UDK 630* 425 + 111 (001)
https://doi.org/10.31298/sl.144.7-8.2

Izvorni znanstveni članci – Original scientific papers
Šumarski list, 7–8 (2020): 351–365

INTERRELATIONS OF VARIOUS TREE VITALITY INDICATORS AND THEIR REACTION TO CLIMATIC CONDITIONS ON A EUROPEAN BEECH (*Fagus sylvatica* L.) PLOT

MEĐUOVISNOST RAZLIČITIH INDIKATORA VITALITETA STABALA I NJIHOV ODZIV NA KLIMATSKE UVJETE NA PLOHI OBIČNE BUKVE (*Fagus sylvatica* L.)

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SUMMARY

Interrelations of various common beech vitality indicators (crown defoliation, foliar chemistry, radial growth) as well as their possible dependencies on climatic conditions were investigated over the course of 12 years in a mature and healthy beech stand. Our results confirm the importance of temperature variables for defoliation, as high temperatures during spring and summer months induce the increase of defoliation. The same negative influence was observed with high maximum temperatures and low precipitation during previous year summer months. Phosphorus, calcium and magnesium nutrition of beech trees suffers from high temperatures during current year summer and benefits from more precipitation. High temperatures in current year May positively influence beech radial growth, while a wide range of minimum temperatures during March and June has a negative effect. In summary, high summer temperatures and low precipitation were shown to have a negative effect on all vitality indicators, and for defoliation and nutrition this effect can last into the following year.

KEY WORDS: defoliation; foliar nutrition; radial growth; drought; vitality

INTRODUCTION
UVOD

The dieback of trees can be complex in its nature, therefore the reasons for the deterioration in the vitality of certain species or stands can be found in specific interactions of stress factors. A common feature of stress impact is the uneconomical use of nutrients and water, leading to alterations in storage patterns in trees, soils and on the ecosystem level (Augustin and Andreae, 1998). At the tree level, this is usually described as decline or dieback processes, influencing tree condition or vitality, which can be assessed through the use of tree vitality indicators such as defoliation, increment, or foliar nutrition.

European beech (*Fagus sylvatica* L.) is a dominant broadleaved tree species in European forests, and on the Medvednica massif. Although common beech is a tree species

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adapted to various conditions, it grows best in areas marked by moderately warm summers and high amount of precipitation (Seletković et al., 2003a).

Climate change and other global changes are supposed to greatly influence the forest ecosystems in Europe (Askeyev et al., 2005, Kellomaki and Leinonen, 2005, de Vries et al., 2014). The forested area is expected to expand to the north and contract in the south (IPCC, 2007). Climatic conditions, especially extreme climatic events such as drought are regarded as critical in the process of forest tree decline, as they govern the water relations (Zierl, 2004). Direct effects of climate change include responses of vegetation to temperature and/or precipitation; indirect effects occur primarily as soil-mediated phenomena, such as the influence of precipitation on soil moisture regimes (Watson et al., 1998).

Defoliation is a non-specific symptom of tree vitality widely used in forest practice (Polák et al., 2006) and forest health monitoring, most notably the UNECE International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests), a pan European forest monitoring program. Dobbertin and Brang (2001) demonstrate that tree defoliation assessed in 5% steps is a useful parameter to predict year-to-year tree mortality. Typically, the defoliation of trees will change from year to year and will rise sharply under heavy stress (such as drought), often not in the same, but the following year (Potočić et al., 2018). Trees are also known to be able to recover from leaf loss, the interval for the return to pre-stress values depending as much on the environmental conditions as on the tree species (Prpić and Seletković, 1992, Potočić et al., 2008).

The cycling and uptake of nutrients have been shown to be critical processes for the health of a forest ecosystem. It is clearly evident from previous research that nutrition has a profound multifarious influence on the vitality of trees (Hallenbarter et al., 1999). Loss of nutrients from the system, disruption of nutrient cycling and uptake, or imbalances in nutrient status may be associated with declines in forest productivity and stability (Nilsson et al., 1995).

Trees respond to environmental stresses, among others, with increment decrease (Dobbertin, 2005). Growth reduction is a consequence of a reduced photosynthetic activity due to limitations in the environment and result in altered carbon allocation. In extreme situations, such as long lasting drought, growth reduction can lead to mortality (McDowell et al., 2011). Radial increment is sensitive to environmental conditions and local and/or regional climate (Fritts, 1976) and as such it can be used as an indicator of tree vitality.

Landmann et al. (1995) consider the results of various research dealing with tree decline lacking as they concentrate only on stands exhibiting great loss of vitality. As with any other influence on a forest ecosystem, climatic change would have a stronger impact on a previously stressed forest stand exhibiting poor vitality than on a forest growing in near-optimal conditions. On the other hand, climate change might have a bigger economic impact on optimal sites than on extreme, less fertile sites. Therefore, it is crucial for practical silviculture and forest management to be aware of the potential reaction of beech to climate change in order to plan mitigation measures to preserve the economic value of beech forests. Furthermore, in contrast with data from large-scale monitoring, case studies are able to provide more data from a limited area, therefore more precisely showing the ecosystem response to a specific set of climatic factors present in the research area (Seletković et al., 2009).

We hypothesise that climate has a significant influence on common beech vitality indicators (crown defoliation, foliar nutrition and radial growth). Higher temperatures and lower precipitation as well as extreme climate events should result in in higher defoliation values and reduced growth. Climate influences the absorption of nutrients, as well as physiological processes within the tree and therefore the effect should be observed on the nutritional status of beech trees. We also expect that it is possible to observe the interconnections between these vitality indicators. Therefore, the aims of this paper are to (i) investigate the interrelations of common beech vitality indicators as well as their (ii) dependencies on climatic conditions in a mature and healthy beech stand.

MATERIAL AND METHODS
MATERIJAL I METODE

Research area – *Područje istraživanja*

Intensive monitoring plot Sljeme, a part of ICP Forests Level II programme (plot number 103) is situated in a European beech - silver fir (*Abies alba* Mill.) community (*Festuco drymeiae – Abietetum Vukelić et Baričević 2007*), at 954 m altitude on a south-exposed slope of Medvednica massif, located in the northwest Croatia (Figure 1). The plot is 1 ha (100 x 100 m) in size. Soil type is dystric umbric cambisol on greenschist parent rock (Potočić et al., 2003). The plot is also a part of UNESCO's Man and the Biosphere Programme (since 1981), when all forest management operations were stopped. The western part of the Pannonian area of Croatia is encompassed by the climate type Cfwbx" according to Koeppen's classification (Šegota and Filipčić, 2017). For this climate type precipitation should occur uniformly throughout the year, with the smallest amount in winter, and precipitation maximums occuring in spring and late summer. According to modelled climate data from E-OBS gridded dataset (Haylock et al., 2008) for the period (1950 - 2007), annual mean temperature for our research plot was 10.8 °C, and annual precipitation was 929.6 mm.

