Species-specific climate response of oaks (*Quercus* spp.) under identical environmental conditions

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Oak forests play a major role in Britain due to their economic, social and historic value. Sudden oak death and general decline symptoms have therefore caused major concerns in the forestry sector over the past decade. Several strategies have been proposed to preserve the economic and social value of oak forests, including the planting of native species with more southerly origins, or non-native species of oak that may be better suited to the projected climate of the future. The Ovington research plots, established 50 years ago at the Bedgebury Pinetum in southeast England, provided the opportunity to compare annual growth rates and climate-growth relationships of five oak species growing adjacent to each other on the same soil type and under the same climatic conditions. Clear differences were evident in annual increment and climate-growth responses for the five *Quercus* species. Growth rates were significantly lower ($p<0.05$) for the two species native to the UK (*Q. petraea* and *Q. robur*) compared to the southern European and American species. A partitioning analysis using key climatic variables separates *Q. coccinea* from the other species due to its negative response to low temperatures. These results were confirmed by pointer year analysis. The analysis suggests that *Q. robur* is likely to be the more resilient of the two native species of oak to the future climate of southern Britain. Of the non-native species of oak evaluated, *Q. coccinea* represents an alternative species to *Q. robur* and *Q. petraea* on very dry, nutrient-poor sites. *Q. palustris* may also have some potential under current conditions for species diversification, but its requirement for higher summer precipitation than the other four species suggests that this potential may not be sustained as climate change progresses. However, if alternative species are selected as more resilient to climate change in terms of growth, it will be essential to consider a range of other issues including impacts on biodiversity, resilience to endemic tree pests and diseases, form and appearance, landscape and timber quality.

Keywords: *Quercus* spp., Species Trial, Dendroecology, Climate-growth Relationships

Introduction

An increase in pest and disease outbreaks as well as projected climate warming constitutes a serious threat to forestry over the coming decades (Bolte et al. 2009, Sturrock et al. 2011). As a consequence of these impacts, individually or in combination, tree vitality and survival may decline resulting in reduced productivity (Leuzinger et al. 2005). The resilience of species to biotic and abiotic stresses, as well as their adaptation potential to changing environmental conditions, is important knowledge to guide sustainable forest management (Arend et al. 2011). Oak comprises the highest percentage of broadleaved woodland in Great Britain but its yield is expected to decline in the south and east under future climate projections (Broadmeadow et al. 2005). These forests possess a high economic and socio-economic value (Evans 1984, Grant & Edwards 2008), raising the question as to whether replacement with another oak species, better adapted to summer drought and wet winters, is an appropriate response to projected climate change. While *Quercus* species are believed to show high competitiveness under drier conditions than currently experienced in southern England (Abrams 1990, Broadmeadow et al. 2005, Eilmann et al. 2006), Thomas et al. (2002) found that a combination of waterlogging in winter and summer drought weakens oak to a level where diseases can attack more readily. Cases of drought-induced mortality have also been reported in Europe (Dreyer 1994, Brasier 1996, Gibbs & Greig 1997, Allen et al. 2010). Modelled results presented by Attorre et al. (2008) suggest that the general assumption regarding drought sensitivity is invalid; instead, the performance of oak is dependent on origin and the characteristics of individual species. Other authors attribute the decline of oak in Europe to a combination of several factors, including infection by *Phytophthora cinnamomi* exacerbated by climatic factors (Brasier & Scott 1994). Thomas & Blank (1996) propose nutrient imbalance as the reason for oak decline, while Andersson et al. (2011) concluded that the decline of oak and its inevitable death is a long process which can begin decades previously.

Tree ring analysis can be used to better understand the potential for an onset of decline driven by responses to climate (Schweingruber 1988, 1990). Despite age and management-related variation in growth, the sensitivity of a species on a given site to environmental changes can be assessed (Friedrichs et al. 2009). Tree-ring analysis is regularly used to evaluate climate-growth interactions as well as establishing the drivers for tree mortality (Cook et al. 1987). While site conditions modulate climate-growth correlations (Wilson et al. 2008, Mérian et al. 2011) information on species-specific climate responses still can be derived (Carrer 2011, Sanders et al. 2012). This approach was the subject of a number of dendrochronological studies (Leblanc & Foster 1992, Dwyer et al. 1995, Eilmann et al. 2006, Danek et al. 2007, Friedrichs et al. 2009, Helama et al. 2009, Di Filippo et al. 2010, Scharnweber et al. 2011). However, a direct comparison of the response to climate of different oak species growing in close proximity has not been undertaken for mature forest stands.

Our aims were: (1) to quantify growth dif-

Fig. 1 - The species trial in Bedgebury, Kent (51° 04' N and 0° 27' East). The oak plots evaluated in this study are all in the north-west corner (orange square) of the plantation and measure 100 m² each. Number codes are: *Q. coccinea* (10), *Q. petraea* (11), *Q. robur* (13), *Q. palustris* (23), and *Q. frainetto* (24). Source: Forestry Commission 2013.

ferences between five *Quercus* species from one plantation in Bedgebury, UK; and (2) to calculate climate-growth correlations based on daily data.

