

MODELLING THE TIMING OF LEAF UNFOLDING IN PEDUNCULATE OAK (*Quercus robur* L.) CLONAL SEED ORCHARD

MODELIRANJE VREMENA LISTANJA U KLONSKOJ SJEMENSKOJ PLANTAŽI HRASTA LUŽNJAKA (*Quercus robur* L.)

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Summary

For ten years, 53 genotypes of Pedunculate Oak were monitored in a clonal seed orchard. The aim of the study was to clarify effects of forcing and chilling temperature as background of leaf unfolding of pedunculate oak through the different kind of prediction models. The Pedunculate Oak is known to have three phenofoms of flushing phases, i.e., early, intermediate and late, and substantially different Growing Degree Days (GDD) requirements were found among these phenological groups. For each of the phenological groups, the GDD interval value required for leaf unfolding was determined, but the values varied between years, rendering the development of a simulation GDD model difficult. For these reasons, other variables – day of year, precipitation and insolation – were included in the assessment. The aim was to examine how these environmental factors determine the GDD requirement for leaf unfolding in the three Pedunculate Oak phenological groups. The results suggest that for all three flushing groups, insolation and the day of year are statistically significant predictors for GDD. Insolation was demonstrated to be the primary factor with the largest influence on the GDD values. In the early flushing group, insolation accounted for 74.1 % of the variation, 90.6 % in the intermediate group, and 78.7 % in the late group. We recommend using the univariate GDD model for the early and intermediate flushing groups ($GDD_{early} = -27.651 + 0.539 * insolation$; $GDD_{inter} = -48.084 + 0.690 * insolation$) and the multivariate model for the late flushing group ($GDD_{late} = -237.839 + 0.559 * insolation + 2.479 * day\ of\ year$). To break the dormancy, chilling is required to be in the range of ± 40 chilling units, and if the values are higher or lower, the trees require significantly higher forcing temperatures.

KEY WORDS: spring phenology, climate change, GDD, environmental drivers, chilling

INTRODUCTION UVOD

The genus *Quercus* is widely distributed across large areas of the entire temperate region of the Northern Hemisphere. The European flora, as part of the European-West Asian formation centre, features 28 species of the genus *Quercus*, among which the Pedunculate Oak (*Quercus robur* L.)

covers the largest areas. In Croatia, the Pedunculate Oak is the most valuable forest tree species and forms the largest continuous oak forest in Europe (the so-called Spačva basin in Eastern Slavonia). The tree's characteristics, such as the fineness, regularity and uniformity of annual rings, golden-yellow colour and durability, all combine to provide old Croatian oakwood with the internationally recognized technical name "Slavonian oak" (Klepac 2000).

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The Pedunculate Oak is an allogamous monoecious species, and the flowering and flushing are largely determined by climatic conditions. Distinct variations in the flushing of the Pedunculate Oak have been noted, and different authors have divided the species into different forms (Mátyás 1967, Stojković 1991) based on differing numbers of categories from very early flushing (*super praecox*) to very late flushing (*tardissima*). The late flushing form (*Q. robur* var. *tardissima*) develops leaves approximately five weeks later than the early form (*Q. robur* var. *praecox*), and both forms occur in the all parts of the species' distribution. This phenomenon is most pronounced in the south-eastern part of the Pedunculate Oak range, where the early and late trees are easily distinguishable (Bacilieri et al. 1994, Wesolowski and Rowiński 2006, Perić et al. 2000). The late flushing types of Pedunculate Oak have a smaller length of crown, are more cylindrical with good straightness of the trunk and are less damaged by the late spring frost than the early types.

The genetic structure and variability of clonal phenofoms in clonal seed orchards were analysed, revealing that there were no significant differences in genetic differentiation among the phenofoms (Katičić et al. 2010). The analysed neutral markers were apparently not associated with adaptive differences between the phenofoms. The variation in flushing phenology is presumably one of the species' defensive strategies against late frosts. There are several reports of significant differences in genetic variability and differentiation among phenofoms within temperate tree species, e.g., late flushing forms of European beech had a higher intrapopulation genetic variability than early flushing forms. Oak trees were found to be more sensitive to temperatures with regard to leaf unfolding over an elevation gradient and were also found to have a lower chilling requirement for dormancy release than European beech (Chmura and Rożkowski 2002, Jazbec et al. 2007, Gömöry and Paule 2011, Dantec et al. 2014). Genetic variations in leaf unfolding timing between and within oak populations are likely due to differences in heat requirement rather than differences in chilling requirement (Dantec et al. 2014).

The technical quality of late flushing Pedunculate Oak trees is likely slightly better due to the delayed budburst and flushing of leaves, which is out of synchrony with eclosing caterpillars and avoids defoliation (Schütte 1957, Hunter 1992, Tikkanen and Julkunen-Tilto 2003). In addition to the early and late types, there are also intermediate phenotypes, which are moving towards one or the other direction.

Because the late flushing Pedunculate Oak (*Q. robur* var. *tardissima*) is more desirable for cultivation in many European countries, the continued selection and collection of acorns from very late flushing trees from natural stands in the beginning of May is recommended. The establishment of clonal seed orchards with late flushing genotypes would

certainly ensure higher quality forest reproductive material with the most advantageous genetic type.

The establishment of clonal seed orchards began with the goal of controlling more regular yield periodicity and obtaining seeds (acorns) with high genetic quality. The leaf unfolding of Pedunculate Oak is largely genetically controlled (Mátyás 1967, Stojković 1991, Baliuckas 2001), which provides an opportunity for legitimate selection of plus trees to achieve lasting phenological uniformity of leafing genotypes from which to establish clonal seed orchards. The phenology of trees is strongly driven by environmental factors, such as temperature, that have already altered the vegetative and reproductive phenology of many forest species. However, the impact of adverse weather conditions, such as heavy rainfall, high relative humidity, frost, low and high air temperatures, and hail, can sometimes disturb favourable phenological uniformity of phenophases in forest stands and within seed orchards (Wolgast 1972, Cecich 1997, Garcia-Mozo et al. 2001). Temperature and photoperiod are widely considered to be a major factors controlling the phenology of boreal and temperate tree species (Sarvas 1972, 1974, Heide 1993, Schwartz 2003, Chuine et al. 2003, 2010, Hänninen and Kramer 2007, Basler and Körner 2012, Fu et al. 2013).

