Effect of tree age on masting signal in tree-ring chronologies of beech in southern Sweden

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Master's Thesis • 30 credits
Swedish University of Agricultural Sciences, SLU
Southern Swedish Forest Research Centre
Sustainable Forest and Nature Management (SUFONAMA)
Alnarp 2023

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Credits:	30 Credits
Level:	Second cycle, A2E
Course title:	Master's Thesis in Forest Science
Course code:	EX0984
Programme/education:	SUFONAMA Master's Programme
Course coordinating dept:	Southern Swedish Forest Research Centre
Place of publication:	Alnarp
Year of publication:	2023
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Keywords:	beech, masting, masting signal, proxy, tree-ring chronologies, age, dominance, social position, southern Sweden, climate change, tree growth, regeneration success

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Abstract

Masting is a synchronous and highly variable production of seeds in tree species. Masting may reflect a reproduction strategy to cope with seed predation. In beech, temperature is the cue controlling annual variability in seeding.

Masting behaviour in beech typically begins around the age of 40 years. This is however based on observations and therefore lacking a formal statistical approach. It is unknown if beech trees younger than 40 years exhibit masting signals in their ring width chronologies. By considering potential masting signals in ring width chronologies, possible underused data can be included to better understand the relationship between environmental variability and seed production. Ring widths can furthermore act as a proxy for the dominance of a tree. More dominant trees may express less pronounced and later occuring masting signals due to their greater accessibility to resources.

This study aimed to 1. Assess the age of appearance of masting signals in tree-ring chronologies of beech in southern Sweden 2. Evaluate the effect of social position on (the onset of) masting signals.

Ring widths were used as a proxy for masting signal and dominance in beech trees. A masting record from a previous study in the same area was used to measure the effect of identified masting years on ring widths, with smaller ring widths indicating a stronger effect of masting. The effect of age and dominance on the expression of masting signal in non-seed producing trees was evaluated by considering the effect of environmental conditions during identified masting years on radial growth. Mixed effect models were developed in Rstudio with a nonlinear model being most suited for this research to capture complexity between variables.

The nonlinear mixed effect model ultimately showed that the onset of masting signal in beech tree ring chronologies in southern Sweden occurs when the cambial age of tree at the breast height (the height at which the growth data were collected) is above 20 years. Samples in this study were obtained at 1.3 m height and thus lack information on the tree growth starting at ground level.

Keywords: beech, masting, masting signal, proxy, tree-ring chronologies, age, dominance, social position, southern Sweden, climate change, tree growth, regeneration success

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1. Introduction

1.1 Defining masting

Masting is a synchronous and highly variable production of seeds in tree species [1]. Seed predation was a likely factor promoting appearance of masting during evolution [2], [3], designed to optimize resource allocation into sexual reproduction [4], [5]. The variability of seed production during masting is driven by weather variation [6], [7]. Annual variability in masting behaviour is mainly controlled by temperature [8], [9].

1.2 Relating mast years to temperature

Masting is found in many temperate tree species such as in the genus *Fagus* [1], [2]. The European beech (*Fagus sylvatica* L.) is a well-studied tree species across Europe [3]–[7]. A pan-European study on beech masting found that the difference in growing season temperatures between the two preceding years (DeltaT) strongly influence seed productivity in the focal year [8]. A cool and moist summer two years before a masting event (Y-2) causes a low evapotranspiration demand favourable for growth, which may result in resource accumulation. A warm year immediately prior to the mast year (Y-1) initiates a shift in meristeme differentiation towards sexual meristems [9], [10]. Accumulated resources in flower buds from Y-2 can therefore boost nut production in Y when the tree switches to reproduction [8]–[10].

1.3 Frequency of mast years

A study focussed on southern Sweden found that the occurrence of beech masting events is best predicted by the sum of growing season temperature instead of temperature regimes in specific parts of the growing season, such as June and July [10]. For southern Sweden, an increase in annual average temperature, summer days[1] and associated increase in the frequency and intensity of heatwaves is predicted [11], [12]. An increase in beech masting frequency in southern Sweden is therefore anticipated and already observed over the past 2-3 decades [13]. However, the recent increase in mast year frequencies may be temporal [9]. A century-long chronology of beech masting in Southern Sweden shows large variability in masting frequencies [9].

1.4 Impact on regeneration and stem growth

Significant seed fall during masting can support successful natural regeneration and hence lower management costs [10], [13], [14]. Thus, increasing temperatures with a greater variability in temperatures between years (deltaT) triggering masting may be beneficial for beech management costs in southern Sweden. However, an increase in the frequency and intensity of heatwaves in southern Sweden could result in failing fruit development after successful pollination in spring [15]. Other environmental conditions such as hailstorms and strong winds can damage beech flowers with fuit development equally failing [16], [17]. Both heatwaves and other environmental conditions may exert a ‘cancelling’ effect on masting events to occur [9]. Furthermore, increased masting frequency due to increased summer temperatures may result in reduced sensitivity of masting to weather cues [18]. This may cause less synchronous flowering which could lead to a pollination deficiency [18], [19], with a resulting regeneration failure and eventual increase in management costs of beech stands [18].

The allocation of resources to seed production during masting years may result in reduced ring-width increments for beech in southern Sweden (Drobyshev et al., 2010, 2014). The high carbon demand into fruit production during masting is not likely to affect stem growth and timber production since beech trees are resilient in growth [20] but see [13], [21]. An increase in extreme weather conditions such as heatwaves together with an increase in masting frequency, as expected for southern Sweden, may however result in a reduced stem growth [20], [22].

Predicting the occurrence of masting events based on weather conditions on a regional scale, and the influence of masting on successful regeneration and stem growth, is therefore of value for the management of beech stands in southern Sweden [9], [10], [14], [18], [23].