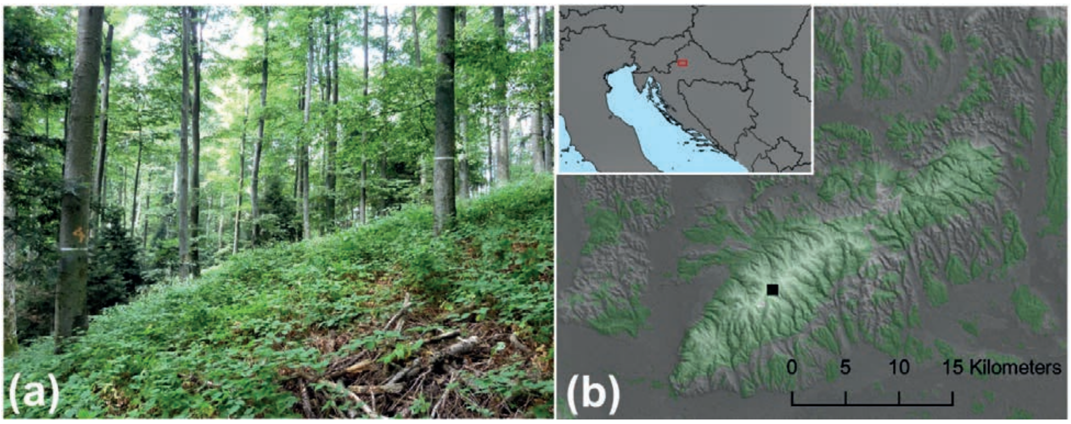

Figure 1. Location of the study site. Photograph of a European beech - silver fir community (a). Positions of the intensive monitoring plot (black square) and forest areas (shaded polygon) (b).

Slika 1. Lokacija istraživačke plohe. Fotografija sastojine obične bukve te obične jele (a). Položaj plohe intenzivnog motrenja (crni kvadrat) i šumskog područja (osjenčani poligon) (b).

Meteorological data – *Meteorološki podaci*

We used climate data from E-OBS gridded dataset (Haylock et al., 2008). Values were extracted using R statistical environment (R Core Team, 2016) with "raster" (Hijmans, 2016) and "rgdal" (Bivand et al., 2017) packages. From the daily dataset we calculated mean monthly temperature (mt), mean monthly minimum temperature (min_m), mean monthly maximum temperature (max_m), absolute monthly minimum temperature (min_a), absolute monthly maximum temperature (max_a), and monthly sum of precipitation (pr). Furthermore, we calculated the quantile range of the central 90% region (0.95–0.05 quantile) of monthly maximum and minimum temperatures (max_Q and min_Q) to investigate the influence of extreme temperature variability on vitality indicators, our assumption being that increased variability of monthly extreme temperatures induces physiological stress that can be detected through vitality indicators. This dataset was also used to generate Standardised Precipitation Index (SPI) and self-calibrating Palmer drought severity index (scPDSI), which are standard indices for quantifying and reporting meteorological drought. Standardised Precipitation Index (McKee et al., 1993) was calculated for the period 1951-2008 on a time scale of three months. To calculate SPI and scPDSI we used R programming environment and package "SPEI" (Beguería and Vicente-Serrano, 2017) and "scPDSI" (Ruida et al., 2018), respectively. Values of SPI above 2 indicate extremely wet conditions, under -2 extremely dry conditions, and normal conditions range from 0.99 to -0.99. Values of scPDSI lower than - 1 indicate moderate drought while values lower than -2 indicate severe drought.

Defoliation assessment – *Procjena osutosti*

Defoliation of sample beech trees on the plot was assessed annually according to the ICP Forests Manual (Eichhorn et al., 2016) in the period 1996-2007. The same two observers performed assessments in late August/early September. Each year 45 trees were assessed but only 29 beech trees that were assessed every year in this period were used in the sample.

Sampling and chemical analysis of foliage – *Uzorkovanje i kemijska analiza biljnog materijala*

Each year the same five trees were sampled from 1997 to 2007. Samples were taken from the upper third of the crown in mid-September. Collected samples were combined in the laboratory based on equal dry mass. Samples of foliage (100 leaves per sample) were dried at 105 °C, ground and analysed for total nitrogen (N) content at Leco CNS 2000 analyser (ISO-13878, 1998). The analysis of other elements content required sample drying, grinding and wet digestion. Phosphorus (P) was determined on UV/VIS spectrophotometer PE Lambda 1A, potassium (K) on flame photometer Eppendorf and calcium (Ca) and magnesium (Mg) by atomic absorption spectroscopy on Perkin-Elmer Aanalyst 700 (Rautio et al., 2016).

The established procedure for the interpretation of foliar analysis is based on the comparison of element concentrations with limit values as according to Raitio (1993). For evaluation of foliar nutrient concentrations, we compared them to the critical values statistically derived from van den Burg's literature compilation which are close to a general optimum range, indicating health and intact resistance mechanisms of these tree species (Mellert and Göttlein, 2012).

Tree-ring measurements – *Izmjera širine godova*

We collected cores from all 29 beech trees that were assessed for defoliation in autumn 2007 (last fully formed ring was in 2007). Each core was mounted and sanded to a high polish