Phenology is the study of the timing of life-history events that occur in a seasonal and repeated pattern. Understanding the processes responsible for macro-scale spatial and temporal phenological patterns is a critical step in developing predictive phenological models (Phillimore et al. 2013). While phenological responses may involve the integration of multiple environmental cues, the spring phenology of many plant species appears to be especially sensitive to temperature. The timing of leaf unfolding is mainly regulated by temperature in cold winter environments. Chilling temperatures break winter dormancy and subsequent warm temperatures induce leaf unfolding, which is why the phenological onset of spring correlates very well with the air temperature of the preceding months (Menzel 2002, Davi et al. 2011). Heat units, expressed in growing degree-days (GDD), are frequently used to describe the timing of biological processes. Approaches that use growing degree-days (GDD) assume a linear effect of temperature on the development rate via enzyme activity (Bonhomme 2000). In the areas of crop phenology and development, the concept of heat units, measured by GDD (°C-day) has vastly improved the description and prediction of phenological events relative to other approaches, such as time of the year or day of year (McMaster and Wilhelm 1997). Growing degree days (GDD) models predict the day on which a phenological event should take place.

Phenological models, used to simulate leaf unfolding, i.e., the start of the growing season, are based on the response

of bud growth to forcing temperatures and/or to chilling temperatures, and this response has been described with different types of mathematical functions (Chuine 2000). The leaf unfolding process is often considered to involve two stages (Cannell and Smith 1983, Hänninen 1990, Kramer 1994, Chuine 2000, Chuine et al. 2003). First, bud dormancy needs to be broken by exposure to cold temperatures during winter, referred to as chilling. Once sufficient chilling has accumulated, the bud enters the second phase of dormancy, during which sufficient warmth is needed to trigger bud burst, referred to as forcing. The accumulation of forcing is based on a linear temperature relationship above a given temperature threshold, and the interaction of chilling and forcing requirements with temperature determines the timing of leaf unfolding.

This work is based on ten years of data recording the leaf unfolding of *Quercus robur* L. in a clonal seed orchard and meteorological data. The parameters are start time (day of year), base temperature, cumulative GDD, precipitation and insolation. From the start time, the daily temperatures above the base temperature are summed, and the model predicts that the phenological event will occur once the cumulative GDD requirement has been met. A number of approaches exist for identifying the best parameters under the GDD model, but most involve the iterative application of combinations of parameters to the temperature data and estimation of one of several related metrics that quantify the difference between the predicted and observed phenology (Bonhomme 2000). The aim of the study was to determine requirements of the GDD values, precipitation and insolation by each phenological group of pedunculate oak, as well as chilling requirements for breaking dormancy of vegetative buds and mutual relationship between chilling and GDD. Thus, the application of GDDs in the future could contribute to better and easier predictions of how phenofoms and pathogens are related, based on their biology and ecology. The values obtained by chilling could be used for the prediction of the required amount of forcing temperature and the occurrence of the leaf unfolding phase.

MATERIALS AND METHODS

MATERIJALI I METODE

Study Area – Područje istraživanja

A clonal seed orchard of Pedunculate Oak (*Quercus robur* L.) was established in the spring of 2001 at the Forest Office Čazma in the lower Sava river provenance region of Croatia. The seed orchard has an area of 26 ha, contains 53 clones (genotypes) selected in seed stands, and features a total of 2,150 ramets (grafts) randomly planted in the orchard. The genotypes belong to a single seed region that includes seven subprovenances. The pruning and training systems

of the grafts in the clonal seed orchard should produce a strong framework and good light penetration in the canopy (Kajba et al. 2008). An oval spindle training system is used after establishment, and the spacing between ramets is 10 × 8 m. The total height of the training shape is up to seven meters with six scaffold whorls.

The clonal seed orchard is located at 45° 45' 55" N and 16° 35' 32" E in the northwest part of Croatia. The climate in this region is moderately warm and rainy with a two short dry period (April and July). The average value of coldest month temperature is between - 3°C and 18 °C, while the mean temperature of the warmest month is not above 22 °C. The mean annual temperature is 9.8 °C, and the mean annual precipitation of 810 mm is evenly distributed throughout the year.

Phenology measurements – Fenološka motrenja

During the 10-year study period (2004-2013), the phenological data of leaf unfolding and meteorological records were studied. Only well-developed individuals (grafts) were chosen for observation. The start date of the leaf unfolding stage is defined as the point at which the entire leaf blade and leaf stalk were visible.

Each year, observation began before any buds began to break, and observation was made every 10 days until the 10th of May. The meteorological data were supplied by the Croatian Meteorological and Hydrological Service, based on data recorded at the Čazma meteorological station, which is located 1 km from the orchard site (DHMZ). Observations were made on ramets of 53 clones randomly selected across the entire area of the orchard. The start of heat accumulation has been taken from the 1st of January. Only positive values of GDD were taken into account to calculate cumulative sums. Insolation is expressed in hours (h) and precipitation in mm. The ten years of leaf unfolding data and the corresponding weather data were used to build the phenology models.

Statistical analysis – Statistička analiza

Growing Degree Days (GDD) were calculated using the Hand Calculating Degree Days method described by Snyder (1985):

$$GDD = \frac{T_{max} + T_{min}}{2} - T_{base} \quad (1)$$

If: $\left[\frac{T_{max} - T_{min}}{2} \right] - T_{base} > 0$ GDD from the days included in final sums;

If: $\left[\frac{T_{max} - T_{min}}{2} \right] - T_{base} < 0$ GDD from the days not included in final sums.