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[1] Summer day: daily maximum temperature above 25 ° C as defined by the SMHI [11]

1.5 Relating mast years to tree age

Dynamics of tree rings exhibit masting signals [14]. During masting the tree allocates its resources to seed production rather than stem growth [10]. Hence, year rings during masting years are smaller compared to non-masting years [10], [14]. Beech masting (vast amounts of seed production) generally occurs from the age of 40 years [24], however this threshold has not been developed using a formal statistical approach. Hence, it is yet unknown how environmental conditions (deltaT) corresponding to identified mast years[2] (if any) affect the growth of non-seed producing trees. By studying tree ring widths, potential masting signals can therefore be detected in non-seed producing beech trees.

Previous studies have mainly studied effects of weather conditions and climatic change on masting [25] . The effect of a tree age (aging) on masting has mainly been ignored so far [25]. Two recent studies reported that the intensity and temporal variability of seed production increased in larger trees (a proxy for tree age), hinting that aging may be an important driver of masting behaviour [26], [27]. A study in north-western France found an increased allocation toward reproduction (seeds and cupules) with an increasing age [28]. Beech trees from 30 years showed a substantial amount of seeds produced [28]. The study furthermore found traces of viable seed production from 14-year old stands [28]. Older and larger trees usually show stronger masting signals with more seed production, yet the relationship between age and masting remains poorly understood [25]. Other studies, for example, have found inconsistent patterns of seed production with tree size, suggesting that changes in reproductive effort are more likely to be stage- rather than age-related [29], [30]. A study in Poland found that over the last five decades, the effect of aging on seed-producing trees was much stronger than abiotic factors such as high temperatures, despite a sharp increase in droughts [25]. Tree age could thus be an important modifier of growth response to masting.

Following this rational, this study will assess from which age masting signals occur in tree-ring chronologies of beech in southern Sweden.

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[2] This study elaborates on a partial reconstructed masting record (see for further specifications section 4.4). Non-seed producing trees in this study are hence assessed based on environmental conditions (deltaT) associated with identified masting years.

1.6 Social position

A trees social position may affect the onset of masting signals and masting signals itself. More dominant trees could exhibit wider ring widths reflecting an increased growth due to their greater accessibility to resources, such as water, nutrients and light radiation [31], [32].

However, extreme weather conditions can reverse this pattern into dominant trees expressing smaller ring widths [31]. Dominant trees may be more prone to extreme weather conditions due to their large tree crown that are more sun exposed [31]. This could become observable in southwestern Sweden considering the expected further increase in heatwaves due to climatic change. Trees in this study were sampled in 2004 and are therefore expected to be less affected by extreme weather events which are occurring with a higher frequency and intensity in more recent years.

2. Relevance & Research Focus

Masting of European beech (Fagus sylvatica L.) has mainly been studied in relation to temperature and climate change. Changing climatic conditions may affect tree growth and regeneration success of beech with an increased frequency of masting and extreme weather events. The effect of tree age on masting in European beech is less studied, especially for younger beech trees. The observed onset of masting in European beech at the age of 40 years has not yet been developed with a formal statistical approach. Aging is furthermore reported as a potential important driver of masting behaviour. By considering potential masting signals in ring width chronologies, possible underused data can be included to better understand the relationship between environmental variability and seed production.

Therefore, this study evaluates the onset of masting signals in European beech with a focus on southern Sweden to narrow down the scope of this research. This study further includes the effect of a trees social position on the onset of masting signals and on masting signals itself. More dominant trees are more likely to express wider ring widths. Hence, this may affect (the onset of) masting signals.

Therefore, assessing the onset of masting while considering a trees social position may ultimately lead to a better understanding of the effect of temperature and climatic change on beech masting behaviour with related tree growth and regeneration success.

3. Research Aim & Questions

My main research objective was to:

Assess the age of appearance of masting signal in tree-ring chronologies of beech in southern Sweden.

Therefore I used ring widths as a for masting behaviour in combination with a masting record for Southern Sweden. To achieve this aim, I formulated as main research question:

From which age does a masting signal appear in tree-ring chronologies of beech in southern Sweden?

The effect of a trees social position may affect the (onset of) masting signal as well. More dominant trees are likely to respond differently in their radial growth due to a greater accessibility to resources essential for growth (sunlight, water, nutrition). Hence, tree dominance could influence masting patterns,

resulting in the second research objective:

Evaluate the effect of social position on (the onset of) masting signal.

With the second question:

How does the social position influence (the onset of) masting signals?

I expected

- The appearance of a negative onset of departures in ring width, associated with identified mast years, for trees from age 30 with an increasing signal towards age 40 of observable nut production.

- An earlier onset of negative departures in ring width, associated with identified mast years, for less dominant trees

4. Methods

4.1 Study area

Samples were collected in nature reserve ‘Biskopstorp’, positioned east of Halmstad in southwestern Sweden, county of halland. Samples were collected from 3 different sites (LT1, LT2, P12) with similar conditions in forest structure and composition, topography, soil, management history and climatic conditions. Biskopstorp is around 900 ha and almost completely covered by forest, of which around 30% broadleaved forest (beech and oak dominated). The region experiences a climate with pronounced oceanic influence, featuring mild winters and cool summers. The annual average temperature and precipitation is 7°C and 1,100-1,200 mm respectively. Average January and July temperature is -1.6°C and 15.5°C respectively. The topography of the area varies, ranging from exposed bedrock on hill sides to gently sloping terrain typically covered by sandy moraines of glacial origin [10], [33].

4.2 Sampling

Samples were collected in 2004. Trees were cored using a Haglöf increment corer for two radii at 1.36 m height. The samples were mounted on wooden support and polished up with 400-grit sandpaper to make year rings visually more distinctive from each other [10]. The prepared samples were subsequently scanned and stored as photographs, which were further used in this study.

