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Ecological, Typological Properties and Photosynthetic Activity (FAPAR) of Common Beech (*Fagus sylvatica* L.) Ecosystems in Croatia

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ABSTRACT

Background and purpose: The purpose of this study was to assess the structural and functional properties of common beech forest ecosystems in Croatia across a wide macro-climatic gradient (Mediterranean, Alpine and Continental) and to gain insight into the ways they adapt to progressing short-term climatic extremes and anomalies.

Material and Methods: Research was undertaken by integration of the expert based, country scale typological delineation of 13 beech ecosystem types, climatic and topographic grids and indices of ecosystem performances such as the JRC FAPAR (Fraction of Absorbed Photosynthetically Active Radiation).

Results: This study reveals preferential environmental conditions for beech ecosystem types together with limiting conditions in three margins of the beech distribution area: highest altitudinal zone, south-eastern continental Pannonian zone and the Mediterranean. The results show that the common beech can adapt to a very wide range of environmental conditions: annual mean temperatures from 2.1°C to 13.5°C, annual precipitation from 739 mm to 3444 mm, and altitudinal range from 20.3 m up to 1576 m above sea level. FAPAR reveals some new insight into the adaptive potential and response mechanisms of the common beech to emerging climate change.

Conclusion: The common beech has great potential to adapt to increasing spring warming by a preterm shift of phenology onset and retain relatively stable productivity during the phenology peak in July and August, unrelated to external climatic forcing. These findings indicate that the flexibility of phenological timing, especially during springtime, present one of the important mechanisms of adaptation and resilience of the common beech.

Keywords: Common beech (*Fagus sylvatica* L.), JRC FAPAR, environmental limits, adaptation, resilience, climate change

INTRODUCTION

The common or European beech (*Fagus sylvatica* L.) is one of the major forest trees in the mountain regions of Europe with an approximated coverage of slightly more than 217,000 km², which is less than one third of the potential beech forest cover of approximately 907,000 km² according to Bohn *et al.* [1]. It has an extremely broad climatic and edaphic amplitude, ranging from the southern regions of the Baltic States to Sicily and from Southern England, Brittany in France, and the Cantabrians in Spain to the lowlands in north eastern Poland, east of the

Carpathians in Moldavia EEA 2007 [2]. Penetration of the beech above the current range of distribution is limited mainly by climatic conditions. A growing season that is too short, low winter temperatures and late frost in spring limits beech distribution at its northern and eastern boundaries and high altitudes [3]. On the other hand, water deficiency limits beech spread to the southern Europe and Mediterranean. The beech gradually expanded in response to the local climate, atmosphere and soils since the last glaciers receded over 10,000 years ago. However,

climate change and intensification of extreme climatic conditions (droughts) are predicted to lead to a drastic reduction in suitable sites for the beech. Regarding the stands in their current zonal position, 56-96% of present day beech forests might be outside their present bioclimatic niche by 2050 [4] mainly in the South of France, Italy and the Balkan Peninsula [5]. Climatic factors limit the progression of the beech in the south-eastern range, most directly expressed throughout Ellenberg's climate quotient [4, 6, 7]. However, future predictions of beech distribution, solely based on long-term averages are prone to uncertainty because of the influence of advanced climatic extremes and intrinsic adaptive capacity of beech. At the xeric edge, subsistence of the beech is more influenced by short-term dry periods than the long-term climatic means [8, 9]. Adaptation to the local environment may lead to genetic and phenotypic structured populations in a few generations, depending on the forest management system applied [5]. Therefore, the adaptive capacity of the beech should not be ignored in the assessment of future distribution. The adaptation strategy of forest trees is receiving growing attention given expected climatic changes. The scarcity of reliable information regarding responses to macroclimatic changes is a central problem and obstacle in planning for the future [6]. To formulate realistic predictions, both the nature of adaptation to past and current climate, and the level of sensitivity to sudden environmental changes have to be understood and properly interpreted.

Due to its very broad environmental niche, the beech constitutes a variety of vegetation types across Europe. This is particularly common in the southern limits of its distribution range, on the Balkan Peninsula, where beech forests are characterized by the high diversity of floral components. This is due to the fact that during the last ice age, the area in the south-eastern periphery of the Alps i.e. the Balkan Peninsula, presented microrefugia that are considered as the main source areas for the subsequent colonization of central and northern Europe by the beech [10]. Nowadays, beech forests in this area contain the variety of "Illyric" floral elements that cannot be found in other parts of Europe, which withstood the last glacial period. Recently, with the goal of placing the EU beech forest on the list of world heritage property, a comprehensive regionalization and formation of Beech Forest Regions was brought about [11]. In the framework of this activity, 12 European Beech Forest Regions were defined, and one of them includes the Illyric Beech Forest Region that covers Slovenia, Croatia and Bosnia-Herzegovina. Another recent comprehensive effort on an EU scale presents the classification of European forest types, Categories and types for sustainable forest management reporting and policy (EEA [2]). EEA classification defines two European beech forest types in the Illyric Beech Forest Region. The Illyrian sub-mountainous beech forest prevails in the Dinarides and mid-Pannonic hills, while in the higher altitudinal range of distribution, beech forests with silver fir and common spruce, forming Illyrian mountainous beech forest type prevail. However, on a local country scale in Croatia, the long-term forest ecosystem studies based on a typological approach [12] have been undertaken. The goal of these studies was in identifying, assessing and mapping the specific forest ecological-managerial types (ecosystems) based on common soil-vegetation properties. The purpose of this classification was to define the optimal productivity (yield tables) of forest stands with respect to site potential and to propose the most suitable means of forest management and regeneration that can preserve ecosystem sustainability in the long-term. As a result of these research activities, a total of 13 beech forest types (ecosystems)

were identified and delineated across the country. Beech forests were also categorized in four broader bioclimatic groups with respect to climate-vegetation relationship.

A broad temperature and precipitation gradient over the narrow geographical range in Croatia (3-17°C of yearly average temperatures and 300-3500 mm of total yearly rainfall) contribute to the variety of macroclimatic conditions. Croatia also intersects four of the main European biogeographical regions on a relatively short spatial extent (Continental, Pannonian, Alpine and Mediterranean). Therefore, delimited beech forest types cover an extensive environmental range; from optimal conditions enabling the highest productivity, to limiting conditions that prevail on the margins of their distribution area. Along the Adriatic littoral region, there is a very sharp transition from the warm and dry Mediterranean climate not suitable for the beech. Beech populations in this boundary region are in environmental limits, partly adapted to the Mediterranean climate. The other xeric limit is on the lowest slopes of the eastern parts of Pannonian hills, in the transition towards the semi-arid South-Eastern climatic zone. The third boundary for the beech is in the highest hilltops of the Dinaric Alps, in the upper altitudinal limits of forest vegetation. This extensive environmental setting across a narrow area is very suitable for assessment of the beech climatic niche width, together with its responses to various climatic anomalies and extreme events that can provide new insights into beech adaptation potential. The regional scale assessment in the transitional area of South-eastern Europe and the Mediterranean could provide important clues as to how beech forest types are coping with a warmer environment and how they are adapting to extreme climatic conditions, such as dry spells.

Consequently, the main objectives of this study were to assess the structural and functional properties of beech forest ecosystems in Croatia across a wide climatic gradient (Mediterranean, Alpine and Continental) and to gain some clues about the means of adaptation to spatio-temporal climatic extremes and anomalies. This was undertaken by: (1) assessing the main ecological properties in terms of the yearly mean temperature, annual precipitation and the Ellenberg climate quotient of 13 previously delimited ecosystem types; (2) assessing the main typological properties such as topography (altitude, slope and aspect) and interactions with edaphic factors; (3) assessing the vegetation activity of beech forests using the proxy remote sensing indices such as FAPAR (Fraction of Absorbed Photosynthetically Active Radiation); and (4) provide an assessment of responses and resilience of the beech forests to climatic anomalies, based on FAPAR datasets for the period of observation (1998-2005).

MATERIALS AND METHODS

Study Area

Croatia is situated in Central and Southeast Europe between latitudes 42° and 47° and longitudes 13° and 20°. The Pannonian Basin, Dinaric Alps and Adriatic Basin constitute the major geomorphographic areas (Figure 1). The major mountain ranges are the Dinaric Alps following the littoral Adriatic zone, ranging from sea level up to 1831 m and the Pannonian hills (Ivančica, Medvednica, Bilogora, Psunj, Papuk, Dilj) in the continental area, ranging up to 1060 m. Parent material in the carstic region of the Dinaric Alps constitute Mesozoic limestones and dolomites with protrusions of silicate and silicate-carbonate clastites and only locally magmatites [13]. Unlike the Dinaric area, the soils

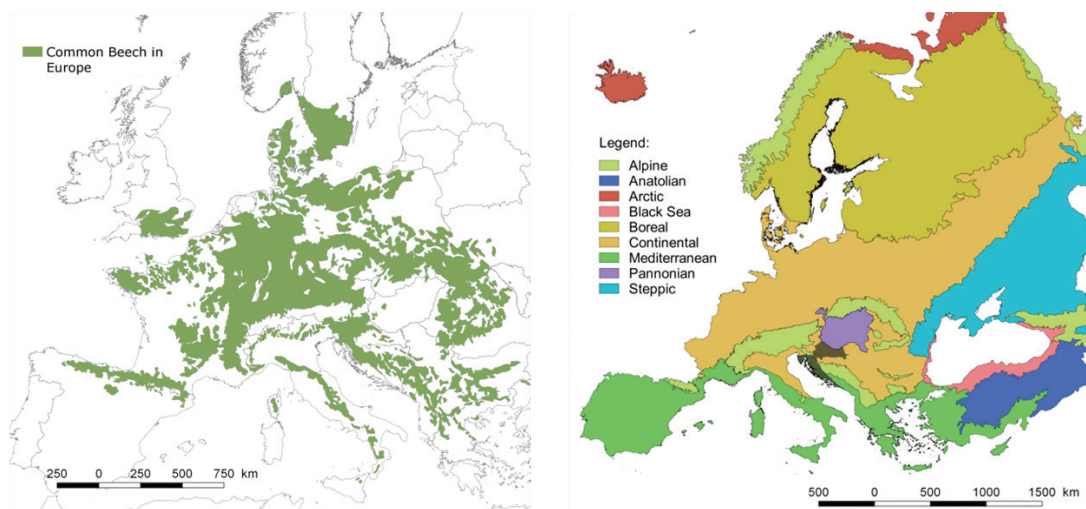


FIGURE 1. Distribution of common beech in Europe (left); European biogeographic regions with Croatia country position (right)

of the beech forests of the Pannonian hills are characterised by predominantly physically easily weathered substrates. They are mainly various unconsolidated clastites, marls, sandstones and metamorphic rocks. Croatia has per-humid, humid and subhumid climates according to the Thornthwaite climate classification [14]. A humid climate is prevalent in a large part of the continental lowlands, a subhumid climate only in the eastern part and a per-humid climate in the highlands [15]. In coastal Croatia, there are per-humid, humid and subhumid climates. In the past 50 years, a significant increase in the mean annual temperature values (from 0.2°C to 0.4°C per decade) is found in Croatia's mountainous region. The overall (annual) positive trend is mainly due to significant positive summer and spring trends (from 0.3°C to 0.5°C per decade). In terms of precipitation, the prevailing trends in the mountains are negative (from -17 mm to -11 mm per decade) except at the highest-altitude stations where the dominant trend is positive (32 mm per decade). An analysis of precipitation [16], based on a dense network of rain-gauge stations in Croatia, reveals a significant decrease in the total annual precipitation amounts of -50.6 mm per decade in the mountainous regions. A significant summer decrease mainly governs the annual trend, and, in the northern part, also partly a spring decrease. Based on available literature, it can be concluded that warming of the climate in the Croatian Highlands is currently occurring, which is especially evident during the warm half-year (spring and summer). This warming is accompanied by drying trends, thus indicating that the mountainous regions in Croatia are prone to significant climate change.

Geospatial Data of Forest Types, Climate and Topography

The definition of 13 beech forest types (ecosystems) used in this research was based on the comprehensive forest ecosystem inventory i.e. typological surveys that were mostly performed between 1970 and 1990 at the Croatian Forest Research Institute. Typological or ecosystem-based assessments were comprised of detail, a plot scale field survey of soil properties including geological and climate characteristics, floristic composition, and stand structural properties in numerous locations. Comprehensive

insights into the results of the aforementioned long-term activities, concerning determined soil and vegetation characteristics that constitute beech ecosystems in Croatia, can be found in the publications of Pernar and Bakšić [13] and Vukelić and Baričević [17]. Geospatial coverage with delineated forest types was produced throughout 2003-2007 in the framework of the project: "Development of the Dynamical geo-information system of forest ecosystems in Croatia". Delineation of forest cover was provided from aerial orthophoto images and available remote sensing data. Further ecosystem stratification was undertaken through expert knowledge and previously gathered information, forest inventory data, draft survey maps, study reports and publications. The resulted map of beech ecosystem types is shown in Figure 2 and Table 1.

Topographic parameters (mean, minimum, maximum of altitude, slope and aspect) were derived from the digital terrain model (DTM) available in 25 m grid resolution (Figure 3), based on topographic maps of Croatia 1:5000 and 1:25 000. For the purpose of this study, the DTM was scaled on a 1000 m grid resolution. The spatial grid of mean annual air temperature (Figure 3) was based on measurements from 152 main and climatological stations in Croatia during the period 1961-1990. The grid of the mean annual precipitation (Figure 3) for the similar period was based on measurements of the mean daily precipitation from 567 main, climatological and rain gauging stations. The resolution of temperature and precipitation grids was also 1000 m. In addition, Ellenberg's climate quotient (EQ) [18] was calculated from grids of the mean temperature of the warmest month (July, T_{07}) divided by annual precipitation (Pa):

$$EQ = 1000 (T_{07} / Pa)$$

Estimation of the FAPAR Values and Resilience Metrics

Freely available, monthly FAPAR (Fraction of Absorbed Photosynthetically Active Radiation) data [19] was obtained from the JRC FAPAR website (<http://fapar.jrc.ec.europa.eu>). Data was acquired in monthly intervals for the period from 1998 to 2005. Basic manipulation and transformation of the data in a

suitable format for SAGA GIS spatial analysis was performed by BEAM VISAT software. Monthly FAPAR images, 96 in total from 1998-2005, were then clipped with the 13 area shape files that represent envelopes of beech ecosystems. Associated FAPAR pixels (with a 1 km spatial resolution) were extracted (Figure 5). However, so as to eliminate the problem of the false high FAPAR intensity (the appearance of extreme FAPAR values during the winter season, very possibly as a reflection of snow cover), only months in seasons with certain vegetation activity (from March to November) were used for analysis. Average monthly FAPAR values for each of the 13 area samples, from March to November within the eight year period, were calculated from related pixels using “Spatial and geostatistic analysis module” in SAGA GIS. Further data processing, statistics and graphical representation were performed in R software for statistical computing.

In order to quantify ecosystem responses indices of resilience were applied that represent the concepts of resistance, recovery, resilience and relative resilience following the procedure of Lloret *et al.* [20], Sánchez-Salguero *et al.* [21], Herrero and Zamora [22] and Pilas *et al.* [23]. In general, resistance is the inverse of performance reduction during extreme drought and presents the ratio between performance during and before drought. Recovery is the ability to recover relative to the performance reduction undergone during drought and presents the ratio between performance after and during extreme drought. Resilience is the capacity to return to pre-drought performance levels and

presents the ratio between the performance before and after drought. Relative resilience is the resilience weighted by the performance reduction during drought. In this study an adapted approach was applied, previously developed by Pilas *et al.* [23] for FAPAR monthly time series. The relationship between mid-season FAPAR in July (F_{ms}) was studied, which is very close to the maximum extent of photosynthetic activity for the season, as well as pre and post mid season vegetation performances. The effect of variations of FAPAR during intensive vegetation growth in the April-June period (F_{pre}) on the mid-season FAPAR performance were analyzed, i.e. resistance ($rt7$) of F_{ms} , and the effect of mid-season FAPAR on the vegetation activity during the later stage and the senescence period in August-October, (F_{post}) i.e. recovery ($rc7$). As a follow up to these calculations we estimated the differences in resilience ($rs7$) and relative resilience of ecosystems ($rr7$) based on intra-annual variations of photosynthetic activity. We calculated these indices using the following formulae:

$$\begin{aligned} rt7 &= F_{ms} / ((F_{ms-1} + F_{ms-2} + F_{ms-3}) / 3) = F_{ms} / F_{pre} \\ rc7 &= ((F_{ms+1} + F_{ms+2} + F_{ms+3}) / 3) / F_{ms} = F_{post} / F_{ms} \\ rs7 &= (F_{ms+1} + F_{ms+2} + F_{ms+3}) / (F_{ms-1} + F_{ms-2} + F_{ms-3}) = F_{post} / F_{pre} \\ rr7 &= F_{post} \times F_{ms} / F_{pre} \end{aligned}$$

where F_{ms} , F_{ms-t} , F_{ms+t} are FAPAR values for the mid-season (July), the previous t months and t months after, respectively, $rt7$, $rc7$, $rs7$, $rr7$ (mid-seasonal resilience indices).

TABLE 1. The dominant soil and vegetation pairs constituting the common beech ecosystems

Bioclimate	Forest ecosystem	Phytocenoses	Dominant soil type (WRB classification)
B	1	(Illyrian) Subalpine beech forest (<i>Ranunculo platanifolii-Fagetum</i> /Ht. 1938/Marinček et al. 1993)	leptic CAMBISOL rhodic
C	1	Dinaric beech-fir forest <i>Omphalodo-Fagetum</i> (Treg. 1957) Marinček et al. 1993	follic CAMBISOL, eutric
	3	Dinaric beech-fir forest <i>Omphalodo-Fagetum</i> (Treg. 1957) Marinček et al. 1993	lithic, mollic LEPTOSOL, humic
	4	Pannonian beech-fir forest <i>Festuco drymeiae-Abietetum</i> Vukelić et Baričević 2007)	haplic CAMBISOL, dystic, endoskeletal
D	1	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	follic CAMBISOL, eutric
	2	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	hyperskeletal, rendzic LEPTOSOL, brunic, skeletal
	3	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	LEPTOSOL, rendzic, mollic
	4	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	gleyic, cutanic LUVISOL, clayic, epidystic
	5	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	cutanic LUVISOL, arenic, siltic
	6	(Illyric) montane beech forest (<i>Lamio orvale-Fagetum sylvaticae</i> Ht. 1938)	follic CAMBISOL, dystic, endoskeletal
	7	Submontane Pannonian beech forests (<i>Cephalathero longifoliae-Fagetum</i> Vukelić, Baričević et Šapić 2012)	gleyic, cutanic LUVISOL, clayic, epidystic
H	1	Sub-mediterranean beech forest (<i>Seslerio-Fagetum sylvaticae</i> /Ht. 1950/M. Wraber 1960)	leptic CAMBISOL rhodic (Calcocambisol)
	2	Termophylic continental beech forest (<i>Ostryo-Fagetum sylvaticae</i> Wraber ex Trinajstić 1972)	LEPTOSOL, rendzic, mollic

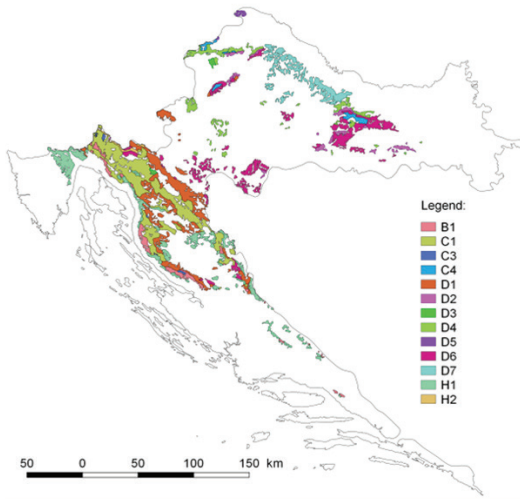


FIGURE 2. Distribution of 13 common beech ecosystems in Croatia

RESULTS

Main Topographic and Climatic Properties

Table 1 shows a summary statistics of the main topographic and climatic grids concerning 13 beech ecosystem types. The results indicate the proportion of area of each individual forest type. The most abundant is ecosystem C1 with an approximate area of 2825 km² and the smallest ecosystem is C3 with 41 km². The obtained results show that the beech appears across a very broad range of environmental conditions, from locations very close to sea level (20.3 m) to the highest altitudinal belts of the Dinaric Alps (1576 m). The average values of the assessed parameters indicate the preferential conditions of a particular ecosystem regarding general macroclimatic properties. However, minimal and maximal values are more influenced by microclimate and specific topographic settings. This is clearly visible in the Sub-Mediterranean beech forest (H1) which, in general, appears at higher average altitudes (886 m) of the coastal zone, but in specific microclimatic conditions such as in north-western slopes of Učka Mountain in the Istrian Peninsula, can reach the lowest elevations of 20.3 m, the boundaries of carstic field Čepić Field in the hinterland. Elevation is noticeable (Figure 6), a very strong differentiating factor of three bioclimatic groups (B,C,D) which are based on relatively uniform vegetation strata. For example, at altitudes of 559 m in the Pannonian and 936-1031 m in the Dinaric region, there is a prevalence of beech – fir mixed forests, while pure beech forests occupy the zones below and above this range. At the inner bioclimatic scale, edaphic factors are more relevant in the differentiation of ecosystem types. Slope also shows a gradual increase across the ecosystem altitudinal range - ecosystems in the lower altitudes (bioclimate D) occupy milder slopes than ecosystems in the higher zones (bioclimates B and C). Aspect is quite invariant across the ecosystem range except for ecosystem H2 (Thermophilic continental beech forest), which presents a specific exception appearing dominantly on the eastern slopes. However, the prevailing “thermophilic” vegetation properties of H2 could also be explained by the character of the

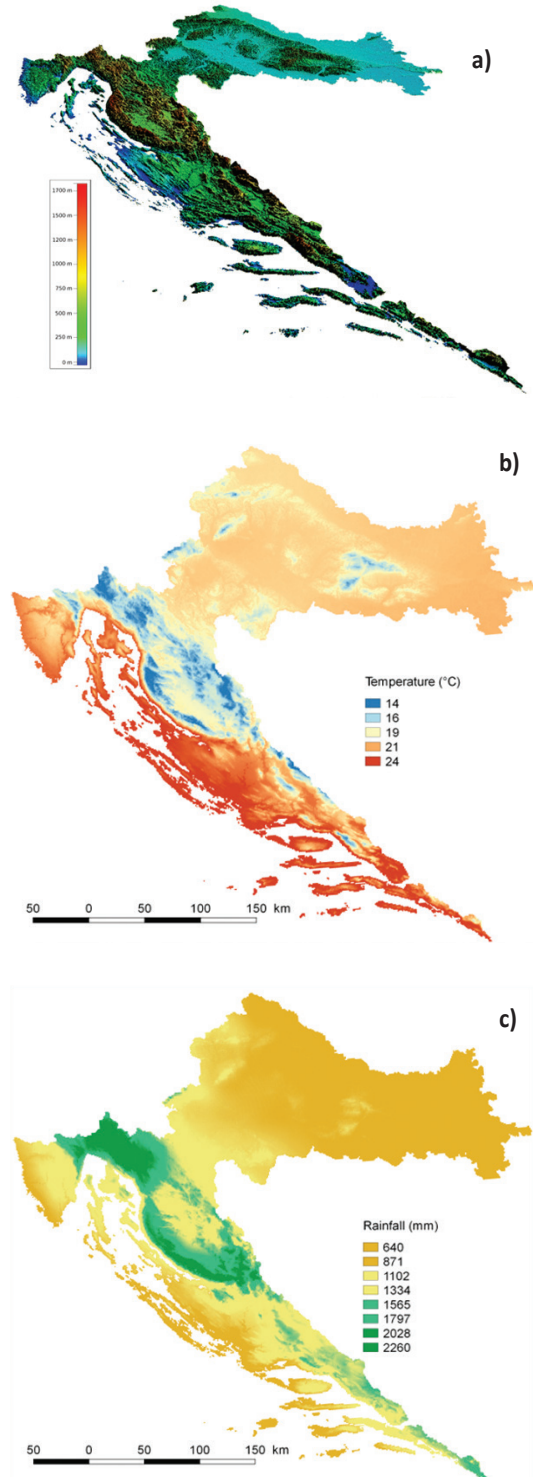


FIGURE 3. Digital elevation model (a), average temperature, based on 1961-1990 average (b), total rainfall, based on 1961-1990 average (c)

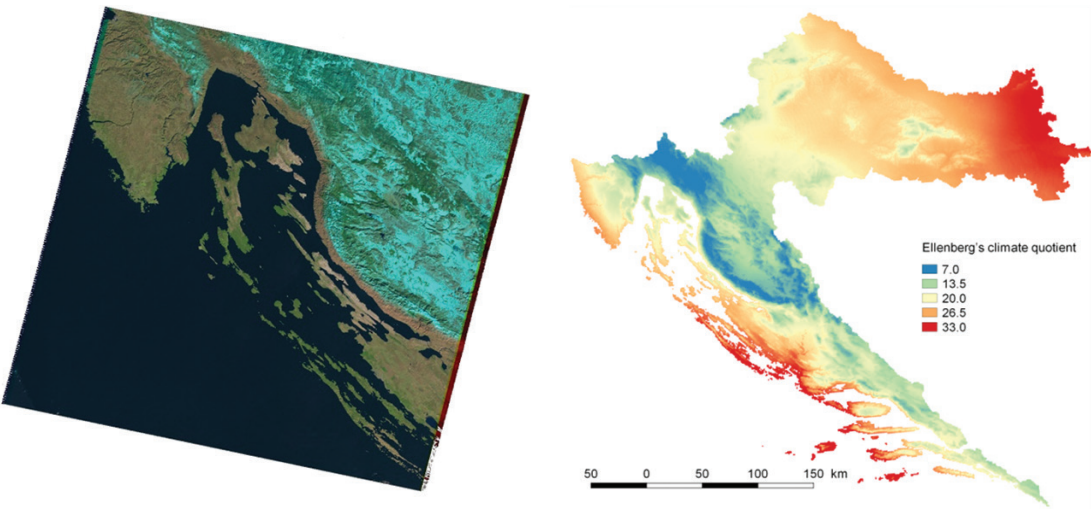


FIGURE 4. Snow boundary indicating the limits of the common beech distribution in Mediterranean (left), spatial coverage of Ellenberg's climate quotient (right)

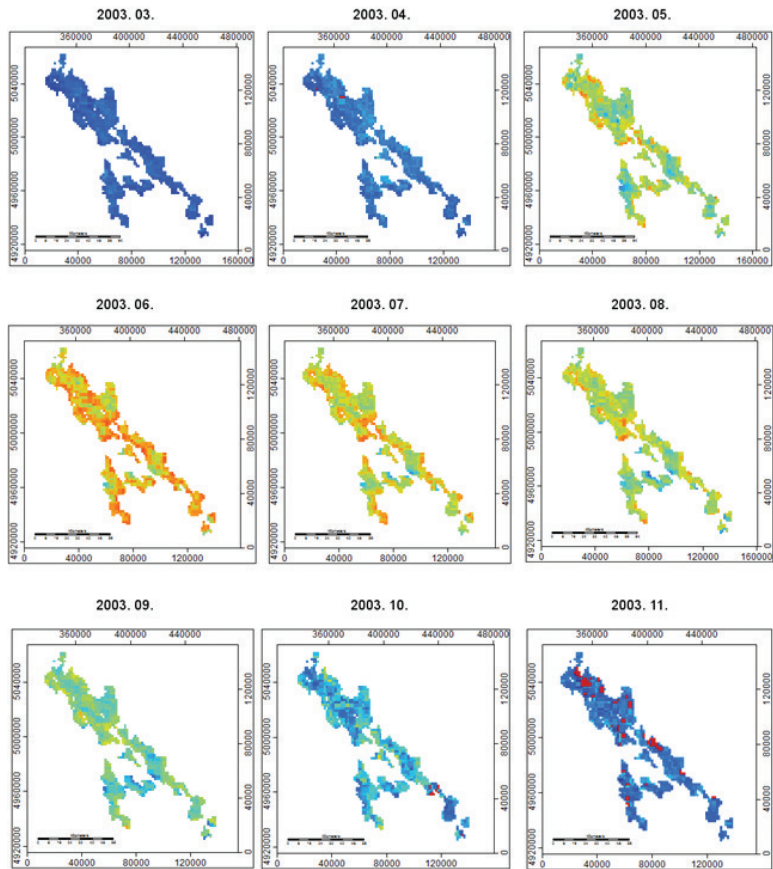


FIGURE 5. Changes of monthly FAPAR for the segment of C1 beech ecosystem during 2003

TABLE 2. Statistics of the main topographic and climatic properties of the beech ecosystems

ELEVATION													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	407	2354	34	186	1648	317	55	841	40	1377	792	1219	79
Min	596.1	245.8	789.3	237.0	114.7	158.6	163.9	123.6	194.0	126.9	109.5	20.3	188.0
Max	1576	1557	1198	958	1316	922	957	1041	364	1341	319	1491	940
Range	979	1312	409	721	1202	764	793	917	170	1214	210	1470	752
Average	1160	936	1031	559	672	328	408	252	292	340	181	886	540
Variance	8892	14688	7366	10054	10640	4871	10879	3562	639	5391	417	16567	16531
Stdev	85	108	68	84	89	59	94	38	25	56	18	108	128
SLOPE													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	407	2354	34	186	1648	317	55	841	40	1377	792	1219	79
Min	0.11	0.05	0.47	0.35	0.02	0.25	0.34	0.03	0.09	0.18	0.04	0.06	0.77
Max	18.98	20.93	20.02	15.50	19.86	12.92	12.28	15.94	3.86	19.37	2.85	23.03	19.68
Range	18.87	20.89	19.55	15.15	19.83	12.67	11.94	15.91	3.77	19.19	2.81	22.97	18.91
Average	6.81	5.52	8.03	5.83	4.72	3.03	3.79	1.99	1.45	2.91	0.78	6.27	6.89
Variance	7.36	7.44	2.77	4.60	6.80	2.08	5.19	1.33	0.36	1.94	0.13	7.24	16.32
Stdev	2.48	2.49	1.10	1.66	2.19	1.20	2.04	0.79	0.60	1.07	0.32	2.35	3.90
ASPECT													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	407	2354	34	186	1648	317	55	841	40	1377	792	1219	79
Min	1.3	0.3	7.9	0.5	0.1	0.2	7.5	0.4	8.2	0.1	0.0	1.8	1.1
Max	358.5	359.6	358.7	359.0	359.8	359.3	343.3	359.7	352.3	359.9	359.9	360.0	351.7
Range	357.2	359.3	350.8	358.5	359.7	359.1	335.8	359.3	344.2	359.8	359.9	358.2	350.5
Average	167.8	178.0	142.0	170.7	164.3	168.7	145.3	159.8	177.1	157.4	183.2	184.5	94.9
Variance	5099.5	10691.6	3450.5	8980.2	8497.1	6801.7	3857.6	8483.4	8595.9	7769.3	8601.0	5081.2	8738.3
Stdev	59.3	97.6	37.9	76.5	82.2	69.9	61.3	78.3	86.0	76.0	85.4	58.2	92.2
Facet	S	S	SE	S	S	S	SE	S	S	SE	S	S	E
TEMPERATURE													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	403	2345	35	188	1661	325	56	841	43	1382	796	1232	78
Min	2.6	2.1	4.8	5.3	4.5	5.2	6.1	4.8	9.2	4.5	8.9	3.0	5.3
Max	10.4	10.6	8.4	9.8	10.8	10.5	10.4	10.6	10.1	10.8	10.6	13.5	10.7
Range	7.8	8.5	3.6	4.5	6.3	5.3	4.3	5.8	0.9	6.3	1.7	10.5	5.4
Average	6.2	6.8	6.5	7.9	8.2	9.3	9.1	9.7	9.6	9.4	9.9	7.9	8.4
Variance	0.4	0.5	0.3	0.3	0.4	0.2	0.4	0.2	0.0	0.2	0.0	0.7	0.6
Stdev	0.5	0.6	0.4	0.5	0.6	0.4	0.6	0.3	0.1	0.4	0.1	0.7	0.8
PRECIPITATION													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	403	2345	35	188	1661	325	56	841	43	1382	796	1232	78
Min	1227	1183	1538	887	912	754	945	739	854	787	816	1145	1396
Max	3444	3234	2643	1343	2816	1930	1904	1581	1101	2300	917	3286	2107
Range	2216	2050	1105	457	1904	1175	959	842	247	1513	101	2141	710
Average	2034	1696	2042	1073	1541	950	1359	968	987	1166	863	1686	1740
Variance	14514	25321	16144	1165	14746	803	3234	934	145	2427	99	20233	10401
Stdev	79	109	93	27	91	22	45	17	11	29	8	100	98
ELLENBERG'S DROUGHT INDEX													
Ecosystem	B1	C1	C3	C4	D1	D2	D3	D4	D5	D6	D7	H1	H2
No samples	115	1246	41	66	889	163	52	393	23	798	499	668	62
Min	3.82	3.63	4.41	12.29	4.87	14.54	8.04	8.84	16.24	5.91	21.03	4.51	8.31
Max	13.63	16.95	14.26	19.33	21.39	26.28	21.24	27.90	23.05	25.77	24.97	18.66	18.86
Range	9.81	13.32	9.85	7.04	16.52	11.73	13.20	19.06	6.81	19.86	3.93	14.15	10.56
Average	7.38	9.01	7.56	17.17	12.47	20.51	15.25	19.47	20.73	17.95	23.34	11.28	12.89
Variance	4.11	6.76	4.52	2.73	5.42	5.83	19.05	13.44	5.69	13.38	0.00	6.33	8.47
Stdev	2.03	2.60	2.13	1.65	2.33	2.41	4.36	3.67	2.39	3.66	0.00	2.52	2.91

predominant soil type, which is dry and relatively shallow molic, rendzic leptosol (rendzina). Overall temperature amplitude for the common beech is between 2.1-13.5°C and precipitation amplitude between 754-3444 mm. There is evidence of a gradual increase of the average temperatures and evidence of more alternating but decreasing trend of average precipitation along bioclimatic gradients (B-C-D). The estimated maximal value of the Ellenberg quotient of 27.9 represents the xeric limit for the beech in the continental region. However, values of the Ellenberg quotient in the Sub-mediterranean ecosystem H1 do not exceed 18.7 that are well below continental limits.

