University of Stirling

School of Natural Sciences – Biological and Environmental Sciences

Spatial and temporal patterns in the climate-growth relationships of *Fagus sylvatica* across Western Europe, and the effects on competition in mixed species forest.

Liam Cavin

Thesis Abstract

Increases in temperature, altered precipitation patterns, and the occurrence and severity of extreme climatic events have been important characteristics of the climate change observed to date. This has had many and diverse impacts upon the living world, with one recent observation being a global reduction in the net primary production of all terrestrial vegetation. Increases in temperature and the frequency of extreme events are predicted to continue throughout the 21st century, and can be expected to have far reaching effects on global terrestrial ecosystems. Increases in temperature and drought occurrence could fundamentally impact upon the growth rates, species composition and biogeography of forests in many regions of the world, with many studies indicating that this process is already underway.

European beech, *Fagus sylvatica,* is one of Europe's most widespread and significant broadleaved tree species, forming an important and frequently dominant component of around 17 million hectares of forest. However, the species is also considered to be drought sensitive. Thus, much research interest has focused on eliciting the details of its physiological response to increased water stress, whilst dendroecological studies have attempted to identify sites and regions where reductions in growth might be found. A significant knowledge gap exists regarding a multi-regional, range-wide view of growth trends, growth variability, climate sensitivity, and drought response for the species. Predicting the potential effects of climate change on competition and species composition in mixed species forests remains an important challenge.

In order to address this knowledge gap, a multi-regional tree-ring network was constructed comprising of 46 sites in a latitudinal transect across the species' Western European range. This consisted of 2719 tree cores taken from 1398 individual trees, which

were used to construct tree-ring chronologies for each site in the network. As a first step in a multi-regional assessment for *F. sylvatica*, a combination of the tree-ring chronologies and environmental data derived from a large scale gridded climate dataset were used in a multivariate analysis. Sites in the latitudinal transect were partitioned into geographically meaningful regions for further analysis. The resulting regions were then studied using climate-growth analysis, pointer year analysis of drought years, analysis of growth trends and growth variability, in order to examine regional variation in the response of the species to climate. Furthermore, a combination of long-term monitoring data from one specific site was combined with tree-ring sampling of multiple cohorts of *F. sylvatica* and one co-dominant competitor, *Quercus petraea*, to study the effects of an extreme drought event in 1976 on mortality and subsequent recovery.

Key results of the multi-regional analysis are that large scale growth reductions are not evident in even the most southerly and driest portions of the species' range. Radial growth is increasing, both in the north and in the core of the species' range, with southern range edge forests maintaining stable growth. However, the variability of growth from year to year is increasing for all regions, indicative of growing stress. Crucially, the southern range edge, which previous studies had identified as an 'at risk' region, was shown to be more robust than expected. Climate sensitivity and drought impacts were low for this region. Instead, forests in the core of the species range, both in continental Europe and in the south of the UK, were identified as having the highest climate sensitivity, highest drought impacts, and experiencing periodic reductions in growth as a result. Northern range edge forests showed little sign of being affected by drought, instead having low climate sensitivity and strongly increasing growth trends.

Extreme drought was found to affect species differently: the dominant species (*F. sylvatica*) failed to recover pre-drought levels of growth, whilst a transient effect of competitive release occurred for the co-dominant species (*Q. petraea*). There was also a long term effect on the relative abundance of the two species within the woodland, due to differences in the levels of drought induced mortality experienced by the species. This shows that in the case of extreme climatic events where thresholds in the ability of species to tolerate water stress are breached, the effects of drought can be rapid and long lasting. Drought impacts can cascade beyond that experienced by the most drought sensitive species, due to changes in competitive interactions between species in mixed species forests.

The implications of this work suggest opportunities, risks and strengths for *F. sylvatica*. In the northern portion of the species' range, predicted increases in productivity are confirmed by recent growth trends, indicating a good outlook for the species. At the southern range edge, *F. sylvatica* forests exist either in locations where precipitation is high or locations where local environmental conditions buffer them from an inhospitable regional climate. These factors result in southern range edge forests which are highly resilient to the effects of increasing climate stress. It is instead in the core of the species' range where the most sensitive forests are found. The effects of extreme drought on a range core forest demonstrated here provide a cautionary note: where drought stress tolerance thresholds are breached, rapid and long lasting effects on growth and mortality can occur, even in regions where drought has not previously been considered to pose a strong risk to the species.

Contents

List of Figures

List of Tables

1. Introduction

Contemporary climate change is characterised by increased temperatures and altered precipitation patterns, alongside a rise in both the frequency and intensity of extreme climatic events such as droughts, floods and storms (Schar *et al.* 2004; Della-Marta *et al.* 2007; IPCC 2007). These changing environmental conditions are affecting ecosystems worldwide, with a slight reduction in the global net primary production of all terrestrial vegetation observed for 2000-2009, attributed largely to regional droughts combined with drying in the southern hemisphere (Zhao & Running 2010). Whilst these global responses mask considerable variation across different regions and ecosystems, drought-related increases in mortality and growth declines have been reported for many forest communities across the globe (Dobbertin 2005; van Mantgem *et al.* 2009; Allen *et al.* 2010).

European beech (*Fagus sylvatica* L.) is a species which is a key component of European broadleaved forests. Due to its ability to utilise a wide range of soil types and habitats, it frequently dominates across Central Europe. The species is distributed widely across Western, Southern and Central Europe, and is also found throughout the British Isles (Packham *et al.* 2012). It reaches its northern range limit in Northern Scotland, and Southern Scandinavia. In the east, it can be found in Eastern Poland, and in Ukraine. Across Southern Europe, *F. sylvatica* is found in the north of the Iberian Peninsula, in Italy, throughout the Balkans and in Greece. There is considerable climatic variation across this wide geographical distribution. In the central and northern part of the species' range, it occupies lowland, hill and lower mountain range sites (Bolte, Czajkowski & Kompa 2007). However, in Southern Europe, it occurs at elevations of up to 2000 m (Magri 2008).

Fagus sylvatica is considered to be a drought sensitive species, with considerable research attention focused on the drought response and its mechanisms for the species due to perceived potential of negative effects of climate change (Peuke *et al.* 2002; Gessler *et al.* 2004; Meier & Leuschner 2008). It has been argued that tree populations living at their equatorial range edge might be particularly at risk to increased water stress due to rising temperatures, due to lower water availability in this portion of their range (Jump, Cavin & Hunter 2010). However, modelling studies have forecast changes in the distribution *F. sylvatica* more widely across its range, alongside reductions in primary productivity of biomass (Broadmeadow, Ray & Samuel 2005; Meier *et al.* 2011). Dendroecological studies conducted in Southern Europe have found reductions in growth rates, and attributed these to a reduction in water availability associated with climate change (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). Additionally, regional scale growth declines have been reported for range core sites, and also attributed to increased aridity due to climate change (Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010). These studies represent a clear warning that predicted negative effects of climate change may already have significantly manifest themselves across the species' range.

The response of trees to changes in environmental conditions is recorded in radial growth long before changes in recruitment and mortality affect the species composition of individual sites, and species' ranges more generally (Leuzinger *et al.* 2005). As tree-core samples taken from living trees provide a time series of growth throughout the life of the organism, they therefore represent an excellent resource for analysing the response of that organism to changing environmental conditions throughout its life. Annual rings formed by trees are themselves an integration of the climatic and stress conditions experienced by the organism both during and before the growing season in which they are formed, and therefore radial growth is an important parameter which allows the growth of the tree to be linked to climate variability (Smith 2008). The establishment of networks of tree-ring chronologies at a regional and continental scale allow for an assessment of the spatial relationships between the growth of forests and geographical climatic variation (Frank & Esper 2005; Buntgen *et al.* 2007; Friedrichs *et al.* 2009; Babst *et al.* 2013). Whilst regional scale networks have been constructed for *F. sylvatica* (Piovesan *et al.* 2005a; Bontemps, Hervé & Dhôte 2010), no networks have been created to date which expressly include the large scale climate gradients that exist when considering the latitudinal range of the species.

Research on the effects of climate change on the living world has largely focused on assessing the response to gradual changes in mean conditions. However, the effects of extreme climate events are increasingly being recognised as being important drivers of the response of organisms and ecosystems to environmental change (Smith 2011b; Smith 2011a). For forests, extreme drought has been implicated in recent forest dieback episodes, alongside non-fatal damage (Peñuelas, Lloret & Montoya 2001; Bigler *et al.* 2006; Bréda *et al.* 2006). Mortality in trees is thought to involve the processes of carbon starvation and hydraulic failure, although considerable debate exists regarding the specific roles of both factors (Sala, Piper & Hoch 2010; McDowell 2011). Recent work has highlighted that most woody plant species in fact operate close to their safety margins for hydraulic failure, indicating that any future shifts in temperature or precipitation could have considerable negative effects (Choat *et al.* 2012). Furthermore, understanding likely variability in drought response within a species, and between species in mixed forest, remains problematic (Martínez-Vilalta, Lloret & Breshears 2011). For *F. sylvatica* specifically, drought has been identified as the cause of elevated mortality levels in regions beyond those generally considered to be most at risk (Peterken & Mountford 1996). Thus, closer investigation of relative mortality rates between species in mixed *F. sylvatica* forest, along with study of the long term recovery of surviving trees, could yield valuable insights.

This thesis describes a targeted attempt to address the knowledge gap regarding the climate response of *F. sylvatica* across its range. Central to this is the development of a multi-regional network of tree-ring chronologies, encompassing samples taken from forests in a broad latitudinal transect in Western Europe, from the north of the species' range in Scotland, to the south of the species' range in Spain. Chapter 2 will describe the sampling methods, laboratory methods, and fundamental steps in the analysis of the radial growth data and climate data that are common to each of the subsequent chapters. Subsequent chapters will be structured along the lines of scientific papers, each with their own introduction, methods, results and discussion sections. Chapter 3 will use data driven methods to identify geographical units within the network of chronologies. Chapter 4 looks at identifying differences in climate-growth relationships for these geographical units, along with an analysis of the response to and drivers of drought induced pointer years. Chapter 5 examines *F. sylvatica* growth trends and growth variability. Chapter 6 describes the effect of a rare extreme drought event on a mixed *F. sylvatica* and *Q. petraea* woodland. Finally, chapter 7 summarises the results of the previous chapters and draws conclusions.

2. Common Materials and Methods

This chapter presents the materials and methods that are common to subsequent data chapters. The sampling sites for the Multiregional Network are introduced, along with the sampling protocols for dendroecological field work. Methods for sample preparation, chronology building and validation are reported along with methods for sourcing and developing climate data.

2.1 The Multiregional Network

The basis for the analysis presented in this thesis is a multiregional dendroecological network of *F. sylvatica* tree-ring chronologies, developed through sampling in 2010 and 2011, and hereafter referred to as the Multiregional Network. Sampling sites were distributed across a broad latitudinal transect, covering from 58.5° to 40.8° N, and from 5.8° to 11.8° E (see figure 2.1 for the spatial distribution of sites). In total, 47 sites contributed to the Multiregional Network across 5 countries: 25 from the United Kingdom, 1 from Belgium, 2 from Germany, 11 from France, and 8 from Spain. At each of the 47 sites, a representative sample of *F. sylvatica* trees were selected for dendroecological sampling. At 1 site (site 16), two *F. sylvatica* chronologies were developed (with the two chronologies representing different drought impacts) along with sampling for a co-dominant competitor species, *Q. petraea*, for a study looking in detail at the response to extreme drought which will be presented in chapter 6. Table 2.1 shows the summary details for all sites included in this study.

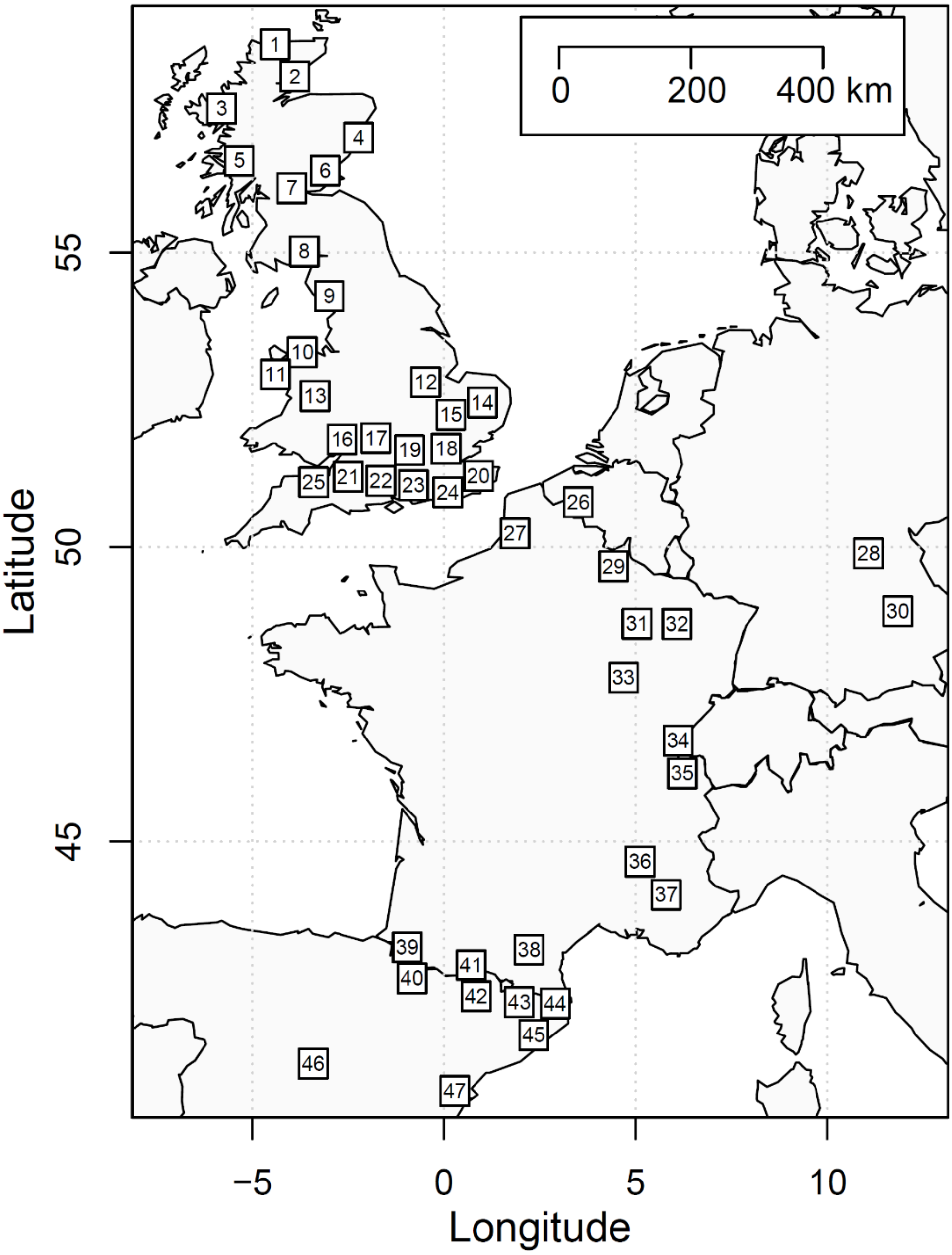

Figure 2.1: Map showing the location of all 47 study sites.

2.2 General Tree-Ring Sampling

For each cohort at each site, a mean of 29 and minimum of 15 canopy dominant or co-dominant trees were selected for coring. Trees selected for coring were; a minimum of

Table 2.1: Summary details for the sites sampled.

ID Number	Site Name	Country	Elevation (m)	Latitude (°)	Longitude (°)	Year Sampled
1	Tongue	UK	60	58.50	-4.41	2010
2	Uppat	UK	30	57.99	-3.89	2010
3	Applecross	UK	20	57.45	-5.80	2010
4	Dunnotar Wood	UK	60	56.95	-2.23	2010
5	Port Appin	UK	60	56.56	-5.34	2010
6	Kinnoul Forest Park	UK	170	56.39	-3.40	2010
7	Lady's Brae	UK	30	56.10	-3.74	2010
8	Mabie Forest	UK	55	55.02	-3.65	2010
9	Linsty Green	UK	55	54.26	-2.99	2010
10	Gloddaeth	UK	130	53.31	-3.80	2010
11	Talhenbont Hall	UK	55	52.93	-4.29	2010
12	Southey Wood	UK	55	52.61	-0.36	2010
13	Gardenhouse Wood	UK	260	52.56	-3.36	2010
14	Two-Mile Bottom	UK	35	52.46	0.72	2010
15	Beechwoods	UK	45	52.17	0.17	2010
16	Lady Park Wood	UK	140	51.83	-2.66	2010
17	Wytham Wood	UK	150	51.77	-1.34	2010
18	Epping Forest	UK	110	51.67	0.05	2010
19	Shirburn Wood	UK	260	51.65	-0.96	2010
20	Foxbury Wood	UK	170	51.21	0.84	2010
21	Roddenbury	UK	145	51.19	-2.29	2010
22	Micheldever Wood	UK	120	51.13	-1.25	2010
23	Wealden Edge Hangers	UK	125	51.05	-0.96	2011
24	West Dean Woods	UK	140	50.93	-0.78	2010
25	Dommet Wood	UK	260	50.92	-3.03	2010
26	Kluisbos	Belgium	120	50.76	3.50	2011
27	Massif Foriester de Crécy en Ponthieu	France	85	50.23	1.85	2011
28	Forcheim	Germany	575	49.89	11.07	2011
29	Massif de Signy L'Abbaye	France	235	49.67	4.42	2011
30	Kelheim	Germany	475	48.91	11.83	2011
31	Forêt de Trois Fontaines	France	240	48.70	5.03	2011
32	Forêt de Haye	France	355	48.69	6.07	2011
33	Forêt de Chattilon-Sur-Seine	France	380	47.78	4.68	2011
34	Forêt Du Lindar	France	765	46.67	6.10	2011
35	La Saleve	France	790	46.16	6.21	2011
36	Massif de Saou	France	460	44.66	5.11	2011
37	Montagne de Lure	France	1310	44.09	5.79	2011
38	Le Massif de la Malepère	France	410	43.16	2.21	2011
39	Forêt de Arbaille	France	570	43.13	-0.96	2011
40	Aztaparreta	Spain	1020	42.93	-0.83	2011
41	Baish Aran	Spain	1080	42.83	0.71	2011
42	La Vall de Boí	Spain	1455	42.56	0.84	2011
43	Sierra Catllaràs	Spain	1135	42.21	2.01	2011
44	Zona Volcanica La Garrotxa	Spain	580	42.15	2.51	2011
45	Montseny	Spain	1205	41.77	2.34	2011
46	Tejera Negra	Spain	1545	41.23	-3.41	2011
47	Parc Natural dels Ports	Spain	1165	40.76	0.28	2011

20 m from each other, to minimise competition effects between individuals in a chronology; a minimum of 20 m from the forest edge to minimise edge effects, such as increased windthrow during storms and increased evapotranspiration; a minimum of 20

m from either running or standing water, to remove the possibility of the individual utilising these water sources during drought periods. Exceptions to these rules occurred at the following sites: site 2, where the forest stand sampled was very small thus in some cases necessitating sampling near neighbours and near edge individuals; sites 38 and 47, where a small proportion of *F. sylvatica* within the forest necessitated in some cases the sampling of near neighbours. Additionally, at site 38 *F. sylvatica* were entirely restricted to a damp ravine with running water, whilst the surrounding area was a more arid Mediterranean forest dominated by *Quercus ilex*. All cohorts sampled were of healthy trees with no visible signs of damage. For each tree, two cores were taken per tree at a height of 1.3 m using a 4.3 mm increment borer (Haglöf: Långsele, Sweden). Samples were then stored and air dried in paper straws before being transported to the laboratory for processing. The circumference of each tree was measured at 1.3 m above ground level, and a GPS unit was used to record its location.

2.3 Tree-Ring Preparation, Measurement and Crossdating

The dried samples were mounted on grooved mounting boards constructed from pine batten wood, and fixed in place using water soluble PVA glue with trachea vertically aligned. Mounted cores were sanded using successively finer grades of sandpaper, with the final sanding at grit size P600. Finished cores were scanned at 1600 dpi, and ring widths measured using CooRecorder v7.5 (Larsson 2003b), with the assistance of a MZ6 stereomicroscope where resolution of the sampled image was insufficient to identify micro-rings (Leica: Wetzlar, Germany). Where annual rings were absent, they were assigned a ring width value of 0. Using the programme CDendro v7.5 (Larsson 2003a), samples were crossdated visually by the comparison of growth curves, and statistically validated using the interseries comparisons of correlations of chronology segments. The programme COFECHA was used as a replication of the statistical validation of crossdating stage for chronologies which proved difficult to crossdate (Holmes 1983). For the final crossdated chronologies, a mean ring width value was calculated for each year for each tree using the total number of cores available from the tree, giving a final ring width series for each tree. Rotten and unreadable cores were excluded from the analysis. In total, 2719 cores from 1398 trees were included in the final 49 tree-ring chronologies.

2.4 Chronology Detrending

A tree ring series can be represented using a conceptual linear aggregate model of unobserved elements (Cook & Kairiukstis 1990):

$$R_t = A_t + C_t + \delta D1_t + \delta D2_t + E_t \tag{2.1}$$

where R_t is the observed series of ring widths, A_t is the age/size related trend contained in the ring widths, C_t is the environmental signal related to climate, $\delta D1_t$ is the signal relating to local endogenous disturbance pulses, $\delta D2_t$ is the signal relating to exogenous disturbance pulses at the stand scale, and E_t represents all variability not captured by the other components. Endogenous disturbances are transient effects which do not impact upon the entire stand, such as gap-phase dynamics in semi-natural forests or thinning cuts in managed forests. Exogenous disturbance pulses are disturbances that affect the entire forest stand, and includes both disturbances that may affect the site alone (e.g. logging) and disturbances that may affect the wider region (e.g. pollution). In order to study the effect of climate on tree growth, it is necessary to perform a series of steps to minimise A_t, $\delta D1_{t,}$ $\delta D2_{t,}$ and E_t, whilst retaining C_t.

The first step in achieving this is to convert each ring width series into a stationary tree-ring index. To accomplish this, each annual ring width is divided by the expected ring width given an estimation of the growth trend (Fritts 1976):

$$I_t = R_t/G_t \tag{2.2}$$

where I_t is the tree-ring index, and G_t is the estimated growth trend.

Many methods are available for estimating G_t. For trees growing in a closed canopy environment, a stochastic method of low-pass digital filtering using a cubic smoothing spline is commonly used. Cubic smoothing splines fit third-order polynomial curves to segments of the ring-width series, whilst smoothing the curves at the connection points. This method has sufficient flexibility to remove not only the age/size related trend from the ring-width series, but also can remove some of the non-climatic variance in growth caused by gap-phase dynamics resulting from either natural or anthropogenic disturbance (Cook & Peters 1981). Thus, the spline gives an estimate of G_t which minimises the components A_t, also partially reduces $\delta D1_t$ and $\delta D2_t$ of equation 2.1. For the purposes of this manuscript, the underlying mathematics of cubic smoothing splines will not be explored, but for a more detailed description of these (and digital filters in general) see Fritts (1976); Cook and Peters (1981); Cook and Kairiukstis (1990), and Zuur *et al.* (2009). The cubic smoothing spline used had a frequency cut-off of 50% and rigidity of 2/3 of the total series curve length, since splines with these characteristics have been shown to be effective in removing long term trends (Cook & Kairiukstis 1990). For a small number of individual tree core ring-width series (number of cores = 6), the spline fitted resulted in a predicted negative ring width value for some years. In these instances, a modified negative exponential curve was used in place of the spline. This simpler deterministic model is adequate for estimating size/age related trends in ring-width, but is unable to model the gap phase dynamics of closed canopy forest stands (Fritts 1976).

In order to remove autocorrelation, and as an additional filter to remove the effects of disturbance, the ring width indices were modelled as autoregressive (AR) processes (Cook 1987), such that:

$$I_t = c + \sum_{i=1}^{n} \tau_i \, I_{(t-i)} + \epsilon_t \tag{2.3}$$

where c is a constant, n is the order of the model, τ_i is the AR coefficient, and ϵ_t is white noise. This method is used in order to decompose the signals $\delta D1_t$ and E_t from the ring-width series', whilst yielding a good estimate of C_t. Akaike's Information Criterion (AIC) was used to determine the order of the AR model (Akaike 1974). The ring width series were then prewhitened by deducting the modelled autocorrelation structure from the ring width indices.

Finally, the detrended and prewhitened ring width indices from each population were then combined into mean chronologies, using Tukey's biweight robust mean (Mosteller & Tukey 1977). This method omits extreme outliers from the mean value calculations, and results in a reduction of error variance for closed canopy forest chronologies. The averaging procedure for combining individual ring width series also has the effect of minimising the $\delta D1_t$ component of equation 2.1. Thus, the final mean chronologies retain the climatic signal on growth, with all other signals minimised. All stages of chronology building (and all subsequent analyses in this manuscript) were performed using the statistical environment R, with the package dplR (Bunn 2010; R Development Core Team 2012).

2.5 Basal Area Increment

Basal area increment (BAI) is well established in forest ecology as measure of tree growth which can be used to study the vigour of individual trees and populations (Biondi 1999; Bigler & Bugmann 2003; Biondi & Qeadan 2008b). BAI tends to increase sharply in juvenile trees before reducing in gradient when the tree reaches the canopy, however it is not expected to decline markedly unless the tree is severely stressed (Pedersen 1998). Other studies have demonstrated that, whilst mature trees can display rising BAI for differing periods of their lifespans, BAI increases taper off to result in a near constant level of BAI growth for healthy and mature trees (Pedersen, 1998, Duchesne, 2002, Duchesne, 2003, Poage, 2002). Thus, decreases in BAI are commonly interpreted as signifying stress, and for *F. sylvatica* declines in BAI for mature forests have been used as indicators of an increase in climate change related water stress (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). However, reductions in BAI can occur as a consequence of other factors that negatively impact tree growth. Here, BAI was calculated by using raw, non-detrended ring widths and circumferences to calculate the area of wood added to a cross section of the tree at breast height (1.3 m) annually:

$$BAI = \pi(R_n^2 - R_{n-1}^2) \tag{2.4}$$

where R is the radius of the tree, and n is the tree ring year.

2.6 Calculation of Summary Statistics

A series of summary statistics were calculated to enable the evaluation of the validity of the tree ring chronologies. Mean sensitivity (MS) is a measure of year to year variability of a ring-width series which has been in use since the early days of dendrochronology (Douglas 1920). Biondi and Qeadan (2008a) define MS as:

$$MS = \frac{2}{n-1}\sum_{t=2}^{n}\frac{|w_t - w_{t-1}|}{w_t + w_{t-1}}$$

(2.5)

where w is the ring width, n the length of the ring-width series, and t the year of the series.

The statistical properties of MS have been criticised as providing little more of substance than standard deviation and first-order autocorrelation (Jansma 1992). However, it has been retained here for use as a simple diagnostic tool in order to gauge how sensitive ring-width series were, and thus how suitable for crossdating they were, and for comparison with other studies.

Mean inter-series correlation ($\overline{r}$, or Rbar) is commonly used as a measure of the signal strength of chronologies (Cook & Kairiukstis 1990). Here, $\overline{r}$ was calculated as the mean of all Pearson's correlation coefficients between pairs of ring-width series within a chronology. Additionally, expressed population signal (EPS), is a measure derived from $\overline{r}$ which is used in as a diagnostic tool to assess chronology quality (Wigley, Briffa & Jones 1984). It is defined as:

$$EPS = \frac{\overline{r}}{\overline{r} + (1 - \overline{r})/N}$$

(2.6)

where N is the number of ring-width series in the chronology. Correlation coefficients were calculated based on the maximum pairwise overlap between cores.

If the aim of chronology building is to combine ring-width time series from individual trees in order to reduce noise and maximise the common climatic signal, then EPS is a measure of how closely the sampled chronology approaches the theoretical population chronology with infinite replication. Each ring-width series was broken into 30 year sections, lagged by 15 years, and used to calculate running statistics for $\overline{r}$ and EPS, thus enabling an evaluation of chronology quality throughout different portions of its length.

2.7 Evaluation of Summary Statistics

The summary statistics for the 53 chronologies are presented in table 2. Mean chronology length ranged from 40 to 162 years for the *F. sylvatica* chronologies, and 175 years for the *Q. petraea* chronology. Standard deviation ranges from 2.3 to 64.4 years, with the largest variability in chronology length found predominantly in those chronologies in excess of 100 years long.

Mean sensitivity was in the region of 0.15 to 0.35 for all chronologies, within the range of 0.1-0.4 judged to be suitable for crossdating (Fritts 1976). For EPS, the generally accepted minimum value for chronologies is 0.85 (Wigley, Briffa & Jones 1984; Cook & Kairiukstis 1990). For two chronologies, this threshold value was not reached: chronology 10 had an EPS of 0.84, and chronology 39 had 0.79. For chronology 10, running statistics calculated over 30 year blocks showed an EPS of 0.86 or higher for the period 1935 to 2009. Therefore, the chronology was truncated to the period 1935-2009 for all further analyses. Chronology 39 had an EPS below the threshold value for much of the time series, and so was omitted from all further analyses.

2.8 Climate Data

Daily climate variables were obtained for all 46 sites used in further analysis (i.e. excluding site 39, as detailed in section 2.7) from the publicly available, high-resolution, E-OBS gridded dataset: daily mean temperature, maximum temperature, minimum temperature

Table 2.2: Summary statistics for all tree-ring chronologies.

Site Number	Name	Period	Mean Length (Years)	SD	MD (mm)	SD	No. Trees	No. Cores	MW (mm)	SD	MS	AR1	Rbar	EPS
Fagus sylvatica														
1	Tongue	1835-2009	114	35.0	502.9	109.9	26	46	2.01	1.07	0.26	0.80	0.41	0.92
2	Uppat	1960-2009	43	4.5	297.1	37.2	21	42	2.98	1.19	0.35	0.38	0.51	0.95
3	Applecross	1812-2009	158	25.3	705.2	136.1	29	55	1.69	0.96	0.25	0.82	0.47	0.95
4	Dunnotar	1961-2009	43	3.4	394.8	60.6	30	56	4.04	1.21	0.16	0.71	0.21	0.88
5	Port Appin	1834-2009	120	34.2	933.6	269.8	27	49	2.42	1.29	0.21	0.84	0.39	0.94
6	Kinnoul	1857-2009	84	21.9	672.2	113.8	28	56	3.47	1.40	0.24	0.75	0.51	0.94
7	Lady's Brae	1952-2009	54	2.7	388.6	46.0	30	59	3.06	1.07	0.23	0.63	0.41	0.95
8	Mabie	1954-2009	52	2.7	549.7	86.1	30	59	3.52	0.97	0.15	0.70	0.28	0.92
9	Linsty Green	1966-2009	40	2.3	466.4	46.3	29	57	3.67	1.19	0.19	0.65	0.36	0.94
10	Gloddaeth	1751-2009	181	64.4	880.8	222.6	28	52	1.40	0.81	0.30	0.76	0.21	0.84
11	Talhenbont	1795-2009	125	37.6	703.8	96.1	28	49	1.88	1.14	0.33	0.77	0.29	0.87
12	Southey	1916-2009	84	12.8	486.2	93.9	30	60	2.68	1.05	0.33	0.50	0.61	0.98
13	Gardenhouse	1810-2009	137	42.8	715.4	198.3	29	55	2.11	1.18	0.32	0.76	0.41	0.93
14	Two-mile-bottom	1818-2009	156	31.3	910.8	153.3	29	58	2.06	1.07	0.35	0.67	0.40	0.94
15	Beechwoods	1840-2009	162	5.9	513.6	110.4	30	30	1.32	0.75	0.30	0.77	0.46	0.96
16A	Lady Park	1856-2009	110	19.0	739.9	167.3	31	67	2.13	1.24	0.32	0.79	0.52	0.96
16B	Lady Park	1832-2009	119	18.2	582.7	144.9	32	68	2.25	1.22	0.28	0.79	0.59	0.97
17	Wytham	1956-2009	50	3.9	554.0	78.3	30	60	4.06	1.32	0.19	0.67	0.26	0.91
18	Epping	1821-2009	124	33.6	682.9	156.0	27	54	2.09	1.14	0.31	0.74	0.39	0.92
19	Shirburn	1801-2009	159	27.0	755.3	147.2	30	59	1.76	1.08	0.30	0.81	0.41	0.95
20	Foxbury	1841-2009	102	21.6	974.6	193.2	19	36	3.10	1.16	0.28	0.62	0.47	0.91
21	Roddenbury	1919-2009	54	7.5	650.5	76.5	30	60	4.30	1.49	0.17	0.79	0.51	0.95
22	Micheldever	1936-2009	59	7.7	663.4	90.5	30	60	3.94	1.32	0.20	0.68	0.24	0.88
23	Wealden Edge Hangers	1889-2010	93	18.9	479.3	155.3	27	54	2.29	1.11	0.24	0.75	0.25	0.87
24	West Dean	1952-2009	50	4.0	619.3	76.4	30	60	4.29	1.53	0.23	0.67	0.46	0.96
25	Dommet	1841-2009	115	29.0	932.4	191.0	30	59	2.54	1.54	0.25	0.84	0.55	0.96
26	Kluisbos	1923-2010	75	7.5	601.5	122.6	30	57	3.50	1.61	0.24	0.75	0.58	0.97
27	Crecy en Ponthieu	1889-2010	102	13.5	707.6	82.8	30	60	2.89	1.14	0.28	0.67	0.47	0.96
28	Forcheim	1913-2010	81	7.8	416.3	53.5	30	60	2.30	0.72	0.25	0.47	0.43	0.95
29	Signy L'Abbaye	1874-2010	85	22.4	656.8	84.7	30	60	3.54	1.40	0.22	0.73	0.37	0.92
30	Kelheim	1897-2010	92	11.4	466.3	44.0	30	60	2.30	0.76	0.22	0.64	0.31	0.92
31	Trois Fontaines	1859-2010	112	18.0	697.4	74.5	29	58	2.67	1.02	0.25	0.66	0.27	0.89
32	De Haye	1921-2010	75	6.5	506.3	61.2	30	60	3.11	1.18	0.33	0.44	0.52	0.97
33	Chattilon-Sur-Seine	1853-2010	133	18.1	643.1	99.5	30	60	2.00	0.95	0.32	0.59	0.68	0.98
34	Colombier	1862-2010	109	30.9	486.2	106.3	30	60	2.14	0.83	0.23	0.71	0.25	0.88
35	La Saleve	1893-2010	92	17.9	473.9	95.8	30	59	2.47	0.91	0.24	0.64	0.44	0.95
36	De Saou	1895-2010	100	12.7	453.3	78.9	30	60	2.05	0.82	0.26	0.65	0.39	0.94
37	De Lure	1877-2010	105	21.6	475.6	71.4	30	60	2.08	0.97	0.23	0.71	0.42	0.94
38	Malapere	1948-2010	58	3.3	315.8	70.8	16	32	2.67	0.99	0.31	0.48	0.58	0.95
39	De Arbaille	1885-2010	67	19.1	535.1	101.7	20	33	3.59	1.21	0.18	0.73	0.26	0.79
40	Aztaparreta	1897-2010	78	12.0	570.8	94.4	30	60	3.04	1.36	0.25	0.75	0.62	0.97
41	Baish Aran	1896-2010	80	19.5	490.7	105.2	30	59	2.76	1.15	0.25	0.68	0.35	0.92
42	Vall de Boi	1904-2010	65	23.5	412.3	63.4	30	59	2.85	1.17	0.25	0.72	0.53	0.95
43	La Bergueda	1838-2010	89	13.8	319.8	71.6	30	60	1.66	0.69	0.23	0.69	0.34	0.89
44	La Garrotxa	1870-2010	107	17.9	389.2	47.1	30	60	0.99	0.40	0.29	0.53	0.38	0.93
45	Montseny	1919-2010	75	13.0	378.2	65.5	30	60	2.34	1.07	0.27	0.70	0.56	0.97
46	Tejera Negra	1837-2010	112	27.2	439.2	104.8	29	57	1.51	0.85	0.31	0.72	0.34	0.91
47	La Senia	1911-2010	60	17.3	331.0	92.3	24	47	2.46	0.79	0.23	0.53	0.41	0.91
Quercus petraea														
16Q	Lady Park	1770-2009	175	42.36	615.2	119.02	30	58	1.59	0.74	0.24	0.70	0.44	0.95

MD: mean tree diameter; **MW**: mean ring width; **SD**: standard deviation of preceding column; **MS**: mean sensitivity; **AR1**: first order autocorrelation; **Rbar**: effective rbar, mean inter-series correlation; **EPS**: expressed population signal.

and precipitation (Haylock *et al.* 2008). This dataset has grid spacing at 0.25° x 0.25° resolution (approximately 17.25 km^2) and covers the period from 1950 to 2012. Whilst primarily used for climatological studies, the E-OBS dataset was designed to be suitable for a wide range of applications and has been applied in fields such as the modelling of vegetation productivity (Maselli *et al.* 2013), and invertebrate adaptation to climate change (Jönsson *et al.* 2013). However, the spread of climate stations used in the E-OBS network is uneven, which can lead to interpolated values being over-smoothed (Hofstra, New & McSweeney 2010). This problem manifests itself most acutely at the southern edge of the study region, where the station network is most sparse. A recent study has shown that for this region, the Iberian Peninsula, the E-OBS grid reproduces most climatological features well, but has serious limitations with regards to extreme indicators (Herrera *et al.* 2012). Despite this limitation, the authors conclude that E-OBS remains the best gridded dataset for European studies currently available.

