



# Relationships between tree growth and weather extremes: Spatial and interspecific comparisons in a temperate broadleaf forest



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## ABSTRACT

Three years of monthly growth increment data identified large interannual differences in growth rate across six contrasting species in a broadleaved, temperate forest with minimum management intervention (Wytham Woods, UK). Growth rates varied by species and canopy position, and were higher in canopy species. Growth rate in 2010 was up to 40% lower than in 2011 and 2012. This can best be explained as an effect of low temperature, which delayed the start of spring and the growing season. This had a greater impact on the growth of sub-canopy trees than that of canopy species. In temperate systems, late spring and summer is an important component of the whole growing season carbon balance because of long day length. In 2010 there were also periods of lower-than-average rainfall, which may additionally have constrained growth during the growing season. Fluctuations and seasonal changes in both temperature and rainfall are projected to continue, so we may expect to see increasing differences in growth and growth rates. A small effect of location relative to the nearest edge was also detected, with higher growth rates only found >50 m from the forest edge. The findings have implications for forest structure and productivity under climate change, and may thus inform current and future forest management.

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## 1. Introduction

Tree growth is sensitive to climate, with the relationship between temperature and moisture driving species' distributions and forest productivity (Boisvenue and Running, 2006). Heat stress can be mediated by moisture availability, while water stress is amplified by high temperature (e.g., Butt et al., 2013a). In temperate and boreal regions, temperature is particularly critical for the onset of spring; warmer temperatures result in longer growing seasons (Polgar and Primack, 2011; Kint et al., 2012).

Tree growth is constrained by water availability: where atmospheric evaporative demand is higher than soil moisture supply, stomata close to reduce water loss and in this way restrict carbon uptake and growth (Bréda et al., 2006; Boisvenue and Running, 2006). Temperature can interact with water availability to either increase growth (where moisture is not limited), or restrict growth (where this leads to water becoming limiting), and there is

evidence that there can be a differential response between canopy and understorey species (Weemstra et al., 2013).

Increasing hydrological stress on trees and forest ecosystems in many areas, leading to increasing frequency and intensity of droughts (IPCC, 2013a), will have implications for forest productivity and carbon storage across all biomes (Pan et al., 2013). Summers in north Western Europe are generally predicted to become hotter, and drier, under low and medium climate scenarios (IPCC, 2013b): in the UK, drought incidence is expected to increase (Jenkins et al., 2008), and severe summer droughts in southern England may become more frequent (Broadmeadow et al., 2005).

As temperate forests and woodlands are often located in areas with long histories of human land use and land use change, associated forest fragmentation is a common feature of these ecosystems (e.g. Rackham, 2008; Riutta et al., 2014). Fragmentation can cause 'edge effects' whereby trees are more exposed to increased solar radiation, wind, temperature fluctuations and soil drying than in the forest interior (e.g. Heithecker and Halpern, 2007; Davies-Colley et al., 2000; Herbst et al., 2007), and larger scale climatic patterns or events may exacerbate these effects. Contrasting landscape characteristics, such as patch size, will affect forest sensitivity to climate, and different species will be impacted differently.

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Ecophysiological stresses can act, individually or in combination, on trees to varying degrees. Climate change will also trigger novel combinations of stresses, which will act differently on different age cohorts and tree types (Niinemets, 2010). Between the canopy and understorey layers stresses vary: understorey trees are more likely to suffer light limitation while canopy trees are more likely to be affected by photoinhibition, or reduction in photosynthetic activity, under high irradiance (Valladares et al., 2005). These effects vary by species and according to light- or shade-adaptation. Taller trees face different stresses to those in the sub-canopy (Kutsch et al., 2009), as their leaves endure higher temperatures and greater wind exposure than trees in the understorey (King, 1990). This may increase hydraulic stress, limiting photosynthesis and thus growth, as has been found in other forest types (Fulton et al., 2014). Hydraulic architectural differences between canopy and understorey trees can lead to lower stomatal conductance, and thus lower photosynthetic rates in larger trees (Niinemets, 2010). Under drought conditions, therefore, canopy trees may be more stressed and grow less than understorey trees (Holmgren et al., 2011).

The objective of the study was to examine the effect of weather conditions (air temperature, rainfall and soil moisture and temperature), on tree diameter growth in a range of species, at different distances to the forest edge, and the interaction of these factors. We would expect that if moisture is not a limiting factor, proximity to edge has only a modestly negative or positive effect, as the increased light availability counteracts the adverse moisture effect. However, due to a higher transpiration rate close to the edge, moisture limitation during drought becomes more severe and, consequently, reduction in tree growth may be more pronounced near the edge than in the forest interior. We tested the following hypotheses: (i) Relative growth rate differs among species; (ii) Tree growth is sensitive to spring temperature and precipitation; (iii) Fragmentation affects growth rate through edge effects.

