

40 **Introduction**

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

47

48 Tree growth is constrained by water availability: where atmospheric evaporative demand is higher
49 than soil moisture supply, stomata close to reduce water loss and in this way restrict carbon uptake
50 and growth (Bréda et al. 2006; Boisvenue and Running 2006). Temperature can interact with water
51 availability to either increase growth (where moisture is not limited), or restrict growth (where this
52 leads to water becoming limiting), and there is evidence that there can be a differential response
53 between canopy and understorey species (Weemstra et al. 2013).

54

55 Increasing hydrological stress on trees and forest ecosystems in many areas, leading to increasing
56 frequency and intensity of droughts (IPCC 2013a), will have implications for forest productivity
57 and carbon storage across all biomes (Pan et al. 2013). Summers in north Western Europe are
58 generally predicted to become hotter, and drier under low and medium climate scenarios (IPCC
59 2013b): in the UK, drought incidence is expected to increase (Jenkins et al. 2008), and severe
60 summer droughts in southern England may become more frequent (Broadmeadow et al. 2005).

61

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

70

71 Ecophysiological stresses can act, individually or in combination, on trees to varying degrees.
72 Climate change will also trigger novel combinations of stresses, which will act differently on
73 different age cohorts and tree types (Niinemets 2010). Between the canopy and understorey layers

74 stresses vary: understorey trees are more likely to suffer light limitation while canopy trees are
75 more likely to be affected by photoinhibition, or reduction in photosynthetic activity, under high
76 irradiance (Valladares et al. 2005). These effects vary by species and according to light- or shade-
77 adaptation. Taller trees face different stresses to those in the sub-canopy (Kutsch et al. 2009), as
78 their leaves endure higher temperatures and greater wind exposure than trees in the understorey
79 (King 1990). This may increase hydraulic stress, limiting photosynthesis and thus growth, as has
80 been found in other forest types (Fulton et al. 2014). Hydraulic architectural differences between
81 canopy and understorey trees can lead to lower stomatal conductance, and thus lower
82 photosynthetic rates in larger trees (Niinemets 2010). Under drought conditions, therefore, canopy
83 trees may be more stressed and grow less than understorey trees (Holmgren et al. 2011).

84

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

95

96

97 **Methods**

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

108

109 *Site description*

110 The plots were located in Wytham Woods, Oxfordshire, UK (51° 46' N, 001° 20' W), within
111 fragments surrounding the main woodland, and the woodland itself. Wytham is a mixed deciduous
112 temperate forest of approximately 400ha (see Savill et al., 2010; Butt et al. 2009). The site is a
113 G1.A22, British [*Fraxinus*] - [*Acer campestre*] - [*Mercurialis perennis*] forest, in the EUNIS
114 classification. The soil is variable across the site as a whole, but all of the study sites in this paper
115 are predominantly surface water gley of the Denchworth series in the England and Wales Soil
116 Survey Classification (Clayden and Hollis, 1984), and Stagni-vertic Cambisol in the FAO system.
117 Mean annual temperature (1993-2009) of the site is 10.1°C and average precipitation is 730 mm
118 (measured approximately 1km from the site by an automatic weather station in an open location,
119 as part of the UK Environmental Change Network monitoring program at Wytham;
120 www.ecn.ac.uk). In total, nine 1 ha plots (or smaller when the forest fragment was <1ha) were
121 situated in the forest core, North and South facing edges, and six fragments of varying sizes (from
122 0.3 ha to 22 ha) around the main woodlands, representing a range of distances from the forest edge
123 (Figure 1).