Photosynthetic Activity (FAPAR)

Figure 7 presents the average values of photosynthetic activity of 13 common beech ecosystem types for the period March-November. The estimated range of average FAPAR is from minimal 0.43 (B1) to maximal 0.55 (C4). FAPAR is decreasing in

ecosystems on higher altitudes (B1, C1, C3) and the Mediterranean (H1). Ecosystem B1 (Subalpine beech forest) has the lowest activity at the upper limit of beech altitudinal zone in Dinaric Alps. On the other hand, the highest photosynthetic activity can be found in ecosystems in the coline belt, D1-D7 (Mountain beech forests), at low to medium altitudes. Overall differences between series of mean FAPAR for an 8 year period, 1998-2005, prove high significance at $p < 0.001$ (AOV test). Multiple comparisons between groups (Figure 8) provide insight into significance amongst ecosystem pairs. The performed test confirms overall differences amongst ecosystems included in bioclimatic hierarchy. However, there is proven significance on intra-bioclimatic level, most obvious between beech – fir mixed forests in the Dinaric and Pannonian region. Productivity of beech and fir forests in the continental Pannonian hills, C4 (Pannonian beech-fir forest) significantly exceeds productivity of the beech and fir forests in the Dinaric Alps, C1 and C3 (Dinaric beech-fir forest). Differences

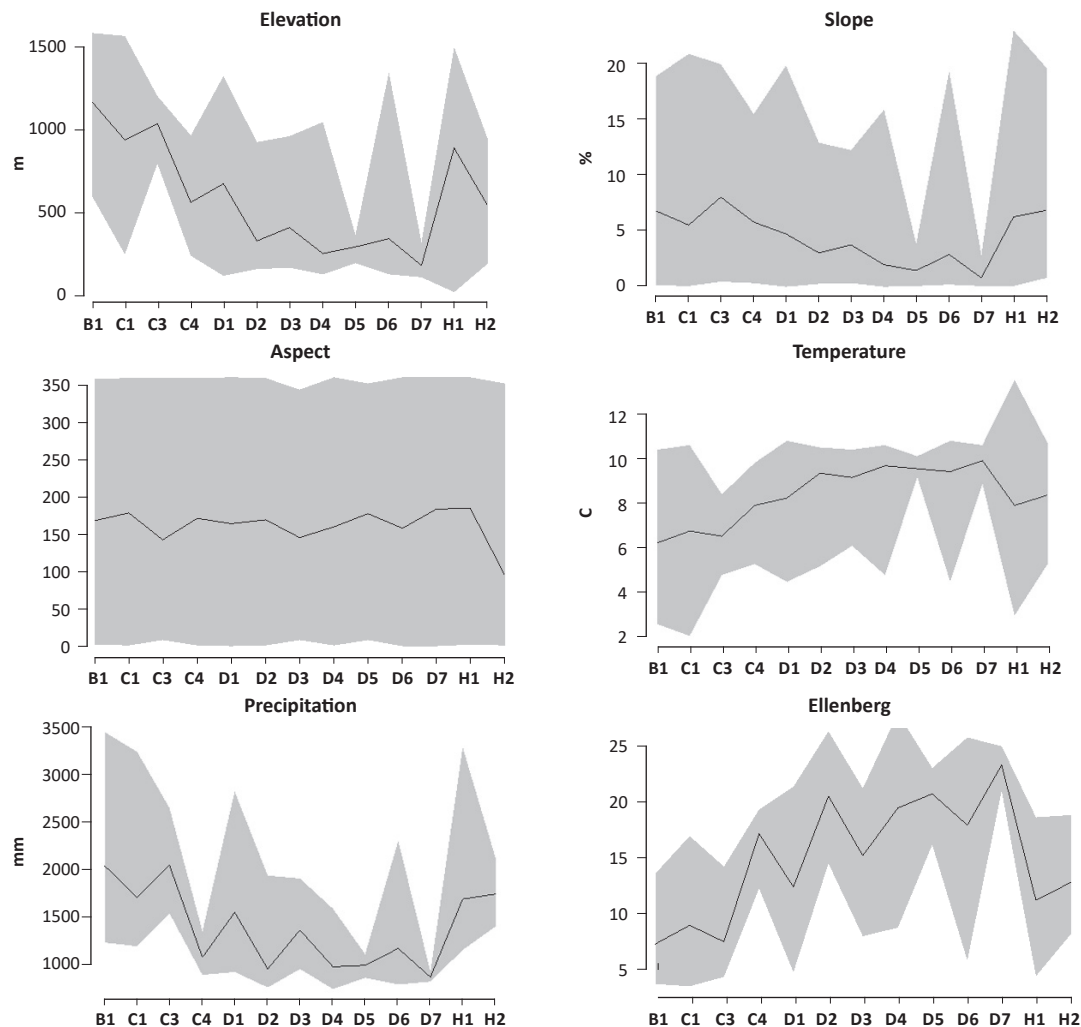


FIGURE 6. Preferential environmental properties and limits of the common beech ecosystem types

inside bioclimatic group D, mountain beech forest vegetation type (Montane beech forest) can be attributed to edaphic factors. Higher productivity is found in relatively deeper soils such as rendzic leptosol (deep rendzina on unconsolidated material), luvisol and dystic cambisol. There is also a noticeable difference amongst types H1 and H2 inside thermophilic beech vegetation group where H1, the sub-Mediterranean beech forest, has one of the lowest productivity and H2, thermophilic continental beech forest is very near to the most productive ecosystems. More intrinsic insight into ecosystems performance can be obtained from the phenological pattern based on monthly FAPAR average series (Figure 9). Ecosystems follow a general pattern of seasonality with vegetation onset in May and rapid inclination of photosynthetic activity during June until maximal values in July. From July to September there is a prevailing stage of maximal photosynthetic activity of forests. Cessation of maximal activity

and the onset of senescence is in October and a sharp decline of activity in November. Apart from this general seasonal pattern there is a visible shift in phenology along bioclimatic range D-C-B. Seasonal distribution of FAPAR swings in absolute values from D to B, retaining a similar shape. The impact of summer drought in the Mediterranean is evident in ecosystem H1 through a more rapid reduction of photosynthetic activity in the mid-season.

More pronounced insight into vegetation timing can be obtained from the contrast of monthly slices of FAPAR (Figure

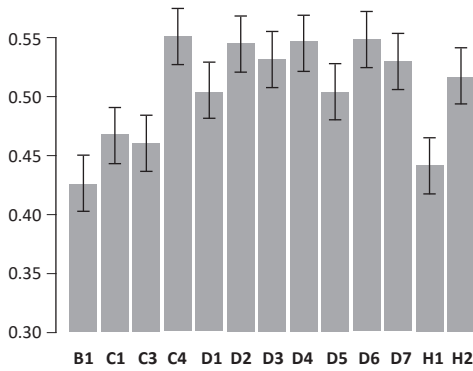


FIGURE 7. Average annual values of FAPAR (March-November)

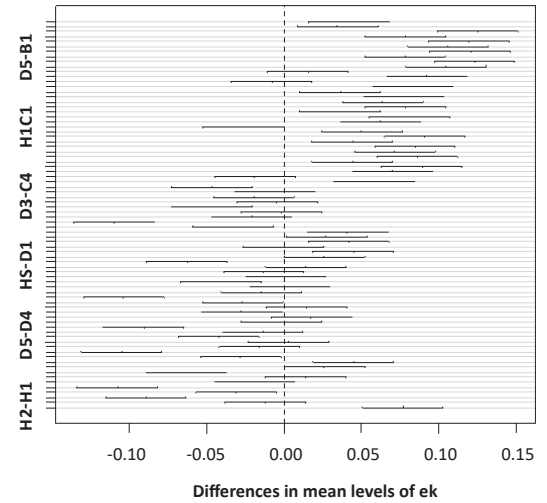


FIGURE 8. Multiple comparisons of yearly differences amongst ecosystems provided by Tukey HSD test

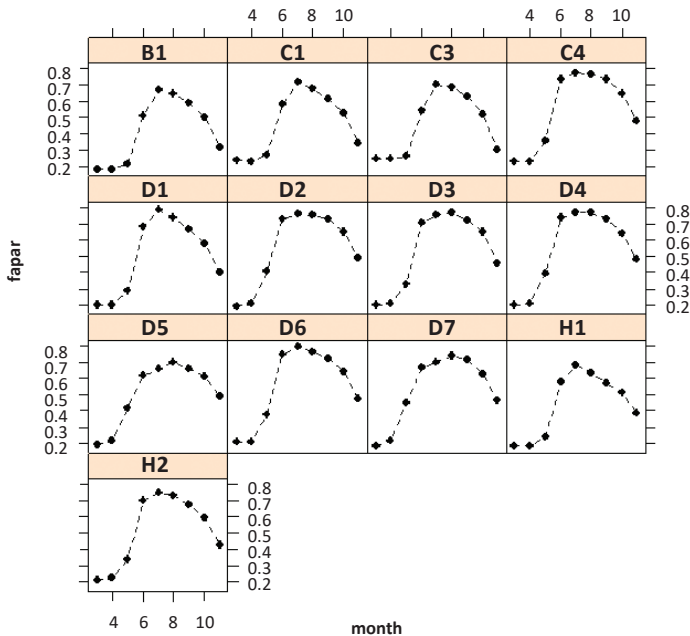


FIGURE 9. The shapes of seasonal FAPAR based on 8 year monthly averages

10). There is a small but noticeable increase in FAPAR during vegetation dormancy (March–April), a consequence of activity of evergreen silver fir in mixed beech–fir forests (C1, C3, C4). Also, there is evident of a gradual boost of vegetation in May, along bioclimatic gradient D–C–B, earliest in D and the latest in B. On the contrary, the start of the senescence period is in November, the earliest in B and the latest in D.

Intra-Seasonal Variations and Ecosystem Responses

Figure 11 presents normalized variations of monthly FAPAR values (z-scores) for the observed period (1998–2005). These deviations are mainly influenced by climatic variations of which the most pronounced events were drought and a heat wave in 2003 and an extremely wet 2005. All ecosystems show the possibility to rapidly adapt their photosynthetic activity in a positive or negative way depending on more or less suitable climatic conditions. From the presented scores, insight into the behaviour of ecosystems under a particular climatic extreme can be noted. The drought and heat wave of 2003 had less influence on FAPAR inside bioclimatic zones C and B. In conditions of excessive precipitation in 2005, only a few ecosystems show a more positive response (C4, D2, D4 and D7). On the contrary, ecosystems B1, C1 and C3 show reduced activity throughout 2005 with the exception of springtime.

Figure 12 presents calculated coefficients of variation for consecutive months which indicates the time or stage with the most pronounced fluctuations of FAPAR. The beech exhibits the highest responses to external anomalies during vegetation onset in spring. Variations gradually recede towards mid season and gradually increase at the beginning of the senescence period. This proves that the beech has very conservative and robust behaviour in relation to climate anomalies during the mid-season with maximal productivity. The highest variations of FAPAR during spring and autumn indicate a specific trait of the common beech in that it can seasonally adjust the kickoff and cessation of its phenology, responding with an earlier onset of vegetation to favourable (warm) climatic settings or forcing a premature drop in productivity during water shortages and drought, while retaining relatively constant FAPAR in the mid-season. Less pronounced variations during the onset of growth were characteristic for C1 and C3 (mixed beech–fir forest) because of the possible stable influence of the silver fir. There is evidence of a gradual shift in the maximal variations amongst ecosystem types so that maximal variations in B1, C1 and C3 (higher altitudes of the Dinaric Alps) occur in June, in most of the ecosystems inside bioclimates D and H (except D5 and D7) in May and D5 and D7, in the lowest positions, in April and March.

Seasonal variations of FAPAR can be applied in a more suitable way to obtain more perceptive insight into the adaptive capacity of beech ecosystems by calculating resilience metrics (resistance, recovery, resilience and relative resilience). Resilience metrics provide a quantitative insight into the intrinsic capacity and responses of beech ecosystems to climate alterations (Fig. 12). The highest resistance is distinctive for ecosystem B1 followed by the group of ecosystems C1, C3, H1 and D1. On the contrary, ecosystems inside bioclimate D (except D1) exhibit the lowest resistance. Recovery, as an inverse of resistance (ecosystems with a smaller drop of FAPAR also have lower recovery), show a relatively opposite picture with pronounced ecosystems D5 and D7. Consequently, the ecosystem with the highest resilience is ecosystem B1, followed by the group of ecosystems inside

bioclimate C together with D1, D3 and H1. The lowest resilience was shown in ecosystems inside bioclimatic group D. With respect to relative resilience, ecosystems exhibit a very heterogenic image where only ecosystems D5 and D7 deviate more from others.

DISCUSSION

Remote sensing FAPAR, with a spatial resolution of around 1 km, presents vegetation indices suitable for assessment of land surface phenology and climatic anomalies on a global or European scale [25]. By performing a global assessment, information about vegetation cover is usually generalized and simplified to a few broad vegetation or land-cover types. By integrating FAPAR and country scale forest ecosystem classification, the power of FAPAR seasonal sensitivity can be extended to provide dynamic linkage with the range of static auxiliary data incorporated into ecosystem structure. With this respect, the results of analysis of auxiliary topographic and climatic features of determined forest types serve to define the environmental conditions and their limits in a more comprehensive quantitative manner. Additionally, supported information can be used as a quantitative mean for evaluation of an empirical classification system such as the forest typological approach in Croatia. This refers primarily to scientific works and surveys in the last 80 years by Horvat [25, 26], Horvat, Glavač and Ellenberg [27], Bertović and Lovrić [28], Cestar *et al.* [29–31], Pelcer and Medvedović [32], Rauš and Vukelić [33], Trinajstić [34], Trinajstić and Franjić [35], Vukelić and Rauš [36], Vukelić and Baričević [37], Pernar and Bakšić [13] and Mesić [38].

Basic Environmental Properties of Beech Forest Types

The obtained results clearly support determined vertical differentiation of the beech bioclimates and ecosystem types over the particular altitudinal ranges, covariant with temperature and precipitation gradients. Based on the yearly average FAPAR, the most productive environmental niches are located in bioclimate D, the area of mountainous and sub mountainous beech forests, in the hillsides of the mountainous continental belt from 181 to 672 m (ecosystem averages). In this mountainous zone with temperature averages of 8.2–9.9°C and yearly precipitation of 863–1541 mm, the beech forms mostly pure homogeneous stands because of its high competitiveness. At higher altitudes, the beech appears with the silver fir forming mixed beech–fir forests (bioclimate C). The average altitudes for beech – fir mixed forests in the Dinaric zone is 936 m (C1), 1031 m (C3) and in Pannonian zone 559 m (C4). Respective average temperatures are 6.5°C (C1), 6.8°C (C3) and 7.9°C (C4) and average precipitation amounts to 1696 mm (C1), 2042 mm (C3) and 1073 mm (C4). Above this zone, in the highest altitudinal range, the subalpine beech forest type (B1) appears forming pure stands with characteristic bended trunks due to the long lasting snow on steep slopes. This type prevails at average altitudes of 1160 m, with an average temperature of 6.2°C and a precipitation amount of 2034 mm. In the Mediterranean littoral zone, the only beech ecosystem, H1, exists at relatively higher altitudes (886 m), with an average temperature of 7.9°C and precipitation of 1686 mm.

Photosynthetic Activity (FAPAR) of Beech Ecosystems

FAPAR [39], used as cumulative metrics, presents a proxy for assessing forest productivity (gross primary production). The

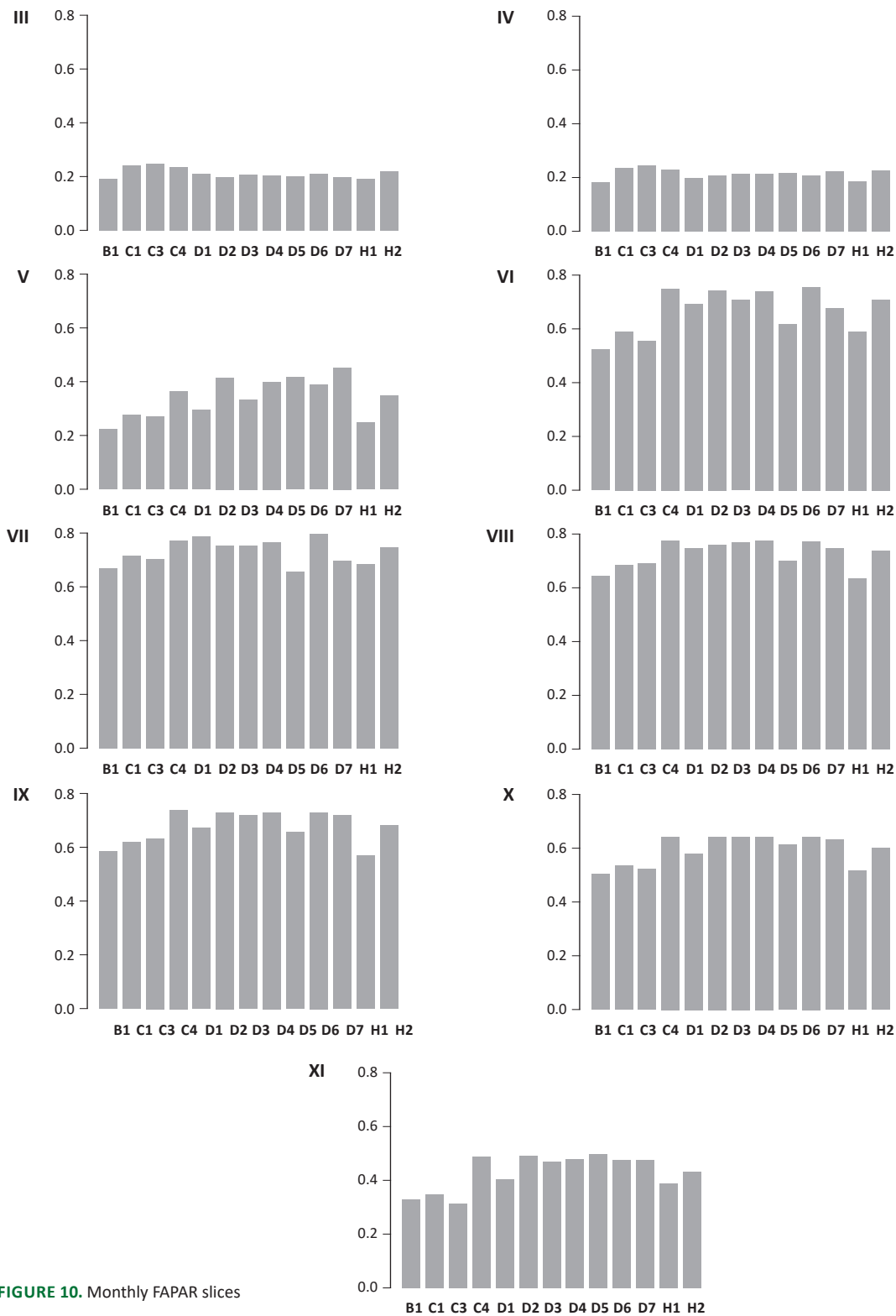


FIGURE 10. Monthly FAPAR slices

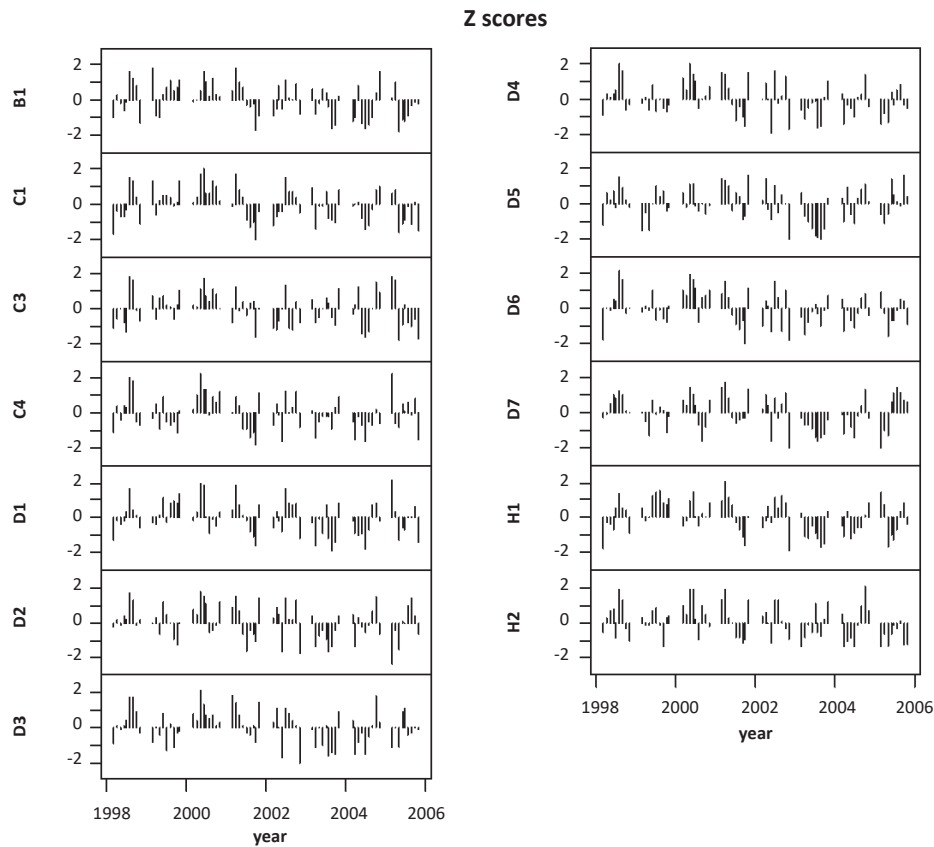


FIGURE 11. Normalized variations (z – scores) of FAPAR during the observation period

results of average FAPAR determine differences in the productivity of beech ecosystems in relation to climate and topography including edaphic factors at the intra bioclimatic level. The overall productivity of common beech forests declines as the altitude increases and towards xeric environmental margins. The common property of soils (rendzic leptosol on unconsolidated material, luvisol, cambisol), in the most productive beech forest types is intermediate to a larger depth (approximate min 60 cm), free drainage capability and a very broad range of soil chemical and physical characteristics that is in accordance with Peters [40] and Sanders *et al.* [41]. There is also evidence that soil properties provide some limitations in productivity. Beech stands on very shallow soils such as cambisols and rendzic leptosol and partly waterlogged soils such as gleyic luvisol show lower values of average FAPAR of all types in the mountainous beech zone (D). The possible influence of edaphic parameters is even more detectable in mixed beech – silver fir forests inside bioclimate C. Very large differences in productivity of mixed stands (C1, C3, C4), in favour of the continental Panonian ecosystem type (C4), could be attributed to more deeper and productive soils (i.e. dystric cambisol in relation to shallow folic cambisol and mollic leptosol).

There is a common trait that altitude has an impact on the duration of the vegetation period as can be corroborated in the

regional phenology studies of the common beech [42, 43]. The earliest onset of the spring phenological phases is observed in the lowest-lying sites and the latest onset in the uppermost sites. The dynamics of the autumn phenological phases had an opposite trend compared to the spring phenophases. This is also evident in our study through an earlier and gradual increase of FAPAR in May and June across bioclimatic vertical zones (D-C-B). The impact of altitude in the cessation of vegetation in October and November is not so pronounced. It is obvious that in the mid vegetation season (July, August), ecosystem productivity retains more constant values than in the onset and senescence periods. This indicates that during mid-season, the peak production of beech ecosystems is relatively uniform across the altitudinal gradient, with small differences related most probably to beech stand structural characteristics. A higher annual productivity in the common beech at lower altitudes can be associated more to the prolonged period of growth than the peak productivity potential of forests by themselves. Ergo, growth duration is most possibly modified by the climatic variations during springtime, during a period of the highest phenological sensitivity that is reflected through the highest FAPAR alternations. Generally, an earlier growth onset is due to the early spring warming and the delay of onset due to the spring chill. An accepted understanding of the impact of global

warming on phenology, given by Rötzer and Chmielewski [44], is that vegetation onset spreads southward at a rate of about 2 days per degree of latitude, the rate of change of the growth season length for forests is in a range of 6.4–6.7 days per °C. Warmer spring temperatures have advanced flowering dates by about 4 days per 1 °C and leaf unfolding by about 3.2–3.6 days per 1°C in Europe. As the possible outcome, a recent dendrochronological study of Tegel *et al.* [45] detected an unexpectedly rapid boost of beech growth after 1990 in the southern Balkan Peninsula (Albania, Macedonia) which is contrary to broad expectations of warming induced suppression of forests productivity in their southern Mediterranean limits. The beech is principally sensitive to excessive summer warming (June–September) that causes a water deficiency and drought as is confirmed in regional studies by Dittmar *et al.* [46], Dittmar and Elling [47], Van der Maaten [48] and Tegel *et al.* [45].

The results of our study reveal that the beech is very adaptable and opportunistic to newly emerging warming conditions because it can easily drift its vegetation onset earlier in the springtime and thus it is capable of prolonging the growing season and increasing its productivity to some degree. However, the smallest fluctuations of FAPAR during the mid-season (July, August, September) indicate that during this period of maximal productivity, the beech is relatively invariant to climate anomalies. One possible explanation is that the plant available water status of the majority of beech forest soils in mountain areas (with the higher total precipitation and lower average temperatures) is not the limiting factor for growth during this mid phenology stage. The prolonged droughts can cause soil water shortage which results

in a decline of productivity and earlier senescence of vegetation in the later stages (October, November) which is obvious due to recurring higher variations of FAPAR in this period. As a consequence, this can contribute to reduced productivity of the beech on an annual scale. In general, according to the provided seasonality of FAPAR variations, it can be concluded that with respect to climatic anomalies, the beech phenology behaves like an intra seasonal teeter, drifting over stable conditions during the mid-season and adapting to opportunities and limitations in springtime and autumn. Warmer conditions in springtime, on the one hand present an opportunity, but on the other, their extension throughout the year produces limitations for productivity in later stages of growth.

In the scenarios of the progression of global warming, there is a strong emphasis on the assessment of the future distribution range of beech forests which has been the subject of modelling and regional simulation studies [4–9]. Therefore, an estimation of environmental conditions on the limits of the beech distribution range, prone to many uncertainties, is of huge interest for the forest management. In this study, the boundary conditions of three marginal limits were assessed: upper altitudinal, south-eastern continental and the Mediterranean. By applying an ecosystem based approach, beech propagation also in relation to prevailing edaphic conditions in the marginal zones can be discussed, as it is often neglected in climate-vegetation modelling and simulations. Based on the maximal and minimal values of topographic and climatic factors, it can be concluded that the current upper altitudinal limit of the beech in Croatia is 1576 m with a minimal yearly temperature of 2.2°C and maximal

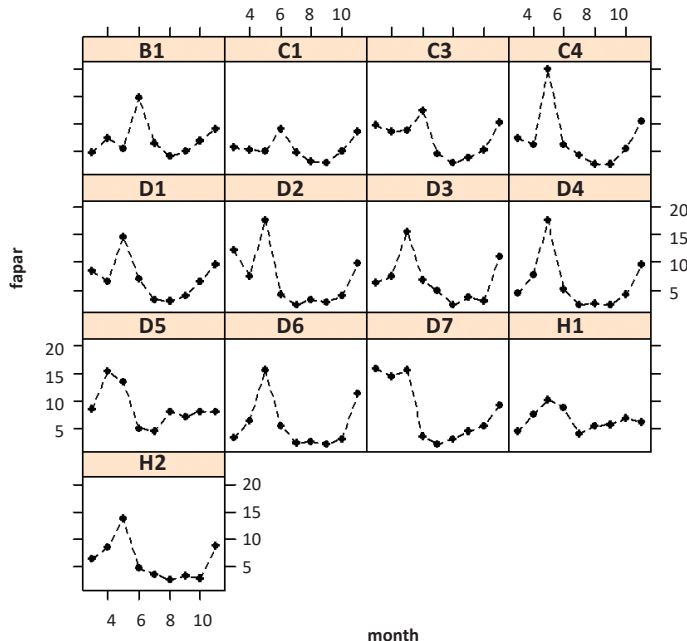


FIGURE 12. Coefficients of variation amongst beech ecosystem types

precipitation of 3444 mm. This shows that the current beech limit is very close to the upper terrestrial boundary determined by the upper ridges and hilltops of the Dinaric Alps ranging from 1750 to 1831 m. However, a future vertical succession of the common beech in this carstic environment is limited by very shallow soils on hard calcareous substrate and by eroded surfaces with plain rocks. On the other hand, the xeric limits for the beech in the continental region is at the lower slopes with a minimal altitude of 109.5 m in the Pannonian hills (max altitudes 900-110 m), on the junction with the Pannonian plain (95-115 m). The estimated maximal average temperature limitation for the beech is 10.8°C and minimal yearly precipitation is 739 mm, which exceeds the xeric limit of 9.3°C and is above the limit of 680 mm provided by Czúcz *et al.* [4]. Maximal values of Ellenberg's climate quotient do not exceed values of 27.9 which is below 28.9 [4], the limiting climatic conditions for the beech in Hungary. Productivity (mean annual FAPAR) of ecosystems at the lower boundary is, in general, below the average for the respective bioclimatic group (D) which could be partly attributed to less suitable edaphic conditions. The lowest lying ecosystem D7, (109.5-319 m) appears on seasonally waterlogged soil (gleyic luvisol) and seasonal oversaturation in soils most probably do not represent optimal conditions for beech growth. The seasonal modification of the Mediterranean climate, in particular an alternation of wet and mild winters and hot and dry summers, present constrains for beech distribution and productivity.