Here, T_{max} and T_{min} are daily maximum and minimum air temperatures, respectively, and T_{base} is the base temperature.

The temperature base was 5 °C, which has been used for other forest tree species as it is presented in formula 1 (Cannel and Smith 1983, Chassagneux and Choisnel 1986, Kasprzyk 2009, Dobrowolska et al. 2011).

Descriptive statistics were calculated for all analysed variables, and the level of statistical significance was set at 5 %. To classify clones by GDD for the study period (2004–2013), we used a k-means clustering that divided all 53 investigated clones into three groups depending on the leaf unfolding (early, intermediate and late flushing groups). By using repeated measures analysis of variance, we tested whether and how other analysed variables (precipitation, day of year, and insolation) differ between the GDD clusters. Our model contains three parameters – effect of GDD groups (between subject) the effect of years, and the interaction years × GDD groups (within subject) – because we wanted to test whether our analysed variables (according to GDD groups) behaved approximately the same throughout the analysed period (Davis 2002). For testing sphericity we use Mauchly's Sphericity test and if sphericity assumption has been violated we use Greenhouse-Geisser Epsilon (G-G) and Huynh-Feldt-Lecoutre epsilon (H-F-L) correction factors which adjust the univariate test degrees of freedom for within subject testing. To determine which of the analysed variables best describes GDD for each GDD group, we used a regression analysis regardless of the clones and the year. First, an univariate regression was performed for each analysed variable. Then, we performed a multivariable (multiple) regression for variables that were statistically significant in the univariate models. Finally, we choose the most appropriate model that served as the best predictor for GDD using differences in R² values as the selection criterion (Sokal and Rohlf 1995).

The chilling accumulation calculations were based on the temperature difference between T_{min} and T_{max} in the period between 1st November and 28th February (formula 2), with ≤ 5 °C adapted from the Thermal Time model (Cannell and Smith, 1983). All statistical analyses were conducted using Statistica 11.0 (StatSoft Inc. 2013).

$$\text{Chilling}(\text{SUM}x) = \sum_{\text{start date}}^{\text{end date}} \begin{pmatrix} 0 & T_{min} = T_{base} \\ x & [T_{base} - T_{min}] \\ x & [T_{max} - T_{min}] \text{ (If } T_{max} < T_{base} \text{)} \\ 0 & T_{min} > T_{base} \end{pmatrix} \quad (2)$$

- If the T_{min} is equal to the T_{base} then the chilling value for that day is 0.
- X represents an interval in degrees between the T_{min} and the T_{base} or between T_{min} and T_{max} if T_{max} is less than the T_{base} .
- If the T_{min} is higher than the T_{base} value then chilling for that day is 0.

RESULTS REZULTATI

The averaged data are clearly segregated between the three groups of *Q. robur* phenofoms (early flushing, intermediate and late flushing) for all measured parameters during the duration of the experiment, as shown in Table 1. The start date of leaf unfolding phenofom is clearly defined by the GDD model (Table 1 and Figure 1).

The mean values of GDD were 118.42 for the early flushing group, 188.34 for the intermediate group and 261.61 for the late group of oak clones. All other measured parameters (precipitation, day of year, and insolation) are similarly separated and are divided into three separate groups (Figure 2). For the early flushing group, the mean day of year is 85 and insolation is 271.04 hours, which achieved the GDD requirements and the clones of that group started with the leaf unfolding. The intermediate group required an average of 98 days and 342.49 hours of insolation, whereas the late flushing group required 109 days and 411.57 hours of insolation. The calculated Coefficient of Variation (C.V. %) values for all parameters are lowest for the late flushing form group, likely because they belong to a group with at least of 9 genotypes. In contrast, the intermediate group contains 13 of genotypes, and the early group contains 31 genotypes.

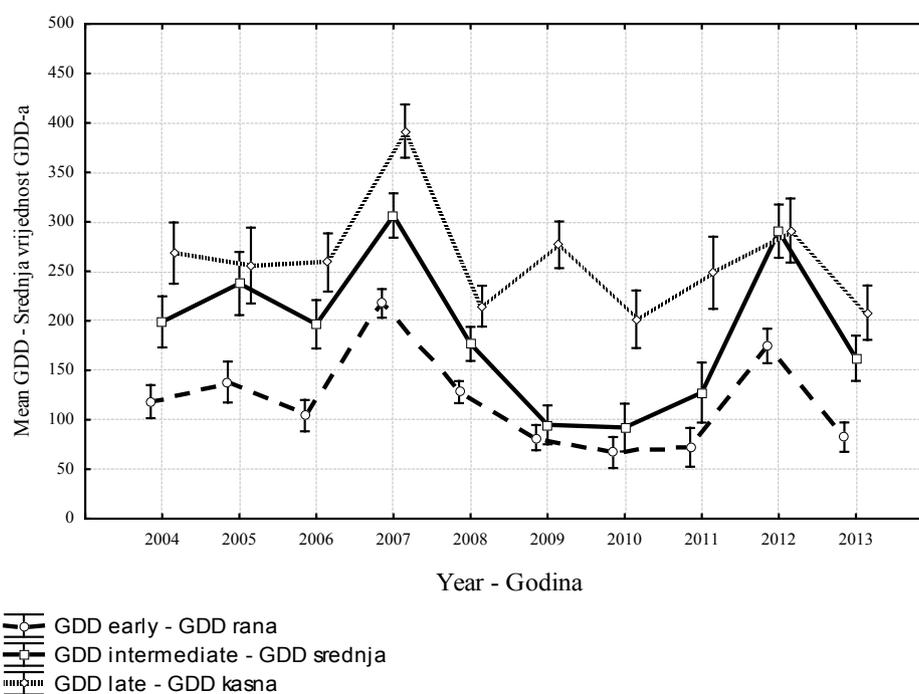
The results of k-means clustering of the clones according to their values of GDD for the period of 2004–2013 are shown in Fig. 1. The clones are clearly classified into three groups (early, intermediate and late flushing).