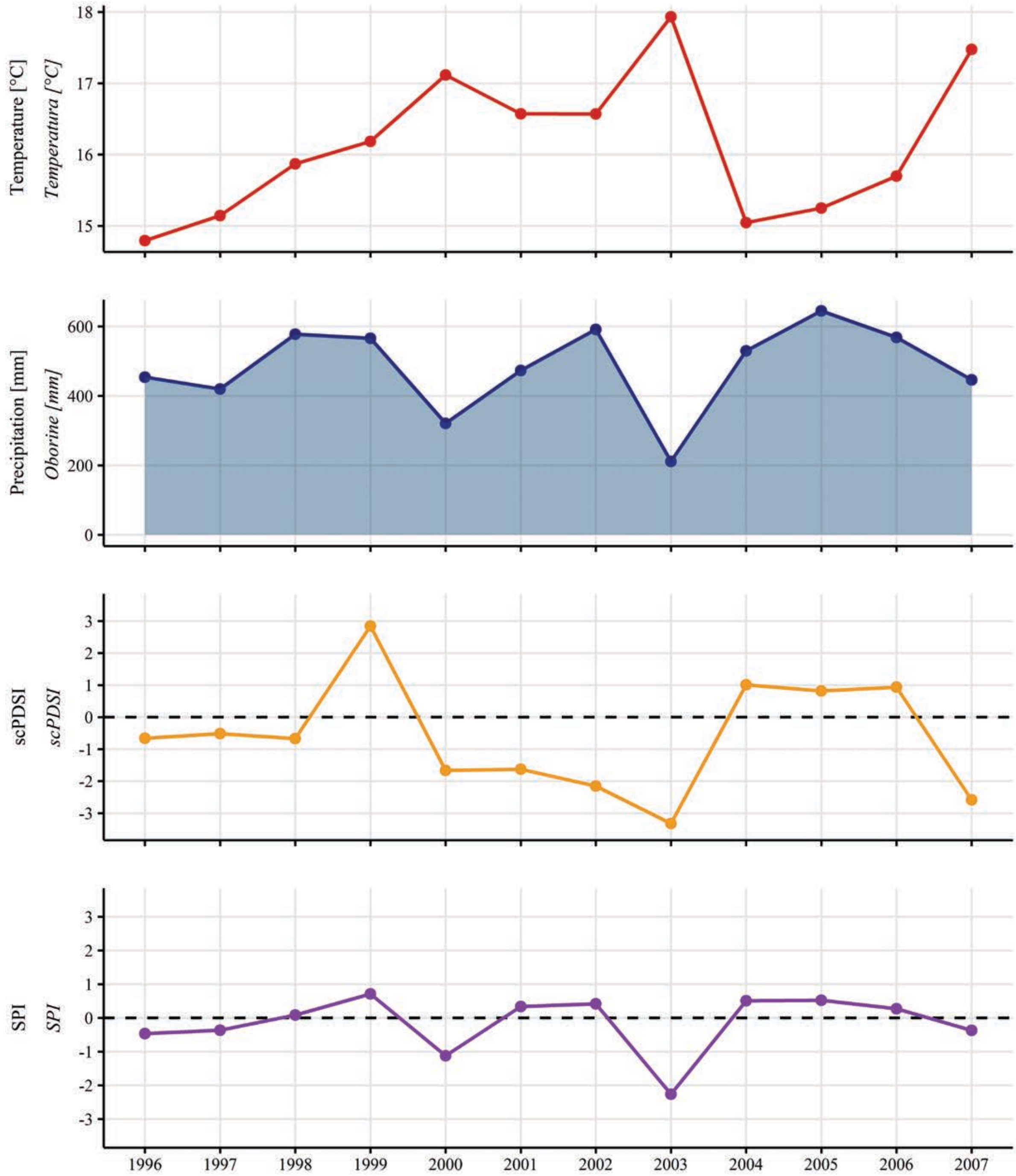

Figure 2. Mean monthly temperature (red line), sums of monthly precipitation (blue line), mean scPDSI (orange line) and mean SPI (purple line) from March to August on plot "Sljeme" in the period 1996 - 2007.

Slika 2. Prosječna mjesečna temperatura (crvena linija), suma mjesečnih oborina (plava linija), prosječni scPDSI (narančasta linija) te prosječan SPI (ljubičasta linija) od ožujka do kolovoza na plohi Sljeme za period od 1996 do 2007. godine.

following standard dendrochronological procedures (Stokes and Smiley, 1968). The cores were then digitized using ATRICS system[1] (Levanič, 2007) and annual radial growth was measured to the nearest 0.01 mm using WinDENDRO software. Each tree ring series was then visually and statistically crossdated using PAST-4. We used the COFECHA program (Holmes, 1983, Holmes, 1994) to check for errors in dating. Tree growth almost universally shows a non-climatic, age-related biological growth trend that must be removed before any dendroclimatological analyses. Individual tree-ring width series were therefore standardised to remove long-term trends (Cook, 1985) using a smoothing loess function. To calculate index chronologies each year's ring width was divided by that year's fitted value to give a dimensionless index with a mean of 1. This procedure removed non-climatic trends due to tree age, size and the effects of stand dynamics (Cook, 1985). Index values were also pre-whitened using an autoregressive model selected on the basis of the minimum

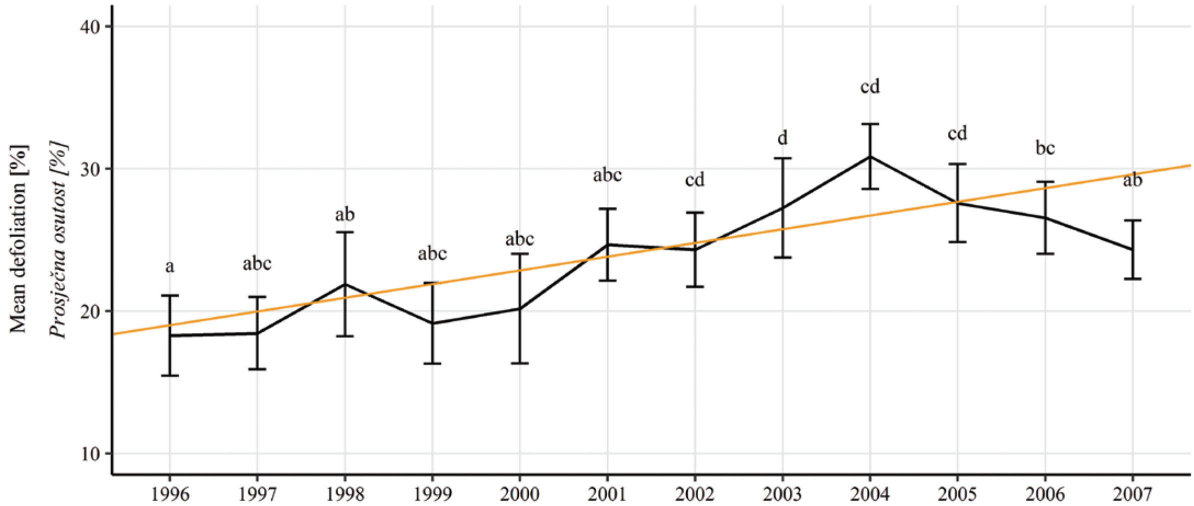

Figure 3. Overall defoliation trend of common beech trees (Tau = 0.62, Sen's slope = 0.962, p= 0.005, orange line) and annual overall mean defoliation (black line). Vertical bars denote 95% confidence intervals. Years that do not share the same letter are significantly different.
Slika 3. Trend osutosti stabala obične bukve (Tau = 0.62, Sen's slope = 0.962, p= 0.005, narančasta linija) te godišnji prosjek osutosti (crna linija). Vertikalni linije označavaju interval pouzdanosti od 95%. Godine koje ne dijele isto slovo statistički se značajno razlikuju.

Table 1. Potassium and calcium ratio in beech leaves in the period 1994 – 2007.
Tablica 1. Omjer kalija i kalcija u lišću bukve u period od 1994. do 2007. godine.

