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Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden

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ABSTRACT

To identify weather controls of beech diameter growth and masting in southern Sweden, we analyze records of monthly weather, regional masting record, and tree-ring chronologies from five beechdominated stands. The results indicate a strong weather control of temporal pattern of masting events in southern Sweden over the second half of the 20th century. Negative summer temperature anomaly 2 years prior to a mast year, coupled with positive temperature anomaly in the year immediately preceding the same mast year, is a characteristic weather pattern associated with known mast years. Strong dependence of beech masting behavior on temperature explains the high degree of regional synchronization of masting events. Growth of beech in southern Sweden is strongly and negatively correlated with previous year's summer temperature and positively - with previous year's October temperature. The present study does not provide a conclusive answer in identifying a full set of direct and indirect effects of climatic variables controlling tree-ring growth, since the negative effect of previous year's summer temperature may be a result of a temperature-controlled increase in the beech nut production in the current year. Consistent and significant negative departures of ring-width index during mast years support the hypothesis about a trade-off between investment of bioassimilates into production of beech nuts and tree-ring growth. Alternative explanation of growth anomalies in mast years, relating such anomaly to a negative impact of previous year's growing season, was not supported by the data. We found a limited effect of masting on diameter growth in the following years, indicating that decline in the overall wood production, associated with heavy masting, is short term and typically occurs in the year of actual masting.

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1. Introduction

Synchronous production of large seed crops, or masting, has been observed in many trees of the temperate regions (Harper, 1977; Koenig and Knops, 2005). Although masting behavior may be an adaptive feature of species strategy to avoid seed predation (Boutin et al., 2006; Espelta et al., 2008), to optimize resource partitioning (Smith et al., 1990; Satake and Bjornstad, 2008) or seed dispersal (Vander Wall, 2001), there is a large body of evidence suggesting that it is the environmental conditions which control the actual timing of masting events (Piovesan and Adams, 2001; Hilton and Packham, 2003; Richardson et al., 2005; Övergaard et al., 2007; Hoshino et al., 2008). In many forested ecosystems, such events are closely linked to regeneration dynamic of species (Hanssen, 2003; Peters et al., 2005; Lazaro et al., 2006; Frey et al., 2007; Read et al., 2008), dynamics of animal populations (Gurnell et al., 2002; Selås, 2003; Hoshizaki and Miguchi, 2005; Shimada and Saitoh, 2006), and even to the temporal pattern of diseases carried by seed-feeding animals (Schauber et al., 2005). Understanding variation in masting-related environmental conditions can, therefore, relate biomass and energy flows to large-scale climatic forcing factors and help trace bottomup and top-down controls in ecosystem functioning (Satake and Iwasa, 2002).

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Masting behavior of beech species (Fagus and Nothofagus spp.) has been actively studied across its wide geographical range in Northern Hemisphere and in New Zealand (Piovesan and Adams, 2001; Yasaka et al., 2003; Richardson et al., 2005; Övergaard et al., 2007, and references therein). Common among these studies is the notion of a high degree of regional synchronization in the production of large seed crops, which was shown for northern Europe (Hilton and Packham, 2003; Övergaard et al., 2007), northern Japan (Kon et al., 2005; Suzuki et al., 2005), and even across North America and Europe (Piovesan and Adams, 2001). Not surprisingly, many studies found an association between masting events and weather conditions in the previous growing seasons. Good beech nut production of the year typically occurs after a year with high summer temperature and low precipitation, preceded by a year with low summer temperature and high precipitation (Piovesan and Adams, 2001). Similarly, in southern Sweden mast years have been followed by growing seasons in which the temperature in July and September was higher than the long-term 30-year mean (Övergaard et al., 2007).

Variation in the frequency of mast years can therefore be related to the variation in the temporal pattern of regional climatic triggers, which induce the formation of flower buds and investment of bioassimilates in nut production. Beech masting frequency, which generally varies between 3 and 10 years, has been reported to increase in many parts of Europe over the 20th century (e.g. Holmsgaard and Bang, 1990; Hilton and Packham, 1997; Schmidt, 2006; Övergaard et al., 2007, and references therein). This increase may be related to the higher frequency of warm periods and to the effect of higher nitrogen availability through atmospheric deposition (Falkengren-Grerup and Eriksson, 1990; Callesen et al., 2007) or direct fertilization of forest stands (Le Tacon and Oswald, 1977). Increased masting frequency could benefit practical forestry since it improves chances for successful regeneration of beech stands. However, even under increasingly less carbohydrate limited growing conditions (Körner, 2000), frequent mast years may also deplete tree's carbohydrate reserves and subsequently limit the amount of biomass allocated to the main stem. Considering regional synchronization of masting events in beech generally, such interaction may have a measurable effect on diameter and volume increments in beech forests.