For 3 sites, a total of 220 daily values were missing: site 1 daily maximum temperature (28 values), site 2 daily mean temperature (44 values), and site 10 mean temperature (148 values). These were interpolated by taking the mean of the adjacent values. As site altitudes differed from those for the E-OBS grid cells, temperature values required adjustment for altitude. The difference between altitude for each grid square and the actual site altitude was calculated. Then, a linear lapse rate adjustment of 6.0 °C per km was applied, giving a value to be added to or subtracted from the grid cell temperatures. This method has been shown to be accurate, compared to a neutral stability algorithm (Dodson & Marks 1997). However, it fails to take into account potential local effects on lapse rate, which are likely to be most pronounced in spatially complex mountain environments (Rolland 2003; Minder, Mote & Lundquist 2010).

Bioclimatic variables were then calculated using the raw daily data, in order to generate a series of variables that were potentially more biologically meaningful. The variables calculated were as follows: annual mean temperature; total annual precipitation; mean temperature of the warmest month; mean maximum temperature of the warmest month; mean temperature of the coldest month; mean minimum temperature of the coldest month; summer precipitation, defined as May to August; continentality index (the difference in mean temperatures of the warmest and coldest months); potential evapotranspiration (PET) calculated using the Thornthwaite method (Thornthwaite 1948); PET calculated for the summer months (May to August), again using the Thornthwaite method and hereafter referred to as summer PET; aridity index, precipitation divided by PET (UNEP 1992); and aridity index calculated for the summer months (May to August), hereafter referred to as summer aridity index.

3. Bioclimatic and Growth Based Zonation of the Multiregional Network

In this chapter, a combination of bioclimatic variables and *F. sylvatica* ring-width chronologies for the Multiregional Network of 46 sites across a latitudinal transect will be analysed, to ascertain to what extent data driven methods can be used to group the various locations within the network. Multivariate techniques will be employed, in an attempt to identify clusters of sites which are both geographically and biologically meaningful, in order to assist our understanding of the broad biogeographical factors which may be driving the growth of *F. sylvatica*, and to guide the analysis of tree-ring chronologies in subsequent chapters.

3.1 Introduction

Given the threat to the living world posed by global environmental change (Thomas *et al.* 2004; Wilson *et al.* 2005; Fischlin *et al.* 2007), assessing the response of species across their ranges to the changes already experienced is an important task. The extent of the geographic distribution of plant species is largely shaped by climate (Woodward 1987), and rapid shifts to those distributions have already been observed (Kelly & Goulden 2008). Studies of range shifts for plants have shown an expansion upwards and polewards at the leading edge of their latitudinal and altitudinal range limits (Walther 2004; Parmesan 2006). Range shifts to higher elevation have been observed at the trailing edge for species ranges, although reports of polewards retractions of range edges are less common (Jump, Matyas & Peñuelas 2009). Furthermore, many studies have reported that species have suffered negative consequences of environmental change widely across their ranges

(Adams *et al.* 2009; Allen *et al.* 2010). Paleological records and ecosystem studies indicate that range wide responses to environmental change can involve spatial and temporal patterning at both a local and regional level (Rietkerk *et al.* 2004; Williams, Blois & Shuman 2011). Therefore, when considering the effects of climate change on a species, it is important to consider its full geographical range, rather than range edges alone. Tree-ring networks which integrate chronologies from multiple sites, and in some cases multiple species, provide a tool to facilitate our understanding of how climatic patterns affect the growth of trees across time and space (Frank & Esper 2005; Buntgen *et al.* 2007; Di Filippo *et al.* 2007). For the Multiregional Network presented in this thesis, a key initial task is to identify geographical groupings of sites on a regional basis, both to frame the subsequent analysis of the network and to identify structure that may inform of likely regional level responses to future climate change.

Fagus sylvatica is considered to be one of the most widespread deciduous broadleaved trees in Europe (Packham *et al.* 2012). The northern portion of its range encompasses the north of the UK (Preston, Pearman & Dines 2002), and Southern Scandinavia (Bjune, Helvik & Birks 2013). In the mid latitudes, *F. sylvatica* can be found across Western and Central Europe, where it has become ever more common through a combination of the conversion of conifer stands to mixed broadleaf (Gessler *et al.* 2007), and natural spread of the species (Peters 1997). In the west, the Atlantic Ocean forms a natural limit of the species range. The eastern range limit is reached at Poland and Ukraine, where increasingly continental climate results in winter extreme temperatures beyond those that the species is able to tolerate (Bolte, Czajkowski & Kompa 2007). In the southern portion of *F. sylvatica's* range, it is found at increasingly high altitudes, where favourable climatic conditions for the persistence of the species exist. In the Iberian Peninsula, populations can be found throughout the Cantabrian Mountains, the Basque region and Catalonia (López-Merino *et al.* 2008). In Italy, populations can be found in locations such as the Apennines, and as far south as Sicily (Piovesan *et al.* 2005b). In South Eastern Europe, *F. sylvatica* forests are found throughout the Balkan region, Bulgaria, and the mountains of Northern Greece (Dzwonko & Loster 2000; Bergmeier & Dimopoulos 2001). Out of this overall geographical range, the Multiregional Network consists of a broad latitudinal transect, from the range edge in the far northern UK, to the southern range edge in the Iberian Peninsula. Thus, the network captures a selection of temperate, continental and Mediterranean regions. However, it does not include sites with extreme winter cold, as in the east of the geographical range.

For trees, dendrochronology is a key empirical tool for the investigation of the connections between annual radial tree growth and environmental conditions, and can be applied to the problem of searching for structure in climatic response within a species' geographical range (Cook *et al.* 2001). Common growth signals across different forests can be used to assess zonation of a species' response to environmental drivers, such as climate. Where common patterns in the growth records of tree populations exist, they can be interpreted to indicate the presence of ecologically and climatically coherent units. In addition to spatial structure in growth patterns due to climate, a genetic signal may be present leading to structure based on provenance (Savva *et al.* 2002; Martinez Meier *et al.* 2008). Studies have utilised multivariate analysis of multi-species dendroecological networks covering large geographical areas to analyse spatiotemporal structure across tree-populations (Cook *et al.* 2001; Fang *et al.* 2012; Babst *et al.* 2013). However, single species studies (including for *F. sylvatica*) have largely remained regional in scope (Piovesan *et al.* 2005a; Di Filippo *et al.* 2007; DeSoto *et al.* 2012). In one notable exception, an extensive network of sites was used to study *Quercus alba* across its range in the eastern USA (LeBlanc & Terrell 2009), which demonstrated that spatial structure in climate response was primarily linked to a precipitation gradient.

Bioclimatic classification systems exist which have been applied to partition geographical areas into ecoregions, which describe patterns of vegetation types (Thompson *et al.* 2004). For example, the Küchler system assesses potential natural vegetation (Küchler 1964), whilst the Bailey system integrates vegetation with assessment of topography and climate (Bailey 1983). However, in the case of studying *F. sylvatica* forests across the species' range, any broad assessment of ecoregion type is likely to be confounded by the fact that all sites themselves consist of a narrow range of vegetation types. Cluster analysis of *F. sylvatica* forests has been applied on a regional scale, using plant community data and ecological indicator values to identify forest types (Marinsek, Silc & Carni 2013). Attempts to identify structure in environmental conditions within the network can draw on this example, along with established methods of multivariate analysis applied to bioclimatic data (Laurent *et al.* 2004; Metzger *et al.* 2005). Classification based on bioclimatic variables should ensure that both summer and winter conditions are considered (Andrew *et al.* 2013).

The primary objective of this chapter is to identify coherent and meaningful biogeographical groups using a combination of environmental and tree ring data from the multiregional tree-ring network. To achieve this, multivariate techniques will be applied to analyse the bioclimatic (see section 2.8) and growth data (see section 2.4) available for the sites within the network. Thus, the aim is to assess geographic structure in both climate and in growth response of *F. sylvatica*. Given recent studies which identify southern range edge populations of *F. sylvatica* as being at risk (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008), this chapter also aims to identify which portion of the network can be classified as being range edge, and to what extent environmental conditions and growth response are homogenous within that zone.

3.2 Methods

Bioclimatic variables

The bioclimatic variables calculated in section 2.8 for each site were used to generate a series of paired plots of all possible combinations of variables. These plots served as a filter to identify and remove any of the bioclimatic variables which were simply linear extensions of others, and thus due to colinearity would lead to the non-independence of predictor variables. The following variables were retained for further analysis: elevation, annual mean temperature, total annual precipitation, mean maximum temperature of the warmest month, mean minimum temperature of the coldest month, continentality index, and summer potential evapotranspiration. These remaining variables were then used to conduct clustering analyses, the overall aim being to enable the grouping of sites based on a data driven assessment of site environmental characteristics.

Agglomerative hierarchical clustering analysis was performed on the bioclimatic variables selected above for each of the 46 sites in the Multiregional Network, using complete-linkage clustering to identify similar clusters (Sørensen 1948). Therefore, distances between groups of sites were calculated as a function of pairwise distances between individual sites. Clustering analysis aims to partition data into a number, *k*, of groups, with the intention of deriving meaningful groups. As the aim here is to resolve biogeographically meaningful clusters, a high number of clusters would run the risk of resolving groups at a local rather than regional scale. Therefore, clustering was initially attempted using cluster sizes of between 2 to 7, with $k = 6$ giving the best agreement between this and subsequent bioclimatic clustering analyses.

In order to examine their structure, discriminant coordinates were calculated for the clusters, with covariances of the different groups given equal weight (Seber 1984). These coordinates were then used to plot the clusters as orthogonal projections in two dimensions, as a discriminant projection plot (Gnanadesikan 1982). Pairwise dissimilarities were calculated for all variables and the resulting dissimilarity matrix was used to generate a silhouette plot for the clusters (Rousseeuw 1987). Silhouette plotting graphically represents the degree to which individual sites fit well within their clusters, and how tight clusters are. Therefore it can be used as a tool for identifying individual sites which may require to be assigned to an alternative cluster, and for a generally assessment of cluster quality. Finally, a bivariate cluster plot was generated by partitioning the bioclimatic variables into 6 clusters around medoids, and then plotting the principal components (Reynolds *et al.* 2006). The results from the different clustering analyses applied here were synthesised to produce a final set of clusters for the study sites based on the environmental variables.

Growth

The individual *F. sylvatica* chronologies for all sites in the Multiregional Network were used for analysis to compare to the bioclimatic parameters dealt with above. The 46 individual site ring width index chronologies were truncated to the time-period common to all chronologies, 1966-2009, and used to calculate a matrix of Pearson's r correlation coefficients, giving pairwise comparisons for each site chronology. The data used in the analysis was non-prewhitened, as analysis using prewhitened chronologies failed to identify geographical structure in the network of sites. This is potentially due to prewhitening removing part of the signal resulting from regional scale response to climate. T-values were calculated using the correlation coefficients and sample sizes, resulting in a matrix of t-values, thus giving estimations of significance levels (Bailey & Pilcher 1973). In order to convert the t-values into a form suitable for cluster analysis, the corrected 1/t method detailed in García-González (2008) was used, with t-values of less than 1 assigned a value of 1. Thus, the linkage dissimilarity matrix of 1/t for all pairwise comparisons consists of values between 0 and 1.

Gleichläufigkeit (Glk) is a measure of the similarity of tree-ring series, which is based upon sign tests (Eckstein & Bauch 1969). Glk was calculated for pairwise comparisons of all chronologies giving a matrix of Glk for all combinations of chronologies. The matrix was then expressed as 1-Glk, converting it into a linkage dissimilarity matrix appropriate for cluster analysis. The dissimilarity matrices for Glk and 1/t were separately analysed by agglomerative hierarchical cluster analysis, with the unweighted pair-group average method of grouping used (Sneath & Sokal 1973). Therefore, the distance between any two clusters is the mean of the dissimilarities between the points in the two clusters. The results were plotted as a dendrogram, and interpreted with reference to the dendrogram previously generated using the bioclimatic variables.

The same 46 ring width index chronologies were used for a rotated principal components analysis (RPCA), in order to identify grouping of sites with similar growth patterns (Richman 1986; Cook *et al.* 2001). RPCA is a type of multivariate analysis derived from principal components analysis. Here, an eigenvalue decomposition of the 46 x 46 correlation dissimilarity matrix was performed, returning eigenvalues, loadings and degrees of fit. Eigenvalues were rotated using the normalised varimax method, in order to give results which are easier to interpret whilst retaining their orthogonality (Cook *et al.* 2001). The number of factors to extract was determined using the non-graphical Cattel's scree test: this test returns a numerical solution giving the number of factors that should be retained in a principal components analysis (Cattell 1966, Raîche *et al.* 2013). Factor loadings were plotted, and the clusters previously identified through hierarchical cluster analysis of the bioclimatic and growth data were examined. For sites where the results from cluster analysis of the bioclimatic parameters was unclear, or conflicted with known site environmental characteristics, the spatial arrangement of the clusters within the factor loading plots were examined. In these cases, sites were reassigned to different clusters where the Euclidean distance within the clusters could be minimised by reassignment. Factor loadings were also examined with sites classified into two groups only: range core (comprising of all range core sites, both temperate and continental) and range edge (comprising of the north western, dry southern and wet southern sites).

In order to assess the relative strengths of different clustering methods for site chronologies, one way ANOVA and regression analysis was performed on the RPCA factor loading outputs for the different clustering methods used (Cook *et al.* 2001). If the grouping of sites into a particular set of clusters is correct, the level of unexplained variance in the ANOVA should be reduced, compared to alternative clustering methods. Alternatively, if a clustering method using RPCA factor loadings to adjust the groups previously identified by cluster analysis of bioclimatic parameters is invalid, then the results should explain less of the variance. Thus, interpretation of the unexplained variance in the ANOVA and regression output can be used as an objective measure to identify the best grouping of sites. The grouping methods examined were: solely bioclimatic clusters (ANOVA), clusters amended by analysis of growth data (ANOVA), clusters simplified to range core or range edge (ANOVA), sites arranged in order of latitude only (regression), and lastly, clusters amended by analysis of growth data but with all southern range edge sites merged into one cluster (ANOVA). If the final assignment groups of sites based on the combination of bioclimatic and chronology analysis is valid, then the level of unexplained variance in the ANOVA of the adjusted clusters should be less than that of the other methods of assigning sites to groups. Alternatively, if the grouping method of using RPCA factor loadings to adjust the groups previously identified by cluster analysis of bioclimatic parameters is invalid, then the results should explain less of the variance.).

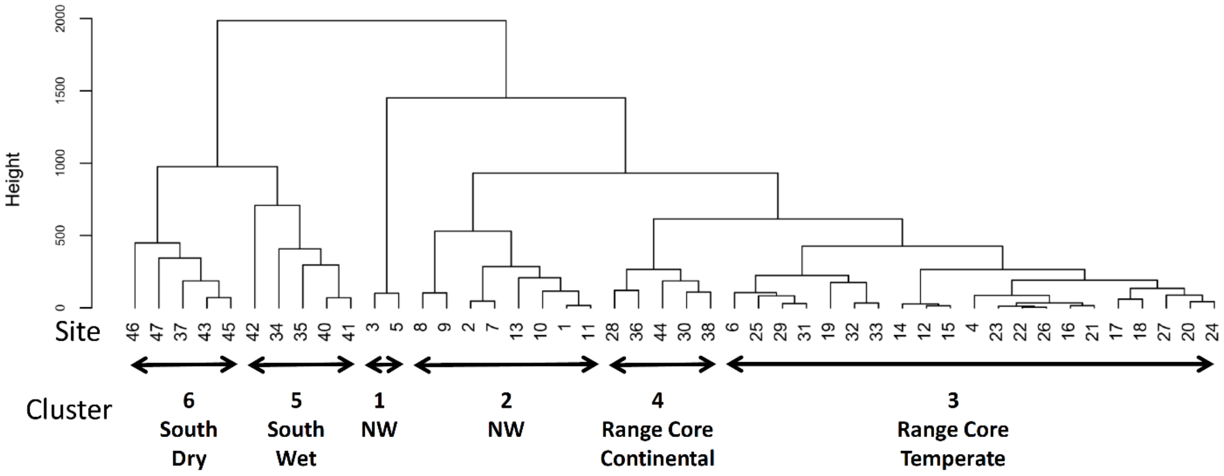

Figure 3.1: Hierarchical clustering dendrogram of bioclimatic variables for the 46 sites.

3.3 Results

Bioclimatic clusters

The results of agglomerative hierarchical clustering analysis, performed on the bioclimatic variables, are shown in figure 3.1. The groups identified were broadly consistent with geographic location, with nearby sites at similar elevations clustering together. Sites 3 & 5 formed the smallest cluster, due to the extreme rainfall at their locations in the west coast of Scotland (see chapter 2, figure 2.1). A second cluster comprises of a further 8 sites from the cool and wet zone of north and west UK (sites: 1, 2, 7, 8, 9, 10, 11, and 13). The third cluster contains the largest number of sites (sites: 4, 6, 12, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 29, 31, 32, and 33), comprising of 19 locations predominantly in South Eastern England, but also two from Eastern Scotland, 1 from Belgium, and 3 from Northern France. This zone has lower precipitation than the North West UK, with higher temperatures. The fourth cluster contains sites from continental Europe (sites: 28, 30, 36, 38, and 44), characterised by medium elevation, high temperature, and a large difference between summer maximum and winter minimum temperatures. The fifth cluster consists

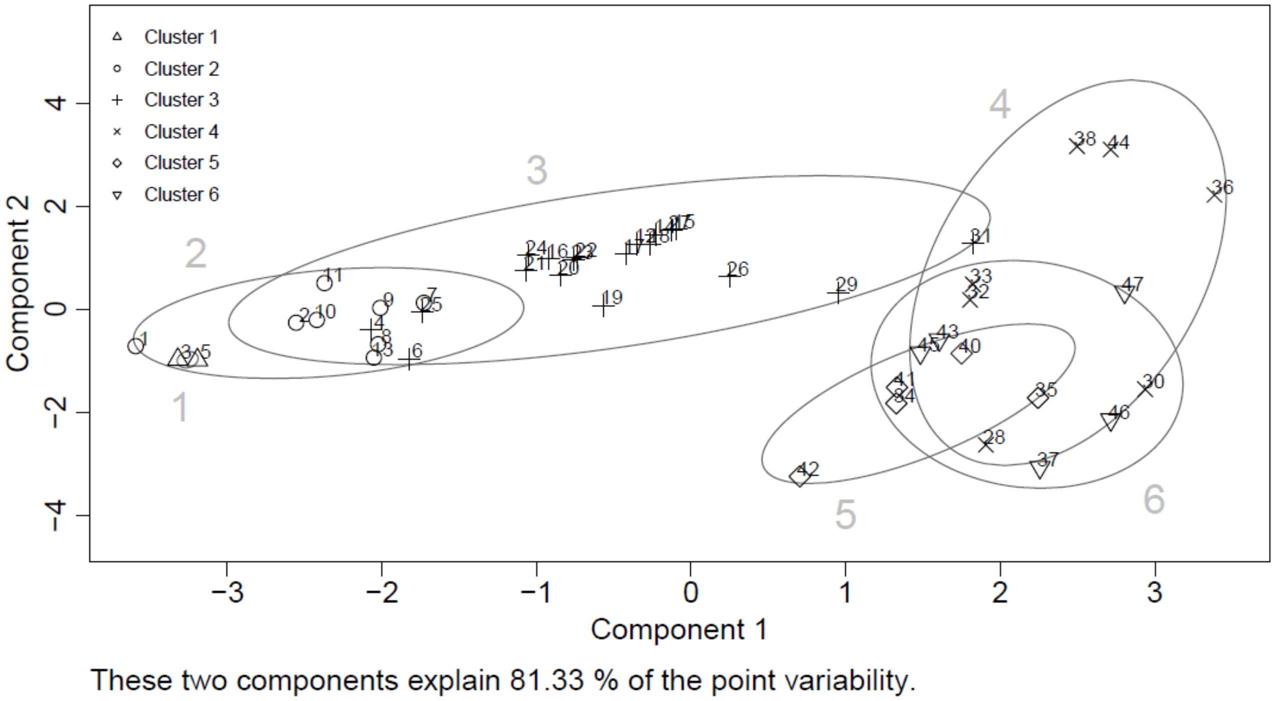

Figure 3.2: Bivariate cluster plot of the bioclimatic variables using k =6 clusters.

of southern sites at high elevation, with high precipitation, and a large difference between summer high and winter low temperatures (sites 34, 35, 40, 41, and 42). Finally, the sixth cluster has southern sites at high elevation, with the lowest precipitation of all clusters (sites: 37, 43, 45, 46, and 47).

The bivariate cluster plot (figure 3.2) broadly separates all sites into two groups; clusters 1, 2, and 3 in one group of cool, low altitude, northern sites; clusters 4, 5, and 6 in a second group of sites characterised by higher altitude, higher summer temperature and higher continentality. Within those two larger groups, individual groupings largely agree with the clusters identified by hierarchical cluster analysis. However, there is considerable overlap between some of the site clusters. Cluster 1 is contained entirely in the ellipse of cluster 2, thus indicating that both North West UK clusters could be combined. There is an area of overlap between clusters 2 and 3, giving reason to question whether sites 4, 6 and 25 were correctly assigned to cluster 3. These sites come from the north and west fringes

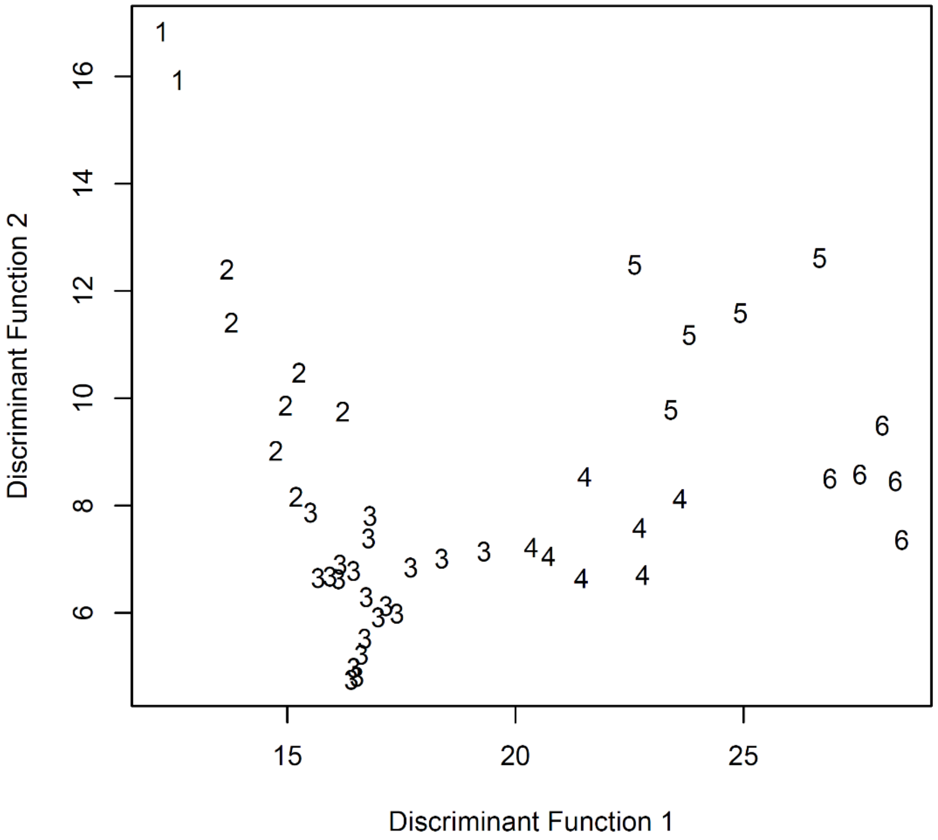

Figure 3.3: Discriminant projection plot of the clusters identified using hierarchical clustering analysis

of the geographical distribution of cluster 3. The greatest ambiguity comes from clusters 4, 5, and 6: figure 3.2 shows considerably overlap from these clusters. The discriminant projection plot created using discriminant coordinates, shown in figure 3.3, corroborates the clustering identified using hierarchical clustering analysis: all clusters are clearly differentiated.

The clusters identified by hierarchical cluster analysis were examined using a silhouette plot (figure 3.4). This is a graphical method which allows the validation of clusters by identifying any objects which fit poorly into their clusters, and for useful information on how well defined individual clusters are (Rousseeuw 1987). Mean cluster width gives an indication of the quality of the cluster, whilst individual object widths indicate whether individual objects (i.e. individual sites) are assigned to the correct cluster. Threshold values for interpreting the silhouette widths are; 0.71 to 1.0, strong structure; 0.51 to 0.70, reasonable structure; 0.26 to 0.50, weak structure; less than 0.25, no substantial structure (Kaufmann & Rousseeuw 1990). The mean silhouette width for all clusters was 0.66. Individually, all clusters had a silhouette width of ≥ 0.50, except for cluster 5, which had a cluster width of 0.28. Two sites had negative silhouette widths, indicating possible assignment to an incorrect cluster. Site 2 had a silhouette width of -0.261, however examination of bioclimatic variables (see appendix 1 for details of bioclimatic variables for each site) show that the site is too cold and wet to be considered a plausible member of a more southerly cluster. Site 35 had a silhouette width of -0.003, and could plausibly be

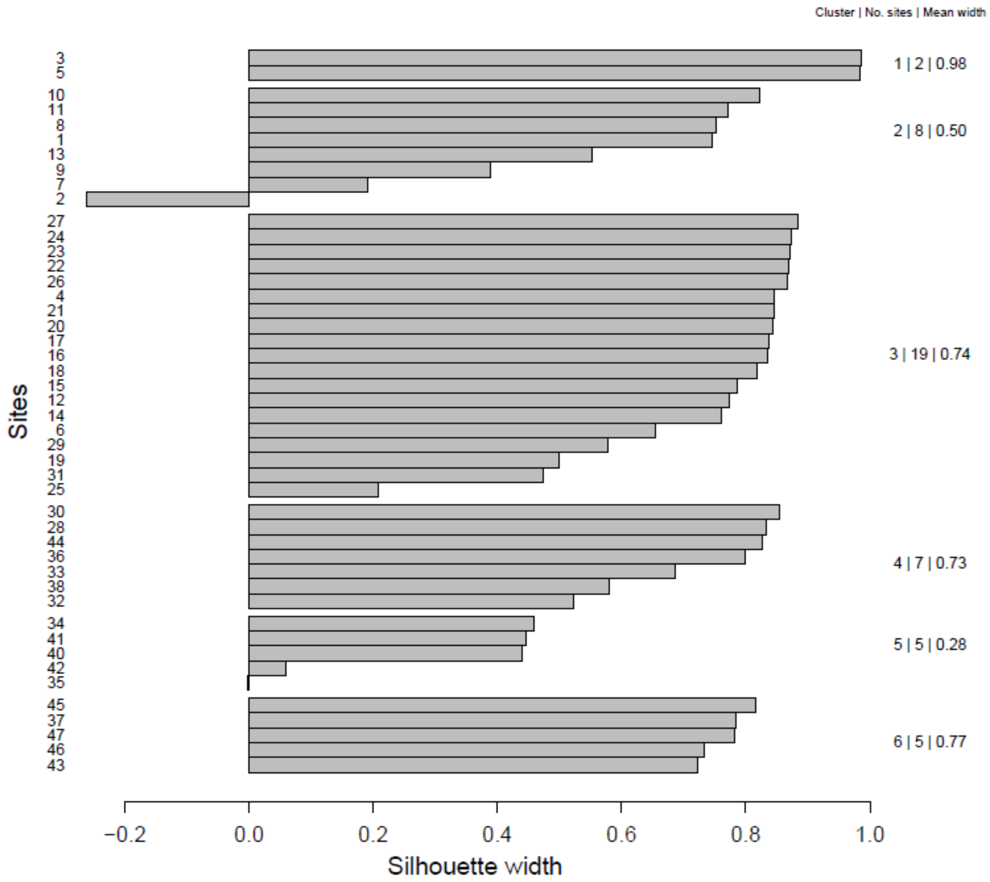

Figure 3.4 Silhouette plot for the clusters identified by hierarchical cluster analysis.

reassigned to cluster 4. Doing so marginally reduces the mean silhouette width for all clusters to 0.65, whilst reducing the silhouette width for cluster 4 to 0.44. Hence, the silhouette plot supports the clustering already identified as a small (n=5) number of sites displayed low or negative silhouette width, and reassignment of these did not result in tighter clusters. Combining the two north western clusters, 5 clusters were identified and will be henceforth referred to by the following names: North West (clusters 1 & 2), Core Temperate (cluster 3), Core Continental (cluster 4), Wet South (cluster 5), and Dry South (cluster 6).

Growth

Hierarchical cluster analysis of the *F. sylvatica* chronologies is presented in figure 3.5. The dendrogram derived from Glk (figure 3.5.A) shows two clusters mainly comprising the Core Continental sites, 2 clusters mainly of Core Temperate sites, one small cluster of North West sites, and one cluster containing mainly Dry and South sites. Many of the North West sites are poorly assigned. Finally, two other sites were not assigned to any of the clusters (sites 47 & 10), both of which are from the geographical periphery of the species range. The dendrogram derived from the 1/t growth model (figure 3.5.B) shows a distinct group incorporating, predominantly, both the Core Temperate and Core Continental sites. The two German sites, 28 & 30, are somewhat removed from this main cluster, reflecting their geographical isolation. 3 Core Temperate sites were not correctly identified (sites 6, 10, and 26). The sites from the geographical periphery of the species range (i.e. from the North West, Dry South and Wet South clusters) are not identified by clear clusters using this method. These sites are intermixed within the remainder of the dendrogram in clusters which make little sense in relation to the spatial distribution of the sites or to the bioclimatic characteristics of the sites. In general, many sites showed disagreement between clustering based on bioclimatic variables, or clustering based on growth data.