124

125 Wytham Woods has been the site of a number of ecological studies that have addressed the
126 sensitivity of carbon uptake and ecophysiology to climate and seasonal patterns. Morecroft and
127 Roberts (1999) measured photosynthetic rates of canopy oak and sycamore trees throughout the
128 growing season showing that oak trees developed photosynthetic capacity slowly, only reaching
129 peak photosynthetic rates at the end of June, while sycamore photosynthetic rates increased more
130 quickly. Morecroft et al (2003) showed that for oak, seasonal changes in photosynthetic capacity
131 would decrease annual carbon uptake per unit leaf area by about 23% compared to that potentially
132 possible if leaves photosynthesised at peak rates throughout the growing season. This difference is
133 likely to be up to 30% larger in years with late budburst, and as low as 18% in years with early
134 budburst. There is also evidence of sensitivity to precipitation, with sycamore in particular showing
135 reduced photosynthesis and growth rates in a three-year period with low rainfall (Morecroft et al,
136 2008).

137

138 *Climatic conditions*

139 Weather variability was high during the three years of the study. We used monthly summaries from
140 the Environmental Change Network (ECN) to characterise the local conditions: mean daily
141 temperature (C°), mean soil temperature at 30 cm depth (C°), monthly rainfall (mm), and mean

142 volumetric soil moisture (%) data were used. In the UK in 2010, there were periods of less-than-
143 average rainfall during May, and between June and August. In addition to this 50% decrease in
144 average rainfall across this part of the country, there was an increase in sunshine totals of up to
145 10% (Met Office 2010). Environmental Change Network (ECN) data for Wytham show that for
146 July 2010 air and soil temperatures were higher than average, while rainfall and soil moisture were
147 below average (Figure 2).

148

149 ECN measurements indicated a delay in spring signals (such as flowering of primrose, *Primula*
150 *vulgaris*) of approximately three weeks (from ECN data long term mean), which was also apparent
151 in the leaf out timings of the canopy species *A. pseudoplatanus* and *F. excelsior* in the study
152 location. ‘Growing degree day’ refers to days > 5°C, considered to be the threshold for
153 photosynthetic/growth activity for temperate trees, and the chilling or non-growing period is when
154 temperatures are < 5°C (Sykes et al. 1996). ECN Growing Degree Day data clearly show the delay in
155 2010 (Figure 3). This followed very low winter and early spring temperatures; rainfall in April
156 2010, just before, during, and just after, leaf out was also very low. The lag effect of rainfall deficits
157 during the growing season, combined with high air temperature and radiation, meant that
158 throughout July and August 2010, soil moisture levels were very low.

159

160 *Dendrometer measurements*

161 Dendrometers were installed on 1256 trees across the plots. In each plot, the stratified random
162 sample was ten stems (or fewer, if there were not ten stems) per species per 10 cm diameter class
163 (5-14 cm, 15-24 cm, 25-34 cm, 35-44 cm, ≥45 cm). The dendrometer bands, made of flexible plastic
164 packaging tape, were fixed horizontally around each trunk approximately 30 cm above the diameter
165 measurement point, and fastened with a stainless steel spring (see
166 <http://www.eci.ox.ac.uk/research/ecodynamics/downloads/pbd-wytham-dec2010.m4v>). As the
167 tree grows, the overlapping end of the band moves away from the original point (marked with a
168 notch), and this distance can be measured with calipers in mm, to two decimal places. The
169 dendrometers were measured regularly (approximately monthly) throughout the growing season
170 over a period of three years (2010 – 2012, inclusive). Data from six species; three ‘canopy’ species
171 – by which we mean those species that can form the upper canopy - (*Acer pseudoplatanus*, *Fraxinus*
172 *excelsior* and *Quercus robur*) and three understory species, (*Acer campestre*, *Corylus avellana* and
173 *Crataegus monogyna*), were cleaned, processed and analysed. Any dendrometer increment < -5mm
174 or >5mm was checked for obvious (primarily transcriptional) error and corrected where necessary.
175 When error was large but the cause was not obvious (e.g. sequential mis-steps), the erroneous value

176 was replaced with the mean of the preceding and subsequent values. In total, 0.58% of
177 measurements were adjusted. Most of the data were collected by volunteer “citizen scientists”, as
178 part of the HSBC Climate Partnership Programme (Shetty 2011), who were trained in methods
179 prior to data collection (Butt et al. 2013b).