Dendrochronologically, European beech is a relatively wellstudied species with the majority of tree-ring chronologies developed in southern and western parts of Europe (Biondi, 1993; Piovesan and Adams, 2001; Rozas, 2001; Lebourgeois et al., 2005; Piovesan et al., 2008). Analysis of beech chronologies from central Italy has shown that temperature during May and precipitation in July-August, together with amount of winter precipitation, are important climatic drivers of diameter growth (Biondi, 1993; Piovesan et al., 2003). In France, soil water deficit in early summer was shown to strongly affect ring increment in beech across a wide range of site conditions (Lebourgeois et al., 2005). It has been suggested that on decadal and centurial time scales the dynamics of beech tree-ring increment may also reflect large-scale atmospheric circulation patterns (Piovesan and Schirone, 2000; Bourquin-Mignot and Girardclos, 2001). However, in Northern Europe and in Sweden in particular, dendrochronological studies of beech are currently absent and to our best knowledge, no regional chronology exists for this species.

In Sweden, beech grows in mixed or pure stands to a latitude of ca. 58N (Dahl, 1998). The importance of this species in maintaining regional biodiversity (Nilsson, 1997) and as a timber resource (Löf, 2001) has been increasingly acknowledged. The interest in the afforestation practices and biological restoration activities, which make use of natural regeneration cycles (Agestam et al., 2003), requires a better understanding of beech reproduction ecology. Although a number of previous studies have analyzed the temporal dynamics of beech masting in Sweden (Carbonnier, 1971; Övergaard et al., 2007), mechanistic explanation of the interplay between environmental variation, diameter growth, and masting behavior in this part of the species distribution range is still inadequate. To address this knowledge gap and to advance our understanding of beech masting behavior and growth at the northern limit of its distribution in Europe, we analyze records of monthly weather, regional masting record, and tree-ring chronologies from five southern Swedish beech stands (Fig. 1). We formulate the following objectives: (1) identify weather variables related to occurrence of mast years, (2) identify main weather variables controlling diameter increment of beech, (3) evaluate the presence of trade-off between diameter increment and beech nut production. To address the first objective we use superimposed epoch analysis (SEA) to study the association between weather variables and masting record. For the second objective, we employ response function and correlation analyses operating with the monthly weather data, output of bioclimatic model, and beech site chronologies. For the third objective, we use linear regression techniques, SEA, and the result of the previous analyses to verify the presence of a trade-off between a masting event and growth. Finally, we discuss the possible applications of the study results in the forest management context.

2. Study area

The data analyzed in the paper were collected in the Swedish counties of Scania and Halland (Fig. 1). The mean annual temperature in this part of southern Sweden is between 6 °C and 8 °C. The mean temperature in January varies between -4 °C and 0 °C, and between 15 °C and 16 °C in July. There is a large variation in precipitation between the western (up to 1200 mm/ year) and the eastern (500 mm/year) parts of the region. The typical range is within 600-1000 mm/year. West or southwest wind prevails (Raab and Vedin, 1995). Growing period with mean daily temperature above 5 °C lasts 180-240 days (Nilsson, 1996). The soils of the study region bear a history of glacial dynamics and are formed on sandy and stony moraines (Fredén, 2002). The region lies in the nemoral and boreo-nemoral zones (Ahti et al., 1968), where the boreal and temperate biomes dominate. Norway spruce (Picea abies (L.) Karst.) and Scots pine (Pinus sylvestris L.) are the main coniferous species. Oaks (Quercus robur L. and Q. petraea (Matt.) Liebl.), European beech (Fagus sylvatica L.), and smallleaved species (downy birch, Betula pubescens Ehrh. and quaking aspen, Populus tremula L.) represent the deciduous component in the forest cover (Nilsson, 1996).



Fig. 1. Study area and location of sampled sites.

3. Materials and methods

3.1. Field sampling and sample preparation

During the summer of 2007 five plots were established in counties of Scania and Halland. Sites analyzed in this study. originally selected to be representative of regional beech forests, were monoculture beech forests and similar in site conditions, tree size distributions, and, except site HU, in mean stand age (Table 1). On each plot 20 trees were sampled on 10 m wide transects stretching across the plot in a random direction. The length of transects varied between 20 and 40 m to allow sampling of a predefined number of trees. The coordinates of the plot centers were obtained with the help of a GPS unit. Trees were cored along two radii at 1.36 m height from the ground with a Haglöf increment corer. Samples were mounted on wood and progressively polished with up to 400-grit sandpaper to allow clear recognition of annual rings under the microscope (using up to $40 \times$ magnification). We used a visual crossdating method (Stokes and Smiley, 1968) to precisely date each sample. Annual rings of prepared samples were measured with an accuracy of 0.01 mm using LinTab measuring stage and TSAP 3.0 software (Rinn, 1996). Verification of dating accuracy was done in COFECHA program (Grissino-Mayer, 2001). After crossdating and measuring of the samples, some of them were filtered out due to the presence of tension wood. The number of sampled trees finally included in the analyses varied between 17 and 19 trees per site.