According to Maselli *et al.* [49], productivity of the Mediterranean beech forest is strongly determined by the start of the dry season. The Sub-Mediterranean beech forest (H1) assessed in this study has one of the lowest productivity. The impact of the summer drought in the Mediterranean can be identified by an earlier decreasing of FAPAR seasonal trajectory starting in August. Sub-Mediterranean beech forest covers the broadest altitudinal range starting from 20 m above sea level up to 1491 m, mostly on the south-western slopes (average inclination of 6.27%) of the littoral flank of the Dinaric Alps. The limiting climatic conditions for the presence of the beech in this region are a mean temperature of 13.5°C and 1145 mm of minimal precipitation. However, the maximal values of EQ of 18.66, well below the determined EQ limits for the beech in the continent, provide clues that the generalization of beech climatic limits using simple climatic indices should be undertaken with great care. Lower values of EQ can induce that, in addition to summer drought, edaphic factors such as shallow soils on limestone with a very limited water retention capacity, contribute to seasonal drought exposure which hinders the productivity and progression of beech forests further in the Mediterranean.

Resilience metrics provided in this study present means to quantify and identify various responses of beech ecosystems to climatic anomalies in the period of observation. Indices of resilience are suitable for quantification of the forest responses on an inter-annual time scale based on some directly measurable environmental

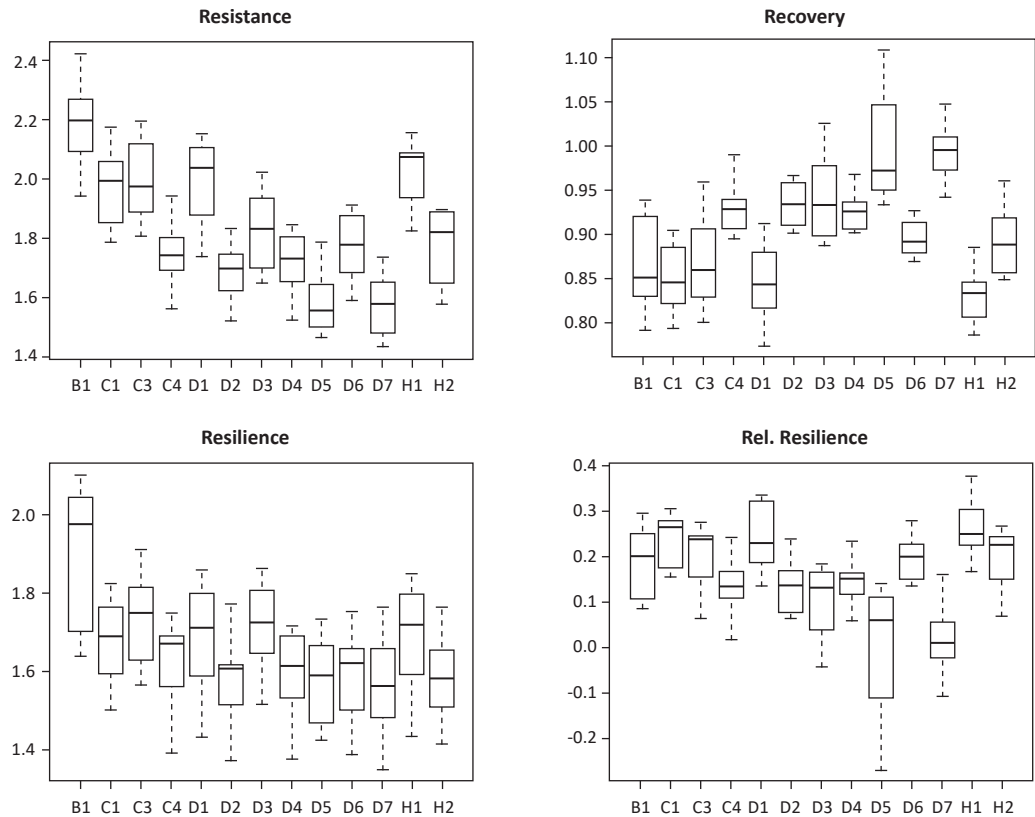


FIGURE 13. Resilience metrics based on intra-seasonal FAPAR variations

tree metrics such as a basal area increment or shoot growth and needle-length in the case of extreme drought conditions. Indices of resilience are mostly based on a single extreme climatic event or pointer years as seen in the studies of Lloret *et al.* [20], Sánchez-Salguero *et al.* [21], Herrero and Zamora [22]. However, applying these indices on an intra-annual scale using a monthly average FAPAR in July as a reference base [23] enables the inclusion of yearly responses for the whole period of observation (1998-2005) and thus, the calculated indices gain more statistical power.

It can be concluded from the calculated indexes of resilience (resistance, recovery, resilience and relative resilience) that the most resilient ecosystems are those occurring on the margins of the beech distribution range that was previously empirically assumed. Highest resistance is exhibited in marginal subalpine (B1) and sub-mediterranean (H1) beech forests. Highest resistance indicates that their springtime phenology is more suppressed by adverse climatic conditions than in other beech ecosystems. On the other hand, these two marginal ecosystems exhibit the lowest recovery rates. There is an obvious gradual increase in resistance with a rise in altitude and recovery in the opposite way, which presents a possible way of response of the ecosystems to climatic hindering and unbounding. Resilience represents a ratio of the average performance in the second half (August-November) and the first half of the vegetation season (April-June). Above all, the most resilient ecosystem is the subalpine beech (B1). Resilience of the bioclimatic types and ecosystems gradually decline towards lower altitudinal zones. Also, there is evidence of one of the highest resilience of the Sub-Mediterranean beech (H1) in comparison to most continental types at low to mid altitudes. At the present, there is confirmed evidence of inherited more adaptive behaviour of beech to droughts in favour of southern populations [50] but looking over a relatively large spatial scale (Germany, Croatia, Bulgaria and Greece). Providing more spatially intensive, ecosystem specific and a confirmatory explanation of beech adaptation, based on aforementioned results could be of the huge benefits for the forest management in the future to cope with the challenges of the global warming.

CONCLUSION

This study confirms the very adaptive potential of the common beech regarding a broad climatic, topographic and edaphic range.

The common beech can adapt to annual average temperature limits from 2.1°C to 13°C and precipitation limits from 739 mm to 3444 mm which presents an environmental spectrum of 11.4°C and 2705 mm respectively. Photosynthetic activity of beech is reducing towards the marginal limits of its distribution range. The most productive beech forest types are in the continental zone from low to medium altitudes, in medium deep soils. The common beech also shows a broad tolerance to edaphic factors. However, some limitations in productivity are observed on partly waterlogged soils in the lowest continental range and also in shallow soils on limestone in the upper zonal belt. This study also reveals how the specific environmental settings of 13 predefined forest types reflect on common beech productivity and phenology. Unfortunately, because of a relatively coarse spatial resolution of FAPAR (1.2 km) and an extensive country scale assessment, this study focuses on univariate macroclimatic relations rather than on specific multivariate interactions (i.e. altitude vs. aspect) which are usually more decisive in the formation of suitable microclimatic conditions for the common beech out of the optimal range.

Through assessment of variations in phenology, this study reveals some new insight into the adaptive potential of the beech to emerging climate change. The common beech has great potential to adapt to increasing spring warming by a preterm shift of phenology onset. The beech retains a relatively stable productivity during the peak of phenology in July and August, unrelated to external climatic forcings, so during this period the impact of summer warming could be possibly minor. By extension of droughts in later phenological stages, the beech can respond with preterm cessation of vegetation activity. These findings indicate that the flexibility of phenology timing, especially during springtime, presents one of the important mechanisms of adaptation and resilience of the common beech to global warming. The beech has likewise shown a very opportunistic response potential to earlier spring warming and in particular circumstances could achieve even higher rates of production throughout the season.

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The Role of Tree Mortality in Vitality Assessment of Sessile Oak Forests

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ABSTRACT

Background and Purpose: The drought-induced vitality loss of sessile oak (*Quercus petraea* (Matt.) Liebl.) has been continuously observed in Hungary for more than three decades. The decrease in stand density as a consequence of drought-induced mortality has not been taken into consideration in most of the monitoring methods.

Materials and Methods: Forest stands without any forest intervention during the last 30 years were selected. Quadrats were designated for the analysis in 18 sessile oak stands along a climatic transect in which foliage transparency and stand density were measured. Drought stress was defined by the water balance approach. By combining the foliage transparency and the relative stand density, a new cumulative assessment method of stand level vitality was introduced to get a more realistic picture about the effects of long-term drought (lasting for several decades) on the sessile oak forests in South-East Europe.

Results: The calculated health status (100% - vital; 0% - dead) of the sessile oak stands was between 70-90% in the moist South-West Hungary and below 50% close to its xeric limit. The individual tree-based vitality assessment method gave considerably higher values on 17 out of 18 sites.

Conclusions: Forest monitoring should also consider stand level-based tree mortality in oak forests while assessing health condition especially close to its xeric limit. The proposed new method provides a more realistic picture about the effects of climate change on sessile oak stands particularly for forest managers interested in changing in the wood stock of forests.

Keywords: *Quercus petraea* (Matt.) Liebl., drought, mortality, stand density, forest monitoring

INTRODUCTION

Global climate change, in particular warming, has been observed in all parts of the world [1], including Europe, where several severe drought periods have occurred during the last decades [2]. The climate of the Carpathian basin has also become more arid during the last 50 years. The mean annual temperature has increased while precipitation during vegetation season has decreased [3, 4]. In the future, the frequency and probability of drought periods may increase, resulting in higher evapotranspiration [5-8] and prolonged water stress.

Since the mid 1970s, droughts tended to occur in subsequent years in Hungary, which led to prolonged water deficits, partly owing to higher evapotranspiration caused by higher temperatures during the growing season [9]. Since

water is one of the limiting resources for trees on the xeric limit, and since it is also needed for transporting nutrients, drought could decrease the vitality of trees [10], reduce tree growth [11, 12], alter their crown leaf structures with increased percentages of defoliation, [13] and ultimately lead to tree death [14], consequently reducing stand density [15].

Sessile oak (*Quercus petraea* (Matt.) Liebl.) forests are one of the most important forest communities in the Carpathian basin, covering 20.8% of the total forested area in Hungary. Since the early 1980s, the severe dry periods have triggered mass mortality of stand-forming forest tree species including *Quercus petraea* [16, 17]. The multiyear drought in the beginning of the 1990s was especially severe

and affected oak forests mainly in the northeastern part of Hungary. These episodic diebacks acted as a self-thinning mechanism to adapt tree density to decreased soil water resources during acute summer droughts.

Different approaches (e.g. ecophysiological, dendroecological, growth modelling) used for the evaluation of stand density change might give different insights [18, 19], but reduced stand density increases water resources, nutrient and light for the retained trees by decreasing competition and canopy interception [20]. Therefore, stand opening could facilitate the regeneration of the surviving trees after drought periods [20, 21]. Improved water availability may reduce the risks of cavitation for trees and thus have a positive effect on stomata opening and consequently also on carbon uptake and growth. The results by McMahon *et al.* [22] indicated an increase for living above-ground forest biomass in the Mid-Atlantic region of the United States, but failed to account past mortality rates that could explain the deviation from the expected rate of biomass change [23]. Improving carbon uptake should mitigate further mortality by allowing the remaining trees to produce enough carbohydrates for their metabolism and defense against biotic attacks [24]. Gracia *et al.* [25] showed that thinning treatments of *Quercus ilex* L. facilitated to overcome severe drought episodes. Nevertheless, stand opening does not ultimately improve water availability since increasing light intensity may lead to a higher temperature at the ground level, which results in higher soil water evaporation and the development of a dense understorey vegetation. A recent study by Misik *et al.* [26] showed that *Acer campestre* L. responded successfully to the foliage gaps of sessile oak trees by forming a subcanopy layer. However, the subsequent establishment of grasses after self-thinning could prevent retained trees from benefiting from increased available soil water [27].

The Europe-wide existing forest monitoring system of ICP (International Cooperative Programme on Assessment and Monitoring of Air Pollution Effects on Forests - Level

I) offers a suitable, continent-wide evaluation of the forest vitality [28]. ICP was designed to detect and monitor changes of the health condition of living tree individuals annually. Thus, stand level data on Level I plots is not taken into account, although it might be an important indicator of the stand productivity for forest managers. In case of scattered and fragmented forest covers, a considerable number of grid intersections may fall outside of the forests, especially in semiarid regions at the retreating edge of the species distribution [29].

We aimed (1) to extend the established and widely used individual tree-based vitality assessment method with a stand level-based approach for oak forests near the xeric limit which incorporates the effects of the former mortality events through stand density. We have compared the results (2) of the different approaches along a climatic transect in Hungary.

MATERIALS AND METHODS

Investigated Stands

Forest stands without any forest intervention during the last 30 years were selected since a middle-aged sessile oak stand under average weather conditions in Hungary could outgrow an intermediate thinning (30%) within three decades [30]. Stands with wind/snow throw, nitrogen deficiency or pest outbreaks were excluded, resulting that the observed tree mortality was triggered exclusively by drought-induced mortality.

A 50x50 m quadrat was designated for the analysis in 18 sessile oak stands along the climatic transect from the humid region in South-West Hungary to the continental-semiarid region in North-East Hungary in 2011 (Figure 1).

The 60-100 years old sessile oak stands are situated in zonal position without major confounding factors among the stands (e.g. exposition, steep slope, seeping water). The mean annual precipitation sum ranges from 550 mm to 730

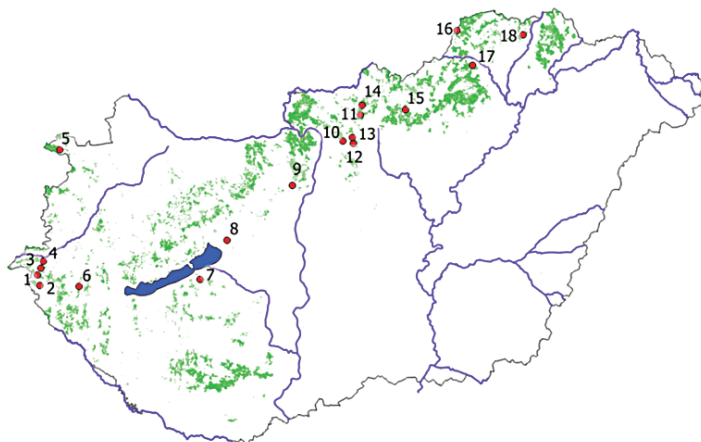


FIGURE 1. The investigated sessile oak stands in Hungary

mm. The mean annual air temperature changes between 8.5°C and 10.8°C [31]. The soil texture of the stands is loam and the soil can be characterized by deep fertile upper layer (>10 cm) in all sites (Table 1).

Foliage transparency is defined as the additional amount of skylight visible through the crown compared to the amount of skylight visible through a fully foliated crown. Foliage transparency was estimated in 5% classes by always the same observer based on the live, normally foliated portion of the crown and branches, excluding branches and large spaces between them [28].

The Definition of the Climatic Water Stress

The water balance model of Thornthwaite and Mather [32] was applied to quantify the climatic water stress for the stands between 1961 and 2010. Monthly weather data were provided by the CARPATCLIM Database [31] and interpolated climate data outside of CARPATCLIM target area provided by the Hungarian Meteorological Service (OMSZ) were used. The maximum extractable soil water (EW_m) was derived from soil texture and rooting depth using soil pit data of the assessed quadrats.

The water stress index (I_s) was calculated according to the methodology of Granier *et al.* [33]. Water stress was

assumed to occur when the relative extractable water ($REW = EW/EW_m$) drops below 0.4 (REW_c) under which transpiration is gradually reduced due to stomatal closure. Soil water deficit (SWD) was calculated as follows:

$$SWD = EW_m \times 0.4 - EW$$

Water stress index cumulates the difference between REW and REW_c for the vegetation period (April–September):

$$I_s = \sum SWD / EW_m$$

Novel Method for the Assessment of the Health Condition

The thinning of the crown and top drying are among the typical consequences of prolonged droughts. Eventually, a major part of the affected trees recover from the decline, but some trees die due to the severe conditions which reduce stand density.

We proposed a new method for the assessment of stand vitality which considered not only the health condition of living trees, but also the effect of mortality on the stand density. The health condition of the forest stand ($H_{sta\%}$) is defined by two indicators:

TABLE 1. Main variables of the assessed quadrats

Stand No.	Annual mean air temperature 1975–2010 (°C)	Mean annual precipitation sum 1975–2010 (mm)	Soil texture	Stand age	Mixing ratio of sessile oak (%)	Mean height (m)	Mean diameter (cm)	Stand density (trees·ha ⁻¹)
1	10.0	725	clay loam	76	95	25.9	39.2	253
2	10.0	717	clay loam	70	98	26.3	38.1	290
3	10.0	715	clay loam	93	96	27.3	34.0	374
4	10.0	708	clay loam	78	90	28.0	41.1	259
5	10.2	675	loam	86	98	22.6	32.6	335
6	9.9	692	clay loam	76	95	29.9	32.8	433
7	10.4	630	loam	77	99	22.4	30.4	340
8	10.8	575	loam	69	91	16.4	23.9	420
9	9.6	549	loam	91	97	21.0	35.7	267
10	9.9	558	loam	65	95	17.3	23.8	400
11	9.3	567	clay loam	69	98	22.2	26.9	370
12	9.8	548	loam	100	89	21.1	30.5	330
13	9.5	550	loam	61	88	18.6	22.6	496
14	9.1	569	clay loam	77	89	23.6	29.4	387
15	8.6	727	loam	75	99	21.6	32.3	389
16	9.1	661	sandy loam	84	93	23.0	28.6	420
17	9.2	571	loam	61	94	20.5	25.2	427
18	9.7	588	loam	86	99	22.3	28.3	417

- 1) Foliage transparency ($H_{fol} \%$) of the selected living tree individuals
- 2) Relative stand density ($D_{rel} \%$), expressed as the ratio of the current density (D_{cu}) and the fully stocked density (D_{fu}) of the stand:

$$D_{rel\%} = (D_{cu} / D_{fu}) \times 100$$

The fully stocked density of a stand is regulated by self-thinning [34, 35]. We have applied the yield tables of sessile oak in Hungary using the average yield class (III.) to determine the fully stocked density corresponding to the mean stem diameter of the stand. The yield tables were defined in the 1960s when there have not been any significant dry periods causing mass oak mortality yet, and therefore we considered these tables describing healthy stands.

These two indicators can be easily combined, i.e. the health status indicated by the foliage transparency is modified by the relative stand density:

$$H_{sta\%} = (D_{rel\%} \times (100 - H_{fol\%})) / 100$$

RESULTS AND DISCUSSION

Relative Stand Density and Foliage Transparency

The relative stand density ranged from 57% to 101% in 2011 in the studied quadrats. As an example, there was a major difference in the relative stand density between two stands (Bak-No.6 and Galgamácsa-No.12) with similar average stem diameters (33 cm and 30 cm respectively) (Figure 2).

The sessile oak stand No. 6 (age: 76 years) is located in the humid south-west part of the country while No. 12 (age: 100 years) is located near the xeric limit of the sessile oak distribution. The prolonged droughts in the past have

reduced the relative stand density to 65% in No. 12, while in No. 6 the stand density was significantly larger with 101 %.

Field observations showed that the mean foliage transparencies were low (below 27%) in all studied stands with varying relative stand density.

The Relationship between the Health Status of the Stands and the Water Stress Index

The stand level-based method showed that the vitality status ($H_{sta\%}$) of the sessile oak stands was between 70% and 90% in the humid southwestern region of Hungary while it was below 50% near its xeric limit in 2011 (Figure 3).

Prolonged droughts triggered a significant decrease of the relative stand density in the semiarid regions, while foliage transparency of the survived trees did not change significantly.

The determination of the relative stand density by using yield tables constituted one of the main uncertainties of the study. We assumed that the yield tables defined 50 years ago showed the stand densities for completely healthy stands. Earlier research on oak in Hungary showed that the oak decline began only in the second half of the 1970s, and therefore this assumption could be justified [36, 37]. Moreover, the applied yield tables were defined for the whole country based on scattered measurements and not for specific forest locations. For this reason, we included only the plots with average yield class in the analysis and used the corresponding values in the yield tables.

The long-term climatic water stress was defined using a simple water balance model [32] which originally was not intended to simulate water balance changes in the forested area. Unfortunately, water balance simulations could not be validated against measured soil water content, although the main aim was only to compare the climate conditions of the sites to each other. The application of a daily water balance model was omitted due to the need of a large number of

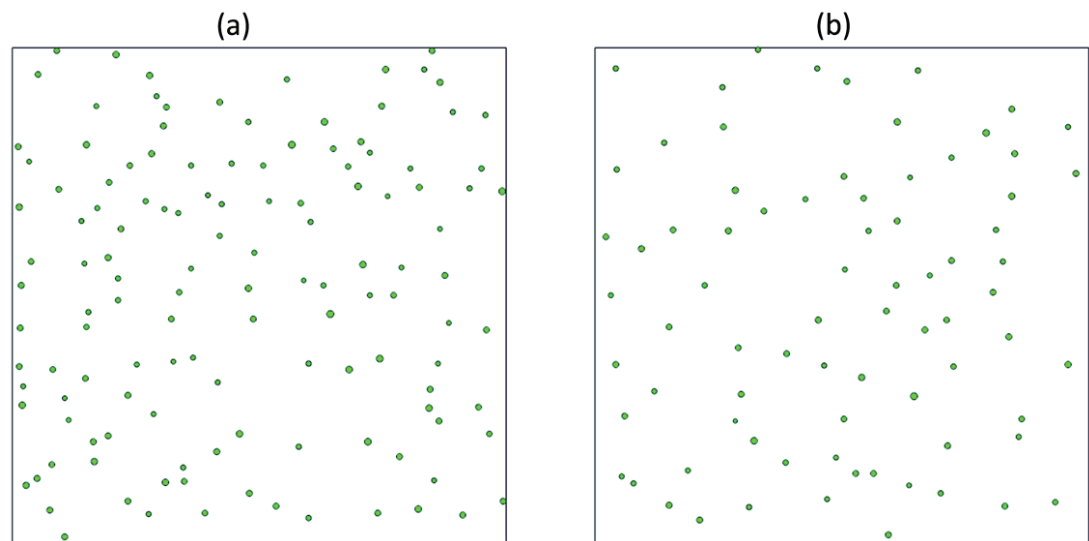


FIGURE 2. The spatial distribution of sessile oak trees in quadrats No. 6 (a) and No. 12 (b)

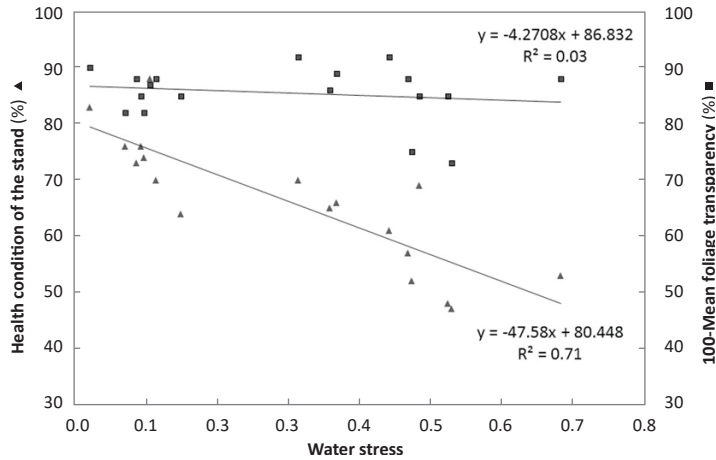


FIGURE 3. The relationship between water stress index (I_s) and the health condition ($H_{sta\%}$) of sessile oak stands (%) with triangles and the mean foliage transparency ($H_{fol\%}$) of sessile oak stands (%) with squares

variables and data to run the model.

The probable cause of the favourable condition of trees in the thinned stands was that transpiration and rainfall interception of the stand have reduced significantly due to the mortality of trees, thus leaving more available water in the soil for the recovery of the survived trees [38]. This way not only the available water in the soil has increased, but also the availability for nutrients.

The potential use of the stand level-based vitality assessment in forest monitoring is limited due to the fact that forest stands without any forest intervention for at least three decades are needed. However, since our results include long-term changes due to drought events, we propose our stand level-based method as complementary to the ICP monitoring. The new method could be implemented on ICP plots situated in national parks, forest gene conservation areas and long-term experiment sites, especially along the xeric limits of tree species.

CONCLUSIONS

We have introduced a new health assessment method for sessile oak which incorporated relative stand density as the indicator of extra tree mortality due to drought events. 18 sessile oak plots were investigated, on which the stand density and the current health status of trees were

determined. Additionally, the water stress was calculated for each plot using a robust water balance model.

The results showed that the current health status of the stands was good in terms of foliage transparency regardless of the magnitude of the long-term water stress. However, if the relative stand density was included in the evaluation then the relationship between the water stress index and the health status became strong. The probable reason for the good condition of the surviving trees was greater availability of water and nutrients due to the extra thinning effect of tree mortality.

The results suggest that forest monitoring should also consider stand-level data in oak forests while assessing the health condition. In our view, this new method provides a more realistic picture about the sessile oak stands, particularly for forest managers interested in changes in the wood stock of forests. The better understanding of the mortality dynamics of oak may also help to predict more reliably the possible shift of its distribution area due to future climate change.

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Stand Regeneration Characteristics of Beech and Fir Forests in Gorski Kotar Region

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ABSTRACT

Background and Purpose: Beech-fir forests cover about 13% of forest land in Croatia, thus being a significant forest resource that is dominantly managed by uneven-aged selection management system. Continuous and successful regeneration is an essential prerequisite for this kind of forest management. Therefore updated and sound information on the present state of regeneration is important, especially in the context of climate change and the actual structure of beech and fir forests. The aim of this paper is to present and analyse current state of regeneration in beech and silver fir forests of Gorski kotar region, with regard to forest ownership (management model), forest communities and habitat characteristics.

Materials and Methods: Field measurement has been done on 313 plots in the beech and fir forests of Gorski kotar region, Croatia. The assessment of regeneration was based on measurement of trees ranging from 0 to 10 cm dbh (species, number of trees, average height) and also the estimation of seedlings up to 1.30 m high (regenerated area in 10% classes, the share of tree species, the origin of stand establishment, regeneration quality).

Results: Attributes like the success of regeneration, the structure of seedlings by species and the recruitment of saplings were analysed with regards to ownership, forest communities and the aim of forest management. The results indicate poor incidence of regeneration especially of silver fir (more than 50% percent of field plots with no regeneration). Silver fir saplings (height > 1.3 m, dbh ≤ 10 cm) are registered on 9% of plots, average number being only 165 per ha (all species together 2044 per ha). The estimated average share of the regenerated area is 16.3% of total forest area, contributed by 5.2% of conifers and 3.8% silver fir. A total of 14 tree species were recorded on regenerated areas, clearly dominated by broadleaves, especially beech (over 50%).

Conclusions: Significant differences in regeneration attributes were proven by ANOVA between ownership categories, forest communities and habitat characteristics. In order to get better insight on the structure of regeneration, it is recommended to improve future assessment by establishing special sub-plots for measurement of seedlings by species.

Keywords: selection forest management, silver fir, European beech, regeneration structure, recruitment

INTRODUCTION

Stand regeneration is a basic task of forest management and therefore natural regeneration with minimal interventions presents a special challenge, as well as the aim of modern forest management planning [1].

Uneven-aged forest management including also selection management approach in circumstances of emphasised multi-functionality and ecological significance of forests on the global level forest science is recognized as the most acceptable management approach. Since the basic

prerequisite for establishing and maintaining selection forest management is continuous stand regeneration through entire stand area, then stand regeneration assessment is more demanding in relation to even-aged management.

Numerous studies of intensity and models of canopy openings in terms of gap size and its enlarging [2], as well as the success of regeneration in selection forests have been published recently. Possibly, due to the complexity of stand regeneration estimations in beech-fir forests which

include assessments of seed plants' abundance, such research in Croatia was mainly carried out on sporadic permanent sample plots or individual management units [3, 4]. Regeneration processes in beech-fir old-growth forests in Croatia and abroad were studied considerably more [5, 6]. The results of influential factors and relations with stand structures and regeneration success were also published, e.g. the impacts of stand opening models [2], light intensity [7], population of herbivores [8, 9] and fellings [10] on quality and abundance of silver fir seedlings.

Integrating research based on permanent sample plots and National Forest Inventory (NFI) data could provide a basis for the development of prediction models of stand regeneration in frame of stand growth simulators [11, 12]. Thereof, the existing stand growth simulators provide possibilities of research of stand openings (selection cut intensity) and their influences on stand regeneration [2].

In Croatia, stand-wise inventory has been conducted periodically every 10 years. However, the estimation of stand regeneration structure has not been included. On the other hand, the estimation of stand regeneration structure is included in almost all national inventories, especially in countries where national inventory has a long tradition [13]. Until now only the first national forest inventory in Croatia has been conducted, in which the assessments and information of forest regeneration are included [14].

It is clear that many factors influence stand regeneration and also that forest trees react by increased seed production in circumstances of stress. On the other hand, the abundance and survival of seedlings depend on ecosystem stability. In the context of climate changes, recent research on climate changes (e.g. the influence of air temperature increase or dry periods on the abundance and growth of seedlings) has special importance [2, 15]. Climate changes can influence the appearance of several tree species in stand regeneration, namely tree species' alterations in stand structure. Climate change in specific areas is characterized by climatic extremes that do not have a clear trend in a short term. In such circumstances, the appearance of pioneer and wide-valent tree species that are adaptive to such conditions can be expected. Consequently, stand regeneration characteristics can be used as valuable indicators of ecosystem stability, the success of forest management in the past and of forest development in the future.

The aim of this paper is to obtain and analyse regeneration characteristics of beech and fir forests in Gorski kotar region, as well as to determine implications of stand regeneration on future forest management in the region, based on the data set obtained from national forest inventory field sample plots. The main assumption is that the abundance and structure of stand regeneration in beech and fir forests in Gorski kotar region during last decades would not sustain establishment and maintenance of selection management, particularly in the sense of maintenance of structural and inter-species relationships in the beech-fir forests. Additionally, significant differences between different site and stand factors and also the impact of management approaches (ownership) on stand regeneration can be expected. Since the success of regeneration directly influences future management

activities, it is assumed that the adaptation of management model to current site and stand characteristics of the beech-fir forests would be needed in the future.

MATERIAL AND METHODS

Study Site

The study site encompasses beech and fir forests in Gorski kotar region (Figure 1). Gorski kotar, known as the "Green heart of Croatia", spreads on 1273 km² [16]. The region belongs to the continental carst area where forests grow on limestone-dolomite substrates (90%) and partly on silicate substrates with basic soils (cambisols and leptosols). The dominant forest type is beech-fir forest community *Omphalodo-Fagetum* [17], while silver fir forests on silicate *Blechno-Abietetum* encompasses smaller part of forests. The altitude ranges between 350 and 1534 m above sea level. The studied area is characterized by continental climate with average annual temperature of 7.3°C and annual precipitation of 2275 mm (meteorological station Delnice). North-east and south-west aspects with many sunny sites are dominant, with inclination reaching above 20% [16].

Field Data

Data on structure and characteristics of stand regeneration in Gorski kotar region were obtained from field measurements and assessments in the first national forest inventory conducted in the area during 2007. The procedures and methods of the inventory are described in Čavlović *et al.* [18]. The estimation of stand regeneration characteristics was based on the assessment of seedlings and saplings. The structure of seedlings up to 1.30 m height was estimated on a circular plot (radius 13 m) with the assessment of 1) regenerated area (plot coverage with seedlings) in 10% classes, 2) the origin of plants (stand establishment), 3) the share of tree species, 4) main tree species, 5) regeneration quality, 6) damage and the cause of damage and 7) the degree of damage. On a sub-plot with radius 2 m trees ranging from 0 to 10 cm dbh were measured according to tree species and diameter classes (0-3.99, 4-6.99, and 7-9.99 cm) and the assessment of average tree heights of several tree species within several diameter class. Qualitative plot data on administrative categories, ownership, site and stand variables were also recorded and used in the analyses of stand regeneration.