In order to use the growth clustering to reassign cluster for sites which were potentially misassigned based on bioclimatic variables alone, agreement between the Glk or 1/t models was examined. Where the two methods disagree regarding the re-assignment of sites relative to the clusters derived from the bioclimatic data (for example, sites 2, 7, 6 & 9), this was not considered to be strong evidence for re-assignment. However, where

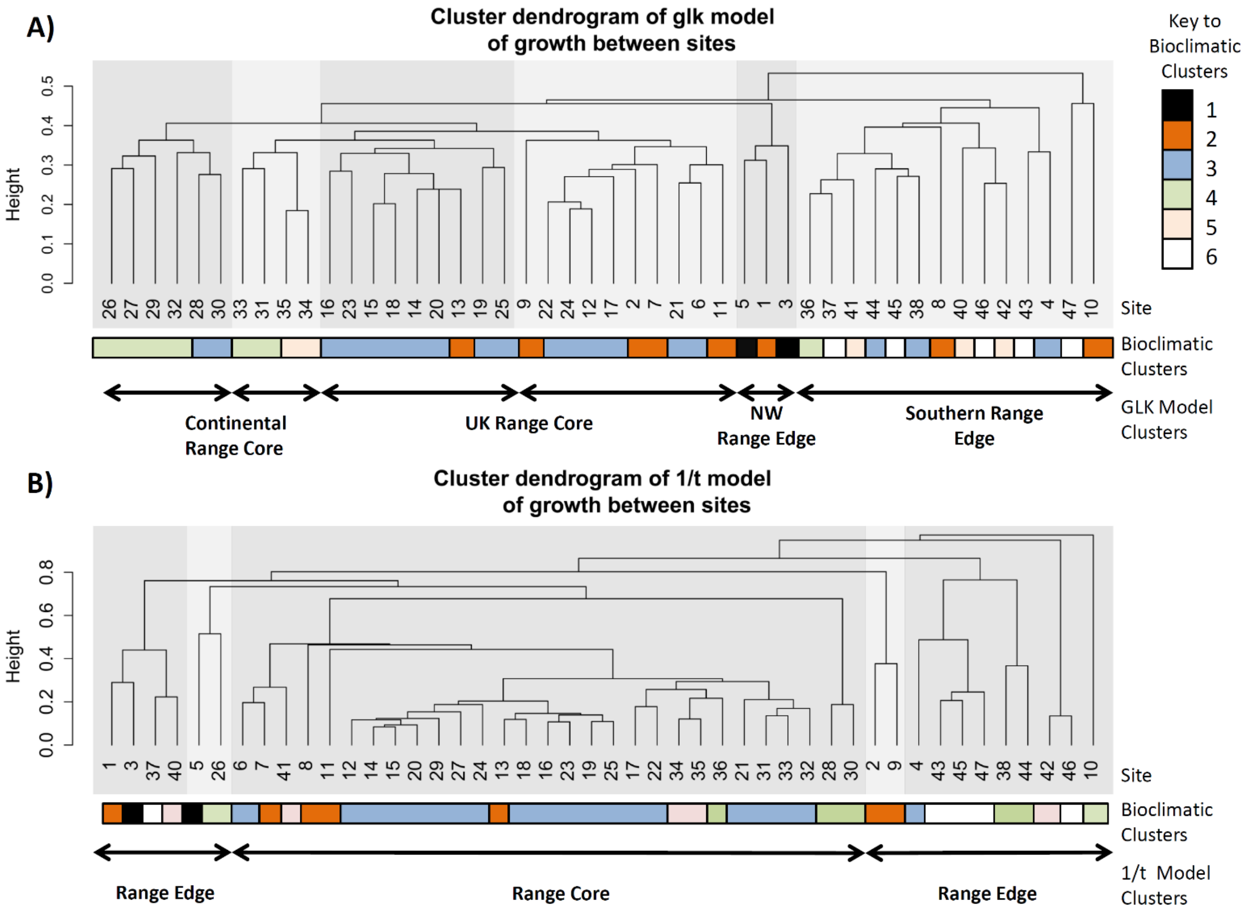

Figure 3.5: Dendrograms for the hierarchical cluster analysis of growth based on a) the Glk and b) the 1/t models. For comparison, the final clusters identified by analysis of bioclimatic variables are marked below each dendrogram.

hierarchical clustering of both ring width metrics agreed on a misclassification, sites were moved from their previous clusters. Thus, both Glk and 1/t clustering identify sites 34 and 35 as being Core Continental sites. This is consistent with the geographical location for the sites, and corrects the ambiguity in bioclimatic clustering identified for this region through bivariate clustering partitioned around medoids. Both methods identified site 13 as belonging to the Core Temperate cluster, rather than North West. Sites 38 and 44 were also identified as Dry South sites and reassigned – consistent with them being southern range edge relict populations at unusually low altitudes. Due to low altitude, bioclimatic analysis grouped them with Core Continental low elevation sites. Finally, both methods identify site 4 as a North West site, and not a Range Core Temperate site. The final clusters derived from joint analysis of bioclimatic and ring width data were: North West (sites 1, 2, 3, 5,7 ,8 ,9 ,10 , and 11), Core Temperate (sites 6, 12, 13, 14, 15, 16, 17, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 29, and 31), Core Continental (sites 28, 30, 32, 33, 34, 35, and 36), Wet South (sites 40, 41, and 42), and Dry South (sites 38, 37, 43, 45, 44, 46, 47). Figure 3.6 shows a map of the spatial distribution of these final clusters.

Cattel's scree test identified the optimal number of coordinates for RPCA analysis as 4, out of a total of 46 eigenvalues. Thus, RPCA utilised 4 significant components, which explained 29.6%, 10.6%, 9.1% and 7.2% of the total variance. The total sum of variance explained by the 4 factors was 57%. Figure 3.7 shows the 4 rotated components, with the amended clusters plotted along their latitudinal gradient, and with cluster box plots. Rotated component 1 displays the clearest separation between the clusters. Values increases with latitude: for the Dry South (mean loading = 0.06), Wet South (mean loading = 0.15), Core Continental (mean loading = 0.45), and Core Temperate (mean loading = 0.75). Component 2 decreases as latitude increases: for the Dry South (mean loading =0.54), Wet South (mean loading = 0.31), Core Continental (mean loading = 0.20), and Core Temperate (mean loading = 0.04). Component 4 performed best for separating the

Core Temperate (mean loading = 0.15) and Core Continental (mean loading = 0.46) clusters. Component 3 poorly differentiated between all clusters, except for the Wet South cluster. Notably, the North West cluster does not clearly separate from the others using any of the four rotated components. RPCA performed on sites classified as range core or range edge revealed strong separation between the two primarily with rotated component 1 (see figure 3.8): mean loadings were 0.67 for the range core , and 0.16 for the range edge sites. ANOVA and regression results for the different cluster groupings are presented in table 3.1, and are used here to assess the alternative sets of final clusters. For components 1 and 4, partitioning all sites into range core and range edge groups resulted in the least unexplained variance. Of the different clustering methods which

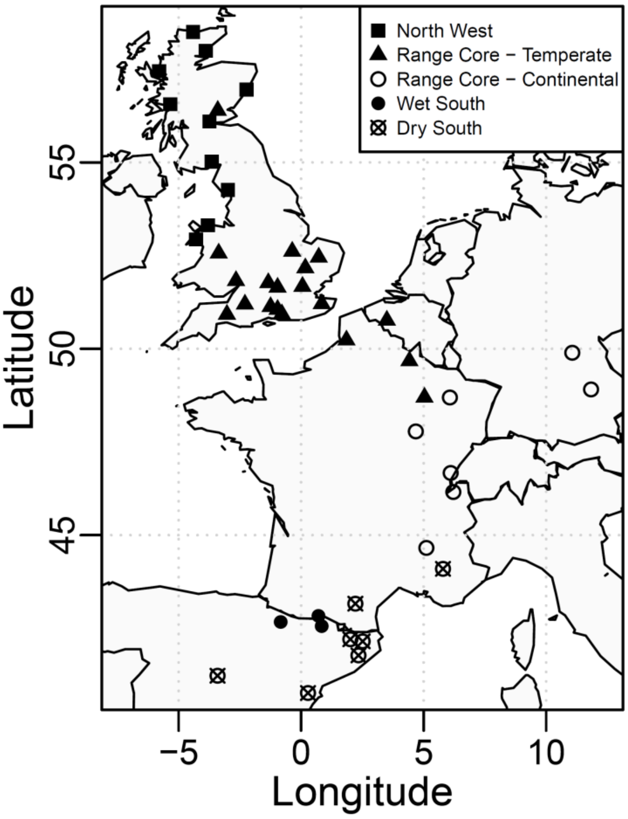

Figure 3.6: Geographical locations for the final clusters from the combined analysis of growth and bioclimatic variables.

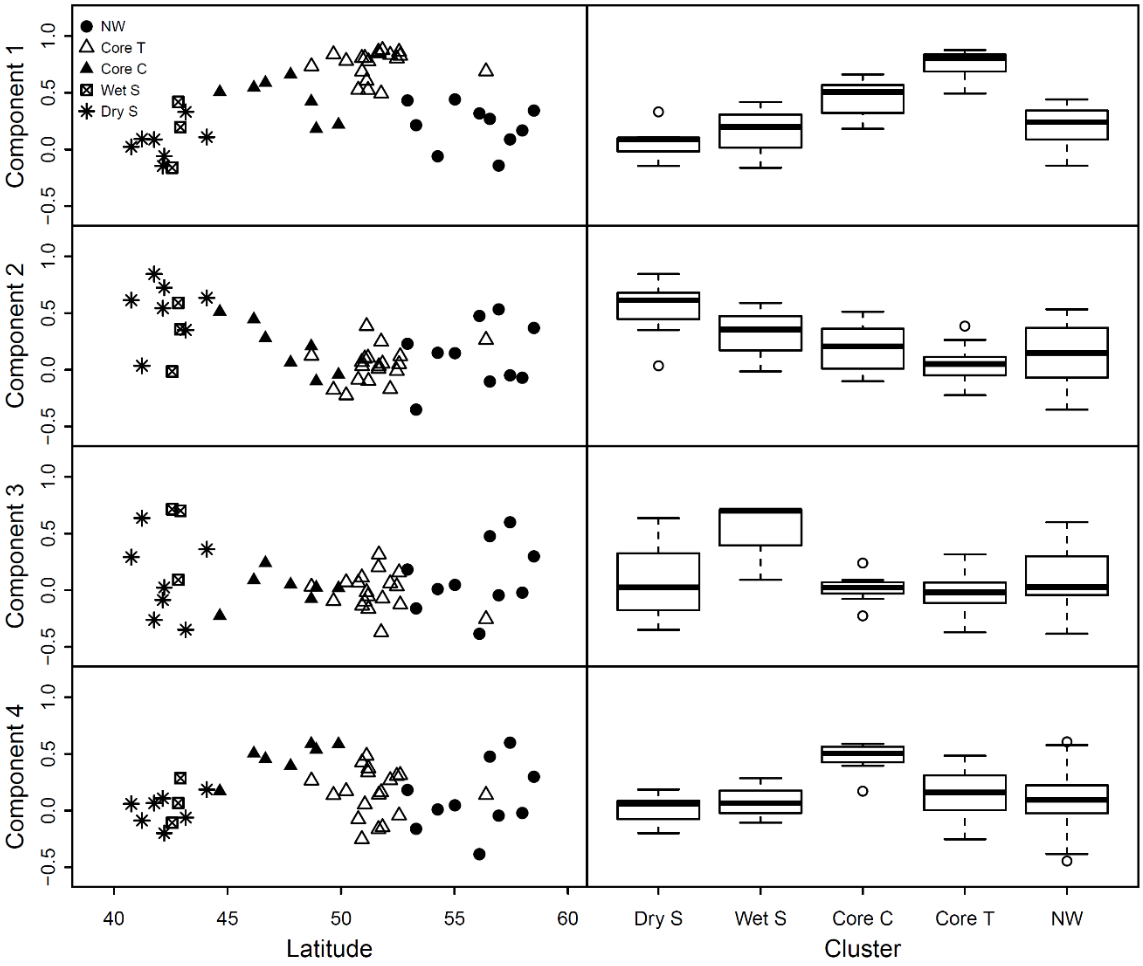

Figure 3.7: The 4 components of the RPCA analysis, with individual site factor loadings plotted against latitude on the left half of the graph. Each point represents an individual chronology. Boxplots on the right show comparisons in RPCA loadings between the 5 clusters: Dry South (Dry S), Wet South (Wet S), Core Continental (Core C), Core Temperate (Core T), and North West (NW).

were used to attempt to partition range edge and core sites further, the clustering derived from a synthesis of bioclimatic and growth data analysis had the highest F score for component 1. The original clusters from bioclimatic analysis alone have the highest F value for component 2. Despite this, due to the higher F score in component 1 (i.e. the

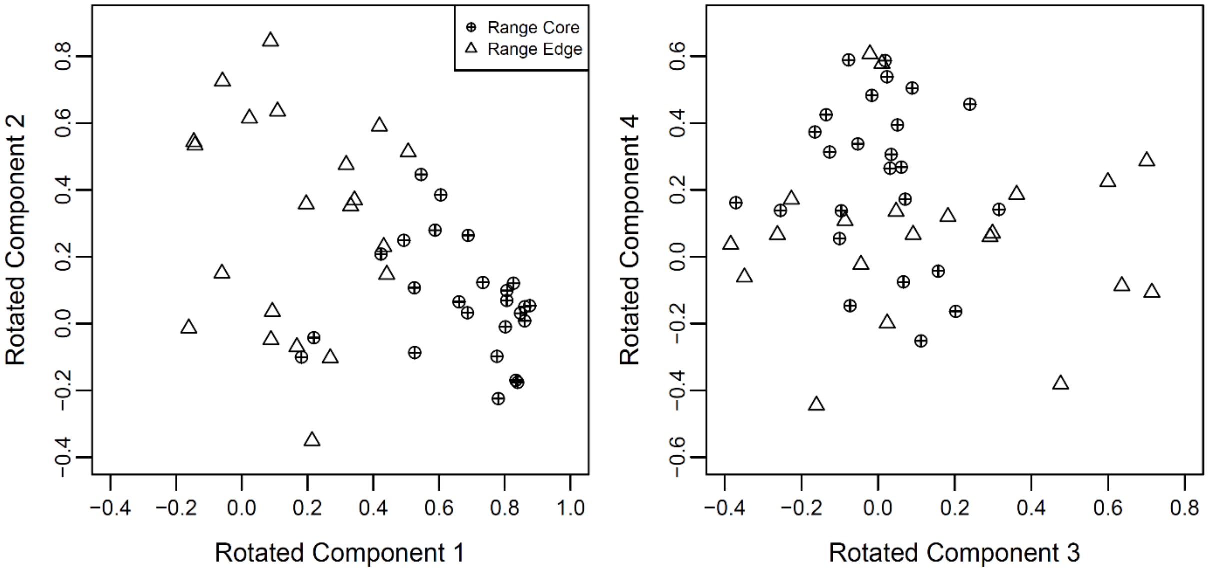

Figure 3.8: Scatter plots for the RPCA loadings for sites partitioned into range core and range edge groups.

component explaining most of total variance), the clusters using bioclimatic variables then amended by growth analysis are judged to provide the best results. Clustering with one group only at the southern edge, and simple arrangement of sites in order of latitude, performed worst.

Table 3.1 ANOVA and regression results of RPCA loadings for the different methods of site grouping. Values shown are F statistics.

Factors	Component 1	Component 2	Component 3	Component 4
Range Core / Range Edge	72.59***	10.98**	3.26 (NS)	5.5*
Bioclimate/Growth Clusters	7.72**	18.88***	1.22 (NS)	0.54 (NS)
Bioclimate Clusters	6.67*	19.48***	2.67 (NS)	0.03 (NS)
Southern Edge Simplified	4.67*	14.29***	1.66 (NS)	0.05 (NS)
Latitude	3.97 (NS)	11.94**	1.27 (NS)	0.12 (NS)

*** $p \leq 0.001$, ** $p \leq 0.01$, * $p \leq 0.05$, (NS) not significant.

Bioclimatic parameters

To examine the environmental characteristics of the clusters, the original bioclimatic variables which were selected for analysis are presented in figure 3.9, with clusters assigned to sites. Variables are shown plotted against latitude to highlight geographical features of the variables plotted are as follows. Sites north of 50° latitude were found at low elevation (< 300m), with the more southerly sites rising in elevation towards the southern range edge. At the southern edge, sites were found at up to 1545 m elevation, although some sites were much lower, where local site conditions permitted the persistence of relict populations. Variance in mean temperature is higher at lower latitudes, driven primarily by variability in winter low temperatures. Core Continental sites generally had lower winter minimum temperatures than the temperate sites.

Table 3.2 Cluster means of bioclimatic variables for the site groupings identified by bioclimatic variables alone, and those identified by a combination of growth and bioclimatic variables.

Cluster	Name	No. of sites	Elevation	Temperature	Precipitation	M	m	Ic	SPET
A)	Clusters identified by analysis of bioclimatic variables alone								
1	North West (1)	2	39 (± 21)	8.67 (± 0.04)	1944 (± 45.7)	17.77 (± 0.06)	1.16 (± 0.02)	10.16 (± 0.13)	91.25 (± 0.18)
2	North West (2)	8	91 (± 30.7)	8.85 (± 0.21)	1182 (± 63.3)	18.54 (± 0.46)	1.02 (± 0.23)	10.90 (± 0.33)	90.71 (± 0.83)
3	Range Core Temperate	19	134 (± 16.2)	9.45 (± 0.15)	723 (± 23.9)	20.79 (± 0.36)	0.69 (± 0.16)	12.80 (± 0.32)	94.57 (± 0.70)
4	Range core continental	7	463 (± 34.0)	10.04 (± 0.81)	754 (± 32.4)	24.55 (± 0.79)	-1.61 (± 0.95)	17.35 (± 0.49)	102.69 (± 1.13)
5	Wet Southern	5	1021 (± 124.9)	8.68 (± 0.32)	1125 (± 62.9)	23.36 (± 0.49)	-2.69 (± 0.30)	16.45 (± 0.49)	94.31 (± 1.62)
6	Dry Southern	5	1271 (± 74.6)	9.14 (± 0.50)	693 (± 53.9)	24.11 (± 0.52)	-2.34 (± 0.67)	16.61 (± 0.40)	94.07 (± 0.80)
B)	Clusters identified by analysis of growth and bioclimatic variables								
1	North West	10	55 (± 9.5)	8.75 (± 0.16)	1277 (± 127.5)	18.19 (± 0.34)	1.06 (± 0.15)	10.64 (± 0.24)	91.0 (± 0.54)
3	Range Core Temperate	19	150 (± 16.7)	9.51 (± 0.14)	729 (± 30.2)	21.01 (± 0.31)	0.67 (± 0.17)	12.97 (± 0.30)	94.7 (± 0.75)
4	Range Core Continental	7	543 (± 66.1)	8.91(± 0.55)	898 (± 76.6)	23.62 (± 0.66)	-2.87 (± 0.66)	17.81 (± 0.35)	100.7 (± 1.34)
5	Wet Southern	3	1185 (± 136.0)	8.83 (± 0.55)	1103 (± 71.5)	23.51 (± 0.82)	-2.26 (± 0.19)	15.72 (± 0.06)	92.2 (± 1.66)
6	Dry Southern	7	1050 (± 153.0)	10.07 (± 0.69)	681 (± 38.8)	24.76 (± 0.55)	-1.36 (± 0.78)	16.41 (± 0.30)	97.0 (± 1.98)

Elevation: site elevation (m); Temperature: annual mean temperature (°C); **Precipitation**: total annual precipitation (mm); **M**: mean maximum temperature of the warmest month; m: mean minimum temperature of the coldest month; **Ic**: continentality index; **SPET**: potential evapotranspiration of the summer months.

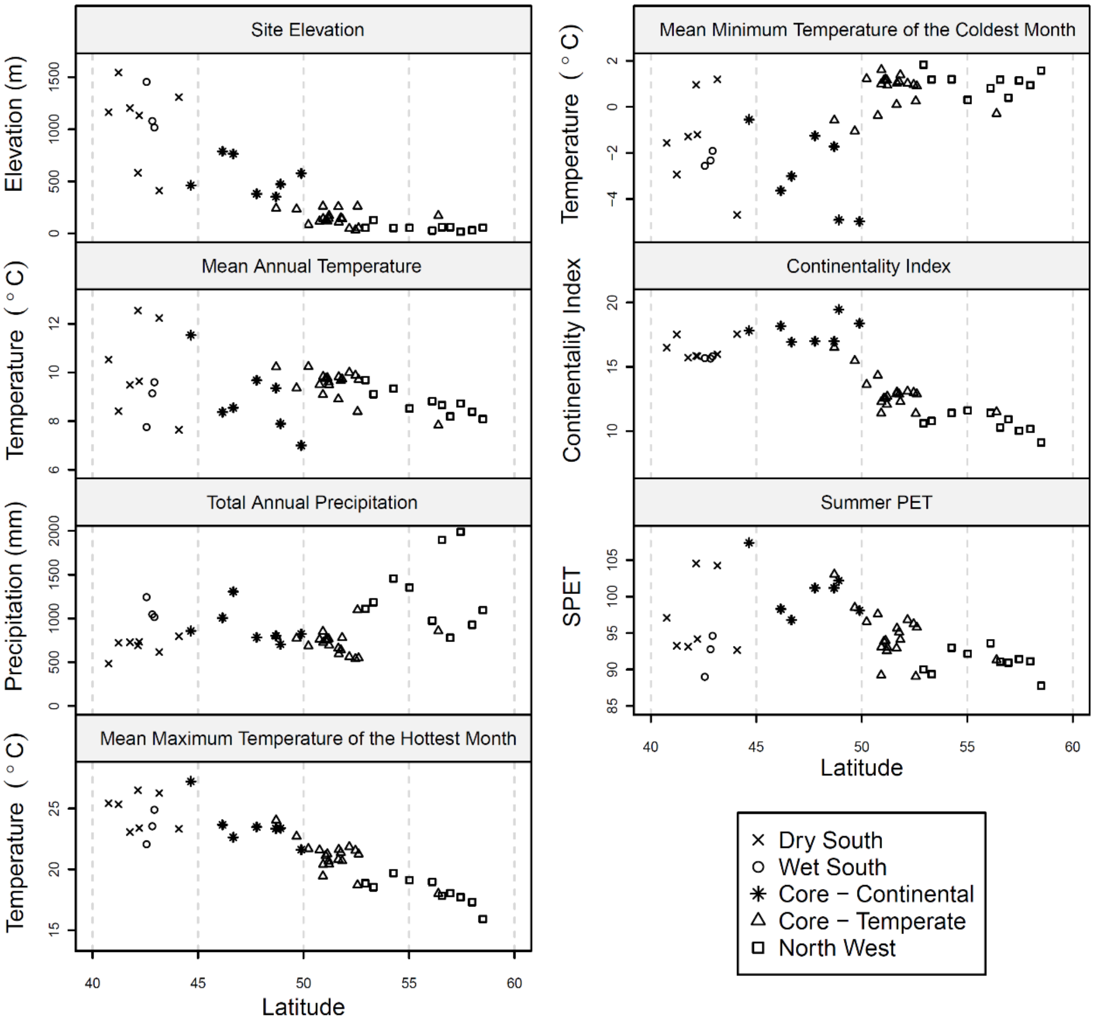

Figure 3.9: Bioclimatic parameters plotted against latitude for the 46 sites, with each site assigned to the final clusters.

Summer maximum temperatures show a linear trend from highs of around 25 °C at the southern range edge, down to around 18 °C in the far north. Broadly, precipitation declines with latitude, however there are some notable features here. Annual precipitation at the temperate range core sites was comparable (729 ± 30.2 mm) to that found at the dry southern range edge (681 ± 38.8 mm). Even at the southern range edge, a precipitation gradient exists east to west in the Pyrenean sites, with a small cluster of sites with high annual precipitation (> 1000 mm). Continentality index splits the sites into two groups: low for UK sites (i.e. above 50.9° latitude), and high for continental European sites. Finally, summer PET generally decreases as latitude increases, with the exception of a cluster of high elevation sites at the southern range edge, which have low values.

3.4 Discussion

An extensive network of bioclimatic and ring-width data was used to identify spatial structure in site conditions and tree growth. The findings of this study indicate that there is evidence for the partition of this network into range core and range edge groupings. At a finer scale (but less well supported by the evidence), the range core can be subdivided into two further groups, and the range edge into 3 groups. Using environmental data, analysis using hierarchical clustering, partitioning around medoids and a dissimilarity matrix was combined to support the partitioning of the sites in the Multiregional Network into 2 clusters geographically located in the core of the species range, and 3 clusters comprising range edge sites. Analysis of tree growth data showed a clear distinction between a well-defined range core, and a more poorly defined range edge. Based on a combination of the findings of both tree-ring and climate analysis, two clusters exist within the range core. One cluster in the temperate west (with low precipitation, and a narrow intra-annual temperature variation), and another in the continental portion of the network (with higher precipitation, and a greater intra-annual temperature variation). The range edge sites can be split into 3 clusters: one in the far north west of the network (with very high precipitation), and two at the southern range edge (one hot and wet, the other hot and dry).

Increasing mean temperatures, altered precipitation regimes and increases in the severity and frequency of extreme events can be expected to result in rapid shifts in plant distribution, which have largely been observed in mountain treelines (Peñuelas *et al.*

2007; Jump, Matyas & Peñuelas 2009). However, at species' trailing edges, variation in topography and climate can ensure the persistence of a limited number of fragmented relict populations whilst climatic conditions in the wider landscape become ever less favourable (Bush 2002; Colwell *et al.* 2008). This study demonstrates the effects of this variation in topography and climate at the southern range edge for *F. sylvatica.* In the Iberian Peninsula, a growth and climate cluster was identified comprising of sites from the central and Western Pyrenees, which were characterised by annual precipitation in excess of other southern and range core populations (see table 3.1). Here, annual precipitation was approximately double the reported physiological lower threshold for *F. sylvatica* (Bolte, Czajkowski & Kompa 2007). The effect of topographical heterogeneity at the southern range edge was demonstrated by 3 sites at lower than 45° latitude at elevations of around 410 to 580 m (see figure 3.9). For these three, the continued persistence of *F. sylvatica* populations depends on features not captured by the data presented in this chapter. At one (site 36, Massif de Saou), *F. sylvatica* exists on the northern side of a perched limestone syncline with surrounding steep cliffs: a natural sheltered amphitheatre which supports temperate forest whilst the region largely has Mediterranean influenced vegetation. At another (site 38, Massif de la Malapere), *F. sylvatica* is restricted to small, sheltered and humid gorges, within a *Quercus ilex* and *Quercus pubescens* forest. Finally, at the last of the three (site 44, La Garrotxa), *F. sylvatica* exists at a relatively low altitude in a valley: the district has a humid Mediterranean climate, and local topography favours temperature inversions which has resulted in an inverse altitudinal distribution of vegetation (Isamat *et al.* 2008). However, despite this climatic and topographical variability between sites, clear differentiation of the southern sites into clusters based on tree growth was problematic. This could be a consequence of the low number of chronologies contributing to southern clusters. For example, only 3 sites belonged to the Wet South cluster. Alternatively, regional synchronisation in drought occurrence could result in a regional tree-ring signal which confounds attempts to partition the sites into different clusters.

According to Bolte, Czajkowski and Kompa (2007), *F. sylvatica* cannot tolerate precipitation of less than 500mm per year and July mean temperatures of greater than 19 °C. All sites within the network had precipitation > 500 mm, except one (site 47, La Senia) which had 484 mm annual precipitation (see figure 3.8). This site is a relict population existing at the very top of a mountain range with many visibly damaged individuals, thus supporting rather than contradicting Bolte's proposed climatic requirements. However, several southern range edge sites had mean temperature for the warmest month (July) above the 19 °C threshold (see appendix 1). The first three of these sites demonstrate the ability of site topography to create clement climatic conditions for a site, allowing the persistence of *F. sylvatica* in a largely unsuitable surrounding region (sites 36, 38, and 44). The final site is an example of a southern range edge population isolated in a location where climate conditions are already beyond the lower threshold of that which can be expected to support *F. sylvatica* population, and where no altitudinal migration is possible (site 47).

A similar precipitation gradient to that in the Pyrenees exists in the south eastern portion of the southern range edge, where a large region of high (>1000 mm per year) precipitation stretches from the eastern Alps, down the eastern Adriatic coast to the north west of Greece (Steinhauser 1970). The identification of at risk southern range edge forests is important due to their significance for the conservation of genetic diversity and the suites of associated species that these relict populations support (Hampe & Petit 2005). These wet regions identified are trailing edge regions where environmental conditions can be expected to favour the continued persistence of *F. sylvatica* populations, and where populations can be expected to be at less risk than those in the drier Mediterranean regions such as the Eastern Iberian Peninsula, Italy, or in north of Greece.

At the northern edge of the Multiregional Network, many of the sites supporting *F. sylvatica* are well beyond the assumed native range in the south east of the UK (Birks 1989; Pott 2000). The North West cluster consists entirely of sites beyond this range limit. However, the native range does not represent a limitation imposed by climatic conditions, instead it represents the extent of northwards post-glacial colonisation by around 1000 years before present (Birks 1989). Human intervention (through plantation, and subsequent naturalisation) has since significantly influenced this distribution, and even the most northerly sites are not limited by the threshold minimum of -3 °C mean January temperature (Bolte, Czajkowski & Kompa 2007). *F. sylvatica* can be found at more extreme latitudes (up to 60.6°) on the oceanic west of Norway, which is also most likely due to human intervention (Myking, Yakovlev & Ersland 2011). Thus, the North West cluster does not represent a true northern range edge for *F. sylvatica,* in the sense that it is not a region where the species is regularly challenged by extreme winter cold. The cold limitation which prevents the colonisation or successful planting of the species at the Northern Scandinavian or Eastern European limits of its range is not present in this Multiregional Network. Instead, the North West cluster represents a region where the species exists with high precipitation and low evapotranspiration, and consequently where extreme drought stress can realistically be expected to be a particularly rare occurrence. Therefore, the difficulty experienced in characterising the northern cluster tree-ring chronologies using RPCA analysis and hierarchical cluster analysis could represent a lack of regional drought driven climatic signal. Alternatively, the North West region consists of populations where *F. sylvatica* has arrived due to human translocation, and come from unknown provenances. Heterogeneous responses of different provenances to regional climate could contribute to the lack of clear regional signal in the chronologies (Savva *et al.* 2002).

The range core portion of the network is the most clearly defined in this study. Separation into temperate and continental clusters reflects the well-known effect of winter cold, which is mainly experienced by *F. sylvatica* sites within the continental portion of the network (Bolte, Czajkowski & Kompa 2007). Additionally, in attempts to characterise forests over such a wide geographical area, regional temporal patterns in climate events such as droughts will affect tree ring patterns (Brubaker 1980). However, the same clustering was apparent using bioclimatic data, in which temporal patterns were subsumed into mean values. The low precipitation values for the range core temperate cluster supports results which predict growing challenges for *F. sylvatica* as a commercial forestry species in this region (Broadmeadow, Ray & Samuel 2005).

Clustering analysis here has demonstrated its utility by revealing ecologically meaningful groups, particularly within the range core and trailing range edge. The further development of regional networks in areas of high conservation value could aid the assessment of prospects for individual sites in a changing climate. However, given the scarcity of conservation resources, the emerging dilemma may be whether to target the most at risk sites, or to focus on preserving sites where conditions are more conducive to long-term survival. The regional units identified by the clustering analyses will be examined in greater detail in the following chapters.

4. Climate Growth Relationships and the Effects of Drought

This chapter will examine the climate response of the sites within the Multiregional Network, and any characteristic geographical patterns. Focusing on the effects of drought, temporal and spatial structure in drought occurrence will be identified. Years in which anomalous low growth occurred will be identified using pointer year analysis, and used to study factors driving the response of *F. sylvatica* to drought.

4.1 Introduction

Climate change predictions for Western Europe forecast increases in temperature, changes in hydrology, and an increase in the occurrence and intensity of extreme climatic events (Schar *et al.* 2004; IPCC 2007; Harris *et al.* 2010). These changes can be expected to have an increasing effect on forests. Increasing drought has already been implicated in the recent decline of forests, particularly in the Mediterranean region where limited water availability provides a strong constraining factor on plant growth (Sarris, Christodoulakis & Körner 2007; Linares, Delgado-Huertas & Carreira 2011; Sanchez-Salguero *et al.* 2012).

Fagus sylvatica is a species which is considered to be particularly drought sensitive. It is one of Europe's most significant late succession, forest forming, tree species which is a frequently dominant component of around 17 million hectares of forest (Petit & Hampe 2006). Dendroecological studies from the southern edge of the species' range have shown a reduction in growth as a response to elevated drought stress associated with climate change, which is expected to result in a reduction in available habitat area in this mountainous part of the species' range (Jump, Hunt & Peñuelas 2006; Piovesan *et al.*

2008). Southern range edge populations are particularly susceptible to negative effects of climate change as they are often living at the edge of the species climatic niche (Jump, Cavin & Hunter 2010). Additionally, growth decline has been reported at a regional scale within the range core of the *F. sylvatica*, and has been attributed to increased drought stress (Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010). However, this range core response is not universal, with increasing radial growth trends also being reported (Dittmar, Zech & Elling 2003). A study of forest ecosystem response to the extreme drought of 2003 in continental Europe reported a reduction in net ecosystem production, with *F. sylvatica* notable for its susceptibility (Granier *et al.* 2007). The study covered most major European forest ecosystem types over a wide geographical range, with monitoring stations in Atlantic, central, Mediterranean and Fennoscandian regions. This reduction in productivity is predicted to be coupled with changes in the future distribution of the species, with modelling studies forecasting an increase in the spatial segregation of *F. sylvatica* with competitor species under climate change scenarios, and a reduction in habitat suitability and biomass yield (Broadmeadow, Ray & Samuel 2005; Meier *et al.* 2011).

The study of the growth response of *F. sylvatica* climate and drought is important, as its sensitivity marks it as a useful indicator species. Given the drought sensitivity of the species, and developing drought threats, our understanding of the relationship between climate and growth of the species needs to transcend the limitations of case studies and regional scale studies. Individual case studies, whilst valuable, are often subject to a publication bias towards unusual results. Whilst regional scale studies avoid this bias by combining chronologies from multiple sites, context is still missing regarding how the region compares to climatic gradients affecting the species across its range. The large number of sites in the Multiregional Network enables a biogeographical view of climate-growth relationships, beyond potentially idiosyncratic population level responses.

This chapter aims to address the following questions: 1) what are the characteristics of the climate growth relationship for *F. sylvatica* across its range in Western Europe, and is there geographical variation in this relationship? 2) To what extent does absolute aridity of a forest stand affect the drought response at the site, compared to drought events which are extreme relative to mean site conditions? 3) In years where drought causes large reductions in growth, what factors affect the severity of the drought damage? In order to address these questions, a combination of classic dendroecological climate-growth analysis will be combined with pointer year analysis, and drought index analysis using generalised additive modelling. These methods will be applied to the Multiregional Network, allowing the identification and analysis of specific drought events which resulted in growth reductions for forest stands.

4.2 Methods

Climate-Growth Analysis

In order to establish the relationships between climate and the resulting growth response of *F. sylvatica*, a climate-growth analysis was performed using annual ring width index chronologies (as calculated using the methods detailed in section 2.4) and climate data (temperature and precipitation, derived from the gridded climate data in section 2.8) for all 46 individual sites within the Multiregional Network. Monthly climate data was used, comprising a 17 month period from May of the year prior to ring formation, up until September of the year of ring formation. Therefore, the climate features considered in the analysis include the previous year’s growing season, intervening winter/spring, and the growing season during the year of ring formation. This method of analysis allows an evaluation of any effects of preconditioning by climate before the growing season (Cook

& Kairiukstis 1990; Biondi & Waikul 2004). Pearson's correlation coefficients were calculated between each of the 46 sites in the Multiregional Network and the 34 climate variables, i.e. 17 months for both temperature and precipitation (Blasing, Solomon & Duvick 1984). Significance was tested by the bootstrap method, using 1000 bootstrap replicates and with 95% confidence intervals, using the R package bootRes (Zang & Biondi 2013). Results for each of the sites were then partitioned into the 5 biogeographical regional clusters identified by analysis of the climate and growth data in chapter 3. Mean correlation function values were calculated for each cluster, in order to identify the climate responses of each group.

Ring-width Indices

Tree ring chronologies for the 46 sites in the Multiregional Network were generated (see section 2.4), and presented for the identification of regional event years, and growth variability. Chronologies were grouped according to the regional clusters identified by analysis of the climate and growth data in chapter 3, and results plotted. The mean series intercorrelation (rbar) for each region was calculated, as a measure of within region homogeneity.

Drought Index

Gridded climate data (see section 2.8) was used to identify drought by calculating the Standardised Precipitation-Evapotranspiration Index (SPEI) (Vicente-Serrano, Beguería & López-Moreno 2010). SPEI is a multi-scalar drought index, which allows the user to calculate drought with individual monthly values derived from a time-period defined by the user, and has been demonstrated to be an effective tool in the study of tree responses to climate (Pasho *et al.* 2011). The index is calculated using PET and precipitation, and so includes the effects of both temperature and water balance. This measure of drought is relative to conditions at the site for which it is calculated, with a value of 0 representing mean drought conditions, and a standard deviation of 1. SPEI was calculated for all sites in the Multiregional Network, using a 12 month time scale (therefore encompassing both current and previous year water availability), with PET derived from the Thornthwaite equation (Thornthwaite 1948), log-logistic distributed indices, and with parameters fitted using unbiased probability weighted moments. SPEI is a measure of drought at a site relative to mean conditions at that site. For a measure of drought which enables the comparison of drought severity between sites, annual summer aridity index (see section 2.8) was calculated for each site over the period 1950-2010.