3.2. Masting data

The regional masting record covered two time periods: between 1950 and 1964, and between 1974 and 2006. The record was a product of data compilation from direct observations, published records, unpublished manuscripts, and anecdotic records (Övergaard et al., 2007). It is important to note that the compiled record used here took advantage of southern Swedish sources only and did not infer occurrence of mast years in southern Sweden from masting records in neighboring regions. Dataset with quantitative assessment of annual beech nut production was available from site Ryssberg (Fig. 1). It covered the period between 1992 and 2006. In this case, we use threshold of 5×10^5 nuts/ha to classify the year as a mast year (Fig. A1 in Appendix 1). The number is related to a potential effect of masting event on beech regeneration: 50 beech acorns/m² were considered as a minimum amount to ensure successful beech regeneration in a Danish study (Henriksen, 1988). The same threshold was also used in a recent analysis of beech masting dynamics in Sweden (Övergaard et al., 2007).

3.3. Statistical analyses

Temporal association between masting events and weather variation was analyzed on the regional scale. Masting record was contrasted against monthly weather variables: average temperature, total precipitation sum, and bioclimatic variables (see next sub-section) in superimposed epoch analysis (SEA) performed in EVENT program (Holmes, 1999). We averaged site-specific weather data into regional variables and contrasted it against previously compiled list of southern Swedish mast years (Övergaard et al., 2007). We limited time frame of the analyses from 1974 to 2006 in all sites, except site HU where it was 1930–2006, with the temporal gap between 1964 and 1974. The reason for restricting the analyses to the most recent sub-set of mast years was the observation that beech masting generally occurs in trees older than 40 years old and, at the stand scale, since the stand age reaches 60–70 years (Simak, 1993). In our study, the start of the selected time period coincided with age of the trees at the DBH level being 45–65 years. Higher age of trees on the site HU allowed extension of this period to the year 1930.

Since our initial analyses pointed to a likely effect of both mast years and previous year's warm summers on the current year growth, we also used SEA to evaluate if the warmest years recorded in the study area over 20th century are associated with negative growth anomalies in the *following* years (*focal years*). A *focal year* was defined as a year with the previous growing season being among the warmest 20% of all years during the 20th century in the study region. We used gridded weather dataset of monthly temperature (0.1667⁰, approx. 16 km, Mitchell and Jones, 2005) and averaged values from all station locations.

We limited our consideration to the period 1950–2006 in order to (a) ensure that both masting record and sub-set of focal years cover the similar time period and (b) obtain similar number of events (mast years and focal years) in these analyses. Year 1950 corresponded to the average age of the trees being within 21 and 81 years. Number of actual years used in SEA varied between 8 and 10 on each site.

The same set of masting years as in masting-climate analysis (see beginning of the sub-section) was contrasted against site treering data to evaluate the relationship between seeding and biomass accumulation. As a source of tree-ring data, we used site residual chronology obtained in ARSTAN program. Crossdated tree-ring chronologies from single trees were detrended in ARSTAN program (Grissino-Mayer et al., 1997) using smoothing spline, which preserved 50% of the variance at a wavelength of 128 years. Each tree-ring curve was modeled as an autoregressive process with the order selected by the first-minimum Akaike Information Criterion (AIC). Index values for site and regional chronologies were computed by the division of the original tree curve values. The residual version of regional beech chronology, obtained by feeding ARSTAN with single tree chronologies from all sites, was used in the analyses of climate-growth and growthmasting relationships at regional scale (see below).

Climate–growth relationships were analyzed at each of the sites. In this case, residual chronologies were used to evaluate climate–growth relationships through response function analyses (Cook and Kairiukstis, 1990). Response function coefficients, in contrast to the common correlation coefficients, are produced using principal component regression analysis (Biondi and Waikul, 2004), which removes autocorrelation present in the climatic data. The response function coefficients were tested using the bootstrap

Table 1

Descriptive data on study sites and respective tree-ring chronologies. *n* refers to the number of dated and measured series for each site, used in the analyses. Age of the stand was estimated at breast height level. Site index is the dominant height of the stand at 100 years (Carbonnier, 1971).