Materials and Methods

Location and soil description

The samples were taken at a species trial in Bedgebury, Kent in the southeast of Britain. Originating from research plots set up by Ovington (1953) in the late 1930's the trial is laid out in plots of a quarter of a hectare each (Fig. 1).

Planting and replanting of different species has occurred over the years and only a handfull of the original Ovington plots still exist. Heavy losses occurred in the 2nd world war resulting in the need to re-establish the oak plots. The Bedgebury plantation has seen heavy damage due to wind throw in the more recent past (1987, 1991); the oak stands, however, have been sheltered from wind damage due to their location in the north-western area at the lowest point of the slope (Howard & Howard 1984). Soils under the oak stands are acidic, permeable loams. Drainage is limited and waterlogging can occur, especially in winter and after heavy rainfall (Howard & Howard 1984). The soils are phosphorus-deficient and generally low in other nutrients (Mitchell & Westall 1972). Soil pH ranges from 5 to less than 4 (Ovington 1953, 1956, Ovington & Madgwick 1958).

Species selection

The *Quercus* stands sampled in this study are in close proximity to one another within a 100 x 200 m rectangle. The stands have been thinned regularly and all have a closed canopy structure. The understory vegetation can be dense with some *Rhododendron* spp. present. Planted in the late 1950's they were about 45 years at time of sampling. Five different oak species were suitable for coring, namely *Q. coccinea, Q. petraea, Q. robur, Q. palustris* and *Q. frainetto* (Tab. 1).

Climate data

The location of the site in the southeast of Britain and its close proximity to the sea (between 15 to 30 km to the south and east respectively) results in a very stable climate. Mean temperature in winter (Dec-Feb) is typically around 4 °C with daily average minima around -6 °C during the reference period (1960-1990). Monthly mean maximum temperature in summer (Jun-Aug) is approximately 27 °C. Late ground frost can occur until June with measured grass temperatures below 0 °C. Climate data was obtained at daily resolution from the Bedgebury Pinetum meteorological record which is taken within the plantation on a cleared area. The record starts on the 1st January 1959 and runs over the complete period of investigation.

Sampling and tree-ring width measurement

Sampling took place in spring 2006. Two cores were taken (Suunto increment borers) from opposite directions on the trunk of five dominant trees, avoiding wounds and reaction wood for each species. Cores were prepared according to standard procedures given in Stokes & Smiley (1968). Individual tree-ring width was measured using a LINTAB measuring table and the software WinTSAP (both Rinntech, Heidelberg, Germany) at 1/1000 mm precision. Cross-dating and chronology building for all respective species was carried out using the same software. Cardinal splines (Fahrmeir & Tutz 1994, pp. 156) were used for indexation (trend removal) of the individual and the species specific tree-ring series.

Statistical analysis

Expressed population signal (EPS) and mean inter-series correlation (Rbar) were calculated using the dendrochronological software library in R (Bunn 2008, R Core Team 2012). Autocorrelation (AR) was calculated using Durbin-Watson statistics, Kruskal-Wallis one-way analysis of variance on ranks and a pairwise multiple comparison procedure (Tukey Test) were performed for the complete, raw and indexed chronologies in SAS (SAS 9.3, SAS Institute Inc.). Annual sensitivity was calculated after Douglass (1928) as follows (eqn. 1):

$$S_a = \left| \frac{2(x_{t+1} - x_t)}{(x_{t+1} + x_t)} \right|$$

Tab. 1 - General information on the five investigated *Quercus* species.

Species	Common name	Natural distribution	Site requirements
Q. coccinea	Scarlet oak	native to eastern and central North America	acidic, poor, sandy soils on dry sides (Minckler 1965)
Q. petraea	Sessile oak	native to Europe	prefers clay or sandy soils with humus
Q. robur	English oak	native to Europe, northern and western Africa	moist and fertile well-drained soil preferred, soil pH is not critical, clay soils
Q. palustris	Pin oak	native to north-eastern and north-central North America	moist, fertile acidic, well-drained soils (Minckler 1965)
Q. frainetto	Hungarian oak	native to south-eastern Europe	Medium to heavy acidic soils, dry and waterlogged tolerated

where S_a is the the annual sensitivity of one chronology, x is the tree ring width, and t is the year. Mean sensitivity is calculated as follows (eqn. 2):

$$S_{mean} = \frac{1}{n-1} \sum_{t=1}^{t=n-1} \left| \frac{2(x_{t+1} - x_t)}{(x_{t+1} + x_t)} \right|$$

where S_{mean} is the mean sensitivity of one chronology and n is the number of years of the chronology. A partitioning analysis was undertaken using annual mean, maximum and minimum temperature and precipitation sums as well as mean wind direction, mean cloud cover and mean sunshine hours (Jump, SAS Institute Inc.). Pointer years were identified for each species using the individually de-trended (exponential spline α = 0.25) chronologies, where increment of 75% of the sample trees deviated by more than one standard deviation from the mean (SAS 9.3, SAS Institute Inc.). Climate-growth correlations were calculated using the CLIMTREG software (Beck 2007, Beck & Heussner 2011). This software uses daily climate variables to calculate climate-growth correlations. Remaining autocorrelation was removed from the indexed series by autoregressive modelling. A common interval analysis was used to detect climate-growth connections. Correlations were calculated using time spans from 21 to 121 days of climate data, starting on the 1st July of the previous year to 31st October of the current year. The deviations of mean temperature and precipitation sums were calculated from the long-term average, correlating the resulting climatic values with the tree-ring index time series (Beck et al. 2013). To verify the results of CLIMTREG, a Pearson's Product Moment Correlation was used. While not as detailed and based on monthly averaged data, it confirmed the general trends between species and climate on this site.

