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

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Abstract

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

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

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

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

Keywords

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

Introduction

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

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

A strong climatic control of beech masting implies that both short- and long-term variations in the frequency of mast years are driven by the frequency of specific climatic conditions. These conditions trigger the formation of flower buds and subsequent shifts in the allocation of bioassimilates towards the production of nuts. Although no published studies looked at the changes in the actual frequency of such triggering conditions, many have reported an increase in the masting frequency across different parts of the European subcontinent over the second half of the 20th century, linking this trend to the changing climate (Schmidt, 2006; Övergaard et al., 2007; Paar et al., 2011). An example of such a trend in Northern Europe was an unusual occurrence of two consecutive mast years reported in Sweden for 1992 and 1993 (Övergaard et al., 2007).

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

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

Study area

The data analyzed in the paper was collected in the south-western Swedish county of Halland (Fig. 1). The mean annual temperature in this part of southern Sweden is between 6°C and 7.5 °C. The long-term mean temperature in January varies between -4 and 0 °C and in July – between 14 and 18 °C. Each year, between 190 and 220 days occur with temperatures above 5 C. The county has one of the largest amounts of annual precipitation in Sweden (1000 – 1300 mm), mainly due to the dominance of westerly and south-westerly winds carrying humid air from the Atlantic (Raab and Vedin, 1995). Geologically, the region is dominated by gneiss rocks and soils formed on sandy and stony moraines (Fredén, 2002). The region lies in the nemoral and boreo-nemoral vegetation zones (Ahti et al. 1968, Fig. 1). Oaks (*Quercus robur* L. and *Q. petraea* (Matt.) Liebl.), European beech (*Fagus sylvatica* L.), and small-leaved species (downy birch, *Betula pubescens* Ehrh. and quaking aspen, *Populus tremula* L.) represent the deciduous component in the forest cover (Nilsson, 1996). Norway spruce (*Picea abies* (L.) Karst.) and Scots pine (*Pinus sylvestris* L.) are the main coniferous species. The tree-ring dataset used for reconstruction was collected in mature and old-growth beech-dominated stands. The main data set originated from of the Biskopstorp nature reserve (Fig. 1). The area encompasses around 900 ha, almost completely covered by forest. The broadleaved forests (beech and oak-dominated) make up approximately 30% of the total forest cover (Fritz, 2006).

Material and methods

Field sampling, sample preparation and development of regional beech chronology

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

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

Analysis of association between climate and mast years

We quantified the association between mast year occurrence and a negative growth anomaly through a superimposed epoch analysis (SEA, Kelly and Sear, 1984), using the regional beech chronology for the county of Halland and the regional mast record. In particular, we checked if the difference in the mean departure of the master chronology in the mast and lagging years was different from the long-term mean. The significance of the SEA was evaluated by bootstrapping the original datasets 500 times and generating a distribution of mean growth index (SEA on tree-ring data) or temperature (SEA on climate data) on the 11-year time frame centered on the focal (mast) year. The SEA was performed in function *sea* of the *dplR* R package (Bunn, 2008).

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

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

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

Reconstruction strategy

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

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

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

The obtained thresholds were used to reconstruct mast years over the period 1795-1895, which was not covered by the observational data. To account for the variability in the initial tree-ring data, we ran the reconstruction algorithm 1000 times on sets of tree ring chronologies randomly resampled with replacement from the original set of chronologies. As a result of each bootstrapping run, we obtained a new master chronology over the 1753-2006, which was later used in reconstruction. In turn, reconstruction resulted in a list of years identified by the algorithm as mast years. This list, which was the final result of a bootstrapping run, was recorded at the end of each reconstruction run. Utlimately, boostrapping produced (a) the chronology of years identified as mast years in at least one run and (b) the associated frequency for that year to be classified as a mast year over the the whole 1000 boostrapped runs. In other words, bootstrapping created a distribution of frequencies, representing the probability for a particular year to be classified as a mast year during 1000 runs. To establish a threshold for the final selection of a year as a mast year, we ran both the reconstruction and the bootstrapping for the period with available observational data and evaluated the frequencies of known mast years.