To examine how the other analysed variables (precipitation, day of year, and insolation) affected the GDD groups, the variables were tested with repeated measures ANOVA to determine whether they individually participate in the GDD groups, their behaviour over years and their behaviour over years under certain clusters. Because sphericity assumption has been violated we use G-G and the H-F-L correction factors. In Table 2 we gave adjusted p value for both. In all tests the p value before and after using correction factors p values were the same ($p < 0.0001$). Sphericity test, G-G epsilon and H-F-L epsilon for Precipitation ($Chi^2=514.61$; $df=44$; $p < 0.001$; $G-G=0.3337$; $H-F-L=0.3574$); Insolation ($Chi^2=348.74$, $df=44$; $p < 0.001$; $G-G=0.4446$; $H-F-L=0.4881$) and day of year ($Chi^2=313.64$ $df=44$; $p < 0.001$; $G-G=0.3994$; $H-F-L=0.4341$).

The results of the repeated measures ANOVA (Table 2) show that there are statistically significant differences between each group for all of the analysed variables. There is a statistically significant difference over the years and significant differences in the interaction between the GDD group and the years, which means that all the analysed variables for individual GDD group over the year do not behave the same (Figure 2).

Table 1: Descriptive data for the seasonal GDD and the other parameters (precipitation, insolation and day of year) according to flushing groups (E – early, I – intermediate, L – late)**Tablica 1:** Deskriptivna statistika za GDD i ostale parametre (oborine, insolacija i broj dana) s obzirom na forme listanja (E – rani, I – srednji, L – kasni).

Year Godina	Parameters (accumulated from the 1 st January) Parametri (početak zbrajanja od 1. siječnja)											
	GDD			Precipitation (mm) Oborine (mm)			Day of year Br. dana			Insolation (h) Insolacija (h)		
	E	I	L	E	I	L	E	I	L	E	I	L
2004	118.38	198.93	268.45	171.02	248.82	276.33	94	107	116	299.37	345.98	393.51
2005	138.15	237.67	255.85	169.63	210.25	210.41	95	111	113	355.73	446.54	468.18
2006	104.19	196.51	258.97	97.83	125.30	144.28	91	105	113	255.67	341.12	389.30
2007	217.59	306.42	391.73	160.83	187.91	189.48	81	99	109	333.62	455.55	556.51
2008	127.98	176.68	214.84	66.60	100.78	114.41	79	92	100	286.72	356.25	403.67
2009	81.91	94.83	276.79	113.41	117.56	129.91	77	83	107	194.92	220.65	377.40
2010	66.86	92.14	201.57	175.85	184.53	230.91	77	83	102	155.43	184.65	296.50
2011	72.13	127.52	248.51	27.18	33.28	45.57	72	83	102	184.62	248.23	373.48
2012	174.58	290.57	291.24	80.73	88.85	88.60	91	110	110	440.28	539.09	534.12
2013	82.45	162.16	208.18	368.07	383.72	385.70	99	109	113	204.04	286.82	323.07
Average – Srednja vrijednost	118.42	188.34	261.61	143.12	168.10	181.56	85	98	109	271.04	342.49	411.57
Minimum – Minimalna vrijednost	66.86	92.14	201.57	27.18	33.28	45.57	72	83	100	155.43	184.65	296.50
Maximum – Maksimalna vrijednost	217.59	306.42	391.73	368.07	383.72	385.70	99	111	116	440.28	539.09	556.51
Range – Opseg	150.73	214.28	190.16	340.89	350.44	340.13	27	28	17	284.85	354.44	260.01
Standard deviation – Standardna devijacija	48.42	74.18	54.72	94.04	99.34	99.83	10	12	6	89.53	112.65	84.20
C.V. % – Koeficijent varijacije (%)	40.89	39.39	20.92	65.71	59.10	54.98	11.14	12.28	5.26	33.03	32.89	20.46

**Figure 1:** Three phenological groups of *Quercus robur* separated by GDD values (early, intermediate and late flushing groups)**Slika 1:** Tri fenološke forme hrasta lužnjaka prikazane prema GDD vrijednostima (rane, srednje i kasno listajuće forme)