4.3 Ring-width measurement, cross-dating and sample selection

I measured ring widths of 133 chronologies from the 3 different sites using CDendro and CooRecorder. Not all piths (first year of growth) were visible in the chronologies. I used the function ‘Set distance to pith’ to estimate the number of rings remaining to the pith. I cross-dated in CDendro using a reference chronology of a beech stand with a similar management history and site and climatic conditions closely located to the 3 stands considered in this study [10].

Out of the 133 chronologies, I selected 24 visually in CooRecorder that showed well distinguishable year rings. I choose for this visual method instead of a statistical method since the samples were from relatively young beech trees that show a great variability in their ring width patterns. The initial correlation test conducted with the reference chronology yielded low significance for many samples, even though they were accurately measured and dated. Consequently, I discontinued this method.

4.4 Data processing and statistical methods

In RStudio I loaded the 24 ring-width chronologies (RWL file) together with the masting record. This masting record was partially reconstructed and therefore not solely based on seed-producing trees [10]. A small proportion of the reconstructed masting record was based on ring widths. The results in this study are therefore partially subject to collinearity which should be considered when drawing conslusions.

I detrended the chronologies using the ‘dplR’ package and ‘Spline’ method with a 32-year window and a moderate smoothing of 0.5. I extracted the standardized growth values for each mast year for each curveID.

I computed average values for years prior and years after each mast year for each curveID as a representation of a trees social position (dominance). By computing the dominance for each mast year for each curveID, I was able to cover different growth conditions throughout a trees life cycle. I initially selected 5 years prior and after since this would likely cover the growth characteristics around a masting year. At a later stage I would test the effect of different windows prior and after the mast year on the model fit using mixed effect models and various metrices (section 4.7). I avoided collinearity by not including the standardized ring width value of the mast year itself.

I corrected the age per masting year by adding the ‘estimated number of rings to the pith’ to the “gross age” to obtain the “net age” for each sample. The “gross age” represented the age related to the last year ring measured in a chronology.

After assembling a data frame containing all variables, I performed the analysis using mixed effect models with the packages ‘lme4’ and ‘ggplot2’. I visualised the mixed effect models using various graphs and metrices which I further discuss in section 4.5-4.7.

4.5 Visual interpretation and model choice

Firstly, I plotted tree age against the observed standardized ring widths with a fitted regression line and associated confidence interval (CI). This served as a first preliminary impression of (non)linearity of my data.
I choose to compute the CI with a nonparametric method based on quantiles that allowed me to assess the uncertainty around the estimated population parameters without relying on specific distributional assumptions.

Based on this plot, I decided to compare linear and nonlinear models since the regression curve was slightly curved.

I generated a total of 11 mixed effect models differing in (in)dependent/random factors and in the years prior and after a masting year (window) for the calculation of the dominance (Table 1).

I decided to test mixed effect models (also known as multilevel or hierarchical models), since those allow to analyse data with nested or hierarchical structures (i.e., complex relationships). Mixed effect models extend the concept of linear regression by incorporating both fixed and random effects and can include multiple predictors.

The mixed effects result in a random intercept model, which means that each level of a random variable (i.e. single trees represented by their respective curveID) has a different intercept and possibly also a different slope/coefficient.

The formula behind the model, for a mixed-effects regression is as follows:
$f(x)=\alpha i+\beta ix+\epsilon$

- αi: intercept (α) per sample (i)
- βix: slope/coefficient of the regression line (β) per sample (i) for a certain predictor value (x)
- ϵ: the difference between the predicted values and actually observed values, i.e., error term

4.6 Models

*Table 1 – **Mixed effect models**.*
-Response (dependent factor): value.my (which is the ring width at a specific mast year for a specific sample
-Fixed effect (predictors/independent factors): value.dom (dominance), age.true (tree age)
-Random factors: curveID (sample), year (which is the masting year associated with a specific curveID and ring width), stand (location of sample)
-*Window:* the years prior and after a masting year as used in the calculation of the dominance

No.	Mixed Effect Model
1	Linear mixed effect model, 5-5 window, random factor (curveID)
	lmer (value.my ~ value.dom + age.true + (1|curveID)
2	Linear mixed effect model, 5-5 window, random factors (curveID, year)
	lmer(value.my ~ value.dom + age.true + (1|curveID)+ (1|year)
3-9	Nonlinear mixed effect models, 5-5/4-4/3-3/2-2/2-1/1-2/1-1 windows, random factors (curveID, year)
	lmer(value.my ~ value.dom + age.true + I(age.true^2) + (1 | curveID) + (1 | year)
10	Nonlinear mixed effect model, 3-3 window, random factors (curveID, year, stand)
	lmer(value.my ~ value.dom + age.true + I(age.true^2) + (1 | curveID) + (1 | year) + (1| stand)
11	Nonlinear mixed effect model, 3-3 window, random factors (curveID, year), autoregressive detrending
	lmer(value.my ~ value.dom + age.true + I(age.true^2) + (1 | curveID) + (1 | year)

Since ‘year’ (masting year) was associated with a specific curveID and ring width (i.e., unique combination), the nestedness of the model was included by summing ‘curveID’ and ‘year’ separately in the model.

The nonlinear model includes the quadratic term ‘I(age.true^2)’ that allows for a curved relationship between tree age and ring width, which can help to capture potential non-linear patterns in the data.

“CurveID” was included as random factor in all models since beech trees are known for showing a great variability in their growth patterns.
“Year” (masting years) was included as random factor in models 2-11. The random effect of ‘year’ was likely to exert a strong influence on the ring width since masting years vary greatly in intensity. The model fit would therefore likely significantly improve when included.
“Stand” was included as random factor in model 10 to include the variability between the different stands. The stands were however similar in growth conditions. Therefore, this would likely not or only slightly improve the model fit.

