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Dependence of tree ring stable isotope abundances and ring width on climate in Finnish oak

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Summary We measured ring widths and isotopic abundances of carbon, oxygen and hydrogen ($\delta^{13}C$, $\delta^{18}O$ and $\delta^{2}H$) from the latewood of tree rings of pedunculate oak (*Quercus robur* L.) in its distributional northern limit in Southern Finland. Ring width was observed to be related to precipitation and relative humidity but not significantly to temperature. $\delta^{13}C$ and $\delta^{18}O$ were significantly related to all studied climatic variables, most strongly to cloud cover. Variations in $\delta^{2}H$ were discovered to be complex combinations of signals from biochemical and physical processes. The results suggest that oaks in Finland can be used as a source of climate information. $\delta^{18}O$ was discovered to be especially promising as it showed the strongest climate signal and highest common signal between trees. The relationship between climate and ring width indicates that water availability is the main control of ring radial growth. This is supported by the isotope data. High correlation between $\delta^{13}C$ and $\delta^{18}O$ time series indicates that photosynthetic carbon assimilation is limited by stomatal control. Therefore, in contrast to the expected temperature limitation, our data indicate that drought limits oak growth more than cold temperatures on the border of its northernmost distribution range.

Keywords: carbon, dendroclimatology, Fennoscandia, hydrogen, oxygen, Quercus robur L.

Introduction

Oaks are long-lived trees that have a common pattern in ring widths which is crossdatable and is frequently used for dating old wooden buildings and wooden objects (e.g., Bartholin and Berglund 1975, Pilcher et al. 1984, Becker et al. 1991, Wazny 2002, Pukiene and Ozalas 2007). However, this pattern has rarely been observed to contain a simple or strong climate signal, which has restricted the use of oak in studies of past climate variability (Pilcher 1995, Helle and Schleser 2004*a*, van der Werf et al. 2007, Etien et al. 2008*a*, Loader et al. 2008, Friedrichs et al. 2009). In order to extract easily utilizable climate reconstructions from tree rings, the growth must be primarily controlled by a single or few environmental variables. This can be accomplished in exceptionally wet or dry growth habitats or in higher altitudes and latitudes, close to the tree species growth limit. In such locations, typically, one or two climatic factors become limiting to growth to the extent that they override other growth controlling factors. This causes ring growth to be highly correlated with the limiting factors. For example, the growth of pine (*Pinus sylvestris* L.) in the vicinity of the treeline in Northern Fennoscandia is largely controlled by temperature (Briffa et al. 1988, Grudd et al. 2002, Helama et al. 2002).

Natural abundances of stable isotopes in tree rings of oaks, on the other hand, have been shown to record a strong climate signal in different sites across Europe. Etien et al. (2008*b*) studied stable isotope ratios of carbon ($\delta^{13}C$) and oxygen ($\delta^{18}O$) in oak tree rings in northern France and discovered especially $\delta^{18}O$ to strongly reflect growing season maximum temperatures. They used a linear combination of $\delta^{18}O$ and grape harvest dates, also used as a temperature indicator, to improve the temperature signal and were able to reconstruct growing season temperatures for the most recent 400 years. Loader et al. (2008) studied stable isotope ratios of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{2}H$ in oak in south western Scotland. They demonstrated that it is possible to extract a summer climate signal from oak trees growing under maritime conditions, where ring widths (or density) do not routinely yield useful climatic information. Ogle et al. (2005) used carbon isotope ratios in tree rings of Irish oak to distinguish past volcanic eruptions. Mayr et al. (2003) studied long-term trends in oak $\delta^{13}C$ and $\delta^{2}H$ in central European millennia long tree ring chronology. They found intervals of agreement and disagreement between the two isotopes and suggested that $\delta^{2}H$ is determined more by temperature and $\delta^{13}C$ by humidity. Robertson et al. (1997) were the first to study carbon isotopes in Southern Finnish oaks from a palaeostudy perspective. They found carbon isotopes in oak tree rings to be a good indicator of climate, better than ring widths, recording a strong signal from rainfall and relative humidity.

