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Masting of European Beech in Seed Stands from Eastern Carpathians

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ABSTRACT

Masting is the process of producing seed crops, which presents annual variation and synchronicity among individuals. Among the major species in Europe, beech is the most common deciduous species, a foundational species in the majority of forest ecosystems, and it has economic, ecological, and environmental benefits. We present the results of a study in masting drivers at stand level in seed stands from Eastern Carpathians. Masting is controlled by stand and climate factors, among which the most important are the canopy position and the crown diameter, together with a surrogate measure for aridity, the Ellenberg quotient (EQ). Known as a factor limiting the beech distribution, EQ seems also to be determinant in masting intensity at stand level more than other analyzed climate factors. The identified parameters are suitable for the selection of the seed forest stands to be used in afforestation programs.

Keywords: masting; ordinal models; canopy position; Ellenberg quotient; crown width

INTRODUCTION

In plant populations, masting is the process of producing seed crops, which presents annual variation and synchronicity among individuals (Pearse et al. 2021). Even in forest trees species the reproduction show large variation within and between populations (Caignard et al. 2019), the masting features are heritable (Bogdziewicz et al. 2020a). The importance of the masting events is related to both forest management and conservation strategies (Chiavetta and Marzini 2021). For example, anticipating masting dynamics could be beneficial for forest management, both in respect to the seed production or to adequate forest planning in response to climate change (Chiavetta and Marzini 2021). In European beech (*Fagus sylvatica* L.) stands, at a large scale, within-species synchronicity between the regions has been reported, while at the population level, a within-plot synchrony higher than in other species (e.g. oak, pine) has been found (Nussbaumer et al. 2016). Recent studies presented a masting spatial synchronization with few underlying climate factors (temperature, rainfall) (Vacchiano et al. 2017, Bogdziewicz et al. 2021). Temporarily, different masting patterns are suggested: a general biennial return (Nussbaumer et al. 2016), a full 5-year cycle (Hilton and Packam 2003), and a mean return between 3.2-3.9 years, based on a long-term series of data (Drobyshev et al. 2014). The main reported factor of influence, especially in large-scale studies, is the temperature, but other factors, are also precipitation (June–July of the before year, Bogdziewicz et al. 2020a), stand structure or stand age (Müller-Haubold et al. 2015), drought (Piovesan and Adams 2001), spring latefrost or wet conditions during the pollination period (Chiavetta and Marzini 2021) seem to have lesser positive or negative influence on masting. Specifically, the reported influences related to masting occurrence refer to the summer temperatures (June-July maximum) of the preceding two years and the preceding year (Lebourgeois et al. 2018, Bogdziewicz et al. 2020a, Chiavetta and Marzini 2021), which had similar precipitation, but combined with the spring requirements (a moist summer and a dry spring of the preceding two years and a dry summer of the preceding year). Moreover, it seems that the moist spring during the masting year is positively related with the seed crop (Bajocco et al. 2021).

Fagus silvatica L. is among the main species in Europe, being the most abundant deciduous and a base species in most forest ecosystems (Leuschner and Ellenberg 2017). It provides ecological, natural conservation and economic value, while in many European countries its wood is used as a primary forest resource (Goncz et al. 2018). The interest in different traits of European beech was supported recently by the development of a database including large-scale phenotypic measurements (217 provenances of the entire species range) (Robson and Garzón 2018), with observed traits related to size, phenology and mortality. This tried to answer to a constant need of increasing the knowledge on the genetic factors, both regarding traits of higher interest (adaptive, wood properties), or those which are more classical (growth, stem form) (Paques 2013). By carefully selecting appropriate populations, long-term forest breeding seeks to enhance the quantity and quality of replanting material that is available. The majority of breeding initiatives begin by selecting additional trees from stands of naturally occurring populations (Paques 2013).

This paper's aim is to analyze the main phenotypic and climatic characteristics which determine the masting of the beech trees from the selected forest genetic resources located at the eastern edge of the natural range. Selecting the best seed stands for planting is one of the most important choices, since it will affect the resulting forest, its long-term health, and preservation (Paques 2013).

