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The influence of masting phenomenon on growth–climate relationships in trees: explaining the influence of previous summers' climate on ring width

Andrew J. Hacket-Pain^{1,4}, Andrew D. Friend¹, Jonathan G.A. Lageard² and Peter A. Thomas³

¹Department of Geography, University of Cambridge, Cambridge, CB2 3EN, UK; ²School of Science and the Environment, Manchester Metropolitan University, Manchester, M1 5GD, UK; ³School of Life Sciences, Keele University, Keele, ST5 5BG, UK; ⁴Corresponding author (ajh220@cam.ac.uk)

Tree growth is frequently linked to weather conditions prior to the growing season but our understanding of these lagged climate signatures is still poorly developed. We investigated the influence of masting behaviour on the relationship between growth and climate in European Beech (*Fagus sylvatica* L.) using a rare long-term dataset of seed production and a new regional tree ring chronology. *Fagus sylvatica* is a masting species with synchronous variations in seed production which are strongly linked to the temperature in the previous two summers. We noted that the weather conditions associated with years of heavy seed production (mast years) were the same as commonly reported correlations between growth and climate for this species. We tested the hypothesis that a trade-off between growth and reproduction in mast years could be responsible for the observed lagged correlations between growth and previous summers' temperatures. We developed statistical models of growth based on monthly climate variables, and show that summer drought (negative correlation), temperature of the previous summer (negative) and temperature of the summer 2 years previous (positive) are significant predictors of growth. Replacing previous summers' temperature in the model with annual seed production resulted in a model with the same predictive power, explaining the same variance in growth. Masting is a common behaviour in many tree species and these findings therefore have important implications for the interpretation of general climate–growth relationships. Lagged correlations can be the result of processes occurring in the year of growth (that are determined by conditions in previous years), obviating or reducing the need for 'carry-over' processes such as carbohydrate depletion to be invoked to explain this climate signature in tree rings. Masting occurs in many tree species and these findings therefore have important implications for the interpretation of general climate–growth relationships.

Keywords: European beech, *Fagus sylvatica* L., growth–climate relationships, growth–reproduction trade-off, masting, plant–climate interactions, seed production, tree growth, tree rings.

Introduction

Tree growth is commonly reported to be influenced by the climate of previous years in a range of ecosystems and species, including studies employing dendrochronology (e.g., [Wettstein et al. 2011](#)), eddy covariance and biometry (e.g., [Capioli et al. 2011](#)), and remote sensing (e.g., [Verbyla 2008](#)). Strong correlations between radial growth and climate of the previous year have been reported in boreal, temperate and tropical forests and in a wide range of tree

taxa (e.g., [Boninsegna et al. 2009](#), [Babst et al. 2013](#)). In *Fagus sylvatica* L., a widespread deciduous tree of European forests, dendrochronological studies report statistically significant correlations with previous summer climate more commonly than any other climate signal (A.J. Hacket-Pain and L. Cavin, unpublished data). However, the mechanism underpinning this lagged response of growth to previous summer climate is still poorly understood, specifically in *F. sylvatica* but also in other tree species.

Annual tree growth depends on photosynthesis during the year of growth to provide the carbon required to build tissues, but stored carbon reserves are also believed to be of importance, particularly during the early part of the growing season when the sink strength from canopy development and wood formation are high (Capioli et al. 2011). For example, Skomarkova et al. (2006) found that 10–20% of total ring width in *F. sylvatica* was formed using remobilized carbon from previous growing seasons. This use of stored carbohydrates is used to explain autocorrelation in tree ring chronologies, and also the influence of previous years' weather conditions on ring width. For example, climate conditions generally unfavourable to carbon reserve accumulation such as high temperatures or drought could reduce the carbon available for remobilization the following year. If growth is subsequently lower in the following year, this will create a correlation between ring width and previous summer climate—a so-called 'carry-over' effect (Figure 1a).

However, it remains unclear to what extent carbon reserves actually are influenced by variation in climate, including unfavourable conditions such as drought. In *F. sylvatica* for example, Hoch et al. (2003) found that carbon reserves were not significantly depleted during unfavourable years. If carbon reserves act as a passive carbon pool (i.e., they simply reflect the balance of

carbon sources and sinks), then these observations indicate that individual years of unfavourable climate are unlikely to deplete reserves sufficiently to cause a growth reduction in subsequent years (Sala et al. 2012b).

A carry-over effect could also be caused by climate-induced plant organ mortality in unfavourable years, leading to reduced growth in subsequent years. For example, drought conditions have been demonstrated to increase fine root, leaf and twig mortality in *F. sylvatica* and many other species (e.g., Peterken and Mountford 1996, Rust and Roloff 2004, Mainiero and Kazda 2006). Leaf or twig mortality may also have an impact on growth in subsequent years due to the cost of replacement, or due to reduced whole-plant photosynthesis (GPP) in the following year if leaf area is lowered. A similar mechanism stems from the observation of Power (1994) that climate conditions influence the formation of *F. sylvatica* leaf buds from which the following year's leaf area will grow, which suggests that unfavourable conditions during bud formation may reduce the number of leaf buds and subsequently whole-plant leaf area.

An alternative explanation for lagged correlations between radial growth and previous summer climate is based on a relationship between climate, seed production and radial growth as proposed by Piovesan and Schirone (2000) (Figure 1b). *Fagus*