4.7 Metrics

To be able to compare the models on how well they would fit the data, I used various statistical methods (metrics). Each of these metrics provided different insights into the model's performance allowing me to assess the suitability of the models.

I used the Shapiro-Wilk test to indicate non-normal distributions (lower p-values), which is of importance since normal distributions are an assumption in regression analysis.
I used the Breusch-Pagan test that tests for heteroscedasticity in a linear regression model and assumes that the error terms are normally distributed. Heteroscedasticity would indicate a “healthy” model since this reflects no or minimal increase of the errors/residuals with an increase of the predictor(s).
Heteroscedasticity is indicated by lower p-values and its contradictor (homoscedasticity) by higher p-values.
I used the AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) that both measure the model fit to the data (lower value = better fit), but differ in the penalty term for model complexity. The penalty term for AIC is calculated by multiplying 2 with no. parameters and for BIC by multiplying the logarithm of the sample size with no. parameters. A model is more complex when this includes more parameters, which is the nonlinear model in this study. Hence, I expected that the nonlinear models would have a higher AIC and BIC indicating a lower model fit due to its higher complexity with added parameter ‘*age.true^2*‘.
I used the Marginal and Conditional R-square that measures the proportion of variance explained by the models. The Marginal R2 considers fixed effects only. The Conditional R2 considers both fixed and random effects.
I used the ICC (Intra-Class Correlation) that measures the proportion of variance in the response variable that is due to the variation between different groups or clusters (random effects).
I used the Chi-square ANOVA test to compare the fit of the models on the data. The chi-square values serve as an indicator of how well the models fit the data.

4.8 Model choice

Based on the metrices, I decided to follow the mixed effect model with a 3-3 window for the dominance, random factors “curveID”/”year” and standardized ring width values based on the Spline method.

4.9 Visual Inspection

I further visually studied the models performance using various plots.

4.9.1 QQ plots

Regression assumes that residuals are e.g., normally distributed. Hence, I firstly tested whether the model was normally distributed with residual (QQ) plots. Deviations of data points from the reference line indicate for which values the model is less good in predicting.

4.9.2 Marginal effect plot

I plotted a marginal effect plot with the function ‘ggpredict’ that calculates predicted values of the response variable for different values of the predictor variable, while holding all other variables in the model constant. The plot contained both predicted data points, the marginal regression line and associated confidence intervals (computed with the Profile Likelihood method) for the marginal effects of the predictor variable.

4.9.3 residuals vs. fitted values plot

I plotted residuals against fitted (predicted) values. The fitted values represent predicted response values (ring width) for each observation (curveID i.c.m. masting years) based on the estimated model parameters (ring width, dominance, tree age, curveID, masting year). The residuals represent the difference between the observed response values and fitted values. I standardised the residuals using the Pearson method, which divides each residual by its estimated standard deviation, resulting in residuals with a mean of zero and a standard deviation of one. The plotted point cloud reflects a healthy model when being unstructured. A structured funnel shaped cloud instead would reflect an increase of the errors/residuals with an increase of the predictor(s).

4.9.4 Box plots by year

I created box plots of ring width by masting year to visualize the effect of masting years upon growth. I interpreted different intensities and frequencies of masting years by comparing the box plots on interquartile ranges, medians and potential outliers.

4.10 Dominance

To answer the second question “*How does the social position influence (the onset of) masting signal?”,* I plotted the marginal effect of dominance on predicted ring widths. This allowed me to asses the relationship between a trees social position and ring widths during masting years. I computed dominance by averaging the 3 years prior and 3 years after each masting year for each curveID.

To assess the effect of a trees social position on the onset of masting signal, I selected dominant and codominant trees. I set a threshold for the dominance values by grouping the dominance values from low to high. Then I selected the dominance value with an equal amount of dominance values above and below (i.e., the median of the number of rows). Trees below this threshold I listed as codominant and trees above I listed as dominant. This allowed me to plot the effect of (co)dominant trees ages on observed related ring widths.

5. Results and Discussion

5.1 Trend in relationship between age and growth.

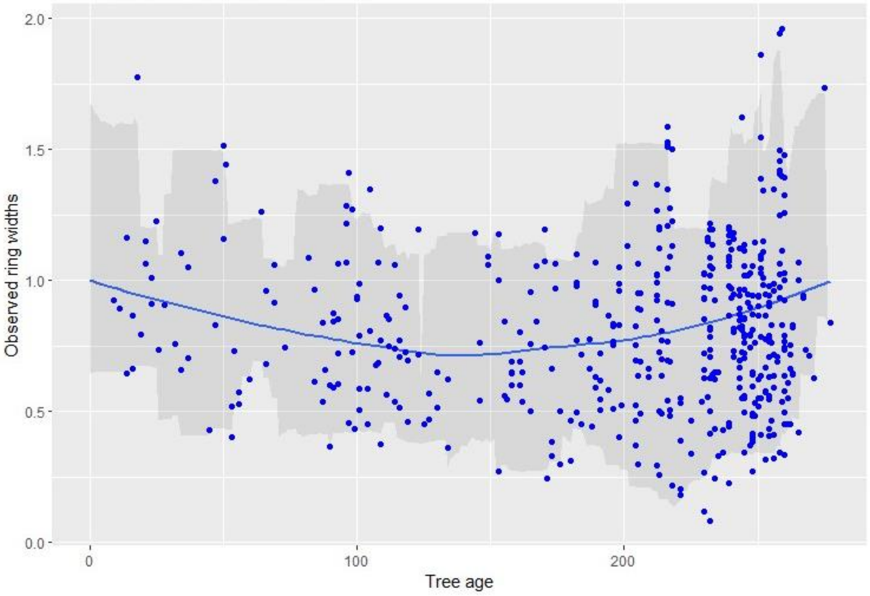

Figure 1 – Tree age vs observed ring width. Visible is a minor nonlinear trend (blue line) between tree age and ring width. Grey area: confidence interval (CI). Blue dots: original data points. Mind: ring width considers standardized values.

