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Citation for the published paper:

Igor Drobyshev, Mats Niklassona, Marc J. Mazerolle, Yves Bergeron. (2014)
Reconstruction of a 253-year long mast record of European beech reveals its
association with large scale temperature variability and no long-term trend
in mast frequencies. *Agricultural and forest meteorology*. Volume: 192-193,
pp 9-17.

<http://dx.doi.org/10.1016/j.agrformet.2014.02.010>.

Access to the published version may require journal subscription.

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1 Reconstruction of a 253 year-long mast record of European beech reveals its
2 association with large scale temperature variability and no long-term trend in
3 mast frequencies

4

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17

18

19 Abstract

20 Synchronous production of large seed crops, or mast years (MYs), is a common feature of many *Fagus*
21 species, which is closely linked to the dynamics of forest ecosystems, including regeneration of canopy
22 trees and changes in animal population densities. To better understand its climatic controls and check for
23 the presence of long-term temporal trends in MY frequencies, we reconstructed MY record of the European
24 beech (*Fagus sylvatica* L.) for the southern Swedish province of Halland over 1753-2006. We used
25 superimposed epoch analysis (SEA) to relate MY (a) to summer temperature fields over the European
26 subcontinent and (b) to the patterns of 500 mb geopotential heights over the 35°-75° N. For the MY
27 reconstruction, we used newly developed regional beech ring-width chronology (1753-2006), an available
28 summer temperature reconstruction, and a discontinuous historical MY record. A Monte Carlo experiment
29 allowed identification of the thresholds in both growth and summer temperature anomalies, indicative of
30 historical MYs, which were verified by dividing data into temporally independent calibration and
31 verification sub-periods.

32 MYs were strongly associated with both the 500 mb height anomalies and average summer temperatures
33 during two years preceding a MY: a mast year (t) followed a cold summer two years ($t-2$) prior to the mast
34 year and a warm summer one year prior ($t-1$) to the mast year. During $t-2$ years, the geographical pattern of
35 500 mb height anomalies exhibited a strong height depression in the region centered in the Northern Sea
36 and extending towards eastern North America and statistically significant ($p < 0.05$) temperature anomalies
37 covering predominantly southern Scandinavia (area below 60 N) and British Isles. A year immediately
38 preceding a mast year ($t-1$) was characterized by a strong regional high pressure anomaly centered in
39 southern Scandinavia with significant temperature anomalies extended [mostly over southern Scandinavia](#)
40 and Germany.

41 The long-term mean MY return interval was 6.3 years, with 50 and 90% probabilities of MY occurrence
42 corresponding to 6 and 15 years, respectively. Periods with intervals significantly shorter than the long-
43 term mean were observed around 1820 - 1860 and 1990 - 2006 (means - 3.9 and 3.2 years, respectively).
44 However, the difference in return intervals between two sub-periods themselves was not significant.

45 Geographically large and temporally rapid changes in atmospheric circulation among years, responsible for
46 summer temperature conditions in the Northern Europe, are likely primary environmental drivers of
47 masting phenomenon. However, decadal and centurial variability in MY intervals is difficult to relate
48 directly to temperature variability, suggesting the presence of conditions “canceling” would-be MYs.
49 Long-term MY reconstruction demonstrates high variability of reproductive behavior in European beech
50 and indicates that a period with shorter MY intervals at the end of 20th may be not unique in a multi-century
51 perspective.

52

53 Keywords

54 dendrochronology / hardwoods / pressure anomalies / Scandinavia / seeding behaviour / Southern Sweden /
55 tree-ring reconstruction

56

57 Introduction

58 Strong variability in annual seed production and occurrence of years with exceptionally large crops often
59 synchronized over large geographical regions, so-called mast years, is a common feature of trees in the
60 *Fagaceae* family (Hiroki and Matsubara, 1995; Hilton and Packham, 2003). At tree level, such events
61 imply large shifts in resource allocation towards reproductive organs, suggesting trade-offs between seed
62 production and biomass accumulation (Monks and Kelly, 2006; Drobyshev et al., 2010). At the stand and
63 regional levels, mast years are important for species regeneration and subsequent canopy dynamics
64 (Emborg, 1998; Frey et al., 2007; Barna, 2011), as well as for dynamics of animal species utilizing beech
65 seeds as a food resource (Schnurr et al., 2002; Clotfelter et al., 2007; Jensen et al., 2012). Mast seeding,
66 specifically of *Fagus* spp., has been widely acknowledged in forestry as a way to promote natural tree
67 regeneration on clearcut areas (Henriksen, 1988; Övergaard et al., 2007; Bileik et al., 2009).

68 Mast years in European beech (*Fagus sylvatica* L.) have been shown to be strongly affected by annual
69 climatic variability. Temperature dynamics apparently plays the major role in controlling mast events
70 (Piovesan and Adams, 2001). Warm and dry conditions were typically observed during the summers
71 preceding the mast year, and cold summers with sufficient amount of precipitation were often observed two
72 years prior to a mast year. A study in southern Sweden has revealed a strong effect of temperature on beech
73 masting behavior (Drobyshev et al., 2010). In line with these findings, physiological studies have
74 repeatedly pointed to European beech as a temperature sensitive species, e.g. relative to the onset of the
75 cambial cell production and growth period (Murray et al., 1989; Prislán et al., 2013), leaf unfolding (Prislán
76 et al., 2013), and leaf growing period (Tikvic et al., 2006).

77 A strong climatic control of beech masting implies that both short- and long-term variations in the
78 frequency of mast years are driven by the frequency of specific climatic conditions. These conditions
79 trigger the formation of flower buds and subsequent shifts in the allocation of bioassimilates towards the
80 production of nuts. Although no published studies looked at the changes in the actual frequency of such
81 triggering conditions, many have reported an increase in the masting frequency across different parts of the
82 European subcontinent over the second half of the 20th century, linking this trend to the changing climate
83 (Schmidt, 2006; Övergaard et al., 2007; Paar et al., 2011). An example of such a trend in Northern Europe

84 was an unusual occurrence of two consecutive mast years reported in Sweden for 1992 and 1993
85 (Övergaard et al., 2007).