Besides the use in palaeoclimatic reconstructions, the information preserved in tree rings can be used for studying ecology of the tree species in question. Oaks are known to suffer from decline events of several years duration, which can be detected by foliage deterioration and increasing mortality rate. During the past decades, such events have been reported to occur more frequently in large parts of Europe (Thomas and Hartmann 1996, Gibbs and Greig 1997, Sonesson 1999, Jönsson et al. 2005). The events have been associated, among other things, with drought and pathogens, but the reasons are also known to be complex, indirect and site specific. These relationships have been successfully studied by comparing living and recently dead trees, studying the timing and severity of growth reductions and linking them with drought and winter frost damages (Drobyshev et al. 2007, Helama et al. 2009).

Stable isotopes, as well, can be interpreted ecologically or palaeoecologically. Since there exists a direct relationship between plant water use efficiency and carbon isotope ratios in plant material (Farquhar et al. 1989), stable isotopes of carbon have been used as an indicator of tree–water relations (Saurer et al. 2004, Betson et al. 2007, Haavik et al. 2008). Oxygen and hydrogen isotopes have been used in differentiating between water sources to the tree. Plamboeck et al. (1999) utilized naturally occurring vertical isotope gradients in soil water to study water uptake. Roden et al. (2009) studied fog events using the distinct isotopic signature of fog water recorded in tree rings. The isotope ratios of H, C and O are not controlled by a single environmental variable, and their combined use can contribute to a better understanding of the environmental controls on tree processes. As an example, variation in carbon isotope ratios may be driven by changes in stomatal conductance, changes in photosynthetic rate or both. Since oxygen isotope ratios are not considered to be strongly influenced by photosynthetic rate, the combined measurement of both carbon and oxygen can be used to identify the likely cause of change in leaf internal CO_2 concentration resulting in more precise interpretations of tree processes (Scheidegger et al. 2000, Keitel et al. 2003, Saurer and Siegwolf 2007).

In Finland, the pedunculate oak (*Quercus robur* L.) grows on the border of its European northernmost distribution range. It is the only oak species in Finland, and its distribution is currently restricted to a narrow zone in the southern part of the country. The population is growing in fragmented, characteristically coastal habitats, most stands being situated near the shoreline or on outcrops of former islands (Ollinmaa 1952, Vakkari et al. 2006). Yet, the oak has been part of the natural flora during the past ~8000 years (Huntley and Birks 1983, Alho 1990, Ferris et al. 1998, Brewer et al. 2002), and it has extended its range further north during warm periods in the past. According to fossil pollen records, oak was present in a wide area in Southern Finland during the Holocene Climatic Optimum (Donner 1995). Additionally, historical records suggest that there were large oak stands ca. 150 km beyond the species current limit during the Medieval Warm Period (Huldén 2001), and it was not until the Little Ice Age (LIA) that oak declined to its current range. Today, the distribution is believed to be limited by climatic factors, cold winter temperatures and short summers in the area (Solantie 1983, Valkonen et al. 1995, Repo et al. 2008) and also by human exploitation (Ollinmaa 1952, Rainio 1977, Raisio 1996).

This study is based on measurements of widths of oak earlywood and latewood and measurements of the natural abundance isotope ratios of $\delta^{13}C$, $\delta^{18}O$ and $\delta^{2}H$ in tree ring cellulose. We study these records for climate-induced signal and the climate–growth relationships in order to quantify the potential of these proxies as a source of palaeoclimatic information. We also address the possible ecological interpretations especially considering the location of the studied trees in the species' northernmost distribution limit.

Materials and methods

Site and sampling

The study site is located in Bromarv (60°00′ 23°05′), on the southern coast of Finland. The habitat is natural grown deciduous unevenaged forest. The common species at the site include *Q. robur*, *Tilia cordata*, *Acer platanoides*, *Sorbus aucuparia* and *Corylus avellana*. The mean July temperature between years 1971 and 2000 measured at the Salo weather station (60° 22′, 23° 03′, 3 m a.s.l.) is 17 °C. The average yearly precipitation sum for the same period is 675 mm. The seven sampled oak trees grow on an east-facing slope towards an open meadow. The stem diameter varies between 60 and 85 cm at breast height. All of the cored trees are more than 100 years old. Trees were sampled from at least two directions with an increment corer during summer and autumn 2004. Additional samples were taken in summer 2008.