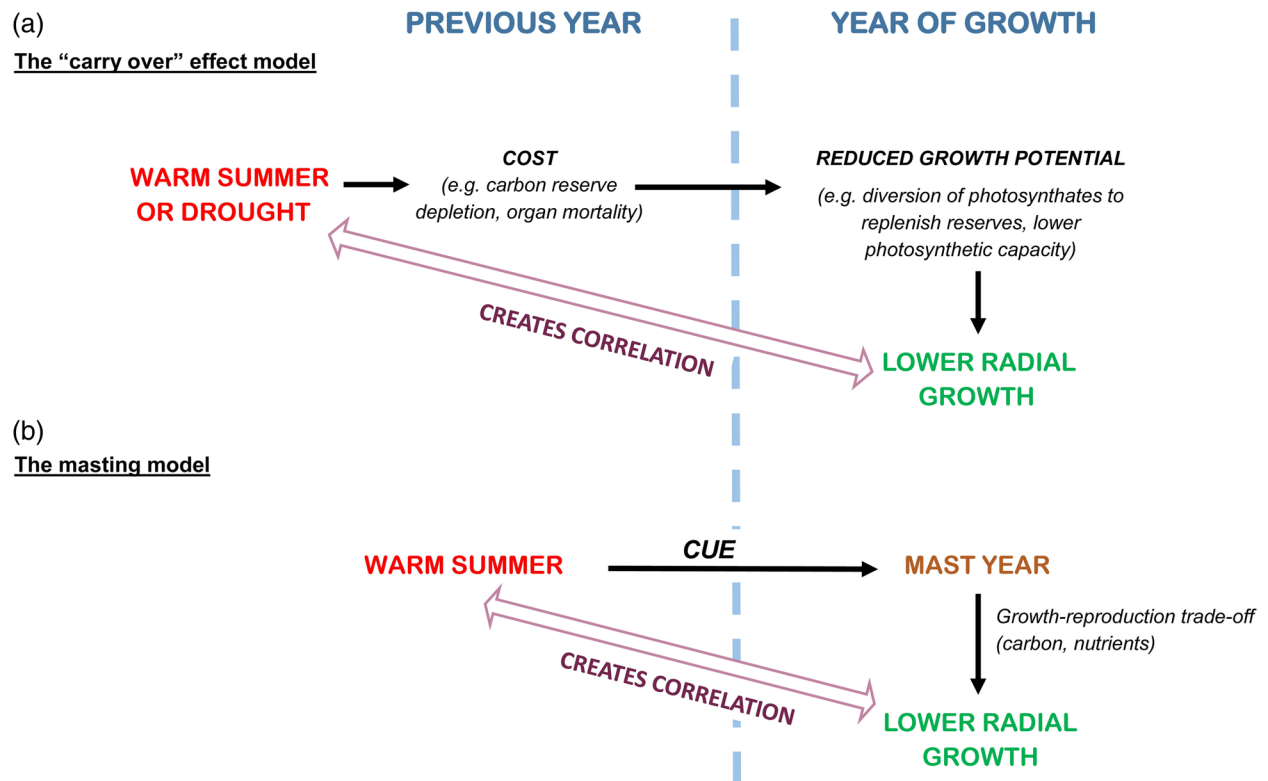


Figure 1. The two alternative models for explaining lagged correlations between ring width and previous summer climate. In the 'carry over' effect model (a), the correlation is created by unfavourable conditions reducing growth the following year due to reduced growth potential. This may be a consequence of either reduced GPP or the allocation of carbon from growth to repair damaged plant organs or replenish depleted reserves. In the masting model (b), warm summers cue a masting event the following year, which in turn reduces ring width due to the growth–reproduction trade-off. This creates the correlation with previous summer temperature.

F. sylvatica is a masting species (Hilton and Packham 2003), along with many other tree genera including *Quercus*, *Pinus* and *Picea* (e.g., Sork et al. 1993, Mencuccini et al. 1995, Koenig and Knops 2005). Piovesan and Schirone (2000) proposed that during years of heavy seed production ('mast years'), radial growth is reduced due to a diversion of resources away from growth and towards reproduction, due to a so-called 'growth–reproduction trade-off'. Masting events in many species, including *F. sylvatica*, appear to be triggered by weather-related cues, particularly previous summer temperature (e.g., Piovesan and Adams 2001, Schaubert et al. 2002). Consequently, weather-related phenomena can produce growth reductions, but these are due to the relationship between climate and masting rather than a direct effect on productivity, creating the correlations between growth and temperature of the previous summer (Figure 1b) (Di Filippo et al. 2007). Drobyshev et al. (2010) investigated this phenomenon in *F. sylvatica* using tree ring chronologies and masting data from southern Sweden. They found that masting events were indeed associated with warm previous summer temperatures, that radial growth was negatively correlated with warm previous summer temperatures, and that radial growth was lower in mast years than non-mast years. However, they did not integrate weather, radial growth and masting into a single analysis, and consequently the potential of this explanation has still not been fully tested in the literature.

In this study, we test the hypothesis that correlations between *F. sylvatica* growth and previous summers' weather are the result of weather-cued masting events, which are strongly associated with a characteristic sequence of a cool summer followed by a warm summer, and lead to a strong growth–reproduction trade-off (and consequently a narrow tree ring). To investigate the relationships between seed production, growth and weather conditions, we used a rare long-term record of seed production and reconstructed tree growth using dendrochronological techniques. We tested whether growth was reduced in mast years, and whether this could create the lagged correlations between growth and previous summers' weather conditions. We believe that this is the first published analysis that has rigorously tested the hypothesis that masting behaviour can explain lagged correlations between growth and previous years' climate in tree species with strong masting behaviour. Although we only investigated this mechanism for *F. sylvatica*, we also discuss how the results may explain observed growth–climate relationships in other tree species, where climate-cued masting behaviour is commonly observed and where correlations between growth and previous years' climate are also frequently reported.

Materials and methods

Study region

The study was conducted in southern England in order to take advantage of an existing long-term regional masting record (see

below). To produce a regional record of tree growth comparable to the regional masting record, tree ring chronologies were created for eight sites across southern England (Figure 2). Table 1 gives details of these sites, including the age of the stands and the local geologies. Southern England has a temperate maritime climate, with a mean annual temperature (1961–2010) of $\sim 10^{\circ}\text{C}$. Annual precipitation is highest in the west ($>1000\text{ mm}$) and declines to the east ($<600\text{ mm}$ in some regions), although there is much less variation in summer precipitation, which is 200–250 mm across most of the study area.

Study species

Fagus sylvatica L. is a shade-tolerant species, typically forming monospecific stands (Peters 1997). The species is one of the most widely distributed tree species in Europe, with a distribution stretching from the mountains of southern Europe to southern Sweden. *Fagus sylvatica* exhibits strong synchronous regional patterns of seed production across wide regions (Hilton and Packham 2003, Packham et al. 2012).

Tree ring data collection and processing

Tree growth at each of the eight sites was estimated using tree rings. Cores were extracted from a total of 186 trees, with two cores taken per tree at all sites, except NET where only one core was removed. Table 2 provides details on the number of trees and cores sampled at each individual site. Cores were extracted at 1.3 m above ground level, and perpendicular to any slope in order to avoid tension wood, as is standard practice in dendrochronology (Grissino-Mayer 2003). Sample preparation followed standard dendrochronological methods (Speer 2010) with samples air dried, and then mounted and sanded with progressively finer paper until the ring boundaries were clearly visible. Cores were then scanned at either 1600 or 2400 dpi

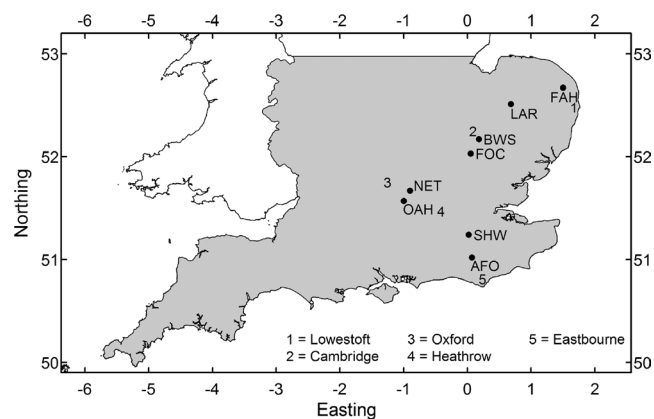


Figure 2. Map of the study region. Black dots represent the sample sites (for full site names and details see Table 1), while the shaded region is the area represented by the UK Met Office southern England climate time series. It also represents the approximate region represented by the southern England beech masting record of Hilton and Packham (2003). The numbers refer to the locations of the meteorological stations used for the analysis of growth–climate relationships for individual sites.

Table 1. The location and description of the eight sampled sites. The site codes are used in Figure 3 and to refer to individual sites in the text.

Site code	Latitude (°N)	Longitude (°E)	Elevation (m)	Mean DBH (cm)	Canopy species	Local Met station (distance, km)
FAH	52.70	1.50	9	68.01	<i>F. sylvatica</i> , <i>Quercus</i> spp.	Lowestoft (27)
LAR	52.51	0.69	27	48.27	<i>F. sylvatica</i> , <i>Acer pseudoplatanus</i>	Cambridge (50)
BWS	52.17	0.17	50	39.97	<i>F. sylvatica</i>	Cambridge (4)
FOC	52.04	−0.06	115	37.95	<i>F. sylvatica</i>	Cambridge (21)
SHW	51.22	0.02	90	75.62	<i>F. sylvatica</i> , <i>Quercus</i> spp.	Heathrow (42)
AFO	51.07	0.07	110	58.03	<i>F. sylvatica</i>	Eastbourne (36)
OAH	51.68	−0.91	250	50.00	<i>F. sylvatica</i> , <i>Quercus</i> spp.	Oxford (26)
NET	51.57	−0.98	172	48.19	<i>F. sylvatica</i>	Oxford (28)

Table 2. Chronology statistics for the individual sites and for the combined southern England chronology (SENG). Statistics are calculated for the period of study only (1921–2010). Period refers to the period of a truncated chronology where the number of cores is >5. All the chronology stats are calculated for this period. MS, mean sensitivity (a measure of the relative change between adjacent ring widths); AC, first order autocorrelation; EPS, expressed population signal; rbar, the average correlation between the tree ring series (tot, all cores; wt, between cores from the same trees; bt, between different trees). Note that two cores were extracted from all sampled trees (except at NET), but the number of cores refers only to those successfully measured and cross-dated and included in the mean chronologies.