86 Although a number of previous studies analyzed climatic controls of beech masting in Scandinavia
87 (Overgaard et al., 2007; Drobyshev et al., 2010), understanding long-term masting patterns and their
88 linkages to the regional climate is still limited. In particular, two aspects warranting further studies are (a)
89 the geographic extent of climate anomalies linked to the masting behavior of beech at its northern
90 distribution limit and (b) the century-long pattern of mast return intervals, which could provide an insight
91 into historic variability of mast year occurrence and its relation to long-term climate variability. Both
92 aspects of beech masting behavior are of direct practical interest since this species is an important timber
93 resource in southern Scandinavia and its practical management (e.g. use of natural regeneration methods on
94 clearcuts) calls for a better understanding of beech reproduction ecology (Ageštam et al., 2003).

95 In this study, we provide a 253-year long reconstruction of mast frequencies in the southern Swedish
96 province of Halland, compiling historical records, a newly-developed dendrochronological reconstruction,
97 and modern observation of mast events. Our main goal was to quantify the pattern and geographical scale
98 of the climatic controls exerted on mast years and identify long-term temporal trends in MY frequencies.
99 Such trends could reflect decadal and century-long changes in summer temperature regime over southern
100 Scandinavia.

101 Study area

102 The data analyzed in the paper was collected in the south-western Swedish county of Halland (Fig. 1). The
103 mean annual temperature in this part of southern Sweden is between 6°C and 7.5 °C. The long-term mean
104 temperature in January varies between -4 and 0 °C and in July – between 14 and 18 °C. Each year, between
105 190 and 220 days occur with temperatures above 5 C. The county has one of the largest amounts of annual
106 precipitation in Sweden (1000 – 1300 mm), mainly due to the dominance of westerly and south-westerly
107 winds carrying humid air from the Atlantic (Raab and Vedin, 1995). Geologically, the region is dominated
108 by gneiss rocks and soils formed on sandy and stony moraines (Fredén, 2002). The region lies in the
109 nemoral and boreo-nemoral vegetation zones (Ahti et al. 1968, Fig. 1). Oaks (*Quercus robur* L. and *Q.*
110 *petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.), and small-leaved species (downy birch,

111 *Betula pubescens* Ehrh. and quaking aspen, *Populus tremula* L.) represent the deciduous component in the
112 forest cover (Nilsson, 1996). Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.)
113 are the main coniferous species. The tree-ring dataset used for reconstruction was collected in mature and
114 old-growth beech-dominated stands. The main data set originated from of the Biskopstorp nature reserve
115 (Fig. 1). The area encompasses around 900 ha, almost completely covered by forest. The broadleaved
116 forests (beech and oak-dominated) make up approximately 30% of the total forest cover (Fritz, 2006).

117 Material and methods

118 *Field sampling, sample preparation and development of regional beech chronology*

119 To obtain tree ring data, we cored trees along two radii at a height of 1.36 m with a standard increment
120 corer. We also used a chainsaw to obtain wedges from both living and dead trees. Core samples were
121 mounted on wood planks and all samples were progressively polished with up to 600-grit sandpaper to
122 allow clear recognition of annual rings under the microscope (using up to 40x magnification). We
123 employed a visual cross-dating method (Stokes and Smiley, 1968) to precisely date each sample, using a
124 regional list of pointer years. In all of the single-tree chronologies ([total number of trees in the analyses, n](#)
125 [= 69](#)), we removed data corresponding to the period when a tree was younger than 40 years to exclude the
126 part of the tree lifespan when mast behavior is not yet well pronounced (Simak, 1993).

127 We removed low frequency trends in tree-ring data (e.g. age- and size-related) by detrending single tree
128 chronologies with a cubic spline with a 50% frequency response at 32 year frequency band. Autoregressive
129 modeling on the detrended ring-width series removed temporal autocorrelation and enhanced the common
130 signal in the tree-ring chronologies. Autoregressive modeling used the *ar* function of the R statistical
131 software (R Development Core Team, 2009) and relied on the values of Akaike's Information Criterion
132 (AIC) to select the optimal order of the autoregressive model. The individual residual series were then
133 averaged together using a biweight robust mean to develop a mean standardized chronology for a site,
134 which retained high-frequency variation and contained no low-frequency trend.

135 *Analysis of association between climate and mast years*

136 We quantified the association between mast year occurrence and a negative growth anomaly through a
137 superimposed epoch analysis (SEA, Kelly and Sear, 1984), using the regional beech chronology for the

138 county of Halland and the regional mast record. In particular, we checked if the difference in the mean
139 departure of the master chronology in the mast and lagging years was different from the long-term mean.
140 The significance of the SEA was evaluated by bootstrapping the original datasets 500 times and generating
141 a distribution of mean growth index (SEA on tree-ring data) or temperature (SEA on climate data) on the
142 11-year time frame centered on the focal (mast) year. The SEA was performed in function *sea* of the *dplR*
143 R package (Bunn, 2008).

144 We tested the association between mast years in Halland (Table 1) and the climate with the SEA, using
145 average summer temperature. As a source of temperature data, we utilized a gridded (2.5° x 2.5°) dataset of
146 reconstructed monthly temperatures over the European sub-continent (Casty et al., 2007), selecting grid
147 points falling within the borders of Halland county.