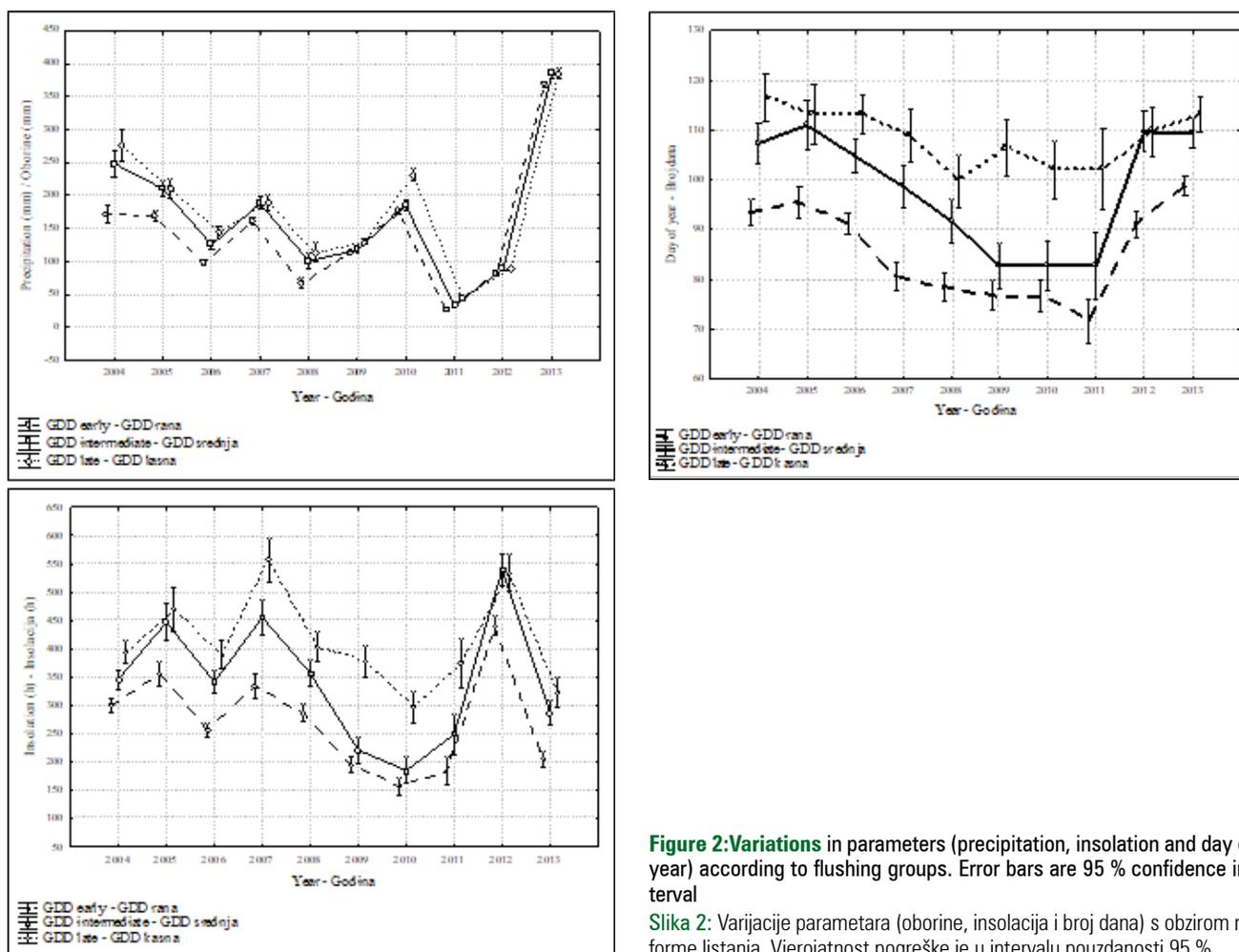


Figure 2: Variations in parameters (precipitation, insolation and day of year) according to flushing groups. Error bars are 95 % confidence interval

Slika 2: Varijacije parametara (oborine, insolacija i broj dana) s obzirom na forme listanja. Vjerojatnost pogreške je u intervalu pouzdanosti 95 %

The results of the regression analysis are shown in Table 3. The goal was to identify the best linear model for prediction of the GDD values for each of the GDD groups. First, univariate linear regressions were calculated for all of the analysed variables (GDD was the dependent variable; Table 2). From the results for all three groups, insolation and day of year are clearly statistically significant predictors for GDD. Although these factors are significant predictors,

their coefficients of determination range from 71 % to 89 % for insolation and from 26 % to 62 % for the day of year. In addition to the univariate models, we created a multivariate model for the variables were shown to be statistically significant in the univariate models, i.e., insolation and day of year.

When we include the value of the day of year to the insolation value for the early flushing group of Pedunculate Oak,

Table 2. Results of the repeated measures ANOVA for GDD flushing groups

Tablica 2. ANOVA s ponovljenim mjerenjima za GDD fenološke grupe

Source of variability Izvor varijabilnosti	df	Precipitation (mm) Oborine (mm)		Insolation (h) Insolacija (h)		Day of year Broj dana	
		F	p	F	p	F	p
GDD group – GDD grupa	2	123.47	<0.0001	146.89	<0.0001	131.17	<0.0001
Error – Pogreška	50						
Years – Godine	9	1280.22	<0.0001*	186.49	<0.0001*	55.53	<0.0001*
Years*GDD group – Godine*GDD grupa	18	14.3	<0.0001*	6.08	<0.0001*	3.8	<0.0001*
Error – Pogreška	450						

Note: * Adjusted p values for G-G and H-F-L correction

Napomena: * Podešene p vrijednosti za G-G i H-F-L korekciju

the total value of GDD does not change, remaining $R^2=74.1$ %. The day of year is not a statistically significant variable in combination with the insolation. Therefore, for the early flushing form of Pedunculate Oak, we recommend the univariate model that features only the insolation as an independent variable: $GDD_{early} = -27.651 + 0.539 * insolation$.

For the intermediate flushing group, both variables (insolation and day of year) were statistically significant, and the total variability of GDD with this model is $R^2=90.6$ %. Based on the univariate model for insolation, $R^2=89.1$ %, which is a difference of only 1.5 %. Therefore, we conclude that the recommended model contains only the insolation variable: $GDD_{inter} = -48.084 + 0.690 * insolation$.

For the late flushing group, both variables (insolation and day of year) were statistically significant, with a total explained GDD variability of $R^2=78.7$ %. The R^2 value for the univariate model for insolation is 70.8 %. Due to the R^2 difference of 7.9 %, we recommend the use of the multivariate model containing the both variables (insolation and day of year): $GDD_{late} = -237.839 + 0.559 * insolation + 2.479 * day\ of\ year$.

A second-degree polynomial has proven to be the best model of the relationship between chilling and GDD ($F(3,7) = 25.71, p < 0.001$), which indicates that if the chilling is

approximately zero, the GDD group needs fewer forcing temperatures, and if the chilling units are above or below the value of ± 40 units, then GDD group requires much more accumulated forcing (Figure 3). Although the parabola is shifted from the centre, the x parameter (0.1644) shows that this shift is not statistically significant ($t = 0.54, p = 0.60$). In contrast, the parameter of the quadratic term (0.012) is significant at the significance level of 9.6 % ($t = 1.92, p = 0.096$). Additionally, to break the dormancy, chilling is required to be in the range of ± 40 chilling units, and if the value is higher or lower than this number, the trees require significantly higher forcing temperatures.