Figure 1 shows a stronger negative growth response during masting years up to age 150 with an increasing age, after which the pattern appears to reverse. This considers a nonlinear trend between tree age and observed ring width values for masting years. The bending of the curve is minimal and should therefore be considered critically when making assumptions about (non)linearity. Hence, in the section below I compare various metrics of linear and nonlinear models to determine the most appropriate model for this research.

5.2 Metrics interpretation and model selection

Table 2 – metrics interpretation

See Table 1 for a further specification on the models

Shapiro-Wilk test indicates non-normal distributions (lower p-values).

Breusch-Pagan test indicates heteroscedasticity (lower p-values) or homoscedasticity (higher p-values) for the variability of the model residuals.

AIC (Akaike Information Criterion) and BIC (Bayesian Information Criterion) both measure the model fit to the data (lower value = better fit), but differ in the penalty term for model complexity. A model is more complex when this includes more parameters, which is the nonlinear model in this study. Mind the minor and negligible differences between the fit_year and nonlinear models. Numbers between brackets state values from the models without “openness” as second predictor.

Marginal and Conditional R-square measure the proportion of variance explained by the models. Marginal R2: fixed effects only. Conditional R2: both fixed and random effects.

ICC (Intra-Class Correlation) measures the proportion of variance in the response variable that is due to the variation between different groups or clusters (random effects).

Chi-square p-values between Linear.55 and Linear.55.year (1.92e^{-13}) and between Nonlinear.33 and Nonlinear.33.stand (0.07).

x	Model	Shapiro-Wilk	Breusch-Pagan	AIC	BIC	Marginal R2	Conditional R2	ICC	Chi-square
1	**Linear.55**	1.31e^{-2}	2.83e^{-2}	96.88	117.14	0.220	0.223	0.00	-
2	**Linear.55.year**	2.81e^{-3}	8.52e^{-2}	43.46	67.78	0.249	0.430	0.24	1.92e^{-13}
3	**Nonlinear.55**	1.65e^{-2}	1.17e^{-2}	64.51	92.88	0.261	0.437	0.24	3.26e^{-2}
4	**Nonlinear.44**	3.15e^{-2}	4.51e^{-3}	106.75	135.00	0.184	0.346	0.20	-
5	**Nonlinear.33**	4.20 e^{-2}	5.07 e^{-2}	**55.06**	**83.43**	0.239	0.418	0.24	-
6	**Nonlinear.22**	1.78e^{-2}	5.26e^{-3}	82.04342	110.375	0.227	0.404	0.23	-
7	**Nonlinear.21**	6.86e^{-5}	2.86e^{-2}	85.21	113.90	0.255	0.457	0.27	-
8	**Nonlinear.12**	2.05e^{-5}	6.80e^{-4}	64.45	93.23	0.297	0.469	0.24	-
9	**Nonlinear.11**	5.14^{-5}	1.33e^{-3}	80.30	109.01	0.268	0.465	0.27	-
10	**Nonlinear.33.stand**	2.70e^{-2}	4.40e^{-3}	108.24	140.53	0.163	0.339	0.21	0.948
11	**Nonlinear.33.ar**	1.00e^{-12}	1.16e^{-4}	265.84	294.89	0.202	0.396	0.24	-

The metrices show a significant improvement of the models when “year” is included as a random factor as indicated by a Chi-square of 1.92e-13 when comparing model 1 with model 2. A nonlinear model instead of a linear model results in a further significant improvement as indicated by a Chi-square of 3.26e-2.

The selection on a nonlinear or linear model for this research I ultimately base on how well it captures the research question. To assess the appearance of masting signal it would be more appropriate to choose a nonlinear model that can capture more complex relationships between variables, allowing for a more flexible representation of the data. Various patterns and relationships (related to e.g., environmental factors such as temperature, resource availability such as nitrogen and phosphorus, physiological processes such as hormonal coordination) have been reported in masting behaviour and its underlying mechanisms [10], [14], [34]. Therefore, a nonlinear mixed effect model is most appropriate.

Based on the metrices I select the nonlinear model with a window of 3 years prior and 3 years after a masting year and random factors “curveID” and “year” as most suitable. The model shows low AIC and BIC values indicating a strong model fit to the data. The Shapiro-Wilk and Breusch-Pagan tests show comparable values with the other models. The conditional and marginal R-square show comparable or higher values than the other models. I ultimately select the nonlinear mixed effect model with a window of 3-3 since this allows me to capture the dominance of a tree around a masting year. Narrowing down the window could result in not capturing the dominance as a complete measure. Expanding the window could result in capturing a trees social position for other parts of their life cycle.

Including “stand” as a random factor in the 3-3 window mixed effect model (model 10) is on overall adverse considering the various metrices results. Using an autoregressive method to compute the standardized ring widths instead (model 11) showed equal adverse affects the models performance.

Hence, I further assess the mixed effect model with a 3-3 window for the dominance, random factors “curveID”/”year” and standardized ring width values based on the Spline method (model 5 indicated in red).

5.3 Visual interpretation

5.3.1 QQ plot

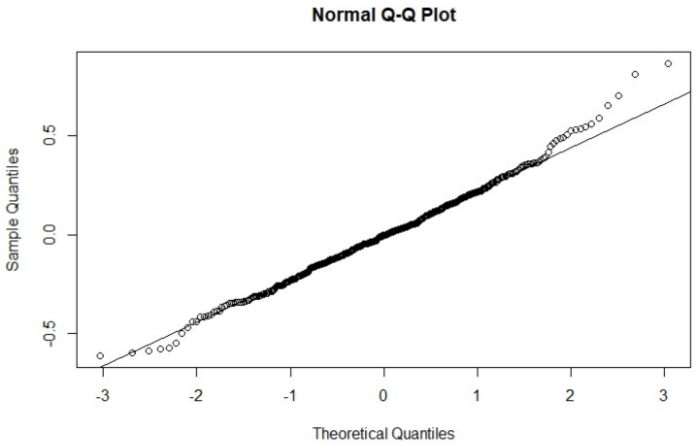

Figure 2 – Residual plot of the selected nonlinear mixed effect model.