## 2. Methods

We were interested in the interactive effects of changing climate and forest fragmentation in the UK, and the use of dendrometers allowed the study of the growth patterns of a large number of trees and their relationships with weather variables to be established. The installation of the Earthwatch/HSBC Climate Partnership forest monitoring plots in Wytham Woods, Oxford, UK (see Butt et al., 2013b) enabled a tree growth experiment to be carried out within the context of relevant climate parameters. Ca. 1300 dendrometers on six species across the temperate broadleaf woodland were installed during the 2009–2010 winter and measured on a several-weekly basis over the following several growing seasons, and examined by species, tree type (canopy/understorey), distance to forest edge, diameter, and compared by year. The wide range of weather conditions experienced during this time allowed us to investigate impacts on tree growth.

### 2.1. Site description

The plots were located in Wytham Woods, Oxfordshire, UK (51°46'N, 001°20'W), within fragments surrounding the main woodland, and the woodland itself. Wytham is a mixed deciduous temperate forest of approximately 400 ha (see Savill et al., 2010; Butt et al., 2009). The site is a G1.A22, British [*Fraxinus*] – [*Acer campestre*] – [*Mercurialis perennis*] forest, in the EUNIS classification. The soil is variable across the site as a whole, but all of the study sites in this paper are predominantly surface water gley of the Denchworth series in the England and Wales Soil Survey Classification (Clayden and Hollis, 1984), and Stagni-vertic Cambisol in the FAO system. Mean annual temperature (1993–2009) of the site

is 10.1 °C and average precipitation is 730 mm (measured approximately 1 km from the site by an automatic weather station in an open location, as part of the UK Environmental Change Network monitoring program at Wytham; [www.ecn.ac.uk](http://www.ecn.ac.uk)). In total, nine 1 ha plots (or smaller when the forest fragment was <1 ha) were situated in the forest core, North- and South-facing edges, and six fragments of varying sizes (from 0.3 ha to 22 ha) around the main woodlands, representing a range of distances from the forest edge (Fig. 1).

Wytham Woods has been the site of a number of ecological studies that have addressed the sensitivity of carbon uptake and ecophysiology to climate and seasonal patterns. Morecroft and Roberts (1999) measured photosynthetic rates of canopy oak and sycamore trees throughout the growing season, showing that oak trees developed photosynthetic capacity slowly, only reaching peak photosynthetic rates at the end of June, while sycamore photosynthetic rates increased more quickly. Morecroft et al. (2003) showed that for oak, seasonal changes in photosynthetic capacity would decrease annual carbon uptake per unit leaf area by about 23% compared to that potentially possible if leaves photosynthesised at peak rates throughout the growing season. This difference is likely to be up to 30% larger in years with late budburst, and as low as 18% in years with early budburst. There is also evidence of sensitivity to precipitation, with sycamore in particular showing reduced photosynthesis and growth rates in a three-year period with low rainfall (Morecroft et al., 2008).