DISCUSSION AND CONCLUSIONS

RASPRAVA I ZAKLJUČCI

Earlier investigations of Pedunculate Oak noticed the existence of different phenological forms that varied from early flushing (var. *praecox*) to late flushing (var. *tardissima*), leading to variations in the leaf unfolding between 1st March and 10th May (Mátyás 1967, Stojković 1991, Perić et al. 2000, Baliuckas et al. 2001, Wesolowski and Rowiński 2006). In this study, the phenofoms were properly separated into three groups – early, intermediate and late flushing types – based on GDD and three other variables (Table 1, Figure

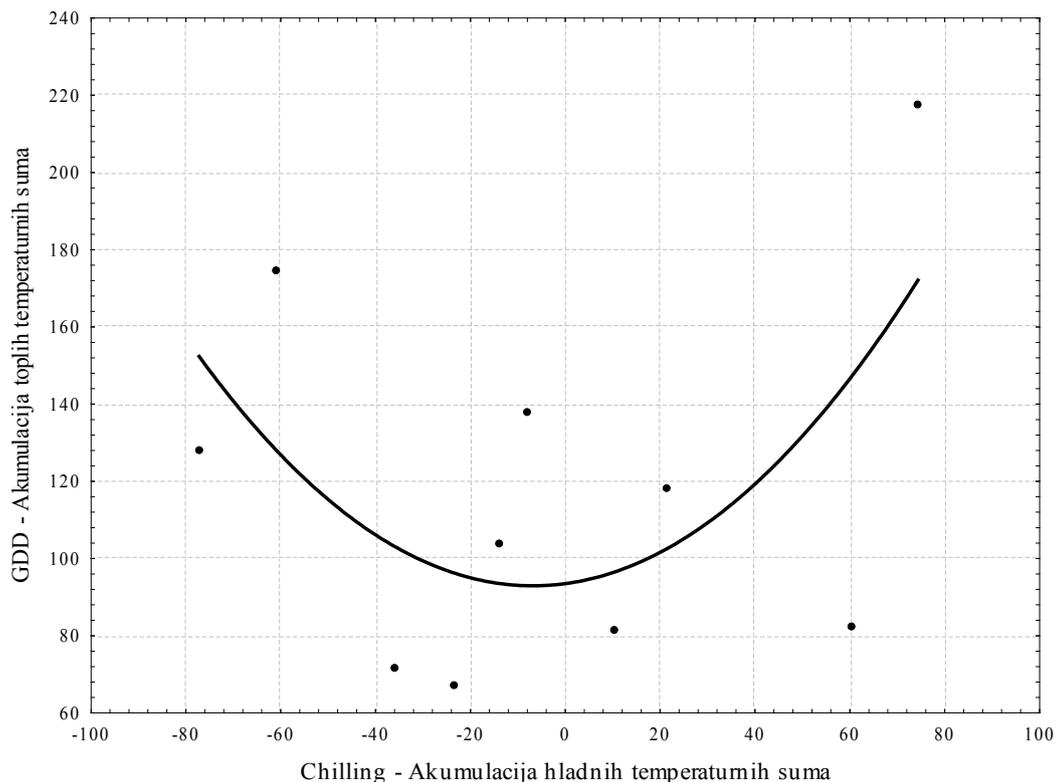


Figure 3: Relationship between the chilling accumulation (chilling units between 1st November and 28th February) and forcing accumulation (accumulated growing degree days between 1st January and 10th May)

Slika 3: Odnos između akumulacije inaktivnih temperatura (hladne temperaturne vrijednosti između 1. studenog i 28. veljače) i proljetnih temperatura (akumulacija toplih temperaturnih vrijednosti između 1. siječnja i 10. svibnja)

Table 3. Results of the regression analysis in which GDD is the dependent variable for each GDD flushing group

Tablica 3. Rezultat regresijske analize u kojima je GDD zavisna varijabla za svaku GDD fenološku grupu

GDD	Univariate model <i>Univarijatni model</i>						Multivariable model <i>Multivarijatni model</i>				
	Variable <i>Varijabla</i>	Intercept <i>Slobodan član modela</i>	PE	SE	p	R ²	Variable <i>Varijabla</i>	PE	SE	p	R ² RMSE
Early <i>Rani</i>							Intercept <i>Slobodan član modela</i>	-25.853	12.815	0.045	0.741
	Precipitation <i>Oborine</i>	118.124	0.002	0.030	0.956	0.000					30.843
	Insolation <i>Insolacija</i>	-27.651	0.539	0.018	<0.001	0.741	Insolation <i>Insolacija</i>	0.541	0.023	<0.001	
	Day of year <i>Broj dana</i>	-100.718	2.260	0.240	<0.001	0.269	Day of year <i>Broj dana</i>	-0.028	0.181	0.878	
Inter- mediate <i>Srednji</i>							Intercept <i>Slobodan član modela</i>	-114.919		<0.001	0.906
	Precipitation <i>Oborine</i>	169.427	0.112	0.080	0.155	0.015					27.351
	Insolation <i>Insolacija</i>	-48.084	0.690	0.020	<0.001	0.891	Insolation <i>Insolacija</i>	0.597	0.031	<0.001	
	Day of year <i>Broj dana</i>	-277.821	4.751	0.327	<0.001	0.622	Day of year <i>Broj dana</i>	1.006	0.257	<0.001	
Late <i>Kasni</i>							Intercept <i>Slobodan član modela</i>	-237.839	40.045	<0.001	0.787
	Precipitation <i>Oborine</i>	274.204	-0.069	0.077	0.375	0.009					34.063
	Insolation <i>Insolacija</i>	-9.618	0.659	0.045	<0.001	0.708	Insolation <i>Insolacija</i>	0.559	0.045	<0.001	
	Day of year <i>Broj dana</i>	-311.111	5.278	0.744	<0.001	0.364	Day of year <i>Broj dana</i>	2.479	0.500	<0.001	

1). Furthermore, the sum of temperature could interact with the other environmental variables.