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

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

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

where *S(t)* is the site survivorship function estimated for a period *t*; *n* is the total number of observations; $\prod$ is the product (geometric sum) across all cases less than or equal to *t*, and *δ (j)* is a constant that is either 1 if the *j*'th case is uncensored (complete); and 0 if it is censored (incomplete).

Results

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

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

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

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

Using the split calibration-verification scheme, we obtained two pairs of calibration and verification results on non-overlapping periods (Table 1). In both versions, the number of mast years suggested by the models didn't deviate by more than 17% from the "true" number of mast years. Realizing that such "true" value might be affected by the quality of the observational record and by the subjectivity of the observers' thresholds used in classifying a year as a mast year, we considered the results satisfactory. We noted that two versions of the reconstruction encompassed the "true" values for respective periods: a version with early calibration and late verification (tree-ring and temperature thresholds -0.777 and 0.015, respectively) showed a slight underestimation, whereas a version with late calibration – early verification (-0.771 and -0.020) overestimated the "true" values. We used threshold values from both versions to produce two final reconstructions.

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

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

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

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

Discussion

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

Climate effects on mast year occurrence and beech growth

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

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

The mast year in beech ring-width chronologies was expressed as a strong negative growth anomaly (Fig. 2B), a pattern regularly reported in literature (see Drobyshev et al. 2010 and references therein). The origin of such an effect may be (a) a trade-off between bioassimilate expenditures associated with the production of large crop and diameter growth, and (b) differences in the timing of resource allocation, used for growth and seeding in European beech. Support for the trade-off hypothesis comes from studies which have revealed the depletion of tree nutrient reserves during mast years (Sala et al. 2012; although see Yasumura et al. 2006) and a competition for resources between seed production and shoot growth (Han et al. 2011). Alternatively, a strong growth anomaly during the mast year may be a result of differences in the timing of resource allocation, used for growth and seeding. A stable carbon isotope study has demonstrated that seed production in European beech is independent from previous year carbon reserves (Hoch et al., 2013). An analysis of carbon stocks and reproductive behavior across multiple species of temperate forests in Japan has found no significant correlations between the carbon accumulation period and the fluctuation of annual seed production (Ichie et al., 2013). These results indicated that it is not the nutrient reserves, but the current year photosynthates which supply resources for seed production during mast years. In contrast, beech growth has been shown to be heavily dependent on the previous year reserves (see above in this section, Dyckmans et al., 2002). It follows then that a negative growth anomaly during a mast year may simultaneously represent unfavorable growth conditions during the previous year and a strong sink of current year assimilates into seed production.

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

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

Temporal variability in mast year frequencies

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

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

Due to strong environmental controls of MYs, a regional mast year chronology could be viewed as a proxy of historical dynamics of pressure and temperature variability. In particular, MY return intervals may reflect changes in frequencies of periods with pronounced inter-annual differences in summer pressure and temperature patterns. However, a comparison of the MY chronology with decadal variability in summer temperature in Halland indicated that the temporal dynamics of two variables might not be well synchronized at decadal and centurial timescales (Fig. 5). Although the most recent (1975-2006) period with elevated MY frequency did coincide with an increased temperature variability, the pattern was less clear for the period at the beginning of the 20th century (around 1900-1930), and literally nonexistent for the period centered around 1840. Similarly, one of the main declines in temperature variability around 1870-1880 had a lower MY frequency. However, the period with the highest temperature variability around 1800 also exhibited a relatively low MY frequency. Expectedly, temporal dynamics of the mean values of the summer temperatures did not point to any pattern associated with MY occurrence.

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

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

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Tables

Table 1.

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

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

Table 2.

