Tree Physiology 37, 744–754
doi:10.1093/treephys/tpx025

Research paper

Drought and reproductive effort interact to control growth of a temperate broadleaved tree species (*Fagus sylvatica*)

Andrew J. Hacket-Pain[1,2,6], Jonathan G.A. Lageard[3] and Peter A. Thomas[4,5]

[1]St Catherine's College, Manor Road, Oxford OX1 3UJ, UK; [2]Fitzwilliam College, Storey's Way, Cambridge CB3 0DG, UK; [3]Division of Geography and Environmental Management, Faculty of Science and Engineering, Manchester Metropolitan University, Chester Street, Manchester M1 5GD, UK; [4]School of Life Sciences, Keele University, Keele, Staffordshire ST5 5BG, UK; [5]Harvard Forest, Harvard University, Harvard Forest, 324 North Main Street, Petersham, MA 01366, USA; [6]Corresponding author (ajh220@cam.ac.uk)

Received November 7, 2016; accepted February 27, 2017; published online March 17, 2017; handling Editor Annikki Mäkelä

Interannual variation in radial growth is influenced by a range of physiological processes, including variation in annual reproductive effort, although the importance of reproductive allocation has rarely been quantified. In this study, we use long stand-level records of annual seed production, radial growth (tree ring width) and meteorological conditions to analyse the relative importance of summer drought and reproductive effort in controlling the growth of *Fagus sylvatica* L., a typical masting species. We show that both summer drought and reproductive effort (masting) influenced growth. Importantly, the effects of summer drought and masting were interactive, with the greatest reductions in growth found in years when high reproductive effort (i.e., mast years) coincided with summer drought. Conversely, mast years that coincided with non-drought summers were associated with little reduction in radial growth, as were drought years that did not coincide with mast years. The results show that the strength of an inferred trade-off between growth and reproduction in this species (the cost of reproduction) is dependent on environmental stress, with a stronger trade-off in years with more stressful growing conditions. These results have widespread implications for understanding interannual variability in growth, and observed relationships between growth and climate.

Keywords: cost of reproduction, masting, resource allocation, ring width, trade-off, tree growth.

Introduction

Current understanding of interannual variations in forest productivity are largely based on the assumption that growth is controlled by carbon supply (i.e., photosynthesis and carbohydrate storage and remobilization) (Körner 2013), although there has recently been an increased recognition that several processes related to growth can also act to limit productivity, even when carbon supply is not limiting (Fatichi et al. 2014). These various carbon supply and growth-related processes operate at different timescales (including across multiple growing seasons), and their timings and rates are all strongly influenced by weather conditions. Consequently, studies using a range of methods have reported strong relationships between tree growth and climate (George, 2014, Vicente-Serrano et al. 2010). Processes related to resource allocation can also have an important control on tree growth (Thomas 2011), although these have frequently been neglected when interpreting variation in tree growth. A number of studies have investigated the importance of resource allocation as a significant control of tree growth, particularly allocation to reproduction (fructification) (Mencuccini and Piussi 1995, Genet et al. 2010, Campioli et al. 2011, Muller-Haubold et al. 2013, Hacket-Pain et al. 2015). In many tree species, allocation to reproduction has high interannual variability, with synchronous production of heavy seed crops across populations that is often cued by species-specific weather conditions (Schauber et al. 2002). This phenomenon is known as masting (Kelly and Sork 2002). It has long been known that years of high reproductive effort ('mast years') commonly correspond to years of low growth in a wide range of species, representing a trade-off, or switch, between growth and reproduction (Woodward et al. 1994, Selas et al. 2002, Monks and Kelly 2006). The strength of this trade-off is species-specific (Thomas 2011, Berdanier and Clark 2016), varies in strength along environmental and stress gradients (Mencuccini and Piussi 1995) and may increase with tree age, reflecting an increase in allocation to reproduction through a tree's lifespan (Genet et al. 2010, Thomas 2011, Wenk and Falster 2015).

Consequently, growth, reproduction and weather conditions are related via complex direct and indirect mechanisms that may operate over multiple years. Allocation processes have important implications for understanding variation in growth (both interannual variation and long-term trends). For example, an increased allocation to reproduction with age (Thomas 2011) may partly explain observed age-related declines in tree growth and aboveground productivity (Guillemot et al. 2015, although see Stephenson et al. 2014). Additionally, variation in allocation may contribute to interannual variation in growth and affect the relationship between annual growth and climate. For example, Muller-Haubold et al. (2013) used data from 12 *Fagus sylvatica* L. stands along a precipitation gradient to demonstrate that inter-annual and inter-site variation in growth could best be explained by variation in the allocation to annual fruit production, rather than variation in weather conditions. Indeed, they found that once variation in reproductive effort was accounted for, growing season precipitation did not have a significant effect on aboveground net primary productivity. In general however, it has proved difficult to separate the effects of weather conditions and reproduction on growth and to identify possible interactions between factors. In previous work we used long time-series of weather conditions, annual reproductive effort and tree growth to demonstrate that mast years in *F. sylvatica* are associated with reduced growth, and that interannual variation in reproductive effort (specifically masting) can therefore explain a significant proportion of variance in growth (Hacket-Pain et al. 2015). However, the relative importance of masting and weather conditions in the year of growth is still unclear, including the potential for an interaction, as is the existence of lagged and multi-year effects of drought and mast events on growth. For example, the most important twentieth century negative tree ring anomaly (i.e., extreme low growth) in northern and central European *F. sylvatica* tree ring chronologies occurred in 1976 (Scharnweber et al. 2011, Cavin and Jump 2016), a year that combined significant drought stress and heavy seed crops across much of this region (Hilton and Packham 2003, Overgaard et al. 2007).

In this study, we make use of time-series of annual tree growth (ring width), reproductive effort (annual seed production) and weather for an *F. sylvatica* stand in the southern UK. Beech has been the subject of a large number of tree-ring based studies, which have frequently linked variation in annual growth with growing season drought, even in central and northern regions of the species distribution (Dittmar et al. 2003, Scharnweber et al. 2011, Cavin and Jump 2016, Hacket-Pain et al. 2016). Additionally, a smaller number of studies have demonstrated that a significant component of variation in growth can also be explained by annual reproductive effort (Drobyshev et al. 2010, Hacket-Pain et al. 2015). The study period includes years of severe summer drought stress (e.g., 1990, 1995 and 2010) and years with heavy seed crops (e.g., 1982, 1987 and 1995). These records are used to investigate the interacting effects of summer drought and reproductive effort on annual growth in beech, a widespread and economically important tree species in European forests (Gessler et al. 2007).

We specifically focus on two key questions:

(i) What is the relative importance of climate and reproductive effort (masting) in explaining interannual variation in growth?
(ii) Do the influences of climate and masting interact to explain additional variation in annual growth?