Ring width chronology construction

All obtained cores were first crossdated visually and then further validated using the COFECHA software package (Grissino-Mayer et al. 1997). The assigned dates were utilized for the isotope chronologies. Tree ring widths were measured from two cores from each of seven trees. The earlywood ring widths (ERW) and the latewood ring widths (LRW) were measured separately, and the total ring widths (TRW) were calculated as their sum. The boundary between latewood and earlywood was distinguished by change in vessel size and vessel distribution. The individual ring-width series were indexed in order to remove the age–size related trend in radial growth. This was done using ARSTAN software (Cook and Holmes 1986). As the growth trend model, we used 67% cubic spline functions with 50% variance cutoff. The tree ring indices were then calculated from each curve by division. The chronologies were produced averaging the annual values of indices for ERW, LRW and TRW (Figure 1). ARSTAN was also used to calculate the residual chronologies

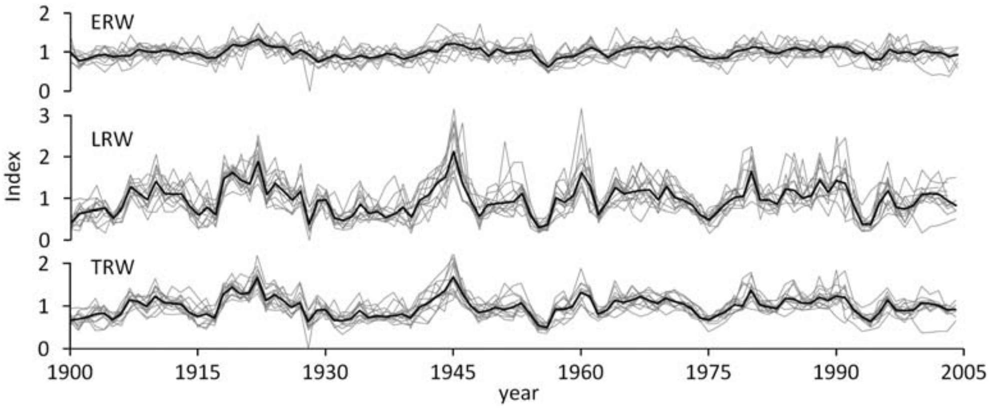

Figure 1. Standardized earlywood (ERW), latewood (LRW) and total ring-width (TRW) series and chronologies. Chronologies are calculated as the average of the individual tree ring series.

(ERW_{res}, LRW_{res} and TRW_{res}). The residual chronology indices are derived by autoregressive modeling, where the autocorrelation is removed from each series before the chronology is compiled.

Isotopic fractionation in trees

Carbon isotope fractionation in plants is dependent on the significance of the various physical and biochemical processes during photosynthetic CO_2 uptake. The model of Farquhar et al. (1982) relates the discrimination in photosynthesis to the ratio of leaf intercellular to ambient CO_2 concentration. This ratio is controlled by the supply of CO_2 through the stomata and demand for it in the photosynthesizing tissue. Other plant compounds will inherit the signature of the photosynthesized carbohydrates. However, the isotope signal can also be altered by some downstream metabolic processes after photosynthetic carbon fixation (Helle and Schleser 2004*b*, Gessler et al. 2009).

Oxygen and hydrogen isotope ratios in the tree ring cellulose record evaporation effects in the leaf and isotopic composition of the source water. The water transported to the leaf becomes enriched with the heavier isotope due to transpiration. The oxygen isotopic composition of synthesized carbohydrates changes due to carbonyl oxygen exchange with the medium water, thus capturing the transpiration signal. A similar exchange also occurs in the stem with stem water when the carbohydrates are utilized to synthesize cellulose (Sternberg et al. 1986, Yakir and DeNiro 1990, Roden and Ehleringer 1999, Sternberg et al. 2006). Also, carbon-bound hydrogen atoms in carbohydrates undergo similar exchange with medium water in the leaf and again in the stem (Sternberg and DeNiro 1983, Yakir and DeNiro 1990, Luo and Sternberg 1992, Roden and Ehleringer 1999, Waterhouse et al. 2002, Augusti et al. 2006, 2008, Sternberg et al. 2006).