Data Analysis

The database of plots according to regeneration state and structure, ownership, site and stand characteristics from sampled 313 plots was designed. Two indicator variables of regeneration were analysed: regenerated area (area covered by juvenile plants in %) and the number of saplings (trees dbh<10 cm). For a more clear presentation, species were grouped in categories (conifers and broadleaves). One-way analysis of variance (ANOVA) was used for testing differences of regenerated area and the number of trees between categories (ownership, forest type (community), canopy closure, soil depth, rockiness, aspect). In the case of significant statistical differences post-hoc LSD test was

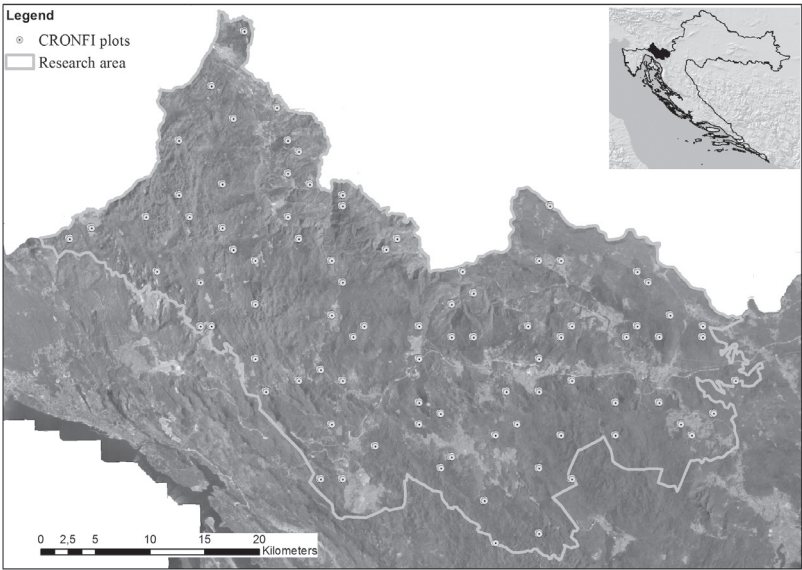


FIGURE 1. Study site area and the sample of field plots

used. All statistical analyses were performed with level of significance being 0.05. The database was designed in EXCEL 2010, while the statistical analyses and the preparation of graphical presentation were performed in STATISTICA 11.1.

RESULTS

Regenerated Area

An average regenerated area of 16.6% was obtained. Silver fir contributes to the seedlings with less than one quarter (3.82%), and by including Norway spruce conifers contribute with the share of 5%. The remaining 11.6% is composed of broadleaved tree species with dominant share of European beech (8.8%) followed by Norway maple (1.8%), while seedlings of other broadleaved tree species in average cover less than 0.2% of the sample plot area (Table 1).

The number of saplings and young trees (0 to 10 cm dbh) amounted to 2044 per ha and can generally be considered sufficient for sustainable selection management. However,

silver fir as the most important tree species in ecological and management sense, contributes with only 165 trees per ha. On the other hand, in the high share of other broadleaves (over 50%) prevails rowan, a species which has no management importance in Gorski kotar region. This fact indicates regeneration problems in the studied forests in the long term, as well as caution in interpreting the importance of saplings and young trees as indicators of stand regeneration. As expected, the number of saplings and young trees is decreasing with the increase of diameter classes as a consequence of competition and tree growth processes.

The results of regenerated area according to six selected management-, site- and stand- characteristics of the studied beech and fir forests (ownership, forest type (community), canopy closure, soil depth, rockiness and aspect) are presented in Figure 2 and Table 2. The area regenerated by conifers was usually lower in relation to broadleaves, with exception of private forests where conifer seedlings cover in average almost 19% of sample plot. Forest type has shown

TABLE 1. Stand regeneration in Gorski kotar represented by average seedling coverage (by tree species) and the number of saplings per ha (by diameter classes and tree species).

Stand regeneration	Tree species				Total
	Silver fir	Other conifers	E. beech	Other broadleaves	
Average share of stand covered by seedlings up to 1.3 m height (%)					
	3.82	1.34	8.86	2.56	16.60
Number of saplings (0-10 cm dbh) per ha by diameter classes					
0 – 3.99 cm	78	66	557	775	1476
4 – 6.99 cm	59	23	107	186	375
7 – 9.99 cm	28	18	59	89	194
Total	165	107	723	1050	2044

influence whereas conifer species have better regeneration success in forest communities with dominant share of silver fir and Norway spruce (coverage up to 10 %), unlike forest communities with dominant share of broadleaved tree species where the obtained average coverage of conifer seedlings is up to 5%. The influence of crown coverage and aspect was shown as unclear, while soil depth showed influence on the abundance of broadleaved seedlings (Figure 2).

The results of one-way analyses of variance showed statistical significant differences of regenerated area according to: ownership for both conifers ($p=0.000$) and broadleaves

($p=0.032$), forest type (community) only for conifers ($p=0.000$), soil depth only for broadleaves ($p=0.0013$), rockiness for broadleaves ($p=0.000$) and aspect for broadleaves ($p=0.020$) (Table 2). The level of canopy closure has not shown to make significant difference neither for conifers nor for broadleaves.

The best regeneration of conifers is observed in private managed forests that are outstanding to other ownership categories (proven significantly different by LSD test, Table 2). For broadleaved seedlings, less differences with only significant difference between state forests and private unmanaged forests were obtained. Forests of Norway spruce and silver fir

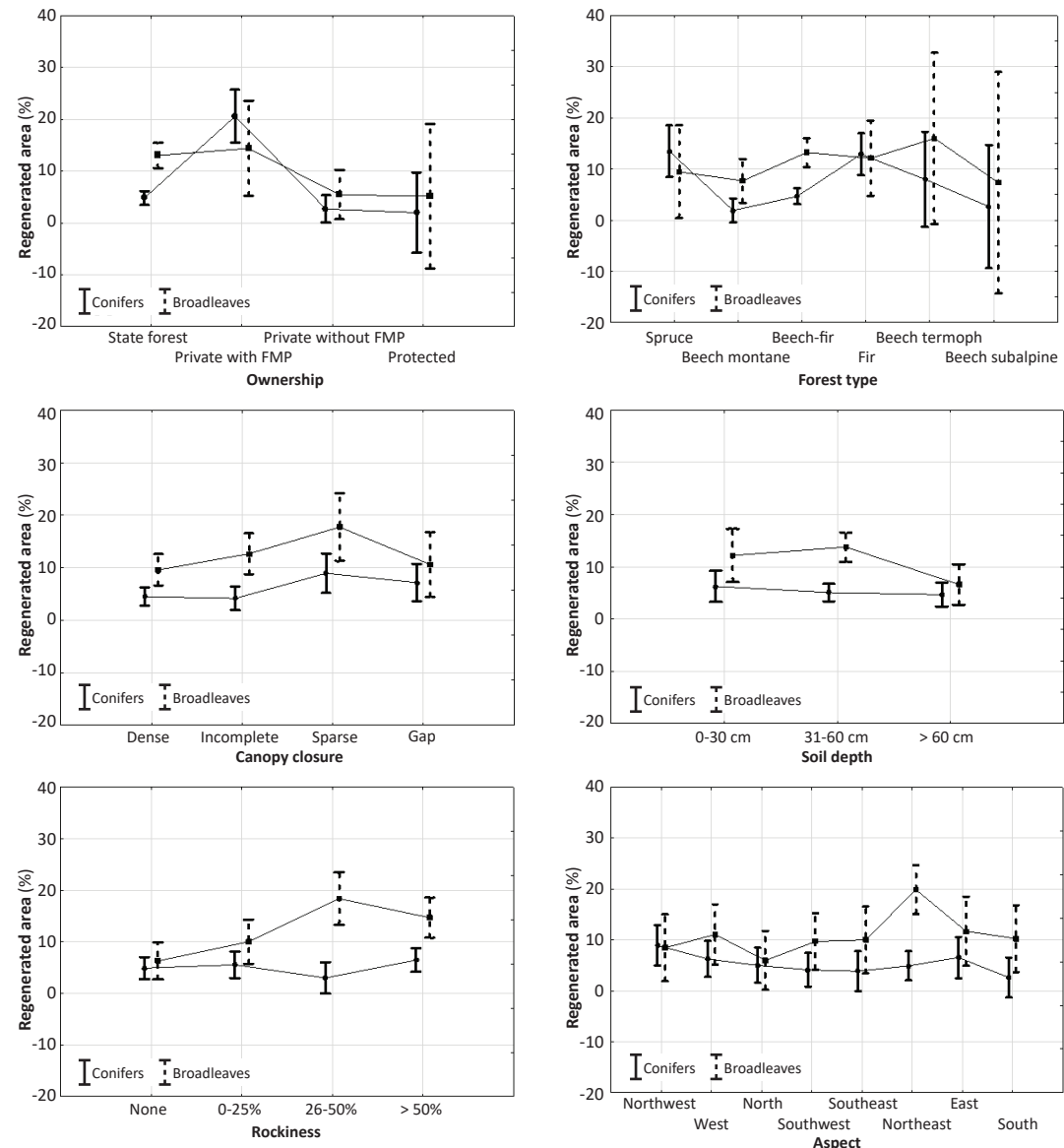


FIGURE 2. Regenerated area (%) according to categories of management, stand and site variables. Vertical lines stand for 95% confidence intervals.

TABLE 2. Descriptive statistics, ANOVA and post-hoc results for regenerated area by ownership, forest type, canopy closure, soil depth, rockiness and aspect.

	Regenerated area (%)								
	Conifers				Broadleaves				
	n	Arithmetic mean	Stand. deviation	ANOVA <i>p</i> value	Post hoc	Arithmetic mean	Stand. deviation	ANOVA <i>p</i> value	Post hoc
Ownership									
State forests	228	4.83	9.47	0.000*	a	11.46	18.90	0.032*	a
Private with FMP	16	20.59	22.96		b	13.02	20.19		ab
Private without FMP	60	2.70	8.99		a	14.41	15.24		b
Protected	7	2.00	3.83		a	5.47	13.86		ab
Total	311	5.17	10.98			11.46	18.90		
Forest type									
Spruce	17	13.47	17.19	0.000*	a	9.47	15.06	0.399	-
Beech montane	76	1.90	6.20		b	7.70	15.58		-
Beech – fir	178	4.68	8.74		b	13.24	20.36		-
Fir	26	12.88	20.93		a	12.12	21.02		-
Beech thermoph.	5	8.00	17.89		ab	16.00	21.91		-
Beech subalpine	3	2.67	4.62		ab	7.33	6.43		-
Total	305	5.21	11.04			11.54	19.03		
Canopy closure									
Dense	152	4.49	11.40	0.091	-	9.59	17.68	0.134	-
Incomplete	91	4.16	8.77		-	12.65	19.94		-
Sparse	33	8.94	12.87		-	17.73	21.82		-
Gap	36	7.17	11.67		-	10.61	17.32		-
Total	312	5.17	10.97			11.46	18.87		
Soil depth									
0-30 cm	52	6.27	9.32	0.707	-	12.19	18.04	0.013*	ab
31-60 cm	170	5.09	11.74		-	13.79	19.75		a
> 60 cm	90	4.70	10.38		-	6.63	16.80		b
Total	312	5.17	10.97				11.46		18.87
Rockiness									
none	102	4.90	11.50	0.341	-	6.28	15.34	0.000*	a
0-25 %	72	5.54	11.45		-	10.01	15.74		ac
26-50 %	51	3.00	6.12		-	18.37	24.91		b
> 50 %	87	6.47	12.03		-	14.68	19.32		bc
Total	312	5.17	10.97			11.46	18.87		
Aspect									
Northwest	31	8.95	16.52	0.445	-	8.47	17.55	0.020*	a
West	38	6.28	10.21		-	11.09	15.00		a
North	40	5.01	13.29		-	5.99	9.44		a
Southwest	44	4.15	6.95		-	9.72	19.02		a
Southeast	31	3.85	10.19		-	10.02	17.55		a
Northeast	58	4.93	10.95		-	19.90	26.36		b
East	29	6.55	11.23		-	11.72	16.25		ab
South	31	2.63	7.78		-	10.27	17.15		a
Total	302	5.22	11.11			11.50	18.90		

*statistically significant

have significant difference in relation to beech and beech – fir forests when abundance of conifer seedlings is considered. Significant differences between categories of rockiness, soil depth and aspect are proven only for broadleaved seedlings as shown in Table 2.

Number of Saplings

The number of saplings (trees with dbh<10 cm) according to the abovementioned categories is presented in Table 3 and Figure 3. Alike regenerated area, the abundance of saplings (number per ha) indicates outstanding difficulties in stand regeneration by conifers, namely silver fir. Almost none of the six characteristics (factors) of the studied forests have shown significant influence on the abundance (appearance) of silver fir saplings. Some differences indicate the influence of forest communities. Thus, in thermophile beech forests there is the highest number of silver fir saplings. However, in such site conditions small silver firs are rarely saplings, but usually these are grown and mature trees. Differences in the number of broadleaved saplings are more expressed. The total number of saplings per hectare seems sufficient, but the fact that rowan contributed to almost one half indicates a low stand regeneration potential. Soil depth (and the resulting site quality) expectedly showed positive influence on the abundance of broadleaved saplings (Figure 3).

One-way analyses of variance showed statistically significant differences of small trees abundance only for soil variables (soil depth, rockiness) as follows: soil depth for broadleaves ($p=0.00001$) and for all species ($p=0.00003$); and rockiness for conifers ($p=0.03504$), for broadleaves ($p=0.02572$) and for all species ($p=0.00427$) (Table 3).

According to post-hoc LSD test for broadleaved and for all tree species small trees, significant differences between the deepest soil and other categories of shallower soil were proven. Similarly, the first category of rockiness (without rockiness) has significant difference in relation to other categories of rockiness for all groups of tree species (conifers, broadleaved, all species) as shown in Table 3.

DISCUSSION

The level and structure of forest regeneration is of special concern for forest management planning. Forest management in Croatia is predominantly based on natural regeneration, whereas in uneven-aged beech-fir stands it is being exclusively used.

However, due to various causes, regeneration in beech-fir selection forests is found to be insufficient. It can be tracked in diameter structure from stand-wise inventories, sporadic research on permanent plots in managed forests [19, 20] and old growth forests [21], and also from the results of the first national forest inventory [14].

Systematic field measurements and assessments performed within national forest inventory on 313 sample plots enabled sound analysis of regeneration in beech and fir forests in Gorski kotar. Spatial stratification according to different criteria helped to track possible influences on regeneration. Specific multilayer structure of selection forest complicates the assessment and measurement of regeneration

and juvenile trees and especially the interpretation of the results [7, 22]. The methodology of measurement used is the same for all forest types and regions, with regeneration being assessed by measurement of trees ranging from 0-10 cm dbh and ocular assessment of regenerated area. While saplings (trees of 0-10 cm dbh) were measured on a small plot ($r=2$ m), regenerated area (seedlings) was assessed on a rather large one ($r=13$ m). The assessment of the regenerated area was therefore time-consuming due to the size of the plot, and it also resulted with rough data (estimate of the area instead of density) with questionable consistency between field crews (subjectivity of assessment). Possible improvement in the next forest inventory would be introducing a small subplot for counting and measurement of seedlings (up to 130 cm height). This approach would improve data collection and make data more precise and less subjective. Categorical variables would however still be necessary for assessing the origin, quality and damage of seedlings.

The acquired data are, however, valuable for the inspection of natural regeneration in selection beech-fir forests. Since silver fir is the fundamental species for these forests, its regeneration is crucial for their survival. Average regenerated area of silver fir was assessed 3.82%, thus clearly indicating problems with natural regeneration. By adding spruce, total conifer regenerated area is about 5%, whereas broadleaved saplings cover about 11%, beech being dominant (about 9%) and sycamore maple following with less than 2%. Other species are sporadically present with regenerated areas less than 0.2%.

The presented results on structure of regeneration clearly indicate evident change in uneven-aged beech-fir forests in Gorski kotar region. The present stage of regeneration will expectedly lead to a decreasing share of conifers (especially fir) in favour of the increasing share of beech and other broadleaves. Possible causes of that change are as following: a) natural substitution of species, b) recovery of beech that was reduced by past management, c) alteration of habitat conditions as a result of climate change, d) management activities that favour broadleaves. Most likely all mentioned causes occur simultaneously and interact with different intensities on each area.

These forests are traditionally characterized by low intensity selection harvests and natural regeneration without any seeding or planting. The results of the inventory confirm this fact - the recorded seedlings are all of natural and mostly generative (97.4% plots) origin. However, due to the present level of regeneration and habitat conditions, it is questionable whether future management can sustainably rely exclusively on natural regeneration. This is specially emphasized in the case of silver fir which is a species of fundamental importance in the selection management. An insufficient level of natural regeneration leads inevitably to the collection and production of seeds and seedlings of silver fir, and also requires planning the planting procedures. At the same time adequate management activities should raise the level and success of natural regeneration [10, 19, 20] wherever and as much as it is possible.

The quality of saplings heavily relies on ecological conditions, especially on the intensity of light. Since this variable was assessed for all species together, detailed analysis

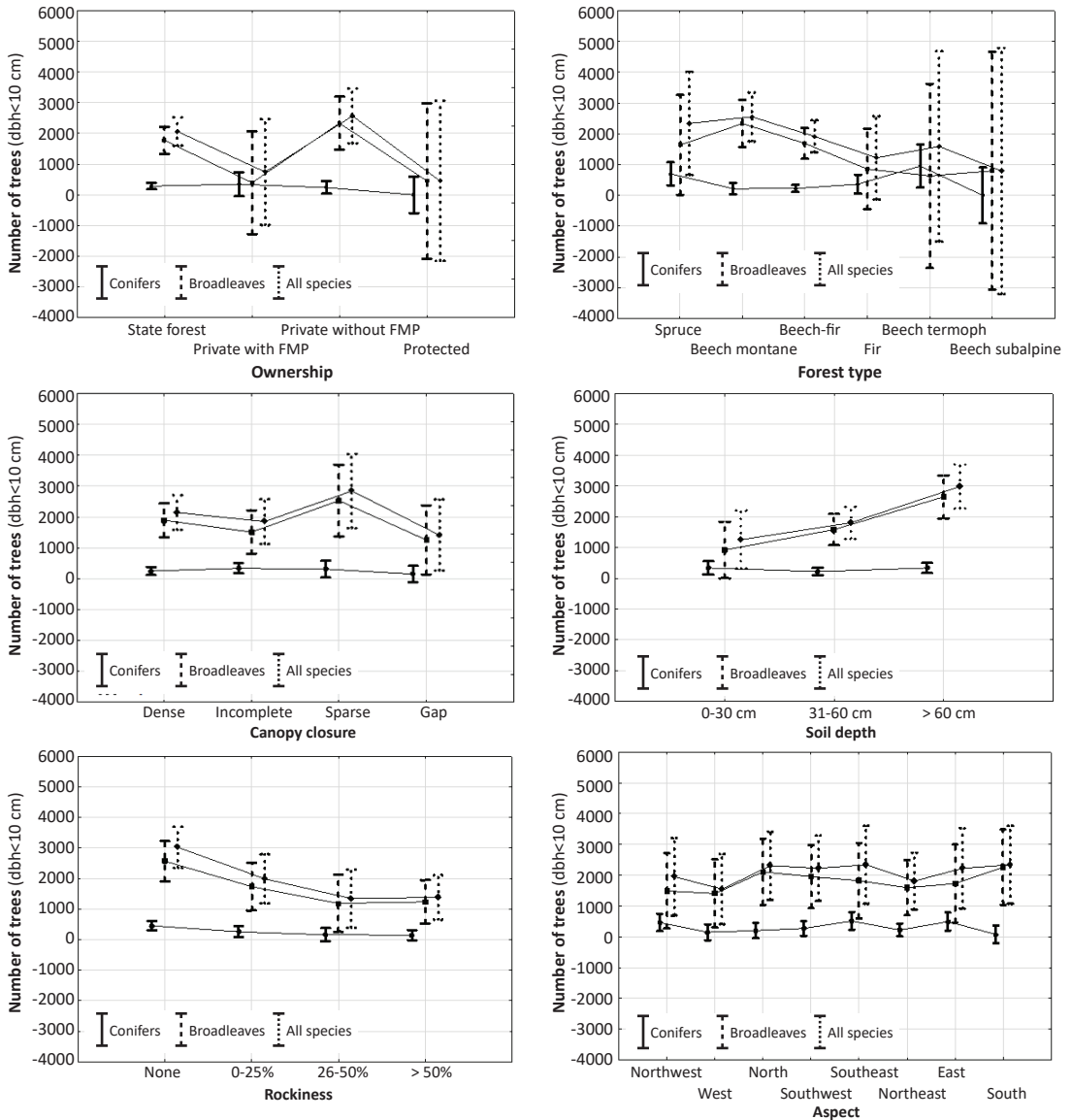


FIGURE 3. The number of saplings (dbh < 10 cm) according to categories of management, stand and site variables. Vertical lines stand for 95% confidence intervals.

is not possible. According to the results, the quality of saplings was assigned as very good and good on 90% of plots. It can be presumed that the results for silver fir would be somewhat different if assessed separately. It can generally be concluded that saplings are of good quality and survive when they appear, thus indicating favourable habitat conditions. On the other hand, management activities do not ensure enough level of sapling occurrence on most areas [20, 23]. Future management influence is, however, supposed to change due to significant change in selection management approach recorded in the past decade [24].

Researched beech-fir stands can be considered to be part of a balanced ecosystem since seedlings were not damaged on 75% of plots. On the rest of the plots, the most common causes of damage were insects and sporadically diseases and herbivores. It is even a more important finding since herbivores are considered to be a significant threat to regeneration in Middle European beech-fir forests [8, 9, 25]. This result can possibly be addressed to successful game management and also to presence of natural predators (lynx, wolf, bear). Other reasons can be close to nature forest management that enables abundance of available feed [26].

TABLE 3. Descriptive statistics, ANOVA and post-hoc results for the number of saplings per ha by ownership, forest type, canopy closure, soil depth, rockiness and aspect.

	Number of trees (dbh<10 cm)												
	Conifers					Broadleaves				All species			
	n	Arithmetic mean	Stand. deviation	ANOVA <i>p</i> value	Post hoc	Arithmetic mean	Stand. deviation	ANOVA <i>p</i> value	Post hoc	Arithmetic mean	Stand. deviation	ANOVA <i>p</i> value	Post hoc
Ownership													
State forests	228	286.2	812.3	0.769	-	1776.5	3490.2	0.153	-	2062.7	3626.0	0.174	-
Private with FMP	16	348.2	709.9		-	397.9	1125.4		-	746.0	1655.7		-
Private without FMP	60	238.7	806.5		-	2334.3	3579.5		-	2573.0	3544.8		-
Protected	7	0.0	0.0		-	454.7	1203.1		-	454.7	1203.1		-
Total	311	273.8	796.0			1783.5	3412.6			2057.2	3518.3		
Forest type													
Spruce	17	702.2	969.8	0.072	-	1638.4	2460.3	0.431	-	2340.5	2616.2	0.577	-
Beech montane	76	219.9	617.8		-	2335.0	4850.7		-	2554.9	4943.7		-
Beech – fir	178	228.0	829.6		-	1689.9	2931.1		-	1917.9	3037.6		-
Fir	26	367.3	818.7		-	857.0	1525.3		-	1224.3	2077.9		-
Beech thermoph.	5	954.9	1307.6		-	636.6	1423.5		-	1591.5	1488.8		-
Beech subalpine	3	0.0	0.0		-	795.8	1378.3		-	795.8	1378.3		-
Total	305	274.0	802.1			1750.7	3397.3			2024.7	3509.2		
Canopy closure													
Dense	152	251.3	811.0	0.647	-	1895.2	3714.4	0.367	-	2146.5	3830.2	0.354	-
Incomplete	91	341.0	864.8		-	1512.8	2812.3		-	1853.9	2975.3		-
Sparse	33	313.5	794.3		-	2532.0	4365.2		-	2845.5	4331.4		-
Gap	36	154.7	496.8		-	1260.0	2213.3		-	1414.7	2322.9		-
Total	312	272.9	794.9			1777.7	3408.6			2050.6	3514.5		
Soil depth													
0-30 cm	52	336.7	950.1	0.439	-	918.2	1714.6	0.008*	a	1254.9	1819.7	0.007*	a
31-60 cm	170	220.0	739.7		-	1582.2	2805.1		a	1802.2	3018.2		a
> 60 cm	90	336.0	800.0		-	2643.7	4765.4		b	2979.7	4754.6		b
Total	312	272.9	794.9			1777.7	3408.6			2050.6	3514.5		
Rockiness													
None	102	452.5	1071.2	0.035*	a	2566.8	4704.4	0.026*	a	3019.3	4781.7	0.004*	a
0-25 %	72	254.2	776.8		ab	1735.2	3133.2		ab	1989.4	3325.6		ab
26-50 %	51	156.0	503.8		b	1185.9	2131.6		b	1341.9	2185.1		b
> 50 %	87	146.3	478.2		b	1234.8	2007.9		b	1381.2	2010.5		b
Total	312	272.9	794.9			1777.7	3408.6			2050.6	3514.5		
Aspect													
Northwest	31	462.1	980.5	0.190	-	1488.9	3533.5	0.964	-	1950.9	3628.4	0.969	-
West	38	146.6	407.7		-	1403.1	2038.8		-	1549.7	2017.8		-
North	40	198.9	643.5		-	2108.8	5899.0		-	2307.7	6035.7		-
Southwest	44	271.3	923.3		-	1953.3	3831.6		-	2224.5	3993.9		-
Southeast	31	513.4	1097.8		-	1822.6	2688.4		-	2336.0	2709.8		-
Northeast	58	219.5	866.5		-	1591.5	2494.3		-	1811.1	2682.3		-
East	29	493.9	835.0		-	1728.7	2724.2		-	2222.7	2880.1		-
South	31	77.0	315.3		-	2259.0	2726.6		-	2336.0	2771.4		-
Total	302	281.9	806.4			1783.9	3430.4			2065.8	3538.3		

*statistically significant

The abundance of saplings indicates successful regeneration during the past decades. However, in beech-fir stands, depending on the site characteristics and stand attributes, trees can be held down for years without reaching large dimensions. This is in particular characteristic of silver fir that is proven to survive more than 50 years in shade without significant growth [3].

A total number of 2044 trees·ha⁻¹ of dbh<10 cm seems adequate to assure sufficient recruitment of saplings. Along with standard management activities it should consequently maintain sustainable uneven-aged selection stand structure.

However, analysis by species reveals a somewhat different picture - the number of thin silver fir trees is very low and it clearly indicates future significant decrease of fir in beech-fir forests. A great share of thin trees are side species - mostly rowan that hardly exceeds dbh 10 cm in given conditions. Also in stands on higher altitudes and unfavourable sites, fir and beech trees under 10 cm dbh cannot all be addressed as a regeneration since it is medium size that trees can reach in such conditions. Therefore the number of trees dbh<10 cm should be interpreted with caution, since just a small share of them represents regeneration, thus consequently pointing on the problem with regeneration in the past. Unfortunately, the quality and damage of saplings were not assessed - such results would better indicate the real state of regeneration and reveal the problems with the transition of saplings (recruitment). Hence the assessment of quality and damage of saplings should be integrated in the following cycles of NFI.

The present state of forests, including intensity and structure of regeneration, is a result of management activities in the past. With assumption that type of ownership also presents specific the type of forest management [27], we analyzed regeneration structure by ownership. Significantly higher regenerated area in private than in state forests indicates inadequate management model in state forests (Figure 2). This is specially emphasized in the case of conifers where regenerated area in private forests is four times greater than in the state forests. High growing stock with great share of conifers and almost even-aged structure is obviously not favourable for fir regeneration, as already reported in previous studies [19, 20, 23]. It is also interesting that thin broadleaved trees are significantly more abundant in state forests but also in private non-managed forests (without management plans), than in private forests managed according to management plans. Those are mostly rowan, maple and beech trees that remain in suppressed layer for years. Such trees have ecological role, but they do not influence future stand structure in managed stands. In the protected area (National Park Risnjak) regeneration is almost absent, especially for fir. It can be attributed to natural dynamics of forests where mature old single layer stands will slowly come to natural regeneration after natural opening of gaps.

The differences in regeneration between forest types (phytocenoses) are clearly demonstrated - conifers successfully regenerate on optimal sites, i.e. on acidophilic soils upon silicate bedrock. In other forest types conifers are significantly less present. Broadleaves regenerate equally well in all plant communities represented on the research area. The number of saplings trees is surprisingly the highest in thermophile beech, which can be attributed to unfavourable site conditions where fir trees can remain stagnant for entire life, and maybe to a small sample size.

Present canopy closure has obviously higher impact on regeneration than on abundance of thin trees. Significantly higher regenerated area is evident in stands with sparse canopy closure in relation to both complete closure and gaps. It suggests that adequate management activities have to be taken to stimulate regeneration - moderate opening of stands will induce regeneration of (mostly) broadleaves. With consequent care of saplings and possible introduction of fir seedlings, stable mixed uneven-aged stands could be achieved.

Ecological factors like soil depth, rockiness and aspect have significant impact on regeneration. It is interesting that plots with deepest soil and least rockiness do not have highest abundance of seedlings, indicating that these are not crucial requirements for plants to grow in the first phase. Saplings are, however, most abundant on those plots, where deepness and quality of soil play an important role, also substituting the lack of light. It is also likely that on shallow and stony soil trees with up to 10 cm dbh form a final and continuous stage of stand development. Although there are differences in regenerated area according to aspect (especially for broadleaves), they cannot be reliably confirmed. Conifers are shown to prefer east and west oriented sites.

Possible other influences, e.g. of climate change, have not been covered in this research. Also, the complex model of individual and mutual influence of stand and site characteristics would surely make a clearer insight on the success of regeneration, and point out the causes of the present state. However, the presented results - poor incidence of seedlings (trees under 1.3 m) and sapling conifer trees - indicate extremely poor regeneration in selection forests, silver fir in particular. Therefore management planning and management activities should be directed in a way to promote fir regeneration and the survival of existing seedlings. It could imply additional involvement in regeneration by the introduction of seeds and seedlings. On the other hand, regeneration of other species (dominantly beech) indicates naturalness and biodiversity of beech-fir forests which should be fostered as much as possible.

CONCLUSION

The level and structure of regeneration in beech-fir forests of Gorski kotar region, based on the results of NFI, is characterized by low regeneration of silver fir, and significantly better success of broadleaves. Common beech regenerates well on the whole researched area. Significant share of other broadleaves (sycamore maple, rowan etc.) indicates well preserved naturalness of forests. Some differences in regeneration structure can be found between forest communities and site conditions - acidophilic sites on silicate bedrock are favoured by conifers, while thermophile and more extreme sites are dominated by beech.

The influence of various owners through different management concepts has also been demonstrated. It can be generally concluded that management models that establish more mixed forests with higher size diversity and lower growing stock enable better regeneration. Management planning should take that into account and adjust future activities into that direction. It will surely help fir regeneration to some extent, while maintaining share of fir over 50% would require aided regeneration by additional

seedlings. It is feasible in the framework of close to nature forest management that it will maintain naturalness and biodiversity of Dinaric beech-fir forests in the long term.

The importance of regeneration as an indicator of both ecosystem stability and the success of forest management requires additional concern in forest inventory. The metho-

dology of measurement and assessment should be improved with special sub-plots for more detailed measurement of seedlings. More reliable and more detailed results on regeneration would lead to better projection of development of forest resources, enabling also more active adaptation of future management activities.

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The Growth of Bosnian Pine (*Pinus heldreichii* Christ.) at Tree-Line Locations from Kosovo and its Response to Climate

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ABSTRACT

Background and Purpose: *Pinus heldreichii* Christ. is a sub-endemic species occurring at tree-line locations in Kosovo and covering an area of 2500 ha. In high elevation sites radial growth is mainly controlled by low temperatures. The main purpose of this study was the analysis of radial growth of *P. heldreichii* and its response to local climate conditions.

Materials and Methods: Research sites comprise of three high elevation stands of *P. heldreichii* with specific site conditions. Core samples were collected from 98 healthy dominant and co-dominant trees at breast height using increment borer. They were prepared and cross-dated using standard dendrochronological methods, while tree-ring widths were measured to the nearest 0.001 mm using the TSAP software. The ARSTAN program was used to standardize the tree-ring widths and to calculate dendrochronological statistical parameters. The growth-climate relationship was investigated using bootstrapped correlation function analysing the residual chronologies of each sampled site as a dependent variable and the climatic data from May of the (n-1) year up to the October of the n year for the common period 1951-2013 as an independent variable.