Results

Environmental conditions

Whilst the soils are typical for lowland area of SE England, they are not optimal for all *Quercus* species planted. While *Q. frainetto* prefers these heavy, acidic soils and can tolerate water-logging, *Q. palustris* and *Q. robur* would benefit from more fertile soils with better drainage. *Q. petraea* and especially *Q. coccinea* are better suited to lighter, sandy soils.

Minimum air temperatures (Fig. 2a) were higher in the period from 1991 to 2005 than in the reference period (1960 to 1990). A general increase in minimum air temperatures is evident over the course of the temperature record which becomes significant (p<0.10) in spring. Grass temperatures (Fig. 2b) decrease (p<0.10) in all but the summer months where a slight increase is observed
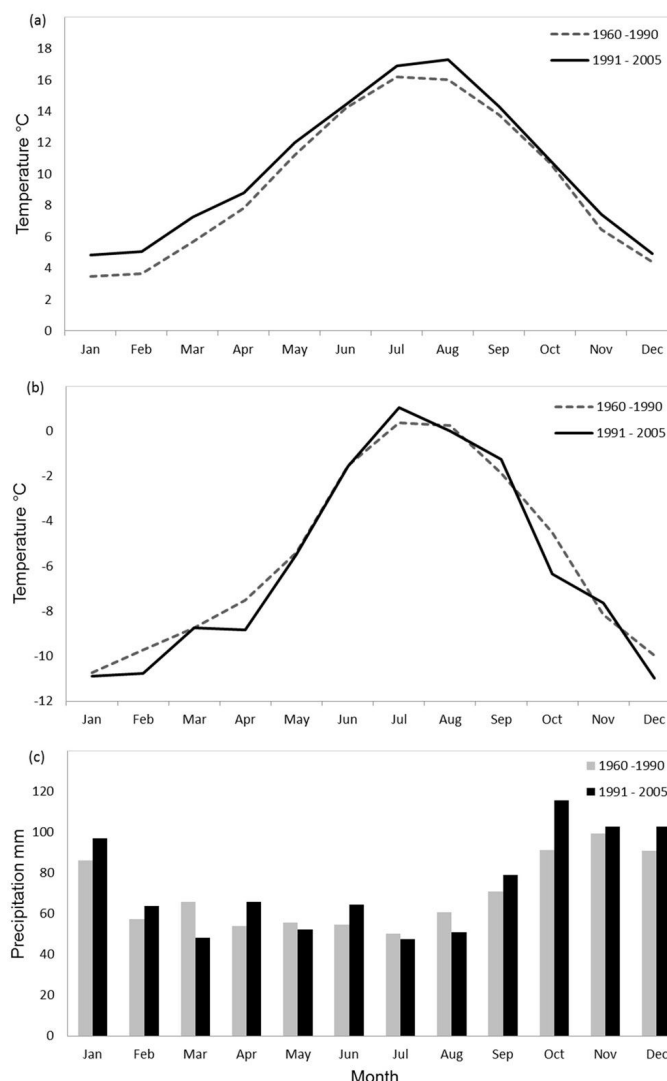

Fig. 2 - Mean temperature (a), grass temperature (b), and precipitation sums (c) for the periods 1960 to 1990 and 1991 to 2005 at the Bedgebury Pinetum.

(not significant). The largest reduction is evident in May and June (p<0.001). A decline in precipitation (Fig. 2c) over the period was significant for January, February and March (p<0.05). A slight increase was found in June, September and October. Year-to-year variation is high for all but grass temperature.

A difference in grass temperature is evident between the two periods (1961-90 and 1991-2005 - Fig. 2b) characterised by colder spring temperatures and warmer autumns in the latter period. Precipitation shows a homogeneous distribution over the years with heavy rainfall occurring in the winters of 1968, 1986, 1998 and 2003. Heavy rainfall in spring was recorded in 2002.
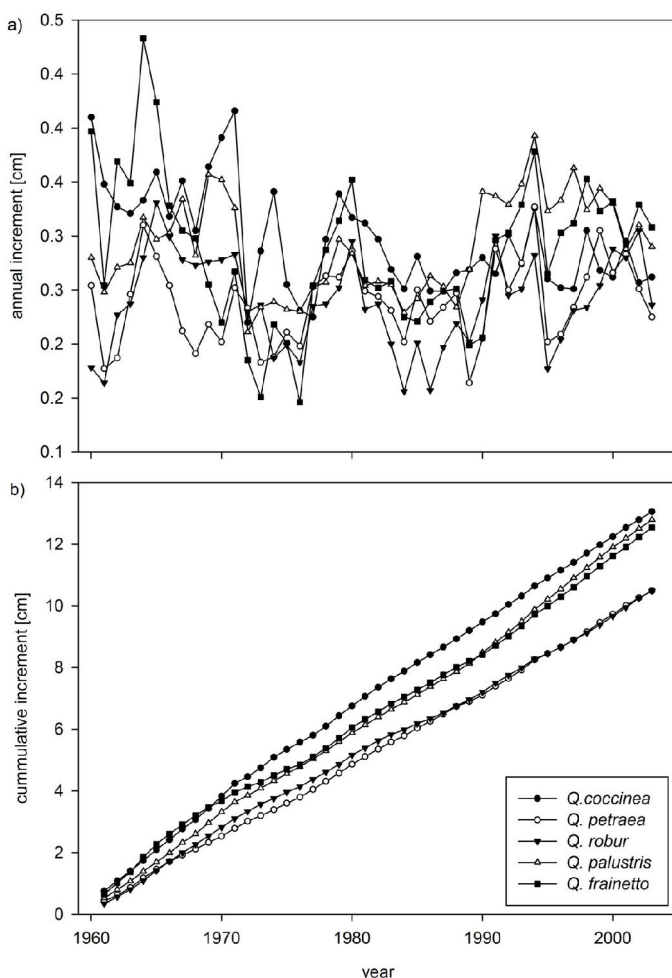
Tree-ring series