Site	No. of trees (cores)	Period	Mean ring width (SD) (mm)	MS	AC	EPS	rbar.tot	rbar.wt	rbar.bt
FAH	20 (36)	1860–2010	1.981 (0.969)	0.298	0.303	0.933	0.382	0.547	0.377
LAR	22 (32)	1958–2009	4.161 (1.049)	0.167	0.329	0.960	0.507	0.651	0.503
BWS	22 (37)	1846–2010	1.078 (0.518)	0.209	0.397	0.929	0.347	0.487	0.343
FOC	21 (35)	1862–2010	1.219 (0.547)	0.170	0.656	0.927	0.346	0.447	0.343
SHW	22 (37)	1913–2009	2.975 (0.932)	0.203	0.326	0.938	0.372	0.469	0.369
AFO	19 (35)	1914–2009	2.491 (0.805)	0.166	0.697	0.902	0.285	0.507	0.279
OAH	24 (42)	1852–2011	2.207 (0.602)	0.185	0.399	0.896	0.244	0.389	0.241
NET	39 (39)	1801–2012	1.284 (0.454)	0.196	0.635	0.881	0.233	–	0.233
SENG	186 (276)	1921–2010	1.534 (0.525)	0.168	0.238	0.981	0.206	0.487	0.205

(the latter where very narrow rings were present in the core), and ring widths were measured using the software *CooRecorder* v7.3 (Larsson 2010b). Cross-dating involved the statistical comparison of patterns of ring widths between individual cores in order to ensure that all rings are assigned to the correct year of growth. Initial cross-dating was conducted in *CDendro* v7.3 (Larsson 2010a), and then checked for each individual site using the standard dendrochronological software *COFECHA* (Grissino-Mayer 2001). The results of the cross-dating for each site are given in Table 2. In total, 276 cores from 186 trees were cross-dated, with a total of 32,109 measured rings.

Raw ring width chronologies typically contain low-frequency (i.e., decadal and longer) signals associated with changes in tree age and size, canopy position and long-term changes in the abiotic environment (Fritts 1976). In order to investigate the relationship between annual growth and climate, this low-frequency variance was removed by detrending using the R package ‘*dplR*’ (Bunn et al. 2012), individually fitting each core’s raw ring width series with a 32-year cubic spline with a 50% frequency cut off. Dimensionless ring width indices were created for each core by dividing the observed ring width by the spline. These individual detrended ring width indices were then averaged across sites for each year in order to produce a mean ring width index (RWI) representative of southern England (SENG, the same region

represented by the masting record). Comparison with other tree ring studies involving *F. sylvatica* in this region suggests that the SENG chronology can be considered representative for the whole of southern England (Wilson et al. 2008, Cavin et al. 2013).

Annual seed production data

Data on masting for *F. sylvatica* across southern England were taken from a mean annual masting record for the region published by Hilton and Packham (2003), with additional previously unpublished data up to 2010. The record is a compilation of records from various sources and locations, and is shown in Figure 3. The record spans from 1921 to 2010, but unfortunately data are not available for 1951 and 1952 as no records exist from these years. The masting record is based on a semi-quantitative five-point scale, from 1 (very poor masting) to 5 (very good masting), with categories 4 and 5 being considered mast years, and represents a regional record of masting across southern England (Hilton and Packham 2003).

Climate data

Both RWI and masting time-series were analyzed with respect to weather conditions. Climate data were taken from the UK Met Office regional climate time-series for southern England (UK Met

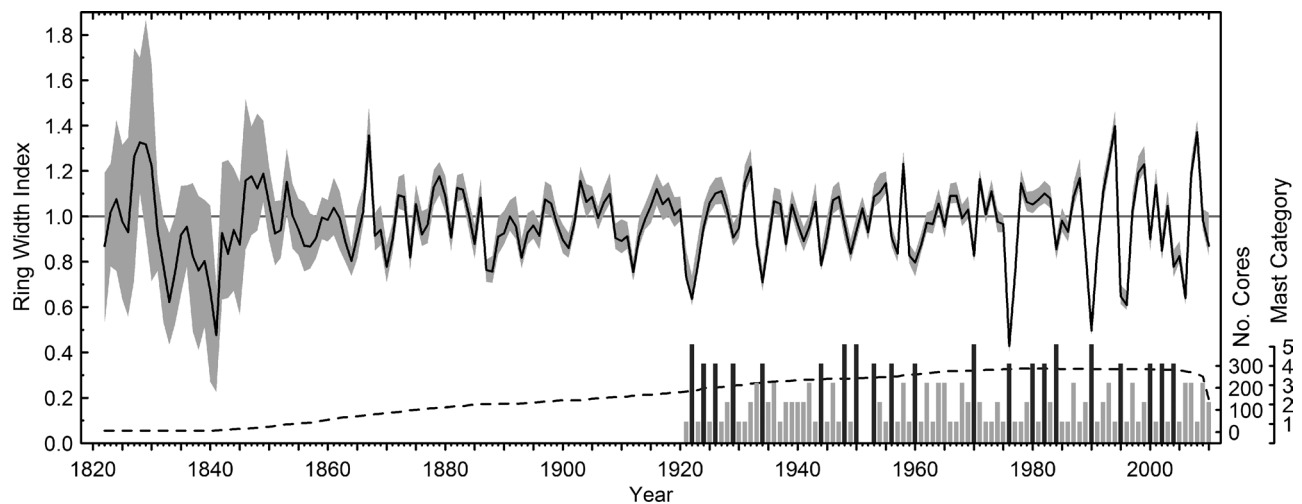


Figure 3. The southern England (SENG) ring width index chronology and masting record. The solid black line is the mean SENG RWI chronology, and the grey region represents the 99% confidence interval, estimated using bootstrapped resampling (1000 resamples). Note that only the period 1921–2010 was used for analysis. The dashed line is the sample depth (i.e., the number of cores contributing to the chronology in a given year). The bars represent the masting record for southern England for *F. sylvatica* L. Annual seed production was recorded on a five-point scale from 5 (very good masting) to 1 (very poor masting). Categories 4 and 5 (black) are considered mast years (i.e., years of high seed production), while categories 1–3 (grey) are considered non-mast years (i.e., low or no seed production). Data taken from [Hilton and Packham \(2003\)](#).

[Office 2013](#)), which represents the same region as the masting and tree ring datasets (Figure 2). Monthly mean daily 24 h maximum temperature (*MAX*) and monthly precipitation (*PREC*) were used as independent variables. Additionally, drought was quantified using the Standardized Precipitation–Evapotranspiration Index (*SPEI*; [Vicente-Serrano et al. 2010](#)) using a 3-month window such that the drought index for July additionally incorporated data for May and June (all months were equally weighted). *SPEI* is a standardized index of the difference between monthly precipitation and potential evapotranspiration. For all independent variables, monthly values from the year of masting, and the two previous years, were examined, with months in the previous calendar year notated in the following analysis using $-t$, with t being the number of years. For example, $PREC_{APR-1}$ represents the monthly precipitation of April 1 year prior to the growth measurement used as the dependent variable.