Statistically significant differences were obtained for all variables (GDD, precipitation, day of year and insolation) and for variable differences between years over the course of the study period. The results are consistent with the observations of significant leaf unfolding variability between years (Morin et al. 2010). The experimental warming and reduced precipitation for several populations of three European oak species (*Quercus robur*, *Q. pubescens*, *Q. ilex*) in this study caused a longer growing season and higher mortality. The leaf unfolding date was not significantly affected by variations in water quantity, but the date varied significantly by year. Certain genotypes may respond to a higher amount of precipitation, which ultimately means that they need a longer time and many more hours of insolation to facilitate leaf unfolding.

Temperature, which is the prime environmental factor regulating the leaf unfolding process, in addition to other environmental cues, such as photoperiod, may modulate

the leaf unfolding process, especially for the late flushing species (Basler and Körner 2012, Caffarra et al. 2011, Heide 1993, Körner and Basler 2010). Several experiments have tested the effects of increasing temperature, and the leaf unfolding date was often advanced by higher temperatures (Repo et al. 1996, Guak et al. 1998, Arft et al. 1999, Hollister et al. 2005, Kilpelainen et al. 2006, Cannel et al. 1999, Menzel et al. 2001). Certain results confirm that continued and intense warming may not result in further advances in the date of leaf unfolding in the late successional species of oak and beech if the warming exceeds a certain threshold that leads to insufficient chilling temperatures for dormancy release (Fu et al. 2012b, 2013). The leaf unfolding of sessile oaks was 2.3 times more sensitive to temperatures over an elevation gradient than that of beech trees (Dantec et al. 2014). The timing of leaf unfolding in deciduous forest trees is genetically determined with respect to temperature changes (Derory et al. 2006, Vitasse et al. 2010), and temperature requirements are under strong genetic control (Rousi and Pusenius 2005, Sanz-Perez et al. 2009). The leaf unfolding date has been shown to be strongly genetically controlled

in several species (Worral 1983, Billington and Pelham 1991, von Wuehlisch *et al.* 1995). The leaf unfolding dates of three species (birch, oak and beech) have been shown to advance significantly with warming in two experimental years (Fu *et al.* 2013). An earlier correlative study revealed that *Q. Robur* flushing in the UK had advanced and that temperatures in the February to April time window were strongly negatively correlated with the first leaf unfolding date (Sparks and Carey, 1995). Altitudinal transplant experiments of *Q. petraea*, a close relative of *Q. robur*, have revealed high levels of temperature-mediated plasticity. For example, a 1 °C rise in mean spring temperature caused leaf unfolding to advance by approximately six (Vitasse *et al.* 2010) to seven days (Phillimore *et al.* 2013).

A phenological model for *Quercus petraea* was formulated to predict the date of budburst and the increase in leaf area as a function of cumulative temperature and of day-length. Budburst occurs when the temperature sum of the past 10 days exceeds a given threshold, which is a decreasing function of day-length (Nizinski and Saugier 1988).

Accumulated GDD is often assumed to be effective for predicting leaf unfolding in trees in present climate conditions (Chuine *et al.* 2000, Chuine and Beaubien 2001). In this research on the influence of variables, such as precipitation, day of year and insolation, on GDD values, insolation is found to be the main factor that best determined the real value of GDD. Insolation predicted the GDD value with an accuracy of 74.1 to 89.1 % (Figure 2). Other parameters do not have as strong an impact on GDD, and only day of year variable contributed significantly, with the values of 1.5 % (for intermediate) and 7.9 % for the late flushing group. Therefore, separate prediction GDD models are used for each of the leaf unfolding groups. Further research should perhaps examine the possibility of using only the insolation as the main variable in the estimation of GDD. The leaf unfolding process is very sensitive to environmental drivers, including both temperature and photoperiod (Basler and Körner 2012, Heide 1993). Comparing the performance of two methods (time-window and GDD) in the prediction of the spatiotemporal variation in the timing of first flushing will provide congruent insights into the cues and processes that underpin geographic variation in the phenology of *Quercus robur* (Phillimore *et al.* 2013).

As a part of this investigation, we decided to apply the GDD method to facilitate future predictions for the leaf unfolding. Natural stands and clonal seed orchards are in constant environmental struggle with various pathogens that to some extent undermine their stability. Thus, the application of GDDs could in the future contribute to better and easier predictions of how phenofoms and pathogens are related, based on their biology and ecology. Late leaf flushing among Pedunculate Oaks serves as an antiherbivore defence, via

the development of leaves that is asynchronous with the eclosion of caterpillars. This trait avoids the costs of defoliation, which may provide benefits later in the growing season (Hunter 1992, Wesolowski and Rowiński 2006). Large intraspecific variation in the timing of budburst of the *Quercus robur* may have a negative effect on herbivores, such as *Operophtera brumata* (Tikannen and Julkunen-Tilto 2003). Late flushing forms are not harmed by late spring frost, which may result in lower damage and better quality trees. The main goal of the testing of the GDD model in this example of oak phenology is to determine the average values of the studied parameters associated with GDD that are required by each phenological group, specifically for the leaf unfolding trait.