The mean segment length is 45 years and average growth rates vary between 2.37 mm and 2.94 mm per year with standard deviations between 0.68 mm and 0.38 mm (Tab. 2).

Tab. 2 - Statistics of tree ring data and chronologies. (MSL): mean segment length; (AGR): average growth rate (mm); (EPS): expressed population signal; (AR): auto correlation (1), Durbin Watson (2); (SNR): signal-to-noise ratio; (MSS): mean signal strength.

Species	T no	S no	Raw data / single trees					Residual chronology		
			MSL	AGR	Std. dev.	AR (1)	AR (2)	Mean sens	EPS	SNR
Q. coccinea	5	10	45	2.94	0.47	0.45*	0.25	0.15	0.87	6.41
Q. petraea	5	10	45	2.35	0.38	0.39*	0	0.12	0.84	5.4
Q. robur	5	10	45	2.37	0.43	0.55*	0.39*	0.19	0.8	4.1
Q. palustris	5	10	45	2.88	0.45	0.69*	0.5*	0.12	0.79	2.44
Q. frainetto	5	10	45	2.83	0.68	0.62*	0.5*	0.15	0.81	4.27

Fig. 3 - Comparison of raw annual growth series over the common period of 45-years (a) and the cumulative growth values of the five oak species (b).

Annual growth variations and sensitivity

The annual increment patterns (Fig. 3a) show similar long-term trends for all five species, with reduced growth evident in the mid-1970s, mid-1980s, mid-1990s and towards the end of the chronologies in 2005. This is consistent with well-documented summer drought conditions in Britain in 1976, 1984, 1995 and 2003 (Innes 1990, Morecroft et al. 2002, Hendry et al. 2005). Negative pointer years (*i.e.*, radial growth is less than one standard deviation from the mean for 75% of sample trees) for *Q. coccinea* occurred in 1956, 1968, 1972 (strongest negative pointer year), 1975-76, 1986, 1995, and 1999; positive pointer years were identified for 1958 (strongest positive pointer year), 1959, 1967, 1969, 1974, 1978, 1994, and 1998. Negative pointer years are evident for *Q. petraea* in 1989 and 1995. None of the other species show significant pointer years in the period covered by the meteorological data. However, the common reaction to the drought years of 1976 and 1995 is apparent. Recovery is quickest for *Q. palustris*, *Q. frainetto*, and *Q. robur*, while *Q. petraea* shows the longest growth depression following the drought years. Cumulative diameter increment, used here as an indication of timber volume (Fig. 3b), shows that *Q. frainetto* experienced suppressed growth in the early 1940s at about 10 years of age, after having the highest juvenile growth rate of the five species.
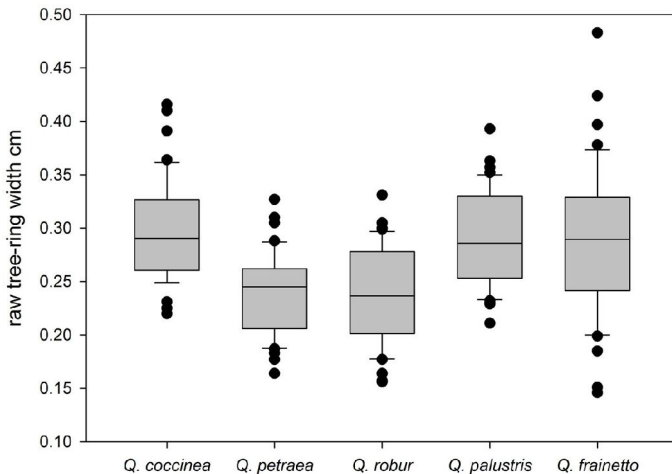
Q. coccinea demonstrates the most consistent growth rate with only a minimal setback at about 20 years of age. The growth rate of *Q. frainetto* is less than that of at the beginning of the chronology. However, no period of suppressed growth is evident for *Q. coccinea* and its cumulative radial growth exceeds that of *Q. frainetto* at the time of sampling. The growth of *Q. palustris* is below the two previous species at until about 30 years of age when it excels *Q. frainetto*. The two species native to the UK, *Q. robur* and *Q. petraea*, show lower growth rates at the beginning of the chronology, but attain the same cumulative diameter growth by time of sampling. A small difference is apparent between eight and 28 years of age when the radial growth of *Q. robur* was greater greater than that of *Q. petraea*. Subsequently the growth rate of *Q. robur* declined compared to *Q. petraea*.