Analysis

In order to investigate the link between masting and lagged correlations between growth and previous summer weather conditions, masting and growth first needed to be shown to share the same climate signals. Previous analysis of part of the seed production dataset used here had demonstrated that mast years were associated with positive summer temperature anomalies and negative anomalies in the summer 2 years prior to masting ([Matthews 1955](#), [Piovesan and Adams 2001](#)). In this study individual correlations between climate and masting category were calculated for all the monthly temperature, precipitation and drought indices described above using ordered logistic regression.

Multiple linear regression models were used to investigate relationships between RWI and monthly climate variables. A subset of

the data (1953–2010) was used for model fitting, with an independent subset of the data (1921–50) used for validation. Although the relationships between growth and climate are expected to be non-linear, a linear approach was employed to maintain a model as simple as possible. The model takes the form:

$$RWI = \alpha + \beta_1(X_1) + \beta_2(X_2),$$

where α is a constant and β_n is the coefficient associated with the independent variable X_n .

Parameters in the regression models were estimated using ordinary least squares with independent variables selected using backward selection. Adjusted R^2 and Akaike Information Criterion (AIC) were used to compare models. The optimal model was then checked to ensure that all independent variables were significant at the 95% confidence level using an *F*-test.

The first model developed included as independent variables only the monthly weather of the year of growth and the two previous years, and is referred to as Growth Model 1 (GM1).

Then, to test the hypothesis that an interaction between climate, masting and growth was responsible for the relationship between growth and previous summer climate, seed production was added as an independent variable (as a five-category factor), and the new optimal model (Growth Model 2, GM2) selected using the same procedure.

If a trade-off between growth and seed production is responsible for the lagged climate signals in the tree ring chronologies (Figure 1b), then, because seed production increases with tree age (as a proportion of whole-plant NPP) ([Genet et al. 2010](#)), the relative effect of masting is likely to increase with age. To test this, Pearson product-moment correlation coefficients were

calculated between previous summer temperature and RWI for each of the eight individual sample sites for the most recent 50-year period common to all sites (1960–2009), and using local meteorological data (see Table 1 and Figure 2). The coefficients were then plotted against mean stand age (estimated as the mean age of the sampled trees). Additionally, moving correlation analysis (MCA) using a 30 year window was used to investigate if the relationship between previous summer climate and RWI changed as the trees at each site increased in age.

Results

Seed production

During the 88-year regional mastling record, 21 mast events (category 4 or 5) were recorded, with no consecutive mast years (Figure 3). Mastling category showed the strongest correlations with MAX_{JUL-1} and MAX_{JUL-2} . These relationships are shown in Figure 4, and demonstrate that mastling has a positive correlation with MAX_{JUL-1} (i.e., high summer temperatures increase the probability of mastling in the following year), while mastling is negatively correlated with MAX_{JUL-2} .

Radial growth chronology

Standard dendrochronological statistics indicated the suitability of the developed tree ring chronologies for dendrochronological analysis (Figure 3 and Table 2). Correlations between the individual tree ring series was generally high at each site (although lower at AFO, OAH and NET), and in all cases within-tree correlations were higher than between trees, as expected. Expressed

population signal (EPS), which is used to estimate the degree to which the sampled trees are representative of the hypothetical chronology including all trees in the population, was above the widely used threshold of 0.85 in all individual chronologies. The chronologies (including SENG) showed high autocorrelation, and so autoregressive models were fitted and the residuals used for all analyses.

Influence of climate on growth

The optimal model of RWI (GM1) included $SPEI_{JUL}$, MAX_{JUL-1} and MAX_{JUL-2} as significant predictors of growth, and explained 56.1% of the variance in RWI (Table 3 and Figure S1 available as Supplementary Data at [Tree Physiology Online](#)). The model validation exercise produced a normal distribution of the residuals, no patterns in the residuals, and a strong linear relationship between predicted and fitted values. It also performed well in predicting the validation dataset, with a strong linear relationship between observed and predicted values ($R^2 = 0.56$).

Table 3. Selected independent variables for optimal Growth Model 1 (GM1). $SPEI_{JUL}$ is a drought index for July of the year of growth, and MAX_{JUL-1} and MAX_{JUL-2} are the mean-maximum temperature of the July in the previous year and the year 2 years previous, respectively. $R^2 = 0.56$, $aR^2 = 0.54$, $AIC = -77.22$.

Variable	Estimate	Standard error	t-value	P-value
Intercept	1.060	0.276	3.842	<0.001
$SPEI_{JUL}$	0.092	0.015	6.015	<0.001
MAX_{JUL-1}	-0.036	0.009	3.513	<0.001
MAX_{JUL-2}	0.033	0.009	-3.919	<0.001

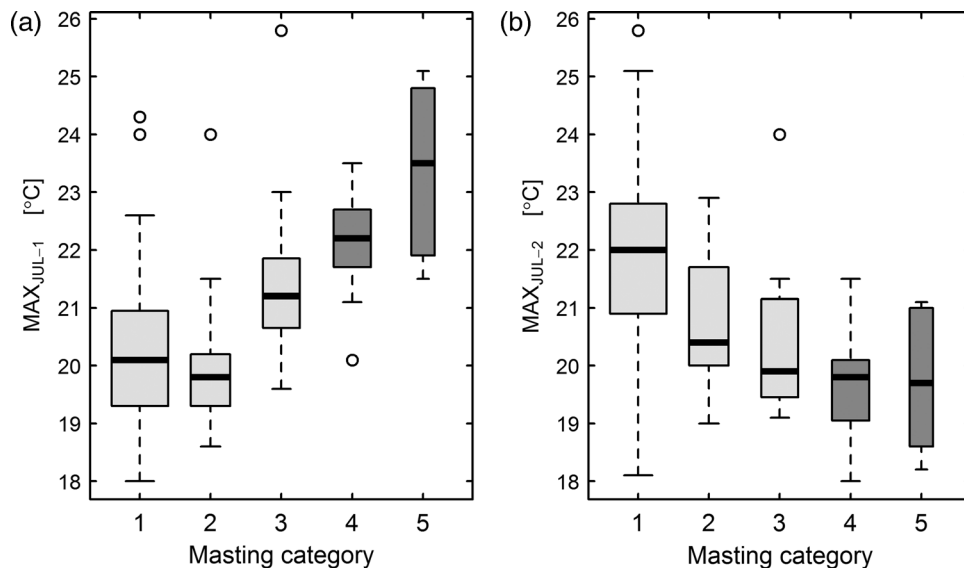


Figure 4. The relationship between mastling and previous summers' temperature. The width of the boxplots is proportional to the number of observations, and the whiskers extend to include all points which are no more than 1.5× the interquartile range from the edge of the box. The dark grey boxes refer to mast years, light grey to non-mast years. (a) Relationship between mastling and MAX_{JUL-1} (mean-maximum temperature of July in year prior to year of growth). Kruskal–Wallis test ($\chi^2 = 34.507$, $df = 4$, $P < 0.001$). (b) Relationship between mastling and MAX_{JUL-2} (mean-maximum temperature of July 2 years prior to year of growth). Kruskal–Wallis test ($\chi^2 = 26.854$, $df = 4$, $P < 0.001$).

Influence of masting on growth

In years with category 4 and 5 mast events, RWI was significantly lower than in category 1, 2 and 3 years (non-mast years) (Wilcoxon rank sum tests, $P < 0.05$, Figure 5). In category 4 years, RWI was 14.3% lower than in non-mast years, and 19.5% lower in category 5 years. The hypothesis that the lagged response of RWI to temperature is the result of masting was tested by fitting a linear model to the same data, but including masting as an additional possible predictor. Refitting the model did not result in masting being selected in place of the previous summer temperatures, but forced replacement of MAX_{JUL-1} and MAX_{JUL-2} with masting as a factor produced a model (GM2) that explained 51.6% of the variance in RWI (Table 4 and Figure S2 available as Supplementary Data at *Tree Physiology* Online), compared with 33.6% when masting was excluded (i.e., only including $SPEI_{JUL}$ as an independent variable).