Materials and methods

Study site and species

The study was conducted at Nettlebed Woods (NET), located in the Chiltern hills in Oxfordshire, southern UK (51.570°N, −0.978°E). The bedrock is Cretaceous chalk, with superficial deposits of Pleistocene age giving rise to thin, stony, acidic soils. Tree ring chronologies at this site are highly correlated with other regional tree ring chronologies for this species (Hacket-Pain et al. 2015), and annual variation in seed production is highly synchronized with the rest of southern England (D.Ascoli, unpublished data). *Fagus sylvatica* tends to favour well-drained soils. Despite this, its intensive, shallow root system restricts it to exploring relatively small volumes of soil very intensively and as such, *F. sylvatica* is susceptible to drought (Packham et al. 2012, Cavin et al. 2013).

Tree ring data

Tree rings were used to measure annual tree growth at the site. One core was extracted from each of 33 mature and canopy dominant or codominant individuals at 1.3 m aboveground level. Cores were air dried, then mounted and sanded with progressively finer sandpaper until tree ring boundaries were clearly visible. Sanded cores were then scanned at 2400 dpi and ring widths measured using the software CooRecorder v7.3 (Larsson 2010*b*). Cross-dating was used to ensure that all measured rings were assigned to the correct year of growth, and was conducted using a two-stage process. Initially, rings were visually cross-dated in CDendro v7.3 (Larsson 2010*a*), and then checked statistically using the standard dendrochronological software COFECHA (Grissino-Mayer 2001).

Raw ring width chronologies contain low frequency variation (i.e., long-term trends) that are associated with processes including changes in canopy position, changes in tree size and age, as well as trends in climate and other abiotic factors

(Fritts 1976). The aim of this study was to investigate the effects of interannual variation in weather conditions and allocation to reproduction on annual ring width, so these low frequency signals were removed by detrending the raw ring width chronologies. The R package *dplR* (Bunn et al. 2012) was used to fit a spline to the ring width chronology from each individual tree. Then, a dimensionless ring width index (*RWI*) was calculated for each tree by dividing the measured ring width by the spline. A 32-year cubic spline with a 50% frequency cut-off was selected to remove the low and medium frequency signal, but retain high frequency (i.e., interannual) variations in ring width. The individual detrended chronologies from each sampled tree were then averaged to create a mean site chronology. In common with many tree ring chronologies, the NET chronology showed strong serial autocorrelation. This was reduced using the prewhitening procedure in *dplR*, creating a prewhitened *RWI*. However, as this serial autocorrelation can be interpreted as a biological signal in addition to a statistical artefact, all analysis was also conducted on the raw *RWI* chronologies (presented in Appendix 1 available as Supplementary Data at *Tree Physiology* Online).

Seed production data

Data on annual seed production at Nettlebed has been collected since 1980, and was used to measure reproductive effort (masting). Reproductive effort was measured by counting seeds for identified individual trees each year using the method described by Hilton and Packham (1997). Seed counts were conducted annually for between two and 12 trees (mean = 5.3), as a result of variation in sampling effort and the addition of new trees to the survey. The individual trees within the site show high intertree correlation in seed count during the period 1981–2012 ($\bar{r} = 0.62$), and also high synchronicity with other local and regional masting records from the UK (Hilton and Packham 1997). The seed count data were standardized to create a dimensionless seed index (*Seed.index*).

Climate data

Climate data was taken from the UK Met Office meteorological station in Oxford (UK Met Office 2016), 28 km from Nettlebed. Summer drought was quantified using the Standardized Precipitation-Evapotranspiration Index (*SPEI*; Vicente-Serrano et al. 2010), a standardized index of the difference between monthly precipitation and potential evapotranspiration. A 3 month window was used for calculation of the index, such that $SPEI_{MJJ}$ incorporates data for May–July, with each month weighted equally.

Modelling

Linear regression models were used to investigate the relationship between *RWI* and $SPEI_{MJJ}$ and *seed.index*, including interaction terms. Previous year $SPEI_{MJJ}$ and *seed.index* were also tested. Parameters were estimated using ordinary least squares, and optimal models were selected using adjusted R^2 and Akaike Information Criterion (AIC). Terms included in optimal models were checked for significance using *F*-tests. Generalized additive models were also used as an exploratory tool to test whether relationships were best described by linear or nonlinear functions.

In order to help address the question of the relative importance of *SPEI* and *seed.index*, the *relaimpo* package in R (Groemping 2006) was used to estimate the relative contribution of each independent variable to the overall explained variance (i.e., to decompose the overall R^2). The metric 'lmg' uses an approach based on sequential R^2, averaging across different orderings of the independent variables (see Groemping 2006 for details), and is recomended by Johnson and LeBreton (2004). While the decomposing of R^2 in multiple regression models is not without criticism (Johnson and LeBreton 2004), it is used in this study, alongside a comparison of the slope parameters to provide a guide to the relative importance of the different variables that influence *RWI*. Model validation follows the recommendations of Zuur et al. (2007), and is detailed in Appendix 2 available as Supplementary Data at *Tree Physiology* Online.

Event year analysis

In order to further investigate possible interactions between drought and reproductive effort an event year approach was used (Schweingruber et al. 1990). Summer drought events were defined as years when $SPEI_{MJJ}$ deviated negatively from the 1921–2012 mean by >1 standard deviation. Event years in reproductive effort were initially defined according to the bimodal distribution of *seed.index* (Figure 1) (Norton and Kelly 1988). The 15 years in the second peak of the distribution were then categorized as (full) mast years (>1 standard deviation from the mean) and intermediate mast years (<1 standard

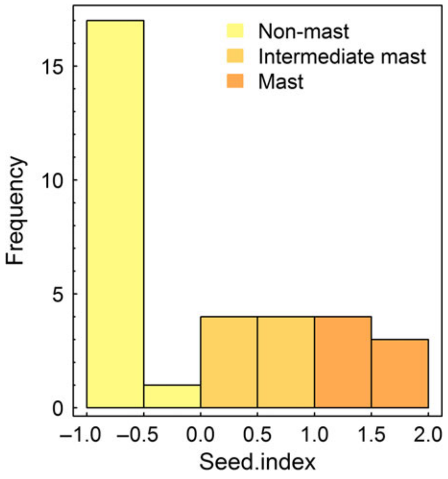

Figure 1. Frequency plot of *seed.index*, showing the bimodal distribution of *seed.index* (annual reproductive effort), and the classification of non-mast, intermediate mast and (full) mast years used in the event year analysis.

deviation). This resulted in the categorization of 7 mast years, 8 intermediate mast years and 17 non-mast years.