The Kruskal-Wallis one-way analysis of variance on ranks showed a significant ($p<0.001$) difference in the mean values between the species. To isolate the groups differing the most, multiple comparison was used showing significant differences ($p<0.05$) between the group of the American and southern European species (*Q. coccinea, Q. palustris* and *Q. frainetto*) and the two species native to the UK (and widely across

Mean signal strength (MSS) is a measure of uniformity between sampled trees of their annual growth response. MSS varies between 0.32 for *Q. frainetto* and 0.55 for *Q. palustris*. The signal-to-noise-ratio (SNR) quantifies the strength of the common signal for all trees in a chronology (Wigley et al. 1984) and falls between 2.4 and 6.4 %. The Expressed Population Signal (EPS) for the residual chronology varies between 0.79 and 0.86. EPS provides an estimate of the explained variance of the sample chronology for the site. Autocorrelation (AR) is a measure of the dependency of annual growth rate on the growth rate observed in the previous years. All species show significant autocorrelation, with the previous year, with the previous two years in the case of *Q. robur* and *Q. palustris* (Tab. 2), while *Q. frainetto* and *Q.palustris* show a significant autocorrelation with the previous three years (not shown).

Fig. 4 - Box-whisker plots of mean growth over the common growth period with variability data for individual cores shown (black dots).

Europe) *Q. petraea* and *Q. robur*.

The mean growth over the common period of study shows, however, not only the highest mean growth rates for *Q. coccinea* but also the high variability for *Q. frainetto* with *Q. coccinea* in second place. The two species native to the UK show the least variability in growth rate combined with the smallest mean growth over the period of study (Fig. 4).

Mean sensitivity for all species lies between 0.12 and 0.19. The greatest sensitivity to environmental conditions is evident for *Q. coccinea, Q. frainetto* and *Q. palustris* (0.41 to 0.62) at the end of the 1950's and 1970's. *Q. robur* has the lowest sensitivity reaching minimum values below 0.1 in the 1960's.

Climate-growth reactions

Partitioning of climate-growth reactions

Tab. 3 - Results of the partitioning analysis for main climate variables of the vegetation period showing threshold values of reaction and the expected change in tree-ring width when exceeding or undercutting the values.

Species	Thresholds for positive responses			Thresholds for negative responses		
	P sum (mm)	max T sum (°C)	min T sum (°C)	P sum (mm)	max T sum (°C)	min T sum (°C)
Q. coccinea	-	-	-	-	-	< 1592 ↓
Q. petraea	> 250 ↑	< 2874 ↑	> 1592 ↑	< 250 ↓	> 2874 ↓	-
Q. robur	-	-	-	< 247 ↓	> 2846 ↓	-
Q. palustris	> 314 ↑	> 2926 ↑	-	< 314 ↓	-	-
Q. frainetto	> 242 ↑	-	-	< 242 ↓	> 2906 ↓	-

(Tab. 3) shows a clear separation between the three European oak species (*Q. petraea, Q. robur, Q. frainetto*) and the two North American species (*Q. coccinea, Q. palustris*).