The QQ plot shows that the data points follow the reference line closely, which suggests a normal distribution of residuals. Hence, the assumption of normal distributions for residuals in regression is met.

The deviations from the reference line at the bottom and top indicate that the model is good at estimating values around the middle range of ring widths but less good in predicting at lower or higher values.

5.3.2 Residuals vs. Fitted values plot

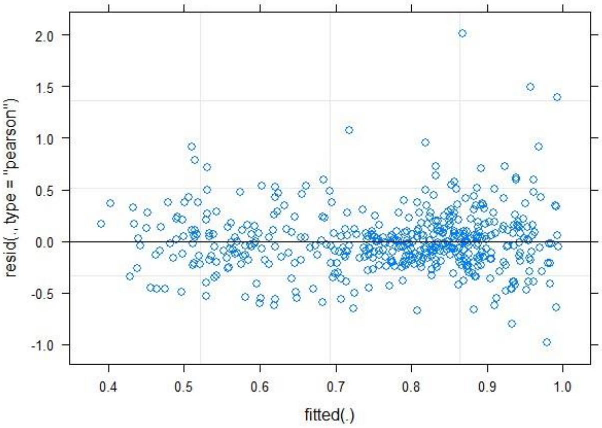

Figure 3 - Residuals vs. fitted values plot for the selected model.

The residuals vs. fitted values plot shows a rather structured point cloud. However, the cluster is still relatively unstructured when compared to a “true” structured funnel-shaped point cloud. Hence, based on the level of heteroscedasticity, the selected model is still suitable.

5.3.3 Box plots by year

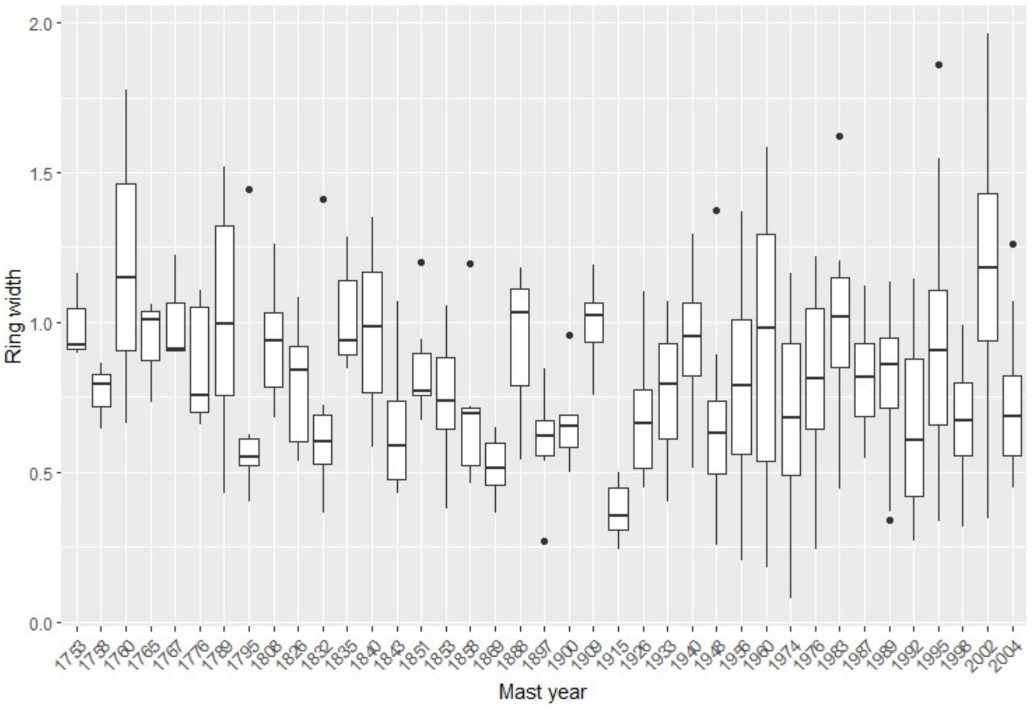

Figure 4 – Box plots of ring widths grouped by masting year. Visible is a varied pattern, which reflects different levels of growth response during masting years.

The variability in interquartile ranges and medians, with no clear pattern, and outliers may reflect different intensities and frequencies of masting years. The outliers can however also be a result of measurement errors. The box plots support the inclusion of masting years as a random factor in the selected model.

The variation in intensity and frequencies between masting years captures a large proportion of the variation observed in ring width patterns. This shows the effectiveness of the nonlinear mixed effect model used in this study, which incorporates the variation of multiple random variables.