In order to extend the period of analysis, and with the particular aim of increasing the sample size of combined mast–drought events, a second masting dataset was used. This also allowed an independent testing of our hypotheses, through use of two independent time periods. In contrast to the site-specific record, this was a regional record of beech masting covering southern England for the period 1921–79 (Hilton and Packham 2003). This regional masting record is categorical (1–5), with the highest two categories considered to represent mast events (Hilton and Packham 2003). The same classification of mast years was used in this study, with no differentiation between heavy and light mast years. Three main classes of event years were created for both study periods (1921–79 and 1980–2012): mast and drought years (M + D), mast and no drought (M + ND), and non-mast and drought (NM + D). Where sample size allowed, each class was then further divided into intermediate and full mast years. Non-drought years were divided into dry years (negative $SPEI_{MJJ}$, but not below the threshold for drought years) and wet years (positive $SPEI_{MJJ}$).

For each class, mean *RWI* deviations in the event year and positive and negative lag years were calculated, both for the period 1980–2012 (using the mast years from continuous site-specific mast data) and for the period 1921–79 (using mast years from the regional masting record). The significance of growth deviations were tested using bootstrapping with 1000 resamples using the 'sea' function in the R package dplR (Bunn et al. 2012).

Results

RWI was significantly correlated with $SPEI_{MJJ}$ and *seed.index*, so that years of low growth were associated with summer drought conditions and high seed production (mast years). Both of these factors were significant in a linear model, which explained 45% of the variance in *RWI* (Model 1 (M1), Table 1). Neither previous year drought stress ($SPEI_{MJJ-1}$) or seed production ($seed.index_{-1}$) was significantly correlated with *RWI*, either individually or when included in the multiple regression model. Additive modelling indicated that linear relationships between *RWI* and both $SPEI_{MJJ}$ and *seed.index* were appropriate (see Appendix 3 available as Supplementary Data at *Tree Physiology* Online). $SPEI_{MJJ}$ and *seed.index* were not themselves significantly correlated, indicating that their individual effects on *RWI* were independent (see Appendix 4 available as Supplementary Data at *Tree Physiology* Online).

As both *SPEI* and *seed.index* were standardized, slope parameters indicated a higher sensitivity of *RWI* to variation in *seed.index* than *SPEI* (Table 1), so growth, as measured by *RWI*, was more influenced by variation in seed production than by variation in summer drought. Additionally, R^2 decomposition using the Img metric indicated that in M1, *seed.index* explained ~30% of the variance in *RWI*, while $SPEI_{MJJ}$ accounted for ~15% (total explained variance, R^2 = 0.45, Table 1). Nevertheless, Figure 2B indicates a possible interaction between drought and masting, with four of the five years of lowest growth associated with both drought and masting. Additionally, drought years that did not coincide with mast years were not associated with strong growth depressions. This potential interaction was explored by adding an interaction to the model.

In this new model (M2) the interaction term was marginally insignificant (P = 0.087), but the adjusted R^2 increased from 0.415 to 0.454 and the AIC was slightly lower (Table 2). Additionally, the interaction term in M2 removed a pattern in the standardized residuals present in M1 (see Appendix 2 available as Supplementary Data at *Tree Physiology* Online). R^2 decomposition indicated that the interaction between $SPEI_{MJJ}$ and *seed.index* explained an additional 5% of the variance in *RWI*. Additive models again indicated that linear models appropriately represented the relationships between *RWI* and the independent variables (see Appendix 3 available as Supplementary Data at *Tree Physiology* Online).

Overall, both models were able to accurately reproduce the observed variation in *RWI* at the sample site, particularly M2, which included the interaction term. In particular, M2 was able to reproduce the narrowest rings with only small residuals (Figure 3, and also see Appendix 2 available as Supplementary Data at *Tree Physiology* Online). However, growth was not reproduced accurately in all years. In particular, the models failed to fully reproduce the observed low growth in 1985 (following a narrow ring in 1984 that was well reproduced by the models), or the narrow ring observed in 2004. Additionally, the models substantially

Table 1. Summary of Model 1, radial growth as a linear function of summer drought and seed production (M1; $RWI = SPEI_{MJJ} + seed.index$).

Variable	Estimate	SE	*t*-Value	*P*-value	Img
Intercept	0.000	0.133	0.000	1.000	
$SPEI_{MJJ}$	0.342	0.137	2.494	0.018*	0.150
seed.index	−0.526	0.137	−3.813	<0.001***	0.302
$R^2 = 0.452$	${}_{\text{adj}}R^2 = 0.415$	AIC = 80.800			

Estimate = parameter estimate; SE = standard error; Img = relative importance metric (Groemping 2006).
*$p < 0.05$.
**$p < 0.01$.
***$p < 0.001$.

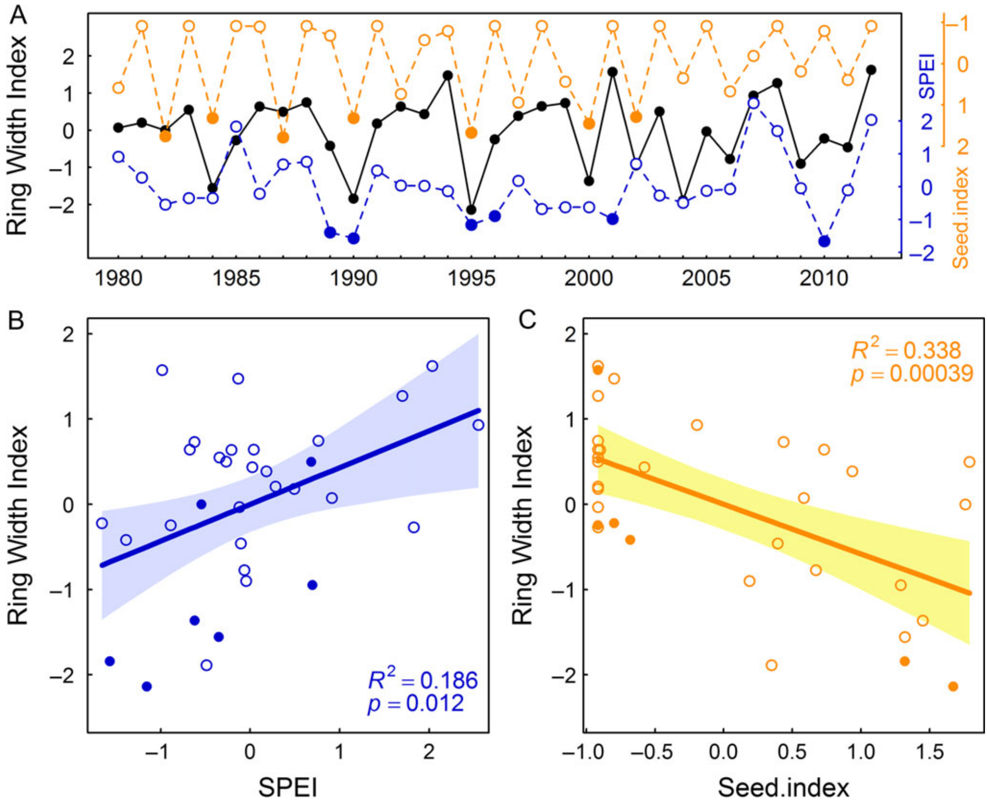

Figure 2. Annual growth and seed production at the study site. (A) Annual growth (ring width index, *RWI*), reproductive effort (*seed.index*) and summer drought ($SPEI_{MJJ}$). Filled circles represent event years in *seed.index* (i.e., mast years) and in $SPEI_{MJJ}$ (i.e., drought years). (B) The relationship between growth and summer drought (filled circles represent mast years). (C) The relationship between growth and reproductive effort (filled circles represent drought years).