MATERIALS AND METHODS

Study Sites and Measurements

This study was carried out in seven beech populations, included in "The National Catalogue of Basic Materials for the Production of Reproductive Forestry Materials" (Pârnuță et al. 2012). The stands were used as seeds sources, while the target of the breeding program was an increase of growth rate and stem straightness for wood production. The stands are distributed in the northern part of Romania, towards the eastern edge of the European beech range, within an elevation range of 360-1150 m, with ages between 105-180 years and canopy cover of 0.7-0.8 (Table 1). In each population, 30 plus trees were measured and observed, randomly selected from the upper canopy (the predominant and dominant classes, according to Kraft classification), on which different traits were estimated (size characteristics, presence of masting). The quantitative data were measured to the nearest centimeter (diameter at breast height – DBH) and decimeter (height, height before live crown, crown diameter). The crown diameter was calculated as an average of two perpendicular diameters of the crown projection, while the qualitative traits (masting intensity, canopy position) were assessed visually. Masting intensity was visually assessed in four classes, graded from absent to weak, good and abundant. Even though visual assessment is a subjective evaluation, in plus trees, such as our evaluated trees, it is one of the types of tree selection, together with the advanced statistical or model-based methods (Kim et al. 2020). All data were collected during autumn of 2010, which was a masting year.

In order to test the influence of different climate variables on the masting intensity, we used daily climatic data from European Climate Assessment & Dataset (Klein Tank et al. 2002). The gridded downloaded data - mean maximum (T_{max}), mean temperature (T_{mean}) and precipitation sum (P_{sum}), with the resolution of 0.1 degree - covering the period 2008-2010, were averaged as previously reported in the literature, as spring, summer and June-July values. Furthermore, the weather data corresponding to the years preceding masting were coded as (-2) - previous year 2008. As an alternative measure to quantify the joint effects of temperature and precipitation on masting, we also calculated the Ellenberg quotient (EQ):

$$EQ=1000\cdot\frac{T_7}{P_{sum}}$$

where T_7 is the mean July temperature, and P_{sum} the sum of annual precipitation, calculated based on Worldclim 2.0 data (resolution 30 s) (Fick and Hijmans 2017). Using the available thresholds of the EQ index for beech (Mellert et al. 2016), the populations were ranked from optimal to marginal (see Table 1).

Data Analysis

Since our dependent variable, masting intensity, has only four levels (absent, weak, good and abundant), we used linear ordinal models of cumulative probabilities with the proportional odds model (logit link). The ordinal models consider that the variable y has a logistic distribution whose mean depends on the predictors; because it cannot observe

Table 1. Characteristics of the seed stand populations.

Seed stand code	Name	Latitude (°)	Longitude (°)	Altitude (m)	Area (ha)	Trees age (years)	Canopy cover	EQ suitability
FA-A140-4	Sighet	47.85000	24.10000	470-620	28.2	110	0.7	optimal
FA-A120-22	Strâmbu Băiuț	47.61667	24.00000	840-1150	47.3	180	0.6	optimal
FA-A220-10	Râșca	47.30000	26.08333	360-430	50.4	160	0.7	intermediate
FA-A150-3	Tăuți Măgherăuș	47.66667	23.46667	360-580	33.6	105	0.7	intermediate
FA-A130-13	Târgu Lăpuș	47.45000	23.85000	670-900	25.2	130	0.8	intermediate
FA-G150-7	Dolhasca	47.38333	26.56667	580-830	22.0	130	0.8	marginal
FA-A240-2	Solca	47.60000	25.91667	460-520	18.6	105	0.8	marginal

Note. The data related to the seed stand populations are taken from the stand description of the forest management plans.

y directly, just which interval (−∞,c1],(c1,c2],(c2,c3],(c3,∞) it falls in, y is a latent variable. The above cut points (the "thresholds" part) are estimated by the model.

Both fixed and random effects were added to the model, with random effects more appropriate when the effect of a variable is expected to vary across different levels of other variables in the model (seed stand in our case), and with the fixed effects more appropriate when the effect of a variable is expected to be constant across different levels of other variables in the model.

We fit a cumulative mixed model to the data:

$$\mathrm{logit}(P(Y_i \leq j)) = \theta_j - \beta_k\,(\mathrm{covariate}) - u(\mathrm{population}_i)$$

with $i = 1, \ldots, n$, $j = 1, \ldots, J - 1$, $k = 1, \ldots, n$. This is a model for the cumulative probability of the i^{th} masting intensity falling in the j^{th} category or below, where i indexes all observations and $j = 1, \ldots, J$ indexes the response categories ($J = 4$). $\{\theta_j\}$ are threshold parameters, the statistically cut-points estimated by the model. The population effects were considered random, and we assumed that its effects are IID normal: $u(\mathrm{population}_i) \sim N(0,\sigma_u^2)$. The model was fitted with the function clmm from the package ordinal of R, which is used for fitting CLMMs for ordinal outcomes with random effects for the intercept and/or slope.