Isotope measurements

Four trees, two cores per tree, were chosen for the isotope analysis. Rings were cut with surgical blades separating earlywood from latewood. Only the latewood portion was used for isotope analysis because the earlywood is likely to be influenced by stored carbohydrates from previous years, whereas the latewood is mainly synthesized from current year photosynthates (Barbaroux and Bréda 2002; Kagawa et al. 2006). For 26 years in the beginning of the study period, isotope analyses were made separately for each tree in order to detect possible differences between sampled trees and to be able to estimate the confidence of the chronology. For the remaining years, the sample material was pooled in annual resolution in order to reduce the number of samples for cellulose extraction and isotope measurements.

α-Cellulose was extracted from the samples following the method of Loader et al. (1997). The cellulose samples were weighed into tin ($\delta^{13}C$ analysis) or silver ($\delta^{18}O$ analysis) capsules. To minimize the effect of air moisture in $\delta^{18}O$ analysis, the silver capsules were preheated (375 °C 1 h) and dried in a vacuum oven. Hydrogen isotopes were measured from nitrated cellulose to avoid the influence of exchangeable hydrogen atoms. Nitration was done following the method of Green (1963). Nitrated samples were weighed into silver capsules and dried overnight. During the measurements, oxygen and hydrogen samples were kept under a cap with Ar gas flow. Samples used for carbon isotope ratio measurement were combusted in an elemental analyzer (NC 2500; Carlo Erba), and samples for oxygen and hydrogen measurements were pyrolyzed in a high-temperature elemental analyzer (TC/EA; Thermofinnigan). The gases were then introduced to mass spectrometers via an interface (ConFlo II or III), CO_2 and CO to Delta^{Plus}Advantage and H_2 to Delta^{Plus}XL (Finnigan). Always at least two replicate samples were analyzed, and the results were calculated as their average. Isotope results are expressed using the conventional δ (delta) notation, where carbon isotope ratios are expressed relative to the Vienna Pee Dee Belemnite (VPDB) and oxygen and hydrogen isotope ratios relative to Vienna Standard Mean Ocean Water (VSMOW) standard.

Carbon isotope values were corrected for change in carbon isotope composition of atmospheric CO_2. This change has occurred during the last centuries due to the dilution of CO_2 with isotopically depleted CO_2 originating from fossil fuel burning and land use changes (Joos et al. 1999). A correction that is based on data from ice cores and instrumental measurements compiled by Leuenberger (2007) was used.

Weather data

Daily temperatures, including daily minimum and maximum temperatures, daily precipitation sum and cloud cover from 1936 to 2004 and relative humidity from 1964 to 2004 were obtained from the Salo weather station (60°22′ 23°03′, 3 m a.s.l.) (provided by the Finnish Meteorological Institute) located at a distance of 40 km from the study site. For the analysis, average daily values for cloud cover were calculated using the morning (observing time 9:00 UTC since 1947) and midday (12:00 UTC) values. Daily average temperature and daily average relative humidity were calculated as the average of morning, midday and evening (observing time 18:00 UTC) values. Monthly climate data were calculated as the average of daily values.

Daily temperature data were used to calculate two agro-climatic indices (Rochette et al. 2004). These indices express the risk associated with freezing injury to deciduous trees during autumn and winter. Cold degree-days (CDD-15) were calculated as cumulate degree-days below a temperature threshold of −15 °C from previous year August 01 to July 31. The first date of autumn frost (FAF-2) is the day of the year when the daily minimum temperature falls below or equal to −2 °C after the beginning of August.