Pointer Years

Identification of pointer years (years where an abrupt growth increase or decrease is recorded in a tree-ring chronology relative to mean growth) can be used to facilitate specific study of the environmental conditions which influenced the growth of a population of trees in that year (Schweingruber *et al.* 1990; Lebourgeois *et al.* 2005; Neuwirth, Schweingruber & Winiger 2007). For the purposes of identifying pointer years, annual ring width values for each individual tree within each site chronology were transformed into Cropper values, through division by their 11 year moving average values (Cropper 1979). The resulting values were then normalised to a mean of 0 and standard deviation of 1. In order to evaluate the Cropper values, the objective threshold values described by Neuwirth, Schweingruber and Winiger (2007) were followed, namely “extreme” > 1.645, “strong” > 1.28, and “weak” > 1, as derived from the probability density function of the standardised normal distribution. The weak threshold value was used, to maximise the number of years for further analysis. Where ≥ 50% of all trees within a chronology exceed the defined threshold, the year was considered a pointer year for that chronology.

In order to identify which pointer years coincided with drought periods, each pointer year identified above within the time period 1951-2004 was compared to SPEI values during the critical growing period of May – August for that year. Where SPEI fell below a threshold value of -1 in any of those 4 months, the pointer year was classed as a drought induced pointer year. This does not account for the fact that during any one of these event years, multiple interacting factors will have influenced tree growth.

Resilience Indices

The effect of disturbance, such as drought, on tree growth can be evaluated using a series of indices described by Lloret, Keeling and Sala (2011), which have the advantages of being easy to calculate and intuitive to understand. These indices quantify different components of tree resilience in response to low growth events, and will be used here to describe the impact of drought events for the drought induced pointer years. The indices evaluate tree growth during a disturbance relative to growth in the 5 years before and after the disturbance, as follows:

$$Pre\ Drought = \bar{x}\{BAI_{i-5}, BAI_{i-4}, \ldots BAI_{i-1}\} \tag{4.1}$$

$$Post\ Drought = \bar{x}\{BAI_{i+1}, BAI_{i+2}, \ldots BAI_{i+5}\} \tag{4.2}$$

$$Drought = BAI_i \tag{4.3}$$

where *i* is the disturbance year, in this study the drought induced pointer year. Resistance is an index describing the severity of the impact of the disturbance in the year it occurred, with low values corresponding to large reductions in growth:

$$Resistance = Drought/Pre\ Drought \tag{4.4}$$

Recovery measures the ability to recover from disturbance relative to its severity, with high values reflecting a large increase in growth post disturbance relative to performance during the disturbance:

$$Recovery = Post\ Drought/Drought \tag{4.5}$$

Resilience is defined as the ability of the system to regain pre-disturbance levels of growth, assuming stable climate between the 5 year periods either side of the disturbance. Low values corresponding to low resilience:

$$Resilience = Post\ Drought/Pre\ Drought \tag{4.6}$$

Relative resilience is the resilience weighted by severity of the disturbance in the event year, high levels of damage in the disturbance event act to reduce this index:

$$Relative\ Resilience = (Post\ Drought - Drought)/Pre\ Drought \tag{4.7}$$

The resilience indices above were calculated for each drought induced pointer year. Pointer years which occurred within 5 years of each other were omitted. Where drought induced pointer years occurred for a site in successive years, the mean BAI of the two years was used to give a single drought BAI for use in calculating resilience indices.

Given the large geographical range covered by the Multiregional Network, spatial and temporal heterogeneity in both the occurrence and severity of drought episodes makes the comparison of individual drought years across sites problematic. Therefore, all drought induced pointer years were pooled and individual disturbance indices calculated for each event at each site analysed using generalised additive modelling (GAM), in other words a generalised linear model estimated using quadratically penalised likelihood estimation (Zuur *et al.* 2009). GAM enables the analysis of response variables with nonlinear-relationships to the explanatory variables, thus fitting a smoothing curve through the data based on one or more smoothing functions. The GAM was fitted using the mgcv package in R (Wood 2011). The values for the smoothing parameters were estimated using generalised cross-validation, a method which is a modified version of ordinary cross validation and has been shown to have computational advantages (Zuur et al. 2009). Values of effective degrees of freedom (edf) are output to indicate the degree of linearity of the smoother: higher values of edf representing strongly non-linear smoothing splines. Results were smoothed using a regression spline with shrinkage. Explanatory variables used were; chronology age in the year of disturbance; latitude; gini coefficient; elevation; aridity, as described by mean summer aridity index (SAI) 1950-2012 (see section 2.8); relative drought intensity, described by the minimum SPEI in May-August of the drought year; absolute drought intensity, described by SAI of the drought year; relative drought intensity of the previous summer; absolute drought intensity of the previous summer. The explanatory variable gini coefficient is a measure of variability in a data set, see Biondi & Quedan (2008a) for a full description of its use as a robust replacement for mean sensitivity in tree-ring analysis. It is calculated as the sum of the absolute difference between all pairs of observations in a data set, scaled by sample mean and sample size according to the equation:

$$Gini = \frac{\sum_{i=1}^{n} \sum_{j=1}^{n} |x_i - x_j|}{n(n-1)} \tag{4.8}$$

The model terms were checked for colinearity and the model was refined to the significant terms using a backwards stepwise selection process.

4.3 Results

Climate-Growth Analysis

The climate-growth correlation functions for the site clusters are shown in figure 4.1. Correlation functions for the North West region failed to display any coherent regional signal in growth response to climate, with high between site variability. There are no apparent features of climate strongly influencing year to year variation in growth within this cluster. The Core Temperate region has a strong regional signal, with a negative association between growth and temperature in the summer prior to ring formation. A weaker effect of current year temperature exists. Summer precipitation, both in the current and prior years, positively influences growth. For the Core Continental region, summer temperature is negatively correlated with growth, both in the previous and current years. High summer precipitation in the current growing season boosts growth, whilst low precipitation results in lower growth. Whilst the Core Continental region has a largely coherent signal, variability in site correlation coefficients is high for winter precipitation, with significant positive correlations with winter precipitation in greater than one third of sites. The correlation functions for both the Core Temperate and Core Continental groups indicate pronounced sensitivity to drought conditions. The Wet South region has low variation in correlations between the sites, however the sample size is low

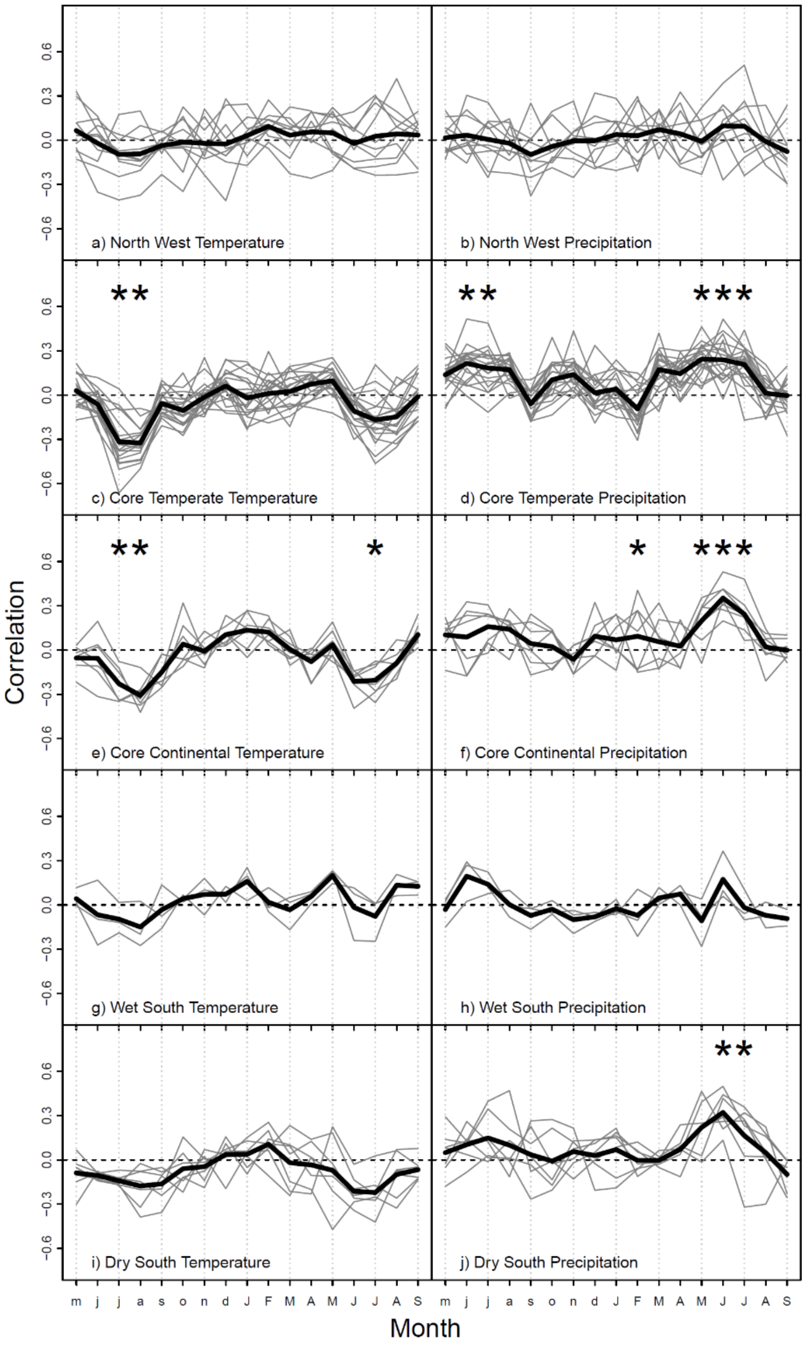

*Figure 4.1 Climate growth analysis results, showing correlation coefficients for annual radial growth and climate factors in the previous and current year. Climate data used is for the period 1950-2009, and monthly factors plotted on the x-axis are May to December of the year prior to ring formation (lower case m – d), and January to September in the year of ring formation (upper case J – S). The 46 sites in the Multiregional Network are plotted in 5 regional groups. Months where significant correlations occurred for greater than 1/3 of sites in each region are marked *.*

(number of sites = 3, see table 3.1 for sample sizes for the regions). Common *F. sylvatica* climate growth relationships are visible, i.e. negative effects of summer temperature, and positive effects of summer precipitation. However, the strength of these relationships is weak: Wet South sites show no indications of being strongly affected by drought. Finally, for the Dry South sites, climate-growth correlations generally have high variability between sites. A strong region wide signal of positive relationship between summer precipitation and growth exists. Negative correlations for summer temperature (previous and current years) are visible, but weak.

Ring-width Indices

Ring width indices are shown, grouped by biogeographical cluster, for the period common to all chronologies (1966-2009) in figure 4.2. Corroborating the lack of regional signal described in the climate growth analysis above, the ring width indices for the North West display high variability between sites (rbar = 0.101), with most years having sites recording both high (index values > 1) and low (index values < 1) growth. Negative growth indices occurred for all sites in this cluster in 1976, which was an exceptional drought year over much of Western Europe. The minimum values of ring widths during periods of low growth were not extreme, with all index values for all sites being greater than 0.5. The Core Temperate region has the highest within-region homogeneity in growth (rbar = 0.575), with frequent synchronised growth reductions throughout the period shown. For example, near universal negative ring width indices were recorded across the cluster for the years 1976, 1989-90, 1995 and 2004. Index values for individual sites were frequently below 0.5 during these synchronised growth suppressions. The Core Continental region shows similar, although weaker, characteristics. Ring index values were higher, although

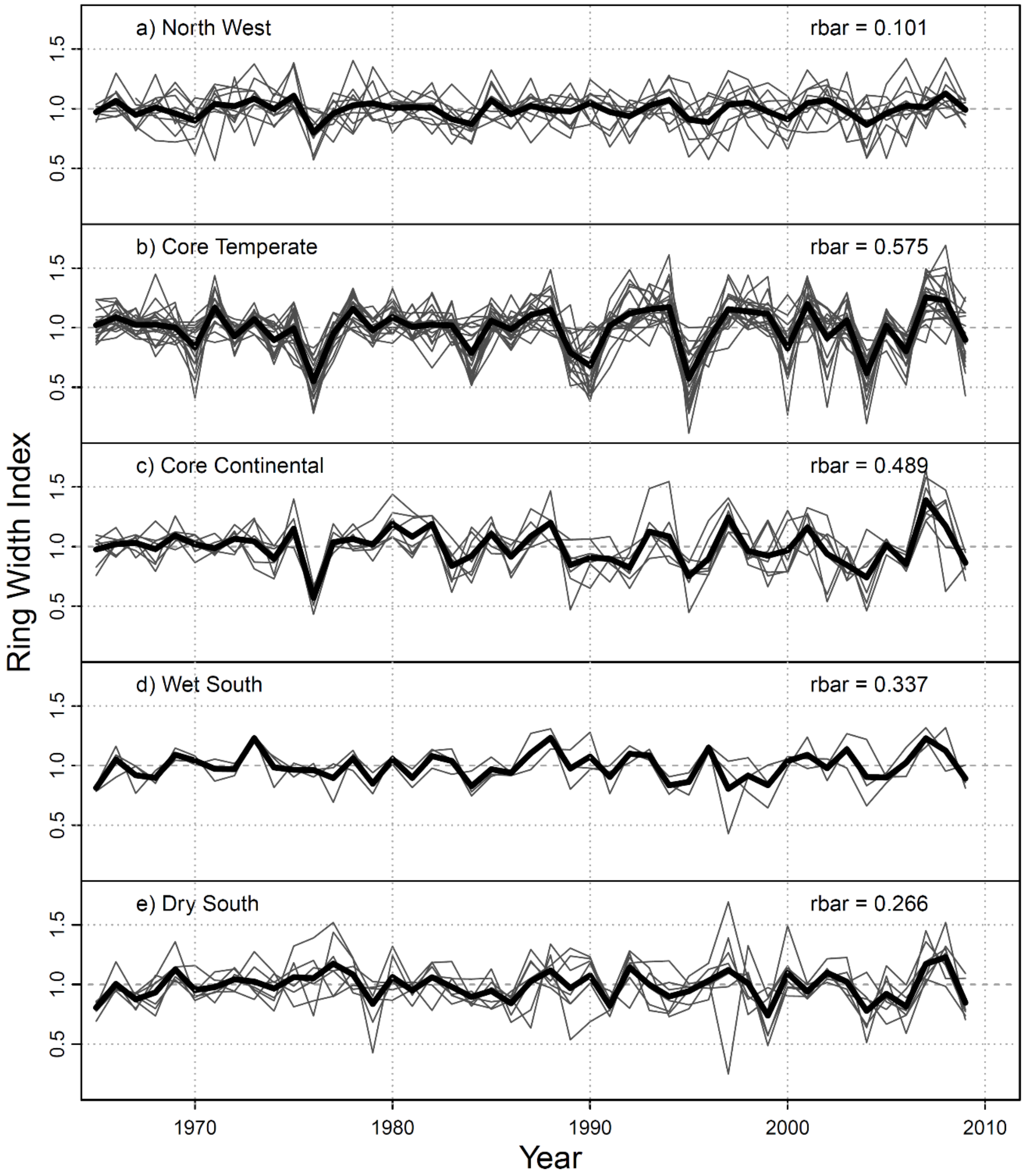

Figure 4.2 Detrended and prewhitened ring-width chronologies for the 46 sites in the Multiregional Network. Sites are partitioned into regional groups, and a mean region chronology plotted in bold. Rbar is the mean series intercorrelation for each region.

strong region wide growth suppressions were evident. Finally, the Dry South region had high variability in growth between sites in individual years (rbar = 0.266). Region wide growth suppressions were recorded in 1979, 1999, and 2004, although these were of a lower magnitude than those experienced in the Core Temperate and Core Continental regions.

Pointer Years

Of 345 pointer years identified using the weak Cropper threshold, 121 were classified as drought induced pointer years. Figure 4.3 shows these drought induced pointer years, displayed as a proportion of sites for each cluster in each year. The timescale plotted

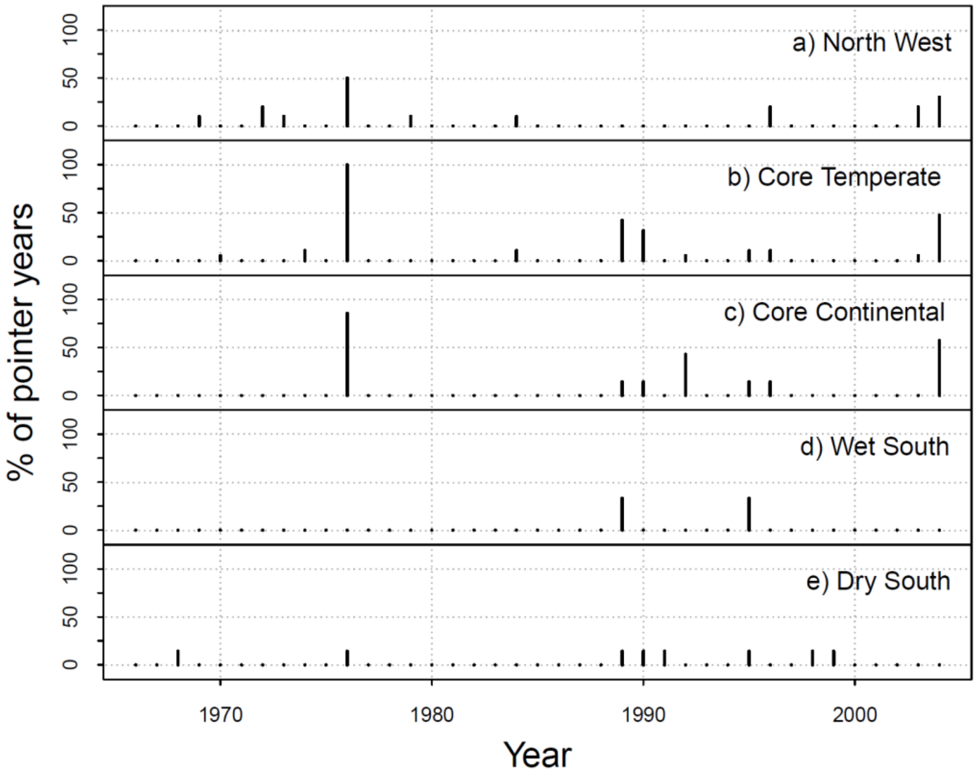

Figure 4.3 Regional drought induced pointer years for the period 1966-2004. Pointer years were identified by calculation of Cropper values, and selection using the weak Cropper value criteria. Weak Cropper years were then matched to drought years using the multi-scalar index SPEI, and proportions of sites within each regional group calculated for comparison.

begins in 1966 (the beginning of the period common to all chronologies) and ends in 2004 (the time period common to call chronologies ends in 2009, minus the 5 years data required to calculate the disturbance indices given in equations 4.5, 4.6 and 4.7) . For the North West, Core Temperate, and Core Continental regions, regional droughts resulted in anomalous low growth episodes across many sites. This was strongest for 1976, which resulted in 50%, 100% and 86% of sites recording drought induced pointer years for the North West, Core Temperate and Core Continental groups, respectively. Lesser drought induced regional growth reductions occurred in 1989/90 and 2004 (following drought conditions in 2003). For the two southern range edge groups, no multi-site regional scale drought induced growth reductions occurred for any year. The drought induced growth reductions recorded for these two groups in figure 4.3 represent in each case an event occurring at a single site.

Drought Indices

Geographical and temporal structure in drought occurrence and strength, relative to climate at any site, is described in figure 4.4. Here, monthly SPEI values are plotted for each site, with site number representing latitude (as sites were numbered in order of latitude, with 1 the most northerly and 47 the most southerly). The regional drought effect described above using drought induced pointer years is clearly shown for the North West, Core Temperate and Core Continental groups. The spatial extent of this drought was limited to the three most northerly groups, with no regional scale drought in 1976 for the Wet South and Dry South clusters. Drought in 1989-90 affected all but the most northerly group, yet this only translated into anomalous low growth in the range core groups. Neither 1989-90, or the range wide drought in 2003 resulted in anomalous low growth for the Wet South and Dry South groups. The drought of 2003 resulted in widespread drought induced pointer years in 2004 for the North West (30% of sites), Core Temperate (47%), and Core Continental (57%) groups.

In addition to the relative drought conditions described above, absolute drought conditions are plotted using summer aridity index in figure 4.5, to allow the comparison

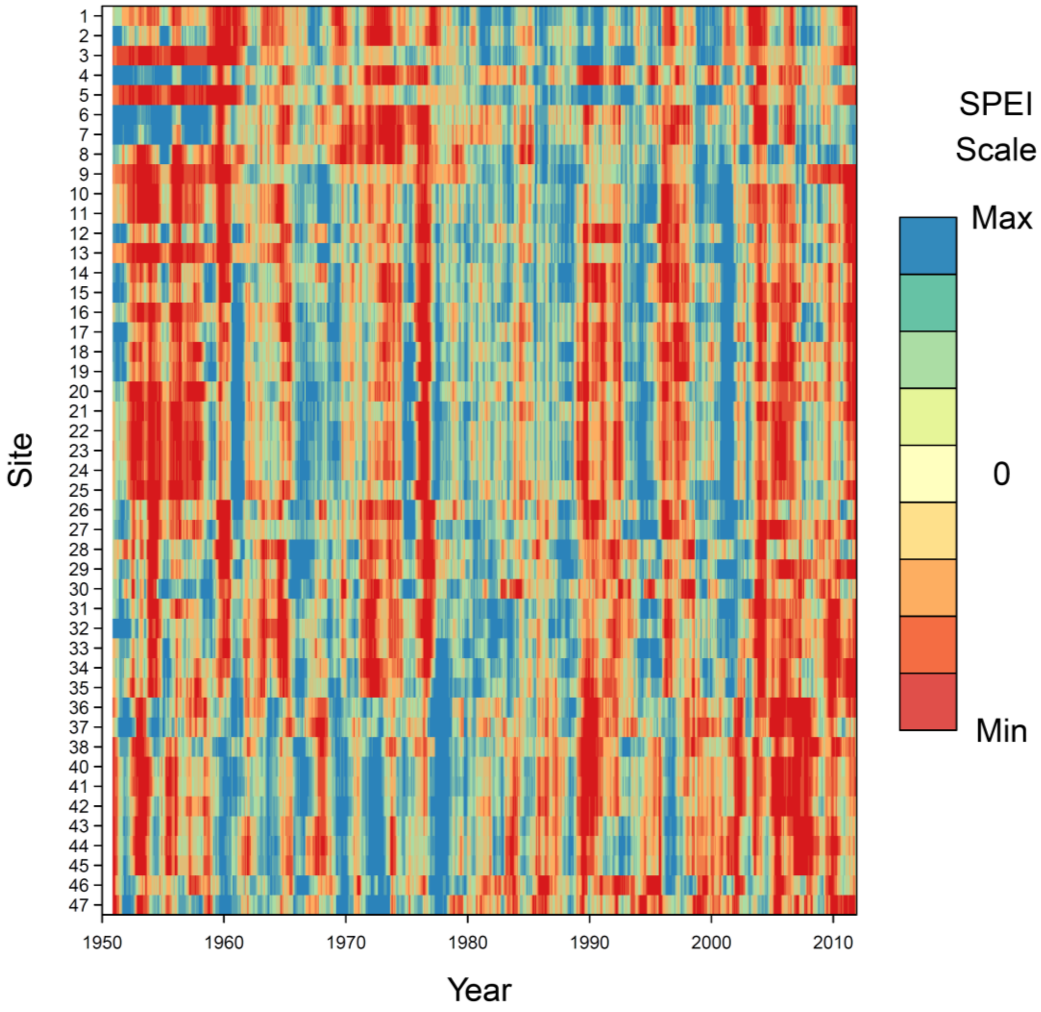

Figure 4.4 Time series plot of the SPEI drought index for the Multiregional Network. Monthly values are plotted for the period 1951 – 2012, using a colour scale which highlights maximum, minimum and mean values. Sites are numbered 1 to 47 in order of descending latitude, i.e. site 1 is the most northerly, and site 47 the most southerly. Values represent drought relative to conditions at each site individually, allowing the comparison of spatial and temporal drought occurrence but not severity between sites.

of water availability between sites. Sites in the Dry South group experience the driest conditions, with near constant aridity at levels equivalent to that only experienced for all other groups during drought events. The Core Temperate region experienced the second highest aridity, particularly for the site in south east England (sites 12, 14-24).

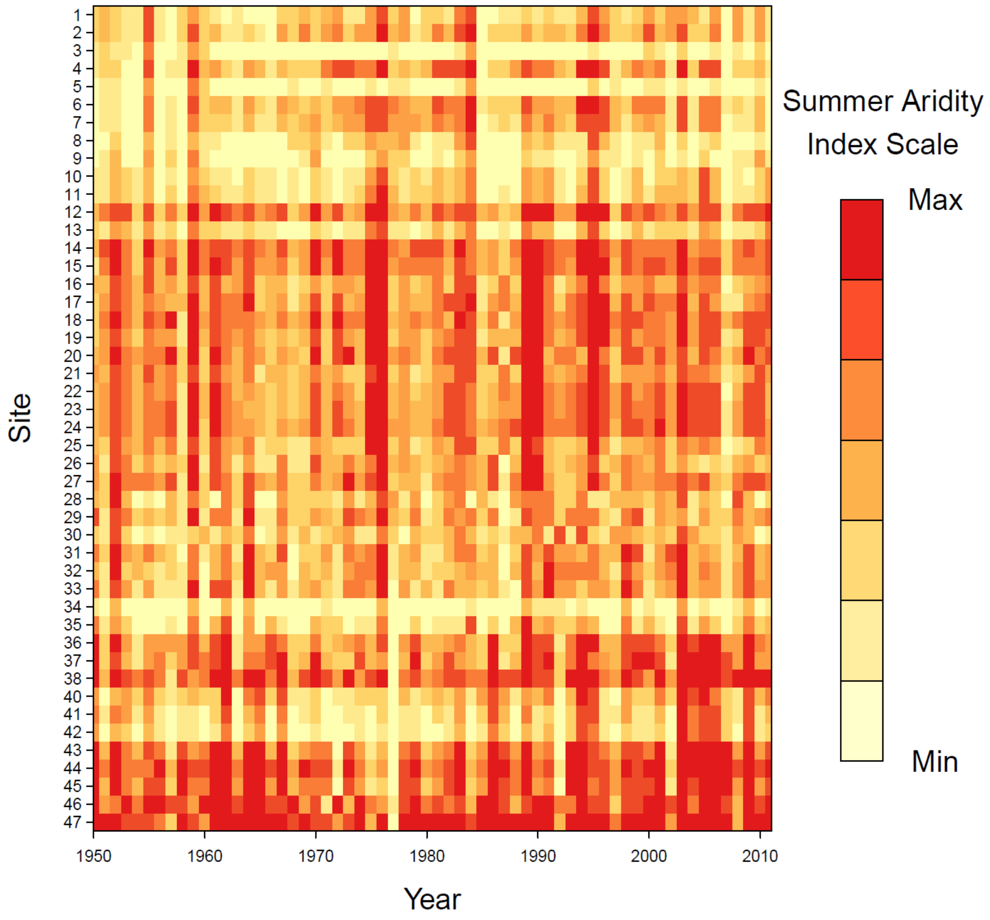

Figure 4.5 Time series plot of Summer Aridity Index (Precipitation/PET calculated for the months May to August). Annual values are plotted for the period 1950 – 2011, using a colour scale which highlights maximum and minimum values. Values represent absolute aridity, allowing the comparison of aridity and drought severity between sites.

For the North West group, aridity was the lowest of all clusters, however, regional droughts in 1976, 1983 and 1995 did result in aridity conditions for a limited number of sites at a level comparable to the more arid groups.

Table 4.1: Generalised additive model results of resilience indices, and predicting factors.

Drought impact index	Factor	e.d.f.	F	p	R^2 (adJ)
Resistance	Age	2.68	3.22	0.024	
	Latitude	8.73	6.19	< 0.001	
	Previous year SAI	1.96	6.18	0.002	
	Whole model				0.566
Recovery	Age	4.12	2.44	0.043	
	Latitude	6.47	5.77	< 0.001	
	year SAI	1.14	6.49	0.005	
	Previous year SAI	2.39	7.50	< 0.0001	
	Whole model				0.546
Resilience	Age	2.89	8.16	< 0.001	
	Latitude	8.83	2.64	0.011	
	Whole model				0.381
Relative Resilience	Age	4.08	3.35	0.009	
	Latitude	5.77	5.29	< 0.001	
	year SAI	1.09	5.05	0.016	
	Previous year SAI	1.18	6.85	0.005	
	Whole model				0.453

Resilience Indices

Of a total of 121 drought induced pointer years, 90 were selected for further analysis: 23 were removed due to occurring within a 5 year window of each other, and a further 8 occurred in consecutive years and thus were combined into a single event. Table 4.1 summarises the GAM selected by stepwise deletion of non-significant terms to examine the factors which drive the drought response. The models explained a moderate degree of the disturbance indices: R^2(adj) ranged from 38% for Resilience, to 57% for Resistance. The relationships between the significant explanatory variables and the resilience indices are shown in figure 4.6. For Resistance, age, latitude and previous year SAI were the significant explanatory variables. Young forests experienced smaller reversals of growth due to drought, and mature forests at around 150 years old larger reversals. However, confidence intervals indicate that the contribution to fitted values is potentially very small. Additionally, for age p = 0.024. Given the uncertainty of p values in the range 0.02 to 0.05 for smoothing functions using estimated degrees of freedom (Zuur *et al.* 2009), these values must therefore be interpreted with caution. Two key features of the relationship between latitude and Resistance are high Resistance for southern range edge populations (< 45°), and low Resistance for sites in the range of 51° to 53° latitude. Latitudinal range of 51° to 53° corresponds to sites in the south east of the UK. A linear relationship exists between previous year SAI and Resistance, with high previous year aridity resulting in low Resistance, and low previous year aridity resulting in high Resistance. For Recovery, age showed a small significant feature of higher values for forests around 170 years old. However, as with age and Resistance, the effect was small and must be interpreted with caution due to the p value of 0.043. Forests at low latitudes (< 45°) had low Recovery. Absolute aridity (SAI), both in the current and previous year, had a positive relationship with Recovery: more arid conditions (i.e. low SAI values) resulted in higher Recovery index values. For Resilience, young forests (< 60 years) showed the highest ratio of post-drought to pre-drought growth. Latitudes covering the Core Continental region had high Resilience, whilst those relating to the Core Temperate region had lower resilience. Finally, for Relative Resilience, the curve for age shows that young forests (< 50 years) were best able to recover performance, weighted by the strength of the drought impact. Southern range edge forests had the lowest Relative Resilience, whilst latitudes relating to the Core Continental group had higher Relative

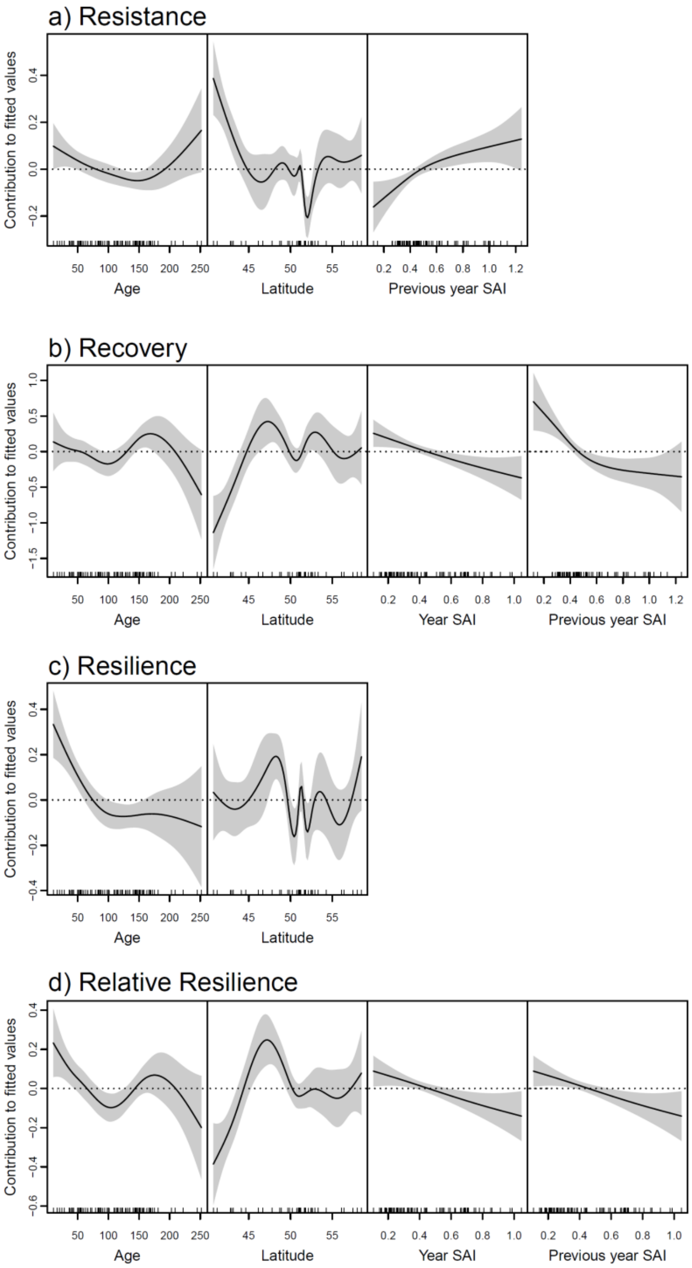

Figure 4.6 Results of GAM analysis for the four drought resilience indices: a) Resistance, the reduction in growth during a disturbance, b) Recovery, ability to recover from damage after a disturbance, c) Resilience, the ratio between pre and post-disturbance growth levels, d) Relative resilience, resilience weighted by the severity of growth reduction during the disturbance. Smoothed curves for significant factors for each index are plotted, with 95% confidence intervals. Notches on the upper side of the x-axis represent sample depth.

Resilience. The relationship with aridity (previous and current year SAI) showed that higher aridity resulted in higher Relative Resilience.

4.4 Discussion

This study identifies key features of the general climate-growth relationship for *F. sylvatica* forests across the species' range, geographical structure in both general aridity and drought occurrence, and the specific drivers of drought response; 1) the drought sensitivity of *F. sylvatica* is strongest in the core of the species' range; 2) high variability in climate-growth relationships, and annual ring widths consistent with low sensitivity to regional drought are apparent at both the northern and southern range edges; 3) southern range edge forests are highly resistant to drought induced reductions in growth; 4) previous year conditions have a strong effect in determining the severity of drought impact; 5) high aridity, drought sensitivity and drought impacts affect *F. sylvatica* forests in southern UK.