We considered the model with only random effects as the null model, the model with climatic covariate (temperature and precipitation of 2008-2010 spring, summer and June-July values and EQ) as the climate model, the model including both phenotypic (DBH, height, crown diameter, canopy position as predominant and dominant), and the above climate covariables as the final model. The percent of variation explained by the random effects was determined by the intraclass correlation coefficient (ICC) and explained it by its value: when zero (or close to zero) suggests that the observations within groups are no more similar than the observations from different groups, making the design of random effects not necessary. In order to select the best model, we performed a selection based on Akaike information criterion (Akaike 1974), Akaike weights and delta AIC (Burnham et al. 2011). In the comparison of all the models, the model with the lowest AIC value is deemed to be the best. As in the 'climate' model, we found also higher correlations among the climate data (Pearson r > 0.8). The search was limited to models including just one of the climatic parameters. The search for the best model was conducted with the function dredge from package MuMIn in R (Bartoń 2024).

To verify the proportional odds assumption, which states that the odds ratios remain constant and that the ordinal dependent variable and the independent variables consistently correlate across all categories, we performed a test on the final model. In order to test this proportional odd assumption, we compared the model fitted under the null hypothesis (parallel effects) with the corresponding model fitted under the alternative hypothesis (non-parallel effects for contact) using a likelihood ratio (LR) test. We then compared these models using the function Anova from R (R Core Team 2024), which runs the LR test. All data were processed with the package ordinal from R (Christensen 2023).

RESULTS

From the variables included in models, the masting presented different degrees of abundance, from sites with all trees having abundant masting (Sighet) to stands with all trees having weak masting (Tăuți Magherăuș) (Table 2). As for social position, most of the stands contained upper layer (predominant) trees. The mean DBH was 55.5 ± 8.3 cm, while crown diameter was 9.1 ± 1.9 m. The average summer maximum temperature two years before masting was 24.8°C.

The best models had as covariates the maximum summer temperature two years before (the climate model), namely EQ, canopy position and crown diameter (the final model) (Table 3). The overall goodness-of-fit of the final model was higher, with the model explaining 76% of the variability in masting intensity, of which 54% is attributable to the fixed effects. By fitting the random effects, which are in latent scale, we considered that the latent ordinal data are subject to the additional random variations due to the grouping of trees in populations (the seed stand). The adjusted ICC was 0.475, which suggests a moderate proportion of the total variation in the masting intensity due to population.

Table 2. Descriptive statistics of the data included in models.

Population	Masting (%)				Canopy position (%)		DBH (cm)		Crown diameter (m)		(-2)summer maximum temperature (°C)
	Absent	Weak	Good	Abundant	Predominant	Dominant	Mean	Stnd. Dev.	Mean	Stnd. Dev.	
Sighet	0	0	0	100	77	23	49.3	7.7	8.7	1.8	24.6
Dolhasca	7	30	33	30	60	40	57.4	7.0	8.4	1.6	26.7
Rasca	0	57	43	0	53	47	61.7	9.3	10.2	1.6	24.0
Solca	0	0	37	63	83	17	48.1	6.0	9.3	2.4	24.9
Strâmbu Băiuț	0	10	37	53	50	50	62.1	11.9	10.0	1.8	21.4
Târgu Lăpuș	0	0	20	80	67	33	61.1	7.8	9.0	2.3	25.5
Tăuți Magherăuș	0	100	0	0	70	30	48.8	8.3	8.3	1.9	26.6
Mean	1	28	24	47	65	34	55.5	8.3	9.1	1.9	24.8

Table 3. Summary of masting intensity models.

	Final model (coefficient, interval of variation, p-value)	**Climate model** (coefficient, interval of variation, p-value)	**Null model** (coefficient, interval of variation, p-value)
Missing|Weak	-10.525	-20.192	-7.559
	[-14.391, -6.658]	[-53.918, 13.534]	[-10.416, -4.701]
	(<0.001)	(0.241)	(<0.001)
Weak|Good	-4.481	-14.058	-1.953
	[-7.824, -1.139]	[-47.618, 19.501]	[-4.203, 0.298]
	(0.009)	(0.412)	(0.089)
Good|Abundant	-2.021	-11.593	0.292
	[-5.305, 1.262]	[-45.126, 21.941]	[-1.934, 2.518]
	(0.228)	(0.498)	(0.797)
EQ Intermediary	-4.095		
	[-7.650, -0.540]		
	(0.024)		
EQ Marginal	-6.608		
	[-10.528, -2.689]		
	(<0.001)		
Canopy - dominant	-1.317	-1.318	
	[-2.029, -0.604]	[-2.029, -0.608]	
	(<0.001)	(<0.001)	
Crown diameter	0.190	0.192	
	[0.008, 0.372]	[0.011, 0.373]	
	(0.040)	(0.038)	
(-2) Maximum summer temperature		-0.534	
		[-1.879, 0.811]	
		(0.437)	
SD (Intercept)	1.725	2.946	2.889
Num. obs.	210	210	210
R^2 Marginal	0.538	0.107	0.000
R^2 Conditional	0.757	0.755	0.717
AIC	295.7	300.9	315.5

Abbreviations: EQ – Ellenberg quotient, SD – standard deviation, Num. obs. – number of observations, R^2 – coefficient of determination, AIC – Akaike information criterion.