Year *Godina*	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007
K/Ca *K/Ca*	0.59	0.66	0.50	0.53	0.56	0.52	1.02	0.75	0.85	1.20	1.01	0.77	0.36	0.51

Akaike Criterion and combined across all series using biweight robust estimation of the mean to exclude the influence of the outliers. ARSTAN produces two types of output chronologies – a standard chronology (STD) and a residual chronology (RES) containing only high-frequency variations (no autocorrelation) (Cook, 1985, Cook et al., 1990). For the purpose of this research, we used RES chronology, which represents a robust estimate of the arithmetic mean and contains no autocorrelation (Cook, 1985). After detrending, the Expressed Population Signal (EPS) was calculated to assess the common forcing (e.g. climate) in tree-ring width chronologies. An EPS of 0.85 or higher is generally accepted to be high enough to show that analysed tree ring series represent the common forcing mechanisms of a larger population of trees (Briffa and Jones, 1990).

Data analyses – *Analiza podataka*

Defoliation trend was tested by Mann-Kendall test (Mann, 1945, Kendall, 1948) and the slope was estimated according to Sen (1968). In order to establish if defoliation statistically differed during the investigated period we performed one-way analysis of variance. Prior to the analysis, defoliation data was checked for normality and homoscedasticity. Since the data did not adhere to the latter assumption we applied the Welch's ANOVA (Welch, 1951). To specify differences between years we conducted the Games-Howell test (Games and Howell, 1976). For the trend analysis we used the "EnvStats" package (Millard, 2013), while the package "userfriendlyscience" (Peters, 2017) was used to conduct ANOVA and the subsequent *post-hoc* test.

Bootstrapped Pearson's correlation coefficient calculated in the package "treeclim" (Zang and Biondi, 2015) was used to identify dependency between the residual chronology and climate variables for the period 1950-2008 and to identify dependency between defoliation and climate variables for the period 1996-2007.

Because foliar nutrition data followed a non-normal distribution we used Spearman's rank correlation coefficient to assess how foliar nutrition relates to climate variables and other vitality indicators. We also tested if previous year defoliation was correlated to current year residual chronology and vice versa. Additionally, we tested if previous year climate variables were correlated to current year vitality indicator values. All analyses were conducted in R statistical

[1] ATRICS stands for Automated Tree-Ring Image Capturing System, system was developed at Slovenian Forestry Institute for use in dendrochronological laboratory

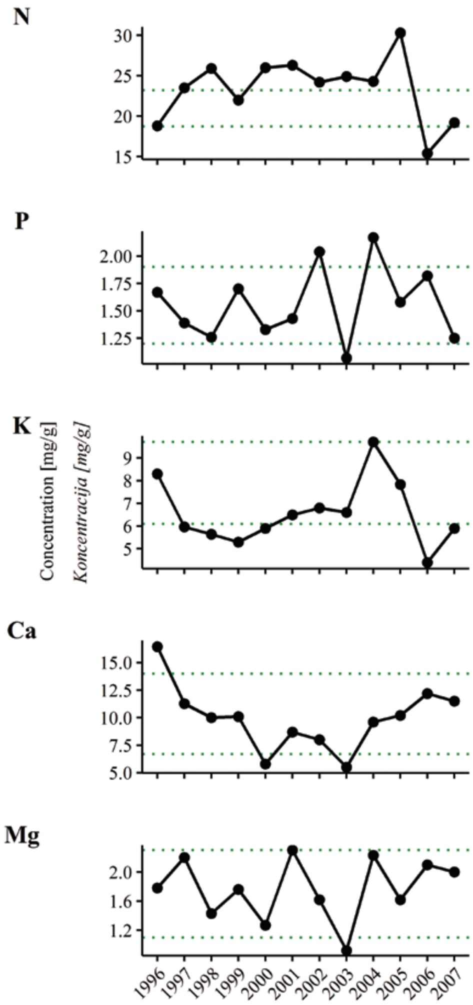

Figure 4. Foliar nutrient status of beech trees. Horizontal, dotted lines represent the normal range of foliar concentrations of macronutrients according to Mellert and Göttlein (2012).

Slika 4. Stanje ishrane stabala bukve. Horizontalne isprekidane linije predstavljaju normalni raspon koncentracija makroelemenata prema Mellert and Göttlein (2012).

environment (R Core Team, 2016) with a probability of type I error of α = 5%. Plots were produced using "ggplot2" package (Wickham, 2009).

RESULTS
REZULTATI

Climate conditions – *Klimatski uvjeti*

High mean temperatures and low precipitation were present especially in years 2000 and 2003, while high temperatures in 2007 were not coupled with low precipitation (Figure 2). Considering the ranges of SPI and scPDSI, water deficits on the research plot could have been expected especially in 2000 and 2003. The scPDSI index also shows the possibility of drought in 2007.

Defoliation – *Osutost*

There is an increasing statistically significant trend of defoliation throughout the observed period (Figure 3). Statistical differences in mean defoliation were established between survey years (Df = 11; MS = 480.3; F = 7.7; $p < 0.001$). Defoliation was higher in the years following a drought year than in drought years but these differences were not significant. However, defoliation in year 2004 was significantly higher than in the years prior to 2003 drought (Figure 3).

Nutritional status – *Stanje ishrane*

Based on the foliar concentrations, plot Sljeme provides satisfactory nutrition for beech trees. Some differences in element values depending on the sampling year are evident. These differences are especially interesting if the values fall below limit values (Figure 4). Ca and Mg deficiency was recorded in drought years (Figure 2). We found that the ratio of K and Ca in beech leaves was high in years 2000, 2003 and 2004 as shown in Table 1.

Tree ring width – *Širina goda*

Beech chronology spans the period from 1904 to 2007 (103 years, Table 2). Since the purpose of this study was not to reconstruct climatic patterns but to evaluate effects of climate

Table 2. Basic statistical data regarding tree-ring series.
Tablica 2. Osnovni statistički podaci analiziranih izvrtaka

	Year *Godina*	Mean *Prosjek*	Standard deviation *Standardna devijacija*	Skewness *Asimetrija*	Kurtosis *Kurtosis*	Mean sensitivity *Prosječna osjetljivost*	1st order autocorrelation *Autokorelacija prvog reda*
arithmetic mean – *aritmetička sredina*	76	1.319	0.566	0.629	3.748	0.339	0.524
standard deviation – *standardna devijacija*	17	0.381	0.138	0.602	2.546	0.057	0.181
median (50th quantile) – *medijan (50og kvantila)*	76	1.249	0.545	0.512	3.029	0.339	0.528
interquartile range – *interkvantilni raspon*	28	0.488	0.108	0.349	1.085	0.092	0.243
minimum value – *minimalna vrijednost*	44	0.878	0.407	-0.081	2.083	0.254	0.060
lower hinge (25th quantile) – *donji kvartil (25%)*	64	1.043	0.482	0.311	2.603	0.293	0.375
upper hinge (75th quantile) – *gornji kvartil (75%)*	92	1.530	0.590	0.661	3.688	0.384	0.619
maximum value – *maksimalna vrijednost*	103	2.483	0.921	3.024	15.082	0.430	0.878

