from laboratory analysis of soil profiles; averages for different soil types (eg. Leptosol, Cambisol and Luvisols) (Table 2). Available water capacity per soil probe AWC' was calculated as a sum value of AWC_i by taking into account the horizon thickness and estimated content of rock fragments (S) (Eq. (2)):

$$AWC' = \sum_{i=1}^n (1 - S) \cdot AWC_i \quad (2)$$

Finally, available water capacity AWC per tree level was calculated as a mean value of AWC' . Bulk density (BD) was calculated using PTF, developed by Kobal et al. (2011) based on organic carbon content (C_{org}) (Eq. (3)):

$$BD = \beta_0 + \beta_1 \cdot C_{org} \quad (3)$$

A detailed stem analysis was performed using software that was written specifically for our study in the R programming language (R Development Core Team, 2013). The software enabled the past growth history of a tree stem to be reconstructed. We used the correction proposed by Carmean (1972) to estimate the height growth of each analysed tree. This method assumes that the annual height growth within a given stem section is constant and that crosscuts occurred in the middle of a given annual height growth. The height increments were calculated for the last 100 years. This time period was selected because of the long period of suppressed growth during which the trees had not reached a dominant canopy position.

The specific basal area increment (SBAI) of a subject tree was chosen as a measure of tree growth rather than the relative growth rate (RGR). Originally, "specific increment" was defined for volume growth (Bevilacqua, 2002), but we applied this concept to basal area growth. SBAI seems to be a more suitable measure for tree growth because growth is expressed per unit cambial length and does not consider the non-productive inner circle part (Bevilacqua, 2002; MacKinnon and MacLean, 2004). The SBAI for the last 5 years was calculated as:

$$SBAI_5 = \frac{BA_0 - BA_{-5}}{CIRC_{-5}} \quad (4)$$

where $SBAI_5$ is the specific basal area increment of the last 5 years, BA_0 is the current basal area of a tree, BA_{-5} is the basal area of a tree before the 5 years and $CIRC_{-5}$ is the circumference of a section at breast height before the 5 years and represents the length of the cambium (Eq. (4)).

As a measure of the competitive influence of neighbouring trees on a subject tree, we calculated the distance-dependent Hegyi competition index (Hegyi, 1974):

$$CI_i = \sum_{j=1}^n \frac{D_j/D_i}{DIST_{ij}} \quad (5)$$

where CI_i is the competition index for subject tree i , D_j is the DBH of the j th competitor, D_i is the DBH of the subject tree i , $DIST_{ij}$ is the distance between the subject tree i and the j th competitor and n is the total number of competitors (Eq. (5)). All species were pooled before calculating the Hegyi competition index. To determine an optimum search radius (maximum $DIST_{ij}$) and an optimum search DBH (minimum DBH_j) above which a tree was considered as a competitor, an optimisation procedure described by Miina and Pukkala (2000), Vanclay (2006) was used. We iteratively revised the relative search radius ($DIST_{ij}$) and relative optimum search DBH (DBH_j) until we reached a stable optimum (maximum) coefficient of determination $adj. R^2$ between the Hegyi competition index and the SBAI.

2.5. Statistical analysis and model selection

Multiple linear regressions were used to relate silver fir growth to corresponding soil attributes at single tree level, e.g. soil depth (minimum, mean and maximum value), mean thickness of soil horizons (A, B_w , B_t and E), share of the soil with different profile development (Fig. 4), soil associations (Fig. 3), modelled available water capacity (AWC) and location of tree in slope position (in sinkhole, out of sinkhole). Tree age and competition intensity were included as additional explanatory variables for height and radial growth of dominant silver fir trees, respectively. Models were compared using partial F -tests and Akaike's Information Criterion (AIC). To define groups of trees with similar soil conditions, we applied a cluster analysis (Ward clustering method, Manhattan distance) considering the mean thickness of the soil horizons around each individual tree. Based on the resulting dendrograms, three groups

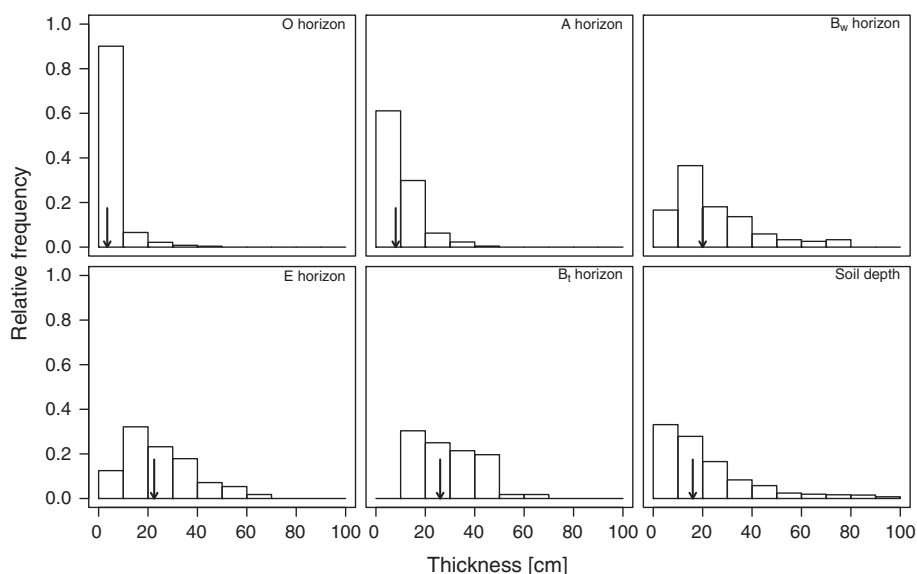


Fig. 2. Depth class distribution for the thickness of soil horizons in the investigated area. Black arrows indicate the median value. The bottom right histogram represents the distribution of the total soil depth.