Site name and ID	Site index	п	Age	Mean DBH	Average mean sensitivity	Signal-to-noise ratio	Signal strength (period, # of trees)
Floen, FL	F30	18	97	47.4	0.277	17.369	1910–2006, 9
Frodeparken, FR	F28	18	77	40.6	0.240	16.481	1940–2006, 9
Hultabugget, HU	F24	18	137	41.5	0.335	18.648	1880–2006, 7
Skarhult, SK	F26	19	87	49.3	0.257	22.501	1929–2006, 6
Trolleholm, TR	F30	17	97	57.2	0.249	17.944	1920–2006, 9

Signal-to-noise ratio is given for residual chronology. Number of trees is given for the value of 0.90 of signal strength (SS) statistics (Wigley et al., 1984).

method (Efron and Tibshirani, 1993) for their statistical significance. This included (1) random re-sampling of the original dataset with replacement, (2) generating a statistical distribution of a response coefficient, and (3) calculating its 2.5% and 97.5% distribution limits. Finally, the value obtained from the original dataset was compared with the bootstrap-generated distribution limits to assess the significance of the coefficient's departure from 0 at the 0.05 probability level. We analyzed the period between July of the previous season and current year July. Preliminary analyses with varying periods confirmed that increasing the number of previous season months had little effect on the outcome of analyses and did not increase the number of significant correlation and response function coefficients. We, therefore, attempted to limit the number of the months analyzed to improve statistical stability of the final results. The analyses were performed with the help of the DendroClim program (Biondi and Waikul, 2004), using mean monthly temperature and the total sum of monthly precipitation. All tests used a significance level of 0.05. To assess the temporal stability of significant response function coefficients in each of the DendroClim analyses, we calculated sets of response coefficients for the window of 55 years moving over the whole period available for a site. This value was the mid-point of the time interval suggested by DendroClim program.

To consider more accurately the temperature and water balance during each year's growing season we employed a bioclimatic model STASH, originally developed to study the effect of climate changes on species distributions and using factors considered to be physiologically important for the individual plant species (Sykes et al., 1996). The model calculated the total amount of accumulated growing season temperature above 5 °C, and the ratio of actual to equilibrium evapotranspiration (AET/EET) as a measure of growing season drought. For AET and EET, we used the algorithms described by Prentice (1993), with the soil water holding capacity set at 150 mm (Sykes et al., 1996). In these algorithms, AET is calculated as the minimum of the supply of water and the atmospheric demand in terms of EET, whereby the latter is driven by the amount of energy provided to the atmosphere through radiation (Jarvis and McNaughton, 1986). The water supply is proportional to soil moisture (Federer, 1982), calculated for a one-layer bucket model (Prentice et al., 1993).

The effect of mast years on diameter increment was analyzed as (a) the relationship between record of beech nut production and growth in the previous years, and (b) a change in the average increment over 2-4 years after a masting event. In the first case (a), we utilized the continuous 15-year record of beech nut production from the site RY (Fig. A1 in Appendix 1) and regional beech chronology, resulting from averaging of all site chronologies. In these analyses, the cumulative diameter growth over the period of 1-3 years was regressed against absolute number of beech nuts produced per ha annually. The 3-year time frame was selected to avoid overlapping with preceding/following masting years. In the second case (b), we used the regional masting record and single site chronologies to calculate the ratio between average increment 1-3 years prior to a mast year and average increment 1–4 years after that mast year. For these analyses we selected mast years which occurred later than 1974 and at least 3 years after the previous mast year. Such an approach allowed us to compare pre- and postmasting growth least affected by previous masting event. Selected years were 1983 and 1998. In addition, we considered a combination of two-in-a-row mast years of 1992 and 1993, a rare phenomenon reported only two times for the region of southern Sweden over the period of 1974–2006 (Övergaard et al., 2007). We hypothesized that if masting draws on tree's carbohydrate reserves, which otherwise will be used to diameter growth, the reduction in growth in such period would be most severe. In the

analyses of 1983 and 1998 we considered a 3-year time frame. In the case of 1992–1993, increments during the masting and the following years were contrasted against average increment over the two previous years to avoid including in the analysis of 1989, a regional mast year. The same approach was used for 1998 to avoid including the mast year 1995. Analyses were performed with the help of the routine IMP ("Impact before and after event") of the Dendrochronological Program Library (Holmes, 1999). For both analyses, non-detrended tree-ring chronologies were used to preserve autocorrelation effects, eventually containing the lagging effect of masting events.