180

181 Annual increment was calculated as the difference between the mean Oct-Mar value of one year to
182 the next. Increments were converted to relative increments (mm growth per cm DBH per year) to
183 control for the effect of tree size and to stabilize the variance, and these relative increment data
184 were then square-root transformed prior to analysis to obtain normal errors. Increments were
185 analysed by Generalized Additive Models in the first instance to check for significant non-linear
186 relationships, and the residuals were checked for spatial autocorrelation. Plot was treated as a
187 categorical fixed effect (i.e., a block), as plot locations were not randomly sampled.

188

189 In addition to the dendrometer measurements, the total tree height, crown height, crown
190 illumination index (five classes from completely exposed crown to crown receiving no direct light)
191 and crown condition (four classes from intact crown to >75% crown missing) were recorded (CTFS
192 protocol, available at [http://www.ctfs.si.edu/data///documents/Metal_Band_Dendrometer_-](http://www.ctfs.si.edu/data///documents/Metal_Band_Dendrometer_-_Protocol_20100330.pdf)
193 [Protocol_20100330.pdf](http://www.ctfs.si.edu/data///documents/Metal_Band_Dendrometer_-_Protocol_20100330.pdf)).

194

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

204

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

207

208

209 **Results**

210

211 *Tree growth*

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

216

217

218

219 Comparing the different years indicates that growth in 2010 was significantly lower than 2011 and
220 2012, which showed similar increments (Figure 4: Equation 1 gives the slope of the line for the
221 2010 vs 2011 growth rate comparison, Equation 2 gives the same for 2010 vs 2012). Individuals
222 which grew fastest in 2011 and 2012 also generally grew most in 2010, despite the overall growth
223 rate being lower as a result of the poor growing conditions.

224 $i_{2010} = -0.161 \pm 0.028 + i_{2012}(0.37 \pm 0.004)$, $r^2 = 0.82$, $df = 1264$ *Equation 1*

225 $i_{2011} = -0.100 \pm 0.056 + i_{2012}(1.01 \pm 0.011)$, $r^2 = 0.88$, $df = 1264$ *Equation 2*

226

227 Analysis of growth rates by species indicated that the canopy species' (*F. excelsior*, *Q. robur* and
228 *A. pseudoplatanus*) growth rates were less reduced during the 2010 growing season than those of
229 understorey species (*A. campestre*, *C. monogyna* and *C. avellana*), and maintained greater relative
230 growth (Figure 5 & Table 2). The reduced growth, given by the 2010/2012 fraction of relative
231 increment, by species was: *F. excelsior* 0.360 ± 0.008 ; *Q. robur* 0.390 ± 0.033 ; *A. pseudoplatanus*
232 0.303 ± 0.016 ; *A. campestre* 0.145 ± 0.015 ; *C. monogyna* 0.213 ± 0.017 ; *C. avellana* 0.241 ± 0.014 .

233

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

237

238 Comparison of relative growth increment and distance-from-edge, by species and by plot, between
239 2010 and 2012 indicated there was no strong edge effect for any of the species, canopy or
240 understorey (Figure 6). Although there is a weak signal suggesting that for *A. pseudoplatanus* the
241 distance-from-edge may have had a negative effect when moisture was not limited (as in 2012), the

242 small differences between 2010 and 2012 are probably related more to the difference in growing
243 season length.

244

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

251

252

253 **Discussion**

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

262

263 Tree phenology is well known to be sensitive to spring temperature. Earlier studies at Wytham
264 Wood have showed that leafing of *F. Excelsior*, *Q. robur* and *A. pseudoplatanus* is sensitive to
265 March temperatures (Morecroft et al. 2008), with date of first leafing advancing by 4- 6 days °C⁻¹.
266 Morecroft et al. (2003) showed for *Q. robur* that this could have a significant impact on total carbon
267 fixation over the course of the growing season: carbon fixation might be as much as 50% higher in
268 years with very warm springs compared to those with very cold springs. This reflects the fact that
269 in this and in many other temperate forest systems there is the potential for high photosynthetic
270 rates during May and June when day length is long. Accordingly, the fraction of annual growth
271 occurring early in the season (to June) was lower in 2010 than in the other years, for most species.

