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Tree rings and masting: considering reproductive phenomena when interpreting tree rings?

A.J. Hacket-Pain[1], A.D. Friend[2], J.G.A. Lageard[3] & P.A. Thomas[4]

[1] *Fitzwilliam College, University of Cambridge, UK*
[2] *Department of Geography, University of Cambridge, UK*
[3] *School of Science and the Environment, Manchester Metropolitan University, UK*
[4] *School of Life Sciences, Keele University, UK*
E-mail: ajh220@cam.ac.uk

Background and justification

Tree ring archives have provided key information for a diverse range of fields, including ecology, archaeology and palaeoclimatology. For example, the statistical relationships between growth and climate form the basis for tree-ring based reconstructions of climate, including regional and global temperature, drought frequency and severity, and atmospheric changes including ENSO and NOA (Cook et al. 2007). In addition, tree rings have been shown to be a reliable record of tree and forest aboveground biomass increment and ecosystem productivity (Babst et al. 2014), and therefore ecologists are increasingly using tree rings to investigate ecosystem dynamics and controls on tree and forest growth. For example, tree rings are being used to determine responses of forest growth to climate changes (Barber et al. 2000, Salzer et al. 2009). Other research is currently focused on the use of tree ring chronologies to detect the effect of increasing atmospheric CO_2 on tree growth in order to resolve outstanding questions concerning the carbon fertilisation effect on the terrestrial carbon sink (Peñuelas et al. 2011, Bowman et al. 2013). A key goal is to determine the sensitivities and vulnerabilities of different tree species to climate change, and predict how the key ecosystem services provided by forests will change in the coming decades. Linked to this, the relationships between growth and climate in tree ring networks have provided a rare opportunity to independently validate the output of Dynamic Global Vegetation Models (DGVMs) (Babst et al. 2013), for example by comparing predictions and observations of the response of forest growth to extreme climate events (Rammig et al. 2015).

Current interpretations of inter-annual variations in tree ring width are based on the assumption that tree growth is controlled by carbon supply and the processes of cell division and expansion (Fritts et al. 1991). These processes may be near-instantaneous (e.g. photosynthesis controlling carbon supply), or involve carry-over processes from previous years (e.g. remobilisation of carbon reserves). Because the rates and timings of these processes are all strongly influenced by weather conditions, strong relationships between ring width and climate can occur. However, in addition to these direct responses, a second class of processes related to resource allocation can also have an important control on annual growth (Thomas 2011). These have frequently been neglected when interpreting tree ring width variability. For example, allocation of resources to reproduction is highly variable, with seed production often varying strongly between years (Allen et al. 2014), and increasing through an individual's lifetime (Genet et al. 2010). Significantly for the interpretation of tree ring variability, allocation to reproduction is associated with a strong trade-off with growth (Obeso 2002), and is itself dependent on weather conditions. In particular, many tree species display strong inter-annual variation in allocation to reproduction (Schauber et al. 2002), a phenomenon known as masting. This allocation strategy typically involves synchronisation of heavy seed production across individuals (mast years), cued by particular weather conditions, with one or several subsequent years of low seed production. The climatic control of masting, combined with a trade-off between growth and reproduction (typically represented by a 20-50% reduction of growth in mast years) (Selas et al. 2002, Sanchez-Humanes et al. 2011, Hacket-Pain et al. 2015)

introduces climate signals into tree ring chronologies, in addition to those directly related to primary production (Fig. 1). However, the influence of allocation to reproduction has not been fully integrated in tree ring studies, despite the potential to explain a substantial component of the inter-annual variance in ring width.
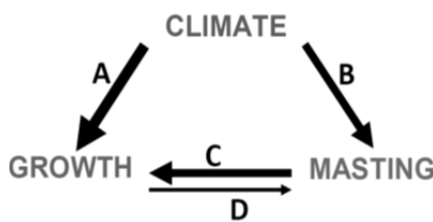
Figure 1. Sketch of the relationships between growth, masting and climate. The width of the arrows provides an indication of previous research effort. High frequency signals in tree rings are usually interpreted in terms of the direct effect of climate on growth (A). However, growth variations can also be caused by masting events (C), which can in turn create complex climate signals in tree ring chronologies as masting events are cued by climate (B + C). A further complication arises because masting behaviour may be influenced by resource availability (D).