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

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

Figures

Fig. 1.

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

Fig. 2.

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

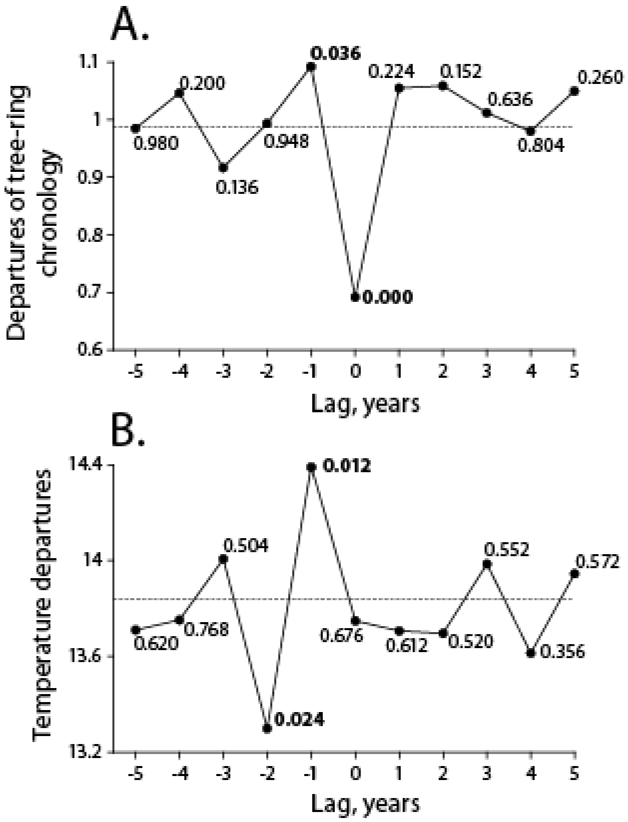

Fig. 3.

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

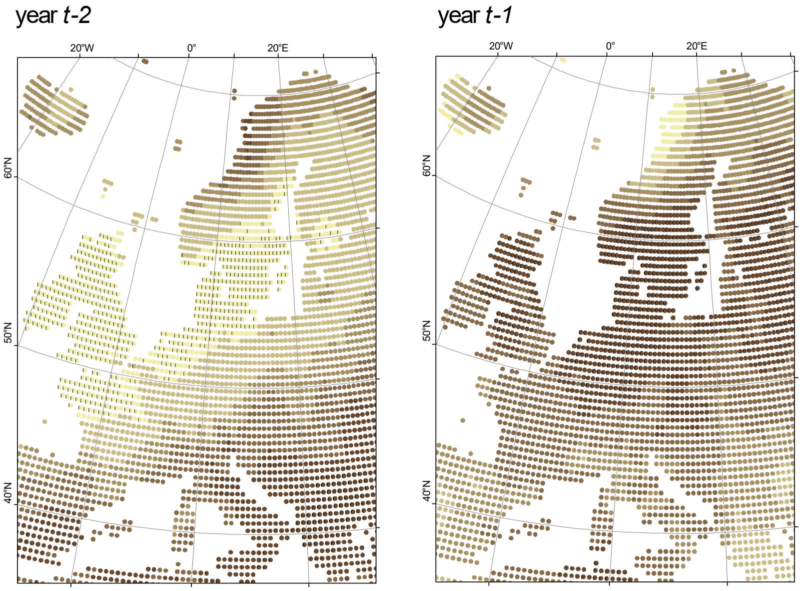

Fig. 4.