Table 3. Expressed population signal and Signal-to-noise ratio statistics, together with within and between tree-ring series correlations.
Tablica 3. Izraženi signal populacije, omjer signala i šuma te korelacije unutar i između serija

effective number of cores *efektivni broj jezgri*	c_{eff}:	1.263	
effective chronology signal *efektivni signal kronologije*	r_{eff}:	0.314	
signal-to-noise ratio *omjer signala i šuma*	SNR:	8.460	
expressed population signal *izraženi signal populacije*	EPS:	0.894	
	Number *Broj*	RBAR *Prosječna korelacija između serija*	Standard deviation *Standardna devijacija*
all series RBAR: *prosječna korelacija između svih serija*	231	0.278	0.253
within-trees RBAR: *prosječna korelacija serija unutar stabla*	12	0.367	0.146
between-trees RBAR: *prosječna korelacija serija između stabala*	219	0.273	0.257

on vitality indicators, for growth data we selected only a relatively short common period 1950-2007 for the analysis. EPS value of beech chronology within studied period (1950-2007) was 0.894, which is well above threshold of 0.85 and Signal-To-Noise ratio is also quite large – 8.460. (Table 3).

Interactions – *Interakcije*

The results of bootstrapped Pearson's correlation indicate a significant influence of extreme temperatures on beech

Table 4. Bootstrapped Pearson's correlation coefficients for correlations between defoliation and monthly climate variables during the vegetation period (March - August). Only significant results are shown ($p < 0.05$). Abbreviations for months of the year in lower case denote previous, and in upper case font current sampling year.
Tablica 4. Bootstrap Personov korelacijski koeficijenti za korelacije između osutosti i mjesečnih klimatskih varijabli za vrijeme vegetacijske sezone (Ožujak – Kolovoz). Prikazani su samo značajni rezultati ($p < 0.05$). Skraćenice za mjesece u prethodnoj godini navedene su malim slovima, a za mjesece u trenutnoj godini velikim slovima.

Climate variable *Klimatska varijabla*	Month *Mjesec*	r *r*
Pr	june	-0.637
max_a	june	0.573
	july	0.747
max_a	MAR	0.737
	JULY	0.610
max_m	JULY	0.597
max_Q	MAR	0.810
min_Q	MAR	0.623

defoliation (Table 4), as well as a significant negative influence of precipitation in June of the previous year.

Results given in Table 5 indicate complex interactions between foliar mineral concentrations and climate variables of the current and previous year. Overall, a general pattern can be observed where current year temperature variables are mostly negatively correlated to foliar mineral concentrations, whereas precipitation and drought indices are positively correlated regardless of nutrient in question. Additionally, we noticed that most climate variables of summer months (June and August especially) are negatively correlated to nutrient concentrations, whereas climate variables during spring months are positively correlated. However, similar patterns cannot be observed when comparing foliar

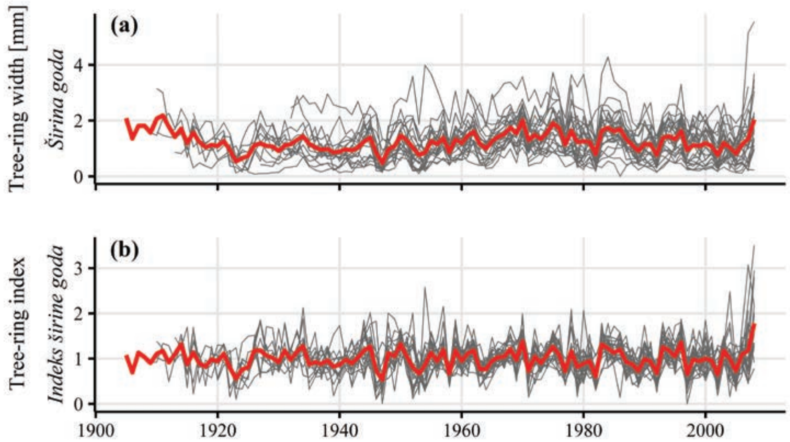

Figure 5. Growth (a) and residual growth (b) of individual beech trees (grey lines) and the mean value (red line) in the period 1908 – 2007.
Slika 5. Rast (a) i rezidualni rast (b) individualnih stabala obične bukve (sive linije) te prosječna vrijednost (crvena linija) u period od 1908. do 2007. godine.

Table 5. Spearman's rho and corresponding p values for correlations between foliar nutrient concentrations and monthly climate variables during the vegetation period (March - September). Only significant results are shown ($p < 0.05$). Abbreviations for months of the year in lower case denote previous, and in upper case current survey year.

Tablica 5. Spearmanov rho i pripadajuća p vrijednost za korelaciju između koncentracije biogenih elemenata i mjesečnih klimatskih varijabli tijekom vegetacijske sezone (Ožujak – Rujan). Prikazani su samo značajni rezultati ($p < 0.05$). Skraćenice za mjesece u prethodnoj godini navedene su malim slovima, a za mjesece u trenutnoj godini velikim slovima.

Element *Element*	**Climate variable** *Klimatska varijabla*	**Month** *Mjesec*	**rho(ρ)** *rho(ρ)*	**Element** *Element*	**Climate variable** *Klimatska varijabla*	**Month** *Mjesec*	**rho(ρ)** *rho(ρ)*
N	Pr	aug	-0.699	P	pr	APR	0.860
		sept	-0.606		mt	AUG	-0.622
	min_a	aug	0.636		max_m	JUNE	-0.580
	min_Q	may	-0.692		SPI	APR	0.790
	max_m	aug	0.643			MAY	0.678
	SPI	sept	-0.748			JUNE	0.692
	max_a	MAR	0.580		scPDSI	APR	0.713
K	Pr	july	-0.602			MAY	0.727
	min_a	june	0.641	Ca	pr	aug	0.594
	max_Q	apr	0.662		mt	mar	-0.776
	max_m	APR	-0.606			may	-0.650
	max_Q	APR	0.637			aug	-0.622
		AUG	-0.644		min_m	mar	-0.825
Mg	min_a	mar	-0.630			may	-0.671
	min_Q	apr	0.581			aug	-0.790
		july	0.634		min_a	mar	-0.685
	max_a	apr	0.648			may	-0.734
	max_Q	july	0.592		max_m	mar	-0.811
	SPI	june	-0.827			may	-0.685
		july	-0.578			aug	-0.587
	Mt	JUNE	-0.701		max_a	aug	-0.678
	min_m	JUNE	-0.689		pr	AUG	0.622
	max_m	JUNE	-0.809		mt	AUG	-0.769
	max_a	JUNE	-0.578		min_m	AUG	-0.839
	SPI	MAR	0.732		max_m	AUG	-0.748
		MAY	0.620		max_a	AUG	-0.748

mineral concentrations with climate variables of the previous year.