148 To understand the relationship between occurrence of mast years and large-scale atmospheric circulation
149 features, we analyzed 500 mb pressure fields over the European sub-continent and north Atlantic over 1871
150 to 2006 using 20th Century Reanalysis V2 data provided by the NOAA/OAR/ESRL PSD, Boulder,
151 Colorado, USA (<http://www.esrl.noaa.gov/psd/> , Compo et al., 2011). The SEA on the pressure data was
152 done in Climate Explorer (<http://climexp.knmi.nl/> , van Oldenborgh and Burgers, 2005), using average
153 summer (June through August) 500 mb heights.

154 To evaluate the geographical extent of temperature anomalies associated with mast years, we conducted
155 SEA on the record of 20th century mast years and the gridded (2.5° x 2.5°) dataset of average summer
156 temperature derived from a dataset of reconstructed monthly temperatures (Casty et al., 2007). For each
157 grid point, we averaged reconstructed temperature values for all mast years in Halland and calculated the
158 percentile based on the distribution of values over a specified time period. By doing so, we evaluated the
159 significance of temperature deviations from the long-term means and the spatial pattern of such deviations
160 during the mast years. Results were mapped by ESRI ArcMap 9.3, using prediction krigging in the
161 Geospatial Analyst module (Anonymous, 2008).

162 *Reconstruction strategy*

163 Mast year reconstruction used two sources of data – a regional beech tree ring chronology and a monthly
164 temperature reconstruction extracted from a reconstruction of Europe-wide temperatures (Casty et al.,

165 2007). Used exclusively, the information from the tree-ring data set might provide an inflated measure of
 166 MY frequency, because not all growth depressions are necessarily characteristic of MYs (Lebourgeois et al.,
 167 2005; Hoshino et al., 2008). To avoid this problem, we used both the tree-ring and the temperature data to
 168 improve the predictive power of our statistical model. Capitalizing on the results from a previous study
 169 (Drobyshev et al., 2010), we assumed that strong growth anomalies in a focal year t , preceded by a large
 170 difference in average summer temperatures between years $t-1$ (a warm year) and $t-2$ (a cold year), would be
 171 indicative of a mast year. In probabilistic terms, we assumed that the probability of a historical mast year
 172 could be expressed as $P_{MY} = P_{GA} * P_{\Delta T}$, where P_{MY} is the probability of mast year occurrence, and P_{GA} and
 173 $P_{\Delta T}$ are the probabilities of growth anomaly below an established threshold and of a temperature difference
 174 between two preceding years (years $t-1$ and $t-2$), respectively. In biological terms, we conditioned the
 175 probability of a mast year on the probability of a temperature anomaly prior to mast year to avoid
 176 considering any strong growth reduction as an immediate indication of a mast year. The reconstruction task
 177 was therefore reduced to finding optimal threshold levels for growth anomaly and for differences in
 178 temperature (ΔT). In the context of the current analyses, optimization of the thresholds consisted in
 179 maximizing the Reconstruction Skill (RSkill):

$$180 \text{RSkill} = (\text{Years}_{\text{Correct}} - \text{Years}_{\text{False}}) / \text{Length of period} ,$$

181 where $\text{Year}_{\text{Correct}}$ is the number of correctly classified years, and $\text{Years}_{\text{False}}$ is the number of incorrectly
 182 classified years, including both false positives and false negatives. Computationally, a program algorithm
 183 screened all combinations of the growth and temperature anomalies, while tracking the values of the *RSkill*
 184 statistics. We obtained threshold values on non-overlapping calibration and verification sub-sets of the
 185 original observational record of mast years, also reversing calibration and verification data to test for the
 186 temporal stability of the relationship. The two periods used at the calibration and the verification steps were
 187 1897-1926 and 1974-2000.

188 The obtained thresholds were used to reconstruct mast years over the period 1795-1895, which was not
 189 covered by the observational data. To account for the variability in the initial tree-ring data, we ran the
 190 reconstruction algorithm 1000 times on sets of tree ring chronologies randomly resampled with
 191 replacement from the original set of chronologies. As a result of each bootstrapping run, we obtained a new

192 master chronology over the 1753-2006, which was later used in reconstruction. In turn, reconstruction
 193 resulted in a list of years identified by the algorithm as mast years. This list, which was the final result of a
 194 bootstrapping run, was recorded at the end of each reconstruction run. Ultimately, bootstrapping produced
 195 (a) the chronology of years identified as mast years in at least one run and (b) the associated frequency for
 196 that year to be classified as a mast year over the the whole 1000 bootstrapped runs. In other words,
 197 bootstrapping created a distribution of frequencies, representing the probability for a particular year to be
 198 classified as a mast year during 1000 runs. To establish a threshold for the final selection of a year as a mast
 199 year, we ran both the reconstruction and the bootstrapping for the period with available observational data
 200 and evaluated the frequencies of known mast years.

201 Beech growth is often sensitive to growing season drought (Dittmar et al., 2003; Scharnweber et al., 2013)
 202 and prolonged periods with drought conditions may lead to strong negative growth anomalies (Dittmar et
 203 al., 2006). This implied that growth anomalies classified as MYs might be a direct product of drought
 204 events during such years. Thus, we examined conditions during reconstructed MYs and long-term drought
 205 conditions. We used an independent reconstruction of growing season Drought Index, a ratio between
 206 actual to equilibrium evapotranspiration (AET/EET), for the region of south-western Sweden,
 207 encompassing our study area (Drobyshev et al., 2011).

208 Final MY reconstruction was compiled from the observational records available for the county of Halland
 209 over three periods – 1753-1795, 1895-1926, and 1974-2006. Distribution of the mast year intervals was
 210 evaluated with a Hollander-Proschan test utilizing only complete (uncensored), observations (Dodson,
 211 1994). Using the composite record (1753-2006), we assessed the probability of mast year occurrence using
 212 survivorship analysis and the Kaplan-Meier estimator (Kaplan and Meier, 1958):

$$213 \quad S(t) = \prod_{j=1}^t \left[(n - j) / (n - j + 1) \right]^{\delta(j)},$$

214 where $S(t)$ is the site survivorship function estimated for a period t ; n is the total number of observations;

215 \prod is the product (geometric sum) across all cases less than or equal to t , and $\delta(j)$ is a constant that is

216 either 1 if the j 'th case is uncensored (complete); and 0 if it is censored (incomplete).