4. Results

4.1. Weather patterns associated with mast years

The temperature of the two previous growing seasons was significantly related to the occurrence of mast years (Fig. 2). A cold growing season followed by a warm growing season, which, in turn, was followed by a mast year, was a pattern replicated in respect to July and August temperatures, as well as in respect to the total growth season temperature. No pattern was present between masting record and total monthly precipitation (results not shown) nor growth season drought index (ratio of actual and equilibrium evapotranspiration, Fig. 2E). We did not find any significant departures during the mast year itself in any of the variables analyzed.

4.2. Weather effects on tree-ring growth

The correlation and response function analyses revealed two consistent patterns in temperature–growth association (Fig. 3). On all sites, growth was negatively correlated with the previous year's summer temperature and positively – with the previous year's October temperature. No pattern was visible in respect to dormant season temperature and current year temperature. On two sites growth was positively correlated with current summer precipitation (sites HU and TR) and with dormant season precipitation (sites FR and TR).

Most of the above-mentioned effects of monthly weather on growth retained its significance when considered over a moving 55-year time frame (Fig. 4). The negative effects of previous year's July temperature became significant when the time frames were centered on 1970 (site FL) and 1960 (site HU). No clear pattern was visible in respect to dormant season precipitation. On three sites (FL, HU, and TR), a negative effect of previous August temperature became significant from 1950. On three sites (FL, TR, and SK) previous year's October temperature showed a period of nonsignificant association with growth, centered around 1960. A period of generally significant association occurred towards the end of the analyzed period. No temporal pattern was identified in respect of previous year's December precipitation on site FR. On site TR, February precipitation lost its correlation with growth since around 1950. On the same site, the effect of current year June precipitation showed a tendency to become significant since 1970.

4.3. Relationship between beech nut production and tree-ring increment

Mast years were associated with a significant decrease in ringwidth increment on three sites and we observed similar and closeto-significant pattern on two other sites (Fig. 5). We used SEA to check whether the negative growth anomaly in mast year was a direct function of warm weather in the previous year rather than of masting. We contrasted site chronologies with a sub-set of years with the previous year being within 20% of the warmest growing



Fig. 2. Superimposed epoch analyses of mast years and weather variables. Departure is the difference between actual and bootstrap-generated values of respective variable for a year. Mast year is shown as an unfilled circle. Dashed lines refer to 95% and 99% distribution limits of respective departure distributions. (A) June temperature; (B) July temperature; (C) August temperature; (D) sum of growing season average daily temperature; (E) growth season drought index.

seasons of the 20th century on each site (Fig. 5). In none of the sites were the growth index departures significant and no trend was visible in the data.

Previous ring increment showed significant positive association with the production of beech nuts in the following year ($R^2 = 0.438$, p = 0.007). However, this pattern was not significant when 2- or 3-year previous cumulative increments were considered ($R^2 = 0.237$, p = 0.065 and $R^2 = 0.092$, p = 0.272). Nut production did not affect diameter growth in the following 1–3 years (p > 0.05 and R < 0.05).

The effect of three selected mast years on beech growth on single sites varied widely across sites and among the years (Fig. 6). The increment in the mast year and the following 2 years could decrease down to 28% of the pre-masting level (years 1992–1993,

site HU), whereas a mast year was not necessarily associated with a growth decline (e.g. site FR after year 1983, site TR after year 1998). A mast year of 1983 generally produced little change in growth over the following 3 years. Mast year 1998 was followed by the recovery of the growth rate, taking place already during the second year after that mast event.

5. Discussion

5.1. Weather controls of masting events

Our results indicate a strong weather control with regard to the temporal pattern of masting events in southern Sweden over the



Fig. 3. Results of correlation and response function analyses on five beech site chronologies. Dots point to the significant response function coefficients at 95% range. Period covered along *X* axis is previous year's July to current year July. Lower-case letters indicate months of previous year and upper-case letters – months of the current year.

second half of the 20th century. A negative summer temperature anomaly 2 years prior to a mast year, coupled with positive anomaly in year immediately preceding a mast year, is a characteristic weather pattern associated with known mast years. We suggest that the observed temporal association is a result of weather effects on specific physiological processes involved in the initiation of flower buds, flower buds' maturation, flowering, and maturation of beech nuts. Lower temperatures 2 years prior to a mast year imply a lower evapotranspiration demand and lower associated cost of maintaining the fine root system during that year. We speculate that such conditions may have promoted the accumulation of bioassimilates and its subsequent investments in cambium tissues. Specifically, cooler conditions may benefit the development of bud meristems, which in European beech are formed 2 years prior to masting (Gruber, 2001). Similar to our results, a study of beech masting (Piovesan and Adams, 2001) over