Table 2. Summary of Model 2, radial growth as a linear function of summer drought and seed production, plus the their interaction (M2; $RWI = SPEI_{MJJ} + seed.index + SPEI_{MJJ} \cdot seed.index$).

Variable	Estimate	SE	*t*-Value	*P*-value	lmg
Intercept	0.045	0.131	0.346	0.732	
SPEI	0.423	0.140	3.019	0.005**	0.150
seed.index	−0.470	0.136	−3.462	0.002**	0.302
SPEI · seed.index	0.275	0.155	1.774	0.087	0.054
$R^2 = 0.505$	aR2 = 0.454	AIC = 79.399			

Estimate = parameter estimate; SE = standard error; lmg = relative importance metric (Groemping 2006).
$^{*}p < 0.05$.
$^{**}p < 0.01$.
$^{***}p < 0.001$.

underestimated growth in several years (i.e., predicted growth was lower than observed growth, e.g., 1982, 1987 (M1 only), 1992, 1994, 1999 and 2001). With the exception of 1994 and 2001 (which are the years with the highest observed ring width), all of these years were full or intermediate mast years that occurred in the absence of summer drought stress (Figures 2 and 3).

A second approach to exploring the interaction between seed production and drought used an event year approach. Mast years that coincided with drought events (M + D) were associated with strong and significant negative growth anomalies in the event year (Figure 4A–C). Two of these combined events occurred in the period 1980–2012, and both were associated with strong and significant negative growth anomalies that corresponded to two of the three narrowest rings formed during the period. In the second period (1921–79), an additional three combined drought-mast events occurred, and negative growth anomalies in the event year were also strong and significant. Despite the strong growth reductions in the event years, no growth anomaly was detected in the following years.

In mast years that did not correspond with drought (M + ND), growth was lower in the mast year during the period 1980–2012 (although the negative growth anomaly was smaller than for

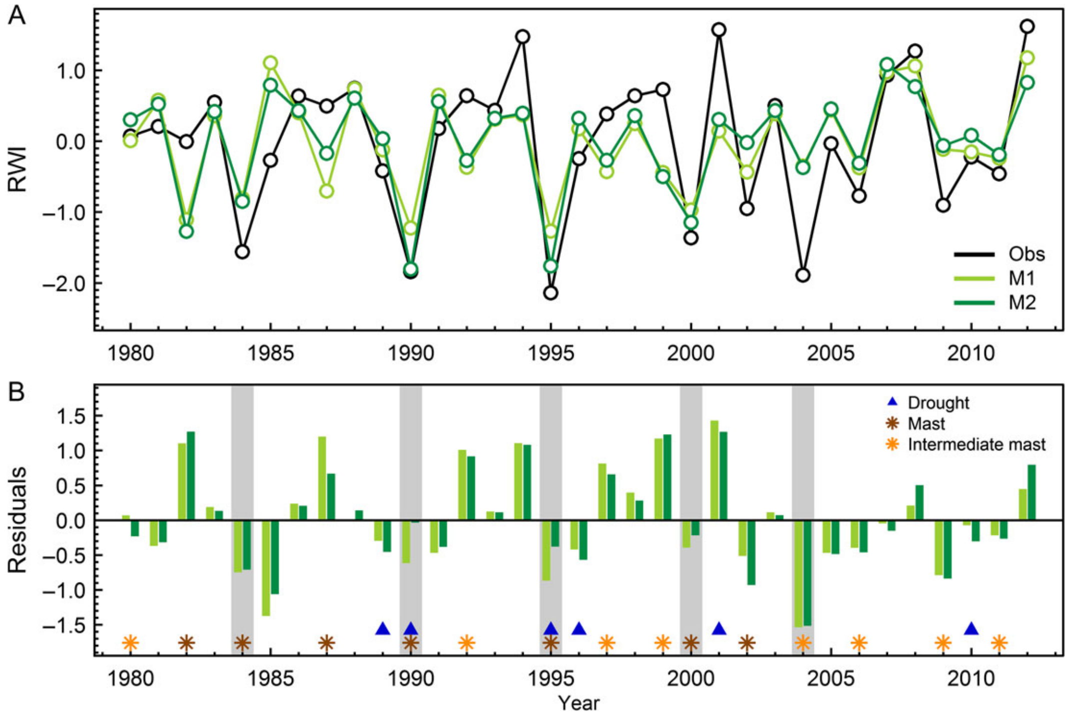

Figure 3. Performance of Model 1 and Model 2. (A) Observed and predicted *RWI*. (B) Residuals of the two models. Grey shading indicates the years with the narrowest observed ring width. Triangles represent drought years, and asterisks indicate (full) mast and intermediate mast years (see Figure 1).

combined mast and drought) (Figure 4D–F), but in some cases positive growth anomalies were found in the following year. For intermediate mast years, the negative growth anomaly was close to zero in the event year (Figure 4D). In the period 1921–79 growth was also slightly lower in mast years, although not significantly. In a combined dataset using both masting time-series (1921–2012), the larger number of mast years that coincided with non-drought conditions ($n = 15$, mast years from both periods, excluding the intermediate mast years from 1980 to 2012) allowed a further division into mast years occurring in dry summers (but not drought) and those occurring in wet summers. Mast years coinciding with dry summers had significant negative growth anomalies, while mast years coinciding with wet summers were not associated with any growth anomaly (Figure 4F). The growth reduction in dry mast years was smaller than the reduction in combined drought-mast years (Figure 4C).

In drought years that did not coincide with mast years (NM + D), no significant growth anomalies were found in either period, although growth was lower the following year (significant in the 1921–79 period, non-significant in the 1980–2012 period, Figure 4G–I). The results showed that the growth response to mast years was highly dependent on summer drought stress (Figure 5). In years with both masting and summer drought, *RWI* was strongly and significantly reduced, while in years with masting and dry conditions *RWI* was also reduced, but the anomaly was smaller in magnitude. In mast years associated with wet summers, and in drought summers that did not coincide with mast events, there was no significant *RWI* anomaly in the event year, although there were significant *RWI* anomalies (positive and negative) in the following years (Figures 4 and 5).