The comparison of the models fitted with parallel effects and non-parallel effects indicated that there is no evidence of non-parallel slopes in our model (likelihood ratio tests p = 0.00021 for Kraft class, p = 0.037 for crown width, and p = 0.021 for EQ suitability). When calculating the relative importance and dominance among the variables determining mast intensity, canopy position has the main importance (52%), followed by site EQ suitability (29%) and crown diameter (19%) (Figure 1). The same order was also observed in the relative dominance of each covariate: EQ is dominated by crown diameter and canopy position, while crown diameter is dominated by canopy position.

The predicted probabilities of the final model (Figure 2) indicate that on the optimal EQ sites, irrespective of canopy position or crown diameter, there is full abundant masting. On intermediate sites, the masting pattern seems to be the same, but with lower probabilities for the dominant trees. A higher probability of weak masting will be on marginal sites, especially for the dominant trees. The probabilities of the difference in crown diameter between narrow and large tree crowns amount to about 25% in abundant masting of predominant trees and weak masting of dominant trees on intermediary EQ sites, as well as weak and good masting of predominant trees from marginal EQ sites.

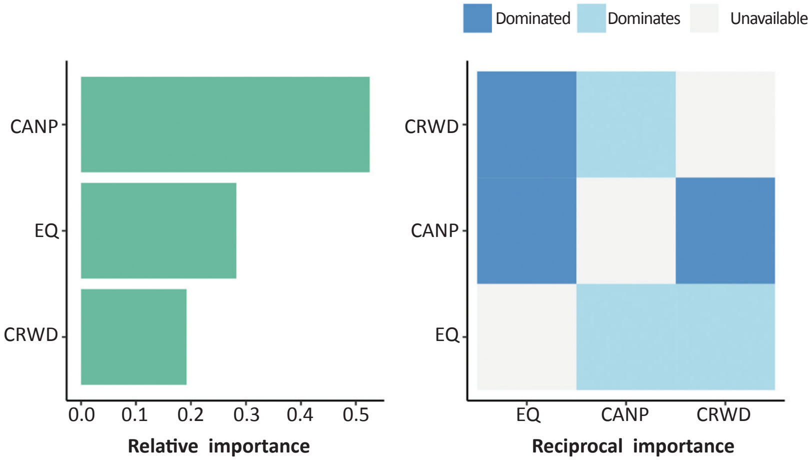

Figure 1. Relative importance of the covariates included in the final model: CANP – canopy position (predominant and dominant trees), EQ – Ellenberg quotient, CRWD – crown diameter.