Climate growth analysis for the sites in the Multiregional Network are in agreement with previous published studies examining the relationship between climate and growth for *F. sylvatica* (Di Filippo *et al.* 2007; Jump, Hunt & Peñuelas 2007; Maxime & Hendrik 2011; Scharnweber *et al.* 2011). Broadly, the response can be described as drought sensitive: positive relationships between summer precipitation and growth, and negative relationships between summer temperature and growth. Additionally, a positive effect of low winter temperatures was found in the most continental portion of the species range, potentially due to recharge of soil water as has previously been shown for Mediterranean *F. sylvatica* forests (Piovesan & Schirone 2000). The results presented here reveal variation in the strength of climate-growth relationships across the latitudinal range of the species in Western Europe: sites categorised as being from the range core display greater sensitivity in growth to climate. Growth was highly sensitive to summer temperature and precipitation for both range core groups. Predictably for a region characterised by extremely high precipitation (see table 3.1), populations from the far northern portion of the Multiregional Network showed no significant regional climate growth relationships, and high variability in climate-growth correlations. This is consistent with forests where stand level environmental conditions are driving growth rather than regional scale climate. The southern range edge region identified as having high precipitation, Wet South (see table 3.1 for mean values of environmental variables for the regions), had low variability in climate-growth relationships, but with no significant relationships. For the *F. sylvatica* populations from the most arid part of the range, drought sensitivity appeared lower than that for the range core, and with high between site variability. This could be the result of adaptation of southern range edge populations to arid conditions, comparable to genetic clines which have been demonstrated to correspond to aridity gradients for other species (Rehfeldt *et al.* 1999; St Clair, Mandel & Vance-Borland 2005). Additionally, as these populations are from climate relict sites where fine-scale environmental conditions favour their persistence, the climate-growth relationships described here can be interpreted as demonstrating the degree of disconnect between regional scale climate and the conditions experienced by organisms at the stand scale (Hampe & Petit 2005; Jump, Matyas & Peñuelas 2009; Hampe & Jump 2011).

Immediate comparisons of the drought response of populations within the network of sites are complicated by the variability in both timing and location of droughts across the latitudinal range. Nonetheless, some key events allow regions to be contrasted. For the latitudinal transect of sites across the western European distribution of *F. sylvatica*, the drought and growth suppression of 2004 is the universal event affecting all regions. Whilst the heat wave of 2003 has been reported to affect the primary production of European vegetation (Ciais *et al.* 2005), the study of tree-rings has revealed a minor impact in this year, attributed to the effect of spring precipitation alongside preconditioning from previous year conditions (Pichler & Oberhuber 2007). This is corroborated by this study, with reductions in growth primarily associated with a 2004 drought identified using the multiscalar index at 12 months resolution. This temporal resolution incorporated both previous summer conditions, alongside dry spells in 2004. However, despite the universal scope of the 2004 event within the network, the effects of this drought were not universal: anomalous low growth (see figure 4.3) affected primarily the mid-latitude forests, and to a lesser extent northern range edge forests. At the southern range edge, both for the arid and wetter regions, regional scale drought did not result in regional scale growth suppressions. For the mid-latitudes, where drought events occurred in synchrony (e.g. 1976, 1990 and 2004: see figure 4.4), reductions in growth were near universal and of a higher magnitude than for other regions (see figure 4.2 b & c). For the northern range edge forests, between site growth variability was high even in drought years: regional scale variation in annual water availability does not result in regional scale coordination of tree growth. The one exception is the drought event in 1976, where all northern range edge sites recorded low growth (see figure 4.2 a). For northern range edge sites, the general lack of drought impact on growth is predictable given that precipitation for this region (see table 3.1) is far in excess of that considered to be limiting to growth (Bolte, Czajkowski & Kompa 2007), and that northern range edge populations for plant species are more generally affected by low temperature (Walther 2004). Southern range edge sites displayed both low magnitude (in the Wet South region, see figure 4.2 d) and high between site variability (in the Dry South region, see figure 4.2 e) in growth response to regional scale drought episodes. Despite significant drought conditions relative to mean site hydrological conditions, and the most extreme aridity relative to conditions throughout the network of sites, climate relict sites at the southern range edge were little affected by drought. These results are in contrast to studies linking reduced water availability at southern range edge populations for *F. sylvatica* to general reductions in growth (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). Climate relict populations have been described as depending upon low variability in environmental conditions, and low chance of extreme events (Hampe & Jump 2011). The results presented here support this, and suggest that the reported growth declines for southern range edge populations could be due to generally elevated water stress, rather than regional scale drought events.

In addition to the assessment of regional variation in climate-growth relationships, analysis of drought induced pointer years using GAM allowed for an evaluation of specific factors which influence the response of *F. sylvatica* to drought. The youngest chronologies were associated with low reductions in growth during drought episodes (see figure 4.6 a) and high post-drought growth levels relative to pre-drought performance (figure 4.6 c & e). However, BAI was used as the metric of growth, which increases rapidly during the juvenile phase of tree growth before either stabilising or continuing to increase at a slower rate around maturity, only decreasing due to stress or senescence (Pedersen 1998; Duchesne, Ouimet & Houle 2002; Duchesne, Ouimet & Morneau 2003; Fekedulegn, Hicks Jr & Colbert 2003; Jump, Hunt & Peñuelas 2006). Therefore, for the youngest chronologies, high post-drought growth performance may simply represent this age related BAI trend. Whilst greater drought sensitivity has been reported for older forest stands for many species (Wang, Chhin & Bauerle 2006; Klos *et al.* 2009; Linares *et al.* 2013), this study finds no clear and strong evidence for such an age-dependent drought effect, with only a small negative contribution to fitted values for mature stand Resilience and Relative Resilience.

Latitudinal variation in the drought resilience statistics corroborates the regional variation in climate-growth relationships and drought pointer year occurrence. *Fagus sylvatica* forest stands at the southern range edge (latitude < 45°) experience lower initial drought impacts in the event year (see figure 4.6 a). Lower Recovery and Relative Resilience indices for southern stands are related to this low drought impact, as these indices are both decreased in the case of low reduction in BAI for the drought year (see formulae 4.5 & 4.7). North continental stands recovered well relative to drought damage, and pre-drought growth levels (figures 4.6 b, c & d). Despite the results of this study implying less drought sensitivity for southern and central European forests, these regions have been highlighted as at risk to future predicted increases in both the frequency and severity of drought stress (Lindner *et al.* 2010; Milad *et al.* 2011). Of the regions considered in this study, forest stands in southern UK were highlighted for experiencing especially elevated reductions in growth performance in drought years (figure 4.6 a & c), consistent with the high drought sensitivity described above from the climate-growth analysis.

Absolute aridity (summer aridity index) was identified as a major driver of drought impact, whereas relative drought (SPEI) was non-significant. The initial reduction of growth in the event year was primarily influenced by aridity in the previous, rather than current, year. Prospective mechanisms for this are the depletion of carbon reserves or damage to the water transport mechanisms within the organisms, as carbon starvation and hydraulic failure have both been implicated in severe drought induced damage and death (McDowell *et al.* 2008; Sala, Piper & Hoch 2010). Potentially, under normal conditions individual *F. sylvatica* trees maintain carbon reserves adequate to avoid severe damage for single year droughts, or are able to tolerate the hydraulic conductivity losses experienced. Multiple interactions between these processes may also shape the response of *F. sylvatica* to drought (McDowell 2011). The relationship of increasing Recovery and Relative Resilience with increasing current and previous year's aridity is most likely due to the effect of a larger event year growth reduction on the calculation of these indices. However, it does indicate that even in the case of the most arid drought events, recovery to prior growth levels is possible. The severity of drought events is generally not at a level which impairs the future growth performance of *F. sylvatica* forest stands.

This study has shown that low sensitivity to climate and low damage from drought are characteristics of southern range edge *F. sylvatica* populations. This applies both to Western Pyrenean wet populations, and to arid sites in the Western Mediterranean basin. Recent climate models have predicted an increase in both the frequency and severity of drought events in the Western Mediterranean region (Giorgi & Lionello 2008). These increasingly arid conditions are expected to impact upon the growth and mortality of tree species within the region (Linares, Delgado-Huertas & Carreira 2011; Granda *et al.* 2013). Whilst southern range edge populations appear currently well buffered against drought stress, it is possible that future conditions may breach threshold values resulting in unexpected and long lasting reductions in growth (Cavin *et al.* 2013). Future research should seek to characterise the site level environmental conditions which permit the continued persistence of the species, buffered from severe drought impacts.

Crucially, this study also reveals that *F. sylvatica* populations in the south of the UK are the most drought sensitive of the regions studied. Modelling has already identified this as a region where the primary productivity of *F. sylvatica* is likely to be severely compromised by future climate scenarios (Broadmeadow, Ray & Samuel 2005). In this region, climate sensitivity is highest, absolute aridity is higher than for any region beyond the Mediterranean basin, and drought induced reductions in growth are the highest throughout the Multiregional Network. Previous study has identified extreme and long lasting drought impacts within this region (Peterken & Mountford 1996). The results of this study suggest that this response could become more widespread in a warming climate. Further work should aim to identify those populations most susceptible to drought, and to monitor the response to future droughts. Management of *F. sylvatica* populations in this region could actively seek to promote drought resistance and resilience, using methods such as selective thinning and the reduction of non-climate related stresses (Jump, Cavin & Hunter, 2010). Such management could help to mitigate any growing negative effects of drought damage to these forests.

5. Growth Trends and Growth Variability

This chapter uses data from the Multiregional Network to examine radial growth trends, and trends in growth variability. Geographical variation in growth and growth variability will be identified. Using a linear mixed effects modelling approach, factors driving growth trends will be examined, alongside differences in their relative strengths between regions.

5.1 Introduction

Environmental change can drive changes in the growth and reproduction of plants. Many studies have examined growth and productivity trends for *F. sylvatica* across Europe over recent history, with predominantly decreasing trends reported (Dittmar, Zech & Elling 2003; Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008; Bontemps, Hervé & Dhôte 2009; Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010; Scharnweber *et al.* 2011; Kint *et al.* 2012). Most studies attribute the observed growth patterns primarily to environmental change, with increasing drought stress being a commonly cited factor leading to reductions in radial growth or increases in climate sensitivity. However, observed trends in radial growth may relate primarily to issues regarding the spatial scale of studies, which range from single site to regional scales. Reviews have shown that the overview from multi-species forest survey studies across Europe, and NPP derived from satellite observations, shows that the overall picture is for increased forest productivity in Northern and Central Europe, along with some increases in parts of Southern Europe (Spiecker 1999; Boisvenue & Running 2006). Given that reported growth trends for *F. sylvatica* conflict with those reported for European forests more generally, the divergence is potentially due to a species specific climate sensitivity. In this case, *F. sylvatica* is predisposed to a negative response to climate change, primarily at its southern range margin. As the species is generally held to be drought sensitive (Fotelli *et al.* 2001; Leuschner *et al.* 2001a; Granier *et al.* 2007), this is a plausible hypothesis. However, the research presented in this thesis in chapter 4 did not identify a strong negative response at the southern range edge. Thus, as an alternative, the possibility exists of a publication bias towards studies reporting negative effects of climate change on forest growth, since reports of populations functioning normally are unlikely to be published. The undue attention given to 'Waldsterben' predictions of large scale forest decline in the 1980s should provide a pertinent cautionary note for current forest ecologists (Skelly & Innes 1994).

To transcend the limitations of studies at scales ranging from individual sites to regions, an approach which considers the growth response of *F. sylvatica* across its range, and over multiple decades, is necessary. Whilst a truly range wide study would be ideal, the Multiregional Network described in this thesis includes sites ranging from the northern to southern range edges in Western Europe. Therefore, this chapter uses the tree-ring records of the Multiregional Network to study temporal trends in *F. sylvatica* growth across multiple regions and decades. One factor widely known to affect tree-rings is tree age, with ring width declining over time (Fritts 1976). However, to circumvent this problem, basal area increment (BAI) can be used as a metric of tree growth for which increasing or stable trends are found in mature trees (Phipps & Whiton 1988; Leblanc 1990; Leblanc, Nicholas & Zedaker 1992). Decline in BAI is commonly interpreted as representing declining tree growth (Pedersen 1998; Jump, Hunt & Peñuelas 2006).

The variability of growth within a tree-ring series has long been used as a measure of climatic signal present in a ring width series, and has been commonly used both to indicate the suitability of a series for cross-dating, and also as a measure of environmental stress (Douglas 1920; Fritts 1976; Cook & Kairiukstis 1990). The characteristics of growth variability are that as site aridity increases, relative ring-width variability can also be expected to increase (Fritts *et al.* 1965). This can be applied to growth variability at a single site over time, and increases in growth variability linked to disturbance patterns for that site. However, when considering a forest growing at a single site, an increase in growth variability over time could represent an increase in endogenous as well as exogenous disturbance. By elevating the scope of a study to incorporate multiple regions, the influence of non-climatic influences on growth acting at a local level can be minimised and the overall signal relating to climate change revealed (Parmesan & Yohe 2003). An additional challenge is that care must be taken in interpreting any temporal trends due to potentially confounding age related effects in tree rings. Recently, assessment of temporal changes in growth variability have been applied to a multi-site study of *F. sylvatica* growing at relatively arid sites (Weber *et al.* 2013). Thus, examination of growth variability at a range wide scale for *F. sylvatica* can usefully inform on any trends in stress experienced by forests due to the common signal of climate change.

This chapter aims to test the following questions relating to growth trends and variability: 1) are the growth reductions in *F. sylvatica* populations reported from the southern range edge common to the species across this region? 2) Due to the increased climate sensitivity and drought susceptibility described in chapter 4 of this thesis, are range core (i.e. in the context of this study Southern UK, Northern and Central Europe) sites also subject to any reductions in growth trend? 3) To what extent are climatic factors the drivers of any growth trends between regions. 4) Are any changes in growth over time accompanied by changes in the variability of tree growth between years, and is growth variability most pronounced in the more arid southern regions? In order to address these questions, a combination of BAI data and gini coefficient from the Multiregional Network will be analysed in tandem with climate variables. Data will be examined using linear regression, generalised additive and linear mixed effects modelling techniques to identify temporal trends and climate drivers of growth.

5.2 Methods

Generalised Additive Modelling of BAI

In order to examine temporal trends in tree growth across the Multiregional Network, BAI data was used (as calculated in section 2.5). Each individual site chronology was truncated to the time period for which sample depth was greater than or equal to 5 trees. The resulting chronologies were further truncated to the time period common to all 46 sites, i.e. 1967 to 2009. As the intention here is to examine growth trends rather than compare absolute growth between sites, BAI for each year was divided by the mean site BAI, to give a dimensionless BAI index. The BAI data was then aggregated into regional datasets, based on the regions determined in chapter 3. Generalised additive modelling (GAM) was then performed on the regional BAI index data, with the sole predictor variable of year of growth, in order to examine temporal trends in BAI. Therefore, the model is of the form:

$$BAI_i = \alpha + f(Year_i) + \varepsilon_i \quad \text{where } \varepsilon_i \sim N(0, \sigma^2) \tag{6.1}$$

where α is the intercept, f is a smoothing spline, and ε represents the residuals. Smoothing parameters were estimated using generalised cross-validation, and the results were smoothed using a regression spline with shrinkage. The aim of this analysis was to identify and describe any non-linear temporal trends in radial growth across the 5 regions identified for the Multiregional Network (see chapter 3), and so the GAM described in equation 6.1 was applied to the 5 regions separately.

Linear Mixed Effects Modelling of BAI

Whilst the GAM approach outlined above is intended to identify and describe growth trends, it yields no information on the drivers of radial growth. To address this question, a linear mixed effects modelling (LMEM) approach was used (Zuur *et al.* 2009). This type of modelling approach can be used to account for the inherently nested nature of tree-ring data from the Multiregional Network, i.e. ring widths from individual trees, trees within sites, and sites within regions (Bontemps & Esper 2011; Kint *et al.* 2012). However, although LMEM has been applied to tree-ring data using individual annual measurements per tree, in the absence of variables which describe within stand factors (such as competition) this approach would simply add a large amount of unexplained noise to the model due to periodic local endogenous disturbance pulses. Therefore, mean site BAI index chronologies for each of the 46 sites were used rather than individual trees, to minimise the effects of disturbances specific to individual trees. Each region was analysed independently, and model selection followed the top down, 'beyond optimal' strategy, where all potential explanatory variables are contained as fixed components allowing for the optimal structure of the random components of the model to be identified. The variables used as the fixed components were: year, summer aridity index (see section 2.8 for this and subsequent climatic variables), PET, mean annual temperature, annual precipitation, summer SPEI (mean annual SPEI calculated for the months May to August, see section 4.2), mean temperature of the hottest month, and mean temperature of the coldest month. A random intercept and slope model was determined as the most appropriate, as assessed using Akaike's Information Criterion (AIC), with year and site chosen as the random effects. Therefore, the model structure allowed for different intercept and slopes to exist for each site within each region. Due to the presence of temporal autocorrelation within the data, autoregressive moving average functions were applied to the random intercept and slope models. The order of the models applied was chosen by applying models using all combinations of auto-regressive and moving average parameters between the values of 0 to 3, and then choosing the optimal model by assessment of AIC. Different covariance structures were applied to the LMEM models for each region, and the most appropriate chosen by assessment of AIC. The fixed structure of the regional models was then optimised using a backwards stepwise selection process, using the maximised log-likelihood method. The final models were then re-fitted using the restricted maximum likelihood method, and models validated by examining the residuals. Whilst calculating an easily interpretable statistic to represent the quality of model fit has proven problematic for LMEM, recent work has proposed a method for calculating marginal and conditional R^2 (Nakagawa & Schielzeth 2013). These facilitate the evaluation of, respectively, the fixed only, and combined fixed and random components in the model, and were therefore calculated for the BAI LMEM models presented here.

Growth variability

Variability in radial growth from one year to the next is a commonly used measure in tree-ring studies of the stress experienced by trees at a site. Tree-ring studies have historically utilised mean sensitivity as a metric of growth variability (Douglas 1920; Fritts 1976). This has received criticism for adding little information over that provided by standard deviation and first order autocorrelation (Jansma 1992). However, gini coefficient is a measure which is widely used across scientific disciplines and has recently been proposed as an alternative measure of variability in tree-ring data which and does not suffer from any of the criticism levelled at mean sensitivity (Biondi & Qeadan 2008a). Therefore, gini coefficient was adopted here as the preferred method of evaluating growth variability. For each ring width chronology for each site within the Multiregional Network, gini was calculated over a moving window of 10 years, giving each chronology a corresponding time series of gini. The moving window for gini was right aligned; thus each value of gini calculated is a representation of the variability in radial growth over the preceding 10 years. In order to assess temporal trends in growth variability across multiple sites and regions, individual site gini time series were normalised by deduction of site mean gini from each yearly value, and then division by the standard deviation of the site gini time series.

To examine temporal trends in growth variability, normalised gini time series for all sites were pooled, and truncated to the time period 1900-2010. Although the exact period selected is arbitrary, data was truncated in order to remove the oldest portion where sample depth is low and chronology quality poorest. Mean gini values were calculated for each year, and linear regression models fitted to the mean value series with AIC used to assess whether simple linear, quadratic, or polynomial models were most appropriate. Site gini time series were then subset into the 5 regions of the Multiregional Network, in order to assess regional differences in gini trends. Focusing on the recent time period during which global rises in temperature have intensified, the regional gini time series were truncated to 1960-2010. Mean annual values were calculated for this time period, linear regression models applied, and model selection conducted using AIC. The same analysis, i.e. linear regression of 1960-2010 annual mean gini values for the 5 regions, was performed for the raw un-normalised gini values in order to compare absolute differences in growth variability between the regions.

As age effects on tree growth are a potential confounding factor in assessing temporal trends in radial growth, it was deemed important to rule this out as a factor affecting gini. Therefore, the 46 sites were split into 3 age classes according to chronology length; the youngest class, consisting of 16 sites with moving gini time series ranging from 1923-2009 to 1976-2009; the middle class, consisting of 16 sites with moving gini time series ranging from 1914-2010 to 1853-2009; the oldest class, consisting of 14 sites with moving gini time series ranging from 1851-2009 to 1761-2009. The three classes were then truncated to the time period common to them all, i.e. 1923-2009, and mean annual values calculated. To examine temporal trends in growth variability for the 3 age cohorts, linear regression models were fitted to the mean value time series, with AIC used to select the most appropriate model.

A remaining question is whether there is a general age related trend in gini. To answer this, all site gini time series were pooled, and aligned by age (approximated using the length of each time series), not by year. Mean gini values were calculated for each age year. At low site sample depth, for the oldest portion of the pooled data, any strong trends for individual sites risk adding bias to this portion of the pooled data. Therefore, the pooled age aligned gini time series was truncated to the portion where the number of contributing sites remained 20 or higher. This gave a final time series of 10 (due to gini being calculated on a right aligned 10 year moving window) to 139 years. Linear regression models were then fitted to the final time series, in order to examine age related gini trends, and the final model chosen by assessment of AIC.

An alternative interpretation of increasing growth variability is that, if climate is itself becoming more variable, any changes in growth could simply represent the trees response to a changing climate rather than stress. Thus, gini coefficient analysis was performed on climate data to identify whether any changes in their variability was evident. Annual mean temperature and sum precipitation were calculated for the summer months (May to August) according to the methods detailed in section 2.8, for each of the sites in the Multiregional network. The resulting time series of annual values covered the period 1950 to 2010. Using methods already applied to the tree-ring data outlined above, a ten year window rolling gini coefficient was calculated for each climate variable, and right aligned. Gini was then normalised by deduction of site mean gini from each yearly value, and then division by the standard deviation of the site gini time series. Values were plotted, along with mean values for each year. Linear models were fitted to the data, with the correct model (linear, quadratic or polynomial) assessed using AIC and plotted.

5.3 Results

Generalised Additive Modelling of BAI

Temporal trends in radial growth were explored using GAM, and model output is summarised in table 5.1. BAI chronologies for the regions and estimated model smoothing curves are plotted in figure 5.1. Models fit to the 5 regions were statistically significant, with R^2 of between 0.11 to 0.24, despite including only a single predictor variable, i.e. year. The estimated degrees of freedom indicate a strongly non-linear temporal trend in the Core Temperate (see figure 5.1g) and Core Continental regions (see figure 5.1h). The temporal trend for these regions is towards higher radial growth. However, strong growth suppressions are presented in both regions centred on 1976 & 2004. Both of these years correspond to regional scale drought events, as discussed at length in chapter 4. Radial growth for the North West region is strongly linear, and towards increased growth (see figure 5.1f). No periodic disturbances in the upwards trend were recorded, although the variability in radial growth between sites was high, particularly from the mid-1990s onwards (see figure 5.1a). For the two southern range edge regions, radial growth rose

Table 5.1: Generalised additive model results of BAI temporal trends for the 5 regions.

Region	Factor	e.d.f.	F	p	R^2 (adJ)
North West	Year	1.63	64.31	< 0.001	0.241
Core Temperate	Year	8.83	13.62	< 0.001	0.125
Core Contintal	Year	8.42	8.73	< 0.001	0.196
Wet South	Year	6.52	3.50	0.001	0.158
Dry South	Year	5.706	5.70	< 0.001	0.11

to a peak at around 1990 (see figures 5.1i & 5.1j) before beginning a slight decline. Broadly however, BAI was stable over the period examined.

Linear Mixed Effects Modelling of BAI

Growth trends for the 5 regions were examined in more detail using the LMEM approach, which indicated differing climatic drivers of radial growth across the regions (see table 5.2). For the North West, Core Temperate and Core Continental regions, year was a significant explanatory factor. Year was a non-significant factor for the southern range edge regions, and thus removed from the models during the model selection process. This corroborates the temporal trends described above using GAM. Across regions, the absolute measure of drought, summer aridity index, was a significant factor driving growth for all but the Wet South region. Marginal and conditional R^2 are measures which allow for the evaluation of the relative contributions of the fixed and random effects portions of the models: in all cases, the random effects added little to the models despite

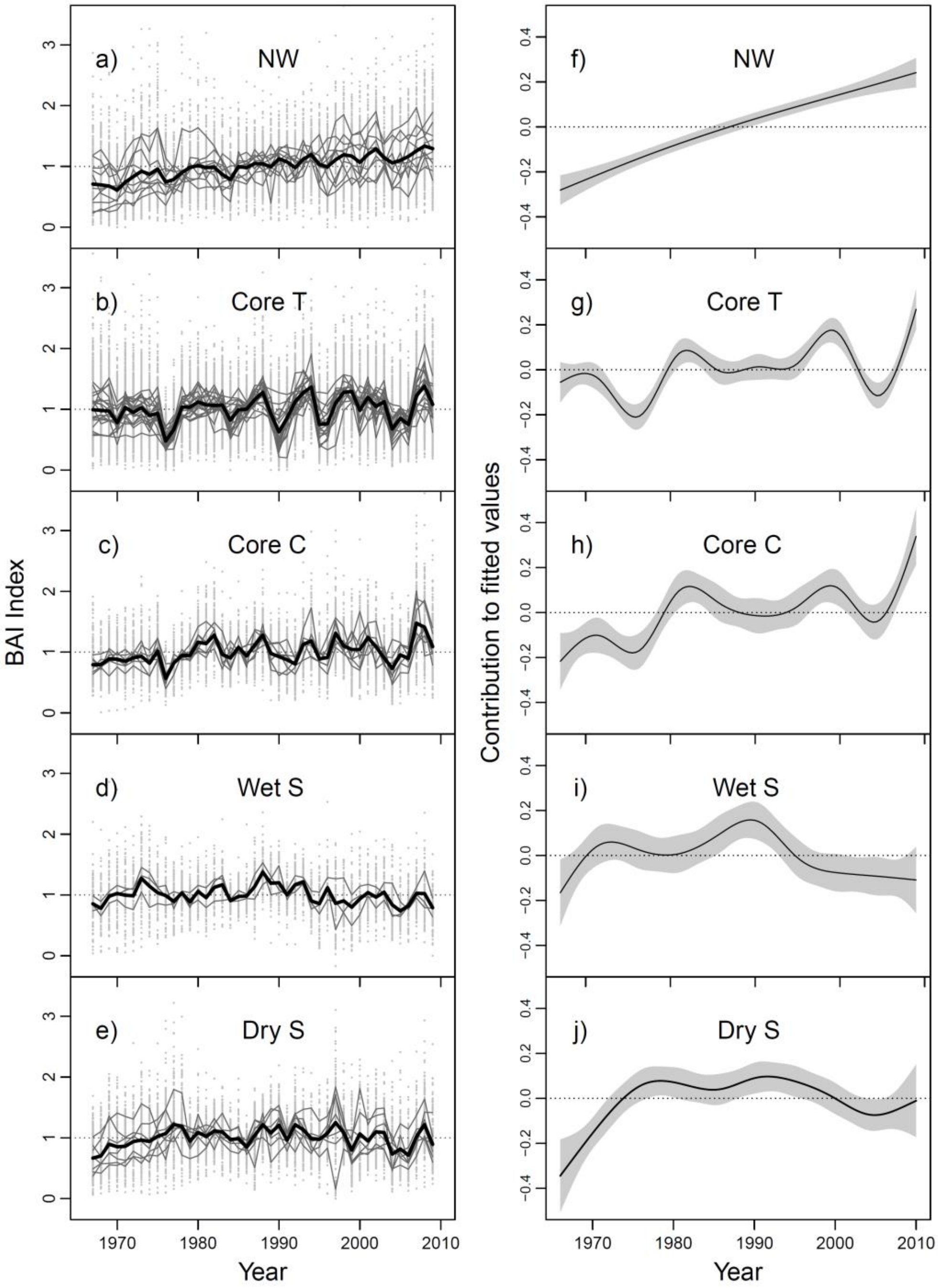

Figure 5.1: BAI chronologies and GAM model smoothing curves for the 5 regions. Left hand graphs show individual BAI index values per site as points, site BAI curves in grey, and regional mean BAI in black. Right hand graphs show the GAM smoothers, with 95% confidence intervals. The regions depicted are North West (plots a and f), Core Temperate (b & g), Core Continental (c & h), Wet South (d & i), and Dry South (e & j).

Table 5.2: Summary of the fitted linear mixed effects models for the 5 regions.

	Value	SE	DF	t-value	p-value	Marg. R^2	Cond. R^2	Corr(P,O)
North West						0.240	0.301	0.904
Year	0.013	0.0022	418	5.83	< 0.001			
Summer Aridity	0.100	0.0339	418	2.96	0.003			
Core Temperate						0.169	0.170	0.660
Year	0.005	0.0017	795	2.87	0.004			
Summer Aridity	0.167	0.043	795	3.89	< 0.001			
Summer SPEI	0.102	0.0087	795	10.88	< 0.001			
Core Continental						0.285	0.286	0.681
Year	0.009	0.002	289	4.42	< 0.001			
Summer Aridity	0.121	0.053	289	2.25	0.025			
Summer SPEI	0.086	0.014	289	5.98	< 0.001			
Tmean C	-0.018	0.007	289	-2.49	0.013			
Tmean H	0.014	0.005	289	2.94	0.004			
Wet South						0.040	0.041	0.358
Tmean H	0.022	0.010	125	2.29	0.023			
Dry South						0.071	0.074	0.530
Summer Aridity	0.251	0.046	293	5.48	< 0.001			

Tmean C: mean temperature of the coldest month of the year; **Tmean H**: mean temperature of the hottest month of the year; **Marg. R^2**: marginal R^2; **Cond. R^2**: conditional R^2; **Corr(P,O)**: correlation of predicted and observed BAI index values.

their inclusion being recommended by an assessment of AIC. This implies that within each region, BAI between sites are subject to the same drivers of growth. The difference between marginal and conditional R^2 is highest for the North West region, where inter-site growth variability is also highest (see figure 5.1a). Model fit (assessed by R^2, see table 5.2) was poor, particularly for the southern range edge. Observed and fitted BAI values for the 5 regions are shown in figure 5.2. Correlation between observed and predicted values was high for the North West region, at 0.904 (due to the strong linear trend in growth and absence of large inter-annual fluctuations). For the Core Temperate and Core Continental regions, correlation between observed and fitted values was also high, 0.66 and 0.681 respectively. The LMEM models for these regions largely predict both good and

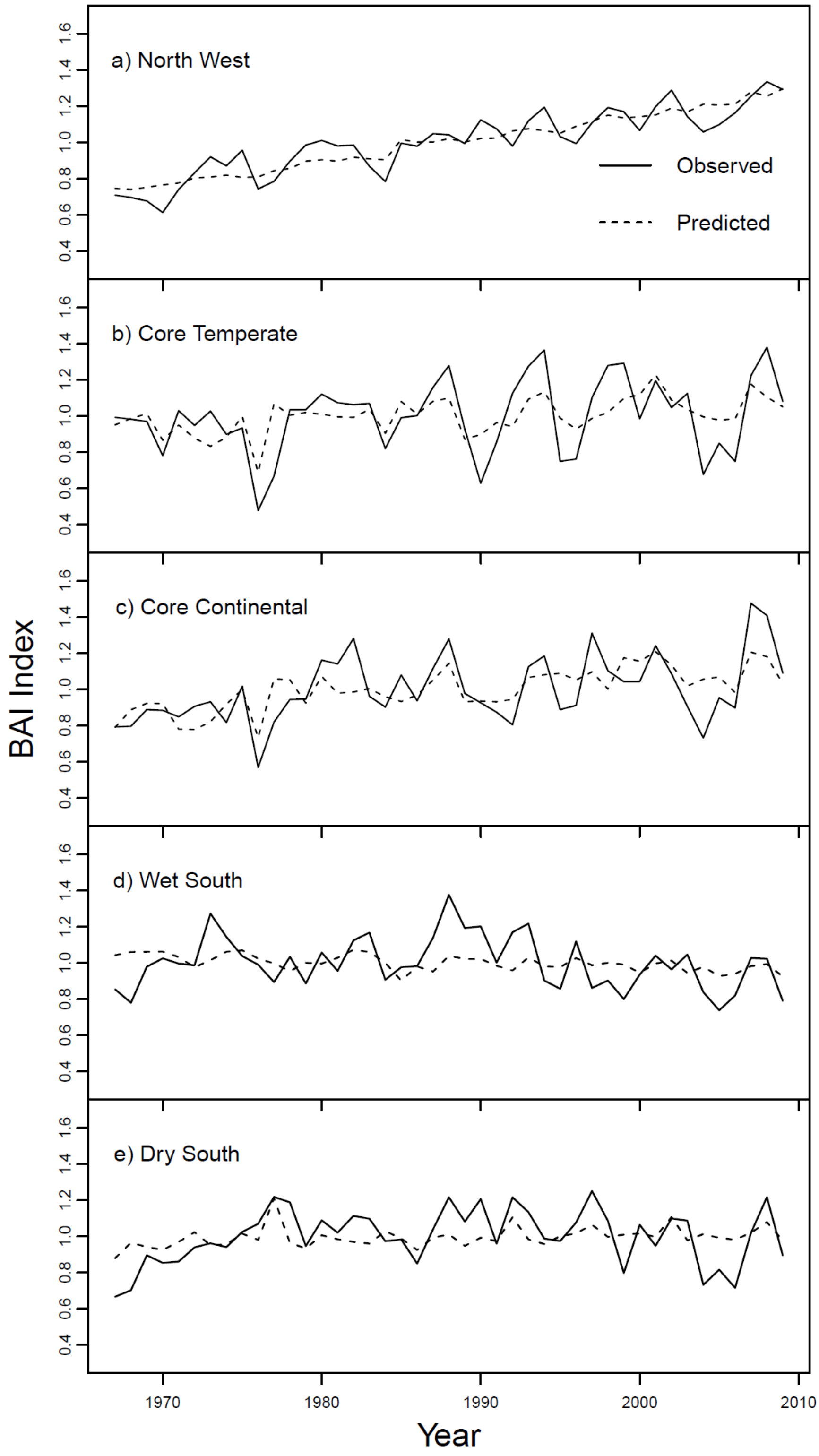

Figure 5.2: Mean regional BAI values for the 5 regions, observed and fitted using linear mixed effects modelling.

bad years for growth, but generally underestimate the strength of growth reductions or expansions. For both southern range edge regions, the LMEM model predicted values explain little of the year to year variation in tree growth.