5.3.4 Dominance

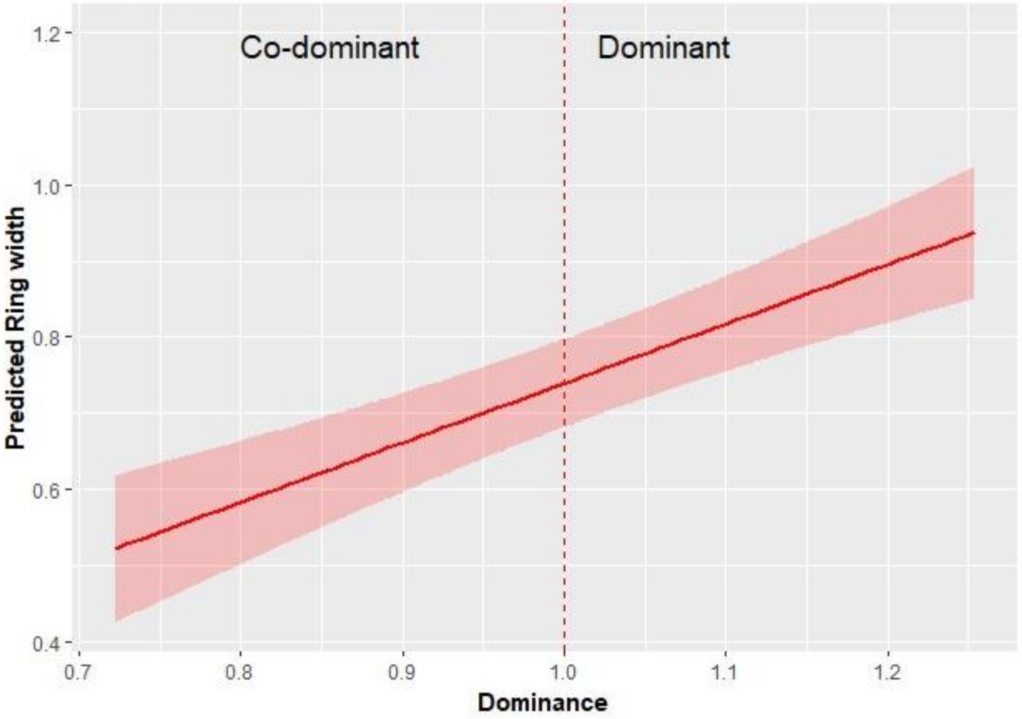

Figure 5 – Marginal effect of dominance on predicted ring widths. See section 4.10 on how the threshold for (co)dominant trees was selected.

The marginal effect of dominance on predicted ring widths shows a strong postivive relationship with an increasing dominance resulting in higher ring widths. This shows that more dominant trees show a larger ring width and therefore a weaker masting signal than codominant trees.

It should be noted however that the dominance in this study was indirectly retrieved based on ring widths. Future studies could record a trees canopy size to have a more direct proxy of dominance. Ring widths however may be able to capture more complex growth patterns and may therefore be more suitable as a proxy for a trees social position.

Figure 6 – Scatter plot of observed ring widths for (co)dominant trees.

Figure 6 shows an onset of masting signal for codominant and dominant trees at the earliest age, when looking at the regression curve. The confidence intervals however show a less clear pattern with onset of masting signal occurring at later ages. The codominant trees show a stronger negative deviation from the standardized mean line. This indicates that codominant trees could be more prone to masting as expressed in their ring widths.

Gap dynamics can modify the availability of resources and therefore may alter diameter growth of beech [35]. This study considered the dynamic nature of a trees availability to resources by expressing the dominance for a specific masting year for a specific tree, with related tree age. Microsite variation is furthermore found to affect light, temperature and soil moisture in ganopy gaps [36], which is embedded by considering tree specific dominance throughout masting years.

5.3.5 The effect of age on masting signal

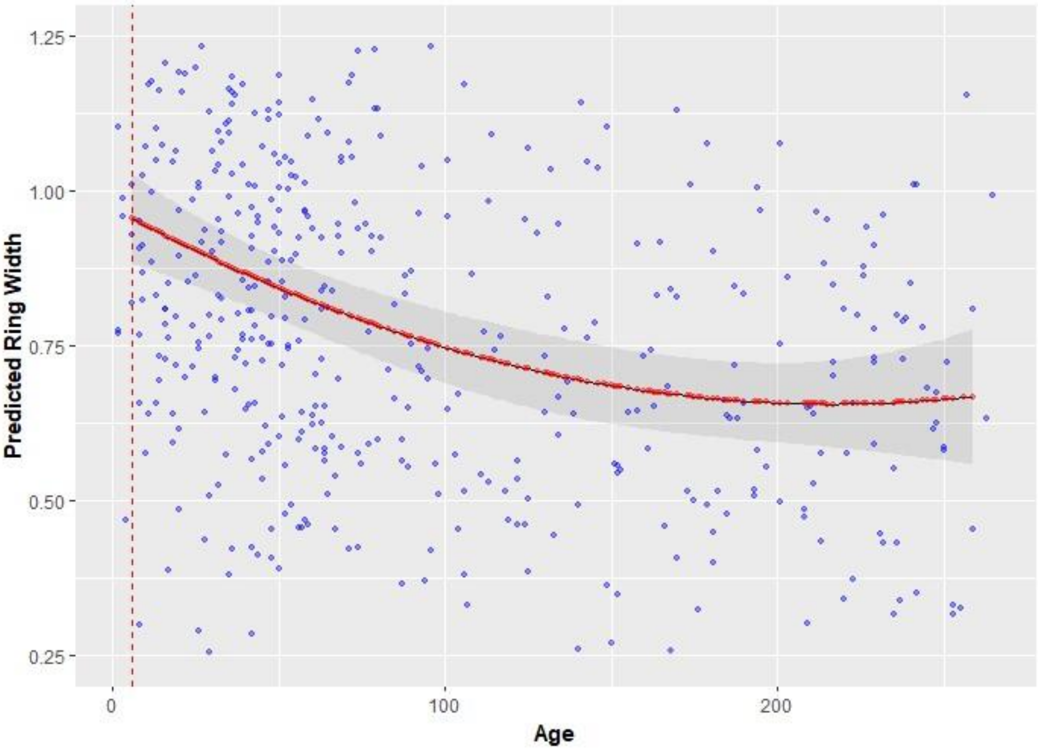

Figure 7 - Marginal effect plot of tree age vs predicted ring width values with fitted marginal regression line (in red) and confidence intervals (Profile Likelihood method.). Red dots: predicted values. Blue dots: observed values. Dashed line: indicates for which age the regression curve goes below the 1.0 mean standardized line, which is at age 0.