Discussion

Combined and interacting effects of masting and drought

Initial analysis of the data (Figure 2) appeared to confirm previous well-established results for *F. sylvatica*, showing that both growing season drought stress (*SPEI*$_{MJJ}$) and annual reproductive effort (*seed.index*) were significantly correlated with radial growth (e.g., Drobyshev et al. 2010, Hacket-Pain et al. 2016). The overall explained variance in M1 and M2 ($R^2 = 0.45$ and 0.51, respectively) was similar to the study by Monks and Kelly (2006), where 41% of variance in *Nothofagus truncata RWI* could be explained using a combination of climate variables and annual seedfall, but less than the 74% of variance in *Picea albies RWI* was explained by a combination of climate variables and seed index in the study of Selas et al. (2002). These results demonstrate that for a variety of species a substantial proportion of the variance in tree growth can be explained by weather conditions and reproductive effort. The physiological basis of growth reductions during drought result from complex interactions between carbon supply (Breda et al. 2006), cell division and expansion (Hsiao 1973), and carbon allocation and transport (Blessing et al. 2015), with responses varying between (and within) species, and according to drought severity (Ryan 2011). Less is known about the physiological mechanisms that are responsible for growth reductions in mast years. Several studies have reported that fruit production is

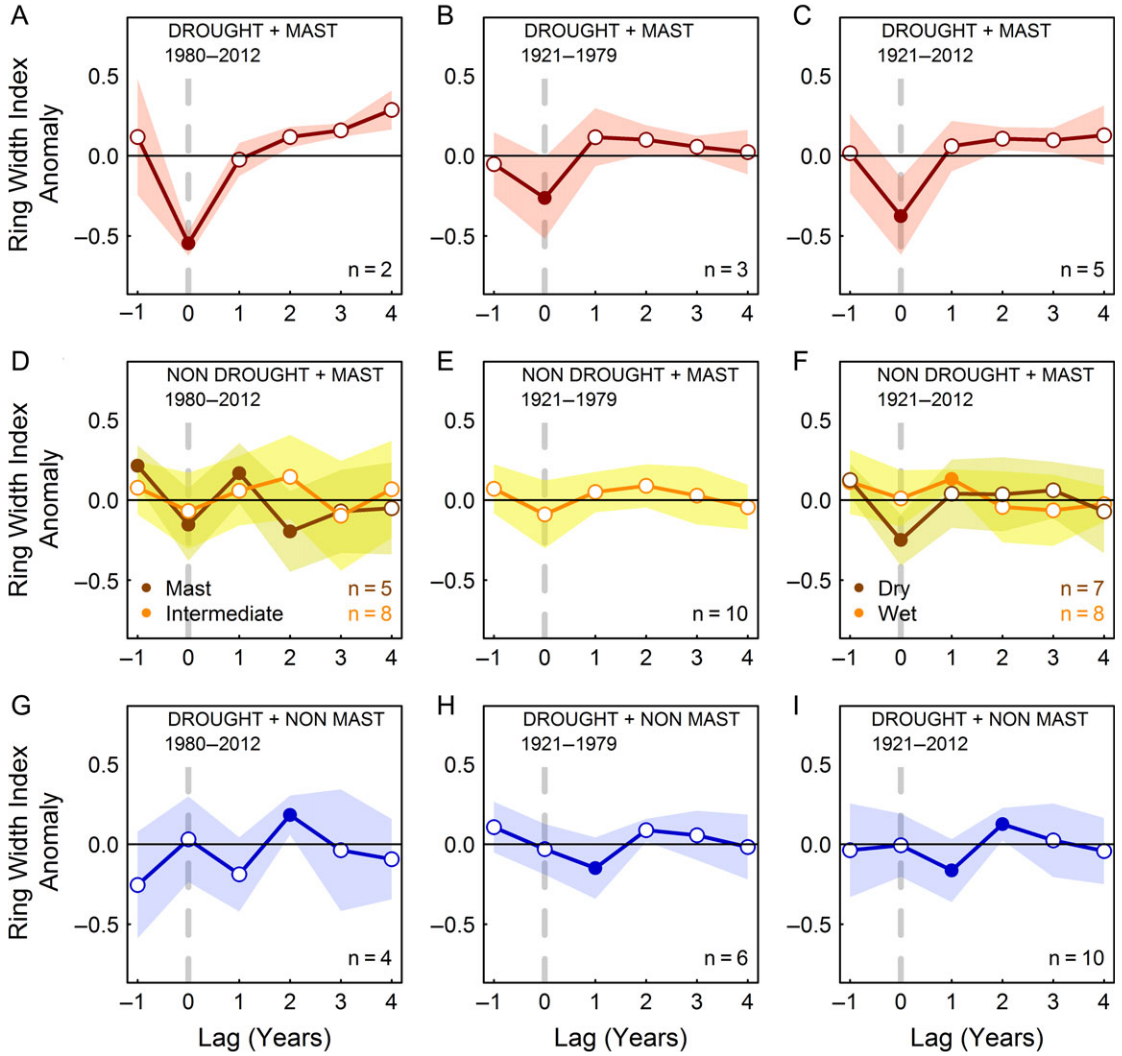

Figure 4. Event year analysis for the period 1980–2012 (site level mast data), 1921–79 (regional mast data) and combined period (1921–2012). Points represent the mean growth anomaly for all event years and the shaded area the standard deviation. Filled circles represent significant anomalies ($P < 0.05$). (A–C) Combined mast and drought years for the periods 1982–2012, 1921–79 and the combined period 1921–2010. (D–F) Non-drought years with masting. In (D) (1980–2012), intermediate mast years plotted in addition to (full) mast years, but were not used in any other analyses. In (F) (1921–2012) mast years were divided into dry (but not drought) and wet summers (note that intermediate mast years were not included). (G–I) Drought years without masting.

dependent on recently assimilated carbon (Hoch et al. 2013, Ichie et al. 2013), with little evidence of declines in stored carbon during mast events. Consequently, growth and fruit production may act as competing sinks for newly assimilated carbon, with a reduction in growth occurring in years where the allocation to reproduction is high. Other factors not considered in the models, such as the effects of late frosts (Príncipe et al. 2016), are likely responsible for part of the unexplained variance in *RWI*.