Correlation analysis based on residual tree ring width chronology and climate data reveals a positive correlation between tree-ring width and multiple temperature-related variables, mostly in May of the same year, and a negative correlation between tree-ring width and the range of minimum temperatures in March and June of the same year (Figure 6).

DISCUSSION
RASPRAVA

The region of south-eastern Europe represents one of the most vulnerable hotspots with expected intensification of severity and duration of droughts and heat waves. As the effects of climate change on forests in Southern Europe will potentially be stronger and more rapid than in the rest of Europe, this area represents an ideal model for studying the impact of changing climatic conditions. This region is already faced with a high frequency of drought events; after 2000, significant droughts and heat-waves were observed in 2002, 2003, 2007-2008, 2011 and 2012 (EEA, 2012). Analyses of meteorological data (Gajić-Čapka et al., 2015) show that in Croatia a change in the temperature and precipitation regime is already present. In the decade 2001–2010 alone, four drought events occurred, and only 13 between 1961 and 2010 (Spinoni et al., 2013). In the future, Croatia is expected to be even hotter and drier (Cindrić et al., 2010, Mihajlović, 2006).

Our results suggest that drought was to be expected on the research plot in years 2000, 2003 and 2007; 2003 was also

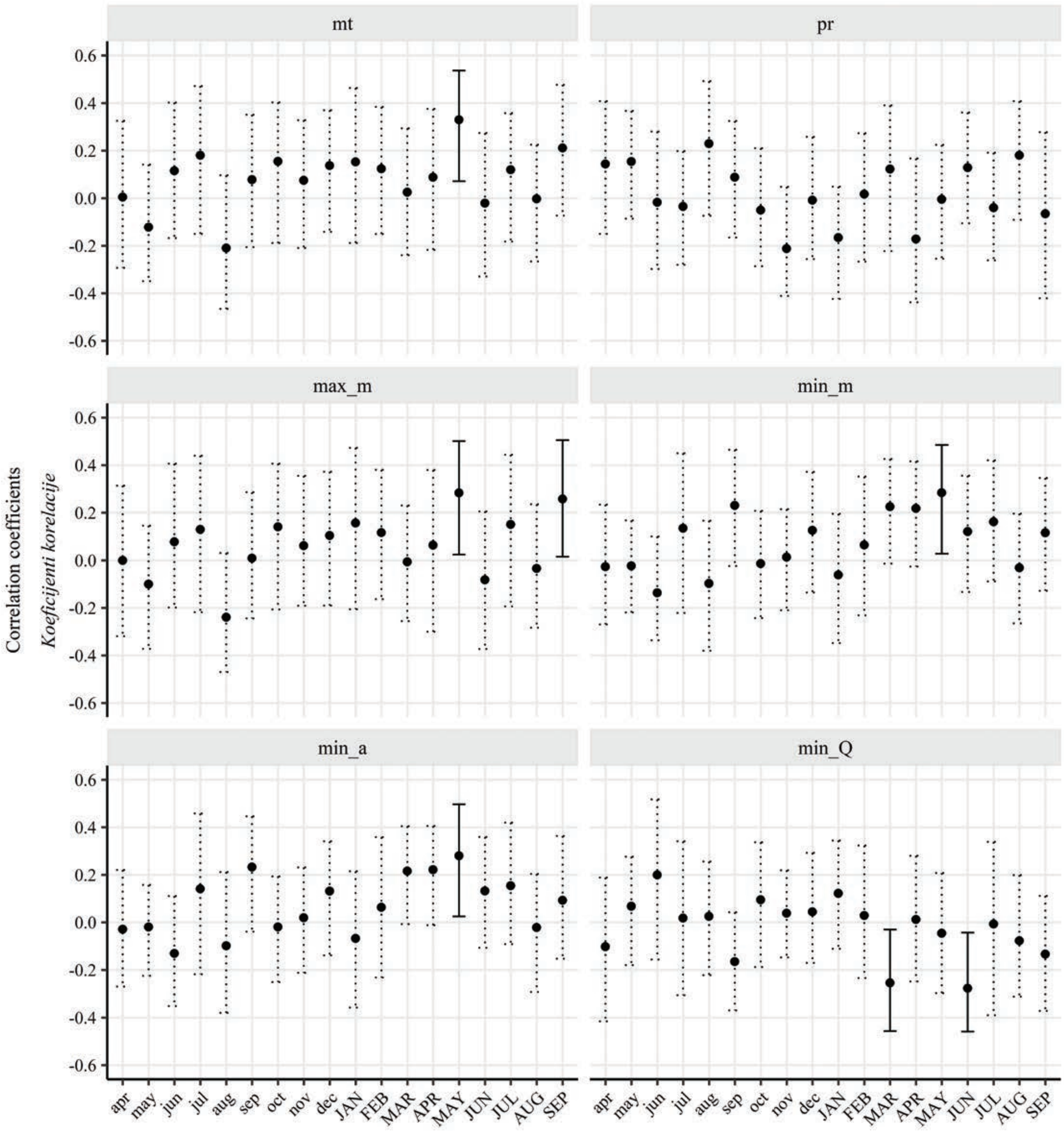

Figure 6. Correlation between residual tree ring width and climate variables from previous year April to current year September. Coefficients significant at the 0.05 are identified by a solid line. Vertical bars denote 95% confidence intervals. Abbreviations for months of the year in lower case denote previous, and in upper case current survey year.

Slika 6. Korelacija između rezidualne širine goda te klimatskih varijabli od travnja prethodne godine do studenog trenutne godine. Ispunjene linije označavaju značajne koeficijenti pri razini od 0.05. Vertikalni linije označavaju interval pouzdanosti od 95%. Skraćenice za mjesece u prethodnoj godini navedene su malim slovima, a za mjesece u trenutnoj godini velikim slovima.

reported as very dry in most of Europe, with adverse impacts on vegetation (Gobron et al., 2005). These results correspond to the more general observations of drought in Croatia in 2000 and 2003 (Cindrić et al., 2010, Mihajlović, 2006)

The results of defoliation assessments seem to show a one –year lag effect, with defoliation rising in the year following a drought year. These results are consistent with previously reported findings (Graf Pannatier et al., 2007). Despite a wide range of ecological conditions present on ICP Forests Level I beech monitoring plots all over Europe, a similar rise in mean plot defoliation above the trend line was recorded in 2001 and 2004 (Timmermann et al., 2017). However, not every rise in defoliation of a tree should be equalled with the permanent decrease of vitality. Crown defoliation is obviously a product of tree crown status from the past several years of growth, which can be misleading if used as a stress indicator when assessing current vitality

(Polák et al., 2006). This can be seen clearly from our results.