For GM2, predicted RWI showed a strong linear relationship with the observed RWI in the validation dataset ($R^2 = 0.52$). In GM2, category 4 and 5 mast events have a significant negative effect on radial growth. The model performed well compared with GM1, and the model residuals showed no relationship with previous summers' temperature, indicating that masting explained the same variance in RWI as MAX_{JUL-1} and MAX_{JUL-2} .

Several other lines of evidence also supported the hypothesis that masting creates lagged growth responses to weather. Figure 6 shows the relationships between SENG RWI and previous summers' temperatures and demonstrates that mast years (black points) were responsible for creating the highly significant relationships between growth and previous summers'

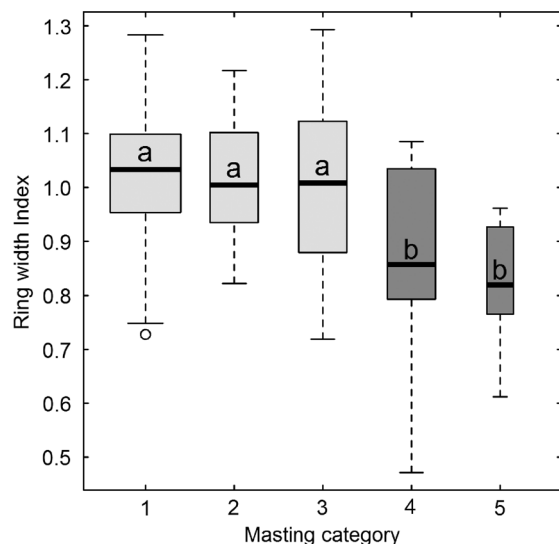


Figure 5. Boxplot of RWI according to masting category. Mast years (categories 4 and 5) are coloured dark grey, non-mast years (categories 1, 2 and 3) are light grey. The width of the boxplot is proportional to the number of observations, the whiskers extend to include all points which are no more than 1.5× the interquartile range from the edge of the box. The letters refer to groups that are not significantly different (non-parametric directional Wilcoxon rank sum test, $P < 0.05$).

Table 4. Selected independent variables for optimal Growth Model 2 (GM2). MAST is a five-category measure of the intensity of annual seed production. MAST.1 is a category 1 mast year, representing very low seed production and MAST.5 a category 5 mast year, presenting the highest seed production. As the mast categories are added to the model as factors, MAST.1 is not included in the model as it is used as the reference. $R^2 = 0.52$, $aR^2 = 0.47$, $AIC = -67.67$.

Variable	Estimate	Standard error	t-value	P-value
Intercept	1.040	0.026	40.288	<0.001
$SPEI_{JUL}$	0.092	0.018	5.123	<0.001
$factor(MAST.2)$	0.001	0.048	0.028	0.978
$factor(MAST.3)$	-0.085	0.047	1.808	0.076
$factor(MAST.4)$	-0.173	0.048	-3.610	<0.001
$factor(MAST.5)$	-0.224	0.095	-2.362	0.022

temperatures. In a subsample including only non-mast years, the relationships became weaker and insignificant in the case of MAX_{JUL-1} . Two further lines of evidence are related to the hypothesis that as investment in seed production increases with age, the strength of the relationship between masting and previous summer temperature should also increase with age. Figure 7 shows that for the eight sampled sites, mean tree age and the strength of the correlation coefficient between RWI and MAX_{JUL-1} were significantly correlated. In the youngest stand, the coefficient was close to zero, but it became more negative with stand age, with the oldest stands exhibiting strong negative correlations (< -0.4). In the MCA, the relationship between RWI and MAX_{JUL-1} was shown to change with age within a stand, with the correlation changing in the five oldest stands from close to zero when the stand is young to strongly negative when chronology age exceeded ~100 years (Figure 8). The different ages of the stands allowed this effect to be isolated from any potential change in the correlation between temperature and growth due to changes in climate.

Discussion

Implications of a growth–reproduction trade-off for growth–climate relationships

Observed correlations between tree growth and monthly climate from previous growing seasons have been linked to a variety of mechanisms, including carbohydrate dynamics (Figure 1a), but this study has demonstrated that in *F. sylvatica*, and probably other masting tree species, correlations with previous summers' temperatures can be explained largely, if not entirely, as a consequence of an interaction between climate, reproductive effort and growth (Figure 1b). This hypothesis has been suggested previously (e.g., Di Filippo et al. 2007), but we are unaware of its rigorous appraisal in the literature. The results of the modelling of RWI presented here strongly support the hypothesis that lagged climate signals in tree ring chronologies from *F. sylvatica* are (at least primarily) the result of masting, which reduces

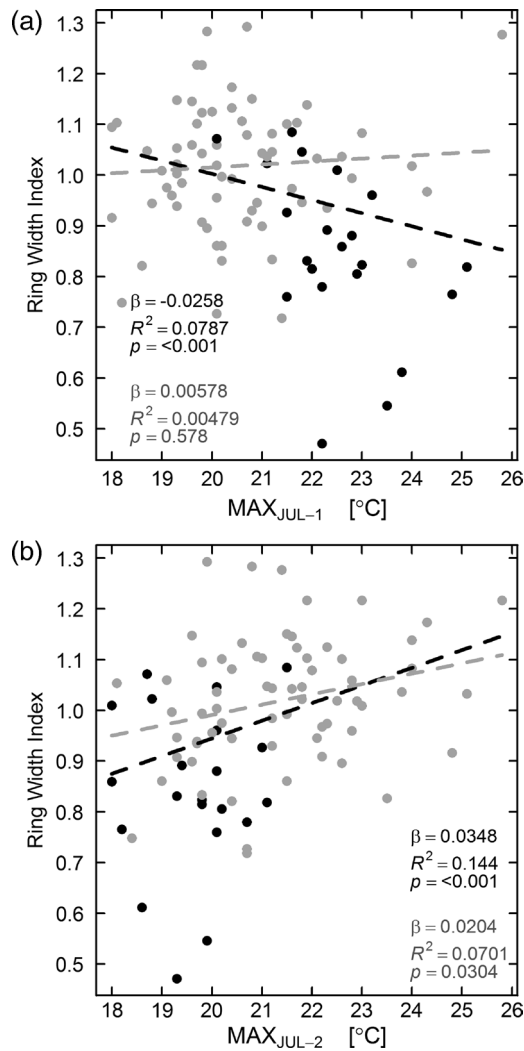


Figure 6. The dependence of growth–climate relationships on mast years. (a) The relationship between RWI and MAX_{JUL-1} . Black points refer to mast years and grey points to non-mast years. The black dashed line shows the linear regression of RWI on MAX_{JUL-1} for all years (black and grey points), with regression statistics in black. The grey dashed line shows the linear regression for only the non-mast years, with regression statistics in grey. (b) As for (a), but for the relationship between RWI and MAX_{JUL-2} .

growth in the year of masting, but is cued by climate in the previous summers. If the relationship between previous summer temperature and RWI were associated with ‘carry-over’ effects (Figure 1a), for example, resource depletion during unfavourable (i.e., warm) years, then the correlation between RWI and MAX_{JUL-1} and MAX_{JUL-2} should exist in both mast and non-mast years. However, Figure 6 demonstrates that when mast years are excluded, the statistical relationships weaken, and become non-significant in the case of MAX_{JUL-1} . This is strong evidence that the relationships between RWI and previous summer’s temperature are caused by the growth reduction associated with mast years.