Fig. 4. Dynamics of relationship between beech tree-ring increment and monthly weather variables. Selection of monthly weather variables was based on the results of correlation and response function analyses (see Fig. 3). Symbols refer to the significant response correlation coefficients between tree-ring data and one of six monthly weather variables for the 55-year period centered at respective *OX* coordinate (e.g. point at year 1972 would correspond to the 1945–2000 period). (\bigcirc) Previous year's July temperature, (\bigstar) previous year's August temperature, (\bigstar) previous year's October temperature, (\bigstar) previous year's December precipitation, (\blacktriangle) current year's February precipitation, (\blacksquare) current year's June precipitation.

different parts of its distribution range in the northern hemisphere, found that a moist and cool summer followed by a drought year increases the probability of a mast year.

Increased growing season temperature is commonly associated with increased production of seeds in the following year in many tree species (Houle, 1999; Selås et al., 2002). In our study, higher temperatures may have been important in promoting differentiation of primordia into flower buds, which occurs in the year immediately preceding the year of nut maturation (Büsgen, 1916; Gruber, 2001). A similar hypothesis relating masting to increased temperature during drought episodes was proposed by Piovesan and Adams (2001). In our study, however, precipitation showed no relationship with masting behavior, which was exclusively a temperature-mediated phenomenon. Temporal pattern of masting events apparently represents beech response to the sum of growing season temperature, and not a response to the temperature regime in a particular part of the growing season. Characteristic total growing season temperature patterns were consistently replicated in each of the summer month. Interestingly, the statistical significance of the effect of cold summer 2 years prior to a mast year was even higher than the significance of the warm period. We interpret this as an indication of the important role of tree nutrient status, which is positively affected by the periods with low evapotranspiration demand.

Our results support the view of European beech as a temperature-sensitive tree. Previously, a study of beech phenology in Croatia has shown a strong relationship between the length of leaf growth period and the mean annual air temperature (Tikvic et al., 2006). A study in Britain has shown a steep response of beech budburst to the length of the chilling period (Murray et al., 1989), which together with photoperiodic control of budburst (Heide, 1993), helps trees avoid damaging effects of late spring frosts (Dittmar et al., 2006; Visnjic and Dohrenbusch, 2004). High temperature sensitivity may be characteristic not only for European beech, but also for other trees in this genus. In a phenological study of North American hardwood species (Richard-



Fig. 5. Superimposed epoch analyses of site tree-ring chronologies with mast years (circles, dashed lines as 95% confidence limits) and *focal years*, i.e. years with warm previous year's growing seasons (stars, dash-dot lines as 95% confidence limits). Unfilled symbols indicate mast year (circle) or *focal year* (star). Record of mast years covered 1974–2004 for all sites except HU (1930–2006, with a temporal gap between 1964 and 1974). Record of focal years covered 1950–2006 for all sites. A set of focal years might include mast years.

son et al., 2006), accumulated degree-days accounted for around 90% of annual variation in the onset of spring canopy development in American beech (*Fagus grandifolia* Ehrh.).

Lack of significant departures in the tree-ring increment in the year preceding the mast year indicates that at this time the primordia differentiation into flower buds does not involve a shift in the allocation of available assimilates towards flower buds at the expense of lateral meristems. In our study, growth in the year before the mast year was positively correlated with the number of beech nuts produced in the following year. It supports the view that more favorable growing conditions could also promote higher primordia differentiation efficiency. The positive effects of higher resource availability on masting have also been reported for red oak (*Quercus rubra* L.) (Healy et al., 1999). The effect, similarly to

our study, was relatively moderate, compared to the role of weather variability.

Since drought stress itself was not related to the occurrence of mast years, the role of water availability in controlling beech masting behavior in southern Sweden appears limited. The observed pattern is probably due to generally sufficient amount of growing season precipitation in this region and the mesic conditions at the sampled sites. In line with our results, a study of dynamics of non-structural carbohydrate reserves showed that summer soil water deficit has a negligible effect on the accumulation of carbohydrate reserves, which continues in beech throughout the whole of the growing season (Barbaroux and Breda, 2002). Precipitation dynamics, however, may be an important factor in controlling masting behavior in other parts of beech's



Fig. 6. Effect of mast years on growth in the years following the mast years of 1983, 1992–1993, and 1998. Note differences in the scale of OY axis.

distribution range. For example, drought has been previously proposed as the main factor affecting beech masting patterns in Europe and eastern North America (Piovesan and Adams, 2001). The cited study, however, did not partition the effects of temperature and water deficit and, therefore, it could not assess the unique contributions of water balance and temperature in controlling masting pattern.