The negative influence of precipitation in June of the previous year, coupled with the aforementioned influence of summer temperatures in the previous year, may point to the lasting effects of drought on defoliation through divergent mechanisms. The example for this is the uninterrupted rise in defoliation from the dry 2000 until 2004 - the years 2001 and 2002 were warm, but with plenty of precipitation; still, the defoliation continued to rise through the dry 2003, reaching peak values in the cool, moist 2004. Similarly, (Králíček et al., 2017) documented significant effect of temperature in July and August of previous year on beech defoliation. Severe drought limits leaf area production by reducing the number and viability of leaf buds and thus the tree's ability to recover an efficient crown development after resuming normal water availability (Bréda et al., 2006). Drought during the year of bud formation decreases the number of new leaves formed in the bud and the new stem segments present. Drought then influences the number of leaves, leaf surface area, and twig extension the following year when those buds expand (Coder and Daniel, 1999). In beech trees, all leaves are completely preformed in winter buds, so the number of leaves is predetermined in the preceding year (Uemura et al., 2000). On the other hand, defoliation can be related to drought events of the current year through a change in intensity of physiological processes such as (slower) leaf expansion or (enhanced) senescence of older leaves (Jackson, 1997), but our results do not show this effect: neither SPI nor scPDSI correlated with defoliation in the current year. This may be because the assessments of defoliation were performed during summer, when the effects of drought may have not occurred yet.

We found that drought affects mostly the foliar concentrations of Ca and Mg, and the ratio of K to Ca. According to Bergmann (1992), the uptake of Ca is negatively affected by irregular water supply and, in particular, by prolonged dry periods. Acting as a counterpart to K, Ca plays a key role in the stomatal movement and regulation of water balance of trees (Raghavendra et al., 2010). Ca and K are also competing for uptake and the lack of Ca in dry years can often be associated with enhanced K uptake (Wallace and Mueller, 1980).

While foliar composition is directly related to weather conditions in the current year through the functioning of uptake mechanisms, the links of current mineral element foliar concentrations and last year's weather conditions have to be considered through storage and remobilization mechanisms which are increasingly recognized as one of the key processes in nutrient conservation in plants and in nutrient cycling in ecosystems (Achat et al., 2018). To maintain growth under a permanently fluctuating availability of soil nutrients, plants use various strategies to optimize nutrient acquisition - nutrient transporters, soil exploration by roots, root exudation, and remobilization of nutrients from storage (Maillard et al., 2015). For mobile nutrients, especially N, remobilization from reserves is very important, as shown in the multiple dependencies of N foliar concentrations on the climate variables of the previous year late summer and autumn months, reflecting the storing of N after the period of intensive vegetative growth is finished (Table 5). In case of elements that are generally not remobilized, such as Ca, we should not consider the effects of storage and remobilization processes: rather, as the growth of roots is dependent partly on the Ca availability (Emanuelsson, 1984), climate conditions in the previous year may modulate the uptake capacity of trees in the current year. However, this effect was not recorded in our study. Also we found no correlations of previous year climate variables and current year P leaf concentrations, although P can be used from reserves stored in the root (Marschner, 2002). Perhaps this is due to the generally very good P nutrition of beech on this site.

Jonard et al. (2010) found that beech defoliation levels were associated with lower foliar Ca and Mg concentrations in a study in Belgian Ardennes, but this relation could not be confirmed in our study: no significant relationship was observed between defoliation and foliar nutrient concentrations. According to Simon and Wild (1998), if the concentration of a certain element remains in the normal range, the decrease in mineral nutrition should be regarded more as a consequence than as the cause of damage. If, on the other hand, the concentrations are inadequate, we can suspect nutrition to be the cause of tree decline. Therefore, the lack of P, Ca and Mg caused by drought in year 2003, may have resulted in enhanced defoliation in the following year (i.e. the lag effect on defoliation).

The growth of trees is a key ecological parameter of forests and thus of high importance as an indicator of forest condition (Dobbertin et al., 2013). Trees generally respond to environmental stresses by increment decrease as a consequence of a reduced photosynthetic activity and altered carbon allocation. Most tree ring studies have observed that trees predisposed to die have lower mean growth rates or greater growth sensitivity to climate in the years proceeding mortality (McDowell et al., 2008). It is clear from our analysis that May average, minimum or maximum monthly temperature plays an important role in the tree-ring formation of the beech. May is critical month for the growth of beech on Medvednica massif, in particular for beech that grows above 800 m a.s.l. Above average temperature in May has a positive influence on tree growth as well as on the tree phenology (Tikvić et al., 2006), this was observed not only at Medvednica massif, but also in Slovenia (Prislan et al., 2019, Čufar et al., 2008) Bosnia and Herzegovina

(Stjepanović et al., 2018), Italy (Piovesan et al., 2005) or Serbia (Stojanović et al., 2018). Favourable May temperature initiate cambium activity and radial growth can start. Contrary, below average temperature in May negatively influences tree growth and hinder cambium development which leads to narrower radial increments in particular year (Dulamsuren et al., 2016, Zimmermann et al., 2015). According to our study precipitation is less critical for beech growth at the Medvednica massif, this could be mainly because precipitation is sufficient for the growth of beech and temperature is not so high that lower amount of precipitation would lead to serious occurrences of drought, this finding is in accordance with Prislan et al. (2018) who found similar lack of response in beech in Slovenia.

Similar to other indicators of vitality such as defoliation or foliar composition, radial growth of trees is an integrative variable of tree response (Seidling et al., 2012). Studies on growth of beech show that it is strongly drought limited (Jump et al., 2006). Several authors state that tree ring width is frequently smaller during years following a severe drought (Le Dantec et al., 2000, Battaglia et al., 1998), but we found no evidence in our data that would support this. Rather, radial growth was linked solely to temperature variables, possibly revealing the shortcomings of an intensive case study in comparison with a study based on a larger number plots with diverse conditions.