However, the present study also assesses the relative importance of these two factors, and their interactive effects on annual growth. Comparison of model coefficients and R^2 decomposition for M1 indicated that variation in reproductive effort (*seed.index*) was more important in explaining variance in growth than growing season drought stress ($SPEI_{MJJ}$) (Table 1). This is an important result, as it shows that at least at this site, annual growth was more sensitive to variance in annual seed production than growing season drought stress. The site is typical of lowland Britain and northern Europe, and tree ring chronologies and seed production time-series show high synchrony with other sites in the southern UK. Additionally, preliminary results using independent data from *F. sylvatica* forests in Sweden show a similar pattern. This suggests our results at NET are likely to be widely applicable to other stands, and that the relative importance of reproductive effort on growth is widespread in *F. sylvatica*, and in other masting trees species (see also Drobyshev et al. 2010, Latte et al. 2016). However, on drier sites, it is possible that drought will play a larger role in determining growth; this warrants further investigation, although it is likely that reproductive effort will still exert a significant effect on growth.

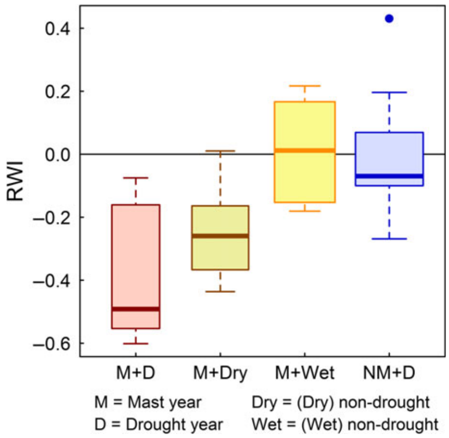

Figure 5. Growth responses to event years for the period 1921–2012. Note that only (full) mast years in the period (1980–2012) are included in the analysis. The width of the boxplots is proportional to the number of observa and the whiskers extend to include all points which are no more than 1.5× the interquartile range.

Closer inspection revealed that the effects of drought and reproductive effort on growth were more complex. Figure 2B indicated that years of combined high seed production and drought were responsible for the narrowest rings, while mast years that did not coincide with drought did not necessarily correspond to low growth. Two approaches were used to investigate this potential interaction further. In the first, adding an interaction term to the model ($SPEI_{MJJ} \cdot seed.index$) explained an additional 5% of variance in *RWI* (Table 2), and increased the ability of the model to accurately reproduce the narrowest rings in the chronology (Figure 3). Additionally, many of the positive residuals in M1 and M2 were associated with mast or intermediate mast years that did not coincide with drought. Both models predicted lower growth in these years than was observed, further supporting the hypothesis that the interaction of masting and drought was important in explaining variation in growth.

Overall, the event year analysis demonstrated similar results, showing that growth at this site responded relatively weakly to mast and drought events that occurred in isolation, and that the strongest growth reductions occurred when heavy seed production and summer drought coincided during the same growing season (Figure 5). For example, the response of growth in mast years was highly dependent on drought: in wet summers even a heavy seed crop resulted in no reduction in growth, while in dry (but not drought) summers, a moderate growth reduction was detected. In drought years however, the combination of masting and drought resulted in strong negative growth anomalies; i.e., an interaction of unfavourable climate conditions and strong growth–reproduction trade-offs resulted in large and highly significant reductions in growth (Figure 5). Similar results were noted by Selas et al. (2002), who reported that very narrow tree rings in *Picea abies* occurred in years with both heavy seed crops and early summer drought. In a recent study, Han et al. (2016) showed that radial growth in *Fagus crenata* was strongly dependent on newly assimilated carbon, while fruit production in *F. crenata* relied initially on stored carbon early in the growing season, before shifting to recently assimilated carbon later in the growing season. This observation may help to explain the interactive effects of drought and masting on growth. In the absence of masting, stored carbon may buffer any carbon shortage in drought years. In contrast, when drought coincides with masting, fruit production would act as a strong early-season sink of stored carbon, reducing the availability of stored carbon for growth. This may be particularly important during the early growing season, when the sink strength is high for fruits (Han et al. 2016) and stem growth (Jezik et al. 2011), potentially creating a temporary carbon shortage (Mund et al. 2010).

These results have important implications for interpretation of the variation in tree ring chronologies and tree growth more generally. For example, tree ring responses to drought events have been used to assess the drought sensitivity of forest trees, including comparisons of the sensitivity of different species (Zang et al. 2014) and populations growing under different mean climates (Cavin and Jump 2016). However, the interaction of masting and drought demonstrated in this study shows that without careful consideration of the confounding effects of annual reproductive effort, such assessments may be compromised in masting species, especially for analysis that focuses on individual years. For example, the major drought in northwestern Europe in 1976 is associated with extreme narrow tree rings in *F. sylvatica*, which has widely been interpreted as indicating drought sensitivity in this species (Cavin et al. 2013). However, this year was also associated with high reproductive effort in *F. sylvatica* across much of northern Europe (Hilton and Packham 2003, Overgaard et al. 2007). Our results indicate that a significant proportion of the growth anomaly observed across northern and central Europe in 1976 could be attributed to the interaction of drought and masting in this year, rather than drought alone (see Appendix 5 available as Supplementary Data at *Tree Physiology* Online).

Variation in cost of reproduction with climate

Additionally, our results are relevant to a more general understanding of the cost of reproduction and its trade-off with growth. The observed variation in growth response to mast years can be interpreted as representing a variation in the strength of the growth–reproduction trade-off along a stress gradient; under stressful conditions (drought years) the trade-off is strong, while under favourable conditions the trade-off is weaker. Such variation in the strength of growth–reproduction trade-offs has been investigated in trees before, but generally by analysing variation between populations or individuals, rather than between years (Berdanier and Clark 2016). These studies have generally reported stronger growth–reproduction trade-offs in stressed trees (Banuelos and Obeso 2004, Iszkulo and

Boratynski 2011, Martin et al. 2015). Such variation in the strength of the trade-off may vary between populations or between years due to climatic control on resource acquisition; Mencuccini and Piussi (1995) suggested that when resources were not limiting, seed production did not act as a substantial cost to the tree. Additionally, in more favourable years the longer growing season may reduce the temporal overlap of allocation to reproduction and growth (Mund et al. 2010, Sletvold and Agren 2015).

Multi-year relationships between weather conditions, mast years and growth

Numerous studies have reported positive growth anomalies in the year prior to masting, interpreted as representing favourable conditions for resources accumulation (Silvertown and Dodd 1999, Drobyshev et al. 2010). Our analysis provided only limited evidence of positive growth anomalies prior to mast years at NET (Figure 4). However, the event year analysis did indicate other complex multi-year connections between climate, masting and growth (Figure 4). The year following a mast year was not associated with a reduction in growth, either when the mast year coincided with drought (Figure 4A–C) or with non-drought conditions (Figure 4D–F). Indeed, in some cases growth was significantly higher in the year following masting (Figure 4D and F). This is contrary to some previous results that have demonstrated multi-year effects of masting on growth (Holmsgaard 1958, Silvertown and Dodd 1999), but is consistent with Drobyshev et al. (2010). This suggests that in mesic sites with generally favourable growing conditions, *F. sylvatica* experiences no long-term costs to growth as a result of mast events, despite strong growth reductions in the year of masting.