272

273 Our results show that growth rates of understorey trees were reduced more in 2010 compared to
274 2011 and 2012 than those of canopy trees, and that *A. pseudoplatanus* was reduced more than *F.*
275 *excelsior* or *Q. robur*. The difference between canopy and understorey may reflect both different

276 light climates and different functional traits. Understory trees are even more dependent on the early
277 spring period as they typically leaf out before canopy trees, and take advantage of high light levels
278 before the canopy closes. Tree organs, such as leaves and roots, differ in their drought sensitivity
279 (Leuzinger et al. 2005), and leaf morphology also differs between species in terms of light and
280 shade response. Canopy leaves in *F. excelsior*, for example, have been found to be less susceptible
281 to drought than those of other species in broad-leaved forest systems (Legner et al. 2013). Previous
282 measurements of rooting depth in other temperate deciduous forests found that some *Quercus*
283 species had deeper roots than other species, and did not respond to drought with an increase in fine
284 root growth (as did other species) (Leuzinger et al. 2005).

285

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

296

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

305

306 The late spring in 2010 is likely to explain most of the difference in growth rates between years,
307 but 2010 was also a dry spring and this may have played a role. Recent work in another European
308 broad leaved forest also found that reduced soil moisture during the growing season inhibited stem
309 growth in both *Fraxinus excelsior* and *Acer pseudoplatanus* (Mund et al. 2010). Fluctuations and

310 seasonal changes (from current baselines) in both temperature and rainfall are projected to continue,
311 so we may expect to see increasing differences in growth and growth rates, as modelled GDD
312 responses indicate (Ashraf et al. 2013). 2010 was an anomalous year, with regard to spring
313 temperatures and timing, and under projected warming we suggest that earlier springs may drive
314 increased forest carbon sequestration by more than would be expected as a simple temperature
315 response, because of the interaction with longer day lengths. With climate extremes and extreme
316 weather events increasing in frequency (IPCC 2013a), there may be an increasing disparity of
317 growth between understorey and canopy species, possibly influencing and altering forest structure.
318 While the earlier-spring carbon uptake effect may be outweighed by drier summers, especially in
319 lower rainfall areas and where soil water capacity is lower, such a shift in productivity towards the
320 spring may have ecosystem consequences in terms of functional processes and the timing of
321 interactions between different components of the forest system.

322

323 **Acknowledgements**

324 This work was funded through the HSBC Climate Partnership (HCP) with the Earthwatch Institute
325 and supported by the Smithsonian Institution and the University of Oxford.

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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. $R^2 = 0.54$.

Predictor	DF	SS	MS	F	p
DBH	1	92.5	92.5	226.9	$<10^{-4}$

Species	5	210.1	42.0	103.0	<10 ⁻⁴
Crown Illum	1	71.6	71.6	175.5	<10 ⁻⁴
log(Edge dist)	1	11.3	11.3	27.7	<10 ⁻⁴
Plot	8	59.4	7.4	18.2	<10 ⁻⁴
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 ⁻⁴
Residuals	1030	420.2	0.4		
Total	1088	914.6			

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Table 2: ANOVA table for relative increment in 2010 vs. relative increment in 2012. $R^2 = 0.88$.

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 × Species	5	92.2	18.4	55.2	<10 ⁻⁴
Residuals	1082	359.8	0.33		
Total	1093	2947.8			