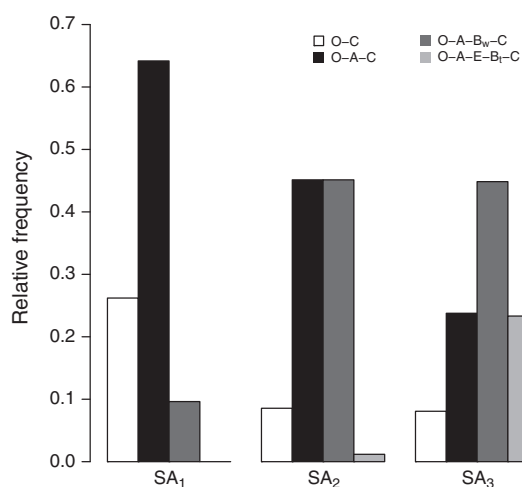


Fig. 3. Composition of soil associations (SA) according to soil development stages: SA₁ – shallow soils with mainly O–C and/or O–A–C horizons; SA₂ – shallow to moderately deep soils with O–A–C and/or O–A–B_w–C horizons; SA₃ – deeper and/or leached soils with mainly O–A–B_w–C and/or O–A–E–B_t–C horizons.

of trees with similar soil conditions were distinguished (Fig. 3). We used an analysis of covariance (ANCOVA) to detect differences in the SBAI between soil associations SA and landforms (grouping factor) while controlling for the effect of competition (a continuous covariate), which is considered a ‘nuisance’ parameter.

3. Results

3.1. Soil description

3.1.1. General soil characteristics

Soil probing ($n = 780$) around each tree revealed different development of soils in the studied area. Shallow soils with depths up to 20 cm were prevalent. Only organic O horizon on parent material was found in 13% of soil probing. Leptosol (profile O–A–C) were found in 44% of the soil probing. Deeper soils with well-developed cambic B_w horizon (Cambisol) or eluvial E horizon in combination

with the B_t horizon, (Luvisol) represented 36% and 7% of the soil cores, respectively. The latter, were most often found at the bottom of sinkholes. At least two different soil profile development were found per tree: in 18 cases two soil development stages; in 33 cases three soil development stages and in 14 cases four soil development stages (Fig. 4). The prevailing thickness of the O and A horizons were 0–5 and 0–10 cm, respectively (Fig. 2). The cambic, eluvial and illuvial horizons were up to 80 cm thick, with median values of 20 cm, 22 cm and 28 cm, respectively. Surface rock outcrops were estimated to be up to 30%.

In general, the soils were silty clay with negligible amounts of sand, neutral pH, high cation exchange capacity and high base saturation (Tables 2 and 3). In the A and B_w horizons of Leptosol and Cambisol, the base saturation (BS) was greater than 99%. Cation exchange capacity (CEC) was highest in the A horizons as a consequence of both high organic matter and high clay content. Eluvial–illuvial processes resulted in decreased pH, organic matter and clay content and base saturation in the A and E horizons of leached soils (Luvisols). Conversely, the highest amount of clay was measured in the B_t horizon. The C/N ratio in the mineral soil was favourable for N mineralisation because it was less than 20 in almost all cases (Table 2). In the organic horizons, the C/N ratio decreased with an increasing degree of decomposition from 41.8 in the litter O₁ to 18.3 in the humified O_h horizon (Table 2). Modelled available water content (see 2.4) ranged from 18 to 78 mm (mean 36 mm), from 25 to 81 mm (mean 53 mm) and 53 to 138 mm (mean 82 mm) in the case of Leptosol, Cambisol and Luvisol, respectively.

3.1.2. Soil clustering according to soil development around the subject trees

Soils with different development stages were found around each subject tree. Cluster analyses of soil properties around each subject tree (based on soil probes and soil profiles descriptions and analyses) suggested the formation of three groups of soil associations with similar properties. In the first soil association (henceforth SA₁), shallow soils with profile O–C (26%) and O–A–C horizons (64%) prevailed, while soils with B_w horizons represented less than 10% (Fig. 3). In the second association (SA₂), soils with profile O–A–C (45%) and O–A–B_w–C horizons (45%) prevailed, while soils with only O–C or with O–A–E–B_t–C horizons represented 9% and 1%, respectively. In the third soil association (SA₃),