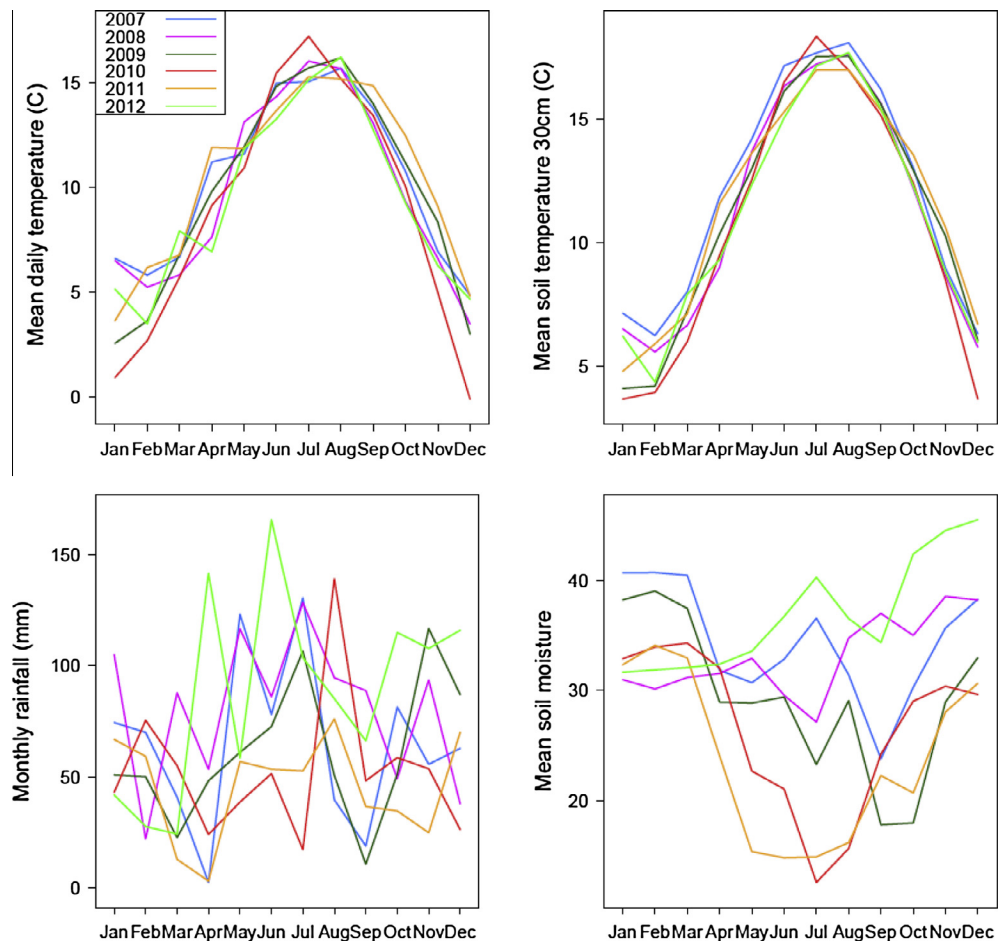
### 2.2. Climatic conditions

Weather variability was high during the three years of the study. To characterise local conditions we used data from an Automatic Weather Station (Didcot Instruments, Didcot, UK) located at Wytham Woods in a standard open grass site (Morecroft et al., 1998) and operated as part of the Environmental Change Network (ECN; Morecroft et al., 2009), a national monitoring network. The AWS records data continuously and we used monthly summaries to compare with growth measurements (Environmental Change Network, 2014): monthly mean air temperature at 1.3 m (°C), soil temperature at 300 mm depth (°C), mean volumetric soil moisture (%) data (Theta Probe, Delta T Devices, Cambridge, UK) and monthly total precipitation (mm). In the UK in 2010, there were periods of less-than-average rainfall during May, and between June and August. In addition to this 50% decrease in average rainfall across this part of the country, there was an increase in sunshine totals of up to 10% (Met Office, 2010). Environmental Change Network (ECN) data for Wytham show that for July 2010 air and soil temperatures were higher than average, while rainfall and soil moisture were below average (Fig. 2).

Phenological records from the site, recorded alongside ECN monitoring, indicated a delay in spring signals (such as flowering of primrose, *Primula vulgaris*) of approximately three weeks (from long term mean), which was also apparent in the leaf out timings of the canopy species *A. pseudoplatanus* and *Fraxinus excelsior* in the study location. Clear-sky measurements taken in the plots throughout the year indicated that full leaf-out was achieved in 2010 by May 16th and in 2011 by April 11th. An integrated measure of the warmth of the growing season is the concept of thermal time, 'Growing degree days' (GDD). We calculated GDD as days >5 °C, considered to be the threshold for growth of temperate trees (Sykes and Prentice, 1996). GDD in 2010 clearly lagged behind the other years (Fig. 3). This followed very low winter and early spring temperatures; rainfall in April 2010, just before, during, and just after, leaf out was also very low. The lag effect of rainfall deficits during the growing season, combined with high air temperature and radiation, meant that throughout July and August 2010, soil moisture levels were very low.