While we found no evidence of multi-year growth response to individual mast years, we did observe a reduction in growth in the year following non-mast drought years, despite no reduction in growth in the drought year itself (Figure 4G–I). While this may be related to lagged responses of growth to drought (Anderegg et al. 2015), we suggest that in this case the lagged effect is due to masting in the year following a drought. Drought years, associated with high temperature and low precipitation, may act as a cue for mast events in the following year (Piovesan and Adams 2001, Drobyshev et al. 2010). Of the four non-mast drought years in the period 1980–2012, two were followed by mast years, and the other two by intermediate mast years. For the period 1921–79, all five non-mast drought years were followed by mast years. As expected based on our results, these years are associated with reduced growth, especially when the summer following the drought year is dry (Figure 4). Consequently, multi-year growth responses to drought events may result not only from direct responses to drought (e.g., resource depletion and organ mortality), but also due to the triggering of mast events. This mechanism may help to explain the commonly observed severe growth reduction associated with the second year of double-year droughts, including 1975–76 and 1989–90, with the first year of drought acting a cue for a mast event in the second year.

Resource switching in **Fagus sylvatica***: masting as an evolutionary strategy*

Negative correlations between reproductive effort and growth have been observed in many species (e.g., Mencuccini and Piussi 1995, Selas et al. 2002, Monks and Kelly 2006), and have been used as evidence of the switching of resources between growth and reproduction in masting species. Monks and Kelly (2006) argued that such resource switching is the most decisive evidence that masting is the result of an evolutionary pressure that acts to exaggerate interannual variation in seed production. However, while a negative correlation between seed production and growth is often interpreted as evidence of resource switching, Knops et al. (2007) have demonstrated that such a negative correlation does not always represent a trade-off. They showed that wet spring weather had a positive effect on growth, but reduced acorn production by limiting pollination. Consequently, in oak species that produced acorns in the same year as pollination, these two independent responses could result in a negative correlation between acorn production and growth, without the need for a causal mechanism linking the two (i.e., a trade-off). Furthermore, they showed that this negative correlation was absent in oak species that produced acorns over 2 years. In our study, seed production did not respond significantly to the same climate signal as growth (summer drought) (see Appendix 4 available as Supplementary Data at *Tree Physiology* Online), and we have demonstrated the presence of a switch in resources even when the main climatic influence on growth (growing season drought) is taken into account. Indeed, our evidence that the reduction in growth in mast years is greater in years of unfavourable climate further supports the existence of resource switching in this species.

Coupling of growth, reproduction and climate

Tree radial growth at NET varied as a function of summer drought and reproductive effort, and their interaction. The degree to which growth at the stand level was reduced in years of high reproductive effort (mast years) was strongly dependent on environmental stress (summer drought). This indicates that the costs of reproduction increased strongly under conditions of environmental stress, and were close to zero under favourable climate conditions. The complex inter-relationships between climate, reproduction and growth that are demonstrated in this study have widespread implications for understanding interannual variation in tree growth. Variation in the growth response of individuals, populations and species to extreme climate events may result from variation in coincident reproductive effort. For example, observed variation in the NPP response of forests to widespread drought events may be linked to variations in masting intensity across space or between species (Nussbaumer et al. 2016), while variation in reproductive effort between trees may contribute to individualistic responses of trees to climate (Carrer 2011).

Supplementary Data

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

Conflict of interest

None declared.

References

Anderegg WRL, Schwalm C, Biondi F et al. (2015) Pervasive drought legacies in forest ecosystems and their implications for carbon cycle models. Science 349:528–532.

Banuelos MJ, Obeso JR (2004) Resource allocation in the dioecious shrub *Rhamnus alpinus*: the hidden costs of reproduction. Evol Ecol Res 6:397–413.

Berdanier AB, Clark JS (2016) Divergent reproductive allocation tradeoffs with canopy exposure across tree species in temperate forests. Ecosphere 7:10.

Blessing CH, Werner RA, Siegwolf R, Buchmann N (2015) Allocation dynamics of recently fixed carbon in beech saplings in response to increased temperatures and drought. Tree Physiol 35:585–598.

Breda N, Huc R, Granier A, Dreyer E (2006) Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. Ann For Sci 63: 625–644.

Bunn AG, Korpela, M, Biondi F, Campelo F, Merian P, Qeadan F Zang C (2012) dplR: Dendrochronology Program Library in R. R package version 1.6.2. http://CRAN.R-project.org/package=dplR (12 April 2016, date last accessed).

Campioli M, Gielen B, Goeckede 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.

Carrer M (2011) Individualistic and time-varying tree-ring growth to climate sensitivity. Plos One 6:e22813. doi:10.1371/journal.pone.0022813

Cavin L, Jump AS (2017) Highest drought sensitivity and lowest resistance to growth suppression are found in the range core of the tree *Fagus sylvatica* L. not the equatorial range edge. Glob Chang Biol 23: 362–379.

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.

Dittmar C, Zech W, Elling W (2003) Growth variations of Common beech (*Fagus sylvatica* L.) under different climatic and environmental conditions in Europe – a dendroecological study. For Ecol Manage 173:63–78.

Drobyshev I, Overgaard 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 Manage 259:2160–2171.

Fatichi S, Leuzinger S, Koerner C (2014) Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. New Phytol 201:1086–1095.

Fritts H (1976) Tree rings and climate. Academic Publishers, New York, NY, p 567.

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.

George SS (2014) An overview of tree-ring width records across the Northern Hemisphere. Quat Sci Rev 95:132–150.

Gessler A, Keitel C, Kreuzwieser J, Matyssek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. Trees 21:1–11.

Grissino-Mayer HD (2001) Crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree Ring Res 57: 205–221.

Groemping U (2006) Relative importance for linear regression in R: the package relaimpo. J Stat Softw 17:1–27.

Guillemot J, Martin-StPaul NK, Dufrene E, Francois C, Soudani K, Ourcival JM, Delpierre N (2015) The dynamic of the annual carbon allocation to wood in European tree species is consistent with a combined source-sink limitation of growth: implications for modelling. Biogeosciences 12:2773–2790.

Hacket-Pain AJ, Friend AD, Lageard JGA, Thomas PA (2015) The influence of masting phenomenon on growth–climate relationships in trees: explaining the influence of previous summers' climate on ring width. Tree Physiol 35:319–330.

Hacket-Pain AJ, Cavin L, Friend AD, Jump A (2016) Consistent limitation of growth by high temperature and low precipitation from range core to southern edge of European Beech indicates widespread vulnerability to changing climate. Eur J For Sci 135:897–909.