Any interaction between masting and tree growth should be dependent on tree age as seed production increases with age,

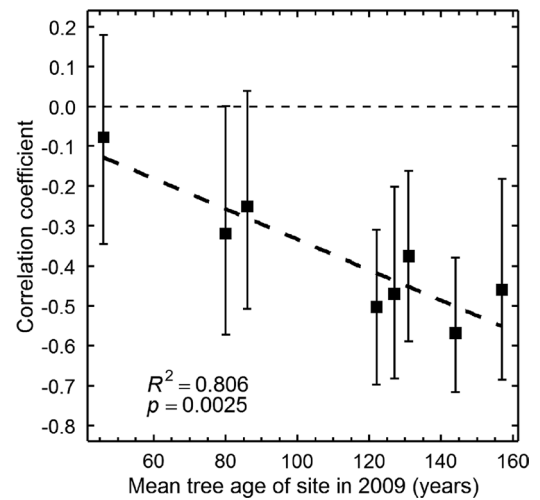


Figure 7. Variation in the Pearson product–moment correlation coefficient between RWI and MAX_{JUL-1} according to stand age for the eight study sites. The error bars refer to the 95% confidence intervals, estimated using a bootstrapping resampling procedure with 1000 resamples. The period 1961–2009 was used for the analysis of all sites.

both in terms of absolute biomass and percentage of the total carbon allocated to reproduction (Genet et al. 2010). Consequently, as juvenile trees invest relatively little in seed production, they should respond less to the temperatures of the previous summers’ from mature trees producing heavy seed crops. It is possible that the strength of the relationship between previous summers’ temperatures and RWI will therefore increase with age. Several lines of evidence support this prediction in our data. The correlation between RWI and MAX_{JUL-1} was close to zero for the youngest stand, and decreased linearly with the age of the site (Figure 7). Additionally, MCA demonstrated that in the oldest five sites, the correlation coefficient varied from close to zero during the youngest periods of stand development to strongly negative during maturity, and that the strength of the correlation increased approximately linearly with age (Figure 8). This observation is consistent with other studies (e.g., Di Filippo et al. 2007, Drobyshev et al. 2010).

Our results have important implications for the interpretation of growth–climate relationships in *F. sylvatica*, but they also have wider implications, as lagged correlations between growth and summer climate of previous years are widely reported for many species (e.g., Miina 2000, Andreu et al. 2007, Babst et al. 2013). Wettstein et al. (2011) reported strong negative correlations between RWI and previous summer temperatures across a range of species throughout the extra-tropical northern hemisphere, which they suggested is ‘potentially puzzling’, but did suggest might be linked to trade-offs with seed production. While long records of seed production are not available for many geographical regions, or for all species, other evidence suggests that these lagged climate correlations may also be due, at least in part, to the interaction between climate, masting and growth. Across all the

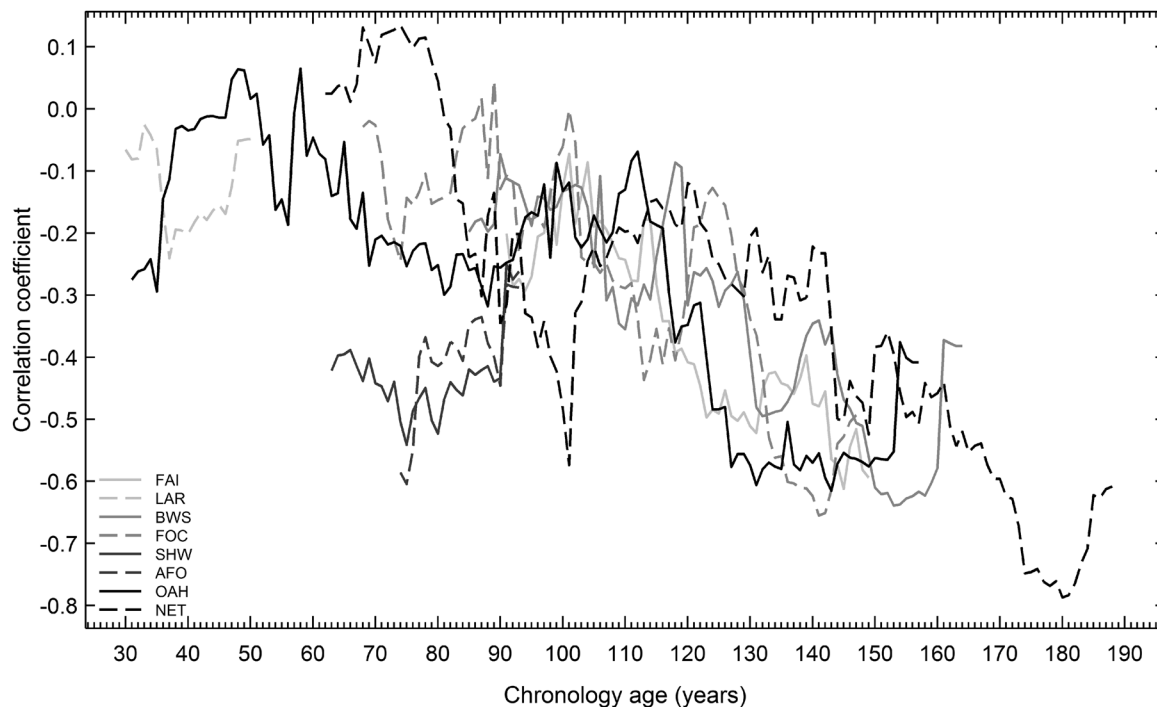


Figure 8. The variation with chronology age of the Pearson product-moment correlation coefficient between MAX_{JUL-1} and RWI, using a moving 30-year window and plotted according to the age of the chronology at the end of the window. Each of the eight sample sites are plotted separately. Moving correlation analysis was conducted with a 1 year time-step.

species included in the analysis of [Wettstein et al. \(2011\)](#), the spatial distribution of correlations with summer temperature in the year of growth showed a marked pattern from strongly positive correlations at the highest latitudes (temperature limited), to strongly negative at lower latitudes (drought limited). However, the correlations with previous summer temperature did not show the same spatial pattern, and were consistently negative for the majority of the chronologies, independent of latitude. The differences in spatial patterns hint at different mechanisms being responsible for the correlations between RWI and climate in the year of growth and the previous year.

The trade-off between growth and masting, and the climatic cueing of masting, has other important implications for analyses based on relationships between tree-rings and climate. Studies using statistical relationships between ring width and climate, such as climate reconstructions and dendroecological studies, rely on extreme observations (particularly the narrowest rings) to create strong correlations between ring width and climate. The interaction between climate, masting and growth suggests that narrow rings may not only be the result of climate, but may be due to masting events (Figure 6). Consequently, narrow rings may not always correspond to years of unfavourable climate, complicating the understanding of what abiotic factors are responsible for these years of low growth, and also complicating the interpretation of statistical relationships between ring width and climate.

Growth-climate relationships are often used to assess the drought sensitivity of species, but the results presented in this study indicate that caution should be taken when interpreting lagged drought signals as these may not in fact reflect direct influences of climate on growth, but instead the influence of climate-controlled masting on growth. Additionally, changes in the strength of lagged climate-growth relationships should be interpreted with care. Within even-aged stands (or wherever the mean cambial age varies throughout a chronology), growth-climate relationships may show variations due to age-dependent allocation between growth and reproduction. This variation in growth-climate relationships could easily be misinterpreted as representing an effect of environmental change, when in reality it may be an expected effect of ontogeny. These results reinforce the importance of considering the mean tree age throughout chronologies used for climate reconstructions, which some but not all studies report (see for example, [Briffa et al. 1998](#), [Wilson et al. 2013](#)).