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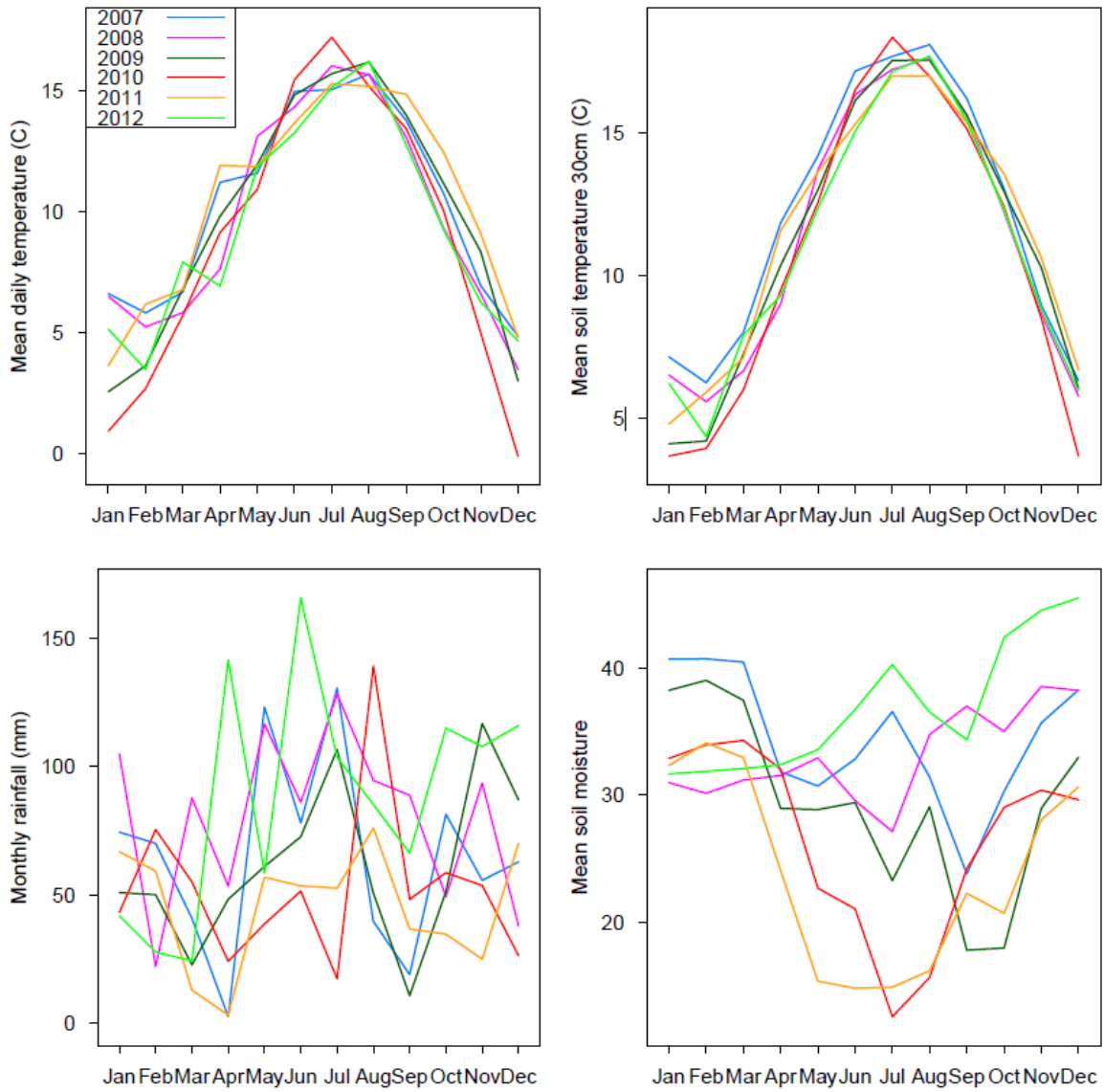
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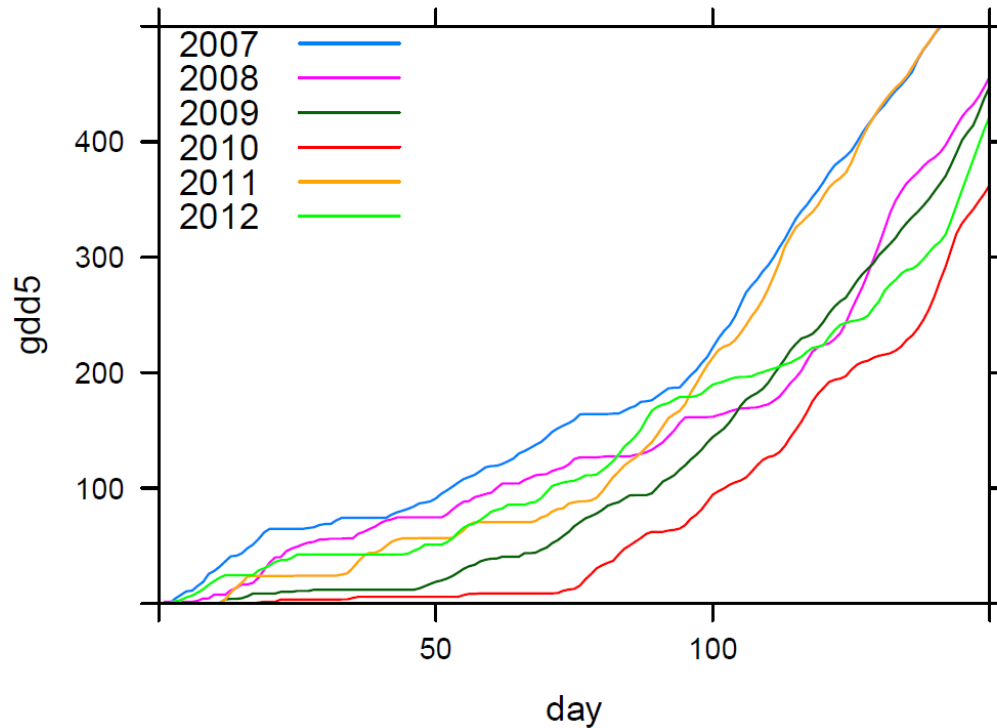
Figure 1: Wytham Woods, near Oxford, and locations of nine ~1 ha study plots. Species composition and forest structure varies across the plots, a function of previous land use. Vegetation types within the plots range from high forest (for example, in the central ‘core’ plot) to coppice with standards (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.