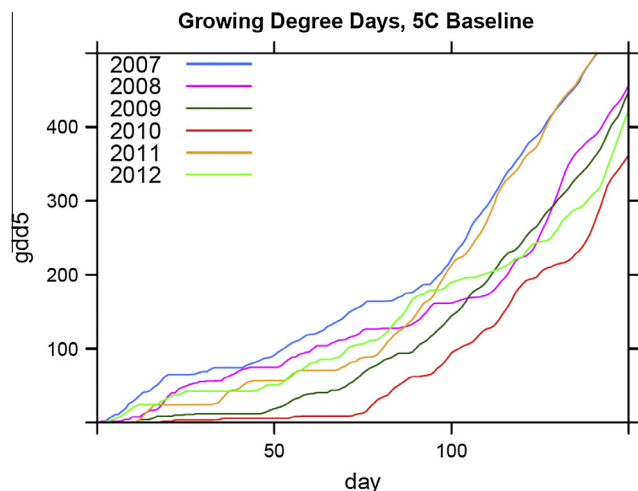


**Fig. 1.** Wytham Woods, near Oxford, and locations of nine ~1 ha study plots. Species composition and forest structure varies across the plots, a function of previous land use. Vegetation types within the plots range from high forest (for example, in the central 'core' plot) to coppice with standards (primarily *C. avellana*). With coppices, new stem development is also a part of tree growth. Most of the plots are mixed in terms of forest types.



**Fig. 2.** Monthly summaries of ecophysiological climate variables, 2007–2012 (ECN): mean daily temperature (°C); mean soil temperature at 30 cm depth (°C); monthly rainfall (mm); mean volumetric soil moisture (%).





**Fig. 3.** Growing Degree Day (GDD5) data for 2007–2012 (ECN), for DOY 0 – DOY 150 (January 1st – May 29th/30th). ‘Growing degree day’ refers to days >5 °C, considered to be the threshold for photosynthetic/growth activity for temperate trees, and the chilling or non-growing period is when temperatures are <5 °C (Sykes and Prentice, 1996). Ranges of tree species across temperate regions are generally linked to growing season length, as defined by GDD5, and to minimum temperature (Woodward 1987; Thuiller et al. 2006). In 2010 (red line) the growing season (spring) commenced later than in the other years of our analysis (2011, 2012). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

### 2.3. Dendrometer measurements

Dendrometers were installed on 1256 trees across the plots. In each plot, the stratified random sample was ten stems (or fewer, if there were not ten stems) per species per 10 cm diameter class (5–14 cm, 15–24 cm, 25–34 cm, 35–44 cm, ≥45 cm). The dendrometer bands, made of flexible plastic packaging tape, were fixed horizontally around each trunk approximately 30 cm above the diameter measurement point, and fastened with a stainless steel spring (see <http://www.eci.ox.ac.uk/research/ecodynamics/downloads/pbd-wytham-dec2010.m4v>). As the tree grows, the overlapping end of the band moves away from the original point (marked with a notch), and this distance can be measured with calipers in mm, to two decimal places. The dendrometers were measured regularly (approximately monthly) throughout the growing season over a period of three years (2010–2012, inclusive). Data from six species; three ‘canopy’ species – by which we mean those species that can form the upper canopy – (*Acer pseudoplatanus*, *Fraxinus excelsior* and *Quercus robur*) and three understory species, (*A. campestre*, *Corylus avellana* and *Crataegus monogyna*), were cleaned, processed and analysed. Any dendrometer increment <–5 mm or >5 mm was checked for obvious (primarily transcriptional) error and corrected where necessary. When error was large but the cause was not obvious (e.g. sequential mis-steps), the erroneous value was replaced with the mean of the preceding and subsequent values. In total, 0.58% of measurements were adjusted. Most of the data were collected by volunteer ‘citizen scientists’, as part of the HSBC Climate Partnership Programme (Shetty, 2011), who were trained in methods prior to data collection (Butt et al., 2013b).

Annual increment was calculated as the difference between the mean October and March value of one year to the next. Increments were converted to relative increments (mm growth per cm DBH per year) to control for the effect of tree size and to stabilize the variance, and these relative increment data were then square-root transformed prior to analysis to obtain normal errors. Increments were analysed by Generalized Additive Models in the first instance to check for significant non-linear relationships, and the residuals

were checked for spatial autocorrelation. Plot was treated as a categorical fixed effect (i.e., a block), as plot locations were not randomly sampled.

In addition to the dendrometer measurements, the total tree height, crown height, crown illumination index (five classes from completely exposed crown to crown receiving no direct light) and crown condition (four classes from intact crown to >75% crown missing) were recorded (CTFS protocol, available at [http://www.ctfs.si.edu/data/documents/Metal\\_Band\\_Dendrometer\\_Protocol\\_20100330.pdf](http://www.ctfs.si.edu/data/documents/Metal_Band_Dendrometer_Protocol_20100330.pdf)).

We assumed that relative growth increment could be influenced by DBH, crown characteristics, distance to the nearest forest edge, and plot, and that each of these effects could differ among species, and between years, reflecting the varying weather conditions during the years. As the increments among years were highly correlated (i.e., similar), most of the analyses were done using the most recent, 2012 increment, and comparing it with the 2010 ‘drought/delayed spring year’ (see *Climatic conditions*, below) value. Linear models were fitted to the data, taking plot as a fixed rather than a random factor, because plots had been installed by deliberate selection rather than randomized sampling across the landscape. Variables were transformed as necessary to stabilize variances and linearize responses.