217

218 Results

219 For the period since 1753, the replication of the chronology exceeded 5 trees (10 trees since 1795) and the
220 values of expressed population signal (EPS) stayed above a generally accepted threshold of 0.85 (Wigley et
221 al., 1984) since 1750 (Supplementary Information, Fig. A). Both the values of EPS and of average mean
222 sensitivity (0.327) suggested the presence of a strong common signal in the dataset.

223 SEA on the residual beech chronology demonstrated strong and highly significant negative departures in
224 beech growth index during the mast years and a moderate, yet significant, positive growth anomaly during
225 the year immediately preceding a mast year (Fig. 2A). SEA on average summer (June through August)
226 temperature over the Halland revealed two significant anomalies – a negative anomaly two years prior to
227 the mast year and a positive anomaly in the year preceding the mast year (Fig. 2B).

228 MYs in Halland were associated with large-scale temperature anomalies over Northern and Western
229 Europe (Fig. 3). A cold year, two years prior to the mast year ($t-2$), exhibited a negative temperature
230 anomaly over the United Kingdom, western France, eastern coastal regions of the Northern Sea, and
231 southern Scandinavia. In its northeastern corner, the zone with significant departures reached up to 60° in
232 the north and 20° to the east. A warm year preceding the mast year ($t-1$) showed a pattern of significant
233 positive temperature anomalies extending down south to 49° N and up to 61° N in the north. In contrast to $t-$
234 2 years, temperature anomalies over the UK were much less common and, the meridional position of the
235 zone with significant anomalies appeared to be shifted towards a more continental part of Europe.

236 The 500 mb height pattern in $t-2$ years (Fig. 4) exhibited strong height depressions centered over the
237 Northern Sea and extending towards eastern North America. In the same year, a strong positive pressure
238 anomaly was observed in the region of Ural mountains. The year immediately preceding a MY year ($t-1$)
239 was characterized by a regional high pressure anomaly centered in southern Scandinavia and moderate, yet
240 significant, low pressure anomaly over the Ural mountains and Greenland.

241 Using the split calibration-verification scheme, we obtained two pairs of calibration and verification results
242 on non-overlapping periods (Table 1). In both versions, the number of mast years suggested by the models

243 didn't deviate by more than 17% from the "true" number of mast years. Realizing that such "true" value
244 might be affected by the quality of the observational record and by the subjectivity of the observers'
245 thresholds used in classifying a year as a mast year, we considered the results satisfactory. We noted that
246 two versions of the reconstruction encompassed the "true" values for respective periods: a version with
247 early calibration and late verification (tree-ring and temperature thresholds -0.777 and 0.015, respectively)
248 showed a slight underestimation, whereas a version with late calibration – early verification (-0.771 and -
249 0.020) overestimated the "true" values. We used threshold values from both versions to produce two final
250 reconstructions.

251 By bootstrapping the original dataset of beech chronologies and running the reconstruction protocol on
252 each of the bootstrap runs, we obtained a distribution of relative frequencies, representing the probability for
253 each year to be classified as a mast year (Fig. B in Supplementary Information). The reconstruction was
254 done on the whole studied period (1753-2006) and included sub-periods with observational data (1895-
255 1926 and 1974-2006). As a result, we were able to evaluate the relationship between frequency of a year to
256 be classified as MY in 1000 bootstrap runs, on one hand, and actual presence of MY in that year, on the
257 other. The analysis suggested that all years which were classified as MY in 50 or more percent of
258 bootstrapped runs of the reconstruction protocol should be considered as MY in the final reconstruction
259 (Fig. B in the Supplementary Information).

260 For the 1756-2006 period, we identified 39 and 41 MYs in the conservative and opportunistic
261 reconstruction schemes, respectively. [The difference between two schemes was the presence of the years](#)
262 [1838 and 1859, which successfully passed temperature qualification thresholds in the more opportunistic](#)
263 [version \(but not in the conservative version\)](#). The distribution of the MY return intervals over the 1753-
264 2006, as well as two selected sub-periods (1825-1855 and 1975-2006) followed the Weibull distribution
265 (Table 2). Over the whole study period, there was a 50% probability of MY occurrence after six
266 consecutive years without masting, and a 90% probability after 14 years without masting (Fig. 6). Since
267 both reconstruction versions were similar (4.9% difference in the reconstructed MYs), we present the
268 results for the more opportunistic version of the reconstruction only (see Supplementary Information Fig. C
269 for results obtained with the alternative reconstruction).

270 **MYs were wetter than average years:** mean and SD values of the drought index was 19.0 ± 4.10 in mast
271 years and 22.5 ± 2.58 for all years (higher values of Drought Index corresponding to higher drought stress).
272 This confirmed that growth depressions were not a direct result of drought stress during the same growing
273 season.

274 Over 1753-2006, MY intervals exhibited a large temporal variability (Fig. 5). Periods of longer MY return
275 intervals were observed during 1800-1825, 1860-1890, and 1950-1975, and periods with shorter intervals -
276 during 1753-1770, 1825-1855, 1900-1925, and 1975-2006. The two periods with the shortest intervals were
277 1825-1855 and 1975-2006, when 50% probabilities of MY occurrence were observed at 3.6 (1825-1855)
278 and 3.0 (1975-2006) consecutive years without mast years. The 90% probabilities of MY occurrence were
279 observed at 6.9 and 5.5 consecutive years for the 1825-1855 and 1975-2006 periods, respectively. Only the
280 later period (1975-2006) differed significantly from the distribution over the complete period: Cox-Mantel
281 test statistics – 2.47 and 1.23, $p = 0.219$ and 0.014 for the 1825-1855 and 1975-2006 periods, respectively.
282 However, two sub-periods did not differ significantly between each other (Cox-Mantel test statistics 1.05, p
283 = 0.294).