Growth Variability

Figure 5.3 shows the moving window gini time series for the 20th and 21st centuries. Gini was stable over the period 1900-1970, before entering a phase of increasing gini from 1970-present, described by the relationship: $Gini = 36210 + 55.9year - 0.029year^2 + (4.9 \times 10^{-6})year^3$, ($R^2$(adj) = 0.673, F = 76.4, $p < 0.001$). As gini was calculated on right aligned 10 year moving window, this period represents growth

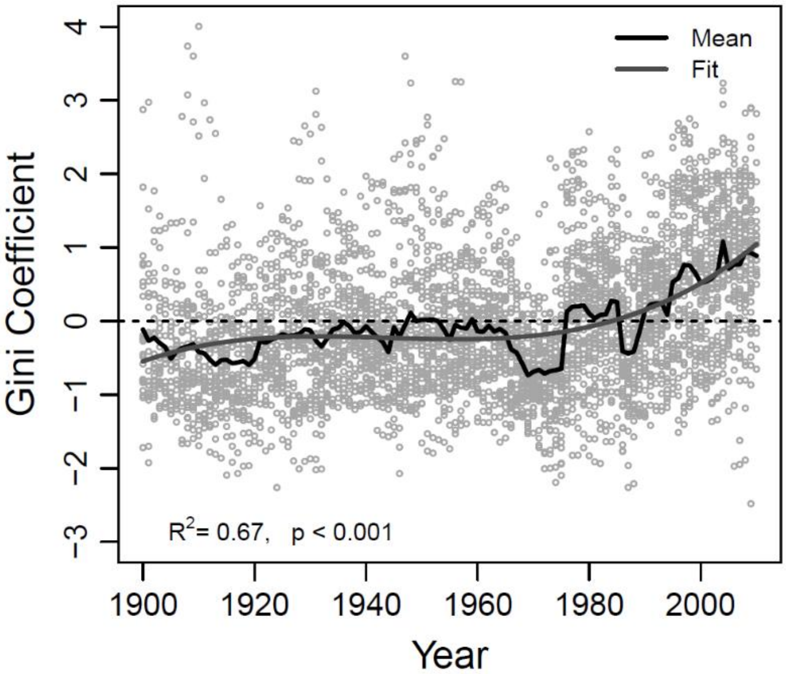

Figure 5.3: Gini coefficient for all sites over the period 1900-2010. Individual yearly values per site are plotted as points, mean of all sites in black, and model fit in grey.

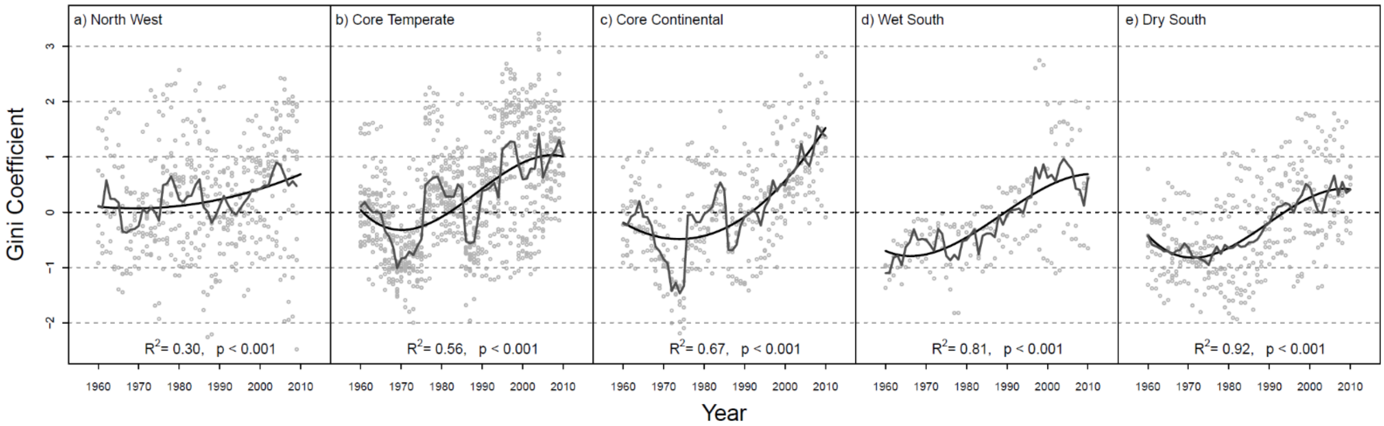

Figure 5.4: Gini coefficient of the 5 regions over the period 1960-2010. Individual year values per site are plotted as points, mean regional gini as a dark grey line, and fitted models in black.

variability over the period 1960 to present. Over this period, normalised gini increased from a low of around -0.7, to a high of around 0.9. Regional gini for the period 1960-2010, is plotted in figure 5.4, showing temporal trends by region over the period of rising gini. Assessment of moving window gini by region reveals an increasing trend to higher growth variability for all regions in the Multiregional Network. The increase in growth variability is weakest for the North West region, increasing from around 0.1 to 0.7 from 1960 to 2010, according to the relationship: $Gini = 1431 - 1.45year + 0.00037year^2$, ($R^2$(adj) = 0.301, F = 11.55, $p < 0.001$). Variability between sites was high, with many sites within the region recording negative gini values. The range core regions, Core Temperate and Core Continental, displayed strong increases in gini over the time period, with final gini in 2010 in excess of 1 standard deviation higher than the historical mean. Core Temperate gini increased from 0 to 1, according to the relationship: $Gini = 415900 - 628year + 0.32year^2 - (5.3 \times 10^{-5})year^3$, ($R^2$(adj) = 0.673, F = 76.4, $p < 0.0001$). Core Continental gini increased the most of all regions, from -0.2 to 1.5 according to the relationship:

$Gini = 6014 - 6.1year + 0.0015year^2$, ($R^2$(adj) = 0.669, F = 51.6, $p < 0.0001$). The two southern range edge regions' gini increased strongly from a low base in 1960 with a rate of increase comparable to the two core regions, however final gini values were lower. Wet South gini increased from -0.7 to 0.7, according to the relationship $Gini = 260800 - 393.6year + 0.198year^2 - (3.32 \times 10^{-5})year^3$, ($R^2$(adj) = 0.811, F = 72.39, $p < 0.0001$). Dry South gini increased from -0.5 to 0.4, described by the relationship: $Gini = 383800 - 578.8year + 0.291year^2 - (4.87 \times 10^{-5})year^3$, ($R^2$(adj) = 0.673, F = 76.4, $p < 0.0001$).

Absolute differences in growth variability are shown in figure 5.5. As with normalised gini, the raw un-normalised gini rose for all regions over the period 1960-2010. Increases and absolute values were highest for the Core Temperate ($Gini = 22190 - 33.5year + 0.017year^2 - (2.83 \times 10^{-6})year^3$, R^2(adj) = 0.601, F = 26.1, $p < 0.0001$), Core Continental ($Gini = 8297 - 12.5year + 0.006year^2 - (1.04 \times 10^{-6})year^3$, R^2(adj) = 0.682, F = 36.8, $p < 0.0001$) and Dry South ($Gini = 12450 - 18.8year + 0.009year^2 - (1.58 \times 10^{-6})year^3$, R^2(adj) = 0.923, F = 200.4, $p < 0.0001$) regions. Gini was lowest,

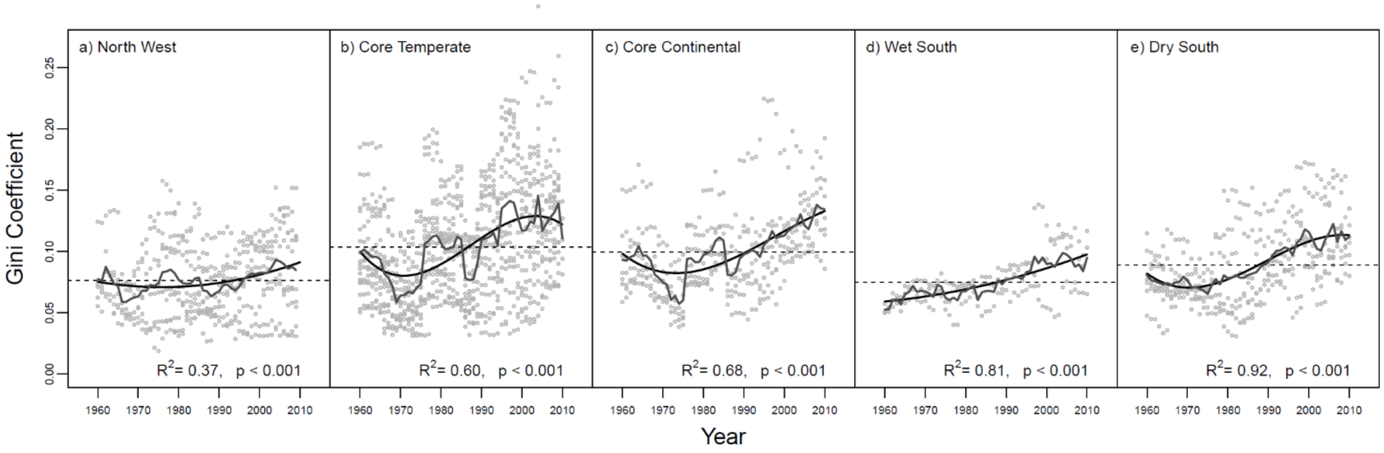

Figure 5.5: Raw, un-normalised gini coefficient for the 5 regions over the period 1960-2010. Individual year values per site are plotted as points, mean regional gini as a dark grey line, and fitted models in black. Regional means are shown as dashed lines.

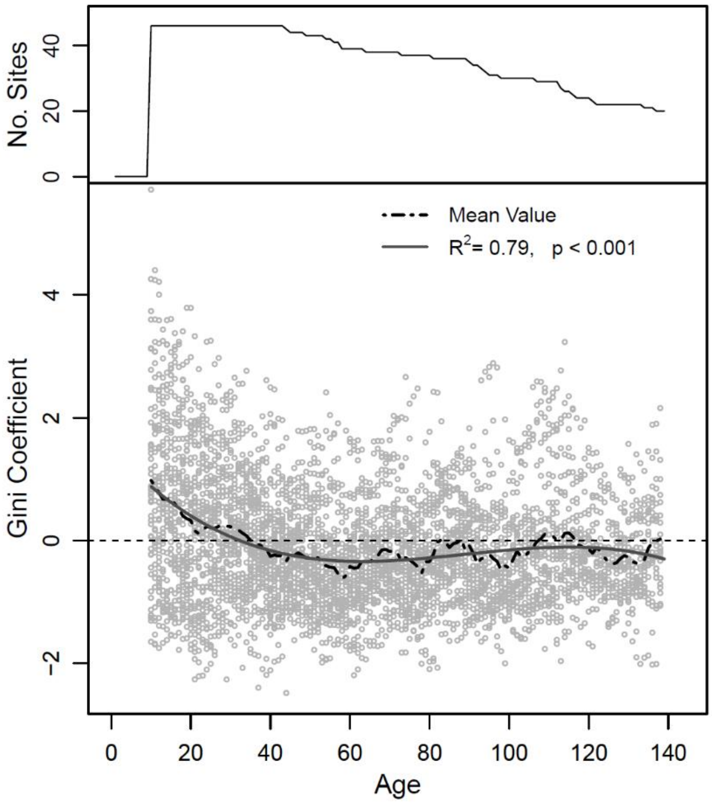

Figure 5.6: Gini coefficient for all sites aligned by age. The top plot shows the sample depth (number of sites). The bottom plot shows individual age gini values per site as points, mean value for all sites as a dashed line, and model fit as a solid grey line.

and had the lowest increases, for the North West $(Gini = 68.2 - 0.069year + (1.75 \times 10^{-5})year^2$, (R^2(adj) = 0.368, F = 15.3, p < 0.0001) and the Wet South region $(Gini = 34.3 - 0.035year + (9.06 \times 10^{-6})year^3$, (R^2(adj) = 0.807, F = 105.8, p < 0.0001).

For the analysis of age related trends in gini over time, figure 5.6 shows the relationship between age and moving window gini up to 139 years. Age has a significant effect on gini, with normalised gini falling from around 1 at 10 years, to around -0.25 at 40 years: $Gini = 1.52 - 0.073age + (8.85 \times 10^{-4})age^2 - (3.31 \times 10^{-6})age^3$ (R^2(adj) = 0.788, F = 160, p < 0.0001). After 40 years of age, growth variability is stable. Potential effects of age on recent gini temporal trends are displayed in figure 5.7. All 3 age classes showed a rise in moving window gini to 0.96 to 1.23 by 2010, described by the regression equations; youngest, $Gini = -88870 + 136.7age - 0.07age^2 - (1.19 \times 10^{-5})age^3$, ($R^2$(adj) = 0.594, F = 43.5, p < 0.0001); middle, $Gini = -66020 + 101.6age - 0.052age^2 - (8.91 \times 10^{-6})age^3$, ($R^2$(adj) = 0.691, F = 66.0, p < 0.0001); oldest, $Gini = 383800 - 578.8age + 0.291age^2 - (4.87 \times 10^{-5})age^3$, ($R^2$(adj) = 0.788, F = 160, p < 0.0001). All age classes show the same temporal pattern in moving window gini: broadly stable

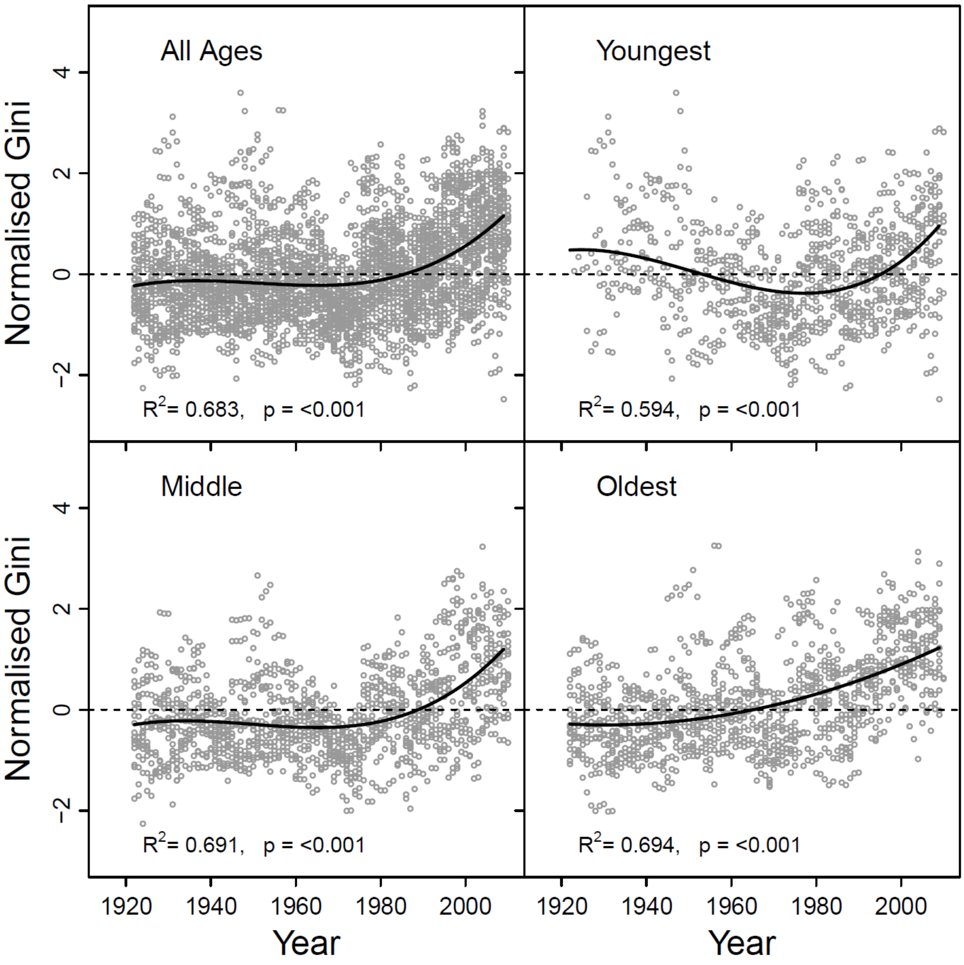

Figure 5.7: Gini coefficient for all sites and for 3 age classes, over the period 1923-2009. Individual site gini values per year are plotted as points, and fitted values as lines.

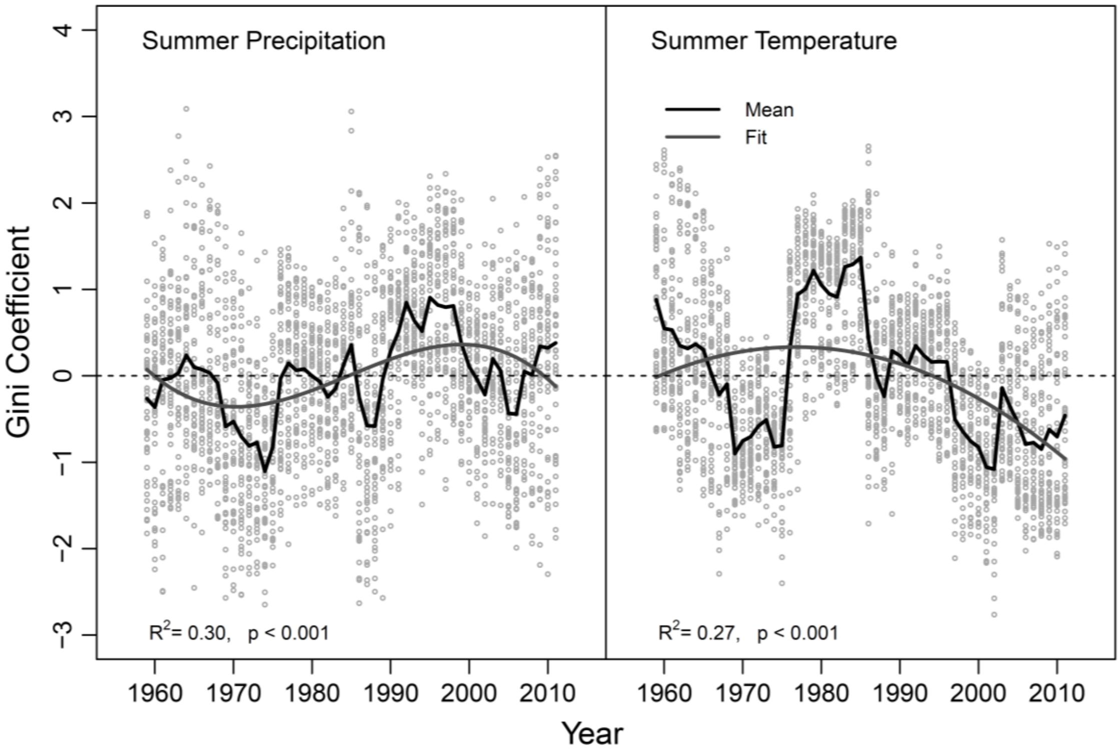

Figure 5.8 Gini coefficient for mean temperature and sum precipitation during the summer months (May to August) for the period 1960 to 2011. Individual site values are plotted as points, with the mean plotted in bold, and fitted values in grey.

gini until the beginning of an increasing phase starting at around 1970 and lasting until the end of the time series in 2010. For the youngest age group, gini was elevated at the start of the period examined, most likely as a result of the age related effect on young tree growth variability described in figure 5.6.

Gini coefficient analysis of the growing season climate data is presented in figure 5.8, representing moving average gini calculated over the period 1950 to 2011. Neither temperature nor precipitation display the same positive trend in variability as evident from the tree-ring data. Summer precipitation gini fluctuated around the mean, according to the relationship: $Gini = -480200 + 725.7age - 0.37age^2 - (6.14 \times 10^{-5})age^3$,

(R^2(adj) = 0.302, F = 7.1, p = 0.0005). Variability in summer precipitation increased from around the mid-1970s to the mid-1990s, but this increase was not sustained for the final decade of the time series, unlike tree-ring gini coefficient. Summer temperature gini peaked from the late 1970s until the mid-1980s: $Gini = -4383 + 4.40age - (1.10 \times 10^{-3})age^2$, ($R^2$(adj) = 0.272, F = 9.3, p = 0.0004). However, from the mid-1980s onwards, variability in growing season mean temperature decreased.

5.4 Discussion

The results presented in this chapter describe characteristics of growth trends and growth variability across the species range for *F. sylvatica*; 1) in the north and centre of the species range radial growth is increasing, whilst growth is stable at the southern range edge; 2) regional scale depressions in growth for range core regions occur in synchrony with large scale drought events; 3) climatic variables predict growth poorly for southern range edge regions; 4) year to year variability in growth is increasing for all regions within the species' range; 5) increases in growth variability are strongest for range core regions; 6) southern range edge regions also display strong increases in growth variability.

The variation in growth trends apparent across the regions of the Multiregional Network highlight opportunities, strengths and emerging concerns for *F. sylvatica*. Growth is increasing most rapidly in the north of the species' range. Research has identified that summer temperature is the major limiting factor on tree growth for poleward range edges (Holtmeier & Broll 2007; MacDonald, Kremenetski & Beilman 2008). However, this explanation for rapid growth increases in the northern UK is not supported by the results of both linear mixed effects modelling (see table 5.2) and climate growth analysis (see figure 4.1), neither of which show an association between summer temperature and growth. Increased growth is in line with modelling predictions for increased future *F. sylvatica* yields for northern UK forests (Broadmeadow, Ray & Samuel 2005). In addition to warming summer temperature, a lengthened growing season can lead to strong increases in growth for forests at the poleward range edge (Shiyatov, Terent'ev & Fomin 2005), which may be a factor for the north west region in this study. It should be restated that the northernmost portion of the Multiregional Network does not represent a treeline in the sense of a region where low temperature imposes a fundamental limit on the growth and recruitment of the species. Rather, human intervention in recent centuries has enabled *F. sylvatica* to establish in Northern UK, where conditions had already been favourable but not yet colonised in the species' northward post-glacial expansion (Birks 1989). Nonetheless, a recent large scale study of over 900 tree-ring chronologies for Europe has found that for North Western Europe, where precipitation is generally not limiting to tree growth, there was a strong positive effect of temperature on tree growth (Babst *et al.* 2013). Thus, the expansion of growth at the north western range edge for *F. sylvatica* may be stronger than for the north eastern range edge, as a precipitation gradient exists in the Scandinavian region from the wet Atlantic west to the more continental east.

For the southern portion of the range, growth was broadly stable. This is in direct contrast to isolated studies at the southern range edge for *F. sylvatica*, where declines in growth were observed (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). This, combined with the poor link between climate factors and radial growth (see figure 5.2d/e), and the lower climate sensitivity demonstrated in chapter 4, implies that southern range edge populations may be more robust than previously thought. Stabilising factors may play an important role in ameliorating increasing drought stress for southern range edge forests, such as the quality of sites to which the species is already restricted at the range edge, along with greater stress tolerance of range edge populations (Lloret *et al.* 2012). For many species at their equatorial range edge, occurrence of the species is already restricted to sites at which local condition strongly buffer the organisms from regional climate (Hampe & Jump 2011). Whilst some studies have found southern range edge populations for multiple species to exhibit low climate sensitivity (Herrero, Rigling & Zamora 2013), many others have reported strong sensitivity to precipitation and growth reductions (Weber, Bugmann & Rigling 2007; Thabeet *et al.* 2009; Martín-Benito, Río & Cañellas 2010). The results presented here for the southern range edge represent the integration of tree-ring data from 13 separate sites, and thus transcend the limitations of case studies, and any potential publication bias towards dramatic results indicating forest decline. However, as this study focuses on *F. sylvatica* alone, that this may be a species specific effect of southern range edge population resilience cannot be ruled out. Furthermore, whilst growth for the southern range edge appears robust, growth variability is increasing, signalling an increase in stress for these regions. The response of forests to increasing water stress due to climate change can involve non-linear threshold processes, with rapid and long lasting effects once tolerance limits are breached (Cavin *et al.* 2013; Lloyd, Duffy & Mann 2013). Consequently, the resilience of southern *F. sylvatica* forests to 20th and early 21st century climate change cannot be assumed to continue indefinitely.

For the range core regions, growth has increased over the period studied. These results contrast with other dendroecological studies, which have reported declining *F. sylvatica* growth for Flanders (Kint *et al.* 2012), across north eastern France (Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010), and for high altitude central European forests (Dittmar, Zech & Elling 2003). Thus, fears of a widespread decline for *F. sylvatica* across its entire range core distribution in Europe are not supported by the large scale, multi-site study presented in this chapter. However, periodic reductions in growth have occurred, tied to regional scale drought events. This finding of periodic growth reductions, combined with the strong increases in growth variability for range core regions, highlights high and increasing sensitivity to climate (and specifically drought). A continent wide assessment of tree growth for Europe reported similarly that the sensitivity of tree growth to drought was higher in central Europe and the south of the UK compared to the Mediterranean region (Babst *et al.* 2013). Recent work has also highlighted the elevated response to drought conditions for *F. sylvatica* forests growing at mesic sites, compared to dry sites (Weber *et al.* 2013), and to increases in drought sensitivity at wetter sites over recent years alongside increases in the occurrence of years during which growth is suppressed (Friedrichs *et al.* 2009; Scharnweber *et al.* 2011). Therefore, the forecast increases in water stress across many central European regions in the 21st century are likely to have significant negative impacts on *F. sylvatica* forests.

Previous studies have examined the tree growth variability for multiple species at sites near their southern range edge in the Mediterranean region, and found an increase in growth variability over time (Tardif *et al.* 2003; Andreu *et al.* 2007). The results presented here demonstrate that this phenomenon is not restricted to range edge populations. In fact, increasing variability in tree growth is a feature of *F. sylvatica* forests spanning the species entire latitudinal range. At the temporal and spatial scale of this study, the influence of individual site conditions and local disturbances can be discounted, suggesting that the common climatic influence for all sites within the study is responsible (Parmesan & Yohe 2003). However, there is no similar increase in the variability of growing season climatic conditions, suggesting that the increase in growth variability is not simply due to a normal response to year to year climate variability. Absolute growth variability is lowest for the regions where precipitation is highest (North West and Wet South regions, see figure 5.5 and table 3.1). Crucially, the increase in growth variability is stronger for forests within the geographical core of the species range compared to southern range edge forests. This appears to contradict the general assumption in tree-ring studies that variability in annual growth increases with site aridity (Fritts 1976). However, relict populations at the southern range edge are likely to exist at sites where fine scale environmental conditions (e.g. edaphic factors or local topography) act to decouple the site from a regional climate which is too hot and too dry for the species (Hampe & Jump 2011). Additionally, high levels of genetic diversity both within and between range edge populations, alongside adaptation to local conditions, mean that range edge populations can be better suited to arid conditions (Hampe & Petit 2005). This prediction is supported by provenance trials which show that provenances from the southern edge of the species range had functional traits which allowed them to perform better in the hottest and driest part of the year when compared to provenances from more mesic core sites (Robson *et al.* 2012). The elevated growth variability for range core populations suggests that climate stress is increasingly manifesting itself in the growth of trees in the form of periodic growth reductions, and that range core populations are often neither adapted to these conditions nor sited where local conditions can buffer them from the worst effects. Southern range edge forests too are experiencing rising growth variability, although large reductions in growth due to drought events appear to be absent from the growth record. Nonetheless, the presence of increasing growth variability for all *F. sylvatica* regions in the Multiregional Network is a strong indicator of a growing challenge to the continued health and productivity of these forests.

This study finds both an absence of growth reductions, and a presence of increasing growth variability across the latitudinal range for *F. sylvatica*. Interpreting these at the broadest level, an increase in stress on *F. sylvatica* forests due to climate is resulting in higher variability in tree growth from year to year. This increase in stress has so far failed to manifest itself in large scale growth reductions for any regions. However, periodic large scale regional reductions in growth are apparent for the most drought sensitive regions – the range core. The degree of dissociation between southern range edge populations and their regional climate is further demonstrated in this chapter through stable growth trends, and the poor explanatory power for climate variables in growth models. Future research should seek to characterise climate and water availability locally for southern range edge sites, in order to determine to what extent climate as experienced by trees at population level differs from regional climate. Additionally, the predictive power of modelling approaches could be usefully combined with climate projection datasets in order to project potential growth and variability trends for future climate scenarios. This study represents an assessment of *F. sylvatica* growth and climate-response at a higher spatial scale than commonly attempted. However, many other published growth data exist for *F. sylvatica*. In combination with the new data that have been collected for the research presented here, tree-ring data for *F. sylvatica* could now enable a truly range-wide assessment of the climate and growth response of the species. Future collaborative efforts to integrate the work of separate research groups holding such data would yield answers to fundamental questions of biogeography and global change biology in addition to informing on the performance of this species in the future and recent past across Europe.

6. Extreme Drought Effects Within and Between Tree Species in a mixed Forest Stand

This chapter presents a study which used mortality data from a long term monitoring programme in the core of *F. sylvatica's* range, alongside annual growth data from tree-rings to examine the effect of, and recovery from, an extreme drought event. Both intraspecific and interspecific drought response in mixed species forest is explored here, as is how differential responses affect competitive dominance between the co-dominant species *F. sylvatica* and *Q. petraea*. This study has been published as a peer reviewed paper, see Appendix 2 for details and the abstract.

6.1 Introduction

Research on biotic responses to climate change has largely focused on assessing the response to gradual changes in mean conditions. However, the effect of extreme events is increasingly being recognised as a key driving force in the response of organisms, species and communities to climate change (Gutschick & BassiriRad 2003; Jentsch, Kreyling & Beierkuhnlein 2007; Smith 2011). Studies of the effect of drought have linked extreme events to increased risk of mortality, reduction in growth of ecosystem dominant species, reduction in ecosystem primary productivity, and altered ecohydrological regime (Breshears *et al.* 2005; Ciais *et al.* 2005; Bigler *et al.* 2006; Gitlin *et al.* 2006; Adams *et al.* 2012). Furthermore, while the response to extreme events differs among species, species-specific impacts can cascade to ecosystem-level effects if dominant or competitor species subjected to extreme events suffer differential mortality (Thibault & Brown 2008).

Given their importance for global carbon and hydrological cycles, and their role in providing and modifying habitat for a wide variety of associated organisms, shifts in species composition of forest trees may have far reaching consequences (Dixon *et al.* 1994; Soja *et al.* 2007; Bonan 2008). It is essential, therefore, to understand how extreme climatic events can affect growth and competition between co-occurring tree species. Recent studies have linked changes in the availability of moisture to increased levels of tree mortality, in temperate and boreal forests (Peng *et al.* 2011; Van Mantgem *et al.* 2009; Hogg *et al.* 2008; Michaelian *et al.* 2011). However, the long term effects of extreme drought and the recovery of surviving trees are poorly documented (Martínez-Vilalta, Lloret & Breshears 2011).

The maintenance of species diversity has been suggested as a means to promote ecosystem resilience in the face of environmental change, through response diversity (Elmqvist *et al.* 2003). Where multiple species perform the same ecosystem function yet display a heterogeneous response to environmental change, biodiversity might provide insurance against ecosystem regime shift, where the ecosystem shifts to a less productive or otherwise less desired state (Folke *et al.* 2004). Monoculture systems, by contrast, can be particularly vulnerable to rapid ecosystem collapse and regime shift once thresholds in environmental conditions are breached (Scheffer & Carpenter 2003). This is particularly true for forests, where the longevity of individual trees means that establishment may have taken place under climate conditions which now occur rarely or have even ceased to exist at that location (Petit & Hampe 2006). However, the response of a single species to environmental change can be expected to display a degree of heterogeneity, as intraspecific competition within any population can be mediated by fine scale environmental site characteristics and variation in drought response traits (Choler, Michalet & Callaway 2001; Bolnick *et al.* 2011). Transplant studies, have demonstrated considerable intraspecific variation in drought traits and responses for seedlings and saplings of provenances taken from different areas of a species' range (Robson *et al.* 2012; Rose *et al.* 2009; Peuke *et al.* 2002; Meier & Leuschner 2008). Recent work using molecular markers has demonstrated evidence that altered climatic conditions can apply a selective pressure within natural populations, resulting in changing genotypic frequencies over time (Jump *et al.* 2006; Bilela *et al.* 2012). Whilst the fine scale spatial patterns of drought response within a species are often patchy, eliciting details of this at the stand scale is challenging (Allen *et al.* 2010; Martínez-Vilalta, Lloret & Breshears 2011). With changing environmental conditions, a competitive advantage for a dominant species may weaken, with increasing frequency and strength of drought conditions acting as a stabilising mechanism favouring coexistence with otherwise less competitive species (Terradas, Peñuelas & Lloret 2009). Once a threshold of drought intensity and frequency has been reached the competitive advantage could switch to the historically less competitive but more drought tolerant species.

Understanding the effect of predicted climatic change on widespread dominant species is, therefore, particularly important to inform on potential future responses at the community level. *Fagus sylvatica* frequently dominates temperate forests over large areas of Europe, but is considered to be particularly drought sensitive, and is predicted to be outcompeted by more drought tolerant species in many regions as the climate warms (Broadmeadow, Ray & Samuel 2005; Czucz, Galhidy & Matyas 2011; Hlasny *et al.* 2011). Dendroecological studies from the equatorial edge of the species' range have shown a reduction in growth as a response to elevated drought stress associated with climate change, which is expected to result in a reduction in available habitat area in this mountainous part of the species' range (Jump, Hunt & Peñuelas 2006; Piovesan *et al.* 2008). However, growth decline has recently been reported in some regions within the range core of *F. sylvatica*, and also linked to increased drought stress (Bontemps, Hervé & Dhôte 2010; Charru *et al.* 2010). Furthermore, the research presented in chapters 4 & 5 of this thesis demonstrates two key points. Firstly, that severe drought induced reductions in growth are not at all typical for southern range edge regions. Secondly, that drought impacts are most pronounced in the range core regions, and in the south of the UK in particular.

Although usually dominant, *F. sylvatica* frequently coexists with competitor species in mesic, multi-species woodlands, with one common co-dominant being sessile oak (*Q. petraea*). Many studies have demonstrated the superior below and above ground competitive ability of *F. sylvatica* over oak (*Quercus sp.*) in mature mixed species woodlands (von Lüpke 1998; Leuschner *et al.* 2001; Hein & Dhôte 2006). By contrast, greater rooting depth, lower fine root sensitivity to drought, differing hydraulic architecture, and lower susceptibility to cavitation of *Q. petraea* all contribute to overall greater drought tolerance (Aranda, Gil & Pardos 2000; Leuschner *et al.* 2004; Aranda, Gil & Pardos 2005). Thus, modelling studies forecast an increase in the spatial segregation of *F. sylvatica* with competitor species such as *Q. petraea* under climate change scenarios, with a reduction in habitat suitability and biomass yield of *F. sylvatica* (Broadmeadow, Ray & Samuel 2005; Meier *et al.* 2011). Ultimately, therefore, differing ecological and physiological characteristics between *F. sylvatica* and its competitors will combine to determine their responses to altered water availability, with the expectation that the competitive ability of *F. sylvatica* may be reduced in many regions throughout its range if droughts become more frequent and more severe.

Consequently, this study seeks to determine the extent to which extreme drought led to changes in the growth and mortality of adult *F. sylvatica* and the competitor species, *Q. petraea* and how these changes modulate inter and intraspecific competitive interactions between these species. The following key issues are focused upon: 1) How do surviving *F. sylvatica* and *Q. petraea* cohorts differ in growth pre and post-drought? 2) How long do the different cohorts and species take to recover from the effects of an extreme drought, and do they return to previous levels of growth? 3) Given expected differences in drought susceptibility and competitive ability between these species, how have their competitive interactions been altered by drought and what are the implications for future forest composition?