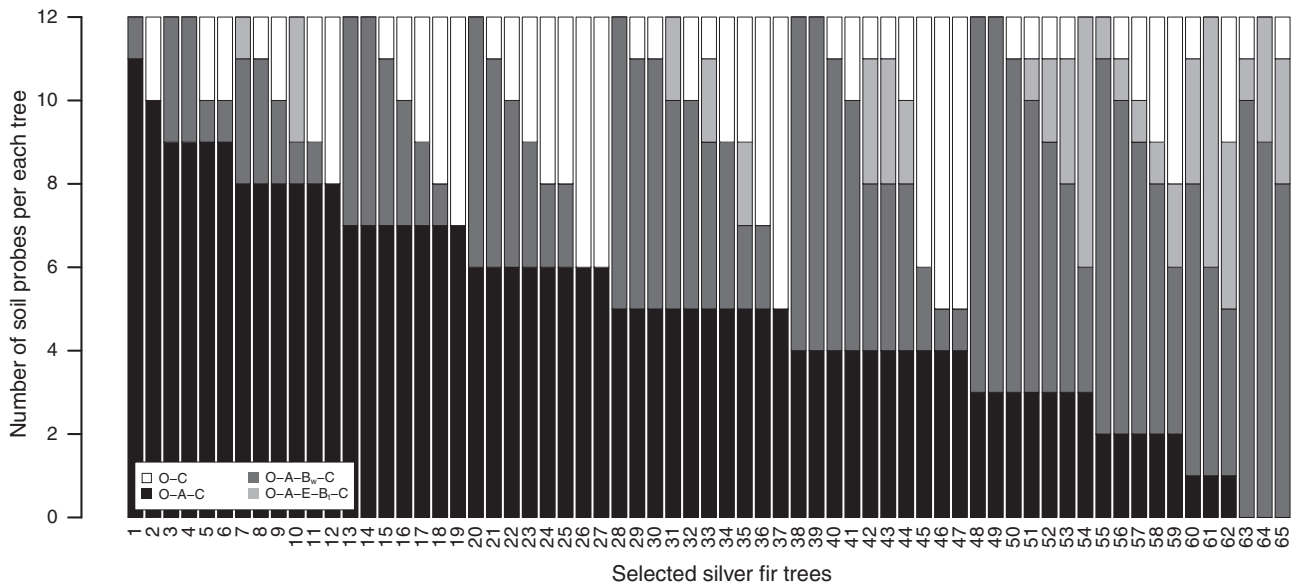


Fig. 4. Number of soil probes regarding soil development stage per tree level.

Table 3
Physical properties of the mineral soil horizons. Twenty-one soil profiles were classified into three soil development stages (SDS) with respect to the properties of the soil horizons. Averages and ranges (in brackets) are presented.

SDS Units	Horizon –	Sand %	Silt %	Clay %	BD g/cm ³
Leptosols	A	2.5 (0.9–2.8)	52.1 (44.5–61.8)	45.5 (33.9–53.7)	0.41 (0.22–0.86)
Cambisols	A	4.0 (1.9–18.4)	51.6 (42.8–60.7)	44.4 (35.9–54.6)	0.58 (0.29–0.86)
	B _w	3.4 (0.8–27.9)	52.5 (29.5–63.6)	44.1 (28.1–69.1)	1.10 (0.84–1.46)
Luvisols	A	4.0 (2.2–6.6)	59.5 (51.5–67.3)	36.5 (27.5–42.6)	0.66 (0.43–0.91)
	E	3.1 (0.5–6.1)	67.9 (58.0–76.0)	29.0 (17.9–38.6)	1.13 (0.88–1.34)
	B _t	3.5 (1.9–11.3)	47.6 (11.7–63.4)	48.9 (31.8–86.0)	1.34 (1.14–1.46)

soils with well-developed B_w horizons (45%) and leached soils with O–A–E–B_t–C horizons (23%) prevailed (Fig. 3).

3.2. Tree growth in relation to soil properties

3.2.1. General information on the subject trees

Dominant silver firs were between 132 and 209 years old (Table 4). The DBH ranged from 41.0 to 72.0 cm, with a mean value of 59 cm. The average height was 34.0 m, and the mean volume was 4.8 m³.

3.2.2. Tree height increment in relation to soil properties

The height increment of silver firs over the last 100 years ranged from 7.4 to 27.7 m. Tree age explained 13% of this variation (M1, Table 5), whereas adding the minimum soil depth around each tree as an additional explanatory variable of height increment did not improve the prediction (M2). The mean (M3) or maximum (M4) soil depth, rather than minimum depth, explained more variability in height increment, but this variable still explained less than 30% of the variation. Stoniness and competition were not statistically significant variables.

The inclusion of individual horizon thickness instead of soil depth as an explanatory variable improved previous models ($\Delta AIC = 22.1$, $p < 0.001$). The thickness of A horizon had a negative effect on height increment (M5), while other horizons' influence was positive, in particular a strong positive was the effect of eluvial E and illuvial B_t horizons, characterised for well developed, deep soils (M6, M8). Similarly higher share of more developed soils (Cambisol and Luvisol) also influenced positively on height growth

Table 4
Summary information about 65 analysed silver fir trees.