Tree rings and masting in *Fagus sylvatica* L.: a review of previous research

We investigated the influence of inter-annual variations in allocation to reproduction on tree ring width index (RWI) chronologies in *Fagus sylvatica* (Hacket-Pain et al. 2015). We showed that, in mast years, allocation of resources to reproduction was associated with a 17-22% reduction in RWI during mast years, which occurred on average every five years. Other studies have reported similar reductions in ring width in beech during mast years (von Jazewitsch 1953, Drobyshev et al. 2010, Latte et al. 2015), and in other species (for example, see the meta-analysis in Thomas 2011). Overall, we found that growing season climate (in this case a summer drought index) explained ~30% of the variance in RWI, but we could explain an additional ~20% by also accounting for masting in our model. We did not establish the physiological cause of the observed growth-reproduction trade-off, but we propose that a combination of direct and indirect trade-off mechanisms may be responsible for the observed reduction in RWI. In a direct trade-off, the increase in investment of carbohydrates in reproductive tissue in mast year reduces the carbohydrate available for woody tissues. Campioli et al.(2011) and Muller-Haubold et al. (2013) found that while growing season weather conditions are the main control of interannual variations in Gross Primary Productivity (GPP) and Net Primary Productivity (NPP) in beech forests, weather conditions in the previous year (previous summer temperature, the main cue for mast events) were the main control on the partitioning of NPP between the wood and fruits, and thus the ratio between GPP and wood NPP. This implies that while growing season weather conditions are the primary control on carbon assimilation (and thus, presumably, carbon availability), masting is a key control on how much of this carbon is allocated to wood production, and hence the width of the resulting tree ring. However, this trade-off between allocation to fruit production and growth may only be seasonal, limited to periods when GPP is low and carbon demand for fruit production is high (i.e. the start of the growing season) (Mund et al. 2010).In addition to influencing the allocation of available carbon (a direct trade-off), mast years may reduce ring width indirectly by reducing GPP, and consequently reducing overall carbon availability (including carbon for growth). Developing fruits are a strong sink for nutrients (Ichie et al. 2005; Sala et al. 2012), with high seed production associated with reduced nitrogen concentration in seed bearing shoots (Alla et al. 2012) and reduced photosynthetic capacity (Han et al. 2008). Furthermore, mast years are associated with smaller whole-plant leaf area (Ferretti et al. 1998; Innes 1992), due to a combination of a lower leaf number and reduced leaf size (Thomas 2011). Together, this reduction in leaf area, and lower photosynthetic capacity as a result of lower foliar nitrogen concentrations may result in reduced carbon assimilation and thus carbon availability.

In addition to demonstrating the strength of growth-reproduction trade-offs in *F.* sylvatica, and the potential to explain significant proportions of variance in ring width by incorporating information on masting behaviour, we have also demonstrated the potential for masting to introduce distinct climate signals into tree ring chronologies (Fig. 1). Mast years are associated with particular

weather cues, which in *F. sylvatica* are most commonly reported to be a sequence of cool temperatures in the summer two years previous, followed by warm temperatures in the summer prior to the mast year (Drobyshev et al. 2010, Hacket-Pain 2013). Importantly, we show that the combination of this climatic cue for mast years, and the strong growth-reproduction trade-off, creates specific correlations between RWI and climate (Piovesan & Schirone 2000, Hacket-Pain et al. 2015). In the case of *F. sylvatica,* we showed that correlations between RWI and previous summer temperature can be explained by this masting-related mechanism (Hacket-Pain et al. 2015). This result has important implications for the interpretation of growth-climate relationships in *F. sylvatica*, particularly as these lagged correlations with previous summer temperature are the most commonly reported correlations in beech RWI chronologies (Hacket-Pain et al. In Prep). However, the results also have wider implications, as lagged correlations between ring width and summer climate of previous years are commonly reported for many species (Wettstein et al. 2011, Babst et al. 2013). Additionally, climates cues of mast years, and growth-reproduction trade-offs have been reported for many tree species (e.g. Selas et al. 2002, Speer et al. 2009, Thomas 2011, Redmond et al. 2012), indicating that a similar mechanism, is likely to also apply in other key tree species used in dendrochronological studies.