If our assumption about high temperate sensitivity of beech masting to temperature holds, it may explain the high synchronicity of mast years over large geographical regions (see e.g. Hilton and Packham, 2003; Kon et al., 2005; Övergaard et al., 2007). Temperature variation, synchronizing meristem activity among trees (Gruber, 2001), generally has a strong regional component and is little affected by site factors, as compared to the stand's water regime, driven by more local pattern of precipitation, which is further modified by the stand's soil profile.

5.2. Dynamics of ring-width increment and trade-off effects

The present study does not conclusively identify a full set of direct and indirect effects of climatic variables controlling beech tree-ring growth. Response function analyses show a strong and consistently negative correlation between beech growth and previous year's summer temperature. This pattern may indicate that a high evapotranspiration demand, resulting in increased costs of maintaining water conductive tissues and fine root system, may deplete structural carbohydrate reserves, therefore limiting potential investments into diameter growth in the following year. Support for this hypothesis comes from the dependence of current year growth on previous year's carbohydrate reserves in European beech (Saurer et al., 1997, but see Lebourgeois et al., 2005). Generally, higher mid-summer aridity in the previous year was often reported as negative for the following year growth in several trees of the European temperate zone, including beech (Lebourgeois et al., 2005), pedunculate oak (Drobyshev et al., 2008), and Scots pine (Drobyshev et al., 2004; Miina, 2000). However, the absence of positive correlation with precipitation during previous year's growing season (Fig. 3) implies that effects of water deficit do not measurably limit tree-ring growth in the studied sites.

Alternatively, the effect of negative correlation between growth and previous year's summer temperatures may be a product of temperature-controlled pattern of beech nut production. Although in the current study we analyzed only the records from large mast years, one could suggest that the same set of factors may be influential in regulating the production of beech nuts also in the non-masting seasons. If this assumption holds, a negative correlation of warm previous growing seasons with current year growth would result from an increased proportion of available assimilates allocated for the production of nuts in the current year, and not from direct effect of high evapotranspiration demand on diameter growth. In our study, however, no sites had both sufficiently long and continuous masting chronology and tree-ring record, a combination that would allow us to partition the direct and indirect effects of previous year's summer temperatures.

The positive association between growth and average temperatures during the previous October could be a result of an extended period of physiological activity at the end of the growing season. This may improve relocation of transportable nutrients from leaves to perennial parts of the tree, making more nutrient and energy reserves available for growth during the next season. Studies on species from the same family support this assumption. For sessile oak (*Q. petraea* Mill.), Barbaroux and Breda (2002) showed that maximum storage of reserves in the wood is reached in October. Similarly, red oak (*Q. rubra* L.) exhibited a peak in translocation of sugars from the leaves to the main stem during late October (Xu and Griffin, 2007). High temperatures of previous year's October may also positively affect pre-winter hardening of the trees. Since the amount of non-structural carbohydrates in plant tissues is generally linked to the degree of frost tolerance (Sakai and Larcher, 1987), a warmer October would mean a higher degree of translocation, which, in turn, may increase the resistance of beech trees to low temperatures during the dormant period.

Although the patterns of weather-growth relationship generally hold while analysis was restricted to shorter subperiods (Fig. 4), our results demonstrate that weather controls of European beech growth are dynamic and may reflect dominant weather at the scale of several decades. Two the most consistent patterns were: (a) disappearance of significant association between previous year October temperature and growth during the period centered around 1950-60, and (b) association of significant effect of the previous summer temperature with the period 1950-70. Although such temporal effects might be caused by similar stand history and reflect impact of a single disturbance event or silvicultural treatments on weathergrowth interactions, synchrony in observed pattern points to the changes in the dominant weather conditions as a likely source of this dynamics. Examination of instrumental weather records (Fig. 7) suggests that the variation in significance of growth-weather relationships was paralleled by changes in the levels of respective monthly variables. Particularly, the period with non-significant October influences was warmer, which may indicate non-linear nature of the effect of this factor on growth. We hypothesize that a gain in efficiency of translocation and/or pre-winter hardening, associated with warmer previous year's October, disappears when mean temperature for that month reaches 8.5 °C.