Value Unit	Age Years	DBH cm	Height m	Volume m ³
Min	132	41	25.2	1.6
1st Quartile	166	55	32.2	3.9
Median	176	59	34.1	4.8
Mean	178	59	34.0	4.8
3rd Quartile	192	63	36.2	5.6
Max	209	72	39.7	8.1

(M10). Positive effect on height growth was also confirmed for the amount of available water, which was mainly a function of soil depth (M11). Cambic horizon B_w had positive effect (M7), but did not improve the model (M9). The influence of the sinkhole is considered in the model 12; trees growing at the bottom of sinkholes were higher for 4.28 m in 100 year. The combination of AWC and location of trees in slope position (sinkhole) also had positive influence on height growth (M13). The prediction of the height increment over the last 100 years was further improved ($\Delta AIC = 9.6$, $p < 0.001$) by considering soil associations in the model (M9). Effect of all available soil variables on height growth are presented in model M14. Statistically significant influence had following variables: tree age, mean thickness of A horizon, share of Luvisol and location of trees in slope position (M15).

3.2.3. Specific basal area increment in relation to soil properties

The SBAI for the last 5 years ranged from 0.097 to 1.528 dm² m⁻¹, and more than half of it was explained by the competition intensity.

Table 5

Results of regressions between height increment over the last 100 years, tree age and soil characteristics. An asterisk (*) indicates that the variable was not statistically significant in the model.

Name	Model	SE	Adjusted R ²	AIC
M1	$\Delta H_{100} = 36.3 - 0.10 \cdot \text{age}$	4.09	0.13	337.6
M2	$\Delta H_{100} = 33.2 - 0.09 \cdot \text{age} + 0.19 \cdot \text{depth}_{\min}^*$	4.07	0.14	338.1
M3	$\Delta H_{100} = 29.9 - 0.08 \cdot \text{age} + 0.17 \cdot \text{depth}_{\text{mean}}^*$	3.72	0.28	327.4
M4	$\Delta H_{100} = 29.3 - 0.08 \cdot \text{age} + 0.08 \cdot \text{depth}_{\max}^*$	3.76	0.26	328.6
M5	$\Delta H_{100} = 43.3 - 0.10 \cdot \text{age} - 0.58 \cdot A$	3.40	0.40	316.7
M6	$\Delta H_{100} = 29.9 - 0.07 \cdot \text{age} + 0.58 \cdot B_t$	3.42	0.39	317.6
M7	$\Delta H_{100} = 35.1 - 0.10 \cdot \text{age} + 0.18 \cdot B_w$	3.87	0.22	332.2
M8	$\Delta H_{100} = 30.6 - 0.07 \cdot \text{age} + 0.69 \cdot E$	3.36	0.41	315.5
M9	$\Delta H_{100} = 30.8 - 0.07 \cdot \text{age} + 4.31 \cdot SA_2 + 8.44 \cdot SA_3$	2.82	0.59	295.6
M10	$\Delta H_{100} = 26.4 - 0.06 \cdot \text{age} + 0.20 \cdot \text{Lpt}^* + 0.05 \cdot \text{Camb} + 0.20 \cdot \text{Luv}$	3.32	0.43	315.8
M11	$\Delta H_{100} = 31.1 - 0.08 \cdot \text{age} + 0.09 \cdot \text{AWC}$	3.62	0.32	324.3
M12	$\Delta H_{100} = 35.6 - 0.10 \cdot \text{age} + 4.28 \cdot \text{Sink}$	3.78	0.26	329.3
M13	$\Delta H_{100} = 31.5 - 0.09 \cdot \text{age} + 0.05 \cdot \text{AWC} + 2.7 \cdot \text{Sink}$	3.69	0.29	327.5
M14	$\Delta H_{100} = 37.1 - 0.09 \cdot \text{age} - 0.48 \cdot A - 0.03 \cdot B_w^* - 0.17 \cdot B_t^* + 0.019 \cdot E^* + 0.02 \cdot \text{Lpt}^* + 0.00 \cdot \text{Camb}^* + 0.11 \cdot \text{Luv}^* + 0.02 \cdot \text{AWC}^* + 1.34 \cdot \text{Sink}^*$	3.14	0.49	314.4
M15	$\Delta H_{100} = 37.1 - 0.08 \cdot \text{age} - 0.41 \cdot A + 0.11 \cdot \text{Luv} + 1.7 \cdot \text{Sink}$	3.01	0.53	314.4

The soil depth for each tree, as minimum, mean and maximum depth among the 12 soil probes, did not statistically improve the model (M17, M18, M19; Table 6). Including the thickness of soil horizons as an explanatory variable in the model resulted in a statistically significant ($p < 0.05$) improvement (M20, M21, M23) except for the cambic B_w horizon (M22). The correlation between basal area increment and the thickness of the B_t , E and B_w horizons was positive, whereas competition intensity had a negative impact on tree growth in all analysed models (Table 6). As in the case of height increment, thickness of A horizon had negative influence on basal area increment (M20). As expected, the amount of available water content influenced positively (M27). Silver fir trees growth locations in slope position (e.g. in or outside sinkholes) improved basal area increment prediction (M28); Combination of both AWC and trees growth locations in slope position in model M30 was not significant. Also, the effect of competition differed among growth locations of silver firs in slope positions (M29).