Furthermore, any interaction between masting and tree growth should also be dependent on tree age as seed production increases as trees become older (and larger) (Nilsson & Wastljung 1987, Genet et al. 2010, Viglas et al. 2013). Consequently, as juvenile trees invest relatively little in seed production, they should respond less to the temperature of the previous summer than mature trees producing heavy seed crops. This would explain the common observation of increasing correlation between RWI and previous summer temperature in *F. sylvatica* chronologies (Di Filippo et al. 2007, Drobyshev et al. 2010, Hacket-Pain 2013), and also the strong relationship between tree age and these lagged correlations that we report in a meta-analysis of published growth-climate relationships in *F. sylvatica* (Hacket-Pain et al. In Prep).

Identification of knowledge gaps and justification for future research

Our study was based on only one regional tree ring chronology and masting dataset, and so the significance of these findings more generally is unknown. We know that allocation strategies, including allocation to reproduction, vary between species, resource availability (i.e. climate) and tree age (Schauber et al. 2002, Genet et al. 2010, Allen et al. 2014, Roland et al. 2014), but the impact of these variations on tree growth and hence tree ring archives is poorly understood. It is likely that allocation to reproduction will influence not only growth-climate relationships, but also other key tree ring 'signals', which are widely used to quantify growth variability and the response of growth to climate (summarised in Table 1 and Figure 2). Furthermore, the potential for masting to influence variation in ring width depends on both the strength of the growth-reproduction trade-off and masting phenomena, including the specific weather cue and the typical return time of mast years, and the size of the seed crop associated with mast years. These processes are poorly understood, but are expected to vary according to: (i) species, (ii) resource availability, and (iii) tree age. We expect these factors to result in strong species-specific spatial and temporal variations in the importance of masting for tree rings, but this has not been considered in the literature. Below we detail the potential ways in which these three factors could influence tree ring signals through masting behaviour:

(i) Species

Physiological differences between species result in different strengths in the growth-reproduction trade-off, which in turn controls the potential for allocation to reproduction to influence tree growth and ring width. Relevant physiological differences include the size and number of seeds produced in mast years (i.e. the reproductive sink strength), the typical interval between mast years, and timing and duration of fruit maturation. Additionally, the specific weather cues for masting and the

strength of the association between cues and mast years may vary between species. Consequently, the strength and patterns of tree ring signals introduced into tree ring chronologies by allocation to reproduction will vary between species.

(ii) Resource availability

The effect of resource availability (e.g. light and soil nutrients) on the influence of masting on tree ring chronologies is likely to be complex. For example, the literature indicates that as growing conditions become increasingly marginal, masting becomes less frequent and seed crops become smaller (Allen et al. 2014). Consequently we hypothesise that in climatically marginal regions the effects of masting on tree rings may be reduced. On the other hand, stronger trade-offs are expected when resources are more limiting. The overall effect is likely to result in spatial variation in the influence of masting on tree rings, and also variation in time if growing conditions and resource availability change. The magnitude of these effects is currently unknown but likely significant, with important implications. For example, tree ring-based reconstructions of climate usually rely on populations of trees growing in climatically marginal areas, and it is therefore important to understand the relative sensitivity of these chronologies to the complicating effects of masting.

(iii) Tree Age

Resource allocation changes according to tree age. Older trees mast more regularly than younger trees, and allocate proportionally more resources to seed production in these mast years (i.e. they mast more regularly and more heavily) (Genet et al. 2010, Viglas et al. 2013). Consequently, the effect of masting on tree rings should increase with tree age. This is important because age-related changes in masting may explain temporal changes in ring width and tree ring signals such as growth-climate relationships. In previous research we found indirect evidence of this effect, with masting-related growth-climate relationships in *F. sylvatica* stronger in older trees (Hacket-Pain et al. 2015, Hacket-Pain et al. In Prep). However, direct evidence of the influence of tree age is still lacking, particularly for the widely used signals summarised in table 1. This is important because tree age at the time of ring formation usually varies with time along a chronology, creating the potential for age-related biases in reconstructions. Numerous studies have compared the relationships between ring width and climate in cohorts of trees of different ages (Esper et al. 2008), but few studies have explicitly tested for an effect due specifically to age-related physiological processes.