The period that was significantly influenced by the previous year's summer temperatures on growth was, in fact, cool at the centurial scale, although the temperature showed an overall increasing trend. A similar non-linear effect seems unlikely in this case as it might be expected that a statistical manifestation of generally negative effect of summer temperatures on growth would be more pronounced during a period with warmer



Fig. 7. Monthly temperature variation in the study area over 1901–2000. Data are the average of site-specific weather datasets for all studied sites. Curves represent 25-year running averages of mean July–August temperature (solid line, right *OY* axis) and mean October temperature (dashed line, left *OY* axis). Running mean window is chosen to approximate half-size of the moving window in the response function analyses (see Fig. 3).

summers. We observed, however, the opposite pattern. Its origin is not clear, but it is worth noting that at that time most of the stands were around 40–60 old, a period when trees start to exhibit pronounced masting cycles (Simak, 1993), which, in turn, may interact with weather–growth relationships. Previously, changes in climate–growth association were documented for many tree species (Biondi, 2000; Smith et al., 1999; Tardif et al., 2001). We propose that in beech, changes in dominate weather patterns may have both direct and indirect effects on growth, the later resulting from strong link between weather and seeding behavior.

Consistent negative departures of ring-width index during mast year support a hypothesis about a trade-off between tree-ring growth and investment of bioassimilates into production of beech nuts. An alternative explanation for the growth anomaly, relating it to negative impact of previous year's growing season, was not supported in the analyses on the sub-set of the 20% warmest years, which were not associated with significant growth reductions in any of the sites. During mast years trees generally invest substantial amount of nitrogen in nut production (Sinclair and de Wit, 1975) and exhibit low concentration of starch in perennial tissues (Owens, 1991), which is indicative of a tree's low nutrient status. Seasonal observations further support the notion of the trade-off effects in European beech timing of nut maturation was associated with lower concentration of storage carbohydrates in stems and branches (Hoch, 2005).

Our results are in line with observation of 40% reduction of diameter increment during mast years in beech (Holmsgaard, 1955) and similar reductions in other tree species during mast years (Eis et al., 1965; Monks and Kelly, 2006; Selås et al., 2002). However, trade-off effect between seed production is not a universal phenomenon in the genus *Fagus*, and in *Fagaceae* in general. A study of *F. crenata* in northeast Japan did not find a consistent reduction in the diameter increment during mast years, suggesting sufficient levels of nutrients in the perennial tissues to support both biomass accumulation and mass production of nuts (Yasumura et al., 2006).

In this study we used population-level data (average site chronology, and regional and site masting data) to analyze trade-off in life history traits. Although this approach is sometimes questioned due to potential differences in data origin (e.g. Monks and Kelly, 2006), we consider it adequate and justified in our study. We can support the use of mean population data by strong synchronicity of mast events across beech trees over geographical regions (Piovesan and Adams, 2001) and within single stands, including the sites analyzed in this paper (Övergaard et al., 2007). On the other hand, obtained tree-ring chronologies showed similarly high level of synchronicity in annual ring growth as it is suggested by high values of signal-to-noise ratio (Table 1).

The effect of masting on diameter growth of beech in southern Swedish beech is short term. Analysis of a continuous record of beech nut production (i.e. including both masting and non-masting years) did not reveal any correlation between the number of nuts and growth in the following years, suggesting that the recovery of carbohydrate reserves already occurs in the season following the mast year. In line with this, growth dynamics in the years following the masting season did not reveal consistent pattern across different mast years (Fig. 6).

5.3. Implication for the practical beech management

The use of natural sources of nuts to ensure regeneration after clear- or partial cuts could considerably reduce the overall management costs of beech stands. Robust climatic controls of beech masting behavior facilitate the use of beech masting events for the regeneration of commercial stands. Regional temperature records within a 2-year time frame are of value in predicting such events. In this context, it is of practical interest to consider absolute values of monthly weather variables associated with mast years. For the cold year 2 years prior to masting event, the mean monthly temperatures were 13.5, 15.5, and 15.3 °C for June, July and August, respectively. Long-term means calculated for the 1901–2001 period were higher (14.4, 16.5, and 15.9 °C, respectively). A warm year immediately preceding masting showed an inverse pattern: 14.8, 17.7, and 16.7 °C, respectively. Approximating these differences for practical purposes, one can conclude that 1 °C difference in mean monthly departures for the June and August, and 2 °C difference for July in two following years, deviating from the long-term means in the negative and then positive directions, should be a good mast year predictor.

We found a limited effect of masting on diameter growth in the years following a masting event, indicating that decline in the overall wood production, associated with heavy masting, is shortterm and is concentrated in the year of actual masting. Finally, improved diameter growth in the previous years translates into higher masting intensity. Better site conditions maintaining high growth rates can therefore ensure higher amount of nuts produced during a mast year. Analyses of heavy masting years and regional growth support this conclusion, although there are at present little data to verify this interaction on a long *and* continuous masting record at the stand scale.

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Appendix A

See Fig. A1.



Fig. A1. Seed production data from Ryssberg (redrawn from Övergaard et al., 2007), representing the longest instrumental *and* continuous masting chronology in southern Sweden.

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