Most of the variability (66%) in the SBAI was explained by the nested model (M25), in which the effect of competition intensity on tree growth was analysed separately between different soil associations. A comparison between the nested model (M25) and previous models (Table 6) using partial F -tests suggested that the nested model was significantly better ($p < 0.05$). There were no significant differences between SA_1 and SA_2 ; however, the SBAI of

trees was higher in SA_2 than it was in the first soil association, SA_1 (Fig. 5). The intercept and the slope of the regression line of SA_3 differed from first two soil associations (i.e., SA_1 , SA_2). A similar amount of variability of radial growth (65%) was explained using combination of competition intensity, mean thickness of A and B_w horizons, share of Leptosol and tree location in slope position (M32).

3.2.4. The cumulative effect of soil properties on tree height growth

Based on the results of the detailed stem analysis, the height increment for the last 100 years was calculated for one-year intervals (Fig. 6). In general, differences in the height increment among the three soil associations increased with a lengthening of the observation period, i.e., from 1 to 100 years. The largest differences appeared when the height increment was considered over the last 86 years (from the year 1921 to the year 2007); soil associations explained more than 62% of the height increment variability (Fig. 6). The statistical significance of the differences in height increments between the soil associations increased with an increasing observation period. The difference in the annual height increment was statistically significant between trees growing on SA_1 and SA_3 . The differences in the cumulative height increment between trees growing on SA_1 and SA_2 became statistically significant after approximately 40 years (Fig. 7).

Table 6

Results of the regressions between the SBAI over the last 5 years, competition and soil characteristics. An asterisk (*) indicates that the variable was not statistically significant in the model.

Name	Model	SE	Adjusted R ²	AIC
M16	$SBAI_5 = 2.08 - 0.75 \cdot CI$	0.26	0.55	12.3
M17	$SBAI_5 = 1.99 - 0.75 \cdot CI + 0.009 \cdot \text{depth}_{\min}^*$	0.26	0.55	13.3
M18	$SBAI_5 = 1.92 - 0.74 \cdot CI + 0.005 \cdot \text{depth}_{\text{mean}}^*$	0.26	0.56	11.8
M19	$SBAI_5 = 1.91 - 0.73 \cdot CI + 0.002 \cdot \text{depth}_{\max}^*$	0.26	0.56	11.9
M20	$SBAI_5 = 2.21 - 0.72 \cdot CI - 0.018 \cdot A$	0.25	0.57	9.8
M21	$SBAI_5 = 1.85 - 0.66 \cdot CI + 0.024 \cdot B_t$	0.25	0.59	7.6
M22	$SBAI_5 = 2.05 - 0.76 \cdot CI + 0.004 \cdot B_w$	0.26	0.55	13.4
M23	$SBAI_5 = 1.86 - 0.66 \cdot CI + 0.025 \cdot E$	0.25	0.59	7.9
M24	$SBAI_5 = 1.92 - 0.67 \cdot CI + 0.15 \cdot SA_2 + 0.30 \cdot SA_3$	0.24	0.62	4.0
M25	$SA_1: SBAI_5 = 1.46 - 0.51 \cdot CI$ $SA_2: SBAI_5 = 1.59 - 0.50 \cdot CI$ $SA_3: SBAI_5 = 2.70 - 1.04 \cdot CI$	0.22	0.66	-1.7
M26	$SBAI_5 = 2.16 - 0.68 \cdot CI - 0.005 \cdot \text{Lpt} - 0.001 \cdot \text{Camb}^* + 0.004 \cdot \text{Luv}^*$	0.24	0.61	6.8
M27	$SBAI_5 = 1.97 - 0.74 \cdot CI + 0.003 \cdot \text{AWC}$	0.25	0.57	10.5
M28	$SBAI_5 = 1.93 - 0.69 \cdot CI + 0.22 \cdot \text{Sink}$	0.25	0.58	8.5
M29	In the sinkhole: $SBAI_5 = 1.79 - 0.62 \cdot CI$ Out of the sinkhole: $SBAI_5 = 3.12 - 1.28 \cdot CI$	0.24	0.61	4.9
M30	$SBAI_5 = 1.91 - 0.70 \cdot CI + 0.002 \cdot \text{AWC}^* + 0.17 \cdot \text{Sink}^*$	0.25	0.58	9.7
M31	$SBAI_5 = 2.53 - 0.62 \cdot CI - 0.022 \cdot A - 0.017 \cdot B_w - 0.005 \cdot B_t^* - 0.02 \cdot E^* - 0.008 \cdot \text{Lpt} - 0.003 \cdot \text{Camb}^* - 0.003 \cdot \text{Luv}^* + 0.004 \cdot \text{AWC}^* + 0.24 \cdot \text{Sink}$	0.23	0.64	6.7
M32	$SBAI_5 = 2.33 - 0.62 \cdot CI - 0.016 \cdot A - 0.014 \cdot B_w - 0.006 \cdot \text{Lpt} + 0.23 \cdot \text{Sink}$	0.23	0.65	0.1