Results: The length of Bosnian pine chronologies ranged from 175 to 541 years. All chronologies had high values of first-order autocorrelation indicating that radial growth of *P. heldreichii* is affected by the climate conditions of the previous growing year. Koritnik chronology had the highest values of the mean sensitivity due to the influence of drought stress. This conclusion is also supported by the result of growth-climate relationship where radial growth is negatively correlated with June temperatures and positively associated with July and August precipitation. We found that radial growth of young trees from Koritnik site is limited by the combined effect of temperatures and summer drought stress. In high elevation sites, temperature is expected to control the growth of *P. heldreichii*, but this effect is becoming more restrictive with age. The positive correlation between radial growth and winter temperatures suggests that favorable thermal conditions during winter months influence snow melting or soil moisture availability and indirectly affect the radial growth of *P. heldreichii* at all three sampled sites.

Conclusions: The first tree-ring width chronologies from Kosovo are an important step towards a denser tree ring network in the Balkan region. Growth-climate relationships indicated that for *P. heldreichii* growth does not depend only on one single dominant factor, but also on various combinations of precipitation and temperature resulting in different climatic sensitivity. Our results provide an important basis for additional tree-ring parameters such as maximum latewood density and stable isotope ratios to be processed, improving the level of knowledge about *P. heldreichii*'s response versus site conditions.

Keywords: *Pinus heldreichii*, growth - climate relationship, tree-line, bootstrap correlation

INTRODUCTION

The direct and indirect effects of global warming on forest ecosystems represent a challenge for human well-being in the near future [1]. Warming trends can influence vegetation patterns by modifying the start and the duration of the growing season, and abrupt air temperature increase can alter growth responses [2].

Climate changes are expected to alter the distribution of tree-line species in mountainous areas, and most predictive models forecast an upward displacement of species, tracking increases in temperatures [3, 4]. However, not all species respond in the same way to climate changes. Special attention must be paid also to species such as *Pinus heldreichii* Christ., which grows in high elevations making it more sensitive to temperature oscillation.

Pinus heldreichii Christ (syn. *P. leucodermis* Antoine) is a sub-endemic species occurring in isolated subalpine locations in the Balkan Peninsula and Southern Italy. The Balkan Peninsula plays a key role as a climatic transition zone between western and eastern Mediterranean and also between the Mediterranean and Central European synoptics [5-9].

Previous studies on *P. heldreichii* have been conducted in Bulgaria [10, 11], Greece [12, 13], and Albania [14], exploring growth-climate relationship of this high elevation species. Moreover, summer temperature was reconstructed (1768-2008) based on maximum latewood density measurements of *P. heldreichii* trees from a high-elevation stand in the Pirin Mountains in Bulgaria [15]. In Albania, a 1391-year tree-ring width chronology (617-2008) was developed and maximum density measurements were acquired on living and dead *P. heldreichii* trees [14].

The overall forest area covered by *P. heldreichii* in Kosovo is accounted to 2150 ha, and it is mostly mixed with species

like silver fir (*Abies alba* Mill.). Some natural forest stands of this species exist in Kosovo, situated in Prevalle (PRE), Koritnik (KO) and Decani (DE) regions respectively, but no dendroclimatic study has been done up to this moment.

The high conservational value of such taxa additionally increases the importance of studies based on tree-ring width that allow a better understanding of the radial growth-climate relationship, as well as the ecophysiological requirements of trees [16, 17]. Changes in annual tree-ring width growth could be due to the effect of environmental conditions, climate and anthropogenic disturbances. To analyze the influence of climatic conditions on growth of coniferous species at the tree-line locations, tree-ring widths (TRW) and wood density chronologies are used [18, 19]. Intra-annual radial growth rates and duration in trees of *P. heldreichii* differ greatly in relation to site conditions. Thus, better knowledge of the relationship between TRW development and climate is needed to improve the current level of dendroclimatic studies in Kosovo and Albania. In this study, we investigated the responses of *P. heldreichii* growth to local climatic variations in three high elevation sites from Kosovo. The aim of this paper was (i) to study the growth – climate relationship of *P. heldreichii* and (ii) to identify the main climatic factors driving its radial growth.

MATERIALS AND METHODS

Study Areas and Sample Sites

The study areas are natural ecosystems located close to the upper distribution limit of Bosnian pine at Prevalle (42°11'N, 20°57'E; 1945 m a.s.l), Decan (42°36'N, 20°14'E; 1830 m a.s.l), and Koritnik (42°04'N, 20°31'E; 1815 m a.s.l) in western and



FIGURE 1. The location of Kosovo (upper left side) in Europe and of the sampled sites (right side)

TABLE 1. Site characteristics of the sampled sites

Sampled site	Latitude / longitude	Altitude (m a.s.l.)	Aspect	Soil / rock formation	Sampled trees
Prevalle (PRE)	N 42°11'01.3" E 20°57'42.0"	1945	SW	Typical rendzina soils on limestone bedrock	30
Decan (DE)	N 42°36'19.8" E 20°14'52.5"	1830	NW	Brown soils on limestone bedrock	38
Koritnik (KO)	N 42°04'46.5" E 20°31'58.6"	1815	NW	Grayish-brown rendzina soils on limestone bedrock	30

southern Kosovo (Figure 1) (Table 1). Soil types are based on limestone bedrocks creating leptosols (rendzinas) and brown soils on higher slopes with slight differences among sites. At all sampled sites Bosnian pine is the dominant species while the ground vegetation comprises of species such as: *Sesleria autumnalis* Ard., *Brachypodium sylvaticum* Huds., *Carex humilis* Leyess., *Thymus balcanus* L., *Fragaria vesca* L., *Festuca heterophylla* Lam., *Dactylus glomerata* L., etc. These forest stands grow under the effect of Continental climate with some influences of Mediterranean climate in the southern Kosovo. Mean annual temperature varies among sampled sites and ranges from 8.0°C (PRE-site) to 8.3°C (KO-site), while the long-term mean annual precipitation ranges from 791 mm (DE-site) to 1029 mm (KO-site) (CRU TS3.22 dataset, period 1901-2013). The weather in the sampled site is characterized by a non-uniform rainfall distribution, with summers that are very short and cold as well as with cold winters with lots of snow.

Maximum precipitation falls from October to December, while the minimum rainfall is recorded from July to August (Figure 2). Moreover, natural forest stands of *P. heldreichii* grow on sites with different slope aspects ranging from NW for DE and KO sites to SW for PRE site.

Tree-Ring Chronology Development

The core samples were collected from old dominant and co-dominant trees with healthy trunks and no sign of human interference. We extracted two cores from each tree at breast height (1.3 m) when possible. Otherwise we tried to avoid compression wood due to steep slopes, compiling a set of 98 new samples from all sites. Core samples were air-dried and glued onto wooden holders and subsequently sanded to ease growth ring identification [20]. The TRW were measured at 0.001 mm precision, with a LINTAB 6 (RINNTECH, Heidelberg) system and TSAP-Win Scientific software. Then they were cross-

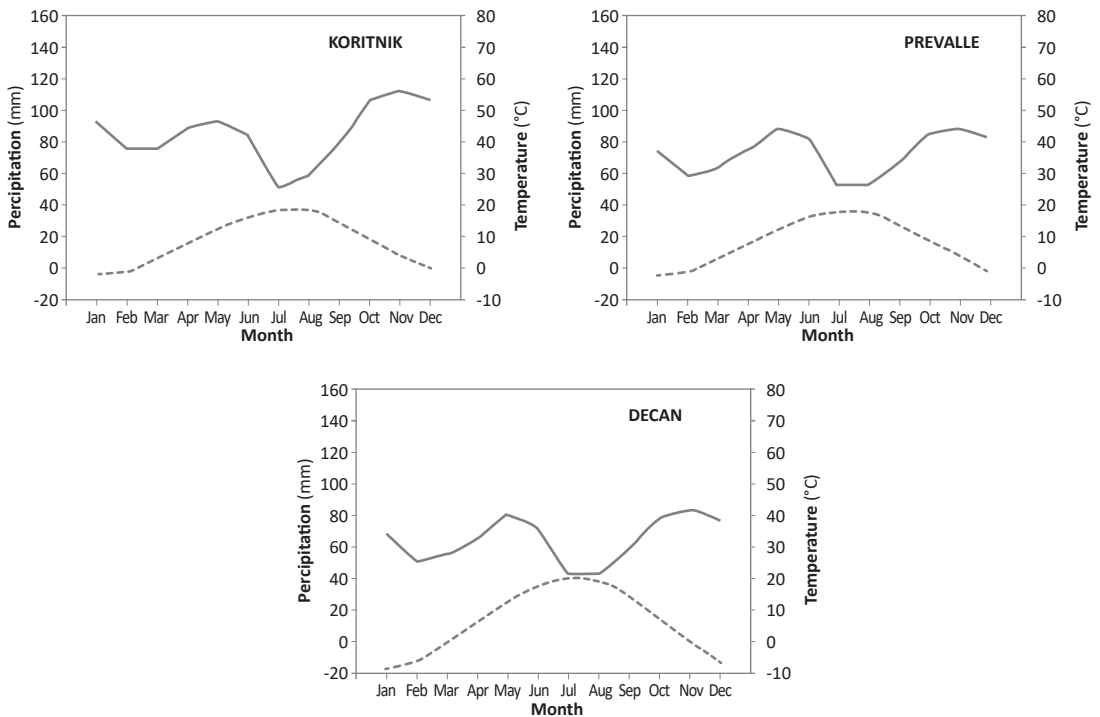


FIGURE 2. Climatic diagrams of the studied sites based on the CRU TS 3.22 data. Dashed line shows temperature, while solid line precipitation values.

dated visually and confirmed statistically using the software COFECHA [21]. The individual raw tree-ring series were standardized in a two-step procedure using ARSTAN software [22, 23]. First, a negative exponential curve was fitted to the ring series. For second de-trending a cubic smoothing spline with a 50% frequency-response of 30 years was used to reduce the non-climatic variation in tree-ring series. This way most of the low-frequency variability in each tree-ring series that is assumed to be unrelated to climate, such as tree aging and forest stand development, was removed. The observed values were divided by predicted values to produce dimensionless indices. The indices were then averaged to obtain site chronologies using a bi-weight robust mean [24]. Common signal in chronology was estimated using expressed population signal (EPS>0.85) which indicates to what extend the sample size is representative of a theoretical infinite population [25]. Residual chronologies are commonly used in dendroclimatic studies because the removal of serial autocorrelation is required for growth- climate analysis.

Climate Data

Total monthly precipitation and mean monthly temperatures were provided from the CRUTS3.22 dataset, with a spatial resolution of 0.5x0.5° (<http://www.cru.uea.ac.uk/>) [26] reaching back to 1901. The only available local climate records belong to Prizreni town, but they were not sufficiently reliable due to the short length of series (series length 1977-1987 and 2009-2014), missing values (from 1988 to 2008) and the lack of homogenization. CRU data used in this study were extracted from the database of KNMI Climate explorer (<http://climexp.knmi.nl/>) for the region encompassed by the coordinates 41.5°-43.5°N and 20°-22°E. However, to the best of our knowledge the CRU climatic dataset is the best available dataset to test long-term changes in radial growth as related to climate in several countries. The gridded climate data for the period 1951-2013 were considered reliable for the growth-climate analysis, because weather station density is high and stable for interpolation of CRU dataset and climate data have been checked and tested for homogeneity.

Growth-Climate Relationship Analysis

To quantify the relationship between residual site

chronologies and monthly climate data (mean monthly temperatures, total monthly precipitation), we calculated bootstrapped correlation coefficients for the common period 1951-2013. The growth-climate relationship analysis was performed with DENDROCLIM2002 software [27]. Bootstrapped correlations were calculated between TRW residual chronologies of Bosnian pine at three sites which were analysed as dependent variables and the climatic data (independent variables) using a 18-month window from May of the year prior to tree-ring width formation (year t - 1) until October of the year of growth (year t). Correlation coefficients were considered significant if they exceeded, in their absolute value, half of the difference between the 97.5th quantile and the 2.5th quantile of 1000 estimates calculated in the bootstrapping procedure [27].

RESULTS

Tree-Ring Chronologies

The length of master chronologies varies among sites. Thus, the chronology from DE- site was the longest with 541 years, spanning throughout the period 1474-2014 with a replication of more than 34 trees from 1770 onwards. The chronology from KO-site was the shortest, 176 years long, with a sample replication of 25 trees, while the chronology from PRE was 243 years long spanning throughout the period 1776-2014 with a sample replication of 25 trees from 1920 onwards (Figure 3, Table 2). The year-to-year persistence (AC) was higher at higher elevation site (PRE) while the inter-annual variability (MS) of growth resulted as greater at KO which suggests that climatic constraints on species growth are more important for this site. All chronologies were correlated (p<0.01) with each other for the common period 1840-2014, but the degree of agreement and similarity appears to be higher between DE and other chronologies, and slightly lower among PRE and KO chronologies. These results indicate that the degree of agreement in radial growth appears to be unrelated to the vicinity between sites (Table 3). Although KO and PRE sites are close to each other and trees belong to the same age class, the low agreement between both site chronologies might be due to slope aspect.

TABLE 2. Statistical parameters of three *P. hedreichii* chronologies from Kosovo

Statistical parameters	Decan (DE)	Koritnik (KO)	Prevalle (PRE)
Time span	1474-2014	1840-2014	1776-2014
Total years	541	176	243
Number of trees in chronology	34	25	25
Mean age	240 ± 69	147 ± 18	116 ± 20
Mean tree-ring width (mm)	1.06	1.81	2.13
Standard deviation	0.498	0.872	0.907
Skewness	1.037	0.995	0.547
Mean Sensitivity (MS)	0.224	0.245	0.212
AC (1)	0.769	0.751	0.783
EPS > 0.85 since	1770	1876	1920

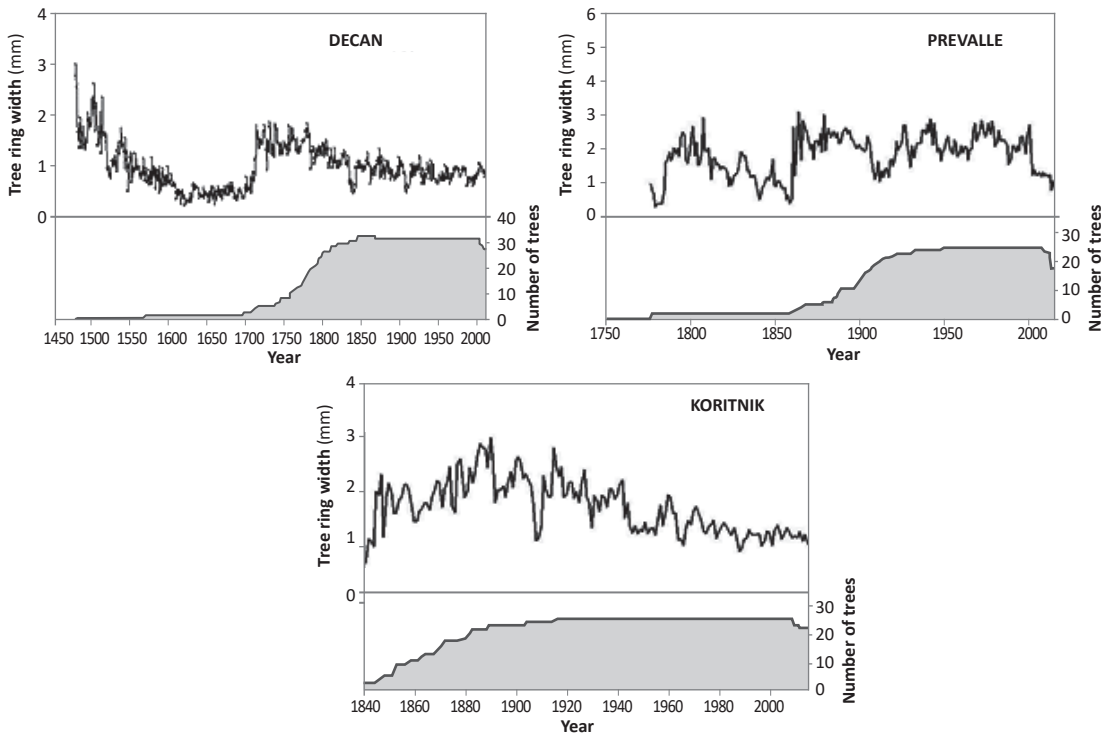


FIGURE 3. Raw tree-ring width chronologies of Bosnian pine (*P. heldreichii* Christ.) from Decan, Prevalle and Koritnik. Upper part in each graph shows the raw tree-ring width chronology while lower part shows tree replication in respective site chronologies

Growth-Climate Relationship

We tested the response to temperatures and precipitation from the previous year's May to the current October of TRW formation for the three site chronologies (Figure 4). All correlations computed over the common period 1951–2013 were not high (maximum *r*-value: 0.37 for DE versus July precipitation). From all 108 correlations calculated for temperature and precipitation together, only 16% reached the 95% significance level. These facts underline the existence of divergent correlation patterns among the three studied sites emphasizing the important role of local conditions on Bosnian pine's growth. Regarding the site-specific patterns, the DE chronology seemed to be slightly more sensitive to current summer precipitation variations than other sites.

In case of KO site, tree growth was correlated negatively

to the temperatures of previous July, August and September as well as June of the current growing year. Moreover, growth-climate relationship showed that *P. heldreichii*'s growth was positively correlated with previous August and negatively associated with current May precipitation. The negative response to previous summer temperatures and the positive correlation to previous July precipitation suggest that *Pinus heldreichii*'s growth from KO site is mainly controlled by drought conditions.

Bootstrap correlation analysis showed that PRE chronology was correlated positively to the temperatures of current January and February and the precipitation of previous May, October and July of the current growing year. An adverse relationship was noted with previous June and current April precipitation. The main climatic factors stimulating growth in this high-elevation site were favorable temperatures during

TABLE 3. Comparison between all three *P. heldreichii* chronologies from Kosovo

Sampled sites	Prevalle (PRE)		Decan (DE)		Koritnik (KO)	
	t-BP	GLK %	t-BP	GLK %	t-BP	GLK %
Prevalle	-	-	7.1	66	6.8	59
Decan	7.1	66	-	-	12.3	71
Koritnik	6.8	59	12.3	71	-	-

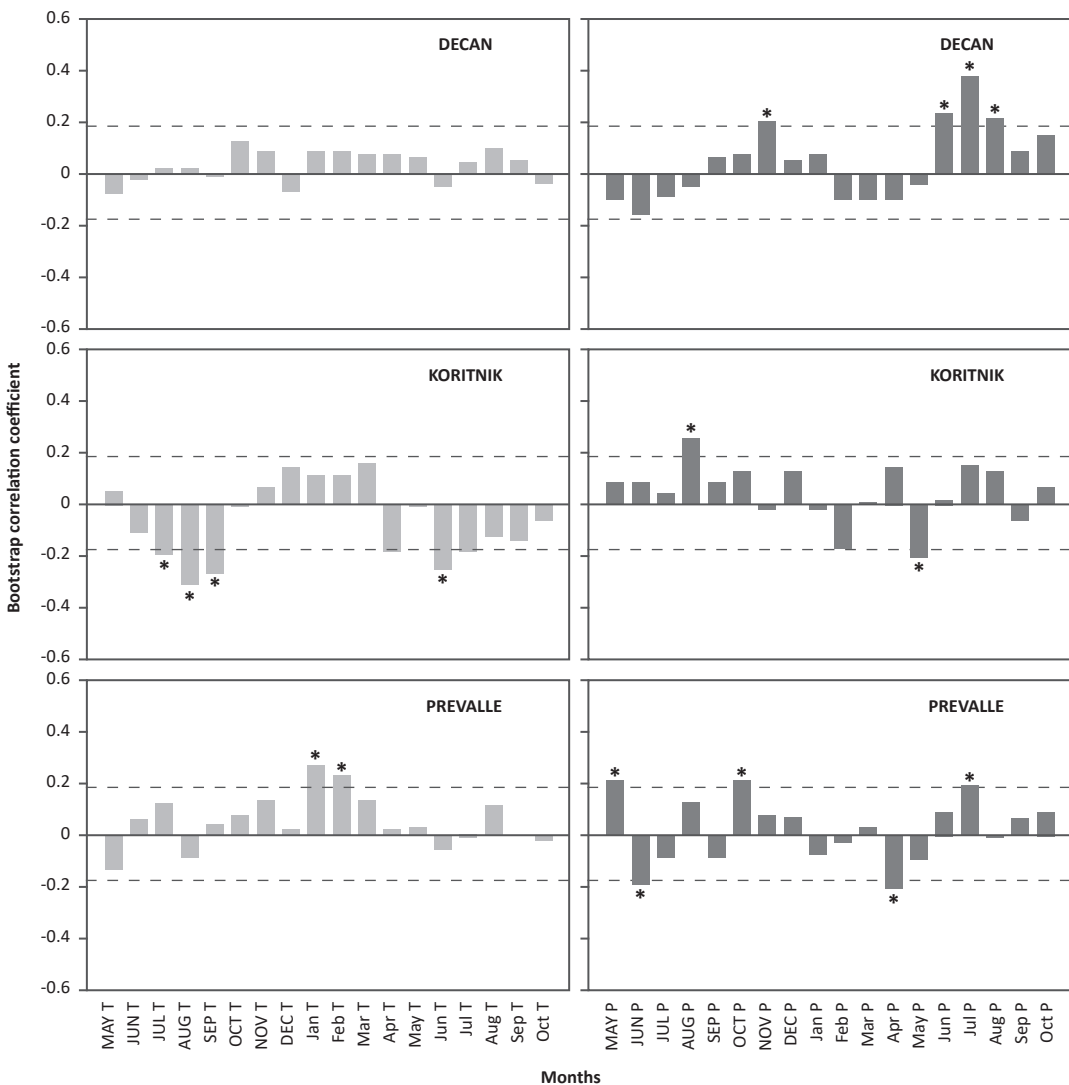


FIGURE 4. Bootstrap correlation coefficients between residual chronologies and temperature (left) and precipitation (right) - asterisks on the top of the bars indicate 95% significance level of the correlation coefficient

current January and February associated with a positive water balance in July. Growth–climate relationships over the last 62 years, however, indicate that tree-ring formation in KO and PRE sites does not depend on one single dominant factor, but rather on various combinations of precipitation and temperature in certain months resulting in a temporal alteration of climatic sensitivity.

DISCUSSION

Chronology Characteristics

We performed this investigation to assess the impact of climate on Bosnian pine’s growth and to evaluate its response.

We were able to develop three TRW chronologies from Kosovo region reaching a maximum of 541 years back in time (from 1474 to 2014). Although the replication of the dataset decreases back in time, the EPS threshold varies among sites spanning from ~1770 for DE-site to 1920 for PRE site. The quality of such chronologies could be further increased in earlier periods by adding more cross-dated series. We note that an increase of tree-ring widths and consequently indices was observed during the de-trending procedure for the last six decades in all chronologies. The most common periods showing a TRW increase were 1965-1970, 1978-1981, and 1987-1991, whereas the periods with radial growth decrease were different between site chronologies. The radial growth which increased during the second half of the twentieth

century has been found in other long tree-ring chronologies and is often attributed to a changing temperature regime [28-30]. Based on CRU climatic data, the common periods associated with mean temperature's rising spanning from 1981 to 2010, while the periods with significant decrease of precipitation records were 1981-1990 and 2010-2014 respectively (Figure 5). These are the first chronologies from Kosovo, but there are also some other built earlier in Italy and the Balkan Peninsula. In comparison, the longest nearby *P. heldreichii* chronologies span periods of 1392 years (617-2008) were found in Albania [14], 762 years (1243 to 2004) in Greece [31], 758 years (1250 to 2008) in Bulgaria [11], and 827 years (1148 to 1974) in Southern Italy [32].

We tried to download these chronologies from International Tree-Ring Data Bank (<http://hurricane.ncdc.noaa.gov/pls/paleox/f?p=518:1:3874104498420267:::APP:PROXY:TOSEARCH:18>) aiming to compare them with ours, but none was available on the website.

Growth–Climate Relationship

Despite the observed climate signal, the response to climate of the three site chronologies was not particularly strong or robust. The low correlation values could at least partly be related to the sparse availability of regional meteorological station data for Kosovo high-elevation sites and also for the whole Balkan region, resulting in a limited representation of

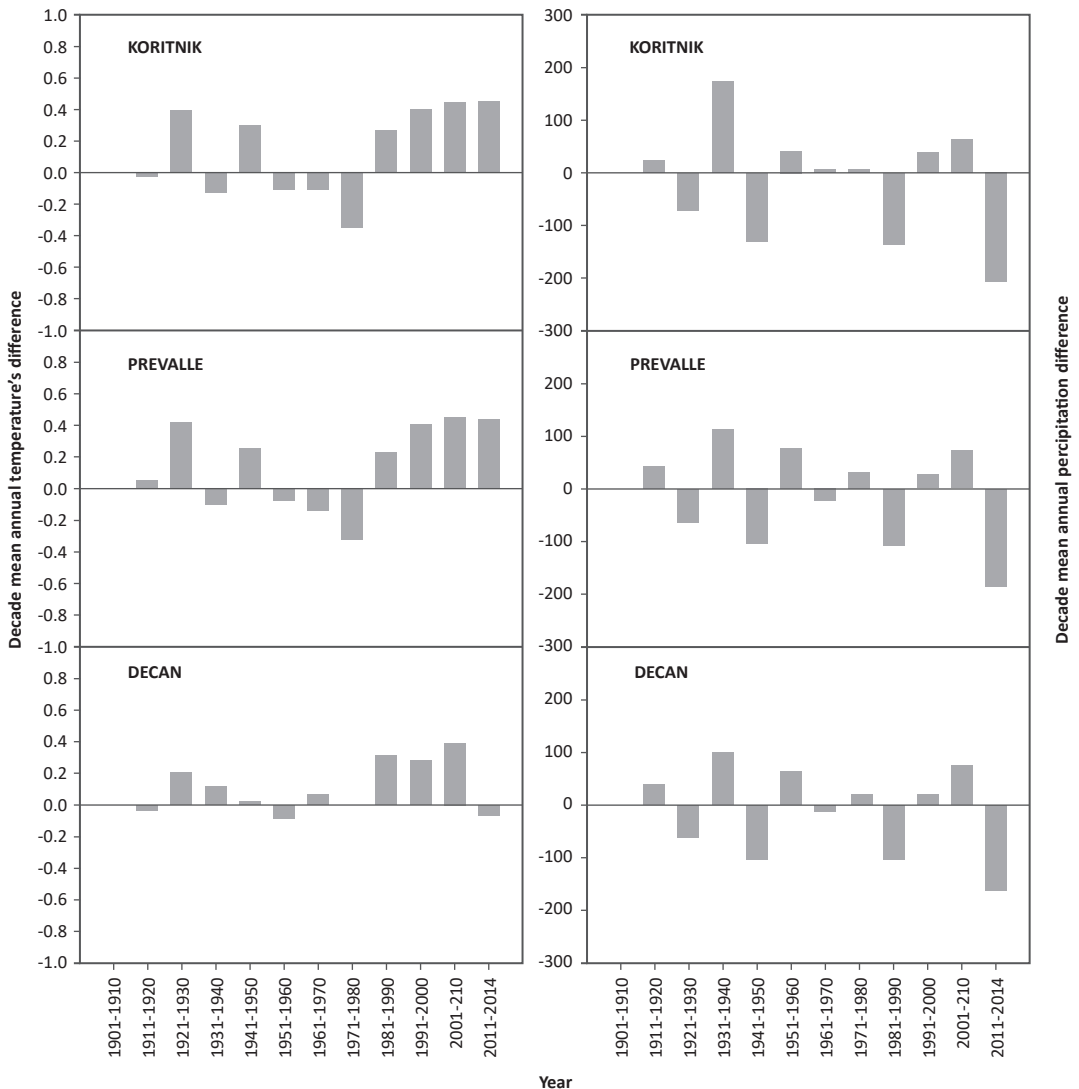


FIGURE 5. Decennial successive differences between mean annual temperatures and mean annual sum of precipitation for the period 1901-2014 (including the period 1951-2013 used as reference in bootstrap correlation analysis)

the gridded CRU data for the study region. In all studies, the correlations between TRW and various instrumental climate data (monthly temperature and precipitation) were relatively weak and not robust over the 20th century proxy-target period. Even for the western Mediterranean basin, similar results based on three conifer species from the Pyrenees were reported [33].

We found strong relationships between tree-ring chronologies and summer precipitation of the current growing year for DE and July precipitation for the PRE site. The location of these stands in high mountainous areas is positively affected by local humid currents helping trees to avoid the negative effects of summer droughts [17]. The strong relationship between KO residual chronology and climate conditions of the years prior to the growth indicates that in this tree-line location, the growing period is relatively short and the most active tracheid formation occurs at the beginning of summer [34]. Therefore, for the production of wide tree rings the combination of early cambial activity start with enough available resources, i.e. stored carbohydrates and other substances produced in the previous growth period, and favorable climate conditions during the late spring and early summer months of the growth year is needed. The effect of climate in the previous year is expressed by strong first-order autocorrelation often found in tree-line trees [35] and also in our series.

Significant correlations with precipitation in certain months of the previous growing season were found at all sites. The persistence of this climatic signal in the subsequent years is linked with soil moisture reserves for the subsequent growing season. Our study revealed that young trees in the KO site growing under drier conditions were more sensitive to summer drought stress, as reflected by the negative correlations with June temperatures and positive correlations with July and August precipitation. Tree age is important not only for tree-ring formation but also for growing trends and should be taken into consideration when exploring the growth-climate relationship. Previous studies have shown that the duration of wood formation in conifers was shorter in old than in young trees [36]. This study reported that young trees were characterized by an earlier onset of xylogenesis, a longer growing season and a higher growth rate, resulting in a higher number of xylem cells. One possible explanation for the earlier onset of xylogenesis in young trees is that the base of the stem is closer to the crown and hence to the source of auxin than in old trees [16]. Moreover older trees have larger diameters and thicker barks, which could negatively influence the spring dynamics of stem warming. Compared to young trees, old trees have a higher hydraulic resistance and lower photosynthetic rates, which might potentially increase the climatic sensitivity reflected in *P. heldreichii* growing at DE site [16, 37, 38].

Positive correlations with current winter temperatures

reported at all three sites showed that mild winters have a positive influence on snow melting or rainfall. From a physiological point of view, winter temperatures cannot directly influence cambial activity since the trees are dormant. However, during warmer winters, more precipitation falls as rainfall, rather than as snow [39]. In our case, it is more probable that precipitation in cases with warmer winter temperatures is in the form of wet snow, which on its side is less prone to wind transport and immediate sliding along steep slopes and therefore could contribute to a deeper snow cover. This can provide more soil moisture after snowmelt and could be a prerequisite for increased cambial activity given that other conditions are favorable.

We expected a stronger thermal signal because the research sites were situated at high elevation and the low temperature is assumed to be the main driver for tree growth. Although sampling in Kosovo was conducted at the highest forested elevations (up to 1945 m a.s.l.), our sampled sites might not fully represent typical tree-line conditions. For instance, the thermal tree line of *Pinus heldreichii* at the Olymp (Greece) ranges from 2200 to 2400 m a.s.l. with the krummholz zone even reaching elevations of 2500 to 2700 m a.s.l. [12]. Körner [40], on the other hand, stated that Mediterranean tree-line sites do not show a clear temperature controlled growth pattern compared to the Alpine region and that it is questionable if sampling at the upper zone provides more defined growth control. Therefore, follow-up studies should be based on tree-ring parameters such as maximum latewood density and stable isotope ratios that are expected to be more climate sensitive in the area.

CONCLUSIONS

The first TRW chronologies from Kosovo are an important step towards a denser tree ring network in the Balkan region. Growth-climate relationships indicated that *P. heldreichii*'s growth does not depend only on one single dominant factor, but on various combinations of precipitation and temperature resulting in different climatic sensitivity. Our results provide an important basis for additional tree-ring parameters such as maximum latewood density and stable isotope ratios to be processed, improving the understanding about *P. heldreichii*'s response versus site conditions.