We calculated the fraction of annual growth occurring in spring (up to June) in each year, to determine how weather variation among years altered the phenology of different species.

## 3. Results

### 3.1. Tree growth

We fitted a model to the square root of mean relative increment during the growing season (March–October) from 2010 to 2012, thus omitting negative increments. The model explained around half of the variance in mean increment (Table 1). The effects of DBH, crown illumination and plot on relative increment varied significantly among species.

Comparing the different years indicates that growth in 2010 was significantly lower than 2011 and 2012, which showed similar increments (Fig. 4: Eq. (1) gives the slope of the line for the 2010 vs. 2011 growth rate comparison, Eq. (2) gives the same for 2010 vs. 2012). Individuals which grew fastest in 2011 and 2012 also generally grew most in 2010, despite the overall growth rate being lower as a result of the poor growing conditions.

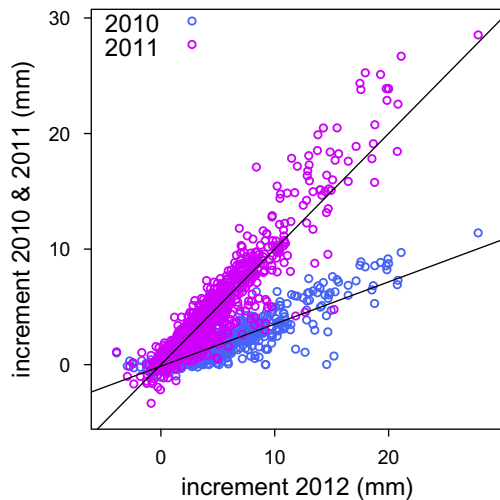
$$i_{2010} = -0.161 + 0.028 + i_{2012}(0.37 + 0.004),$$

$$r^2 = 0.82, \quad df = 1264 \quad (1)$$

**Table 1**

ANOVA table for predictors of mean relative annual increment, 2010–2012. Relative increment was square-root transformed, and edge distance was log-transformed, for analysis.  $R^2 = 0.54$ : the model explained around half of the variance in mean increment; the effects of DBH, crown illumination and plot on relative increment varied significantly among species.

Predictor	DF	SS	MS	F	p
DBH	1	92.5	92.5	226.9	<10 <sup>−4</sup>
Species	5	210.1	42.0	103.0	<10 <sup>−4</sup>
Crown Illum	1	71.6	71.6	175.5	<10 <sup>−4</sup>
Log(Edge dist)	1	11.3	11.3	27.7	<10 <sup>−4</sup>
Plot	8	59.4	7.4	18.2	<10 <sup>−4</sup>
DBH * species	5	9.5	1.9	4.6	0.0003
Illum * species	5	6.6	1.3	3.2	0.007
Edge * species	5	3.9	0.8	1.9	0.086
Plot * species	27	29.5	1.1	2.7	<10 <sup>−4</sup>
Residuals	1030	420.2	0.4		
Total	1088	914.6			



**Fig. 4.** Absolute increment in 2010 and 2011 vs. 2012, for all trees. Regression lines in black. Growth in 2011 is the same on average to that in 2012, but growth in 2010 was 37% of that in 2012.

$$i_{2011} = -0.100 + 0.056 + i_{2012}(0.01 + 0.011),$$

$$r^2 = 0.88, \quad df = 1264 \quad (2)$$

Analysis of growth rates by species indicated that the canopy species' (*F. excelsior*, *Q. robur* and *A. pseudoplatanus*) growth rates were less reduced during the 2010 growing season than those of understorey species (*A. campestre*, *C. monogyna* and *C. avellana*), and maintained greater relative growth (Fig. 5 & Table 2). The reduced growth, given by the 2010/2012 fraction of relative increment, by species was: *F. excelsior*  $0.360 \pm 0.008$ ; *Q. robur*  $0.390 \pm 0.033$ ; *A. pseudoplatanus*  $0.303 \pm 0.016$ ; *A. campestre*  $0.145 \pm 0.015$ ; *C. monogyna*  $0.213 \pm 0.017$ ; *C. avellana*  $0.241 \pm 0.014$ .

Investigation of the effect of crown illumination on relative growth rates by size class and species indicated that relative increment was largely independent of DBH, but that large trees generally have emergent crowns (Fig. S1).