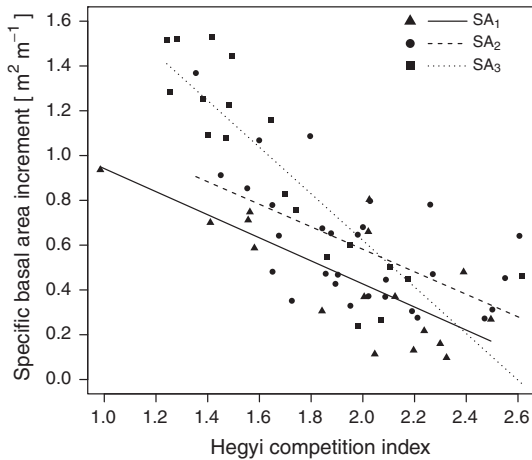


Fig. 5. The nested model for the SBAI of silver fir between soil associations.

4. Discussion

Recently, individual tree growth models have become a commonly accepted tool for sustainable forest management (Hasenauer, 2006; Pretzsch, 2009). These models perform well in uneven-aged, mixed forest stands and in pure, even-aged forests and forest plantations (Trasobares et al., 2004; Hasenauer, 2006). Because of their flexibility, individual tree growth models can be a useful support tool in soil quality assessment and forest ecology research.

A direct relationship between soil properties and tree growth was achieved using a concept called “plant’s zone of influence” (Casper et al., 2003; Berger et al., 2004). Using this concept, the area where soil conditions were assessed with detailed soil probing was reduced to the level of individual subject trees. Because of the significant correlation between the above-ground and below-ground size of trees (Schenk and Jackson, 2002), the soil probing was not performed at the same distance for all trees, but it was adjusted to each individual tree according to its dimensions. In our case, a radius of 4–8 m around each tree was used throughout the study. Other authors have reported the presence of fine roots at

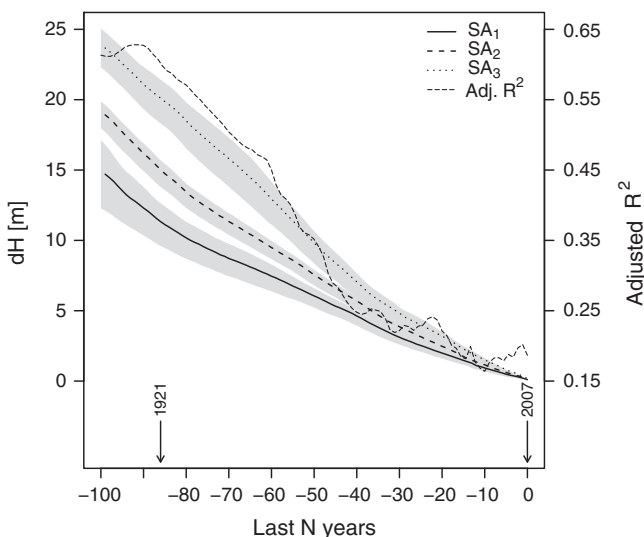


Fig. 6. Height increment over the last 100 years, derived from a detailed stem analysis among soil associations (SA). The grey shade indicates the 95% confidence interval. The thin dashed line represents the adjusted coefficient of determination, which was highest for the cumulative height increment over the last 86 years.

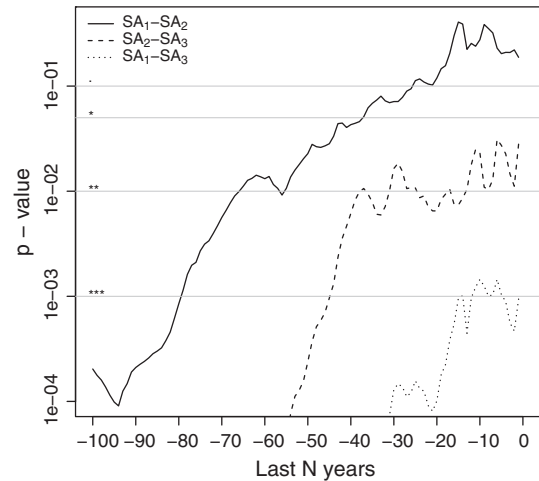


Fig. 7. Statistical significance of the differences among three soil associations (SA) over an increase in the length of the observation period.

similar distances, which are most important in the uptake of resources (Casper and Jackson, 1997; Brunner et al., 2004; Göttlicher et al., 2008). In addition, soil samples were frequently collected at similar distances from a stem (Johansson, 1999; Bergès et al., 2005).

The chemical and physical characteristics based on the analyses of 21 soil profiles were favourable for plant growth (pH, texture, cation exchange capacity) and were similar for soils with O–A–C horizons (Leptosols) and O–A–B_w–C horizons (Cambisols). Homogeneity of the chemical properties was expected due to similar parent material, climate conditions and tree species composition, which could explain the chemical properties of soils, especially of undisturbed, naturally developed horizons in forest soils. There were slightly less favourable parameters in leached soils with O–A–E–B_t–C horizons (Luvisols), especially the lower pH and cation exchange capacity in upper horizons. In addition to concentration, soil depth dependent total nutrient content and water stock, as well as a combination of concentration, bulk density and horizon thickness, could influence plant growth (Salifu et al., 1999; Tamminen and Starr, 1994).