The core of our interest was, however, in disentangling the relations of growth and other vitality indicators. Only a few authors report on the relationship between tree growth and defoliation, and the patterns are not always uniform (Dittmar et al., 2003, Rybníček et al., 2015). Often the studies relating crown condition and tree growth suffer from the fact that the data is provided from different groups of trees and therefore is plot-related rather than tree-related (Seidling et al., 2012). We used the same trees for tree-ring analysis and for defoliation assessments, which enabled us to make direct comparisons. Despite our sampling strategy, we did not record any significant relationship between radial growth and defoliation. This could be explained by a very narrow range of defoliation values on our plot, since several authors reported on the relationship between radial growth and defoliation but using a wide range of defoliation values in their studies. Solberg (1999) found considerable growth depressions for Norway spruce already at slight levels of defoliation, and Drobyshev et al. (2007) reported that radial increment of oaks in Sweden was highest in trees with healthy crowns. Information on the relation of radial growth and defoliation for common beech is largely missing, Seidling et al. (2012) state that increment and crown defoliation represent only partially the C allocation or C assimilation of a tree, hence a functional relationship of these parameters might not exist. However, Bréda et al. (2006) found that severe and long drought produced stress symptoms (premature leaf fall, yellowing), resulting in large number of individuals being in a weakened condition, with low radial growth. Dittmar and Elling (2007) related decreasing increment of beech in Switzerland to defoliation, suggesting that increment decline preceded crown decline. Our study, however, could not confirm this conclusion, even when taking into consideration various combinations of current and previous year observations.

The relation of growth and tree nutrition has also been extensively studied, mostly in studies dealing with characterization of forest soil productivity or stand fertilization/liming experiments (Fox et al., 2007, Sikström, 2002) with varying results. Improved nutrition is reported to have a positive effect on tree vitality and growth in some studies (Mohamed et al., 1993, Van Praag and Weissen, 1976). Similarly, several studies (Spohn et al., 2018, Yang et al., 2016) found that beech has a high metabolic flexibility to cope with low soil P stocks by growth adjustment. However we can expect long-term negative effects of prolonged drought (enhanced vulnerability to stresses, reduced growth) on beech trees, as the effects of low P are similar to drought-induced decreased stomatal conductance (Zavišić and Polle, 2018). Nys (1989) found that the addition of $CaCO_3$ had a positive effect on the nutrition, defoliation and increment of beech in the French Ardennes. While liming in Belgian Ardennes improved foliar Ca and Mg status of beech trees and significantly limited the decline in crown condition triggered by the summer drought in 2003, it had no effect on basal area increment (Jonard et al., 2010). Compared to fertilization experiments, the analysis of naturally occurring mineral foliar concentrations is more demanding in that the differences in nutrient status are smaller and more difficult to detect. In our study K concentrations correlated to residual tree ring chronology, although this relation was not particularly strong. It is unlikely that this is due to any direct negative K effect on growth, but rather shows the elevated uptake of K and restricted uptake of Ca in hot and dry years. This is important because Ca has a direct influence on the capacity of plants to regulate the intensity of transpiration (Berkowitz, 1998) and tree water deficits can reduce radial growth as well as bud production (Bréda et al., 2006). Therefore, although we could not relate radial growth to precipitation directly, there is some evidence of indirect linkages of nutrition, growth and defoliation patterns.

CONCLUSIONS
ZAKLJUČCI

In this study, we were able to determine that high maximum temperature variables of current year early spring and summer months, as well as previous year summer months caused an increase of defoliation. Low precipitation during

June of the previous year also caused an increase of defoliation, indicating that defoliation status depends on the climate conditions through various mechanisms that influence tree vitality. Beech was especially sensitive to drought or warmer than average years appearing in succession.

A similar relationship was observed between climate conditions and foliar nutrient concentrations where high temperatures during current year summer months negatively influenced nutrient uptake. Furthermore, we established that P and Ca concentrations in beech leaves are sensitive to the lack of precipitation. Temperature variables and precipitation in the previous year influenced the nutritional status of beech trees in the current year, although the results differed according to element in question and month of the year.

High temperatures in May positively influenced beech radial growth, while a wide range of minimum temperatures during March and June had a negative effect. Precipitation was shown to have no apparent effect on beech radial growth, perhaps due to the growth resilience of a healthy beech stand, maintaining radial growth in spite of less than ideal conditions.

Although we were not able to detect direct, significant links among vitality indicators, they all reacted to temperature variables within a current, or the previous year. The negative correlation of K to radial growth points to the effects of K/Ca antagonism in dry years and underlines the importance of nutrition for the health status of beech.

Overall, both high summer temperatures and low precipitation were shown to have the most negative effect, influencing the vitality of beech trees also in subsequent years.

ACKNOWLEDGEMENT
ZAHVALA

We acknowledge the E-OBS dataset from the EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the data providers in the ECA&D project (http://www.ecad.eu). Tom Levanič was supported by the following programmes and projects supported by the Slovenian Research Agency: Program and Research Group "Forest biology, ecology and technology" P4-0107, basic research projects J4-5519 "Paleoclimate data enhances drought prediction in the W Balkan Region" and J4-8216 "Mortality of lowland oak forests - consequence of lowering underground water or climate change?"

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SAŽETAK

Međuovisnosti različitih uobičajenih indikatora vitaliteta obične bukve (osutost krošnje, stanje ishrane, širina goda) kao i njihove moguće ovisnosti o klimatskim uvjetima istraživani su tijekom razdoblja od dvanaest godina u zreloj i zdravoj sastojini bukve na plohi intenzivnog motrenja br. 103 (Sljeme). Ploha se nalazi u sastojini bukve i jele (*Festuco drymeiae – Abietetum Vukelić et Baričević 2007*) na Medvednici, na 954 m nadmorske visine i južnoj ekspoziciji.

Naši rezultati potvrđuju važnost temperature za osutost, jer visoke temperature tijekom proljetnih i ljetnih mjeseci utječu na porast osutosti. Isti negativan utjecaj je zabilježen u slučaju visokih maksimalnih temperatura i niske količine oborine u ljeto prethodne godine. Bukva je bila osobito osjetljiva na sušne godine ili natprosječno tople godine koje se pojavljuju u nizu.

Ishrana bukovih stabala fosforom, kalcijem i magnezijem lošija je u slučaju visokih temperatura tijekom ljeta tekuće godine, a poboljšava se porastom oborine. Također, u našem istraživanju utvrdili smo negativnu korelaciju koncentracije kalija u lišću sa širinom godova. Smatramo kako se ne radi o negativnom učinku kalija na rast bukve, već o posljedici slabijeg usvajanja kalcija u sušnim godinama.

Visoke temperature u svibnju tekuće godine pozitivno utječu na prirast, dok široki raspon minimalnih temperatura tijekom ožujka i lipnja ima negativan učinak. Nije utvrđen izravan utjecaj oborine na širinu goda.

Ukratko, visoke ljetne temperature i niske količine oborine negativno utječu, izravno ili neizravno, na sve istraživane indikatore, a kod osutosti i ishrane taj efekt može biti značajan i u sljedećoj godini.

KLJUČNE RIJEČI: osutost; stanje ishrane; širina goda; suša; vitalitet