Comparison of relative growth increment and distance-from-edge, by species and by plot, between 2010 and 2012 indicated there was no strong edge effect for any of the species, canopy or understorey (Fig. 6). Although there is a weak signal suggesting that for *A. pseudoplatanus* the distance-from-edge may have had

**Table 2**

Analysis of growth rate by species: ANOVA table for predictors of relative growth increment in 2010 vs. relative growth increment in 2012. Canopy species' growth rates were less restricted than those of understorey species in 2010.  $R^2 = 0.88$ .

Predictor	DF	SS	MS	F	p
Increment 2012	1	2425.0	2425.0	7259.7	$<10^{-4}$
Species	5	70.8	14.2	42.5	$<10^{-4}$
Inc. 2012 $\times$ species	5	92.2	18.4	55.2	$<10^{-4}$
Residuals	1082	359.8	0.33		
Total	1093	2947.8			

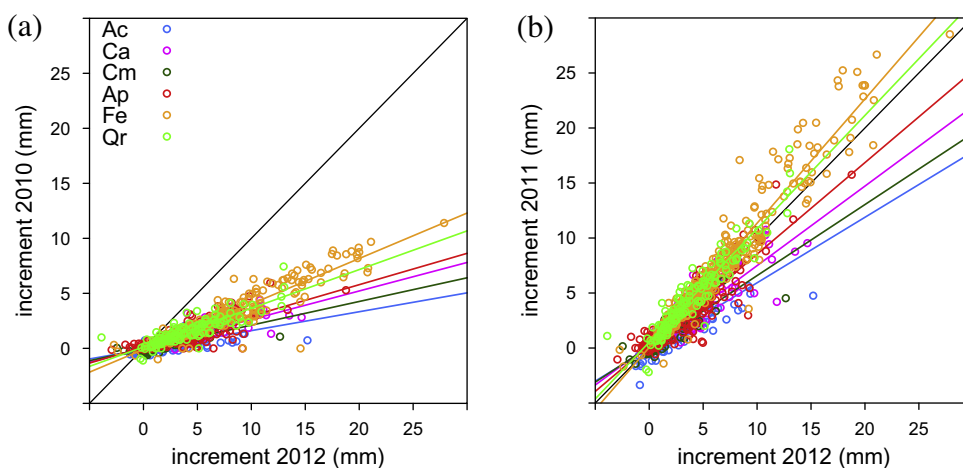
a negative effect when moisture was not limited (as in 2012), the small differences between 2010 and 2012 are probably related more to the difference in growing season length.

The fraction of annual growth occurring early in the season (to June) was lower in 2010 than in the other years, for most species (Fig. 7). *C. avellana*, in particular, had low spring growth fraction in 2010 and 2012. Overall, tree species and plot were the greatest predictors of diameter change, with crown illumination also important. The delayed spring in 2010 caused a significant decrease in diameter increment, more markedly in understorey than canopy species: canopy species maintained greater relative growth.

#### 4. Discussion

Trees exhibited different growth rates, according to species and canopy position: *F. excelsior* and *Q. robur* had the highest growth rates and *A. campestre* the lowest. Relative growth rates in 2010 were significantly lower for all species, compared with the other years of the study, 2011 and 2012. This is best explained as an effect of the cold spring and consequent delay to the start of the growing season. The growing season began three weeks later than recent average spring commencement times (ECN) (Fig. 2). Temperatures did not reach GDD5 level until this point (three weeks later than average), and were too low for the tree species to begin growth activity (Woodward, 1987; Thuiller et al., 2006).

Tree phenology is well known to be sensitive to spring temperature. Earlier studies at Wytham Wood have showed that leafing of *F. excelsior*, *Q. robur* and *A. pseudoplatanus* is sensitive to March temperatures (Morecroft et al., 2008), with date of first leafing advancing by 4–6 days  $^{\circ}\text{C}^{-1}$ . Morecroft et al. (2003) showed for *Q. robur* that this could have a significant impact on



**Fig. 5.** (a) Increment in 2010 vs. 2012, (b) 2011 vs. 2012, for common species. Coloured lines show linear regressions, black line shows 1:1 slope. The greater the slope, the less that species was affected by the 2010 climate. Ac = *Acer campestre*, Ap = *Acer pseudoplatanus*, Ca = *Corylus avellana*, Cm = *Crataegus monogyna*, Fe = *Fraxinus excelsior*, Qr = *Quercus robur*. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