Detailed soil probing revealed variations in the soil horizon development, mainly as a consequence of diverse micro topography and specific limestone weathering (Furlani et al., 2009), which is well known for the Dinaric Mountains. To explain the relationship between dominant silver fir growth and site characteristics 32 models were calculated and are presented in Tables 5 and 6. Tree age explained 13% of the silver fir height growth variability (M1). Unexpectedly, total soil depth (M2, M3, M4) explains less variability in height growth than thickness of individual soil horizons (M5, M6, M8). The specific soil development on limestone parent material and diverse topography confounded the effect of soil depth. Furthermore our results and field observations indicate that soil with high depth developed not only in sinkholes but also in other landforms (soil pockets).

Even though the upper soil layers with nutrient-rich patches represent sources of nutrients (Brunner et al., 2004) after mineralisation of organic matter (Berg, 1986), the influence of humus accumulative A horizon (M5) was negative. Soil probing revealed greater thickness of A horizon in the less developed soils (Leptosol) compared to the better developed soils (Cambisol, Luvisol), as was also confirmed with negative correlation between thickness of A horizon and soil depth ($r = -0.59$, $p < 0.001$).

Height increment of silver firs was positively correlated with available water capacity ($r = 0.43$, $p < 0.001$). Jackson et al. (2000)

showed that deep soil layers are important sources of water for woody plants due to their clay content, usually higher than in superficial soil layers. Positive correlations between clay in subsoil layers and forest productivity have been reported also by Kõlli (2002). In our case, all soils contain high amounts of clay due to the limestone parent material. Cumulative thickness of mineral horizons explained a large share of soil available water capacity ($r = 0.90$; $p < 0.001$), while correlation between thickness of A horizon and modelled AWC was negative ($r = -0.39$, $p = 0.002$). The effect of available water capacity in the model was lower compared to soil profile structure, which is logical in the light of high amount and evenly distributed precipitation over the year (2150 mm). Nevertheless, it has been proven in the past studies (Levanič, 1997) that rainfall is vital for the growth of forest stands in the Dinaric region. Due to limestone bedrock, the majority of precipitation quickly disappears underground and only a fraction of it is retained within the soil layer (Vilhar et al., 2005). Consequently, trees sensitively react with a growth decrease through years with reduced amount of precipitation. This is becoming more and more important (and critical) as frequency of dry to extremely dry years is increasing. The analysis of precipitation record (source: www.meteo.si) showed 10 dry (with record breaking extremely dry year 2003) and only 3 wet years within the 1980–2013 period (10th and 90th percentile was used as criterion for dry and wet year). Compared to the 1841–1979 period, in which 11 dry (including extremely dry years 1920, 1921, 1935 and period 1944–1947) and more than 16 wet years within the 139 year long period were identified, this is unprecedented and clearly points towards drier growing conditions. However, consistent with studies about the importance of soil water capacity to silver fir growth in the Vosges Mountains (Pinto et al., 2007; 2008), as well as in the case of silver fir growth in the Dinaric Mountains, the smaller effect of available water capacity was evident for the height increment (M11 and M12) rather than radial growth (M27 and M28). Measurements of young silver fir trees (Kadunc and Kotar, 2003) indicated that intensive height growth last only 40 days with the highest increment at the beginning of June, before water could become limiting factor, because of the high rate of precipitation in this period. On the other hand, Rathgeber et al. (2011) showed that duration and rate of xylem production lasted longer for dominant, mature silver fir trees and the duration of the growing season varied from 3 to 5 months.

Competition intensity was the key factor controlling radial tree growth. Soil characteristics slightly improved model prediction. Influence of humus accumulative A horizon and mineral (B_w , E and B_c) horizons thickness on basal area growth was similar to height growth. The thickness of O horizons did not additionally explain variability in tree growth. Our study revealed the same findings like Pinto et al. (2007), who found higher correlation between radial growth and topography rather than with available water capacity. In the last 100 years, the height increment for the dominant silver fir trees consistently revealed differences among two groups of silver fir formed according to slope positions (0 = no sinkhole, 1 = sinkhole). The SBAI of trees in sinkholes was higher than for other trees for the last observed 2002–2007 period, whereas competition intensity had a stronger negative impact on the basal area increment (M28). Our study revealed relative small soil available water capacity (from 18 to 138 mm). According to modelling AWC based on 21 soil profiles only Luvisol with AWC from 53 to 138 may have sufficient AWC, e.g. more than 100 mm as was suggested as the threshold value for AWC in the study of stand chronologies for the 33 studied stands in France (Lebourgeois, 2007; Lebourgeois et al., 2010).