The fitted marginal regression curve follows a negative trend below the mean standardized line of 1.0 from age 0. The confidence intervals show a negative trend below the standardized line of 1.0 from age 20. Hence, I reject my hypothesis with masting signal starting at age 30. The observed appearance of masting signals reflects a limitation in tree growth by identified mast years from approximately 20 years based on the confidence intervals. Young beech stands may therefore be at an increased risk from reduced growth during identified masting years and related environmental conditions (deltaT). The negative trend of the fitted marginal regression curve indicates an increasing negative effect of an increasing age on ring width (smaller rings) as a proxy for masting signal. Climatic change with an increased masting frequency may put beech furthermore at an increased risk on regeneration failure due to for example a reduced sensitivity to weather cues with reduced pollination efficiency.

The exact timing of the onset of masting signal is difficult to assess since the age estimates of the samples were obtained at 1.3 m height. As a shade-tolerant tree, beech may establish under the main canopy and exhibit slow growth [37], [38]. The appearance of masting signal may occur for a later tree age if the missing ring widths from growth below 1.3 m height would be included. Hence, future studies could consider coring at the stem base to more accurately determine the age of onset of masting signal in beech trees.

Alternatively, seed production of beech trees could be recorded from the start of a trees life cycle. This provides direct observations on the onset of masting based on actual seed production. However, masting signal may be expressed earlier in ring widths as indicated by this study and can therefore provide valuable information to better understand the relationship between environmental variability and seed production.

The curve approaches a horizontal pattern from at around age 150. This indicates a decreasing negative effect of an increasing age on the ring width. The curve remains below the mean standardized line, indicating a continuous negative association of age on ring widths during masting years. A possible explanation could be a decrease in seed production with an increased allocation towards growth instead. A previous study reported a declining seed production for beech trees of the age of 175 in an earlier study [28]. The flattening of the curve may equally be an effect of reduced re-allocation towards growth while seed production maintained equal, considering that this study used ring widths as a proxy for masting signal instead of actual seed production. Finally, the wide confidence intervals for age 150 onwards reflect a higher uncertainty in the regression curve. Hence, no firm conclusions can be drawn for trees of age 150 and older.

The masting record in this study was partially reconstructed, based on ring widths, which likely has induced collinearity (section 4.4). Future studies could avoid collinearity by excluding masting years which were reconstructed based on ring widths.

6. Conclusion

The onset of masting signal in tree ring chronologies of beech in southern Sweden appears from approximately age 20 (Figure 7). By including masting signal of tree ring chronologies of young beech trees, potential underused data can be included to better understand the relationship between environmental variability and seed production. This is of high importance considering climatic change and related potential adverse affects on tree growth and regeneration success.

A decreasing negative effect of an increasing age on the ring width in trees older than 150 years is an interesting finding warranting further investigation. Whether those trees actually reduce their seeding or reduce their re-allocation towards growth during the mast years is unclear, as no tree-specific mast data were available for this study. I noted that there is a large variability in growth departures during mast years among these trees, suggesting that there are factors, not studied here, modulating the tree response.

The dominance of a tree is likely influencing the expression and onset of masting signal. More dominant trees showed a less negative deviation from the mean standardized ring width and therefore a weaker masting signal than codominant trees. Codominant trees furthermore could be more prone to masting considering their larger negative deviation from the mean standardized ring width. Hence, codominant trees may be more prone to climatic change and related potential adverse effects on tree growth and regeneration success. A combination of masting years with extreme weather conditions however, may reverse this effect, with codominant trees becoming more susceptible to climatic change.

This study concludes that beech trees can express masting signal in their ring-width chronologies from approximately 20 years. More dominant trees can express a later onset of masting signal. The relationship between environmental variability and seed production can be better understood by including masting signal of younger beech trees and the effect of a trees social position which is ultimately of importance considering climatic change and its potential adverse effects on tree growth and regeneration success.

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8. Popular science summary

Young-adults: young beech trees behave grownup based on their ring-widths

Beech trees can produce enormous amounts of seeds as a reproduction strategy to cope with seed predation. Doing so, beech forests can produce up to 250 kg of seeds per hectare. Such an event is called masting, which is for beech mainly triggered by temperature. Beech trees from around 40 years are observed to start showing masting behaviour. This study evaluates the effect of masting events on non-seed producing beech trees by evaluating their ring widths. Each tree is unique and therefore this study also includes the effect of a trees dominance on masting signals.

"This study found that masting signals occur from approximately 20 years"

This study focused on southern Sweden since the ring width samples were obtained in this region. Southern Sweden is faced and anticipated to endure more droughts as a result of climate change. Droughts could severely impact beech trees to reproduce themselves and simultaneously affect their growth. It is thus of upmost importance to better understand the relationship between the environment and seed production of beech trees. This study does so by including previously unused data of non-seed producing beech trees. This study used computer models that included different variables such as the age, dominance, differences between masting years and differences between trees. By doing so, this study found that masting signals occur from approximately 20 years. More dominant trees showed a less strong response to masting and could thus be more resilient to climate change. Future studies can consider a masting signal in non-seed producing beech trees to better anticipate the consequences of climate change on beech reproduction and growth.

Acknowledgements

I am very thankful for the spirited, insightful and to-the-point support from my supervisor Igor Drobyshev during the writing of my master thesis.

I am also very thankful for the support, interest and insightfull perspectives from all my friends and family.

I am thankful to the Erasmus Mundus SUFONAMA (Sustainable Forest and Nature Management) programme and the SLU (Swedish University of Agricultural sciences) that provided the research facilities to conduct this research.

I am furthermore thankful to have the opportunity to conduct this research considering its importance in times of climate change and due to my passion for the European beech tree.

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