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Generating Virtual Even-Aged Silver Fir Stand Structure Based on the Measured Sample Plots

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ABSTRACT

Background and Purpose: The aim of this article is to create a virtual forest stand based on the field measurement of spatially separated sample plots and to examine its credibility based on the deviation of the basic characteristics of the virtual stand as compared to the field measurements.

Material and Methods: Field measurements were made on 20 circular sample plots with a 20 m radius, set on a 100x100 m grid. By using the univariate Ripley's *K* function the regularity of the spatial pattern of trees was analysed. The diameter distribution and the frequencies of height within individual diameter class were mathematically fitted and used for generating the virtual stand. The whole process of generating the virtual stand was done in the *R* software. Area of study are even-aged silver fir stands in the Croatian Dinarides.

Results: The main unit of the virtual stand is a tree, with the purpose that the virtual stand can then be used as a basis for forest stand growth simulators. The result of the research was a virtual stand of 3 ha whose characteristics only slightly differed from the field measured plots. Within the virtual stand, special emphasis has been put on tree heights, which were generated according to the variability of tree height for trees of the same diameter at breast height.

Conclusions: Considering the distribution of diameters at breast height, tree heights, the number of trees, basal area and volume, the virtual stand has minimal deviations from the situation in the field and it adequately shows variability measured in the field.

Keywords: virtual forest, forest planning, Ripley's (*K*) analysis, distribution fitting, *R* software

INTRODUCTION

Prior to planning forest management, field measurements have to be done in order to obtain main forest characteristics. Because of its complexity and labour cost, field measurements are usually carried out on a previously chosen sample area, and not in the entire forest area [1-3]. This assumes that the unmeasured parts of the stand have the same or similar characteristics as the measured parts with the given confidence interval. The sample usually consists of many relatively small and spatially separated areas (e.g. 500 m² in size) in order to estimate the variability in statistical analysis, but it does not enable insight into the entire stand. By compilation of spatially separated plots into a single coherent plot, forest stand can be shown in its absolute area [4-7] and as such it can be used in forest tree growth simulators [8] for the purpose of planning

future forest management [4, 9-12]. Also, the compilation of spatially separated plots into a single coherent plot reduces the costs of the total measurement of structural elements of the entire stand [9]. Apart from the possibility of using virtual stands as a starting point for future forest management simulation, they can also be used for comparison between the present and the future value of forest resources [13].

Trees which belong to a stand can be classified according to their mutual position into three basic spatial patterns: i) clustered, ii) random, iii) regular [14]. This classification treats forest as two-dimensional in its form, which differs from defining its structure as three-dimensional [11]. Pommerening [11] also stressed that most of the measures which describe the forest structure can be classified into two groups according to mathematical relations:

distance-independent and distance-dependent. The spatial distribution of trees and their interrelationship based on tree species, diameter and similar factors, is primarily the result of the impact of habitat, but also of forest management. Stands consisting of several different tree species of different age and size are the most complicated for modelling [5, 11], unlike even-aged and pure stands.

Generating virtual forest stand is conditioned by the type of simulator which will simulate future theoretical and/or practical management. According to Pretzsch *et al.* [15] and Ngo Bieng *et al.* [5], there are three levels of forest stand growth simulators (single-tree level, diameter class level and stand level). The classification is always conditioned by the basic input data [15], while it refers to the level of simulation [16]. Simulators based on individual trees are the most complex and they require detailed data about every single tree in the stand. It is especially important that the virtual stand of a single-tree level realistically represents the measured stand [17] so that the results of the simulation of management would be more realistic. When generating such a virtual stand, the spatial distribution of trees plays a crucial role. By directly joining separated spatial sample plots, the resulting spatial distribution of trees would not match the spatial distribution in the field because of the marginal trees of spatially adjoining plots. Therefore the spatial distribution of trees in a virtual stand has to include all the factors of spatial occurrence of trees in the field [8, 11, 17]. Virtual stand can cover a much larger area than the spatial sample based on which it was generated [4-6, 8], which is one of the reasons for creating a virtual stand in the first place. The aim of this article is to create a virtual forest stand based on the field measurement of spatially separated sample plots and to examine its credibility based on the deviation of the basic characteristics of the virtual stand as compared to the field measurements.

MATERIAL AND METHODS

Study Site and Data Collection

The study was conducted on an area of even-aged pure forests of silver fir (*Abies alba* Mill.) in Lika region, located in central Croatia (management unit Škarnica 44°58'N, 15°08'E). In forest of management unit Škarnica altitudes vary between 430 and 828 m a.s.l. Main soil types are limestone and dolomite. According to Köppen classification, the climate is marked as Cfbwx. Because of being even-aged and consisting of only one tree species (>95% of growing stock), this type of forest is rarely found in forest management of European fir forests [18]. Stands which belong to the observed forest are extremely similar to each other in terms of timber stock, stand basal area and increment [10]. The study site (management unit Škarnica) covers an area of 1833 ha, while the spatial sample obtained by field measurements is narrowed to a section (subcompartment) of 22.21 ha (Figure 1a).

Within a 100 m square grid oriented according to cardinal directions a total of 20 circular sample plots with 20 m radius were positioned. All trees within the plot (silver fir, beech (*Fagus sylvatica* L.) and other broadleaved

hardwoods (OBH)) with a diameter at breast height (dbh) over 10 cm were measured. For every tree, its species, the specific position in the three-dimensional space, dbh, and absolute height were determined according to the Croatian National Forest Inventory (CRONFI) field procedures [19]. Regarding the tree species and the status of the tree (dead/alive) four subpopulations were determined: fir-alive, fir-dead standing, beech, and broadleaved hardwoods. The total sampled area was 2.512 ha, which makes 11.3% of the studied stand's area. Field measurements were conducted during 2013 after selective felling.

Spatial Structure Analyses

Ripley's $K(r)$ is a univariate function [20-22] used for the analysis of spatial structure. This function is based on the distance between all of the trees in a two-dimensional space [21], and it is often used in the analysis of spatial point patterns of forest ecosystems [23]. According to Ripley [20] and Ngo Bieng *et al.* [5], "Ripley's K function is a function of the mean number of other trees found within distance r from a typical tree and it defines different degrees of random, clustered or regular spatial organisation". In this study distance r around every tree is represented by a sequence of concentric circles with 0.5 m intervals. According to Besag and Diggle [24], $L(r)$ square-root transformation of the main $K(r)$ function was used.

The null hypothesis of the univariate function $K(r)$ claims that there is no statistically significant difference between the spatial pattern of trees and the totally random spatial pattern, i.e. claiming that trees are randomly distributed. The confidence interval of totally random pattern was calculated by Monte Carlo simulation [25] with 99 repetitions of Poisson's distribution [26]. The analysis was done with R software [27] using the "spatstat" package [28].

Generating Virtual Stand

Based on the analysis of spatial structure on all 20 plots a virtual stand was generated with a given condition that the spatial pattern of trees for all subpopulations is identical to the pattern in the field. The spatial pattern was generated with "stats" package, which is part of the R software [27]. The generated virtual stand is square-shaped and has an area of 3 ha (Figure 1b).

Furthermore, the virtual stand is assigned with additional conditions which describe positions measured in the field. The simulated positions of trees are associated with the corresponding subpopulation (tree species and the condition of being alive/dead), dbh and tree height. The association process consists of several parts:

- i) The category of subpopulation (tree species and the condition of being alive/dead) has to be the same as in field measurements;
- ii) The dbh distribution in spatial structure. According to Jaworski and Podlaski [29] and Burkhart and Tomé [30], the diameter distribution with diameter classes of 5 cm is fitted by using one of the following functions: normal distribution [31], logarithmic normal distribution [32], Weibull's function [33] or gamma distribution. The fitted distribution which has the lowest values of parameters AIC and BIC is

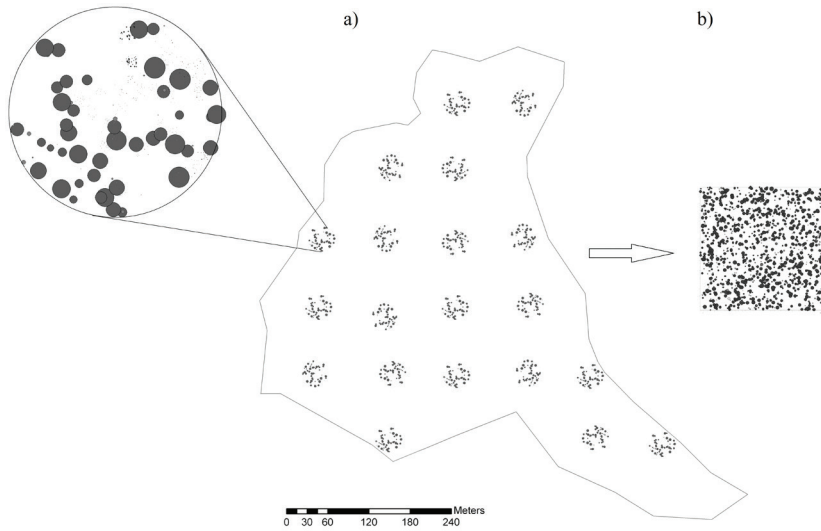


FIGURE 1. The spatial pattern of field measurements (a) and the generated virtual stand (b).

taken to be optimal, as according to Dziak *et al.* [34]. The fitting was done using the “fitdistrplus” package [35], which is a part of the R software [27]. The fitted distribution is associated with the allocation of the corresponding subpopulation in the area.

- iii) The distribution of tree heights depending on dbh. The measured heights within a diameter class (5 cm) always include some variability. The measured heights were taken for every diameter class separately and their distributions within the class were mathematically fitted as described in ii). After this, the fitted distribution of heights was associated with the corresponding fitted dbh.

Virtual Stand Validation

Deviation of the measured characteristics of the virtual stand from the field measurements were analysed by diameter classes for every stand variable separately (the number of trees, basal area and volume). Also, two-sided K-S test [36, 37] was used for determining the statistically significant difference between them using the “stats” package [27], with significance level being 0.05. The test was conducted separately for each specific subpopulation (tree species, alive-dead) and in total for all the subpopulations together, i.e. for the entire stand.

RESULTS

Field measurements (Table 1) confirmed silver fir as the most frequent tree species in the study area. More than 80% of silver fir’s timber stock is concentrated in diameter class’s span between 37.5 cm and 62.5 cm, with diameter distribution characteristic for an even-aged stand (Figure 3a). Other subpopulations (dead standing fir trees, beech,

other broadleaved hardwoods) in timber stock are together represented by only 2.47% and on average do not achieve dbh greater than around 30 cm (Table 1).

The analysis of the spatial structure with the univariate Ripley’s K function was conducted for every sample plot separately (Figure 2). On a total of 19 plots, the spatial distribution of trees is random and it follows Poisson’s distribution while trees are grouped on one of the plots. The criterion of random spatial distribution of trees is reflected in the comparison of the transformed Ripley’s $L(r)$ analysis for individual plots and Poisson’s random distribution (Figure 2). The result of clustered spatial patterns are groups of young trees (dbh=15-25 cm), which are situated on more open parts of the stand. From the results of the two-dimensional analysis it can be observed that the clustered pattern of trees is an exception, while random pattern prevails. Silver fir trees form the main stand (the upper storey), while other tree species can be found individually in the bush layer, i.e. in the lower storey.

According to the characteristics of the measured stand (Table 1), the number of trees in the virtual stand which were generated contained 375 trees·ha⁻¹, out of which 315 trees·ha⁻¹ were silver fir (alive), 43 trees·ha⁻¹ were silver fir (standing dead), 12 trees·ha⁻¹ were beech and 5 trees·ha⁻¹ other broadleaved hardwoods. The spatial distribution of dbhs (Figure 1b) was generated based on the analysis of spatial patterns of individual subpopulations (Figure 2). The relative coordinates (x, y) within the stand were associated with the fitted diameter distribution (Figure 3). Although in some subpopulations the field measurements did not determine the presence of trees in every diameter class (Table 1), in the process of distribution fitting all classes were used for generating the virtual stand (Figure 3).

The coefficients of determination (r^2) ranged from 0.70 to 0.85. The fitted distribution for the subpopulation of alive

TABLE 1. Stand structure based on the measured field plots: stand density (N, trees·ha⁻¹), basal area (G, m²·ha⁻¹), volume (V, m³·ha⁻¹).

dbh (cm)	<i>Abies alba</i> Mill.			<i>Abies alba</i> Mill.			<i>Fagus sylvatica</i> L.			OBH*			Σ		
	Alive			Dead standing			Alive			Alive			N	G	V
	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)			
12.5	13	0.16	0.89	20	0.24	0.95	7	0.08	0.43	2	0.02	0.15	41	0.51	2.42
17.5	22	0.54	4.19	11	0.27	1.55	2	0.05	0.38				35	0.85	6.12
22.5	20	0.83	8.83	6	0.24	1.85	1	0.03	0.21	2	0.07	0.62	29	1.16	11.51
27.5	27	1.62	19.36	3	0.19	1.12	1	0.05	0.71				31	1.86	21.19
32.5	33	2.78	35.62	1	0.09	1.00				1	0.04	0.37	36	2.91	36.99
37.5	44	4.91	67.49				1	0.05	0.63				45	4.96	68.13
42.5	45	6.26	89.64	1	0.06	0.90				1	0.10	1.44	46	6.42	91.98
47.5	47	8.38	122.93				1	0.07	1.09				48	8.45	124.02
52.5	31	6.65	99.44	1	0.08	1.18							32	6.73	100.63
57.5	20	5.19	78.51										20	5.19	78.51
62.5	9	2.67	40.01										9	2.67	40.01
67.5	2	0.85	12.97										2	0.85	12.97
72.5	1	0.15	2.28										1	0.15	2.28
77.5	1	0.37	5.66										1	0.37	5.66
Σ	315	41.36	587.83	43	1.18	8.55	12	0.33	3.46	5	0.23	2.58	375	43.09	602.41
Share (%)	84	95.99	97.58	11	2.73	1.42	3	0.75	0.57	1	0.52	0.43	100	100	100

* other broadleaved hardwoods

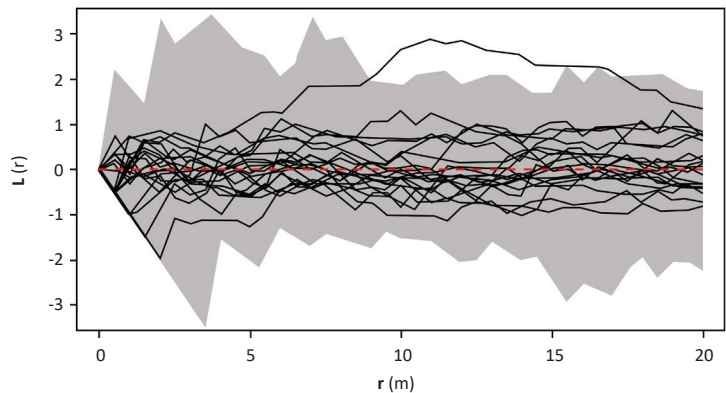


FIGURE 2. The results of univariate Ripley's (K) analysis for silver fir on all plots. Black lines represent the transformed values of Ripley's (K) analysis for the distance 0-20 m for each plot. The area of Poisson's random distribution with confidence interval of 95% is shown in grey.

silver fir had the highest coefficient of determination, which was 0.85. For the subpopulation of dead standing beech the coefficient was 0.79, for beech it was 0.70, and for other broadleaved hardwoods 0.82.

Tree height is a function of the tree's dbh, which at this stage of generating virtual stand is already determined by its dimension and position. Figure 4 shows the comparison between the measured and the generated heights of alive and dead standing silver fir trees. Every diameter class was

associated with the number of tree heights proportional to the number of heights of that diameter class measured on the plots. Tree heights of beech and other broadleaved hardwoods were not generated by mathematical fitting because of the extremely small number of them (beech 12 trees·ha⁻¹, other broadleaved hardwoods 5 trees·ha⁻¹), but field measured heights were used instead.

The virtual stand generated this way includes the variability of the sampled actual stand. Mathematical

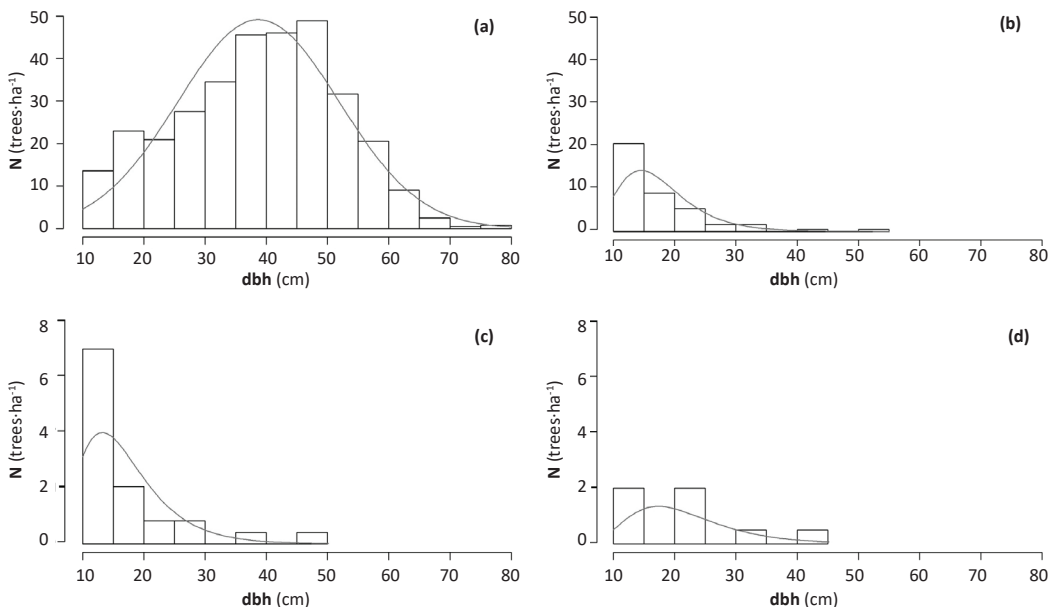


FIGURE 3. Diameter distributions for: alive silver fir (a), dead standing silver fir (b), beech (c), other broadleaved hardwoods (d); histograms represent sample plot data, line - mathematically fitted distribution.

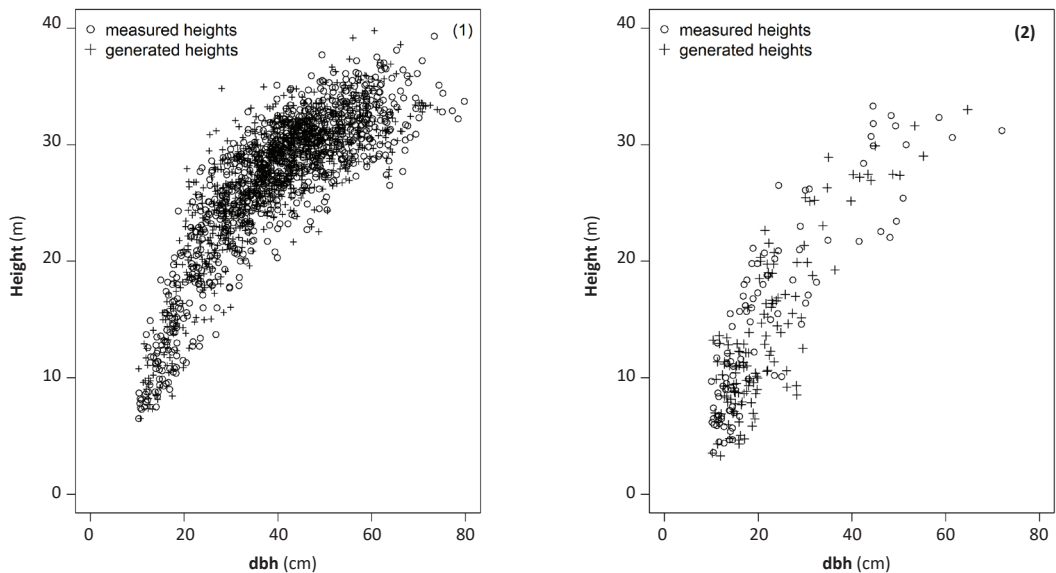


FIGURE 4. The comparison of measured and generated heights for alive (1) and dead silver fir trees (2).

fitting of diameter distribution and the distribution of tree heights resulted in particular deviations from the actual situation (Table 2). The comparison shown in Table 2 was done on the level of one hectare. The greatest deviations in distributions were recorded for alive silver fir trees (the

number of trees -5 trees·ha⁻¹, basal area 0.36 m²·ha⁻¹, and volume 4.21 m³·ha⁻¹). The results show that diameters at breast height for silver fir of medium diameter classes (37.5-62.5 cm) have the greatest deviations, while for the lowest and highest diameter classes the deviations are significantly

TABLE 2. The deviation of the structural elements of the virtual stand from the plot data: stand density (N, trees·ha⁻¹), basal area (G, m²·ha⁻¹), volume (V, m³·ha⁻¹).

dbh (cm)	<i>Abies alba</i> Mill.			<i>Abies alba</i> Mill.			<i>Fagus sylvatica</i> L.			OBH*			Σ		
	Alive			Dead standing			Alive			Alive					
	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)	N (trees·ha ⁻¹)	G (m ² ·ha ⁻¹)	V (m ³ ·ha ⁻¹)
12.5	-5	0.00	-0.11	-8	0.00	-0.30	0	0.00	0.00	0	0.00	0.00	-13	0.00	-0.41
17.5	-9	0.00	-1.29	5	0.00	1.67	0	0.00	0.00	0	0.00	0.00	-4	0.00	0.38
22.5	-1	0.00	-0.03	4	0.00	1.76	0	0.00	0.00	0	0.00	0.00	3	0.00	1.73
27.5	8	0.40	5.54	1	0.00	1.17	0	0.00	0.00	0	0.00	0.00	9	0.40	6.71
32.5	1	0.10	0.99	1	0.00	1.55	-1	0.00	-0.10	0	0.00	0.00	1	0.10	2.44
37.5	6	0.70	9.81	1	0.00	0.32	0	0.00	0.00	0	0.00	0.00	7	0.70	10.13
42.5	6	0.90	11.60	-1	0.00	-0.10	-1	0.00	-0.20	0	0.00	0.00	4	0.90	11.30
47.5	-10	-2.00	-27.60	0	0.00	0.00	0	0.00	0.00				-10	-2.00	-27.60
52.5	-6	-1.00	-22.90	-1	0.00	-1.20							-7	-1.00	-24.10
57.5	1	0.30	5.20										1	0.30	5.20
62.5	1	0.40	5.64										1	0.40	5.64
67.5	1	0.30	4.98										1	0.30	4.98
72.5	2	1.20	18.00										2	1.20	18.00
77.5	-1	0.00	-5.66										-1	0.00	-5.66
Σ	-5	0.40	4.21	2	0.00	5.48	-2	0.00	-0.30	0	0.00	0.00	-6	1.30	8.74
Average	-0.43	0.03	0.30	0.22	0.03	0.54	-0.25	0.00	-0.04	0.00	0.00	0.00	-0.43	0.05	0.62
St.dev.	5.44	0.80	12.40	3.70	0.10	1.00	0.46	0.00	0.07	0.00	0.00	0.00	6.30	0.80	12.60

* other broadleaved hardwoods

smaller. The difference of the virtual stand to the sample plots was calculated only up to those diameter classes for which the presence of trees was determined by field measurements.

In total, in the virtual stand the volume is greater only by 8.74 m³·ha⁻¹, basal area is greater by 1.30 m²·ha⁻¹, and the number of trees is smaller by 6 trees·ha⁻¹ (Table 2) as compared to the results of field measurements (Table 1). The deviation for volume, shown in percentage (%), is 1.46%, for basal area it is 1.36% and for the total number of trees -1.06%.

Table 3 shows the results of the Kolmogorov-Smirnov test (K-S test) for the distributions of measured and generated values for dbh, tree height and volume of individual trees. With respect to the D value of the K-S test, deviations between the cumulative relative distributions of the two stands (measured and generated) are tested. The K-S test deviations for the subpopulation of beech were minimal, but the statistically significant difference between dbh and volume was recorded for the subpopulation of dead standing silver fir. According to this test, the subpopulation of alive fir does not have a statistically significant deviation from the situation in the field, which is especially important because this subpopulation makes 97% of growing stock and 84% of the number of trees in the stand. Also, in total (the comparison on the level of the entire stand) the difference is not significant.

DISCUSSION

Directly joining spatially adjacent plots into a single coherent plot would result in an incorrect spatial structure of trees in the areas where the adjacent plots are connected [11], but there is also a possibility of using such plots as a basis for forest stand growth simulators [38]. In the virtual stand the simulated spatial organisation (x, y) does not have identical distances between trees to those measured in the field, but the whole virtual stand meets the requirement of the spatial pattern (regular, clustered or random) with respect to the results of Ripley's spatial analysis of individual subpopulations [5, 8-10]. Some authors [5, 6, 9, 11] agree with the claim that random distribution of trees is the most common and that generating a virtual stand according to random distribution is a less significant mistake. The only possible mistake caused by spatial pattern of trees might be found if the virtual stand is connected with forest stand growth simulators. In that case, the result of the stand's future development can to some extent be influenced by the mutual position of subpopulations [9, 39, 40]. The disadvantage of the majority of virtual stands is not taking into account the three-dimensional aspect of the forest [41]. The analysis of spatial structure, as well as the generating of the relative coordinates (x, y), generally refers to the analysis of horizontal projections of trees' positions. However, it is possible to generate relative coordinates of

TABLE 3. The results of the Kolmogorov-Smirnov test for the comparison of the distribution of the measured and generated values.

K-S test	<i>Abies alba</i> Mill.			<i>Abies alba</i> Mill.			<i>Fagus sylvatica</i> L.			Σ		
	Alive			Dead standing			Alive					
	dbh	Height	Volume	dbh	Height	Volume	dbh	Height	Volume	dbh	Height	Volume
N1/N2*	800/933			75/135			30/33			915/1111		
D	0.054	0.061	0.061	0.290	0.102	0.216	0.069	0.042	0.072	0.043	0.035	0.040
p value	0.1585	0.0763	0.0792	0.0005	0.4911	0.0219	1.0000	1.0000	1.0000	0.2950	0.5434	0.3679

* the ratio between the number of measured and the total number of generated trees

D – maximum difference of cumulative values

trees by using digital terrain model (DTM), but the horizontal projections would be identical. This is also corroborated by the characteristics of forest stand growth simulators which mostly work with horizontal surfaces [15]. The object of this research is characterised by up to 10% of inclination which could be ignored without having any significant mistakes as a consequence in further simulations of this stand's management.

In this research, the analysis of spatial distribution was done with the univariate Ripley's function for every individual subpopulation. Even though the subpopulation of silver fir (alive) holds more than 97% of timber stock, the bivariate analysis was not done because the contribution of other subpopulations was too small. In case there are more subpopulations and all of them are represented by 10% or more, it is possible to conduct an adequate bivariate analysis for all populations, as it was done by Pretzsch [8], Goreaud *et al.* [42] and Grabarnik and Särkkä [43]. In other words, in this paper the subpopulations were analysed independently of each other because only one subpopulation was dominant. In case of an even-aged pure stand of silver fir, the assumption taken was that there was no significant spatial interaction between the subpopulations.

Tree height is a function of its diameter at breast height and it is natural that trees of the same diameters at breast height are of different heights [44-47]. In this study tree heights were not associated with their corresponding diameter based on height-diameter equations (e.g. by using Michailoff's function [48]), because the fitted height curve does not describe variability within the same diameter class and thus reduces the variability of heights of real forest stand. Therefore in this study the variability of heights was associated with the corresponding diameter at breast height in a way that the distribution of heights within the same diameter class were taken into account (Figure 4). The presented way of generating virtual stand in this segment differs from the majority of similar studies.

When simulating a virtual stand it is fully expected that some deviations from field measurements will occur (Table 2). The comparison presented in Table 2 has been done on the area of one hectare, which is an adequate measure for this purpose. The virtual stand was generated based on a methodology which will always, on average, result in the

same characteristics, no matter the size of the area. The Kolmogorov-Smirnov test was done for all measured trees in the field (2.512 ha) and all trees belonging to the 3 ha area of the virtual stand. The deviations were primarily a result of the mathematical fitting of diameter distribution and the variability of tree heights within the same diameter class. Although the best possible fitting functions were used, they are still equations, and therefore they cannot completely stochastically describe all the variability in a forest stand [29]. In Figure 3 it can be seen that particular subpopulations are not continuously represented in all diameter classes, but appear intermittently in fitted distribution. In such cases, due to using continuous mathematical functions, the result of fitting always has to be greater than zero (Figure 3). There are no deviations for the subpopulation of other broadleaved hardwoods because the dimensions are identical to those measured in the field, so neither the K-S test is shown in Table 3. The distributions for this subpopulation are identical in the measured and in the virtual forest because of a very low frequency of only five trees per hectare, which was easier to generate.

The final result of this study is a virtual stand of 3 ha. According to Čavlović *et al.* [49], and Čavlović and Božić [50], that is the minimal area on which it is possible to establish a selective structure in the range of beech-fir forests of the Croatian Dinarides. On the other hand, the minimal stand area for sustainable even-aged forest management is one hectare. Therefore this generated area of the virtual stand is at the same time the universal and the minimal area for further management simulation in its two basic forms: the selective and the regular form. This is corroborated by the fact that silver fir supports both forms of management [10]. For the aforementioned management simulation, the virtual stand should be connected to one of the forest stand growth simulators on the level of one tree. Although this is a virtual stand in which for every tree many characteristics are known (position, species, diameter, height), the projection of future management which involves felling on the level of a single tree would be made difficult and very impractical for a virtual stand with a larger area (e.g. 10 ha, 20 ha or 50 ha). An area of 3 ha enables the user to decide in a relatively short period of time which tree should be cut, but that the result of management simulation is the same as the result

from a much larger area.

Before generating a virtual stand, data have to be collected by field measurement. Forest management and inventory is prescribed by the regulations of a particular country. In intensive standwise inventories forest stands are measured cyclically every ten years in order to develop management plans. However, those data are still not enough for generating a virtual stand. What is missing are the data about the spatial pattern of trees. This kind of research leads to the possibility of updating the abovementioned data with the spatial structure which can be determined in a relatively short time and at low cost. Stands are already organised based on the structural similarities within them so it is expected that the spatial pattern and analysis within them would be the same. This way it is possible to create entire virtual forests [16].

CONCLUSION

Considering the distribution of diameters at breast height, tree heights, the number of trees, basal area and volume, the virtual stand has minimal deviations from the situation in the field and it adequately shows variability measured in the field. Variability is an inherent component

of the most common stand characteristics which has to be determined when planning and managing forests. It is obvious that the characteristics of ground vegetation, shrubs, ground water and the like would not match the situation in the field. However, the presented methodology can have its role in ecology and can upgrade the process of generating virtual stands.

The virtual stand generated as part of this research can be used as a basis for forest stand growth simulators whose basic unit is a single tree and this way it can examine various future scenarios for managing both forest stands and entire forests. In that case, a virtual stand has to be generated for every part of the area managed as a separate stand (sub-compartment), because the virtual stand represents only a single stand within the entire forest. Virtual stands can be used in several different branches of forestry for which the size of the area is the most important factor, for example in landscape management. As part of a long-term forest management planning, generating virtual stands and using them in forest stand growth simulators should become a standardized procedure with the aim of predicting future forest characteristics as realistically as possible. The logical continuation of such plans is using forestry economics in order to provide an answer to the question of which potential future scenarios are economically justifiable.

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HPLC/MS-TOF Analysis of Surface Resins from Three Poplar Clones Grown in Serbia

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ABSTRACT

Background and Purpose: Poplar clones grown in Serbia are fast growing tree species important for many different purposes in forestry and industry. In this study chemical content of the surface resins of three poplar clones grown in Serbia - M1, B229 and PE 19/66 was analyzed, aiming at their potential usage as a source of natural products important for pharmacy and chemotaxonomy.