Due to large differences in soil development, typical of the Dinaric Mountains (Urbančič et al., 2005; Kobal, 2011), three soil associations were identified and tested in the models: SA₁ – shallow

soils, SA₂ – shallow to moderately deep soils and SA₃ – deeper and/or leached soils (Fig. 3). Soil condition (the number of different soil development stages) per tree level is evident from Fig. 4. Under conditions of low competition when light and nutrients are not limited, the SBAI are highest on deep or even leached soils – SA₃ (Fig. 5). This observation can most likely be explained by the benefit of available soil water due to total soil depth and the topographic position of leached soils, which were, in our case, most often found at the bottom of sinkholes. The SBAI of trees on shallow soils (SA₁) was not statistically significantly lower than the SBAI of trees on moderately deep soils (SA₂). It is hypothesised that soil pockets occurred in both SA₁ and SA₂ and they represent nutrient-rich patches and the storage of soil water (Hutchings et al., 2003; Brunner et al., 2004; Vilhar et al., 2005), where trees could develop their roots and take up resources.

Under conditions of high competition, trees growing on moderately deep soils with O–A–B_w–C profiles seem to be the most efficient, most likely due to favourable chemical and physical parameters and sufficient soil depth. The decrease in the SBAI with an increase in competition intensity was most evident for leached soils with an O–A–E–B_t–C profile, where the less favourable chemical and physical characteristics should be limiting factors for tree growth. A large decrease in the basal area increment with increasing competition intensity on leached soils can be explained by the observation that relative root growth tends to decrease with an increasing water supply (Wilson, 1988). This could be a reason why trees growing on leached soils with sufficient amounts of available water developed smaller root systems and were not, in the case of high competition intensity, capable of competing for resources (Fig. 5). According to the results of the present study, the stem density should not be very high in sinkholes if faster diameter growth is to be achieved. In shallow soils, lower thinning intensities are reasonable.

It has been assumed in the forestry literature that height growth of dominant trees responds less to stand density (Pretzsch, 2009) and, consequently, that the effect of competition on tree height growth should be less important. Based on the literature assumptions (e.g., Lanner, 1985), we did not include competition in the height increment models, which enabled us to reconstruct tree height dynamics for the last 100 years. A calculation of both the coefficient of determination (Fig. 6) and the statistical significance (Fig. 7) of the relationship between height growth and soil association for the last 100 years emphasised the cumulative effect of soil condition on tree height growth. In both cases, the statistical measures increase with an increase in the length of the observation period. The benefit of well-developed soils (SA₂) compared with shallow soils (SA₁) was expected (Fig. 6). Unexpectedly, however, leached soils (SA₃) are also favourable, which can most likely be explained by the spatial distribution of leached soils. Leached soils were most often found in the terrain depressions, i.e., sinkholes (Urbančič et al. 2005), which have a naturally lower elevation than surrounding locations. Consequently, trees growing at the bottom of sinkholes were situated lower and were deeply shaded in comparison with neighbouring trees. Such growth conditions stimulate inferior trees to grow rapidly in height to reach favourable light conditions (Muller-Landau et al., 2006; Coomes and Allen, 2007).

To study height increment of silver fir trees in the last 100 years, the soil sampling distance seems to be critical, especially due to high soil variability at study site. However, variability in soil development is also high within each tree growing site (“plant’s zone of influence”) and sampling distance for estimation soil properties, based on soil probing, did not play a crucial role in defining soil characteristics for each tree. We believe that soil probing at a distance of 4–8 m from the subject tree stem represented a reliable picture of soil characteristics and soil (site) vari-

ability for each selected subject silver fir tree. This could be confirmed by the highest coefficient of determination of height increment model on the base of soil associations as dependent variable in comparison to individual soil horizon thickness and soil depth. Similar findings were confirmed also in the case of specific basal area increment in the 2002–2005 period. In this case, soil probing well defines soil characteristics according to the “plant's zone of influence” concept, but the effect of soil associations was greater than the effect of individual soil horizons.

5. Conclusions

The results of our study emphasise soil as an important site parameter that influences tree height growth and basal area increments. As a result, soil should be considered in forest management, especially in the adaptation of thinning intensities to the variations in micro topography over short distances. Our study revealed that addition to tree age and competition intensity, soil parameters e.g. soil depth, thickness of genetic soil horizons, share of soil types around each tree and soil associations were the factors controlling tree growth. Results do not allow us to highlight available water capacity as a key factor for tree growth, but in the case of climate change with increasing temperature and evapotranspiration and decreasing amount of precipitation the AWC as a result of soil depth and lateral water inputs due to topography should be a key factor for tree vitality and distribution.

The presence and thickness of particular soil horizons, which define soil types and consequently soil associations, seem to be simple and effective soil quality indicators. Such an approach is suitable mainly for natural, undisturbed soils, such as soils in uneven aged forests, and for areas where short-range spatial variability in environmental parameters and soil development prevails. The practicability of such an approach cannot be questioned because soil type and soil association assessment, which are based on expert judgement in the field, are cost effective compared with the expensive and time-consuming soil chemical and physical analyses. In the future, we also suggest the use of high-resolution digital elevation models, which could be obtained from airborne laser scanning ALS and LiDAR data, digital soil mapping using digital terrain analysis and statistical modelling integrated into GIS.

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