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

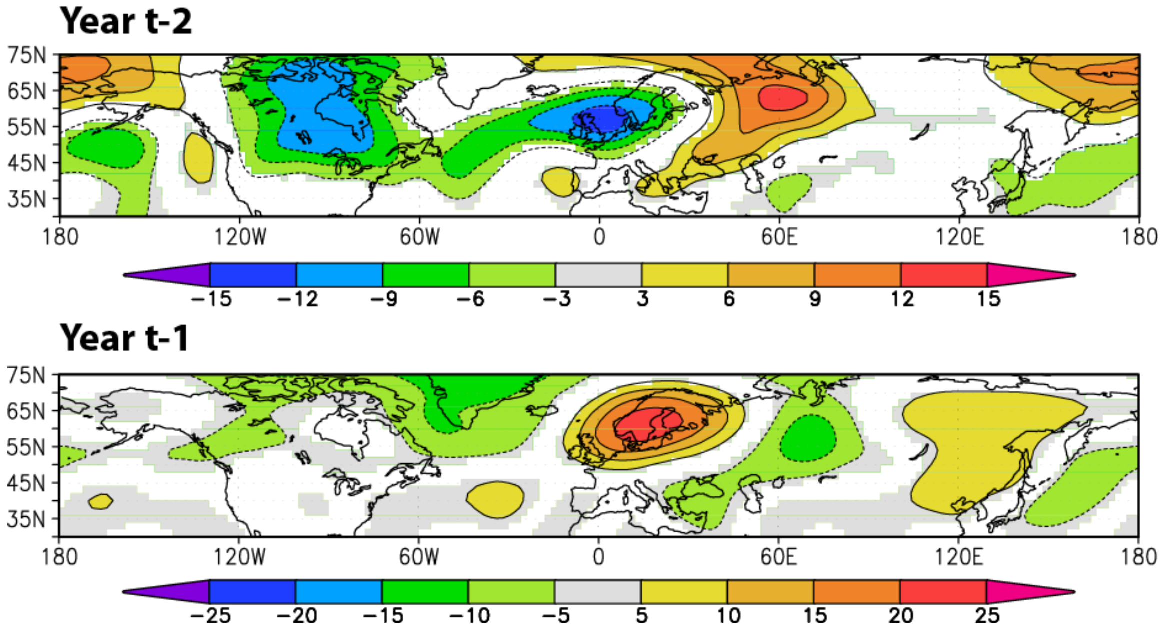

Fig. 5.

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

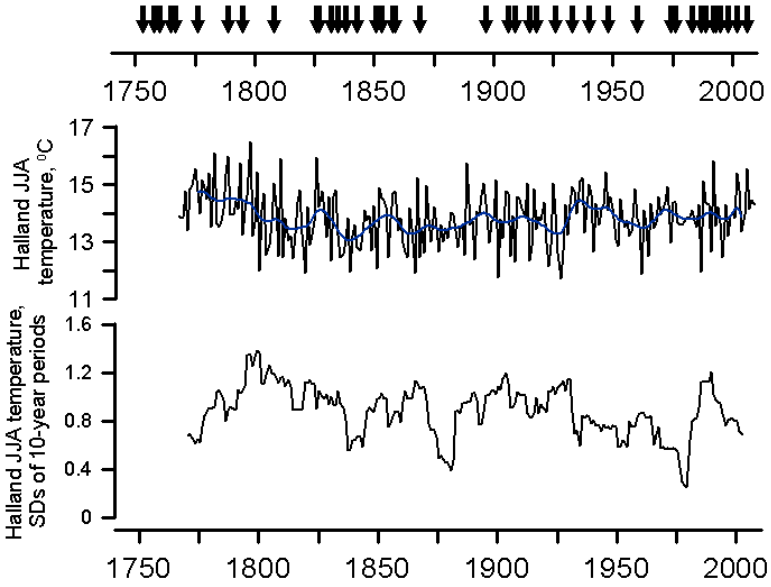

Fig. 6.

Probability of beech mast occurrence in the province of Halland during 1753 – 2006 and two sub-periods. For each sub-period, the probability function is shown with its respective 95% confidence envelope. The results represent a version of the reconstruction done with the early calibration of the model. Results of the reconstruction obtained with the late calibration are available in Supplementary Information Fig. C.