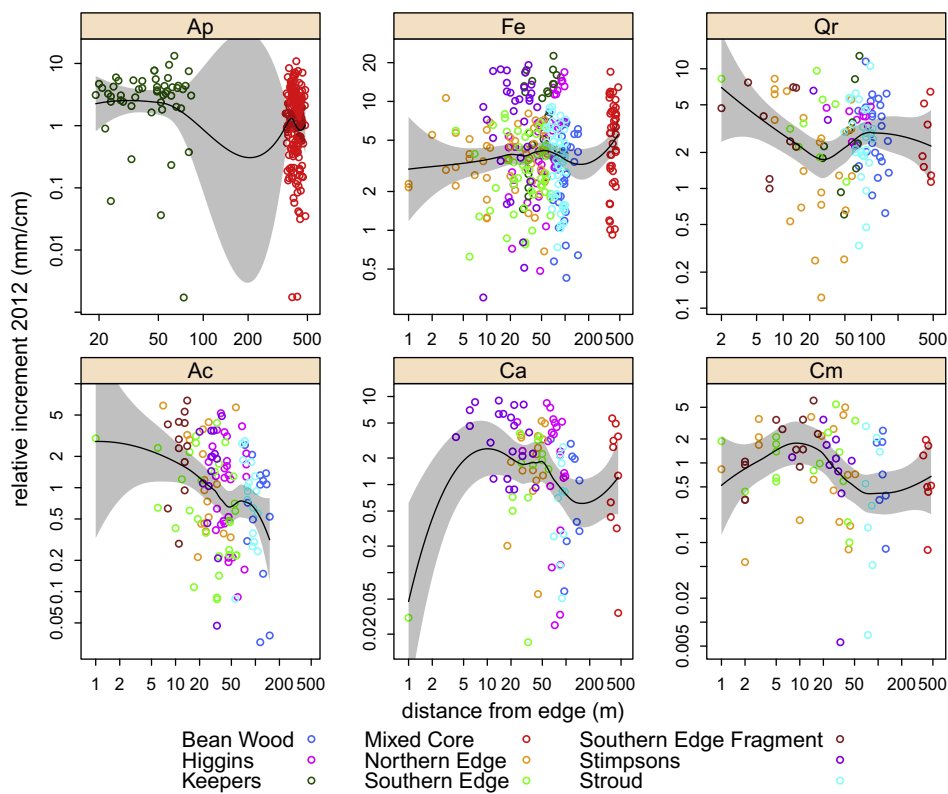


Fig. 6. Mean annual growth increment against distance-from-edge, by species and plot for 2012. Smoothed curves fitted by loess, with 95% Confidence Limits.

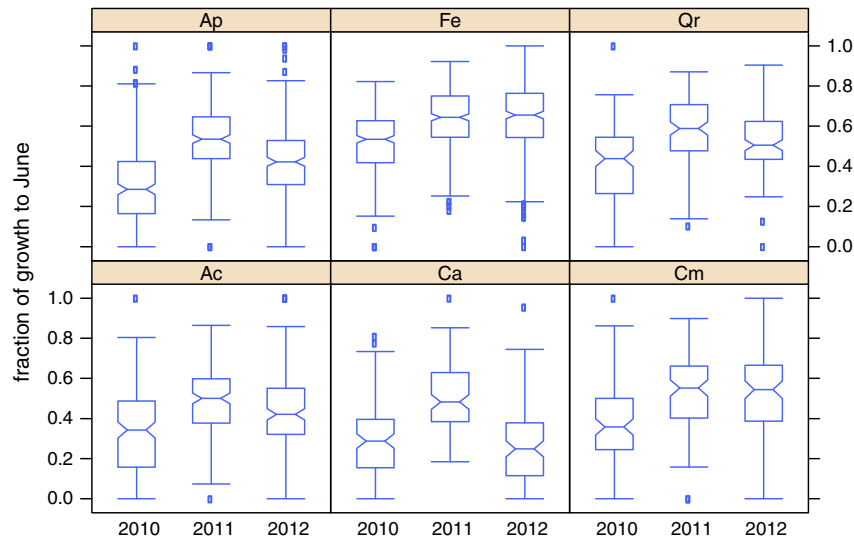


Fig. 7. Fraction of annual growth occurring in spring (to June) in each year, by species. Upper row shows canopy species (Ap = *A. pseudoplatanus*, Fe = *F. excelsior*, Qr = *Q. robur*); lower row shows understorey species (Ac = *A. campestre*, Ca = *C. avellana*, Cm = *C. monogyna*). Boxes show medians and interquartile ranges, whiskers show data to 1.5 x the interquartile range, points show extreme outliers. Non-overlapping notches are indicative of significant differences among years by species. Spring growth fraction varied among plots ( $F_{8,1075} = 21.4$ ,  $p < 0.001$ ), and the difference among years varied significantly by species ( $F_{10,2139} = 11.9$ ,  $p < 0.001$ ).