The duration of the growing season may increase the vegetation period. Due to climate change, this duration is an important feature for carbon sequestration (Delpiere *et al.* 2009) and to the growth response (Kramer *et al.* 2000). Several studies have documented advances in the leaf unfolding and flowering dates of 2 to 3 days per decade on average during the last 64 years (Menzel 2000). Certain experimental results showed that future warming should continue to advance the tree species leaf unfolding dates, but other results also suggest that the phenological response of three European oak species to increased temperatures is nonlinear and can vary strongly among species (Morin *et al.* 2010).

A negative relationship is known to exist between required chilling and forcing, and Murray *et al.* (1989) reported that a negative exponential equation was the best fit across all fifteen investigated woody species. The findings of Fu *et al.* (2013) suggest that a constant forcing requirement could be used to predict the timing of leaf unfolding in oaks only when the chilling requirement is either far too low or fully reached. In between, a linear (negative) relationship between chilling and forcing needs to be applied. The relationship between GDD and chilling units (CU) was sigmoidal; GDD was not correlated with CU both at very low (< 40 CU) and very large (> 80 CU) chilling unit values. When chilling was less than 40 CU, the forcing requirement of oaks no longer increased and even appeared to become uncoupled from the accumulated chilling units. The breakdown of the negative linear relationship between forcing requirement and chilling at very low chilling units may be related to the influence of photoperiod. A long photoperiod may partially compensate for a lack of sufficient chilling (Caffarra *et al.* 2011, Garber 1983, Nienstaedi 1966, Wareing 1953). The values obtained by chilling could be used for the prediction of the required amount of forcing temperature and the occurrence of the leaf unfolding phase, which may indicate accurate protection from pests/diseases in clonal seed orchards or in natural stands of Pedunculate Oak.

For each of the phenoform groups (early, intermediate and late flushing groups), an appropriate model for the prediction of the unfolding trait is specified and selected. The timing of leaf unfolding is also an important characteristic related to pests and insects and to the occurrence of the late spring frost. The models based the observations obtained over ten years should be applied to other clonal seed orchards and natural stands of Pedunculate Oak to verify their universality and to maintain their constancy and applicability.

ACKNOWLEDGMENTS

ZAHVALE

This work was supported by Croatian Science Foundation through the research project FRAXINPRO [IP-11-2013].

The authors gratefully acknowledge Dr. Francois Lefèvre and Dr. Yongshuo H. Fu for constructive comments. Special thanks to Marina Antulov, MSc and Bernarda Bukovac, MSc for their kind support in collecting of data in seed orchard.

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Sažetak

Biološki mehanizam listanja pod izravnim je utjecajem okolišnih čimbenika. Razvijeni su mnogi modeli i objavljene različite studije s ciljem što boljeg opisa pojedinog biološkog mehanizma fenoloških svojstava, a koji su izloženi upravo okolišnim čimbenicima tijekom svoga života. Temperatura je neminovno jedan od najbitnijih čimbenika za pokretanje mnogih procesa u biljci i upravo je ona okosnica većine izrađenih modela. Growing Degree Days model se temelji na minimalnim i maksimalnim temperaturama, te na baznoj temperaturi, odnosno temperaturnom pragu iznad kojeg se aktiviraju procesi u biljci.

Istraživanja u ovome radu temelje se na desetogodišnjem monitoringu početka listanja hrasta lužnjaka u klonskoj sjemenskoj plantaži koja sadrži ukupno 53 genotipa. Cilj je bio utvrditi ponašanje svojstva listanja te implementirati dobivene rezultate u GDD model. S obzirom da je već poznato da hrast lužnjak ima svoje tri fenološke forme listanja (rane, intermedijarne i kasne), bilo je potrebno dokazati da se te tri grupe jasno diferenciraju i po temperaturnim sumama, odnosno GDD-u. Razdoblje monitoringa u svakoj godini bilo je oko 130/131 dan, odnosno od 1.siječnja do 10.svibnja. Izračunom GDD-a i povezivanjem tog modela s dobivenim vrijednostima početka listanja, iskazala se jasna segregacija na već spomenute tri forme. Svako fenološkoj grupi, dodijeljen je interval vrijednosti temperaturnih suma koje su potrebne da bi ta fenološka forma započela s listanjem. S obzirom na godišnje vrijednosti temperaturnih suma koje su potrebne pojedinoj formi da krene s listanjem, evidentno je bilo da vrijednosti značajno variraju kroz godine, i to za kompletno promatrano razdoblje. Upravo to variranje onemogućava da se putem GDD modela izradi simulacijski model, koji bi mogao, uz određena manja odstupanja, predvidjeti početak listanja za iduće razdoblje. Važnost predviđanja nije jednostrana, naprotiv, cijeli je niz sinergijskih čimbenika koji su izravno ili neizravno vezani za početak listanja pojedinih vrsta šumskog drveća, među kojima možemo spomenuti stadijni razvoj entomofagnih i fitopatogenih štetnika, koji su svojom biologijom usko vezani za biologiju određene vrste drveća.

S obzirom na izraženo variranje vrijednosti temperaturnih suma, po fenološkim formama, u istraživanja su uključeni i drugi okolišni čimbenici, kao što su količina oborina (mm), insolacija i broj dana. Cilj je bio ispitati kako se ova tri čimbenika ponašaju s obzirom na kretanje GDD vrijednosti, odnosno koji od ispitivanih čimbenika je preciznija poveznica za svojstvo početka listanja. Statističkom obradom podataka, jasno su i s visokim postotkom isključeni količina oborina i broj dana kao čimbenici koji definitivno ne utječu ili utječu s jako malim učešćem na kretanje vrijednosti GDD-a. Insolacija se iskazala kao čimbenik koji s najvećim udjelom sudjeluje u kretanju GDD vrijednosti i to za ranu fenološku formu sa 74,1 %, za intermedijarnu formu sa 90,6 %, te za fenološku formu kasnog listanja sa 78,7 %.

KLJUČNE RIJEČI: fenologija listanja, promjena klime, GDD, klimatološki parametri, hladne temperaturne jedinice.