To address these questions, I used tree condition and mortality data derived from a long-term monitoring site where individual tree growth and condition have been assessed since 1945, in combination with new dendroecological data (Peterken & Jones 1987; Peterken & Jones 1989). At this site, the extreme drought in 1976 led to divergent responses of condition and mortality within and between co-occurring species (Peterken & Mountford 1996), thereby enabling an exploration of the intra and interspecific responses to drought and post-drought recovery.

6.2 Methods

Study Site

Lady Park Wood National Nature Reserve (southwest UK, 51°49’N, 2°39’W, see figure 6.1) is a 35.2 hectare, ancient, mixed species, deciduous woodland which has been managed as a minimum intervention forest reserve for ecological research since 1944 (Peterken and Mountford, 1996, Peterken and Jones, 1989). The most abundant canopy dominant tree species are: *F. sylvatica*, *Q. petraea*, *Fraxinus excelsior* L. (common ash), *Tillia cordata* and *Tillia platyphylos* (small-leaved lime and large-leaved lime respectively). The site is in

Figure 6.1: Location of the study site in relation to the geographical range of F. sylvatica within the British Isles. The range of F. sylvatica is shown in grey, representing the presence of both native and non-native populations (Source: New Atlas of the British & Irish Flora, http://www.brc.ac.uk/plantatlas/)

a steep sided valley, where the River Wye has cut through the underlying carboniferous limestone. Thin well-drained acidic brown earth and skeletal, organic loam rendzina soils cover much of the upper slopes where the old growth predominates (Peterken & Jones 1987). The regional climate is temperate, with 803 mm of precipitation annually and a mean temperature of 9.3 °C (using the baseline period 1961-1990). Since *F. sylvatica* extends from Southern Fennoscandia in the north to the Mediterranean region in the south, and from the edge of Western Europe to the Carpathian Mountains in the east, our study site is at the western edge of the core of the species climatic distribution (see figure 6.1), although human intervention has significantly advanced its postglacial geographical distribution in more northern parts of the UK (Birks 1989).

Climate Data & Drought Indices

Climate data for the site was obtained from the Met Office UK 5 km^2 gridded dataset, covering the period 1914-2006 (Perry & Hollis 2005). Using this dataset, annual values were calculated for mean temperature and total precipitation for 1914-2006, and regression analyses performed to identify any temporal trends (see figure 6.2).

Droughts were identified by using the Standardised Precipitation-Evapotranspiration Index (SPEI). This method has the advantage over alternatives, such as the Palmer Drought

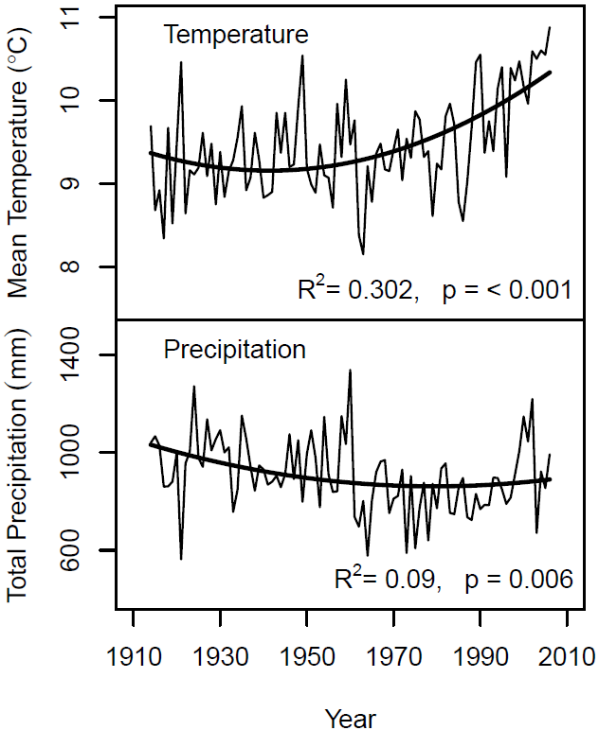

Figure 6.2: Temperature and precipitation for the study site, using 5 km^2 gridded climate data for the period 1914-2006 (Perry & Hollis 2005). Temporal trends were described using regression analyses: $Temperature = 1073 - 1.096year + (2.824 \times 10^{-4})year^2$, *($R^2$ adj = 0.302, p < 0.001),* $Precipitation = 157100 - 157.8year + 0.040year^2$, *($R^2$ adj = 0.09, p = 0.006).*

Severity Index, of enabling the calculation of drought utilising a time scale relevant to the study system in question (Vicente-Serrano, Beguería & López-Moreno 2010). In combination with the Standardised Precipitation Index (SPI), the SPEI enables an evaluation of the degree to which climate warming contributes to drought. SPEI uses monthly precipitation and potential evapotranspiration (PET) as input data, whilst SPI uses only precipitation data. PET was calculated using the Thornthwaite method, using monthly mean temperature and a correction coefficient derived from latitude (Thornthwaite 1948). SPEI and SPI were calculated at 12 month time-scales, with monthly index values derived from climate data over the previous 12 months, and using log-logistic distributed indices with parameters fitted using unbiased probability weighted moments. This timescale represents current and partial previous year conditions for tree growth. The difference between the two indices was calculated ($SPEI - SPI$), representing the contribution of PET to drought (Vicente-Serrano *et al.* 2011). Linear regressions were performed on SPEI, SPI and the difference, to identify any temporal trends. SPI and SPEI were compared by calculating Pearson's r correlation coefficients between monthly values.

The Thornthwaite method for calculating PET used above has recently received criticism for causing assessments of drought to be overestimated (Sheffield, Wood & Roderick 2012). The Met Office UK 5 km^2 gridded dataset includes data for mean monthly cloud cover and wind speed for the period 1969-2004 (Perry & Hollis 2005), enabling PET to be calculated by other methods. To validate drought indices calculated over the longer 1914-2006 period using the Thornthwaite method, we additionally calculated SPEI for this shorter time-period, using PET derived from the Penman-Monteith equation (Allen *et al.* 1994). Correlation analysis and linear regression were then used to compare it to SPEI calculated using the Thornthwaite method, and to identify any trend.

Tree Ring Sampling

Previous research at this site assigned individual *F. sylvatica* drought survivors into two classifications according to the level of drought damage sustained in 1976 (Peterken & Mountford 1996). Severely damaged individuals had suffered extensive canopy dieback, bark necrosis, trunk scarring and limb loss. Minimally damaged individuals escaped with only minor canopy dieback. These two classes, along with the individuals that perished, were intermixed throughout the old growth stand. This study focused on assessing pre-drought growth differences between these damage classes and their post-drought recovery rate, to identify if growth- or size-related factors might predispose individuals to drought-induced growth decline.

Three sets of mature, canopy dominant or co-dominant trees were identified using existing site stem maps for the woodland, in combination with examination of individuals in the field. These three sets were: severely damaged *F. sylvatica* (n = 32), minimally damaged *F. sylvatica* (n = 33), and *Q. petraea* (n = 30), as described in table 1. In 2010,

Table 6.1:. Descriptive statistics for the tree-ring chronologies; BAI, basal area increment; $Rbar$*, mean inter-series correlation; EPS, expressed population signal.*

	No. of trees	No. of cores	Mean series length (years)	Series Duration	Mean BAI (mm^2)	Mean Sensitivity	Rbar	EPS
Fagus sylvatica (severely drought damaged)	31	62	109.6	1856 - 2009	2523 ± 94	0.29	0.35	0.94
- pre-drought subset				1929 - 1975	2973 ± 92	0.24	0.41	0.96
- post-drought subset				1976 - 2009	1902 ± 128	0.39	0.34	0.94
Fagus sylvatica (minimally drought damaged)	32	68	111.8	1832 - 2010	2905 ± 95	0.32	0.42	0.96
- pre-drought subset				1929 - 1975	3265 ± 97	0.22	0.49	0.97
- post-drought subset				1976 - 2009	2407 ± 152	0.35	0.43	0.96
Quercus petraea	30	58	174.6	1770 - 2009	2530 ± 51	0.23	0.45	0.96
- pre-drought subset				1929 - 1975	2428 ± 66	0.22	0.43	0.96
- post-drought subset				1976 - 2009	2671 ± 80	0.21	0.38	0.95

Core samples were extracted, prepared, measured and crossdated using the methodology described in chapter 2.

Permanent Transect Inventory

A series of permanent transects were established in the woodland in 1945, covering 0.9 ha of the 14 ha of old growth (Peterken & Jones 1987). These were 20 m wide transects running down slope and recorded in 1945, 1955, 1977, 1983, 1986, 1992, 2000 and 2010, thus providing a 65 year record of tree growth, mortality and recruitment for all individual trees and shrubs present (Peterken & Mountford 1996). Each tree or shrub attaining a height of 1.3m was mapped, and circumference at breast height recorded. Records were also made of canopy position, crown size, crown dieback, and notes of the condition of individual stems. For each case of tree death, the primary cause of death was attributed based on survey assessment and classified as either drought (i.e. severe drought damaged as described above, followed by death), competitive exclusion (overtopping by neighbouring trees, followed by decline and death) or other factors. Mortality of canopy *F. sylvatica* (n = 102) and *Q. petraea* (n = 34) was examined from 1955-2010 using records from the permanent transects. 1955 was used as a baseline date, as no canopy trees of either species died during the period 1945-1955.

Data Analysis

Basal area increment (BAI) is well established in forest ecology as measure of tree growth which can be used to study the vigour of individual trees and populations (Biondi 1999; Bigler & Bugmann 2003; Biondi & Qeadan 2008b). BAI tends to increase sharply in juvenile trees before reducing in gradient when the tree reaches maturity, however it does not display the same age-related trends as raw ring widths, and is expected not to decline markedly during the mature phase of a tree’s growth unless the tree is severely stressed (Pedersen 1998). Here, BAI was calculated using raw, non-detrended ring widths and radii using equation 2.4 (page 12). BAI was then plotted using a 9 year running mean to facilitate the visual identification of the long term growth trend (Jump, Hunt & Peñuelas 2006). The inflection point at which post-release growth started to plateau was identified as being the beginning of the mature phase of growth, mature growth being 1929-2009 for the severely damaged *F. sylvatica*, 1927-2009 for the minimally damaged *F. sylvatica*, and 1883-2009 for *Q. petraea*. The same 1929-2009 mature phase of growth was subsequently used for all three BAI series, to allow the comparison of the series over the same period. All further BAI analysis used the raw BAI data, not the running means. The 3 mature growth series were then split into pre-drought (1929-1975) and post-drought (1976-2009) subsets.

In order to compare pre-drought growth rates for the *F. sylvatica* cohorts, pre-drought BAI for each tree was prewhitened by fitting an autoregressive model, selected using Akaike's information criterion (AIC), and combined into pre-drought chronologies. Pre-drought growth was then compared by pooling the severely and minimally damaged BAI chronologies, with dummy variables assigned according to cohort of tree. Linear regression was then performed on the pooled data, with the statistical significance of the dummy variable used to assess differences in pre-drought growth between the cohorts (Draper & Smith 1998).

Post-drought growth for all *F. sylvatica* and *Q. petraea* cohorts was assessed using linear and non-linear growth models (Paine *et al.* 2012) fitted to mean BAI chronologies, and with the most appropriate models chosen by evaluation of AIC. The best performing models selected for post-drought BAI were: two parameter asymptotic regression models for both *F. sylvatica* series, and a four parameter log-logistic model for *Q. petraea*. Subsequently, post-drought BAI was standardised by dividing individual year growth values by the mean pre-drought annual BAI, thus transforming BAI into a dimensionless and comparable index, and then plotted to illustrate relative recovery.

In order to assess whether the 1976 growth response was extreme for *F. sylvatica* at the study site, BAI for the severely damaged *F. sylvatica* was compared to SPEI. Growing season mean SPEI was calculated for the period April to September, giving a value for the drought stress during the growing season which was then transformed using the formula $\log(-SPEI + 1)$, to obtain a normally distributed data set. BAI and growing season mean SPEI for the period 1929-1975 were then converted to z-scores, and plotted with normal probability contours added as data ellipses around the scatterplot. The 1976 value was then added for comparison to the probability contours of the 1929-1975 data.

Trees stressed by environmental factors (such as aridity) will generally produce rings with higher year-to-year variability than less stressed individuals (Fritts, 1976). Therefore, inter-year growth variability can be used as an indicator of plant stress. Gini coefficient (G) is a common measure of data heterogeneity, and has been proposed as being particularly appropriate for the analysis of tree-ring data (Biondi & Qeadan 2008a). Therefore, G was calculated for the pre (1929-1975) and post (1976-2009) drought portions of the mature phase of tree growth for all groups. G for the minimally damaged *F. sylvatica* was transformed using $\frac{1}{G^{0.5}}$ to obtain normally distributed data. G was then compared within and between groups using t-tests and paired t-tests (utilising the same transformation for comparison with the minimally damaged data). Given recent efforts to integrate the use of effect size statistics in the biological sciences as a way of evaluating the biological importance of the factor under investigation (Nakagawa & Cuthill 2007), standardised mean difference (Cohen's d, the difference between the two means divided by the standard deviation) was calculated to evaluate effect size, and reported using established values of effect size, i.e. small$(0.2 < d < 0.5)$, medium $(0.5 < d < 0.8)$ and large $(d > 0.8)$ (Cohen 1988).

The relationship between tree growth and climate was examined using response function analysis, a variant of multiple regression analysis which uses monthly climate predictor variables, orthogonalised as principal components, to elicit the climate drivers of growth (Zang & Biondi 2012). In this analysis, a series of coefficients were calculated, relating the ring width indices from the de-trended chronologies (according to the methods in section 2.4) to monthly climate variables covering from the beginning of the previous year's growing season until the end of the current year's growing season (Cook & Kairiukstis 1990; Biondi & Waikul 2004). Monthly precipitation and temperature values from the 1914-2006 climate dataset described above were used, with a 17 month window from May of the previous year until September of the current year. 1000 bootstrap replicates were used (Biondi 1997), and significance calculated at the 95% level. The analysis was repeated using Pearson's product moment correlation functions.

6.3 Results

Climate and Drought Indices

Temperature has increased over time, with the rate of increase accelerating from the mid 1960's onwards (see figure 6.2). Temperature increased by 1.02 °C over the 40 years 1966-2006, according to the relationship: $Temperature = 1073 - 1.096 year + (2.824 \times 10^{-4}) year^2$, ($R^2$ adj = 0.302, $p < 0.001$). Precipitation declined over the study period, but has remained stable since the 1960's. Mean precipitation for the period 1996-2006 was 853 mm ± 20.4.

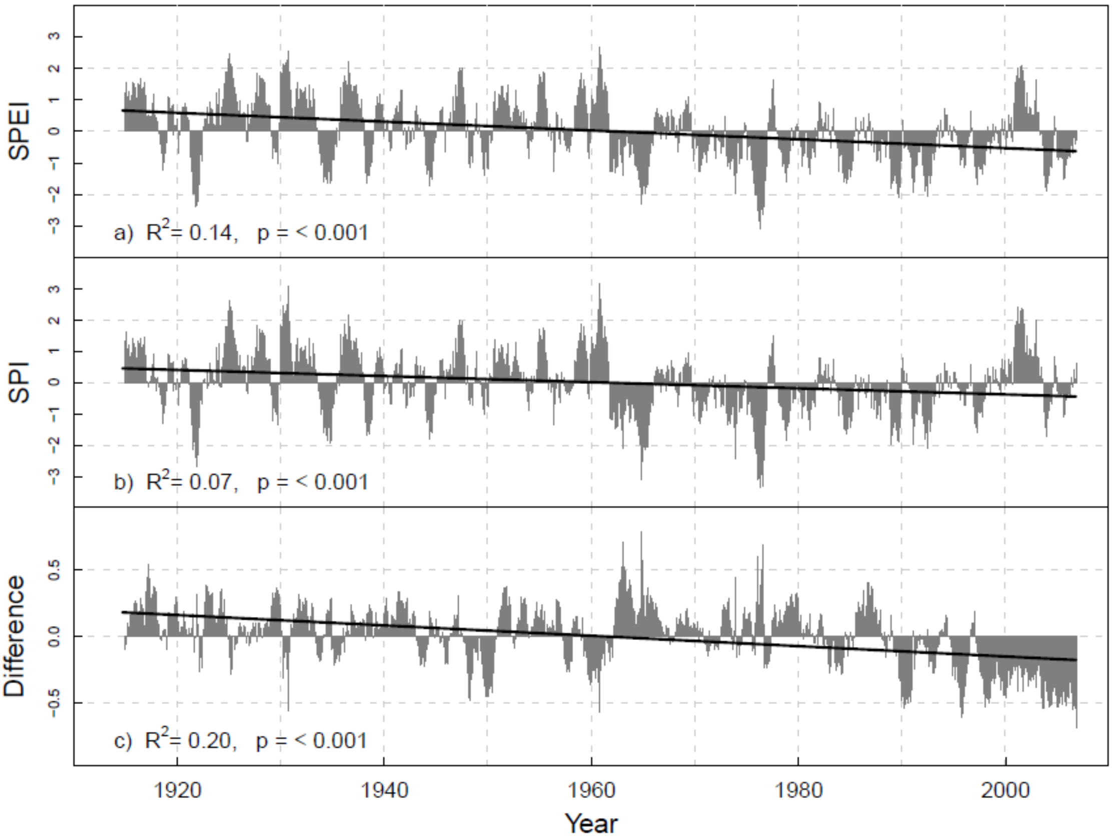

Figure 6.3: Drought indices for the study site, calculated using 5 km² gridded climate data. The indices shown are: a) Standardised Precipitation-Evapotranspiration Index (SPEI), b) Standardised Precipitation Index (SPI), and c) Difference (SPEI – SPI). Monthly values are plotted, calculated over a 12 month time scale.

Comparison of SPEI calculated using the Penman-Monteith and Thornthwaite methods showed that both methods produced similar results (Pearson's r correlation coefficient = 0.987). Linear regression of $SPEI(Thornthwaite) - SPEI(Penman)$ revealed a small but statistically significant positive trend ($R^2 = 0.10$, $p < 0.001$), i.e. SPEI (Penman) gave results showing a stronger drought trend. Consequently, the more conservative approach using calculation of SPEI based on PET calculated by the Thornthwaite method over the longer timescale (1914-2006) is used in all further analyses.

The drought indices SPEI and SPI show that the 1976 drought was the most exceptional drought during the period 1914-2006 (see figure 6.3). Using the minimum recorded index value as a measure of peak drought intensity, the 1976 drought exceeded the second most intense drought (in 1921) by 30.8%. The minimum SPEI value recorded during the drought was -3.08. Index values were almost constantly negative throughout the period

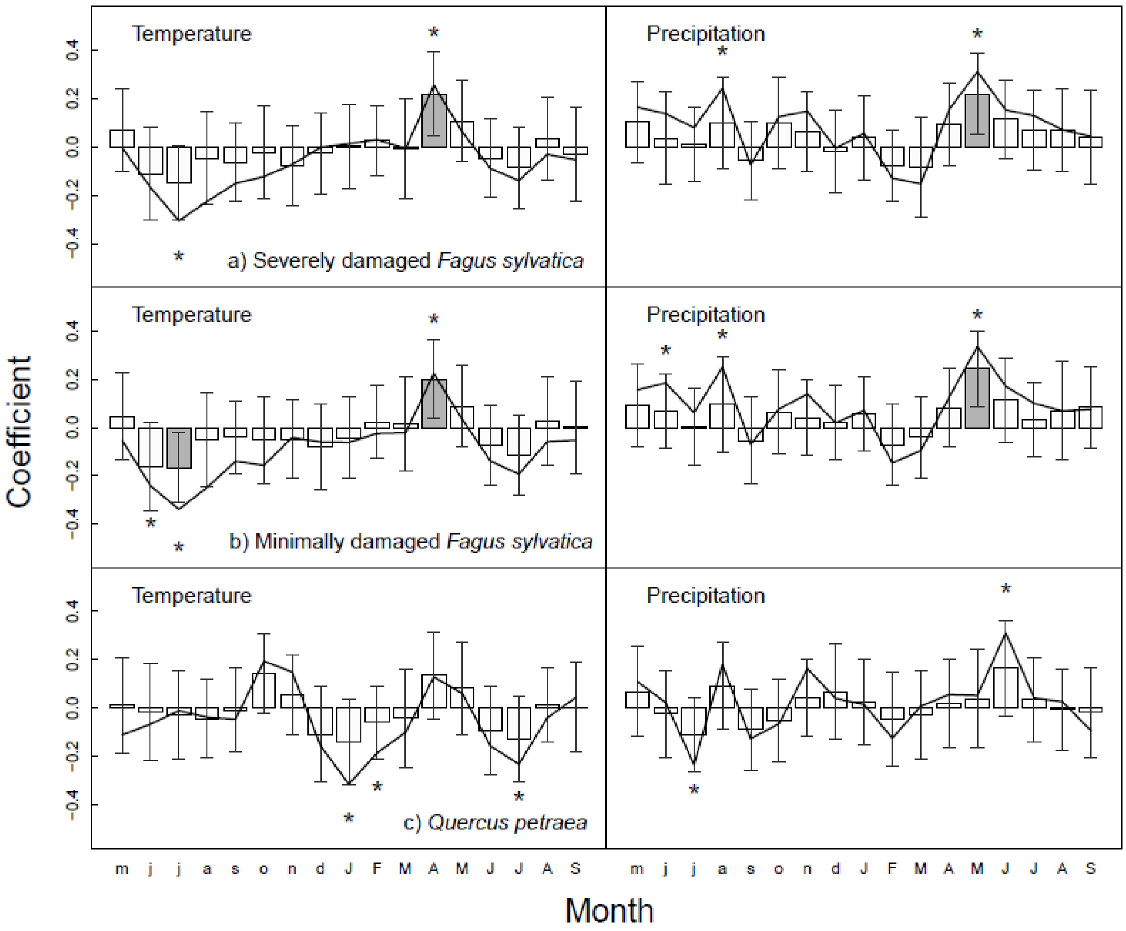

Figure 6.4: Climate growth analysis for the three cohorts of trees, showing the relationship between annual radial growth and climate factors in the previous and current year over the period 1914-2006. Response function coefficients are plotted using bars (shaded bars represent significant monthly factors), and correlation function coefficients are plotted using lines (asterisks represent significant monthly factors). On the x-axis, lower case letters represent months in the previous year, and upper case letters represent months in the current year.

1970-1976, representing a prolonged period of moisture deficit. The long term trend for SPEI is for increasing drought ($SPEI(t) = 26.99 - 0.138t$, where t = time, $R^2 = 0.14$, $p < 0.001$) and also increasing, but more weakly, for SPI ($SPI(t) = 19.34 - 0.099t$, $R^2 = 0.07$, $p < 0.001$). The two indices are highly similar with a Pearson's r correlation coefficient of 0.97. However, despite this strong similarity, the difference plot reveals a deepening contribution of PET (and therefore of climate warming) to drought stress ($Difference(t) = 7.65 - 0.004t$, $R^2 = 0.20$, $p < 0.001$).

Climate Growth Relationships

Response function analysis shows that for both *F. sylvatica* damage classes, warm springs and wet summers in the current year favour growth. There is a negative effect of high temperatures in the previous summer for the minimally damaged group (see figure 6.4). However, whilst the same negative effect is present for the severely damaged group, it is weaker and narrowly fails to achieve statistical significance. *Q. petraea* has no statistically significant relationships between climate and growth in any month demonstrating that, at this site, the growth of *F. sylvatica* is more sensitive to climatic variation than that of *Q. petraea*. These results were corroborated by similar output from correlation function analysis.

Mortality

On the permanent transects, of 102 initial live, mature and canopy dominant *F. sylvatica* recorded in 1955, 28 had died by 2010 with 24 of those occurring between 1977-2010. In figure 6.5, tree mortality is broken down over time by cause of death, revealing a strong pulse of mortality in *F. sylvatica* following the 1976 drought. *Q. petraea* mortality, by contrast, was predominantly due to competition, i.e. through exclusion by overtopping

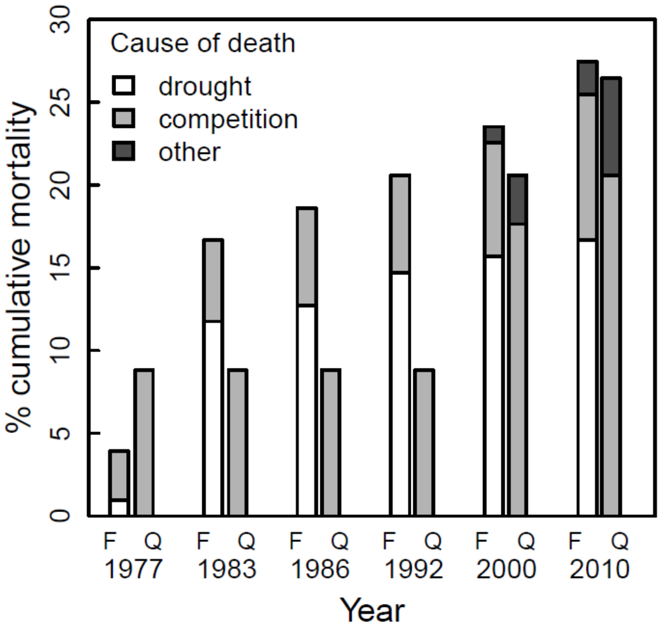

Figure 6.5: Mortality of canopy trees assessed in survey years on the permanent transects from 1977-2010, with cause of death apportioned. On the x-axis, F= F. sylvatica, and Q = Q. petraea.

from neighbours. No *Q. petraea* death occurred during the period 1977-1992 immediately following the drought, whereas 17% of *F. sylvatica* died. Other causes of death for both species reported were: windthrow (n = 3) and squirrel debarking (n = 1).

Ring Width Index Chronologies

Summary statistics for the three chronologies are given in table 1. *Q. petraea* (175 years mean series length) were older than *F. sylvatica* (110 and 112 years mean series length for the severely and minimally damaged respectively). Mean sensitivity was in the region of 0.22 – 0.37 for all series, within the range of 0.1-0.4 judged to be suitable for crossdating (Fritts 1976). Lower $\bar{r}$ (inter-series correlation) was recorded for all three chronologies after the drought compared to before, i.e. the growth response to climate was more variable between trees in each chronology after the drought. EPS was consistently high, with a minimum value of 0.94 being comfortably above the threshold minimum of 0.85 (Wigley, Briffa & Jones 1984; Cook & Kairiukstis 1990). Figure 6.6 shows de-trended and standardised chronologies. Both *F. sylvatica* chronologies record their lowest ring width index (RWI) values over the whole time series following the 1976 drought. This was followed by a rapid recovery to a >1 RWI value by 1980 for the minimally damaged chronology, comparing with approximately a full decade before >1 RWI was regained for the severely damaged individuals. The subsequent droughts of 1990 and 2004 also had an effect on tree growth, with low RWI values recorded. By contrast, the *Q. petraea* chronology shows no strong suppression effect related to drought years, and in general RWI is much less variable over time, suggesting less growth sensitivity for this species to climate conditions at this site.

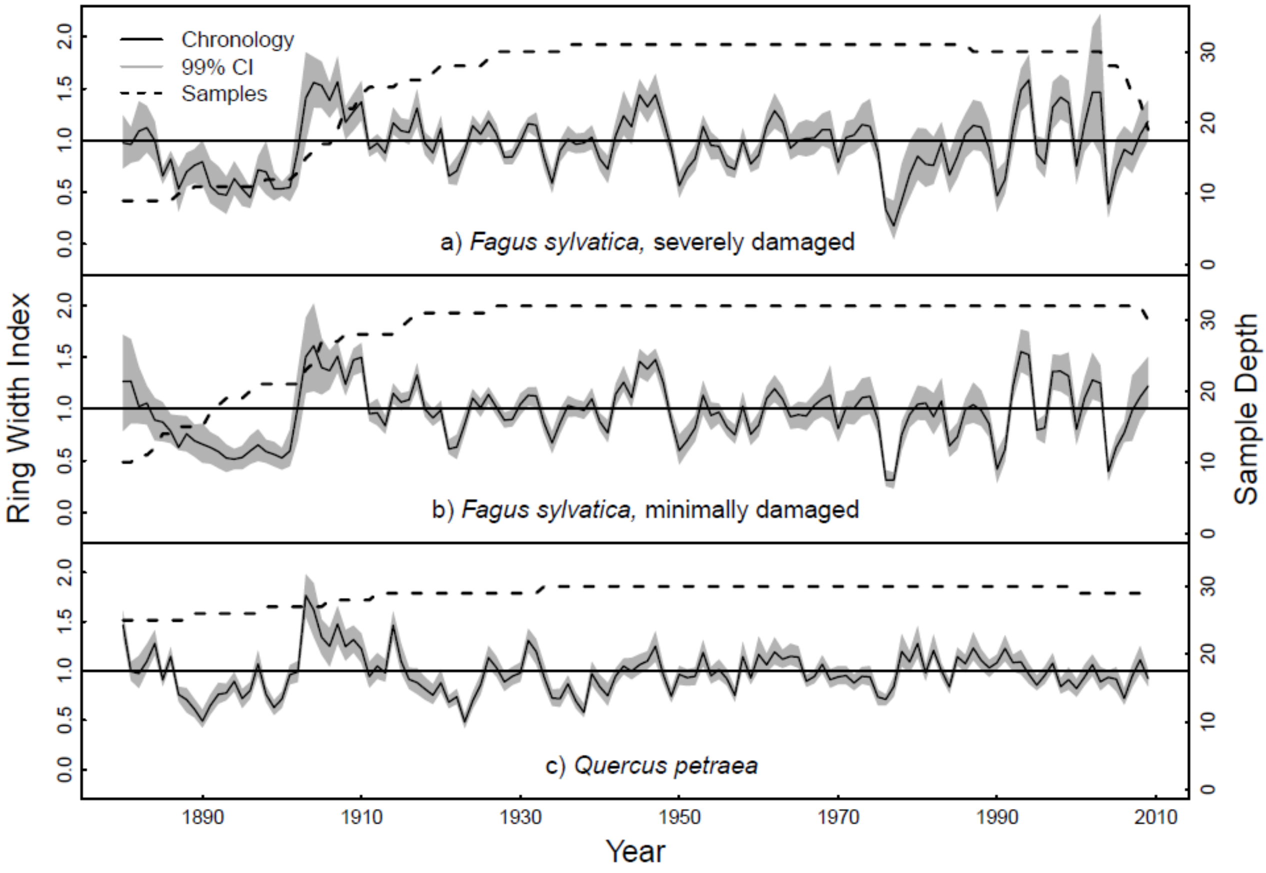

Figure 6.6: Detrended ring width indices for the three cohorts of trees, with 99% bootstrapped confidence intervals (using 1000 bootstrap replicates).

Growth Variability

Analysis of growth variability using Gini coefficient for the series, show that G increased post-drought for the severely damaged *F. sylvatica* (t = 8.67, df = 50.77, p < 0.0001) with a large effect size (d = 2.17, 95% CI 1.54/2.80), and also increased for the minimally damaged *F. sylvatica* (t = 6.50, df = 53.13, p < 0.0001) again with a large effect size (d = 1.41, 95% CI 0.86/1.96) (see figure 6.7). There was no significant difference between the severely damaged and minimally damaged trees before the 1976 drought (W = 634, p = 0.059; small effect size: d = 0.45, 95% CI -0.05/0.95). Post-drought, G was higher in the severely damaged trees compared to the minimally damaged trees (W = 714, p = 0.003; medium effect size: d = 0.74, 95% CI 0.22/1.24). G did not change in *Q. petraea* following

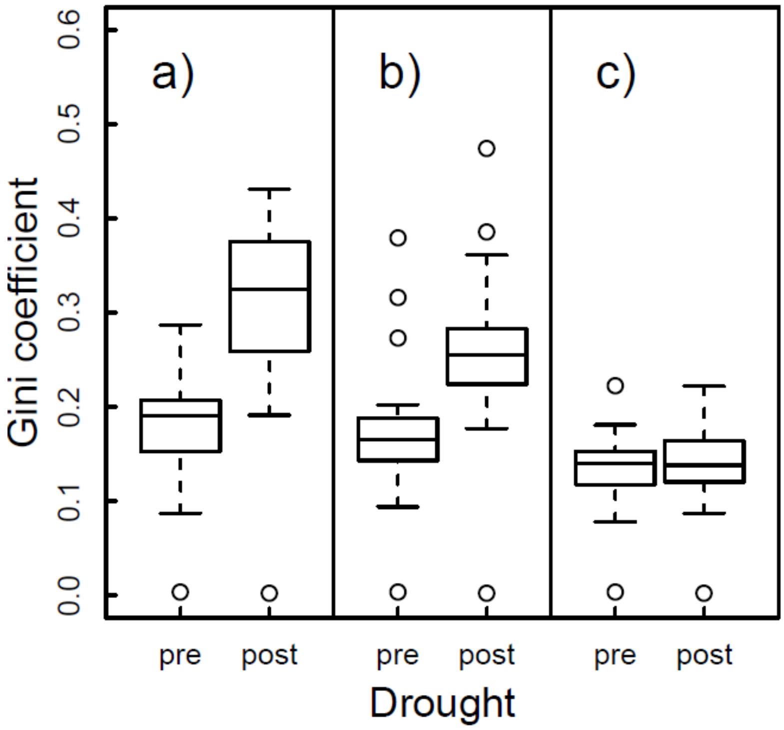

Figure 6.7: Gini coefficients for the three tree cohorts, pre- (1929-1975) and post- (1976-2009) drought. The 3 cohorts are: a) severely damaged F. sylvatica, b) minimally damaged F. sylvatica, c) Q. petraea.

the drought (t = 0.23, df = 56.96, p = 0.82).

Basal Area Increment.