Q. frainetto, Q. robur and *Q. petraea* all show a decline in growth below a precipitation sum for May to September of less than than 242, 247 and 250, respectively, while the strongest response of *Q. coccinea* is to minimum temperatures. *Q. palustris* shows a positive response to maximum temperatures with tree-ring growth further enhanced when May to September precipitation is above 314
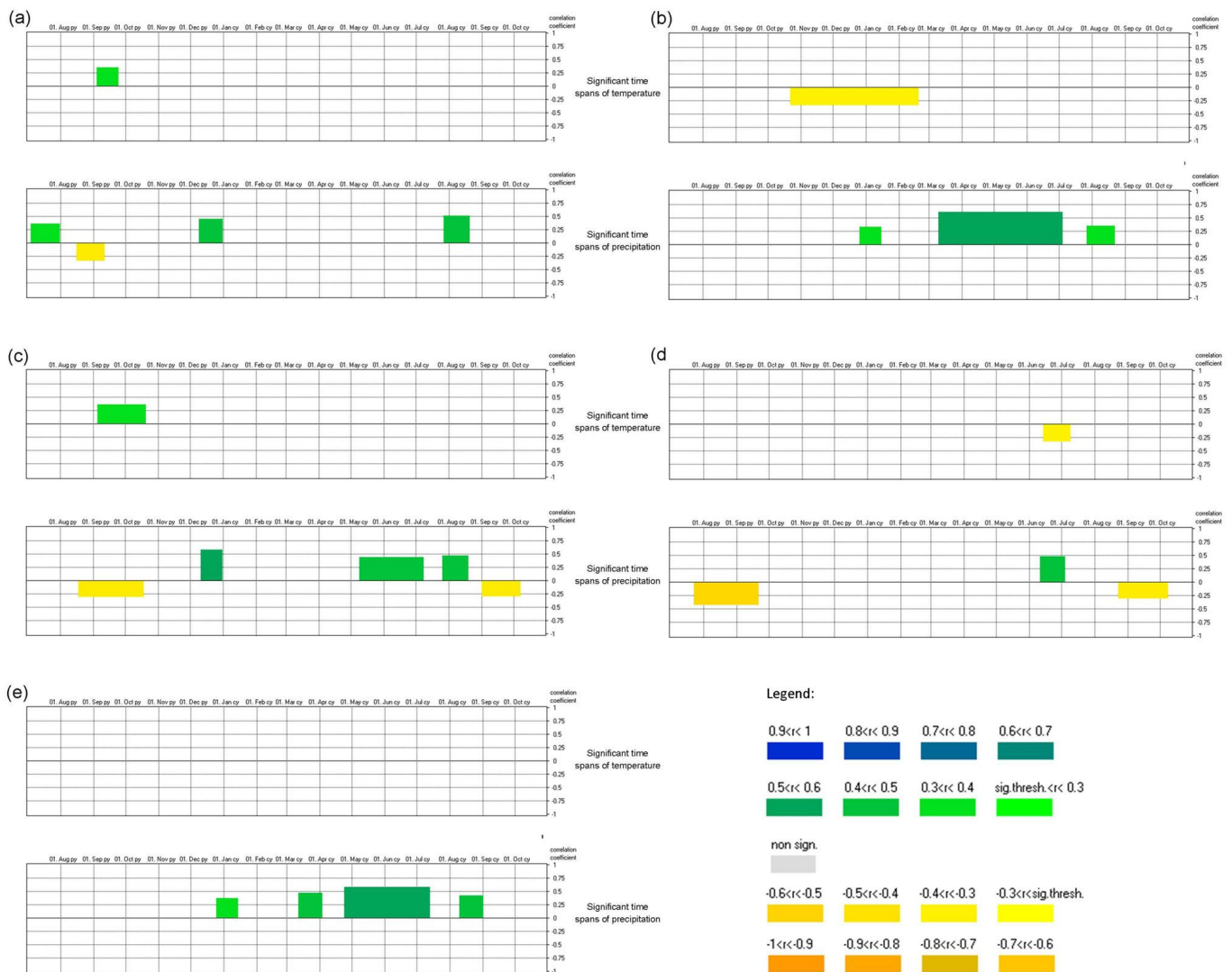

Fig. 5 - Climate-growth correlation between temperature (top) and precipitation (bottom) for *Q. coccinea* (a), *Q. petraea* (b), *Q. palustris* (c), *Q. robur* (d), and *Q. frainetto* (e). Significance levels range from +1 (dark blue) to -1 (red) and are additionally provided on the right y-axis for each individual diagram. The width of the columns provides information on the length of persistence of each correlation with the dates given on the top x-axis of each diagram, beginning with the 1st June of the previous year and ending with the 31st October of the current year.
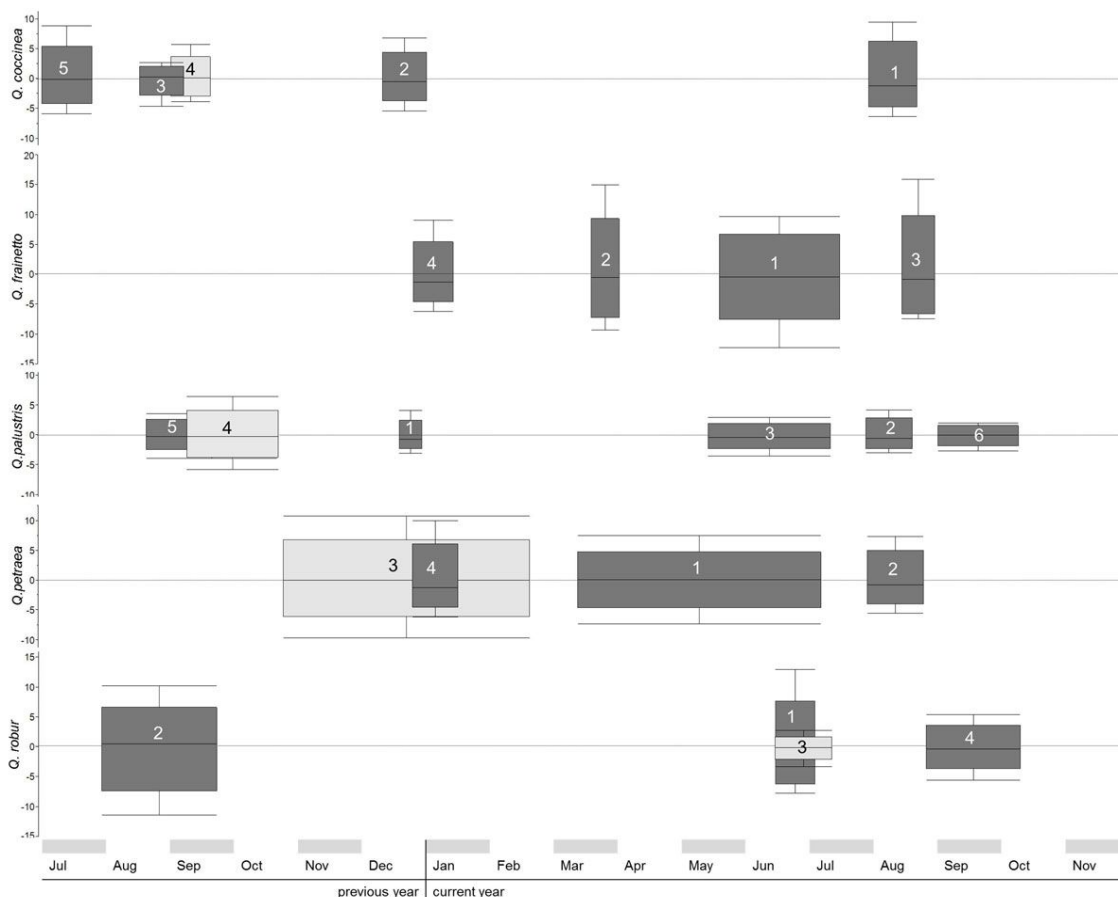
Fig. 6 - Explained variation in tree-ring width to precipitation (dark grey) and temperature (light grey) of *Q. coccinea, Q. petraea, Q. palustris, Q. robur*, and *Q. frainetto* from July previous year to November current year; scale indicating 10% variance for the top three species and 15 and 20% for the bottom two, respectively.