Materials and Methods: Using HPLC/MS-TOF we gained the first information on chemical compounds which comprise of resins on terminal twigs cuttings of commonly grown poplar clones. Provided from the nursery of the Institute of Lowland Forestry and Environment (Serbia), terminal twigs cuttings with leaves of different development stage from two year old seedlings of M1 poplar clone (*Populus euramericana* L.), PE 19/66 clone and B229 clone (both belonging to *Populus deltoides*) were sampled. The washing of the surface resins from terminal twigs cuttings of every sample was done with methylene-chloride until the samples were prepared for HPLC/MS-TOF analysis.

Results: Out of 38 different compounds which were identified, M1 clone qualitatively differed for 14 compounds as compared to two other clones. Generally, the results showed that the composition of the resins consisted of different phenolic acids, phenolic esters, flavonoids and other contents.

Conclusion: These three poplar clones are potent producers of pharmacologically and chemotaxonomically potent compounds in forest ecosystems, especially M1 clone.

Keywords: phenols, poplars, resins, terminal twigs

INTRODUCTION

The genus *Populus* from *Salicaceae* family consists of about 30 species, growing in southern and central Europe, in central Asia, Siberia, and North America, characterized and differentiated by the presence of different flavonoids, phenolic derivatives, and terpenoids in particular in young leaves, buds, and bud exudates [1]. Several species of *Populus* have been traditionally used in medicine, especially for their anti-inflammatory properties [2]. Nowadays, large-scale poplar production is based on clone culture production of controlled hybrids. The complex chemistry of poplar bud exudates includes about a hundred different phenolic and terpenoid compounds

[3], several of which are involved in biological processes [1]. Poplar biomass is a potential resource for natural production of bioactive molecules which could be substituted for some synthetic compounds associated with human and animal medicine [1]. Buds from *Populus* species are the main source of resins in propolis in Europe and North America ("poplar type" propolis) [4]. Resins comprising flavonoids and related phenolic acids represent approximately half of the propolis constituents [5]. Still, the chemical composition of the bee glue is extremely dependent on the plants found around the hive, as well on the geographic and climatic characteristics of the site.

Less commonly, species such as *Betula*, *Ulmus*, *Pinus*, *Quercus*, *Salix* and *Acacia* are also used in the production of propolis by bees [6, 7]. For the first time, the chemical composition of the cuticular waxes of poplar clones from Serbia was done and the results of GC/MS analysis showed that there are no significant differences in presence of alkanes: *n*-nonacosane, *n*-hexacosane, *n*-untriacosane and *n*-octacosane within leaf wax of these three clones [8].

Chemical content of the surface resins from three poplar clones was in the focus of this research. This type of chemical analysis of the surface resins from any fast-growing tree species from Serbia has previously not been undertaken.

MATERIALS AND METHODS

The Sampling of Plant Material

Five terminal twigs cuttings with healthy leaves of different development stage from two year old seedlings of M1 (Panonnia) poplar clone (*Populus euramericana* L.), cl. PE 19/66 and cl. B229 (both belonging to *Populus deltoides*) were sampled at the same time from the nursery collection of the Institute of Lowland Forestry and Environment, University of Novi Sad. The collections were grown as separate plantations, consisting of seedlings of the same age and origin, and influenced by the same climatic and weather conditions since they have been grown in the open. The two *Populus deltoides* clones B-229 and PE 19/66, and the hybrid *P. x canadensis* clone M-1 have previously been reported to be suitable for high biomass plantations [9-11]. *Populus deltoides* clones such as PE 19/66 were showed greater net photosynthesis than hybrid poplars (e.g. M-1), but hybrids were superior in water use efficiency [12]. The collections are part of the experimental Kač Forest estate located north-east from the city of Novi Sad, near the Kač village (N45° 17' 41" E19° 53' 30"). The genetic structure of the M1 and B229 clones has previously been determined through SSR and AFLP marker system and published, confirming the specific DNA profile of two different species originating from this nursery collection [13]. As the objective of the study was to examine the chemical composition and not the variability between single plants, the results were obtained for one pooled sample of terminal twigs cuttings with leaves from five plants per cultivar.

Preparation of Resin Extracts

Terminal twigs cuttings were immediately transported in sterile plastic bottles (5 mL volumes) on ice to laboratories of the Centre for Instrumental Analysis in Belgrade. Poplar clones' surface resins were washed out from the terminal shoots with 10 mL dichloromethane. Afterwards, the extracts were evaporated under a stream of N₂ for 23 minutes and dissolved in methanol at a concentration of 10 mg/mL, respectively.

HPLC/MS-TOF Analysis

High-resolution Liquid Chromatography/Photo-Diode Array/Electro Spray/Time of Flight mass spectra (HRLC/PDA/ESI/TOF MS) were measured on a HPLC instrument (Agilent 1200 Series) equipped with an autosampler, using a Zorbax Eclipse Plus C18 analytical column (1.8 µm particle size, 4.6 × 150 mm i.d., Agilent Technologies), and a PDA detector (DAD)

coupled with a 6210 TOF LC/MS system (Agilent Technologies).

The mobile phase for HRLC/PDA/ESI/TOF MS was 0.2% formic acid in water (A) and acetonitrile (B), and analyses were carried out under the following conditions: (0-3 min) 10% B, (3-8 min) 10-25% B, (8-11 min) 25% B, (11-18 min) 25-30% B, (18-48 min) 30-40% B, (48-68 min) 40-60% B, (68-88 min) 60-90% B, (88-100 min) 90% B, (100-101 min) 90-10% B, and (101-120 min) 10% B. The flow rate was 1.20 mL·min⁻¹, the injection volume was 5 µL, while the temperature of the column oven was set at 40°C. UV Spectral data from all peaks were accumulated in the range of 190-450 nm and chromatograms were recorded at 280 nm. MS data have been collected by applying the following parameters: ionization, negative ESI capillary voltage 4000 V, gas temperature 350°C, drying gas 12 L·min⁻¹, nebulizer pressure 45 psi, fragmentor voltage 140 V, mass range 100-2000 *m/z*. A personal computer system running MassHunter Workstation software was used for data acquisition and processing.

Exact mass measurements of pseudomolecular ions of analytes performed with a time-of-flight (TOF) mass spectrometer in negative polarity mode enabled the determination of molecular formula of most of the constituents. All identified compounds exhibited quasi-molecular ion [M-H]⁻ in the negative mode, confirming the molecular mass. Peak identification was mainly tentative, by comparison of their retention time, mass, and UV spectra with the literature data. For nine compounds we had standards for additional conformation of identification.

RESULTS AND DISCUSSION

Thirty-eight different compounds in resin extract of M1 clone and 24 common compounds within resin extract of B229 and PE 19/66 clones (Table 1, Figure 1) were identified. Fourteen compounds were unique for M1 clone, giving possibility to use them as potential species specific chemotaxonomic markers. Those are the compounds belonging to the caffeic, coumaryl and pinobaksin groups of compounds.

Our HPLC/MS-TOF analysis confirmed that Serbian poplar clones mainly consists of three groups of phenolic compounds: phenolic acids (caffeic acid, *p*-coumaric acid, cinnamic acid), phenolic esters, and flavonoid aglycons of flavanones (pinocembrin, pinobaksin), flavonols (galangin, quercetin and kaempferol), flavones (chrysin and its derivatives, apigenin). We have also identified salicylate like populin. The results obtained in the experiment were compared with literature data on *P. nigra* HPLC bud and propolis analysis in the following text. Black poplar buds are coated with a viscous substance, an exudate which contains different varieties of phenolic compounds: flavonoid aglycons and their chalcones and phenolic acids and their esters [2]. Also, the chemical characterization of bud exudate has allowed the identification among the flavonoid aglycons of some flavanones such as pinocembrin and pinostrobin, some flavonols such as galangin, quercetin and kaempferol, some flavones such as chrysin and apigenin [14-16] and some esters of phenolic acids, similar to our data when it comes to the phenolic content. Such compounds have also been reported in propolis [17]. Bud extract of *P. nigra* was mainly composed of phenolic acids (caffeic, *p*-coumaric, ferulic,

TABLE 1. A list of identified compounds within surface resins of three poplar clones. Abbreviation NI means Not Identified. Compounds marked with * were previously reported in Trudić *et al.* [20]. Bolded compounds are compounds identified by internal standards.

No.	UV max	Quasi-molecular ion [M-H] ⁻	Exact mass	Molecular formula	Compound name	M1 Clone	B229 Clone	PE19/66 Clone
1	198; 216; 274	109,0287	110,0360	C ₆ H ₆ O ₂	Benzenediol	+	+	+
2	198; 216; 274	123,0442	124,0515	C ₇ H ₈ O ₂	Methyl benzenediol	+	+	+
3	230; sh296; 324	179,0341	180,0414	C ₉ H ₈ O ₄	Caffeic acid *	+	+	+
4	sh290, 310	163,0372	164,1445	C ₉ H ₈ O ₃	<i>p</i>-Coumaric acid *	+	+	+
5	244; sh296; 322	423,1294	424,1364	C ₂₀ H ₁₂₄ O ₁₀	Furanocoumarin	+	+	+
6	234; 288	285,0762	286,0835	C ₁₆ H ₁₄ O ₅	Pinobaksin-5-methyl-ethar	+	+	+
7	242; 268; 300	389,1226	390,1309	C ₂₀ H ₂₂ O ₈	Populin *	+	+	+
8	292	271,0604	272,0677	C ₁₅ H ₁₂ O ₅	Naringenin *	+	+	+
9	264; 310	267,0654	268,0727	C ₁₆ H ₁₂ O ₄	Chrysin-5-methyl-eter	+	+	+
10	264; 338	269,0452	270,0525	C ₁₅ H ₁₀ O ₅	Apigenin *	+	+	+
11	292	271,0604	272,0676	C ₁₅ H ₁₂ O ₅	Pinobaksin *	+	+	+
12	266; 364	285,0396	272,0676	C ₁₅ H ₁₀ O ₆	Kaempferol *	+	+	+
13	236; 288	269,0812	270,0885	C ₁₆ H ₁₄ O ₄	NI	+	+	+
14	254; 372	315,0504	316,0576	C ₁₆ H ₁₂ O ₇	Isorhamnetin	+	+	+
15	264; 348	299,0554	300,0626	C ₁₆ H ₁₂ O ₆	Luteolin-3'-methyl-ethar	+	+	+
16	254; 356	329,0660	330,0733	C ₁₇ H ₁₄ O ₇	Quercetin-dimethyl-ethar	+	+	+
17	260; 302; 352	283,0603	284,0676	C ₁₆ H ₁₂ O ₅	Galangin-methyl-ethar	+	+	+
18	232; 286; 324	327,0869	328,0942	C ₁₈ H ₁₆ O ₆	Pinobaksin-5-methyl-ethar-3-acetate	+	+	+
19	244; 294sh; 326	315,0844	316,0919	C ₁₇ H ₁₆ O ₆	NI	+	+	+
20	268; 312	253,0497	254,0570	C ₁₅ H ₁₀ O ₄	Chrysin	+	+	+
21	296; 326	247,0967	248,1040	C ₁₄ H ₁₆ O ₄	Caffeic acid prenyl ester	+	+	+
22	294sh; 328	269,0810	270,0883	C ₁₆ H ₁₄ O ₄	Caffeic acid benzyl ester	+	+	+
23	290	255,0655	256,0728	C ₁₅ H ₁₂ O ₄	Pinocembrin	+	+	+
24	266; 360	269,0445	270,0518	C ₁₅ H ₁₀ O ₅	Galangin	+	+	+
25	290	285,0760	286,0833	C ₁₆ H ₁₄ O ₅	Pinobaksin-7-O-methyl eter	+	+	+
26	294	313,0712	314,0784	C ₁₇ H ₁₄ O ₄	Pinobaksin-3-O-acetate	+	+	+
27	298; 328	283,0968	284,1041	C ₁₇ H ₁₆ O ₄	Caffeic acid Phenylethyl eter	+	+	+
28	264; 312	283,0603	284,0676	C ₁₆ H ₁₂ O ₅	Methoxy-Chrysin	+	+	+
29	230; 290sh; 310	231,1015	232,1088	C ₁₄ H ₁₆ O ₃	<i>p</i> -Coumaryl prenyl ester	+	+	+
30	220; 314	253,0861	254,0935	C ₁₆ H ₁₄ O ₃	<i>p</i> -Coumaryl benzyl ester	+	+	+
31	220; 288sh; 312	231,1017	232,1089	C ₁₄ H ₁₆ O ₃	<i>p</i> -Coumaryl prenyl ester	+	+	+
32	248; 316	295,0967	296,1040	C ₁₈ H ₁₆ O ₄	Caffeic acid cinnamyl ester	+	+	+
33	238; 232sh; 324	311,2222	312,2294	C ₁₈ H ₃₂ O ₄	NI	+	+	+
34	294	327,0868	328,0941	C ₁₈ H ₁₆ O ₆	Pinobaksin-3-O-propionate	+	+	+
35	314	267,1017	268,1090	C ₁₇ H ₁₆ O ₃	<i>p</i> -Coumaryl phenylethyl ester	+	+	+
36	268; 312	279,1016	280,1097	C ₁₈ H ₁₆ O ₃	<i>p</i> -Coumaryc cinnamyl ester	+	+	+
37	294	341,1020; 377,0788	342,1093	C ₁₉ H ₁₈ O ₆	Pinobaksin-3-O- butyrate	+	+	+
38	292	355,1172; 391,0958	356,1245	C ₂₀ H ₂₀ O ₆	Pinobaksin -3-O pentanoate	+	+	+

isoferulic, *di*-O-methyl caffeic and cinnamic acids) (5.2%), followed by salicylates (salicin) (1.8%) and flavonoid aglycons (pinobaksin 5-methyl ethar, pinobaksin and pinocembrin) (1.5%) [18].

Data comparison of poplar bud absolute markers after true quantitation by derivatization-GC-MS and HPLC-PDA was also reported in study of Rubiolo *et al.* [18]: benzoic acid, cinnamic acid, *p*-methoxycinnamic acid, *p*-coumaric acid,

dimethoxycinnamic acid, isoferulic acid, ferulic acid, caffeic acid, 1,1-dimethylallyl caffeate, pinostrobin, pinocembrin, tectochrysin, chrysin, galangin. Salicyl aldehyde in fresh 0.2% and in dried 1.4% plant material of *P. nigra* L. was also identified in study of Jerković and Mastelić [15]. This compound may originate from salicin and/or populin by hydrolysis and oxidation and as mentioned before, we identified populin in our resins extract. Jerković and Mastelić [15] have also

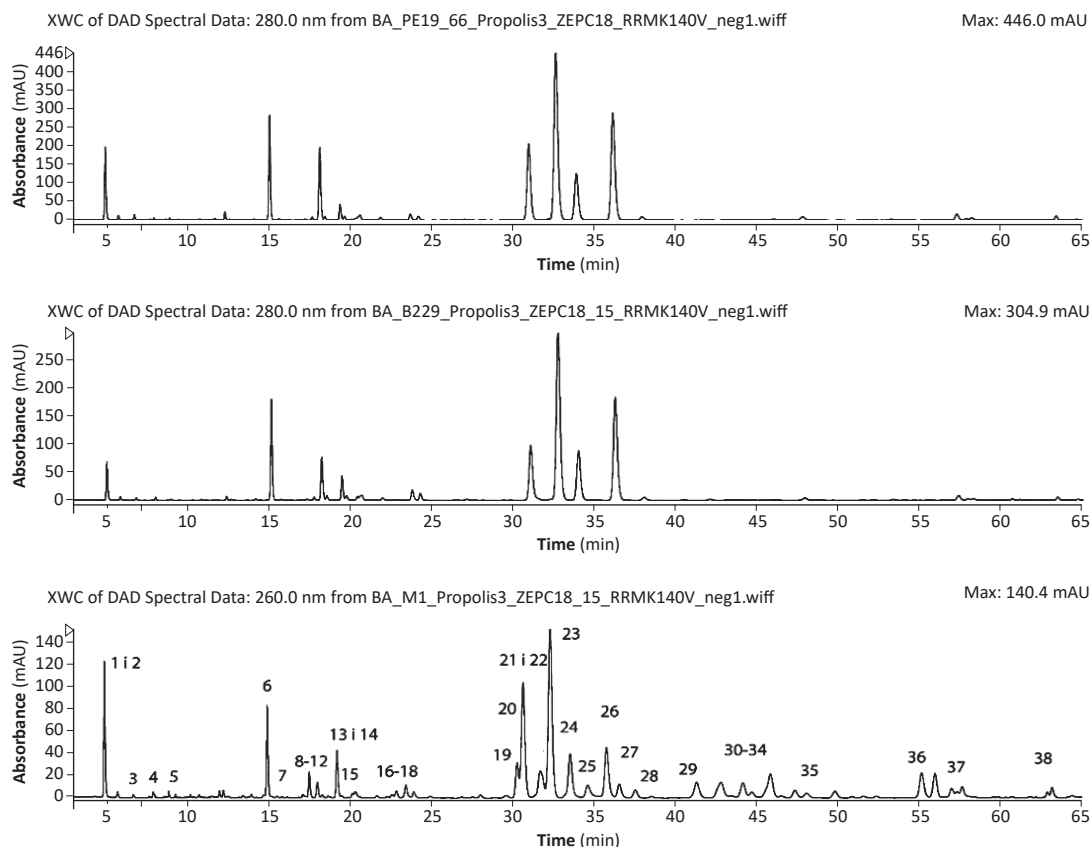


FIGURE 1. DAD chromatograms of identified resin compounds measured on 280 nm, 65 minutes. Peak numbers refer to those reported in Table 1.

reported prenyl alcohols with higher percentage (7.6%) in dried buds. Non-terpenes presented 9.8-13.5% of the total isolate. The gross compositions of non-terpenes were aliphatic and aromatic alcohols, carbonyl compounds and aliphatic acids. Benzyl alcohol and 2-phenylethanol were previously identified (ca. 0.2%) in the bud extract of *P. candidans* [19]. The analysis of the phenolic extract of Portuguese propolis allowed the detection of dihydroflavonols, flavones, flavanones and flavonols, either as a free form or their methylated/esterified forms [7]. In particular, it was possible to identify the aglycones forms of apigenin, pinobaksin, pinocembrin and chrysin, the esterified derivatives pinobaksin-3-O-acetate, pinobaksin-3-O-propionate, pinobaksin-2-O-butyrate or isobutyrate and pinobaksin-3-O-pentanoate or 2-methylbutyrate and the methylated derivatives pinobaksin-5-methyl-ether, pinocembrin-5-methyl-ether, chrysin-5-methyl-ether, and chrysin-6-methyl-ether. In propolis from temperate zones, the most frequently reported phenolic acids are caffeic acid, ferulic acid and the cinnamic acid [4]. We reported the following esters and ether derivatives: *p*-cinamyl cinnamyl ester, pinobaksin-3-O-butyrate, pinobaksin-3-O-pentanoate, pinobaksin-5-methyl-ether, luteolin-3-methyl-ether, quercetin-dimethyl-ether,

galangin-methyl-ether, pinobaksin-5-methyl-ether-3-acetate, caffeic acid prenyl ester, caffeic acid benzyl ester, pinobaksin-7-methyl-ether, pinobaksin-3-O-acetate, 2-phenylethyl caffeate, coumaril prenyl ester, coumaril benzyl ester, coumaril prenyl ester, caffeic acid cinnamyl ester, pinobaksin-3-O-propionate. Similarity with the chemical profile of *P. nigra* might indicate that some of those phenolic compounds and its ester might be common for the genus *Populus*, but further analysis within more *Populus* species is needed to confirm such hypothesis.

CONCLUSIONS

Direct assessment of antioxidant activity of resins is required through FRAP, DPPH, ORAC, ABTS, lipid peroxidation and other tests to screen its radical scavenging capacity and correlate it with quantity analysis of its bioactive compounds. In this case, 70% ethanol should be used as a common and nontoxic solvent for extraction. It is also possible that isomers can be present, although further NMR analysis must be performed.

The results presented in this study shows application in:

- Chemical compounds identified so far can be applied in pharmaceutical research and thus involve more nursery production of poplar clones' biomass as a resource of those molecules;
- To understand the chemical profile of propolis, since resins are the starting material for its production by bees;
- Chemotaxonomy, since we confirmed that there is a quite different chemical profile of surface resins between two species of poplars from our collection. In our study, 14 compounds were specifically characteristic for M1 clone (*P. euramericana* L) surface resin extract, indicating their species-specific

significance. However, further comparative study with other poplar species is needed to determine the presence/absence of those compounds within genus.

- To monitor and predict poplar's biomass pharmaceutical potential and label them as a nursery with ecosystem service significance.

Acknowledgements

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The Impact of Drought, Normal Watering and Substrate Saturation on the Morphological and Physiological Condition of Container Seedlings of Narrow-Leaved Ash (*Fraxinus angustifolia* Vahl)

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ABSTRACT

Background and Purpose: Narrow-leaved ash (*Fraxinus angustifolia* Vahl) is one of the most important tree species of lowland floodplain forests in the Republic of Croatia. Recent significant climate changes, reflected in extreme temperatures and long dry periods, have had a direct impact on the dynamics and levels of groundwater, as well as on the dynamics of precipitation and floodwater, which are of decisive importance for the success of narrow-leaved ash. Our study aims to determine the morphological and physiological characteristics of seedlings of narrow-leaved ash after 72 days of drought, normal watering and substrate saturation.

Materials and Methods: The experiment was established in three treatments (drought, normal watering and saturation), and each treatment included two containers or 24 seedlings. A total of 72 seedlings were replanted. After 72 days, height growth and increment, water potential, photosynthetic efficiency and the total chlorophyll content in the leaf mesophyll were measured.

Results: Seedlings from the drought treatment wilted immediately. Seedlings saturated with water up to the root collar manifested better height and diameter growth, high water potential and a lesser physiological stress response as compared to the seedlings that were watered normally.

Conclusions: Seedlings of narrow-leaved ash, which is a hygrophytic tree species, do not tolerate dry conditions and no watering. Seedlings saturated with water for 72 days showed a better morphological-physiological status than the seedlings that received normal quantities of water.

Keywords: water potential, photosynthetic efficiency, CCI index, seedling morphology, seedling physiology

INTRODUCTION

Narrow-leaved ash (*Fraxinus angustifolia* Vahl) is one of the most important tree species of lowland floodplain forests. In the Republic of Croatia, this tree species is found in pure stands, but more commonly mixed with other broadleaves, including pedunculate oak, black alder, lowland

elm, spreading elm, poplars and other species. The basic ecological factors that determine the occurrence of this forest tree species are micro-depressions in which water is retained after frequent flooding, and clayey alluvial soil which prevents water drainage. Due to these factors, forests of narrow-leaved

ash are exposed to long-lasting effects of surface water and high groundwater. According to Anić [1], in terms of micro-relief narrow-leaved ash is the euryvalent species of floodplain forests. The habitats in which it grows range from wetland sites, where narrow-leaved ash forms a wetland forest boundary towards a swamp, to fresh micro-elevations (humid micro-elevations - "grede" in Croatian). However, it reaches its ecological optimum in wetland habitats where it faces no competition [2].

The degradation of lowland forests is a serious problem not only from a commercial and non-commercial standpoint, but also from a biological and ecological aspect. Tree decline in forest ecosystems may have different causes, such as competition between species and individuals, the effects of diverse natural phenomena (climatic excesses, thunder, wind, wet snow, icy rain, long-lasting flood, biotic factors), changes in natural ecological conditions, i.e. a drop in groundwater levels, changes in floodwater dynamics, waterlogging and drying of habitats, the pollution of flood and precipitation water), and the consequences of adverse human activity [3]. The dieback of narrow-leaved ash results from a synergy of climate change, biotic factors and anthropogenic effects on water conditions. Climate has recently undergone significant changes manifested in extreme temperatures and long dry periods that directly affect the dynamics of ground water levels and the dynamics of precipitation and floodwater, all of which are of decisive importance for the growth of narrow-leaved ash. Retentions constructed in order to prevent the consequences of high water levels have exposed forests in retention areas to exceptionally high floodwater levels. Floodwater levels are much higher now than they were during flooding before the retentions were constructed. As expected, this has a negative effect on the vitality of forests in these areas. Air pollution, flooding in the vegetation period and the absence of regular winter and spring floods, coupled with consecutive dry periods, are crucial stress factors that exert an adverse impact on these forests [4-7].

This research aims to determine the following:

- Height and diameter increment (mm) of container seedlings of narrow-leaved ash under conditions of substrate saturation and normal watering in the period from 5 May to 15 July 2015 (72 days);
- Water potential (Ψ) of seedlings under conditions of substrate saturation and normal watering;
- Photosynthetic efficiency (F_v/F_m) of seedling leaves under conditions of substrate saturation and normal watering;
- Total chlorophyll content of mesophyll (CCI) in the leaf of seedlings growing in saturated substrates and under normal watering conditions;
- Correlation between diameter increment (mm) of seedlings and their physiological condition (water potential (Ψ) and the maximum quantum yield of photosystem II (F_v/F_m));
- Correlation between the maximum quantum yield of photosystem (F_v/F_m) and water potential (Ψ) of normally watered seedlings.

MATERIALS AND METHODS

This research involved one-year-old seedlings of narrow-leaved ash with bare roots which were replanted in 12-hole AM-POLIM multi-containers of 620 ml. Replanting was performed on 5 May 2015. The trial was established in three treatments (drought, normal watering and saturation), and each treatment included two containers or 24 seedlings. A total of 72 seedlings were replanted. The initial morphological seedling characteristics were measured prior to replanting (total height and diameter of the root collar). In the drought treatment, the seedlings were not watered during the experiment. Data on the overall monthly precipitation quantity for the meteorological station Zagreb Maksimir were used during the normal watering treatment. Watering was done with the previously determined quantity of water in $\text{mm}\cdot\text{m}^{-2}$. During the substrate saturation treatment, a constant water level was retained in the bath with the containers so that the water was above the seedling root collars. Seedlings from all treatments were covered in order to prevent precipitation from disrupting the experiment. Seedlings from the drought treatment died immediately after the experiment was established. On 15 July 2015, height and diameter increment were measured on the survived seedlings. The physiological properties of the seedlings (water potential, chlorophyll fluorescence "a" and the total chlorophyll content index (CCI) in the leaf mesophyll) were also measured on the same day. The seedling water potential (Ψ) was measured with a portable instrument for measuring water potential (Model 600 Pressure Chamber Instruments, Corvallis, ORE). One leaf per seedling from the tip part of the crown was selected for measurement. The measurement of chlorophyll fluorescence "a" and the determination of the maximum quantum yield of photosystem II (F_v/F_m) were accomplished with a portable device FluorPen FP 100 (Photon Systems Instruments). Measurement was performed on 1 leaf in 20 seedlings from the normal watering treatment and 20 seedlings from the saturation treatment. The total chlorophyll content index was measured with a portable chlorophyll metre CCM-200 (Opti-Sciences, Tyngsboro, MA). The total chlorophyll content index was determined on the basis of five measurements per leaf on a randomly selected spot, but the main leaf vein was avoided. Under three different conditions (drought, normal watering and saturation) and two repetitions, substrate temperature ($^{\circ}\text{C}$) and volumetric substrate moisture (%) were measured from 5 May to 15 July 2015. The measurements were performed every full hour using the measuring station Spectrum (N=1705 data). Climate data were processed with SpecWare 8 Professional software, and the data were statistically processed (descriptive statistics, ANOVA) using Statistica 7.1 software [8].

RESULTS

Table 1 shows the results of descriptive statistics of seedling height and diameter increment under substrate saturation and normal watering between 5 May 2015 and 15 July 2015. The mean height increment of narrow-leaved ash seedlings under substrate saturation conditions between 5 May 2015 and 15 July 2015 reached 110 mm (19-199 mm),

while diameter increment amounted to 2.20 mm (9.54-4.43 mm). The mean height increment of seedlings under normal watering conditions between 5 May 2015 and 15 July 2015 amounted to 48 mm (0-119 mm) and diameter increment amounted to 0.39 mm (0.00-1.31 mm). A t-test was used to determine a statistically significant difference ($p=0.000033$) in the height increment of narrow-leaved ash seedlings under substrate saturation and normal watering conditions between 5 May 2015 and 15 July 2015. The seedlings under substrate saturation conditions showed better height increment of 62 mm on average compared to the normally watered seedlings. A t-test was used to determine a statistically significant difference ($p=0.000000$) in diameter increment of narrow-leaved ash seedlings under substrate saturation and normal watering conditions between 5 May 2015 and 15 July 2015. Seedlings growing in saturated substrates had a diameter increment that was higher by 1.81 mm on average compared to normally watered seedlings.

Table 2 shows the results of descriptive statistics of the seedling water potential (Ψ) under substrate saturation and normal watering conditions on 16 July 2015. The mean water potential of narrow-leaved ash seedlings under substrate saturation conditions amounted to 5.6 bar (4.4-9.0 bar), whereas under normal watering condition it was 36.1 bar (15.5- 40 bar and more). In 10 plants (45.45%) pressure could not be taken due to instrument limitation of 40 bars. A t-test was used to determine a statistically significant difference in the water potential of narrow-leaved ash seedlings with regard to treatments ($p=0.000000$). Seedlings that were watered needed pressure that was higher by 30.5 bars on average for water to appear on the surface of leaf cross-section. Under

conditions of substrate saturation lasting for 72 days (5 May 2015 - 16 July 2015), the seedlings were under a low water stress or high water potential in relation to the seedlings that were watered, in which a low water potential or high water stress was detected.

Table 3 shows the results of descriptive statistics of the maximum quantum yield of photosystem II (F_v/F_m) of seedlings under substrate saturation and normal watering conditions on 16 July 2015. The mean values of the maximum quantum yield of photosystem II (F_v/F_m) in seedlings treated by substrate saturation amounted to 0.82 (0.77-0.84), and in seedlings that were watered normally it was 0.65 (0.02-0.84). A t-test was used to determine a statistically significant difference ($p=0.000000$) in the success of photosynthetic efficiency of narrow-leaved ash seedlings with regard to the treatments. Watered seedlings had on average a lower maximum quantum yield of photosystem II by 0.17. The lower the F_v/F_m values are, the stronger the physiological shock of the seedlings is.

Table 4 provides the results of the descriptive statistics of the total chlorophyll content in the leaf mesophyll (CCI) of seedlings under conditions of substrate saturation and normal watering on 16 July 2015. Seedlings of narrow-leaved ash under conditions of substrate saturation had an average total chlorophyll content index (CCI) in the leaf mesophyll of 17.8 (7.8-32.6), whereas in the case of watered seedlings the above index was 18.3 (3.1-65.1) on average. The t-test results did not show the existence of a statistically significant difference ($p=0.6818$) in the total chlorophyll content index (CCI) in the leaf mesophyll of narrow-leaved ash seedlings under conditions of substrate saturation and normal watering on 16 July 2015.

TABLE 1. Descriptive statistics of height (mm) and diameter (mm) increment of container seedlings of narrow-leaved ash (*Fraxinus angustifolia* Vahl) under conditions of substrate saturation and normal watering between 5 May 2015 and 15 July 2015

Variable	N	Treatment	Mean	Median	Minimum	Maximum	Variance	Std. Dev.
Height increment (mm)	24	Saturation	110	121	19	199	3203	57
Diameter increment (mm)			2.20	2.12	0.54	4.43	0.79	0.89
Height increment (mm)	24	Watering	48	46	0	119	845	29
Diameter increment (mm)			0.39	0.33	0.00	1.31	0.17	0.42

TABLE 2. Descriptive statistics of the seedling water potential (Ψ) under substrate saturation and normal watering conditions on 16 July 2015.

Treatment	N	Mean	Median	Minimum	Maximum	Variance	Std. Dev.
Saturation	24	5.6	5.4	4.4	9.0	1.3	1.1
Watering	22	36.1	39.5	15.5	40.0	36.7	6.1

TABLE 3. Descriptive statistics of the maximum quantum yield of photosystem II (F_v/F_m) of seedlings under substrate saturation and normal watering conditions on 16 July 2015

Treatment	N	Mean	Median	Minimum	Maximum	Variance	Std. Dev.
Saturation	20	0.82	0.83	0.77	0.84	0.00	0.02
Watering	20	0.65	0.73	0.02	0.84	0.04	0.20

A negative and significant correlation ($r=-0.4507$) was found between diameter increment (mm) of narrow-leaved ash seedlings under conditions of substrate saturation and water potential (bar) on 16 July 2015 (Figure 1).