284 Discussion

285 European beech is an important component of the European forests and understanding its reproductive
286 biology should advance our ability to study population dynamics and model population-level responses to
287 future climate variability. By compiling an original reconstruction based on tree-ring and temperature data
288 with fragmentary observational records, we presented a regional 253-year mast record of *F. sylvatica*. To
289 the best of our knowledge, it is the longest record of its kind currently available for Europe. Our analyses
290 suggested that beech masting behavior was strongly controlled by large-scale atmospheric circulation
291 anomalies during two and one years prior to mast year, probably explaining a high level of synchronization
292 of beech MYs across Europe. Large variability in mast year return intervals, revealed by the reconstruction,
293 indicated that the recent increase in mast year frequency, although regularly noted as unusual, may be not
294 unique in the multi-century perspective. Below we discuss details of these findings.

295 *Climate effects on mast year occurrence and beech growth*

296 A combination of a cold year and a warm year preceding a mast year pointed to the important role of
297 internal physiological triggers controlling occurrence of a mast year (Fig. 2A). We speculate that a cooler
298 year two years prior to a mast year might promote development of bud meristems, which in European
299 beech occur two years prior to masting (Gruber, 2001). A warmer year immediately preceding the mast
300 year may be important both as a period of favorable growth conditions, facilitating accumulation of
301 bioassimilates, and as a trigger for the differentiation of primordia into flower buds, which in beech happens
302 in the year preceding the year of nut maturation (Büsgen, 1916; Gruber, 2001). [Rapid changes in hormone
303 levels, forced by a strong change in summer temperatures between years, appear as a likely driver linking
304 temperature variability and changes in primordia differentiation pathways. Future biochemical studies will
305 be of help to test this hypothesis.](#)

306 [The pattern of tree growth prior and during the mast year suggests complex, possibly not self-excluding,
307 mechanisms regulating the allocation of photoassimilates within the tree. We envision two possible
308 interpretations for a significant increase in ring width during the years immediately preceding the mast year
309 \(Fig. 2B\).](#) First, since years preceding MY tend to be warm, the effect might suggest a positive effect of
310 growing season temperature on growth. Such positive temperature effects has been reported for several
311 species of this genus (Hoshino et al., 2008; van der Maaten, 2012), although a combination of elevated
312 temperature and low precipitation have a negative effect on European beech in western Europe
313 (Scharnweber et al., 2011; van der Maaten, 2012). Alternatively, a positive growth anomaly could also be a
314 result of cooler conditions during the previous year resulting in a lower evapotranspiration demand and a
315 strong dependence of the beech growth on the assimilation efficiency of the previous year. A study on
316 European beech seedlings using labeled isotopes revealed that current year assimilation of nitrogen
317 contributed only around 7% for the leaf production in that year. Similarly, only 18% of carbon consumed
318 during a year was synthesized in that year, the consumption relying heavily on reserves from the previous
319 year (Dyckmans et al., 2000; Dyckmans et al., 2002).

320 [The mast year in beech ring-width chronologies was expressed as a strong negative growth anomaly \(Fig.
321 2B\), a pattern regularly reported in literature \(see Drobyshev et al. 2010 and references therein\). The origin
322 of such an effect may be \(a\) a trade-off between bioassimilate expenditures associated with the production
323 of large crop and diameter growth, and \(b\) differences in the timing of resource allocation, used for growth](#)

324 and seeding in European beech. Support for the trade-off hypothesis comes from studies which have
325 revealed the depletion of tree nutrient reserves during mast years (Sala et al. 2012; although see Yasumura
326 et al. 2006) and a competition for resources between seed production and shoot growth (Han et al. 2011).
327 Alternatively, a strong growth anomaly during the mast year may be a result of differences in the timing of
328 resource allocation, used for growth and seeding. A stable carbon isotope study has demonstrated that seed
329 production in European beech is independent from previous year carbon reserves (Hoch et al., 2013). An
330 analysis of carbon stocks and reproductive behavior across multiple species of temperate forests in Japan
331 has found no significant correlations between the carbon accumulation period and the fluctuation of annual
332 seed production (Ichie et al., 2013). These results indicated that it is not the nutrient reserves, but the
333 current year photosynthates which supply resources for seed production during mast years. In contrast,
334 beech growth has been shown to be heavily dependent on the previous year reserves (see above in this
335 section, Dyckmans et al., 2002). It follows then that a negative growth anomaly during a mast year may
336 simultaneously represent unfavorable growth conditions during the previous year and a strong sink of
337 current year assimilates into seed production.

338 The pressure and temperature patterns associated with MY suggested that geographically large and
339 temporally rapid changes in atmospheric circulation among years, responsible for summer temperature
340 conditions in Western and Northern Europe, were likely primary environmental drivers of masting
341 phenomenon. Negative 500 mb height anomaly developing over northern Europe and centered over the
342 Northern Sea (Fig.4) caused lower temperatures over a large part of southern Scandinavia and along the
343 Atlantic coast between approximately 47 and 55° N (Fig. 3). Geographical patterns of low 500 mb heights,
344 stretching over the Atlantic and further to the east-northern part of North America, suggested that it might
345 be a product of westerly transfer of cooler Arctic air masses in the Atlantic sector. A warm year
346 immediately preceding a mast year, on the contrary, appeared to be a result of a regional high pressure
347 system centered over the southern Scandinavia. More “continental” patterns of $t-1$ pressure anomalies were
348 well reflected in the pattern of temperature departures for that year, which were centered in more
349 continental positions, as compared to “cold year” departures.