mm; however, the decline in growth below the precipitation threshold is not statistically significant.

The climate-growth correlations using daily data (Fig. 5a-e) show the different responses to climate for the five species grown under the same environmental conditions.

Q. coccinea responds positively to temperature during the the previous autumn. Positive correlations with precipitation are apparent for the previous year's summer and winter periods, and with summer in the current year. Small negative correlations with precipitation are found from mid-August to mid-September of the previous year. *Q. petraea* responds negatively to temperature from mid-October all the way through to mid-February (*i.e.*, growth in the current year is higher when conditions were cold in the previous early autumn). Correlations with precipitation are positive and evident at the beginning of January, from the beginning of March to early July and, again, between the end of July to mid-August. *Q. palustris* displays a positive correlation to temperature in the previous year's autumn. Positive correlations to precipitation are strongest in December of the previous year. Also significant are positive responses to precipitation from May to July and, again, in August of the current year. Negative reactions to precipitation are found, albeit weaker, in the au-

tumn of both the previous and current years. The correlation to temperature of *Q. robur* is weakly negative from mid-June to the second week of July. During the same period, a positive correlation with precipitation is apparent. Negative correlations with precipitation are evident in the late summer of both the current and previous years. No significant correlations with temperature are found for *Q . frainetto* but positive correlations with precipitation occur in mid-winter, mid-March, from the end of April until mid-July and at the end of August.

Using these climate-growth correlations for each species we calculated the explained variance in growth (Fig. 6). For each significant climate-growth correlation, the maximum, mean and minimum tree-ring width is used to produce individual box-plots. The width of the box plots corresponds to the period (in days) of the significant correlations for each species. The mean of the box-plots gives the likely variance in tree-ring width (indexed) caused by a change in climate in the respective periods. The height of the boxes indicates the 25th and 75th percentile respectively as well as absolute maxima and minima (whiskers). Presenting the results in this way allows a comparison to be made between the five species of the strength of the response to these two climate drivers of tree growth. *Q. robur* and *Q.*

frainetto show the strongest variation in radial increment to temperature and precipitation. Tree-ring width of the other species varies less.

The response of *Q. petraea* and *Q. frainetto* are notably to the current year's conditions, in contrast to the other species where precipitation of the previous year are important (*Q. robur* and *Q. coccinea*), and temperature for *Q. palustris*.

Discussion

Studies on climatic influences on the growth of *Q. robur* and *Q. petraea* are extensive (*e.g.*, Anderson & Adams 1978, Friedrichs et al. 2009, Arend et al. 2011, Mérian et al. 2011, Mérian & Lebourgeois 2011). The same is true for several controlled experiments (Broadmeadow & Jackson 2000, Hu et al. 2013, Kuster et al. 2013). The situation is similar for *Q. coccinea* (Abrams 1990, 1996, Jenkins & Pallardy 1995, Speer et al. 2009) but less so for *Q. palustris* (Robertson 1992, Leavitt 2002) in America. For *Q. frainetto* there is a lack of research (Chatziphilippidis & Spyroglou 2004) particularly for climate-growth analysis using tree-rings. Griggs et al. (2007) reported that *Q. petraea, Q. robur* and *Q. frainetto* share a common climate signal at their southern distribution but were unable to distinguish the species due to the historic

source of the timber. These findings could not be confirmed in this study, neither for *Q. petraea, Q. robur,* nor for *Q. frainetto* at this western edge of its distribution. The sensitivity to the two climate variables investigated in this study was low for all five species, indicating that none of them were close to the edge of their climatic envelope. The low year-to-year variability and the significantly high AR is a sign of stable growth conditions (Beck & Heussner 2011).