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Figure 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 (%).

Growing Degree Days, 5C Baseline



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

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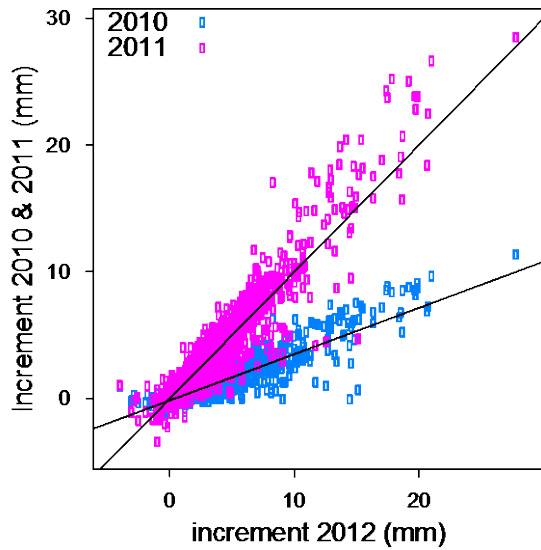
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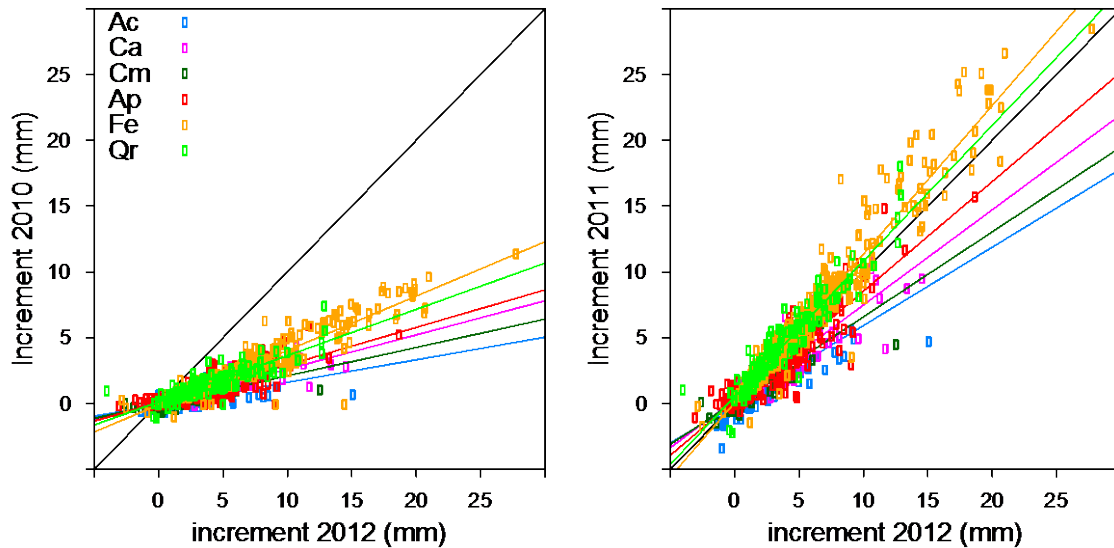
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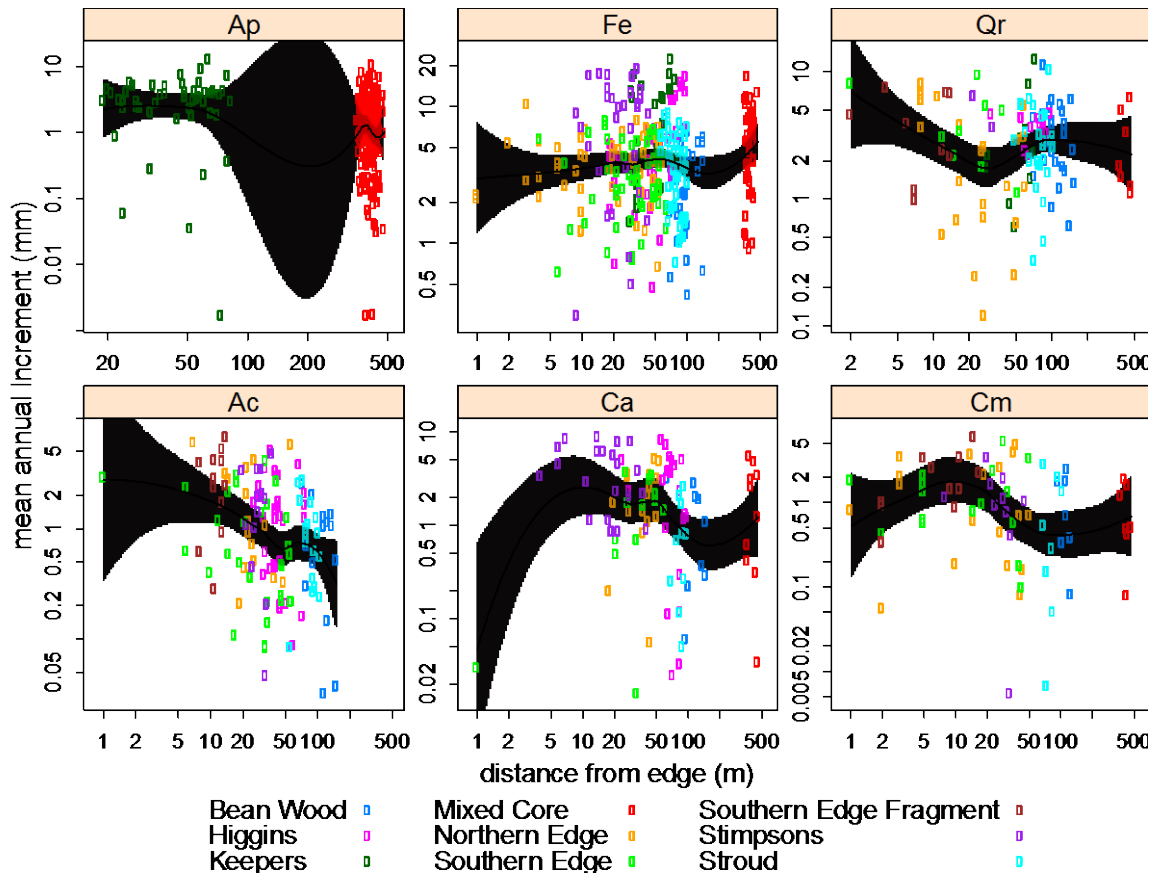
Figure 4: Absolute increment in 2010 and 2011 vs. 2012, for all trees. Regression lines in black. Growth in 2011 is the same on average to that in 2012, but growth in 2010 was 37% of that in 2012.