350 Strong climate control of MY, and specifically – the role of summer temperature as a synchronizing factor,
351 explains regular occurrence of MYs which were simultaneously observed across Northern Europe (Hilton
352 and Packham, 2003). For example, comparison of Halland mast chronology with the one from Denmark
353 (Holmsgaard and Olsen, 1960; Jenni, 1987) over the 1846 - 1982 revealed 13 common mast years (43% of
354 the total number of MY for this period), which corresponded to less than 10^{-4} probability of observing this
355 number given the independent occurrence of MY in each of these regions.

356 *Temporal variability in mast year frequencies*

357 Possibilities to detect temporal changes in mast frequencies are inherently dependent on the length of a
358 continuous MY record. A regional 253-year mast record, developed in this study, revealed a pronounced
359 decadal variability in the MY return intervals. Although the long-term probability of MY occurrence was
360 six years, there were two periods when it was below four years – during 1820 - 1860 and 1990-2006. This
361 finding suggests that a period with shorter MY intervals at the end of 20th may be not unique in a multi-
362 century perspective. Previous studies have indicated an increase in the seeding and mast events of European
363 beech (Schmidt, 2006; Övergaard et al., 2007; Paar et al., 2011), although not all analyses have found this
364 temporal trend (Hilton and Packham, 2003).

365 Our result did not support a hypothesis (Övergaard et al., 2007) of recent changes in MY frequency being a
366 result of increased nitrogen deposition (Jonsson et al. 2003; Akselsson et al., 2013). The periods in the
367 middle of the 19th century and in the late 20th century likely had contrasting background levels of N
368 deposition. However, we did not observe significant differences in MY frequencies between them (Fig. 6).
369 Although long-term trends in N deposition did not appear to be a driving factor of mast frequencies, it
370 might act as a contributing factor. We observed a strong coupling between MYs and climate and similar
371 increases in MY frequency in the past. Consequently, we propose that the temperature variability at
372 geographically large scale was the primary factor behind MY dynamics.

373 Due to strong environmental controls of MYs, a regional mast year chronology could be viewed as a proxy
374 of historical dynamics of pressure and temperature variability. In particular, MY return intervals may
375 reflect changes in frequencies of periods with pronounced inter-annual differences in summer pressure and

376 temperature patterns. However, a comparison of the MY chronology with decadal variability in summer
377 temperature in Halland indicated that the temporal dynamics of two variables might not be well
378 synchronized at decadal and centurial timescales (Fig. 5). Although the most recent (1975-2006) period
379 with elevated MY frequency did coincide with an increased temperature variability, the pattern was less
380 clear for the period at the beginning of the 20th century (around 1900-1930), and literally nonexistent for the
381 period centered around 1840. Similarly, one of the main declines in temperature variability around 1870-
382 1880 had a lower MY frequency. However, the period with the highest temperature variability around 1800
383 also exhibited a relatively low MY frequency. Expectedly, temporal dynamics of the mean values of the
384 summer temperatures did not point to any pattern associated with MY occurrence.

385 Difficulties in relating MY occurrence to the regional temperature variability might be due to conditions
386 “canceling” would-be MYs. Strong spring temperature depressions, hailstorms, and even strong winds have
387 been reported as factors damaging beech flowers (Hilton and Packham, 2003; Gruber, 2003) and can
388 potentially eliminate mast crops. Taking this component of environmental variability into account would
389 likely improve the correlations between MY and temperature variability. However, such events occur at
390 much shorter temporal scales and their long-term records and reconstructions are inherently difficult to
391 obtain.

392 Whatever the reason for the lack of the temporal trend in MY frequencies, it may imply a low sensitivity to
393 changes in long-term means of average summer temperatures, as suggested earlier for other masting trees
394 (Kelly et al., 2013). Our results indicated that it is, instead, the degree of annual variability in the large scale
395 pressure patterns over the Atlantic and Northern Europe which synchronize and likely modify temporal
396 pattern of masting in European beech across its distribution range. Further studies aimed at partitioning
397 between environmental signals that induce and cancel MY should improve our understanding of long-term
398 temporal trends in MY frequencies.

399 Acknowledgements

400 I.D. thanks Stiftelsen Stina Werners Fond for financial support (grant SSWF 10-1/29-3). The study is done
401 within the framework of the Nordic-Canadian network on forest growth research, supported by the Nordic
402 Council of Ministers (grant # 12262 to I.D.), and Swedish-Canadian network for cooperation in forestry

403 research, supported by the Swedish Foundation for International Cooperation in Research and High
404 Education STINT (grant # IB2013-5420 to I.D.). We thank Geert Jan van Oldenborgh (The Royal
405 Netherlands Meteorological Institute) for technical support during data analyses in KNMI Climate Explorer
406 and Andy Bunn (Western Washington University) for help with *dplR* package. [We thank two anonymous](#)
407 [reviewers for constructive comments on an earlier version of the manuscript.](#)

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- 534

535 Tables

536 Table 1.

537 Skill of most year (MY) reconstruction on two alternative calibration and verification periods. N refers to
 538 the number of most years in the calibration period. Percentages of correctly and incorrectly classified
 539 years were calculated as the ratio between the number of reconstructed MYs (MY_{rec}) and the observed
 540 number (MY_{obs}).

541

Calibration period	Verification period	N	% correctly classified as MY	% incorrectly classified as MY	MY_{rec} / MY_{obs} , %	RSkill in verification
1897 - 1926	1974 - 2000	6	87.5	0.0	87.5	0.875
1974 - 2000	1897 - 1926	7	87.3	33.3	116.7	0.500

542

543

544 Table 2.

545 Statistics of the return interval distributions for the beech mast years over the 1753-2006, and two selected
 546 sub-periods. For the 1753-2006 and 1825-1855 periods, results are presented for both early and late
 547 calibration runs of the reconstruction model (EC and LC, respectively). For the 1975-2006 period,
 548 calculations were done on the observational data.