total carbon fixation over the course of the growing season: carbon fixation might be as much as 50% higher in years with very warm springs compared to those with very cold springs. In May and June, day length is long, so there is potential for high rates of carbon uptake, but this potential can only be realized if leaf photosynthetic capacity and leaf area index have developed. Accordingly, the fraction of annual growth occurring early in

the season (to June) was lower in 2010 than in the other years, for most species. Similar slow development of the leaf canopy and photosynthetic capacity have been found in other temperate forests (Bréda et al., 1993; Ogink-Hendriks, 1995; Reich et al., 1991; Wilson et al., 2000; Bassow and Bazzaz, 1998) indicating that a similar effect might be found elsewhere, although further work is needed to establish how general this may be.

Our results show that growth rates of understory trees were reduced more in 2010 compared to 2011 and 2012 than those of canopy trees, and that *A. pseudoplatanus* was reduced more than *F. excelsior* or *Q. robur*. The difference between canopy and understory may reflect both different light climates and different functional traits. Understory trees are even more dependent on the early spring period as they typically leaf out before canopy trees, and take advantage of high light levels before the canopy closes. Tree organs, such as leaves and roots, differ in their drought sensitivity (Leuzinger et al., 2005), and leaf morphology also differs between species in terms of light and shade response. Canopy leaves in *F. excelsior*, for example, have been found to be less susceptible to drought than those of other species in broad-leaved forest systems (Legner et al., 2013). Previous measurements of rooting depth in other temperate deciduous forests found that some *Quercus* species had deeper roots than other species, and did not respond to drought with an increase in fine root growth (as did other species) (Leuzinger et al., 2005).

In terms of photosynthesis, *Q. robur* takes several weeks to develop full capacity (Morecroft and Roberts, 1999), even once the leaves have developed. By contrast *A. pseudoplatanus* develops capacity more quickly. This is consistent with the difference between ring porous and diffuse porous patterns of wood formation. Ring porous species, including *F. excelsior* and *Q. robur*, lay down a band of growth at the start of the growing season, using carbohydrate accumulated during the previous year (Barbaroux and Bréda, 2002): it is not until later in the growing season that the effect of the previous year is outweighed by the current season, and we would therefore expect that growth rates in diffuse porous species (such as *A. pseudoplatanus* and the three understorey species) would be more influenced by the current season. Ring porosity has also been linked to lower cavitation risk leading to higher resistance to drought in *Quercus* species (Leuzinger et al., 2005).

The results support our first two hypotheses, that relative growth rates differ among species, and that growth is sensitive to spring temperature and precipitation. Fragmentation has a demonstrated impact on various ecosystem processes (Riutta et al., 2012), and moisture-driven edge effects can be important in Wytham Woods (Crockatt and Bebb, 2014). However, while there was some indication that *A. campestre* growth decreased with increasing distance from the edge, the edge effect here was very weak overall, and was not a key driver of growth differences. The results therefore do not strongly support the third hypothesis, that fragmentation significantly affected growth rates through edge effects.

The late spring in 2010 is likely to explain most of the difference in growth rates between years, but 2010 was also a dry spring and this may have played a role. Recent work in another European broad leaved forest also found that reduced soil moisture during the growing season inhibited stem growth in both *F. excelsior* and *A. pseudoplatanus* (Mund et al., 2010). Fluctuations and seasonal changes (from current baselines) in both temperature and rainfall are projected to continue, so we may expect to see increasing differences in growth and growth rates, as modelled GDD responses indicate (Ashraf et al., 2013). 2010 was an anomalous year, with regard to spring temperatures and timing, and we suggest that under projected warming, earlier springs may drive increased forest carbon sequestration by more than would be expected as a simple temperature response, because of the interaction with longer day lengths. With climate extremes and extreme weather events increasing in frequency (IPCC, 2013a), there may be an increasing disparity of growth between understorey and canopy species, possibly influencing and altering forest structure. While the earlier-spring carbon uptake effect may be outweighed by drier summers, especially in lower rainfall areas and where soil water capacity is lower, such a shift in productivity towards the spring may have

ecosystem consequences in terms of functional processes and the timing of interactions between different components of the forest system.

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## Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.foreco.2014.09.006>.

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