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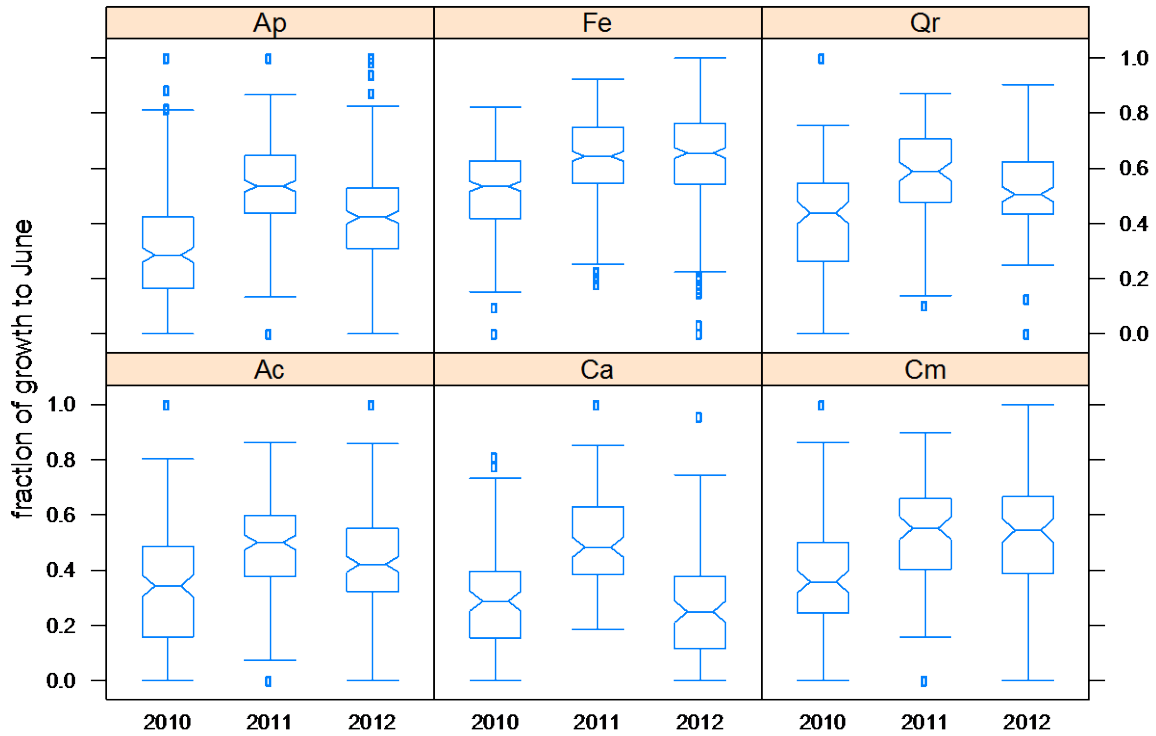
Figure 5: a) increment in 2010 vs. 2012, b) 2011 vs 2012, for common species. Coloured lines show linear regressions, black line shows 1:1 slope. The greater the slope, the less that species was affected by the 2010 climate. Ac = *Acer campestre*, Ap = *Acer pseudoplatanus*, Ca = *Corylus avellana*, Cm = *Crataegus monogyna*, Fe = *Fraxinus excelsior*, Qr = *Quercus robur*.

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



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Figure 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 ($F_{10,2139} = 11.9$, $p < 0.001$).