549

Period	Scale parameter \pm SE	Shape parameter \pm SE	Hollander-Proschan test statistics & p
1753-2006	EC: 6.93 ± 0.874	EC: 1.33 ± 0.15	EC: 0.278, $p = 0.786$
	LC: 7.35 ± 0.912	LC: 1.39 ± 0.16	LC: 0.245, $p = 0.806$
<i>Sub-periods</i>			
1825-1855	EC: 4.49 ± 0.89	EC: 1.97 ± 0.55	EC: -0.011, $p = 0.991$
	LC: 5.27 ± 1.05	LC: 2.10 ± 0.69	LC: -0.320, $p = 0.749$
1975-2006	3.63 ± 0.57	2.13 ± 0.50	0.129, $p = 0.897$

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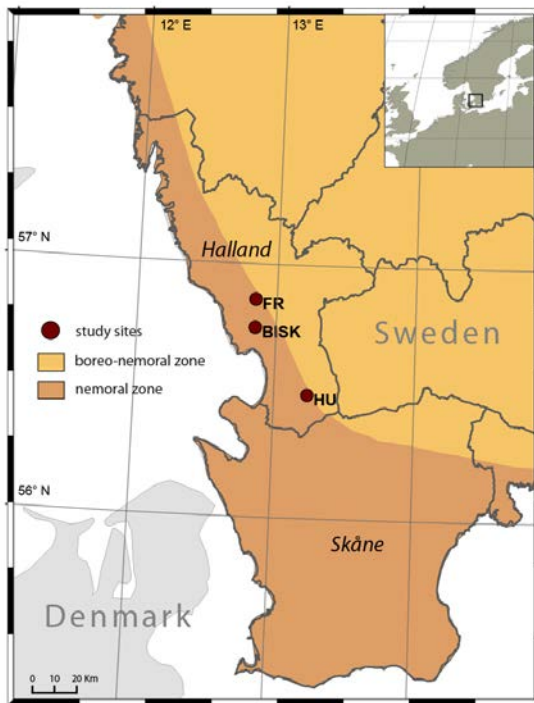
553 Figures

554

555 Fig. 1.

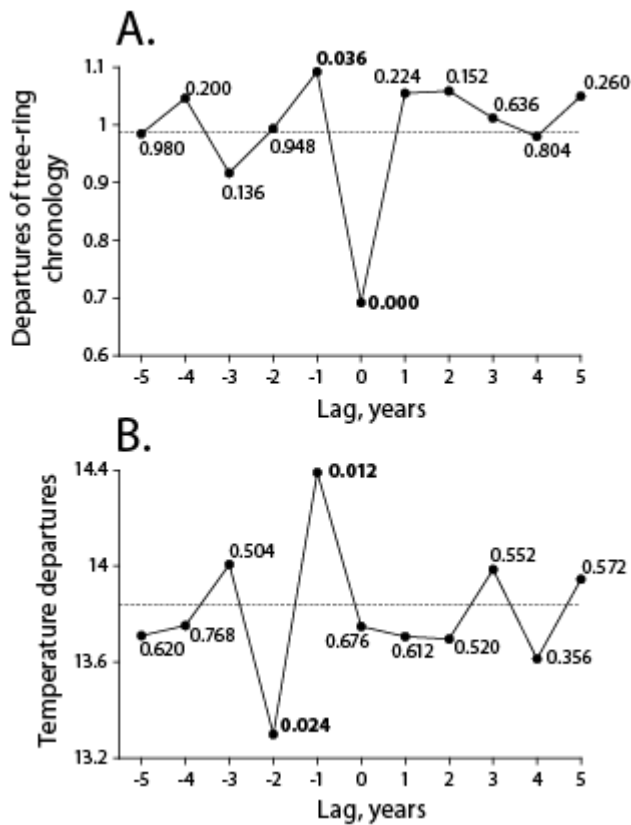
556 Location of the study sites and the Swedish county of Halland.

557



558

559 Fig. 2.
 560 Results Superimposed Epoch Analysis (SEA) using Halland mast year record and (A) regional beech tree-
 561 ring chronology, and (B) average Halland summer temperature over the period 1900-2000. Year with a
 562 zero lag corresponded to mast year. Numbers at the points indicate bootstrap-derived significance of
 563 departures from the mean value of the respective dataset. Bold font indicates departures significant at 0.05
 564 level.
 565

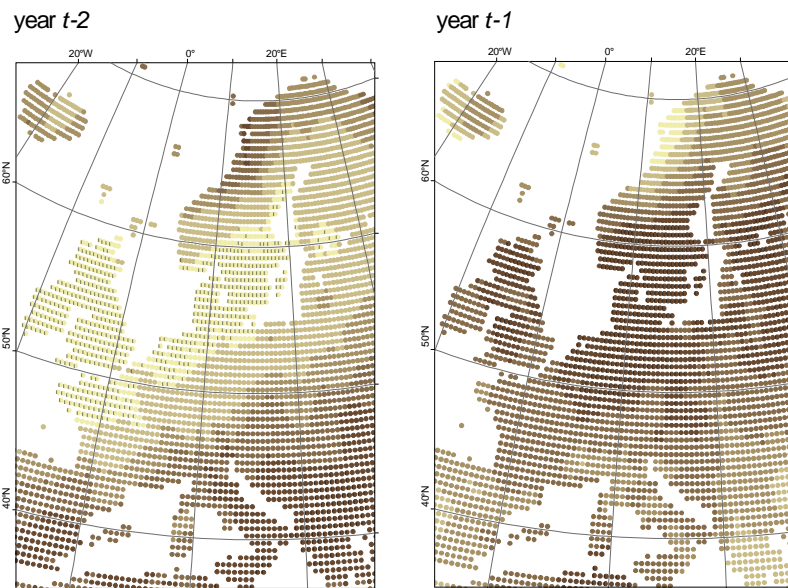


566

567 Fig. 3.

568 Superimposed epoch analysis (SEA) of average summer temperature over the European sub-continent and
569 the 20th century beech mast year record for the Swedish county of Halland. t indicates a mast year, and $t-2$
570 and $t-1$ refer to two and one years preceding the mast year, respectively. Gradient towards darker colors
571 indicate a temperature gradient from negative towards positive temperature anomalies. Asterisks indicate
572 grid points with significant (at 0.05 level) temperature departures during mast years.