Tree ring signals and masting

While the importance of allocation strategies for tree growth and tree ring chronologies can be appreciated in general terms, several key uncertainties remain. For example, while some studies directly rely on the analysis of raw tree ring data, many ecological and biogeographical studies use derived statistics to quantify components of tree ring variability (tree ring 'signals'), summarised in table 1. These include measures of the interannual variability in ring width, and the frequency of extreme growth anomalies ('pointer years'). All of these are used to assess stress in tree populations and the responses to climate variations (e.g. Lenz et al. 2014; Latte et al. 2015), and have the potential to act as early-warning signals for tree/forest mortality events and ecosystem collapse (Suarez et al. 2004, Scheffer et al. 2009, Linares et al. 2010). Lower-frequency variations in growth such as decadal growth trends are also used to detect and monitor forest health, while growth-climate relationships and the responses of growth to climate extremes are used to understand which climatic factors drive these changes in growth. However, the potential role of masting in influencing these signals in poorly understood. For example, previous research has shown that mast years have a tendency to cluster, particularly during periods of more variable climate (Drobyshev et al. 2014). This may introduce two important signals into tree ring

chronologies which are often interpreted as indicating forest decline: increased variation in ring width and negative trends in growth (Fig. 2).
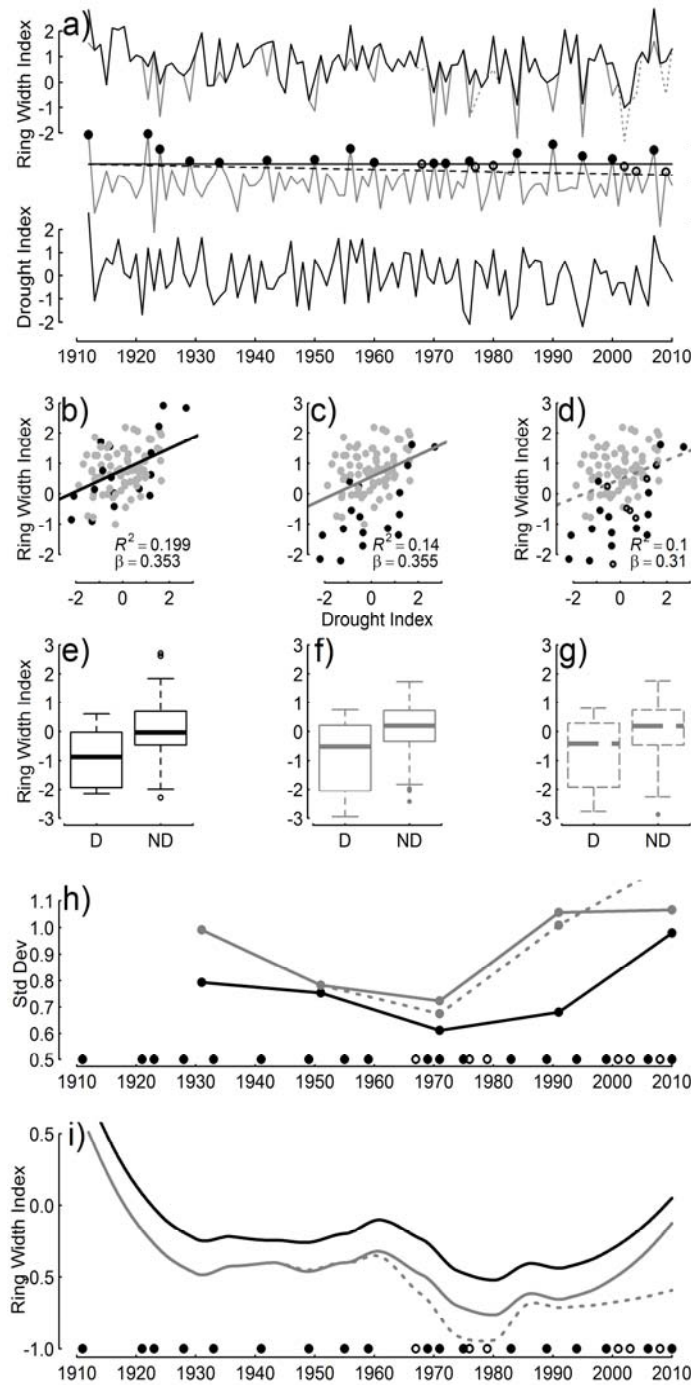