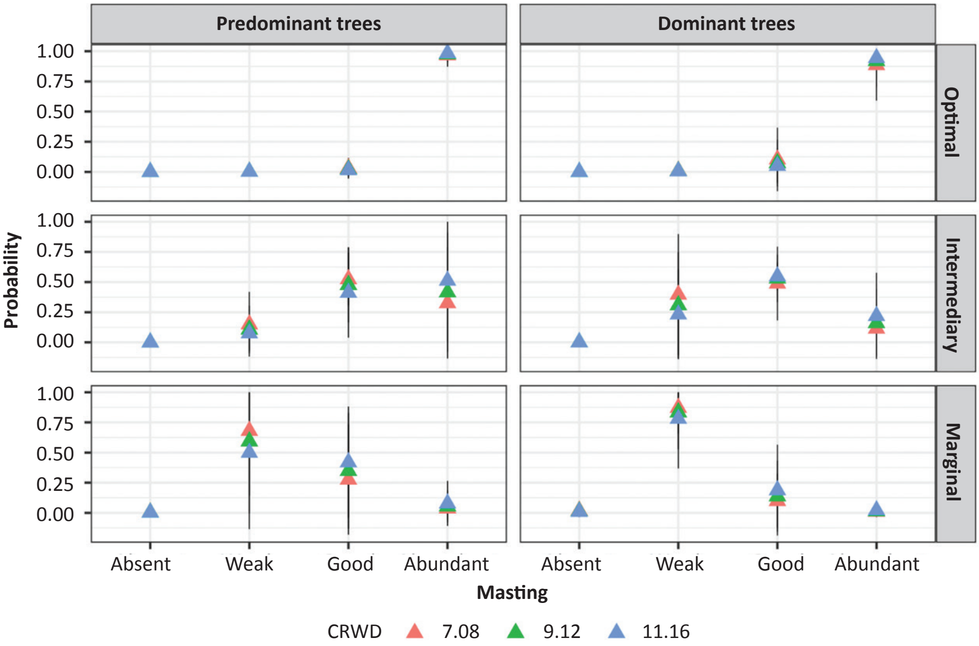

Figure 2. Probabilities of masting intensity function of canopy position (predominant, dominant trees), EQ suitability (optimal, intermediary, and marginal) and crown diameter (CRWD).

DISCUSSION

Our work identified the main covariates that influence masting in beech mature seed stands from Eastern Carpathians. Previous models separated the entire beech distribution in regard to masting into three clusters (into northern, southern, and a separate branch in Eastern Europe) (Vacchiano et al. 2017). The differences between these studies, conducted especially at large scale vs. at a regional or local scale (our study), are related to the way of computing the realized ecological niche of the species, which is a matter of spatio-temporal scale. The whole distribution range refers to the entire niche, while the others can be just partially realized niches.

Our study suggested a moderate effect of the seed stand - the within-plot masting synchrony, in line with studies indicating to be higher in beech than in other species (Nussbaumer et al. 2016). A positive relationship between the amount of leaves in the canopy and fruit production has been reported before (McCarthy and Quinn 1992), while Camarero et al. (2010) found in *Quercus ilex* that seeding may be regarded as the consequence of the gradual increase of canopy foliage. Nevertheless, stand characteristics (structure, stand age) have been found to have less influence on the masting intensity (Müller-Haubold et al. 2015). Our data support the first findings, where the predominant trees, higher in size than the dominated trees, with larger crowns, will present a higher masting intensity probability. Some studies related the masting occurrence to the summer temperatures or precipitation of the preceding years (Lebourgeois et al. 2018; Chiavetta and Marzini 2021), coupled with some specific requirements during spring (e.g. moist springs positively correlated with the abundance of seed crops) (Bajocco et al. 2021). The mean July temperature and annual precipitation may be summarized in terms of climatic aridity using Ellenberg's climate quotient (EQ; Ellenberg 1988). In statistical modelling of climate change, EQ has been rediscovered as an important proxy (Mellert et al., 2016). We found the EQ to be the second factor in determining the masting of beech in the studied stands and a decrease in masting intensity towards the aridity sites, with EQ better explaining the masting intensity than the summer maximum temperature two years before, as pointed the literature (Lebourgeois et al. 2018; Bogdziewicz et al. 2020a; Chiavetta and Marzini 2021). Our work is based on one year of observation data and this could be seen as a drawback of the study; however, the final results include some stand structure characteristics and the threshold values of the EQ index as masting determinants, based on the long-term combination of precipitation and temperature (the Worldclim data), with the related temporal variability included.

Furthermore, other climatic studies (Mátyás et al., 2010) indicated the EQ as one of the most differentiating and consistent predictor factor, which could contribute to the way of carefully selecting the seed stands for the replanting material. Apart from obtaining seeds from areas which can be classified according to aridity by an easy index, their further planting will consider the ecological areas located in similar conditions as the seed stands (Paques 2013). Greater selection will lead to more variation and synchronization of masting over time since masting traits are heritable. This, together with information on habitat appropriateness, will help in the identification of cultivation risks that might result in: (i) shortened life spans, (ii) restricted regeneration, (iii) diminished competitiveness, and (iv) increased susceptibility to biotic hazards. Our results suggest species cultivation on higher habitat appropriateness, as opposed to those that are closer to their niche boundary (Mellert et al., 2016).

CONCLUSIONS

At a local scale, masting is controlled by stand and weather factors, among which the most important are the canopy position and the crown diameter, together with a surrogate measure for aridity, the Ellenberg quotient. Known as a factor limiting the beech distribution, the EQ seems also to be determinant in masting intensity at stand level more than other climate factors. The identified parameters are suitable for selecting accordingly seed source forest stands to be used in afforestation programs.

Author Contributions

MT, CE, AB, MCT conceived and designed the research, MT carried out the field measurements, MT and MCT processed the data and performed the statistical analysis, MT secured the research funding, supervised the research and helped to draft the manuscript, MT, EC, AB and MCT wrote the manuscript".

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Conflicts of Interest

The authors declare no conflict of interest.

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