Han Q, Kagawa A, Kabeya D, Inagaki Y (2016) Reproduction-related varaition in carbon allocation to woody tissues in *Fagus crenata* using a natural ^{13}C approach. Tree Physiol 36:1343–1352.

Hilton GM, Packham JR (1997) Sixteen-year record of regional and temporal variation in the fruiting of beech (*Fagus sylvatica* L) in England (1980–1995). Forestry 70:7–16.

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, 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.

Holmsgaard E (1958) Effect of seed-bearing on the increment of European beech (*Fagus sylvatica* L.) and Norway Spruce (*Picea abies* (L.) Karst). In: Papers of the Twelfth Congress of the International Union of Forestry Research Organizations. International Union of Forestry Research Organizations, Oxford.

Hsiao TC (1973) Plant responses to water stress. Annu Rev Plant Physiol Plant Mol Biol 24:519–570.

Ichie T, Igarashi S, Yoshida S, Kenzo T, Masaki T, Tayasu I (2013) Are stored carbohydrates necessary for seed production in temperate deciduous trees? J Ecol 101:525–531.

Iszkulo G, Boratynski A (2011) Initial period of sexual maturity determines the greater growth rate of male over female in the dioecious tree Juniperus communis subsp. communis. Acta Oecol 37:99–102.

Jezik M, Blazenec M, Strelcova K, Ditmarova L (2011) The impact of the 2003-2008 weather variability on intra-annual stem diameter changes of beech trees at a submontane site in central Slovakia. Dendrochronologia 29:227–235.

Johnson JW, LeBreton JM (2004) History and use of relative importance indices in organizational research. Organ Res Meth 7:238–257.

Kelly D, Sork VL (2002) Mast seeding in perennial plants: why, how, where? Annu Rev Ecol Syst 33:427–447.

Knops JMH, Koenig WD, Carmen WJ (2007) Negative correlation does not imply a tradeoff between growth and reproduction in California oaks. Proc Natl Acad Sci USA 104:16982–16985.

Körner C (2013) Growth controls photosynthesis – mostly. Nova Acta Leopoldina 114:273–283.

Larsson L-A (2010*a*) CDendro. Cybis Elektronik and Data AB. Saltsjöbaden, Sweden.

Larsson L-A (2010*b*) CooRecorder. Cybis Elektronil and Data AB. Saltsjöbaden, Sweden.

Latte N, Lebourgeois F, Claessens H (2016) Growth partitioning within beech trees (*Fagus sylvatica* L.) varies in response to summer heat waves and related droughts. Trees 30:189–201.

Martin D, Vazquez-Pique J, Carevic FS, Fernandez M, Alejano R (2015) Trade-off between stem growth and acorn production in holm oak. Trees 29:825–834.

Mencuccini M, Piussi P (1995) Production of seeds and cones and consequences for wood radial increment in Norway spruce (*Picea abies* (L.) Karst.). Giornale Botanico Italiano 129:797–812.

Monks A, Kelly D (2006) Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). Austral Ecol 31:366–375.

Muller-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.

Norton DA, Kelly D (1988) Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Funct Ecol 2:399–408.

Nussbaumer A, Waldner P, Etzold S et al. (2016) Patterns of mast fruiting of common beech, sessile and common oak, Norway spruce and Scots pine in Central and Northern Europe. For Ecol Manage 363: 237–251.

Overgaard R, Gemmel P, Karlsson M (2007) Effects of weather conditions on mast year frequency in beech (*Fagus sylvatica* L.) in Sweden. Forestry 80:553–563.

Packham JR, Thomas PA, Atkinson MD, Degen T (2012) Biological flora of the British Isles: *Fagus sylvatica*. J Ecol 100:1557–1608.

Piovesan G, Adams JM (2001) Masting behaviour in beech: linking reproduction and climatic variation. Can J Bot 79:1039–1047.

Príncipe A, van der Maaten E, van der Maaten-Theunissen M, Struwe T, Wilmking M, Kreyling Ju (2016) Low resistance but high resilience in growth of a major deciduous forest tree (*Fagus sylvatica L.*) in response to late spring frost in southern Germany. Trees. doi: 10.1007/s00468-016-1505-3

Ryan MG (2011) Tree responses to drought. Tree Physiol 31:237–239.

Scharnweber T, Manthey M, Criegee C, Bauwe A, Schroeder C, Wilmking M (2011) Drought matters – declining precipitation influences growth of *Fagus sylvatica* L. and *Quercus robur* L. in north-eastern Germany. For Ecol Manage 262:947–961.

Schauber EM, Kelly D, Turchin P, Simon C, Lee WG, Allen RB, Payton IJ, Wilson PR, Cowan PE, Brockie RE (2002) Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. Ecology 83:1214–1225.

Schweingruber FH, Eckstein D, Serre-Bachet F, Bräker OU (1990) Identification, presentation and interpretation of event years and pointer years in dendrochronology. Dendrochronologia 8:9–38.

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.

Silvertown J, Dodd M (1999) The demographic cost of reproduction and its consequences in balsam fir (*Abies balsamea*). Am Nat 154:321–332.

Sletvold N, Agren J (2015) Climate-dependent costs of reproduction: survival and fecundity costs decline with length of the growing season and summer temperature. Ecol Lett 18:357–364.

Stephenson NL, Das AJ, Condit R et al. (2014) Rate of tree carbon accumulation increases continuously with tree size. Nature 507:90–93.

Thomas SC (2011) Age-related changes in tree growth and functional biology: the role of reproduction. In: Size- and age-related changes in tree structure and function, Springer Netherlands, Vol. 4. pp 33–64. http://link.springer.com/chapter/10.1007%2F978-94-007-1242-3_2

UK Met Office (2016) Historic station data: Oxford, http://www.metoffice.gov.uk/pub/data/weather/uk/climate/stationdata/oxforddata.txt (12 April 2017, date last accessed).

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.

Wenk EH, Falster DS (2015) Quantifying and understanding reproductive allocation schedules in plants. Ecol Evol 5:5521–5538.

Woodward A, Silsbee DG, Schreiner EG, Means JE (1994) Influence of climate on radial growth and cone production in sub-alpine fir (*Abies lasiocarpa*) and mountain hemlock (*Tsuga mertensiana*). Can J For Res 24:1133–1143.

Zang C, Hartl-Meier C, Dittmar C, Rothe A, Menzel A (2014) Patterns of drought tolerance in major European temperate forest trees: climatic drivers and levels of variability. Glob Chang Biol 20: 3767–3779.

Zuur AF, Ieno EN, Smith GM (2007) Analysing ecological data. Statistics for biology and health. Springer, New York, NY, 672 pp.