Increment is highest for *Q. coccinea*, a species known for its rapid growth (Minckler 1965) on a variety of soil types in a wide range of climates. However, it is generally found in regions with a relatively moist climate characterised by more than 760 mm annual precipitation; despite this, observations suggest that it is better suited to dry, well-drained soils. In this study its high average increment is accompanied by high inter-annual variability and the highest number of pointer years. *Q. coccinea* shows a strong negative reaction to summer drought but it also demonstrates the strongest positive response to temperature. This might give the species a competitive advantage under warming conditions in years not characterised by summer drought. *Q. palustris* on the other hand is, as its common name "Spanish swamp oak" implies, tolerant of moist soil conditions and grows primarily on poorly drained and seasonally (winter) flooded sites. In this study a positive response to summer precipitation was evident, but with low inter-annual variability in increment. However, exposure to declining summer precipitation might change this as the climate changes. Both native oak species would be likely to decline in response to climate projections of rising temperatures and declining summer precipitation; however *Q. robur* seems to be more able to tolerate an increase in summer temperatures and is slightly less affected by summer drought than *Q. petraea*, on the basis of responses to climate variables over the chronology covered by this study. The results also suggest that *Q. frainetto* is likely to experience the severest decline under climate change projections of hotter drier summers. This is consistent with observations from Greece where its distribution is limited by summer drought and soil nutrient availability (Spyroglou & Chatziphilippidis 2007). The relative response of the five species to climate variables outlined in the partitioning analysis (Tab. 3) is consistent the results from the climate-growth analysis. While the drought-tolerant species *Q. coccinea* only shows a growth decline when temperatures in the "vegetation period" are below the threshold sum of 1592 °C, none of the other species show a negative reaction to low temperatures.

The Expressed Population Signal (EPS) is a measure of the strength of the common sig-

nal within a chronology, where the threshold is set at 0.85 (Wigley et al. 1984); however, this threshold value is not universally applied (Wigley et al. 1984, Franklin 2013). Where there is a strong common signal within a chronology (*i.e.*, high EPS value), this is generally driven by climatic factors pointer years clearly evident. The chronologies for all five species presented in this study show consistent annual growth and high autocorrelation (AR), indicating relatively limited climatic influences on growth rates. While the low EPS values could result from the low sample size, they could also be explained by the low sensitivity to climate and the high AR. This argument is strengthened by the low SNR-values, providing further evidence of the limited effects of climate on the growth of *Q. robur, Q. palustris* and *Q. frainetto* during the period of the chronologies (Oberhuber et al. 1998) on the sites for the species. Rozas (2005) found similar low values for SNR and EPS for young *Q. robur* growing in Spain, while Pilcher & Baillie (1980) report low SNR values for a modern oak chronology in Ireland. In Germany EPS-values of less than 0.84 were reported for *Q. petraea* and *Q. robur* by Friedrichs et al. 2009. Even lower values have been reported for some other species, including *Fagus sylvatica* (0.818 - Tardif et al. 2001) and *Nothofagus* (0.77 - Cullen et al. 2001). The variability reported here is higher than that reported by Rozas (2005), possibly due to the younger age of the oak trees sampled.

Q. petraea the slowest growing species over the course of the study was highly sensitive to climatic variables and exhibited the longest period of reduced growth following pointer years. *Q. robur* represents a more suitable species to plant in the UK as an adaptation measure given projections of hotter, drier summers and its ability to make a more rapid recovery following negative pointer years.

Conclusion

Analysis of growth variability of five species of oak at a southern British site has enabled a comparison of their response to climatic variation over nearly 50 years. This has provided new information on the extent of their reaction and speed of recovery to extreme climatic events, and highlighted that the growth of some species is dependent on antecedent conditions in previous years. The analysis has provided some of the vital background needed to inform current forestry policy, which is establishing appropriate adaptation measures to respond to the threats of climate change (see Ray et al. 2010).

Q. petraea was the slowest growing species over the course of the study, and appeared to be highly sensitive to climatic variables exhibited the longest period of reduced growth

following pointer years. *Q. robur* therefore represents a more suitable species to plant in the UK as an adaptation measure given projections of hotter, drier summers and its more rapid recovery in growth rate following extreme climatic events. The results indicate that the planting of some species of oak, not native to the UK, offers potential as an adaptation measure, either to diversify species choice or to replace native species of oak on very dry sites. Of the three non-native species evaluated in this study, *Q. palustris* showed the smallest response to changes in climate variables and may therefore have some potential as an alternative species. However, the partitioning analysis indicated that reduced growth rates occurred at a lower precipitation sum than for the two native species, which may be more significant if summer droughts were more intense than those experienced during the course of this study. In terms of overall growth rates *Q. coccinea* is superior to the other four species investigated in this study, with no negative impacts of drought apparent. It could therefore be a suitable choice as an adaptation measure in dry areas with poor nutrient supply, particularly on sandy soils. The sensitivity of *Q. frainetto* to summer drought suggests that the species is unlikely to represent an appropriate alternative to native species of oak.

Apart from the evaluation of future climatic suitability presented in this study, a much wider range of factors, including timber quality, needs to be taken into account when considering whether to select alternative, non-native species as a climate change adaptation measure when planting new woodland. Non-native species of oak, particularly those from outside Europe may not support the same biodiversity as native species of oak, while they may also be susceptible to pests and diseases that are endemic to the UK, but not present in their native range. There are also a number of landscape and cultural issues to consider, as the form and appearance of both *Q. palustris* and *Q. coccinea* is very different to that of the two native species.

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