The influence of climate and masting on growth

The results of the modelling of RWI reveal that early summer drought in the year of growth is a significant factor influencing radial growth in the sampled *F. sylvatica* stands. This is a common finding in studies investigating the relationship between growth and climate in *F. sylvatica*, which is widely considered a drought sensitive species ([Packham et al. 2012](#)). Additionally,

the importance of MAX_{JUL-1} is expected, as this is one of the most common significant correlations reported for tree ring chronologies from this species. However, the selection of MAX_{JUL-2} as a significant predictor of RWI is somewhat unexpected, as correlations between growth and climate are rarely investigated for >1 year prior to growth. However, it is in agreement with Piovesan et al. (2008), who reported a significant positive correlation between growth and temperature of the summer months (June–August) 2 years prior to growth for a *F. sylvatica* ring width chronology from the Apennines, Italy.

Figure 5 shows that RWI is 14% lower in category 4 mast years, and 20% lower in the heaviest mast years (category 5). This finding is in agreement with numerous studies that have demonstrated a negative correlation between plant reproduction and growth in tropical (Nakagawa et al. 2012), temperate (Drobyshev et al. 2010), Mediterranean (Barringer et al. 2013) and boreal ecosystems (Selas et al. 2002). This growth–reproduction trade-off may result from either direct or indirect trade-off mechanisms. In a direct trade-off, increased investment of carbohydrates in fruit production reduces investment in woody tissues without any reduction in whole-plant photosynthesis. This direct trade-off with growth may be especially strong as a result of the apparent lack of stored carbohydrate use in masting in beech (Hoch et al. 2013), which suggests fruit production will act as a major competing sink for newly fixed photosynthates. In a recent study, Muller-Haubold et al. (2013) demonstrated that while total above-ground NPP of *F. sylvatica* was strongly controlled by current year weather conditions, the partitioning of above-ground NPP between wood, leaves and fruit was closely linked to weather conditions in the previous year, supporting this direct mechanism for the growth–reproduction trade-off. This trade-off-induced shortage of carbon for growth in individual trees may be restricted to particular periods of the growing season rather than across the entire year, due to strong seasonal variation in GPP and carbon demand (Mund et al. 2010).

However, in addition to influencing sink strength and carbon allocation, masting may also reduce radial growth indirectly by reducing GPP, and consequently reducing the overall carbon availability. For example, developing fruits are strong sinks for nutrients (Ichie et al. 2005, Sala et al. 2012a, Han et al. 2014) with high seed production associated with reduced nitrogen concentrations in seed bearing shoots (Alla et al. 2012) and reduced foliar nitrogen and photosynthetic capacity (Han et al. 2008) (although not in all studies; see Yasumura et al. 2006). Furthermore, masting may reduce whole-plant leaf area and subsequently whole-plant photosynthesis. Leaf number may be reduced due to lower shoot growth and higher bud mortality in mast years (Ishihara and Kikuzawa 2009), and because flower buds replace potential leaf buds (Innes 1994). In *F. sylvatica*, mast years are also associated with reduced leaf size (Innes 1992), with a combination of smaller leaf size and fewer leaves

resulting in lower stand leaf area index during mast years (Innes 1994, Ferretti et al. 1998). In addition, Olesinski et al. (2012) found that fine root biomass in *Abies balsamea* (L.) Mill. is reduced in mast years, which may reduce water or nutrient supply in mast years, also reducing GPP.

Relationships between tree growth, climate and seed production

This study has found strong relationships between regional-scale patterns of tree growth, seed production and climate in *F. sylvatica*, with climate-cued masting events creating lagged correlations between RWI and weather conditions in the previous summers. We interpret this phenomenon to occur as a consequence of a trade-off between growth and seed production during mast years. This conclusion has important implications for our understanding and interpretation of the relationships between tree growth and climate at scales from individual trees and forest stands to distribution-wide analysis of growth–climate relationships, but needs to be tested in other species where long records of seed production exist. Additionally this study used regional records of growth and seed production, but stand- and individual-based analysis of these relationships is also required. However, as long records of seed production are rare, an alternative approach would be to investigate the relationship between lagged climate correlations and tree age, as life-history theory predicts that older trees will invest a greater proportion of available resources into reproduction (Genet et al. 2010, Viglas et al. 2013), resulting in a stronger reproduction–growth trade-off and therefore a stronger influence of the cues of masting on radial growth.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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References