The BAI series of the 3 tree cohorts are shown in figure 6.8. The difference in pre-drought BAI (1929-1975) between the two *F. sylvatica* groups, analysed using dummy variables regression, was 358 mm^2 ± 109, which was statistically significant (t = 3.278, p = 0.0015) but with a small effect size (d = 0.44, 95% CI -0.06/0.95). For the severely damaged *F. sylvatica*, 1929-1975 mean annual growth of 2973 ± 92 mm^2 fell to a minimum value of 374 mm^2 in 1977 (12.6% of pre-drought mean growth). Non-linear growth modelling shows a recovery to an asymptotic level of 2218 ± 152 mm^2 after the drought ($BAI(x) = d(1 - \exp\left(-\frac{x}{e}\right))$, where d = 2218, p < 0.001 and e = 5.10, p = 0.004). In comparison, for the minimally damaged *F. sylvatica*, pre-drought annual mean BAI of 3265 ± 97 mm^2 fell to a minimum value of 862^2 mm (26.4% of pre-drought mean growth), and recovered to 2527 ± 145 mm^2 (d = 2527, p < 0.001 and e = 1.99, p = 0.020). The higher parameter 'e'

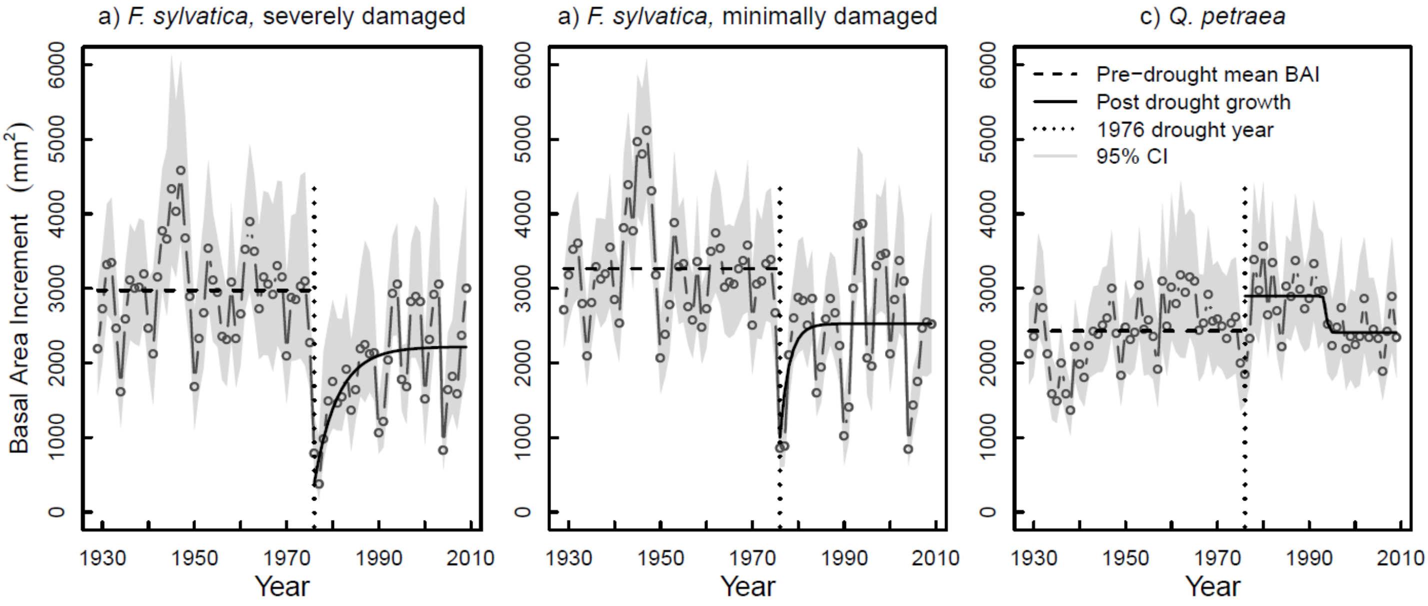

Figure 6.8: Mean basal area increment of the three tree cohorts. Yearly values are represented by open circles, with 95% confidence intervals shaded in grey. Mean growth

pre-drought (1929-1975) is shown by the dashed lines, and post-drought (1976-2009) growth derived using non-linear modelling shown using solid lines.

for the severely damaged *F. sylvatica* represents a lower slope gradient and therefore a slower recovery rate. Therefore, the minimally damaged trees had higher BAI rates than the severely damaged trees both before and after the drought, and both groups had a clear step change reduction in BAI after the drought. For *Q. petraea*, pre-drought annual mean growth of 2428 ± 66 mm^2 fell to a minimum value of 1845 mm^2 (76.0% of pre-drought mean growth), increasing immediately after the drought to 2897 ± 90 mm^2. The initial increase in BAI underwent a further rapid reduction to 2410 ± 98 mm^2 around an inflection point in 1994 ($BAI(x) = c + (\frac{d-c}{(1+\exp(b(\log(x)-(\log(e))})$, where b = -86.07 (p =

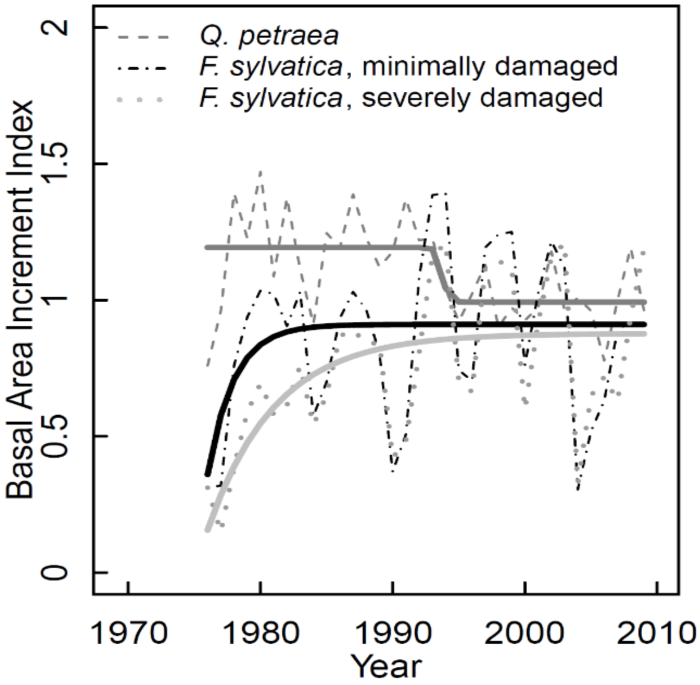

Figure 6.9: Basal area increment index for the post-drought period (1976-2009), for the three tree cohorts. Index values were calculated by dividing annual radial growth by the mean value for the pre-drought period (1929-1976). Non-linear post-drought growth models are shown as solid lines.

0.63), c = 2897.1 (p < 0.001), d = 2410.3 (p < 0.001) and e = 2.93 (p < 0.001)). Focusing on the post-drought trends, the standardised BAI recovery (see figure 6.9) shows that the partial recovery for both *F. sylvatica* groups reached their asymptote at around 75% of pre-drought BAI. Whilst the initial increase in growth for *Q. petraea* was temporary, overall pre-drought BAI levels were maintained for this species. The inflection point of the step reduction in *Q. petraea* growth occurs at 1994 - the same point in time as the severely damaged *F. sylvatica* BAI approaches its asymptote (with the minimally damaged having recovered around a decade earlier), and also at the same time as a strong surge in *F. sylvatica* growth. The extremeness of the 1976 BAI response to drought is further

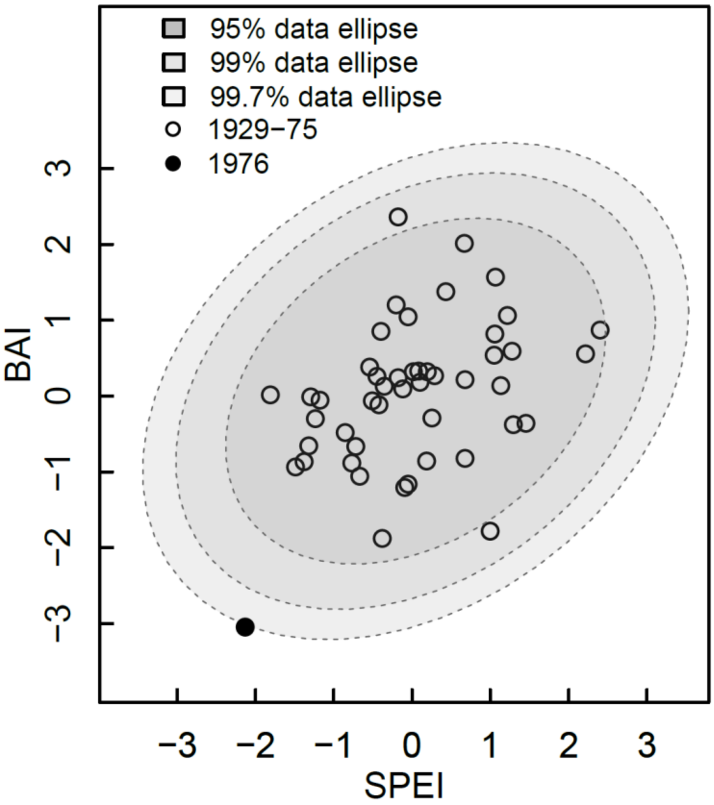

Figure 6.10: Comparison of basal area increment to SPEI, for the severely damaged F. sylvatica cohort. Annual mean values were converted to z-scores, and plotted with normal probability contours added as data ellipses. Open circles represent the years 1929-1975, and the filled circle represents the drought year 1976.

demonstrated by the comparison of BAI for the severely damaged *F. sylvatica* to growing season mean SPEI where the 1976 response lies at around the 99.7% normal probability contour for the pre-drought data (see figure 6.10).

6.4 Discussion

This study highlights key effects of an extreme drought on the subsequent recovery of a mixed species forest; 1) intra and interspecific variability in the response of the focal species; 2) long term failure of the dominant species to regain pre-drought growth rates; 3) a divergent response of a normally less competitive co-dominant, with no decrease in long-term growth following an initial competitive release; 4) a long-term effect on relative abundance, due to differential sensitivity to drought and reduced competition induced mortality of the two focal species.

In assessing the impact of an extreme climatic event (ECE) as defined by Smith (2011), it is essential that both the climate driver and the ecological response are extreme. The drought investigated here can be considered extreme as a climatic event – it was the most severe drought episode of the period studied, exceeding the 2nd most severe by around 30% in peak severity. Furthermore, from an ecological perspective, the drought affected *F. sylvatica* through a growth and mortality response unmatched by the prior variation (see figures 6.5 & 6.8). For *Q. petraea*, no such extreme response occurred. Our study relates to the “hierarchical-response framework” (HRF) conceptual framework for evaluating ecosystem responses to climate events (Smith, Knapp & Collins 2009), by demonstrating ecosystem response to a large scale resource alteration with a permanent shift in species abundance, described according to the HRF as species reordering. As predicted, the mechanisms specified in the framework have occurred simultaneously, with species reordering occurring alongside responses at the individual species level.

The growth analysis reported here demonstrates substantial intraspecific variation in the response and recovery of *F. sylvatica*. Furthermore, divergent interspecific responses resulted in step-wise changes in competitive interactions in response to extreme drought. For all *F. sylvatica,* radial growth dropped in response to drought, with a prolonged recovery period culminating in stable growth at around 75% of pre-drought levels. It is this failure to recover fully, combined with the differential effect on the species' abundance through mortality, which marks the effect of drought as an ECE. Furthermore, the comparison of normalised BAI with SPEI (see figure 6.10) shows that the response to ECE is not simply a linear extension of previous behaviour, but has involved the breach of drought tolerance thresholds.

There is no evidence for pre-conditioning by the ECE for a further extreme response to subsequent droughts, as recovery from subsequent droughts was rapid (see figure 6.8). *F. sylvatica* cohorts differed in growth before the drought, with the severely damaged trees having lower growth (low effect size: d = 0.44). This slightly lower growth may have predisposed these trees to greater drought response later, consistent with previous research showing higher drought mortality for poorly growing canopy trees (Peterken & Mountford 1996; Bigler *et al.* 2007; Das *et al.* 2007). Despite the small difference in growth prior to the ECE, the *F. sylvatica* cohorts diverge in response with the most severely damaged cohort taking longer to recover, in addition to greater inter-annual growth variability. This lagged recovery is a crucial feature of the ECE response at ecosystem level, as is the fact that recovery falls short of pre-ECE radial growth rates (figure 6. 9). Intraspecific differences in drought resistance traits have been reported between tree populations (Mitton, Grant & Yoshino 1998; Kavanagh *et al.* 1999), and shown to be related to genetic variation. The population studied here showed intraspecific variation amongst individuals which were physically intermixed and with only small differences in growth before the ECE. This raises the possibility that this population level intraspecific response diversity could be related to genotypic differences in susceptibility, and merits further investigation.

The ECE impact described above was not universal across both species studied: *Q. petraea* increased its growth rate by approximately 20% in the period immediately following the drought. Climate growth analysis shows considerable differences in climate sensitivity between the species (see figure 6.4), and therefore drought could be expected to affect *Q. petraea* less, as has previously been shown for these species (Michelot *et al.* 2012). The increase in growth seen post-drought for this species is most likely due to competitive release as a result of drought induced mortality and canopy damage, potentially acting in combination with reduction in carbohydrate reserves, and drought-induced damage to the root systems of previously dominant *F. sylvatica* individuals (Lloret, Siscart & Dalmases 2004; McDowell 2011). Furthermore, in contrast to the response of *F. sylvatica*, *Q. petraea* did not increase its growth variability post-drought. *Q. petraea* became the more productive species in terms of absolute radial growth immediately following the ECE. However, this effect was transient. In synchrony with the recovery of radial growth to near asymptotic levels for the severely damaged cohort, and with good growth in 1994 for all *F. sylvatica*, a rapid reversal of *Q. petraea* growth back to pre-drought levels occurs (see figure 6.10). The timing of this shift in growth is consistent with the resumption of competition induced mortality for *Q. petraea* (see figure 6.5). As the drop to pre-drought growth for *Q. petraea* occurs in synchrony with the delayed recovery of the severely damaged *F. sylvatica*, it suggests a direct consequence of poor resilience of the dominant species on its competitor's growth rate.

Abrupt and non-linear ecosystem responses have previously been observed for some short-lived organisms, with population size and biomass productivity responding to abrupt changes in climate drivers (Bestelmeyer *et al.* 2011). Here we demonstrate that the effects of extreme drought can cascade beyond the reduction in growth of a dominant species, resulting in the temporary release from suppression of a co-dominant competitor followed by a non-linear threshold response upon recovery of the dominant species. These switches in ecosystem state are both sudden, threshold processes and, although stable growth is regained, it is to a lower level than that prior to the ECE for the dominant species (see figure 6.10).

Climatic limitations on growth have combined with intraspecific competition to drive the dynamics of this mixed species woodland ecosystem. Other recent studies have also shown a greater climate sensitivity of *F. sylvatica* over *Quercus spp*., and a decline in competitiveness of *F. sylvatica* (Scharnweber *et al.* 2011; Bontemps *et al.* 2012). Our study builds on these findings by combining growth modelling and long term mortality data to demonstrate the lagged pulse of *F. sylvatica* mortality following extreme drought. Consequently, competition induced mortality relaxes for the competitor species, alongside an increase in growth rate. Differential mortality rates as a result of drought have previously been shown to affect the species composition of woodland ecosystems (Mueller *et al.* 2005). Resumption of competition induced mortality for *Q. petraea* is tied to partial recovery of the dominant *F. sylvatica*, alongside a resumption of pre ECE growth rates for *Q. petraea*. This adds significant detail to our understanding of the mechanisms at work within mixed species woodlands as a result of extreme drought stress. It has been shown here that in this mixed species system, an ECE has been a significant factor in maintaining species diversity, by promoting (at least temporarily) the normally less competitive, though more stress tolerant, species. Such species richness can insure against negative effects of climate change, as the long term resilience of forest ecosystems is increased when key species display a diversity of response to climate stress (Elmqvist *et al.* 2003; Bodin & Wiman 2007). Regional scale networks of paleoecological records have provided evidence that communities can respond rapidly to ECE, with site specific factors contributing to a temporal mosaic of responses to the climate driver (Williams, Blois & Shuman 2011). Thin, freely draining soils at the study site potentially make this site an early indicator of a drought response which could become more widespread as climate change intensifies. Further work should seek to elucidate the current extent of regional drought response, alongside examination of the thresholds that lead to the extreme response shown here.

Over the long term, the continued presence of a species within a community depends not only on the growth rates of adults and their mortality, but also on reproduction and subsequent establishment (Hurtt & Pacala 1995). In the absence of critical thresholds for rapid species loss being reached, the species composition of woodlands can be expected to be resilient to change given the longevity of organisms such as trees (Chapin *et al.* 2004). Therefore, the changes reported here may not herald a sudden shift in community composition as the climate warms, since adult longevity is likely to combine with recruitment in favourable years (Lloret *et al.* 2012). Furthermore, the presence of both intraspecific and interspecific variation in drought susceptibility is likely to significantly buffer against rapid changes at the ecosystem level, ensuring that temperate forest remains, even though the abundance of the dominant species is likely to vary over time in response to climatic variation (Elmqvist *et al.* 2003; Folke *et al.* 2004). Critically, the results demonstrate that responses to extreme climatic events are non-linear threshold processes that can result in sudden changes in growth and competition within natural populations, and that the recovery of the dominant species can itself trigger threshold effects in its competitors.

7. Summary and Conclusions

The programme of research presented in this thesis has applied tree-ring analysis methods to samples taken from sites covering a latitudinal transect across the Western European distribution of *F. sylvatica*: the Multiregional Network. After constructing tree-ring chronologies for all sites, the first stage of the analysis used multivariate techniques to identify if there was a data-driven justification for partitioning the sites into regions (Chapter 3). In comparison to other published work on clustering *of F. sylvatica* populations based on tree-ring data from the Italian peninsula and Eastern Alps (Piovesan *et al.* 2005a; Di Filippo *et al.* 2007), the results of clustering in Chapter 3 displayed less cohesive groupings. For these previously published studies, a higher concentration of site chronologies within a smaller geographical area may account for the better results. For the Multiregional Network, sampling over such a large geographical area means that site chronologies are often responding differently (in timing and intensity) to climate events. Pre-whitening the tree-ring data serves to remove much of the signal of low frequency variation in growth related to regional scale climate, whilst retaining year to year variation (Cook & Kairiukstis, 1990). This method is commonly applied to hierarchical cluster analysis of tree-ring data (Piovesan *et al.* 2005a; Di Filippo *et al.* 2007, García-González 2008). It is notable that in this study, meaningful geographical clustering of populations based on tree-ring data only emerged using non-prewhitened data, i.e. where the low frequency regional scale variation had not been removed. Despite the challenges of basing regional clustering on populations over such a wide geographical area, the combination of clustering using bioclimatic variables and growth is judged to be sufficiently robust and produces clusters which make intuitive sense when mapped (figure 3.6).

With regional groupings of sites within the Multiregional Network identified, subsequent analysis focused on identifying the response of the growth of forests within these regions to climate. A key finding is that case studies describing population level growth declines at the southern range edge

(Jump *et al.* 2006; Piovesan *et al.* 2008) are not typical when examining the growth of the species more widely in the Iberian Peninsula and Southern France. Climate sensitivity was low in this region (Wet South & Dry South regions, see figure 4.1), drought induced low growth years were rare (figure 4.3), and radial growth was broadly stable (figure 5.1). These results are echoed in a recently published study, which looked at *F. sylvatica* populations at two sites in the Eastern Mediterranean, and found no decline in growth (Tegel *et al.* 2014). Instead, growth was increasing. In the Multiregional Network, the regions with the highest climate sensitivity and drought impacts are the core regions (Core Temperate and Core Continental). The case study of the effect of an extreme drought on *F. sylvatica* (Chapter 6) comes from within one of these regions, the Core Temperate region. However, the long-term effects of the 1976 drought on *F. sylvatica* growth are not apparent more widely in the region, and in fact growth is increasing in both range core regions (figure 5.1). Other studies identifying similar increases in growth for European tree species interpreted the increases as potentially being due to a CO_2 fertilisation effect, and N_2 deposition (Martinez-Vilalta *et al.* 2008; Koutavas 2013). However, great uncertainties remain regarding the strength of CO_2 fertilisation effects on forests (Dobbertin 2005; Peñuelas, Canadell & Ogaya 2011), and N_2 deposition has been shown to negatively affect *F. sylvatica* growth in a network of Belgian chronologies (Kint *et al.* 2012). An alternative explanation is that an extension of the growing season may stimulate greater growth, resulting in the increases in BAI evident for the North West, Core Temperate and Core Continental regions.

The inter-annual variability of tree-ring series have long been interpreted as an indicator of drought stress experienced by trees (Douglas 1920). A study from the Western USA used gini coefficient analysis to show that trees from mesic environments had lower inter-annual growth variability when compared to trees from xeric environments (Biondi & Qeadan 2008). This is consistent with fundamental expectations of the behaviour of tree-rings (Fritts 1976). Biondi and Quedan (2008) also demonstrated a small temporal trend in gini coefficient, with values increasing in the 20th century. This is corroborated in the work presented in this thesis. For the extreme event case study (figure 6.7), growth variability was shown to increase strongly for *F. sylvatica*, and for the most drought affected trees in particular. However, increasing growth variability was a notable characteristic of all regions within the Multiregional Network, to a greater or lesser degree (figures 5.4 & 5.5). This feature of *F. sylvatica* growth was not simply a normal response to climate variability (figure 5.8), and was strongest in (but not limited to) the range core regions where drought impacts were greatest. Further work should seek to identify whether this is a feature which is replicated in *F. sylvatica* populations in other regions of Europe, and also other species.

Examining the effect of an extreme drought event in detail revealed key features of the long term recovery from drought for *F. sylvatica*, alongside the effect of drought on competitive interactions between species in mixed species forest. The temporary reversal of competitive dominance between *F. sylvatica* and *Q. petraea* is in line with studies showing the drought sensitivity of *F. sylvatica*, and the competitive balance in *Fagus-Quercus* forests (Leuschner *et al.* 2001a; Leuschner *et al.* 2001b; Friedrichs *et al.* 2009; Scharnweber *et al.* 2011). The partial recovery was not replicated in any of the other chronologies within the Multiregional Network either individually or regionally, suggesting that the extreme drought response was largely due to site specific factors, such as the steep gradient and freely draining soils (Peterken & Mountford 1996). However, within the range core regions *F. sylvatica* is likely to be found occurring at many sub-optimal locations. Paleo-records indicate that as climate changes, site-specific factors lead to a temporal and spatial mosaic response (Williams, Blois & Shuman 2011). In other words, species can have a varying response to climate at different locations at different times, dependent on the suitability of site conditions. It is not intuitive that extreme drought impacts were identified within the range core (Chapter 6), alongside high levels of climate sensitivity and drought stress more generally (figures 4.1. and 4.6) whilst the most arid region in the south of the species’ range displays lower climate sensitivity and low drought impact. However, in the context of the temporal and spatial mosaic, it should be remembered that the sub optimal sites in the south of the species range have long ceased to support *F. sylvatica* populations. The remaining populations occur at sites where local conditions buffer an unfavourable regional climate, thus allowing the persistence of relict populations (Hampe & Jump 2011).

Across much of the range core for the species, *F. sylvatica* forests are managed for silviculture. Trends in management over recent decades are for the gradual conversion of coniferous plantations to broadleaf forests, with *F. sylvatica* often favoured (Spieker *et al.* 2004). As the implications of global climate change become evident for forestry, management strategies to promote adaptation and the conservation of forest structure are actively being discussed (Bolte *et al.* 2009; Lindner *et al.* 2010). Commonly, temperature and precipitation for a given site are used to guide decisions on the selection of species to promote. One major implication for the management of *F. sylvatica* forests from these findings is that higher tolerance of drought impacts can make *Q. petraea* a better choice of species for withstanding extreme events. A recent study predicted that a buffer exists within predicted climate conditions resulting in a favourable outlook for *F. sylvatica* until at least 2050 (Mette *et al.* 2013). However, beyond this time frame, *F. sylvatica* is expected to perform more poorly than *Q. petraea*. Given the long timescales involved in managing trees as a crop, it would be prudent to begin altering the species mix of range core *F. sylvatica* forests in favour of more drought tolerant competitors. Management towards a mixture with *Q. petraea* would promote resilience to future droughts.

As a complete body of work, this thesis adds significantly to our current knowledge of the effects of climate change on *F. sylvatica* forests. It shows that despite previous concerns regarding their sensitivity, at the regional scale southern range edge forests are resilient to the current levels of climate warming experienced. Variation in response at the population level means that some sites may show drought related growth declines, but at the regional scale such declines are not evident. This is attributed to two main factors: to the presence of climate gradients within Southern Europe which result in wet conditions for many forests, and to forests in dry regions occurring in locations where site conditions buffer the forest from a more inhospitable regional climate. Furthermore, this thesis demonstrates that an emerging risk exists for range core forests, particularly in the south of the UK. Finally, this thesis shows that for *F. sylvatica* forests, once thresholds of drought tolerance are surpassed by an extreme drought, the result can be long lasting due to failure to regain pre-drought growth rates, and differing rates of mortality in mixed species forest.

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Appendix 1 – Bioclimatic Variables

Table showing the bioclimatic variables for the individual sites in the Multiregional Network.

Site Number	Name	Elevation	Temperature	Precipitation	M	m	Ic	SPET	Tmin	Tmax	Ps	Pw	PET	SPET	Aridity Index	Summer Aridity Index
1	Tongue	57	8.09	1095	15.90	1.58	9.11	87.79	3.97	13.1	279.6	318.96	49.75	87.8	1.83	0.80
2	Uppat	32	8.38	928	17.29	0.95	10.17	91.12	3.65	13.8	258.9	260.94	50.54	91.1	1.53	0.72
3	Applecross	18	8.73	1990	17.71	1.14	10.03	91.43	4.06	14.1	447.5	620.65	51.08	91.4	3.25	1.23
4	Dunnotar	60	8.20	780	18.03	0.39	10.92	90.92	3.13	14.1	246.1	200.49	50.05	90.9	1.30	0.68
5	Port Appin	60	8.66	1898	17.83	1.19	10.28	91.07	3.86	14.1	450.2	584.79	50.82	91.1	3.11	1.24
6	Kinnoul	171	7.83	857	18.00	-0.30	11.49	91.31	2.42	13.9	258.5	238.60	49.40	91.3	1.45	0.72
7	Lady's Brae	28	8.82	974	18.97	0.81	11.42	93.61	3.45	14.9	280.9	277.23	51.33	93.6	1.58	0.76
8	Mabie	54	8.52	1354	19.11	0.31	11.60	92.15	3.06	14.7	361.0	396.62	50.54	92.2	2.23	0.99
9	Linsty Green	53	9.34	1457	19.69	1.20	11.42	92.96	3.97	15.4	392.8	421.61	51.91	93.0	2.34	1.07
10	Gloddaeth	129	9.11	1185	18.53	1.19	10.79	89.36	3.98	14.8	312.0	346.82	51.01	89.4	1.94	0.88
11	Talhenbont	54	9.69	1110	18.85	1.82	10.61	90.04	4.63	15.2	295.0	320.00	52.03	90.0	1.78	0.82
12	Southey	53	9.71	548	21.24	0.90	12.88	95.78	3.63	16.5	196.0	128.03	52.67	95.8	0.87	0.52
13	Gardenhouse	261	8.39	1098	18.71	0.25	11.37	89.05	3.07	14.4	306.2	311.55	49.69	89.0	1.84	0.87
14	Two-mile-bottom	33	9.88	539	21.55	0.96	13.00	96.25	3.68	16.7	189.0	126.62	52.98	96.2	0.85	0.49
15	Beechwoods	47	10.00	561	21.84	1.02	13.09	96.82	3.80	16.9	197.1	131.60	53.24	96.8	0.88	0.51
16	Lady Park	140	9.73	781	20.70	1.39	12.29	94.11	3.97	16.3	234.8	214.45	52.46	94.1	1.24	0.63
17	Wytham	149	9.67	639	21.37	1.09	12.87	95.12	3.67	16.5	212.6	161.68	52.43	95.1	1.02	0.56
18	Epping	109	9.82	595	21.62	1.03	13.03	95.64	3.68	16.7	193.8	148.90	52.74	95.6	0.94	0.51
19	Shirburn	258	8.91	660	20.81	0.10	12.89	92.92	2.87	15.8	210.4	169.62	50.81	92.9	1.08	0.57
20	Foxbury	171	9.49	695	20.41	0.94	12.70	93.02	3.46	16.2	199.3	188.20	51.79	93.0	1.12	0.54
21	Roddenbury	144	9.61	767	20.67	1.16	12.07	92.54	3.97	16.0	224.0	216.25	52.00	92.5	1.23	0.61
22	Micheldever	118	9.78	759	21.26	1.19	12.55	93.95	3.84	16.4	211.0	216.32	52.43	94.0	1.21	0.57
23	Wealden Edge Hangers	123	9.75	751	21.12	1.15	12.55	93.83	3.82	16.4	205.9	214.80	52.35	93.8	1.20	0.55
24	West Dean	142	9.83	726	20.40	1.61	12.28	93.07	4.00	16.3	194.1	209.21	52.38	93.1	1.15	0.53
25	Dommet	261	9.09	851	19.44	0.99	11.39	89.22	3.79	15.2	234.3	253.56	50.73	89.2	1.40	0.66
26	Kluisbos	118	9.50	760	21.58	-0.38	14.33	97.60	2.47	16.8	260.6	185.01	52.30	97.6	1.21	0.67
27	Crecy en Ponthieu	85	10.24	685	21.69	1.22	13.62	96.53	3.57	17.2	221.3	171.22	53.54	96.5	1.07	0.58
28	Forcheim	577	7.00	823	21.62	-4.97	18.37	98.10	-2.23	16.1	299.9	207.78	47.01	98.1	1.46	0.77
29	Signy L'Abbaye	234	9.36	774	22.70	-1.05	15.47	98.50	1.71	17.2	260.0	203.08	52.02	98.5	1.24	0.66
30	Kelheim	474	7.89	705	23.37	-4.91	19.45	102.20	-2.01	17.4	313.8	144.24	49.25	102.2	1.19	0.78
31	Trois Fontaines	241	10.23	802	24.04	-0.58	16.49	103.05	2.07	18.6	269.3	214.04	54.09	103.1	1.23	0.66
32	De Haye	353	9.36	800	23.35	-1.72	16.99	101.18	0.91	17.9	271.6	215.10	52.10	101.2	1.28	0.68
33	Chattilon-Sur-Seine	382	9.68	783	23.48	-1.26	16.99	101.17	1.26	18.2	270.8	201.99	52.65	101.2	1.24	0.68
34	Colombier	764	8.55	1307	22.63	-3.01	16.92	96.80	0.32	17.2	437.9	346.42	49.52	96.8	2.20	1.14
35	La Saleve	788	8.37	1007	23.66	-3.64	18.16	98.30	-0.52	17.6	332.5	257.65	49.16	98.3	1.71	0.86
36	De Saou	462	11.54	858	27.23	-0.55	17.81	107.38	3.02	20.8	241.0	194.14	56.65	107.4	1.26	0.57
37	De Lure	1309	7.64	797	23.33	-4.69	17.54	92.67	-0.65	16.9	205.4	196.72	46.61	92.7	1.43	0.57
38	Malapere	412	12.24	616	26.27	1.20	15.97	104.25	4.67	20.6	177.4	157.18	57.55	104.3	0.89	0.44
40	Aztaparreta	1020	9.60	1016	24.90	-1.91	15.83	94.65	2.31	18.1	272.9	282.77	51.17	94.6	1.65	0.73
41	Baish Aran	1081	9.14	1050	23.57	-2.32	15.65	92.80	1.88	17.5	305.8	271.93	49.90	92.8	1.75	0.84
42	Vall de Boi	1455	7.76	1245	22.06	-2.55	15.67	89.02	0.83	16.5	327.9	334.40	46.42	89.0	2.24	0.94
43	La Bergueda	1134	9.64	733	23.39	-1.21	15.82	94.18	2.41	18.2	197.7	172.91	50.94	94.2	1.20	0.54
44	La Garrotxa	582	12.55	691	26.51	0.96	15.85	104.55	5.24	21.1	180.6	164.24	58.03	104.5	0.99	0.44
45	Montseny	1204	9.49	729	23.06	-1.29	15.71	93.13	2.34	18.0	190.7	171.05	50.49	93.1	1.20	0.53
46	Tejera Negra	1545	8.41	722	25.35	-2.94	17.51	93.26	0.67	18.2	157.6	216.68	47.76	93.3	1.26	0.43
47	La Senia	1164	10.53	484	25.44	-1.57	16.49	97.10	2.81	19.3	131.9	100.07	52.92	97.1	0.76	0.35

T: mean annual temperature (deg C); **P**: total annual precipitation (mm); **M**: mean maximum temperature of the hottest month of the year; **m**: mean minimum temperature of the coldest month of the year; **Tmin:** mean temperature of the coldest month of the year; **Tmax:** mean temperature of the hottest month of the year; **Ps:** total summer precipitation (May-August); **Pw:** total winter precipitation (December-February); **PET:** potential evapotranspiration; **SPET:** summer potential evapotranspiration (May-August); **Aridity Index:** P/PET; **Summer Aridity Index:** P/PET (May-August).

Appendix 2 – Peer Reviewed Papers

The following peer reviewed papers were published arising from work conducted as part of this PhD:

Cavin, L., Mountford, E.P., Peterken, G.F. & Jump, A.S. (2013) Extreme drought alters competitive dominance within and between tree species in a mixed forest stand. *Functional Ecology*, doi: 10.1111/1365-2435.12126

Abstract:

1. The effect of extreme climate events on ecosystems is an important driver of the biotic response to climate change. For forests, extreme drought has been linked to negative effects such as large scale mortality and reduced primary production. However, the response of plant communities to extreme drought events remains poorly understood.

2. We used mortality data from a long term monitoring programme in the core of the focal species' ranges, in combination with annual growth data from tree-rings, to study the effect of, and recovery from, an extreme drought event. We examined both the intraspecific and interspecific drought response and explored how differential responses affect competitive dominance between the dominant species Fagus sylvatica and Quercus petraea.

3. Mortality for the most drought-susceptible species, F. sylvatica, occurred alongside a temporary reduction in competition-induced mortality of Q. petraea, resulting in the long-term alteration of the relative abundance of the two species.

4. Significant intraspecific variation occurred in post-drought recovery in surviving F. sylvatica, with two distinct cohorts identified. A prolonged recovery period was coupled

with the failure to regain pre-drought growth levels in this species, whereas for Q. petraea no severe drought impacts were observed. This species instead experienced competitive release of growth.

5. Our results demonstrate that ecosystem responses to extreme drought can involve rapid, non-linear threshold processes during the recovery phase as well as the initial drought impact. These sudden changes can lead to the reordering of dominance between species within communities, which may persist if extreme events become more frequent.

Jump, A.S., Cavin, L. & Hunter, P.D. (2010) Monitoring and managing responses to climate change at the retreating range edge of forest trees. *Journal of Environmental Monitoring,* 12, 1791- 1798.

Abstract:

Rising temperatures and increasing drought severity linked to global climate change are negatively impacting forest growth and function at the equatorial range edge of species distributions. Rapid dieback and range retractions are predicted to occur in many areas as temperatures continue to rise. Despite widespread negative impacts at the ecosystem level, equatorial range edges are not well studied, and their responses to climate change are poorly understood. Effective monitoring of tree responses to climate in these regions is of critical importance in order to predict and manage threats to populations. Remote sensing of impacts on forests can be combined with ground-based assessment of environmental and ecological changes to identify populations most at risk. Modelling may be useful as a ‘first-filter’ to identify populations of concern but, together with many remote sensing methods, often lacks adequate resolution for application at the range edge. A multidisciplinary approach, combining remote observation with targeted ground-based monitoring of local susceptible and resistant populations, is therefore required.

Once at-risk regions have been identified, management can be adapted to reduce immediate risks in priority populations, and promote long-term adaptation to change. However, management to protect forest ecosystem function may be preferable where the maintenance of historical species assemblages is no longer viable.