A positive and significant correlation ($r=0.40762$) was observed between diameter increment (mm) of narrow-leaved ash seedlings under conditions of normal watering and maximum quantum yield of photosystem II (F_v/F_m) of seedlings on 16 July 2015 (Figure 2).

A negative and significant correlation ($r=-0.4195$) was found between the maximum quantum yield of photosystem II (F_v/F_m) and water potential (bar) in normally watered seedlings on 16 July 2015 (Figure 3).

Table 5 presents descriptive statistics of the analyzed microclimatic elements. The differences between the minimal and maximal values, i.e. maximal oscillations in substrate temperature in dry conditions amounted to 24.2°C, in saturated conditions to 15.9°C, and in normal conditions to 23.7°C. Absolute oscillations in the values of volumetric soil moisture reached 27.5% in dry conditions, 112.1% in saturated conditions, and 27.6% in normal conditions.

According to the results in Table 6, significant differences were found in mean values of substrate temperature and

volumetric substrate moisture for the observed cases of drought, saturation and normal watering.

DISCUSSION

According to Hrašovec *et al.* [9], drought has an important effect on the growing intensity of narrow-leaved ash dieback. If water supply is poor, then important physiological processes are decreased or halted, which affects plant growth [10].

In our research, seedlings under drought treatment died very soon after the establishment of the experiment. Seedling mortality can be explained by the biological properties of narrow-leaved ash (hygrophyte) and by adverse ecological conditions (lack of moisture in the soil and extremely high substrate temperature inside the containers). During flooding, the air in soil pores is replaced by water, which leads to oxygen concentrations that are 30 times lower than those in aerated soils [11]. Because the seedling root collars were submerged in water all of the time, hypertrophic lenticels were developed, while adventitious roots on the bottom part of the stem did not grow. Jaeger also reached the same result [12]. The European ash covered by floods during the entire vegetation

TABLE 4. Descriptive statistics of the total chlorophyll content in the leaf mesophyll (CCI) of container seedlings of narrow-leaved ash (*Fraxinus angustifolia* Vahl) under conditions of substrate saturation and normal watering on 16 July 2015

Treatment	N	Mean	Median	Minimum	Maximum	Variance	Std. Dev.
Saturation	120	17.8	16.8	7.8	32.6	34.9	5.9
Watering	115	18.3	17.1	3.1	65.1	89.6	9.5

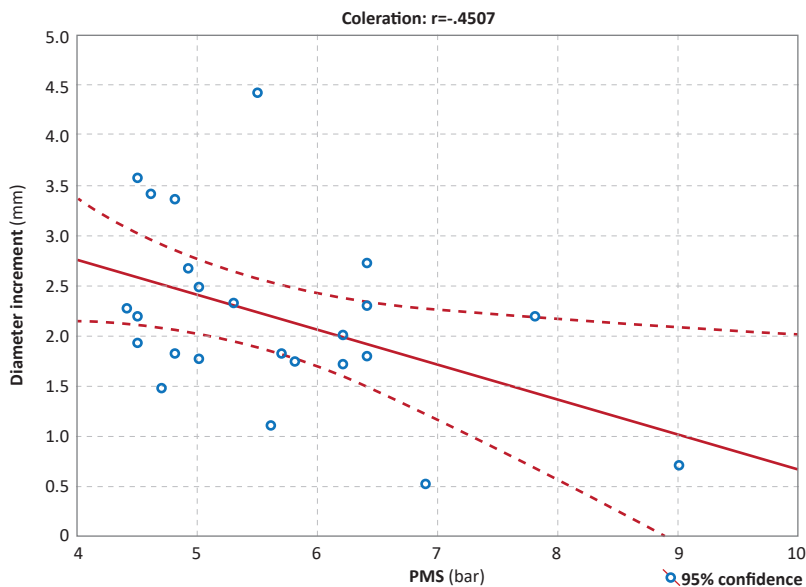


FIGURE1. Correlations between diameter increment (mm) of container seedlings of narrow-leaved ash under conditions of substrate saturation and water potential (bar) on 16 July 2015

period (April - September) manifests a considerable decrease in height increment and biomass [13, 14].

Our research showed that the height increment of narrow-leaved ash seedlings growing in saturated substrates was by 62 mm better on average as compared to the seedlings that received normal quantities of water. Evidently,

the European ash and narrow-leaved ash are species with diverse ecological requirements.

The development of plant hypertrophy as a morphological response to flood conditions in which plant aeration is increased [15] was recorded in the species *Fraxinus excelsior* L. [13]. This phenomenon was observed

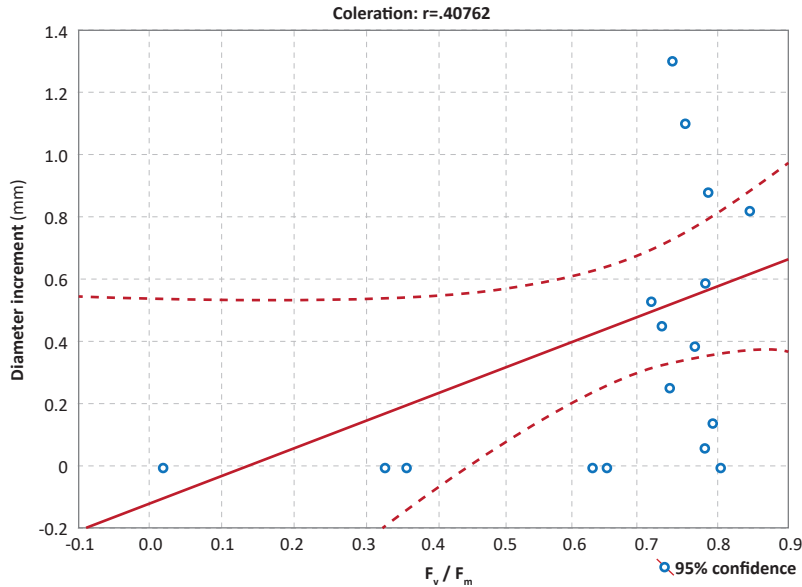


FIGURE 2. Correlations between diameter increment (mm) of container seedlings of narrow-leaved ash and the maximum quantum yield of photosystem II (F_v/F_m) in normally watered seedlings on 16 July 2015

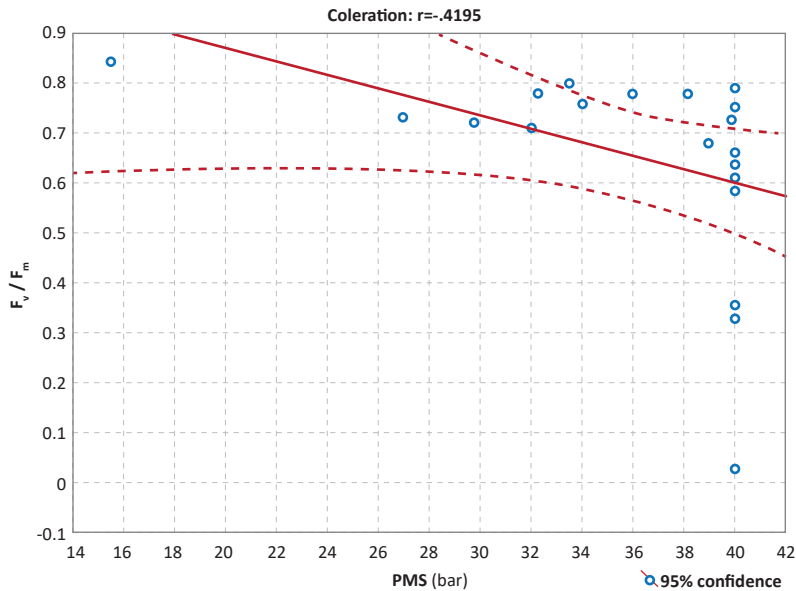


FIGURE 3. Correlations between the maximum quantum yield of photosystem II (F_v/F_m) and water potential (bar) in normally watered seedlings on 16 July 2015

in the provenance “Rhine” from alluvial stands, but not in the provenances “Alb” and “BFor”, which indicates specific provenance adaptations to site conditions [12]. Morphological and anatomic adaptations of species of floodplain forest to floods are discussed by [16-19]. Our research confirmed what was mentioned above. Diameter increment of seedlings growing in saturated substrates was higher by 1.81 cm on average in relation to seedlings that were watered normally.

The plant root is in the soil with a high water potential, while the above-ground parts are surrounded by air, whose water potential is low. The existing water potential gradient enables transpiration course by which water is transported from the soil through the plant with no energy consumption and is released in the atmosphere. If low pressure (3 bars or 45 psi) is sufficient for water to emerge on the surface of a leaf cross-section, then the plant is under a relatively low water stress (high water potential) and probably has enough water for growth processes. If a pressure of 20 bars is needed for water to appear on the surface of the cut, the water stress is relatively high (low water potential). Water potential values differ from species to species. Succulents or young shoots may wilt at a low pressure of 7-8 bars, and certain physiological processes, such as photosynthesis, may be decreased at pressures lower than 10 - 15 bars. In our research, the average seedling water potential under substrate saturation was 5.6 bars (4.4 - 9.0 bars), and in

normal watering conditions it was 36.1 bars (15.5-40 bars and higher). At 10 plants (45.45%), the pressure could not be taken due to the instrument being limited to 40 bars.

Photosynthesis is a very sensitive and early indicator of plant vitality [20, 21]. One of the first responses of a plant to unfavourable conditions is reflected in lower photosynthetic efficiency and in inhibitions of different molecular mechanisms. In this sense, the analysis of chlorophyll fluorescence is an excellent tool for determining different photosynthetic parameters that can be used for photosynthesis optimisation and control in field cultures. Chlorophyll fluorescence provides useful information about the photosynthetic efficiency under abiotic stresses [22]. Chlorophyll fluorescence analysis is a powerful tool for the study of species under normal and stressful conditions [23, 24]. Chlorophyll fluorescence can be used to assess plant vitality and stress. The parameter F_v/F_m is calculated from the minimum fluorescence value (F_0) and the maximum value (F_m) using the formula $(F_m - F_0)/F_m$. It reflects the efficiency of electron transfer in photosystem II and is used as an indicator of the success of photosynthetic efficiency.

The difference between maximum and minimum fluorescence is called variable fluorescence (F_v). An optimum yield of photosystem II, F_v/F_m is calculated from these data. This ratio represents a measure of the potential maximum quantum yield of photosystem II.

There are photosystems I and II. In the centre of

TABLE 5. Descriptive statistics of substrate temperature (°C) and volumetric substrate moisture (%)

Conditions	Mean	Min.	Max.	Std. Dev.
Substrate temperature (°C)				
Drought	20.7	10.4	34.6	4.5
Saturation	19.6	12.0	27.9	3.2
Watering	20.1	9.1	32.8	4.8
Volumetric substrate moisture (%)				
Drought	19.8	6.1	33.6	7.2
Saturation	41.3	36.7	148.8	16.1
Watering	22.8	6.6	34.2	8.1

TABLE 6. The comparison of mean values of substrate temperature and volumetric substrate moisture in different conditions

Conditions	Microclimatic elements	
	Substrate temperature (°C)	Vol. substrate moisture (%)
Drought	20.7 ± 4.59 ^a	19.8 ± 7.2 ^a
Saturation	19.6 ± 3.2 ^b	41.3 ± 16.1 ^b
Watering	20.1 ± 4.8 ^c	22.8 ± 8.1 ^c

^{a, b, c} Values within the column marked with a different letter significantly differ (p<0.05). Values are presented as the mean ± std. dev.

photosystem I there is a chlorophyll molecule which has maximum absorption at a wavelength of 700 nm, while a chlorophyll molecule in photosystem II has maximum absorption at a wavelength of 680 nm [25].

Chlorophyll fluorescence can be used to assess vitality and stress of several cultivars, as well as analyze different cultivars in terms of their response to stress factors. Franić *et al.* [26] state that in general, the lowest Fv/Fm values were measured in treatments with insufficient water/5mg Cd in the soil, and the highest in treatments with sufficient water without cadmium, which points to the negative effect of a combination of water stress and cadmium-induced stress. Identical results were obtained by our studies (without cadmium). The average value of the maximum quantum yield of photosystem II (F_v/F_m) in seedlings treated by substrate saturation was 0.82, and in seedlings that were watered normally it was 0.65. In the majority of plant species, the potential maximum quantum yield of photosystem II is about 0.83. The maximum quantum yield of photosystem II in watered seedlings was lower by 0.17 on average, which indicates that the seedlings were under a stronger physiological shock. The chlorophyll metre works by emitting light at a wavelength of 653 nm (the red part of the solar spectre) and of 931 nm (the infrared part of the solar spectre) through the leaf mesophyll filled with chloroplasts that contain chlorophyll. The chlorophyll content index (CCI) is obtained on the basis of the relative quantity of the emitted, i.e. absorbed light by the chlorophyll. Measurements of the chlorophyll content index during the vegetation period can help us determine the optimal time for fertilization and the application of other pomotechnical treatments in nurseries, cultures or clonal seed orchards, thus improving the quantity and quality of the increment or seed yield. No statistically significant differences were found in the total chlorophyll content index (CCI) in seedling leaf mesophyll under substrate saturation and normal watering conditions.

Seedling diameter increment decreases with an increase in water potential values, as stated by Jaeger [12]. At normal watering, seedling diameter increment increases as the maximum quantum yield of photosystem II increases. An increase in the water potential value of seedlings under normal watering decreases the maximum quantum yield of photosystem II.

Consecutive dry years have a significant impact on the dieback of pedunculate oak and narrow-leaved ash, which are hygrophytes in terms of their ecological requirements for water. As for floods, the only difference is that pedunculate oak's dieback is affected by the occurrence of floods, whereas narrow-leaved ash's dieback is affected by the absence of floods. Here, the issue is probably the duration of flooding. Pedunculate oak cannot tolerate long-lasting floods, unlike narrow-leaved ash which is a more hygrophytic forest tree species. Narrow-leaved ash is a distinct hygrophyte capable

of tolerating stagnant water on the soil surface, the surplus of carbon dioxide and the lack of oxygen in swampy soils. Of importance is the fact that narrow-leaved ash cannot thrive under swampy conditions when water stagnates on the soil throughout the vegetation period. Changes in the onset and size of floods are the consequence of climate change and global warming. Large-scale floods will occur with rising frequency. There will be fewer small-scale floods [27]. Changes in climate that are expected in lowland Croatia will probably bring about a rise in air temperatures and a drop in precipitation quantities. The current status of hydrological conditions, which severe droughts occurring in the past several decades have changed significantly, are becoming ever more unfavourable for the survival of lowland forests with regard to their water requirements and the dependence of lowland species on groundwater [28]. Among all studied climatic elements and indices, it is lower precipitation quantities that have had a significant effect on the dieback of narrow-leaved ash [9].

The most favourable temperatures for the growth and development of an organism are those at which all the processes are best coordinated [29]. In terms of the requirements for air temperature and soil, narrow-leaved ash belongs to the eurithermal tree species, which are hardly susceptible to winter cold and summer heat, but highly susceptible to winter frost.

CONCLUSIONS

Containerized narrow-leaved ash seedlings saturated with water for 72 days showed a better morphological-physiological status than the seedlings that received normal quantities of water.

A statistically significant difference was confirmed in the morphological status of seedlings under conditions of substrate saturation and normal watering. Seedlings growing in saturated substrates attained bigger height increment by 62 mm and bigger diameter increment by 1.81 mm on average, compared to seedlings that were watered normally.

A statistically significant difference was obtained in the physiological status of seedlings. The water potential of watered seedlings needed pressure that was higher by 30.5 bars in order for water to appear on the surface of the leaf cross-section. Seedlings growing in saturated substrates were under a low water stress or high water potential compared to watered seedlings, in which a low water potential or high water stress was observed. Photosynthetic efficiency of watered seedlings had a lower maximum quantum yield of photosystem II by 0.17 on average, which indicates that they were exposed to a bigger physiological shock.

Seedlings of narrow-leaved ash as a hygrophytic tree species do not tolerate dry conditions and no watering.

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The Influence of Changing Climate Extremes on the Ecological Niche of Pedunculate Oak in Croatia

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ABSTRACT

Background and Purpose: Forest trees are adapted to the specific climatic conditions and other ecological factors that dominate within their distribution range. However, the climate is in constant flux. In addition to natural climatic oscillations, the climate has also been changed directly or indirectly by human activities. The issue of climate change is tied mostly to air temperature and precipitation. The objective of this study was to assess the potential influence of climate change on a part of the ecological niche of pedunculate oak (*Quercus robur* L.) in Croatia.

Materials and Methods: A forecast model was developed for the ecological niche of pedunculate oak in Croatia from the present day to 2080 using logistical regression, on the basis of a climate change model.

Results: Within the lowland areas of Croatia, the model forecasts an increase in the minimum temperatures of the coldest month and maximum temperature of the warmest month, and reduced precipitation in both the driest and wettest months.

Conclusion: The results indicate that climate change will negatively impact the ecological niche of pedunculate oak in the future.

Keywords: climate change, ecological niche, pedunculate oak

INTRODUCTION

The climate is a complex and direct ecological factor that is described using various climatic elements, appearances and indices. Flora is dependent on both weather and climatic conditions. The forest tree species of lowland Croatia are adapted to the specific climatic conditions and other ecological factors that dominate in those areas. However, those climatic conditions change over time, which is reflected on the growth and development of all types of organisms. In recent years, climate changes have been documented worldwide. Hasselmann [1] indicated that the average air temperature has increased 0.5°C over the past century. Reduced precipitation has been confirmed in Russia [2], Turkey [3], South Africa [4] and in China [5]. However, no changes in precipitation extremes were recorded at 19 meteorological stations in northern and central Europe [6]. The minimum temperatures increased virtually everywhere, and the maximum and mean temperatures increased in northern and central Europe, Russia and Canada [7]. In

Croatia, Seletković *et al.* [8] analysed weather data over the past century from the Zagreb – Grič station, indicating that changes to the temperature and precipitation regime have already begun in Croatia.

According to the Fifth National Report of the Republic of Croatia, in line with the United Nations Framework Convention on Climate Change [9], a tendency towards increasing temperatures was found throughout the whole of Croatia. This positive trend has become strongly pronounced over the past 50 years, and particularly in the past 25 years. The increasing mean annual air temperature in the past 50 or 25 years was statistically significant at all weather stations. The total annual precipitation was found to be declining throughout Croatia, during the entire 20th century.

An ecological niche is the position of a species in the ecosystem, in the place where it survives (its habitat) and the way it lives. Every species has specific living conditions and poses various demands towards the habitat it lives in.

If the ecological niche is examined from the perspective of a population in a certain geographic area, then the climatic and geomorphological factors are of critical importance for the spatial distribution and size of the species range. In addition to air temperature, which is dependent on cloud cover and insolation, water is the most important factor for the development of vegetation, as it presents the main source of moisture in the soil that is required for physiological processes. When the relationship of air temperature and precipitation is considered, it is necessary to take into account that the extreme amounts (minimum and maximum values) of these two ecological factors are the limiting factors for the survival of certain species. Pedunculate oak (*Quercus robur* L.) requires a large quantity of water for transpiration, which most often can exceed the quantity of precipitation falling in the vegetation period. For that purpose, pedunculate oak must have access to additional water, such as ground water [10]. The annual transpiration of a 108-year old stand of pedunculate oak is 1,030,000 litres per hectare [11].

With changes to the climate elements, the appearance of the vegetation cover of an area also changes. With the activity of climatic elements, certain species are able to move into new areas or to higher elevations, while their place is taken by other species suited by the altered ecological conditions. Understanding the ecological niche is of key importance for getting better insight on how forest ecosystems function. Understanding the interaction of climate and vegetation is one of the most important segments in studying geographic distribution and the success of species. Therefore, the objective of this study was to establish the potential changes in the ecological niche based on a global climate change model to the year 2080.

MATERIALS AND METHODS

Pedunculate oak is the most valuable tree species in Croatia, accounting for 27% of the wood mass in Croatian forests [12]. The rotation for pedunculate oak is 140 years [13]. Croatia currently has 201,739 ha of pedunculate oak forests, with a growing stock of 41.5 million m³ [14]. Natural pedunculate oak sites in Croatia are located in the valleys of large rivers and their tributaries, such as the Sava, Drava, Kupa, Danube and others. The most common soil type in these forests is gleyic soil with its subtypes [15]. According to the Köppen classification, there are two climate types within the pedunculate oak forest distribution area in Croatia. The Cfbw"x" type, the temperate rain zone climate, prevails in the west part of the Pannonian Plain. The eastern area between the Sava and Drava rivers is the domain of the Cfbw"x" type climate. This is also a temperate rainy climate, but with only one pronounced precipitation maximum. The mean annual air temperatures range between 10.0 and 11.5°C. Rainfall ranges from a maximum of about 900 mm occurs in the western part to less than 600 mm, in the eastern part. The precipitation is relatively evenly distributed throughout the year [16].

The CCM3 (Climate Change Model) model, which represents a concentration of greenhouse gases in the atmosphere twice that of the present day [17], was used to

develop the climate change forecast to 2080. To build the forecast model, the extreme values of climatic elements were used as follows: maximum temperature in the warmest month of the year, the minimum temperature in the coldest month of the year, precipitation in the wettest month in the year and precipitation in the driest month of the year.

Data on the presence of pedunculate oak in the Republic of Croatia were taken from the most recent research on the distribution of forest habitats [18], and the Flora Croatica Database [19]. Modelling the ecological niche was performed in the program MAXENT [20]. Climatic data used to model the ecological niche were taken from the WORLDCLIME database for the period 1950 to 2000 [21]. The ecological niche model for the distribution range of pedunculate oak today and in the year 2080, based on the climate change model, was created using logistical regression [22]. The obtained spatial distribution maps of the ecological niche (GRID format) were converted to a TIFF and visualised in ESRI ArcMap 9.2.

RESULTS

According to the global climate change model, the minimum temperature of the coldest month and the maximum temperature of the warmest month will increase by 2.2°C and 6.7°C, respectively. The precipitation in the driest and wettest months of the year will decrease by 18.5 mm and 5.8 mm, respectively (Table 1).

Figure 1 shows the probability (%) of the appearance of pedunculate oak in Croatia, with regard to the climatic conditions. Yellow areas are those with a lower probability of their appearance, while green areas indicate areas where pedunculate oak has a higher probability of appearing with regard to climate. The spatial distribution of the ecological niche of pedunculate oak in the period from 1950 to 2010 corresponds to the actual species distribution range (Figure 1).

With regard to the changing climatic elements, changes in the ecological niche to the year 2080 can also be forecast. Based on the model of global climatic changes, the model forecasts less favourable conditions for pedunculate oak in the area of the Spačva Basin and Podravina (yellow), while there will be more favourable condition in central parts of Croatia (Figure 2).

DISCUSSION

Global climate change, regardless of how it arises, is a current and ongoing occurrence on Earth. With air temperature, which depends on cloud cover and insolation, precipitation is most significant for the development of vegetation, as this is the primary source of moisture in the soil. A lack of precipitation, with the appearance of high air temperatures, weakens plant resistance, as increased transpiration consumes large quantities of water. The regional climate model used for the scenario of climate changes in Croatia was developed by Dickinson *et al.* [23] and Giorgi [24]. In the scenario of climate change based on the regional climatic model in Croatia, the mean values of the 30-year

TABLE 1. Mean climatic element values for ecological niche modelling for the periods 1950–2010 and 2080

Climatic factors	Period		Difference
	1950 – 2010	2080	
Min. temp. coldest month (°C)	3.6	5.8	+2.2
Max. temp. warmest month (°C)	28.9	35.6	+6.7
Precipitation driest month (mm)	38.6	20.1	-18.5
Precipitation wettest month (mm)	137.3	131.5	-5.8

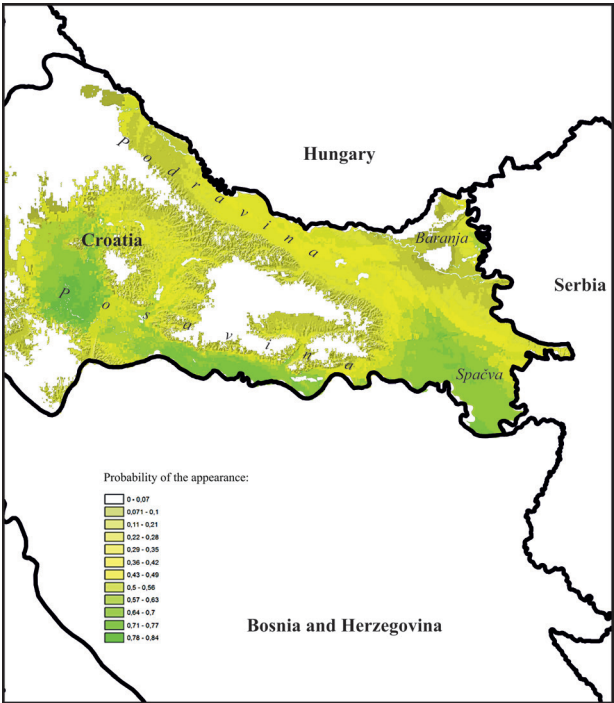


FIGURE 1. Spatial distribution of the ecological niche (potential habitat) of pedunculate oak for the period 1950 to 2010

future climate period (2041-2070) were compared with the 30-year climate average of the reference period (1961-1990). According to that scenario, climate change in all seasons will result in increasing air temperatures, which is statistically significant with a 99% confidence level. Small changes in precipitation are often accompanied by large increases in the appearance of precipitation extremes [25, 26]. The regional climate model for Croatia envisaged a reduction in the total quantity of precipitation in three seasons (spring, summer and fall), primarily in the coastal, southern and mountainous parts of Croatia [9]. Climate change can lead to changes in the spatial distribution of forest vegetation that can be seen in the representation of the current forest types, the possible disappearance of existing or appearance of new types, changes in population densities in certain tree types, productivity of forest ecosystems, ecological stability and vitality of forests, and in changes to the total production and general values of forests ecosystem services.

Pedunculate oak is a tree species with a very narrow ecological amplitude in terms of water demand. Over the past century, large changes have a great role in the lowland forest habitats, primarily due to changes in the hydrological conditions. This has affected the reduced stability of the pedunculate forests and of individual tree stability [27].

The effects of climate change can have a negative effect on the ecological niche of one tree species, while other species are positively affected, and the spatial distribution of the ecological niche of those species is increased. Climatic elements, such as the maximum temperature of the warmest month and minimum temperature of the coldest month, and precipitation in the driest and wettest months represent the limiting values of climatic elements that influence the appearance and existence of a species.

The limit values of the presence of a species in most logistical regression models are 0.5 [28]. A higher probability indicates a habitat that is suitable for the appearance of

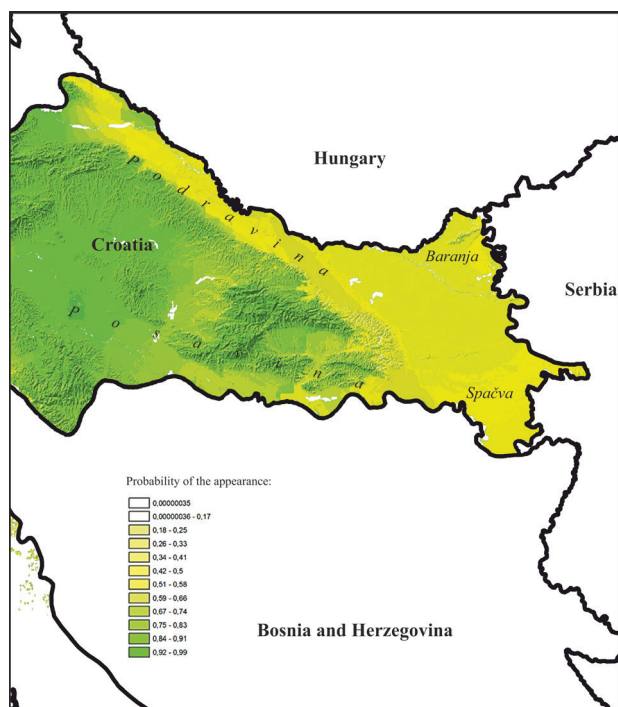


FIGURE 2. Probability of the presence of pedunculate oak to the year 2080 in relation to simulated climatic factors

pedunculate oak with regard to climate elements. Taking into account the changing climatic elements, changes in the ecological niche of pedunculate oak to 2080 can be forecast. According to the forecast model, negative changes to the ecological niche can be expected in the Savačva area (eastern Croatia), while the western part of the Podravina area (northern Croatia) will become unfavourable for the growth of pedunculate oak. The Baranja area will have favourable conditions, while the Posavina area will not see any changes in the ecological niche of pedunculate oak (Figure 2). The natural adaptation of vegetation to climate change occurs on a small percentage of vegetation affected by the climatic elements. A vegetation model indicated that successful adaptation is possible only with very small changes in climate, less than 0.1°C per 10 years, and an absolute change in climate of less than 1°C [29]. A study on the palaeontological and recent climates in Croatia showed that secular or long-period climate changes, warming or cooling, did not negatively affect the composition of the climazonal vegetation [30]. Those changes only caused a shift in the vegetation belt in the direction from lower elevations towards higher elevations (in the case of warming) and vice versa (in the case of cooling). On the basis of such findings, it can be expected that the future natural climate change or changes caused by the direct or indirect human activities will also cause a shifting of the climazonal vegetation forms, depending on how the climate is changing [30, 31].

With regard to the context of the relationship between vegetation and climate, it should be considered that

vegetation directly influences and changes the climatic conditions in a certain area through the processes of assimilation and the sequestration of atmospheric CO_2 [32]. As such, changes to climate elements result in changes to certain parts of the ecological niche of a species. It is difficult to differentiate and fully elucidate the exclusive activity of climatic elements on the ecological niche of a species, and with that its spatial distribution. An example of this is pedunculate oak, which requires high ground waters and flood waters [27, 33, 34].

The range of temperature and precipitation values for an individual species shows the significance of climatic elements for the appearance of a species. Research on the effect of climatic factors on the ecological niche of a species gives important knowledge on the relationship of the vegetation at the species level towards the environment, particularly towards climate. The current comprehension of the exceptionally large significance of various forms of water (ground water, flood waters and stagnant waters) on the appearance of pedunculate oak should be considered in synergy with climatic elements, particularly temperature.

Forest ecosystems today are very exposed to changes, whether those changes are caused by natural variability or by human activity. Considering the overall synergy of all the ecological factors on the appearance of a specific tree species is one of the fundamental segments in the study and understanding of forest vegetation functioning. Forecast models of climate change should also be taken with a certain reserve, and with consideration of the various possible

outcomes. Modelling ecological niches and understanding the relationships between vegetation and ecological elements, particularly climate, should be considered at the level of the entire population. However, it is necessary to also consider the possible spatial parts of the population that became adapted to the local climatic conditions over time, and that the ecological niche of these populations varies from that of the remaining part of the population (ecotypes). In that case, future research of the relationships of climate and vegetation should also include studies on genetic variability within populations of the same species.

The climate model used in the present study assumes twice the present level of greenhouse gases in the next hundred years. However, a shortcoming of climate forecast models is that they tend to not consider the influence of vegetation on the global carbon cycle, aerosols, cloud cover and the oceanic-atmospheric links of climate [1]. At the local level, other factors other than climate elements can be of key importance, such as herbivore population density, pathogenic organisms, commercial activities, changes in soil properties, competition, meso- and micro-climatic factors and more.

Models that predict global climate change contain a large amount of entropy, as they do not include all those factors that directly or indirectly affect climate. Future research should continue to model the population densities of pedunculate oak or the ratio of the species at the level of the actual ecological niches in competition with other tree species, including their population growth mechanisms.

CONCLUSIONS

According to the climate change model, the minimum and maximum air temperatures in the coldest and warmest months will increase, while precipitation of the driest and wettest months of the year will decrease. Climate changes in the future will alter the ecological niche of pedunculate oak, dependent on other ecological factors. Future research should continue to analyse and spatially model the groundwaters and forest soil properties as independent variables in the forecast. Research of the ecophysiological reactions of pedunculate oak to changing ecological factors and competition would also be a valuable addition to such research.

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