- Alla AQ, Camarero JJ, Maestro-Martínez M, Montserrat-Martí G (2012) Acorn production is linked to secondary growth but not to declining carbohydrate concentrations in current-year shoots of two oak species. *Trees* 26:841–850.
- Andreu L, Gutierrez E, Macias M, Ribas M, Bosch O, Camarero JJ (2007) Climate increases regional tree-growth variability in Iberian pine forests. *Glob Chang Biol* 13:804–815.
- Babst F, Poulter B, Trouet V et al. (2013) Site- and species-specific responses of forest growth to climate across the European continent. *Glob Ecol Biogeogr* 22:706–717.
- Barringer BC, Koenig WD, Knops JMH (2013) Interrelationships among life-history traits in three California oaks. *Oecologia* 171:129–139.
- Boninsegna JA, Argollo J, Aravena JC et al. (2009) Dendroclimatological reconstructions in South America: a review. *Palaeogeogr Palaeoclimatol Palaeoecol* 281:210–228.
- Briffa KR, Schweingruber FH, Jones PD, Osborn TJ, Harris IC, Shiyatov SG, Vaganov EA, Grudd H (1998) Trees tell of past climates: but are they speaking less clearly today? *Philos Trans R Soc Lond B Biol Sci* 353:65–73.
- Bunn AG, Korpela M, Biondi F, Campelo F, Merian P, Qeadan F, Zang C (2012) dplR: Dendrochronology Program Library in R. R package version 1.5.6. <http://CRAN.R-project.org/package=dplR>.
- Campioli M, Gielen B, Göckede M, Papale D, Bouriaud O, Granier A (2011) Temporal variability of the NPP-GPP ratio at seasonal and interannual time scales in a temperate beech forest. *Biogeosciences* 8:2481–2492.
- Cavin L, Mountford EP, Peterken GF, Jump AS (2013) Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Funct Ecol* 27:1424–1435.
- Di Filippo A, Biondi F, Čufar K, de Luis M, Grabner M, Maugeri M, Saba EP, Schirone B, Piovesan G (2007) Bioclimatology of beech (*Fagus sylvatica* L.) in the Eastern Alps: spatial and altitudinal climatic signals identified through a tree-ring network. *J Biogeogr* 34:1873–1892.
- Drobyshev I, Övergaard R, Saygin I, Niklasson M, Hickler T, Karlsson M, Sykes MT (2010) Masting behaviour and dendrochronology of European beech (*Fagus sylvatica* L.) in southern Sweden. *For Ecol Manag* 259:2160–2171.
- Ferretti M, Baratozzi L, Cenni E, Cozzi A, Savini P (1998) Crown transparency of beech (*Fagus sylvatica* L.) in the northern Apennines (Italy)—status, changes and relationships with site characteristics and other indices of tree condition. *Chemosphere* 36:1037–1042.
- Fritts HC (1976) *Tree rings and climate*. Academic Press, London.
- Genet H, Breda N, Dufrene E (2010) Age-related variation in carbon allocation at tree and stand scales in beech (*Fagus sylvatica* L.) and sessile oak (*Quercus petraea* (Matt.) Liebl.) using a chronosequence approach. *Tree Physiol* 30:177–192.
- Grissino-Mayer HD (2001) Crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree Ring Res* 57:205–221.
- Grissino-Mayer HD (2003) A manual and tutorial for the proper use of an increment borer. *Tree Ring Res* 59:63–79.
- Han Q, Kabeya D, Iio A, Kakubari Y (2008) Masting in *Fagus crenata* and its influence on the nitrogen content and dry mass of winter buds. *Tree Physiol* 28:1269–1276.
- Han Q, Kabeya D, Iio A, Inagaki Y, Kakubari Y (2014) Nitrogen storage dynamics are affected by masting events in *Fagus crenata*. *Oecologia* 174:679–687.
- Hilton GM, Packham JR (2003) Variation in the masting of common beech (*Fagus sylvatica* L.) in northern Europe over two centuries (1800–2001). *Forestry* 76:319–328.
- Hoch G, Richter A, Körner C (2003) Non-structural carbon compounds in temperate forest trees. *Plant Cell Environ* 26:1067–1081.
- Hoch G, Siegwolf RTW, Keel SG, Körner C, Han Q (2013) Fruit production in three masting tree species does not rely on stored carbon reserves. *Oecologia* 171:653–662.
- Ichie T, Kenta T, Nakagawa M, Sato K, Nakashizuka T (2005) Resource allocation to reproductive organs during masting in the tropical emergent tree, *Dipterocarpus tempehes*. *J Trop Ecol* 21:237–241.
- Innes JL (1992) Observations on the condition of beech (*Fagus sylvatica* L.) in Britain in 1990. *Forestry* 65:35–60.
- Innes JL (1994) The occurrence of flowering and fruiting on individual trees over 3 years and their effects on subsequent crown condition. *Trees* 8:139–150.
- Ishihara MI, Kikuzawa K (2009) Annual and spatial variation in shoot demography associated with masting in *Betula grossa*: comparison between mature trees and saplings. *Ann Bot* 104:1195–1205.
- Koenig WD, Knops JMH (2005) The mystery of masting in trees. *Am Sci* 93:340–347.
- Larsson L-A (2010a) CDendro. Cybis Elektronik and Data AB, Saltsjöbaden, Sweden.
- Larsson L-A (2010b) Coorecorder. Cybis Elektronik and Data AB, Saltsjöbaden, Sweden.
- Mainiero R, Kazda M (2006) Depth-related fine root dynamics of *Fagus sylvatica* during exceptional drought. *For Ecol Manag* 237:135–142.
- Matthews JD (1955) The influence of weather on the frequency of beech mast years in England. *Forestry* 28:107–116.
- Mencuccini M, Piussi P, Sulli AZ (1995) Thirty years of seed production in a subalpine Norway spruce forest: patterns of temporal and spatial variation. *For Ecol Manag* 76:109–125.
- Miina J (2000) Dependence of tree-ring, earlywood and latewood indices of Scots pine and Norway spruce on climatic factors in eastern Finland. *Ecol Model* 132:259–273.
- Müller-Haubold H, Hertel D, Seidel D, Knutzen F, Leuschner C (2013) Climate responses of aboveground productivity and allocation in *Fagus sylvatica*: a transect study in mature forests. *Ecosystems* 16:1498–1516.
- Mund M, Kutsch WL, Wirth C, Kahl T, Knohl A, Skomarkova MV, Schulze ED (2010) The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed beech forest. *Tree Physiol* 30:689–704.
- Nakagawa M, Matsushita M, Kurokawa H et al. (2012) Possible negative effect of general flowering on tree growth and aboveground biomass increment in a Bornean tropical rain forest. *Biotropica* 44:715–719.
- Olesinski J, Krasowski MJ, Lavigne MB, Kershaw JA Jr, Bernier PY (2012) Fine root production varies with climate in balsam fir (*Abies balsamea*). *Can J For Res* 42:364–374.
- Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological Flora of the British Isles: *Fagus sylvatica*. *J Ecol* 100:1557–1608.
- Peterken GF, Mountford EP (1996) Effects of drought on beech in Lady Park Wood, an unmanaged mixed deciduous woodland. *Forestry* 69:125–136.
- Peters R (1997) *Beech forests*. Geobotany 24. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Piovesan G, Adams JM (2001) Masting behaviour in beech: linking reproduction and climatic variation. *Can J Bot* 79:1039–1047.

- Piovesan G, Schirone B (2000) Winter North Atlantic oscillation effects on the tree rings of the Italian beech (*Fagus sylvatica* L.). *Int J Biometeorol* 44:121–127.
- Piovesan G, Biondi F, Di Filippo A, Alessandrini A, Maugeri M (2008) Drought-driven growth reduction in old beech (*Fagus sylvatica* L.) forests of the central Apennines, Italy. *Glob Chang Biol* 14:1265–1281.
- Power SA (1994) Temporal trends in twig growth of *Fagus sylvatica* L. and their relationships with environmental factors. *Forestry* 67:13–30.
- Rust S, Roloff A (2004) Acclimation of crown structure to drought in *Quercus robur* L.—intra- and inter-annual variation of abscission and traits of shed twigs. *Basic Appl Ecol* 5:283–291.
- Sala A, Hopping K, McIntire EJB, Delzon S, Crone EE (2012a) Masting in whitebark pine (*Pinus albicaulis*) depletes stored nutrients. *New Phytol* 196:189–199.
- Sala A, Woodruff DR, Meinzer FC (2012b) Carbon dynamics in trees: feast or famine? *Tree Physiol* 32:764–775.
- Schauber EM, Kelly D, Turchin P et al. (2002) Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* 83:1214–1225.
- Selas V, Piovesan G, Adams JM, Bernabei M (2002) Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Can J For Res* 32:217–225.
- Skomarkova MV, Vaganov EA, Mund M, Knohl A, Linke P, Boerner A, Schulze ED (2006) Inter-annual and seasonal variability of radial growth, wood density and carbon isotope ratios in tree rings of beech (*Fagus sylvatica*) growing in Germany and Italy. *Trees* 20:571–586.
- Sork VL, Bramble J, Sexton O (1993) Ecology of mast-fruiting in three species of North American deciduous oaks. *Ecology* 74:528–541.
- Speer JH (2010) Fundamentals of tree ring research. The University of Arizona Press, Tucson, USA.
- UK Met Office (2013) Regional climate values. <http://www.metoffice.gov.uk/climate/uk/datasets/>.
- Verbyla D (2008) The greening and browning of Alaska based on 1982–2003 satellite data. *Glob Ecol Biogeogr* 17:547–555.
- Vicente-Serrano SM, Beguería S, López-Moreno JI (2010) A multiscalar drought index sensitive to global warming: the Standardized Precipitation Evapotranspiration Index. *J Clim* 23:1696–1718.
- Viglas JN, Brown CD, Johnstone JF (2013) Age and size effects on seed productivity of northern black spruce. *Can J For Res* 43:534–543.
- Wettstein JJ, Littell JS, Wallace JM, Gedalof Z (2011) Coherent region-, species-, and frequency-dependent local climate signals in northern hemisphere tree-ring widths. *J Clim* 24:5998–6012.
- Wilson R, Miles D, Loader NJ, Melvin T, Cunningham L, Cooper R, Briffa K (2013) A millennial long March–July precipitation reconstruction for southern-central England. *Clim Dyn* 40:997–1017.
- Wilson SM, Broadmeadow M, Sanders TG, Pitman R (2008) Effect of summer drought on the increment of beech trees in southern England. *Q J For* 102:9.
- Yasumura Y, Hikosaka K, Hirose T (2006) Resource allocation to vegetative and reproductive growth in relation to mast seeding in *Fagus crenata*. *For Ecol Manag* 229:228–233.