573

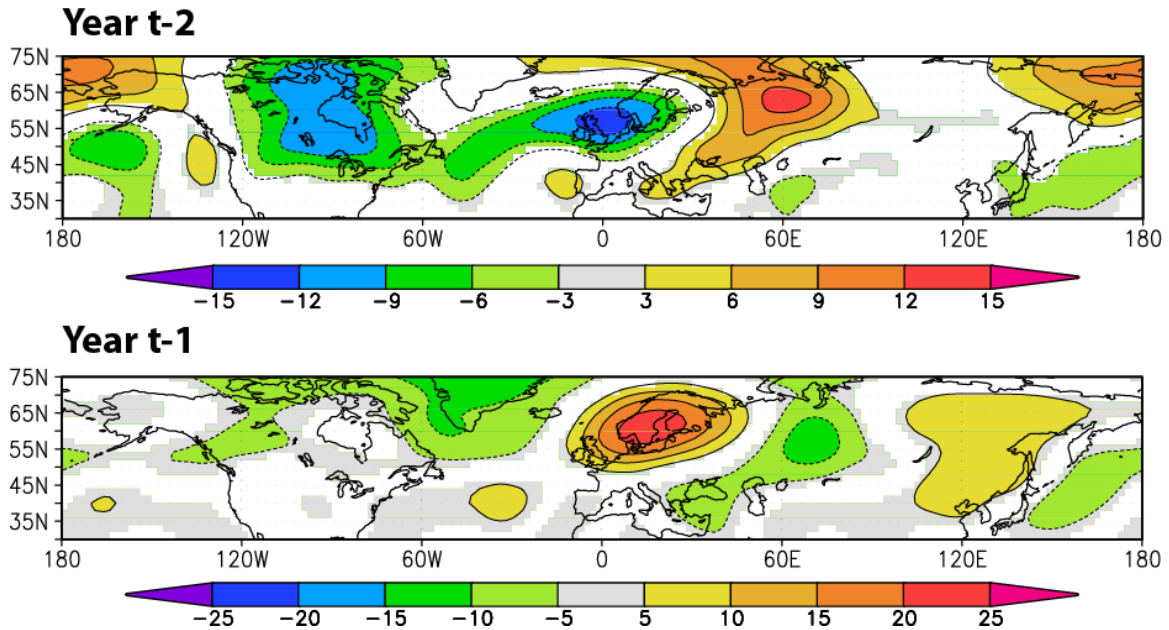


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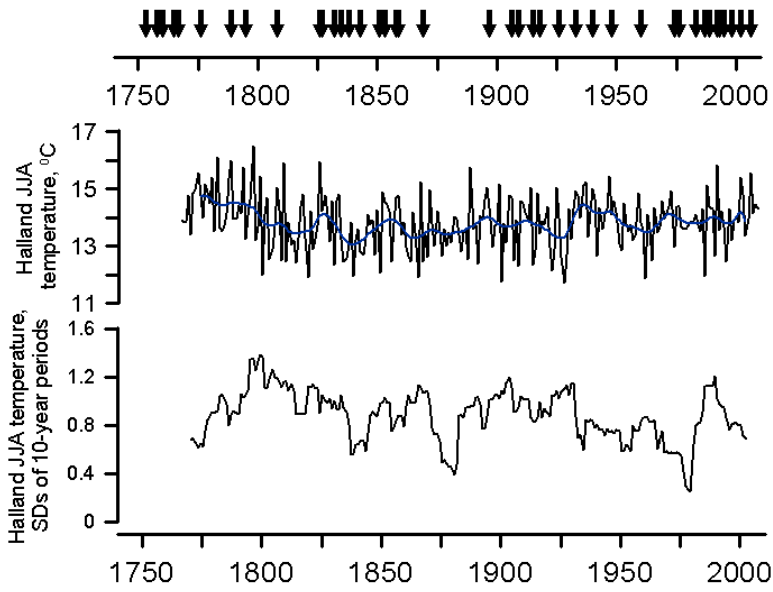
577 Fig. 4.
578 Pattern of circumpolar 500 mb geopotential height anomalies during years preceding most years in the
579 province of Halland as revealed by SEA on composite records of most years over 1872 - 2006. Distribution
580 of values in highlighted areas fell below 95% (year $t-2$) or exceeded 95% (year $t-1$) of the long-term
581 distribution for that area.
582



583

584

585 Fig. 5.
 586 Beech mast year chronologies for the county of Halland (arrows) over 1753-2006 and variability in
 587 Halland's summer temperature, expressed as running standard deviation (SD) of 10-year periods. Mast year
 588 chronology is a compilation of observational data and reconstruction results obtained with early calibration
 589 period (1897 – 1926). Source of the temperature data – Casty et al. 2007.
 590



591

592

593 Fig. 6.

594 Probability of beech mast occurrence in the province of Halland during 1753 – 2006 and two sub-periods.

595 For each sub-period, the probability function is shown with its respective 95% confidence envelope. The

596 results represent a version of the reconstruction done with the early calibration of the model. Results of the

597 reconstruction obtained with the late calibration are available in Supplementary Information Fig. C.

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