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# 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). 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.

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