Figure 2: Overview of possible effects of masting on tree rings, using simulated data.
a) *RWI (black line) was simulated using an index of summer drought and random noise. Two modified RWI chronologies were also created that included a growth reduction in mast years. Mast years were predicted as a function of ΔT ($T_{JUL-1} - T_{JUL-2}$), with either a constant threshold (solid line, filled points, corresponding to the solid grey RWI curve) or a decreasing threshold (dashed line, filled and empty points, corresponding to the dashed grey RWI curve). The declining threshold for mast events was a simplification to simulate increasing frequency of masting with tree age.* ***b-d)*** *Relationships between RWI and summer drought index b) RWI, c) RWI with mast years, d) RWI with mast years from decreasing threshold. Growth-climate relationships change despite no direct relationship between mast events and drought. Additionally, increases in mast frequency/intensity may act to reduce the strength of the growth-climate relationship through time, as an increasing percentage of variance is explained by masting events rather than drought (not shown).* ***e-g)*** *RWI in drought and non-drought years for the three chronologies. The drought group includes the 10 driest years in the drought index. If drought years tend to coincide with mast years or non-mast years, the apparent reduction in growth associated with drought may be overestimated or underestimated respectively.* ***h)*** *Growth variability in the three chronologies (standard deviation), calculated for 20-year windows. As mast years are associated with low RWI, trees that mast more frequently have greater growth variability.* i) *Growth trends for the three chronologies, represented using loess curves. Periods of more intense masting correspond to lower growth and potentially negative growth trends. If masting increases in frequency/intensity with age then this may influence long-term growth trends.*

Also, while greater variability in ring width is normally taken to indicate increased direct impacts of climate on growth (e.g. through greater drought frequency), this response might actually be due to more frequent mast years (e.g. driven by climatic changes or aging), despite there being no increase in tree stress (Fig. 2). Additionally, a cluster of narrow rings resulting from a cluster of mast years (caused by a period of increased climate variability, for example) may also create a multi-year reduction in growth, despite no actual decline in vitality (Fig. 2).

Table 1: *Possible effects of masting on the interpretation of tree ring archives.*

Tree ring signal	Masting effect on tree ring chronology interpretation
Growth-climate relationships	*In F. sylvatica, correlations between growth and previous summer temperature are created by weather-cued masting (Hacket-Pain et al. 2015). Similar effects are expected for other species (Selas et al. 2002), but have not yet been demonstrated. Correlations between growth and growing-season climate may also be affected (Figure 3 b-d).*
Event years (extreme climate years)	*The response of trees to known individual years of extreme conditions will be influenced if a mast year coincides. As mast years may not be synchronous across species or across space, this complicates comparisons of the response of different populations to extreme events.*
Negative pointer years	*Mast years are associated with reduced growth, and so extreme narrow rings are created when drought coincides with mast years. Additionally, strong mast years may result in strong growth reductions in the absence of severe climate conditions during the growing season. If allocation to reproduction is dependent on tree age or resource availability, then the frequency of negative pointer years in a chronology may not be a direct measure of tree stress.*
Interannual growth variability	*Inter-annual growth variability is summarised using statistics such as standard deviation, mean sensitivity or the Gini coefficient. It is expected to increase when masting is more frequent (Figure 3 h). Increases in growth variability may therefore be expected as trees become older. Additionally, variations in growth variability between populations may be created by differences in tree age.*
Growth trends	*Periods of more frequent or intense masting may be associated with lower average growth and negative growth trends. Additionally, increased frequency or intensity of masting with age may be a contributing factor to long-term declines in growth.*

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