Statistical methods

The confidence of the site chronologies was examined using the expressed population signal (EPS), which is a measure to express the common signal in a time series (Briffa and Jones 1990). A value of 0.85 or higher is commonly considered as acceptable (Wigley et al. 1984). Mean sensitivity, which is the relative difference from one year to the following (Fritts 1976), was calculated for ring-width series using COFECHA. The dependency of an isotope or a ring-width value on the respective value of the previous year was examined using autocorrelation analysis (Fritts 1976). Before this analysis, a linear trend, determined by least squares method, was removed from the isotope series. To compare the structure of correlation among chronologies, Pearson correlation coefficients and principal component analysis (PCA) were calculated using program R (version 2.2.1) (library Vegan). The option to standardize the data prior to the PCA was used. PCA involves a procedure that transforms possibly correlated variables into uncorrelated variables called principal components (Girardin et al. 2004, Tardif and Conciatori 2006).

Shifting correlations were used to define the interval during summer when climate influences tree ring growth or isotope value. Daily weather measurements were averaged over 30 consecutive days, and these averages were calculated starting every 10th day, the first period starting from mid-May and the last period continuing to the end of September. Pearson correlations between chronologies and 30-day averages were calculated. Daily climate data from years 1936–2004 were used in this analysis. Since the available climate data from the early observations is mainly available as monthly averages and since in the literature it has been common to use monthly averages to calibrate tree ring proxies with climate records, we tested our time series also against monthly climate data. This was done using Pearson correlation coefficients.

Results

Description of the chronologies

The descriptive statistics for the isotope series are presented in Table 1. After correcting the trend caused by atmospheric $\delta^{13}C$ depletion, all series exhibit an increasing linear trend with time that is statistically significant ($P = 0.000$ for $\delta^{13}C$, $P = 0.021$ for $\delta^{18}O$, $P = 0.000$ for $\delta^{2}H$) (Figure 2).

The EPS value was calculated for all of the chronologies using the period 1901–1926. The particular years were chosen because for these years separate isotope measurements exist for each tree. The period is short but shows a guideline for the approximate confidence of the chronologies. The EPS value was 0.83 for $\delta^{13}C$, 0.87 for $\delta^{2}H$ and 0.95 for $\delta^{18}O$ using all four trees. For LRW, the EPS value is 0.94, for ERW 0.86 and for TRW 0.94. Thus, the obtained EPS values exceed the commonly accepted value of 0.85 for all the other chronologies apart from $\delta^{13}C$. The average mean sensitivity calculated for standardized ring-width series is 0.17 for ERW, 0.36 for LRW and 0.21 for TRW. Autocorrelation analysis was carried out for the standardized ring-width chronologies and for the detrended isotope chronologies. The ERW chronology was observed to contain the most significant autocorrelation, which was significant on lags 1 to 3 (ERW_{std}: $r = 0.65$ $P < 0.001$ on lag 1; $r = 0.39$, $P < 0.001$ on lag 2; $r = 0.23$, $P < 0.05$ on lag 3). The LRW and TRW chronologies were observed to contain autocorrelation that is significant on lags 1 and 2 (TRW_{std}: $r = 0.62$, $P < 0.001$ on lag 1; $r = 0.33$, $P < 0.001$ on lag 2; LRW_{std}: $r = 0.53$, $P < 0.001$ on lag 1, $r = 0.23$, $P < 0.05$ on lag 2) (Figure 3). The $\delta^{13}C$ and $\delta^{18}O$ chronologies did not contain statistically significant autocorrelation. However, the $\delta^{2}H$ chronology did contain weak autocorrelation on lag 1 ($r = 0.25$, $P < 0.05$).

The Pearson correlation coefficient value calculated for the $\delta^{13}C$ and $\delta^{18}O$ chronologies was high (Table 2). Both of the

Table 1. Descriptive statistics of isotope series including the number of years covered by the chronologies.

	$\delta^{13}C$	$\delta^{18}O$	$\delta^{2}H$
Mean	−24.78	25.6	−93.4
Minimum	−26.77	23.8	−107.4
Maximum	−22.98	28.2	−53.4
n	104	104	104

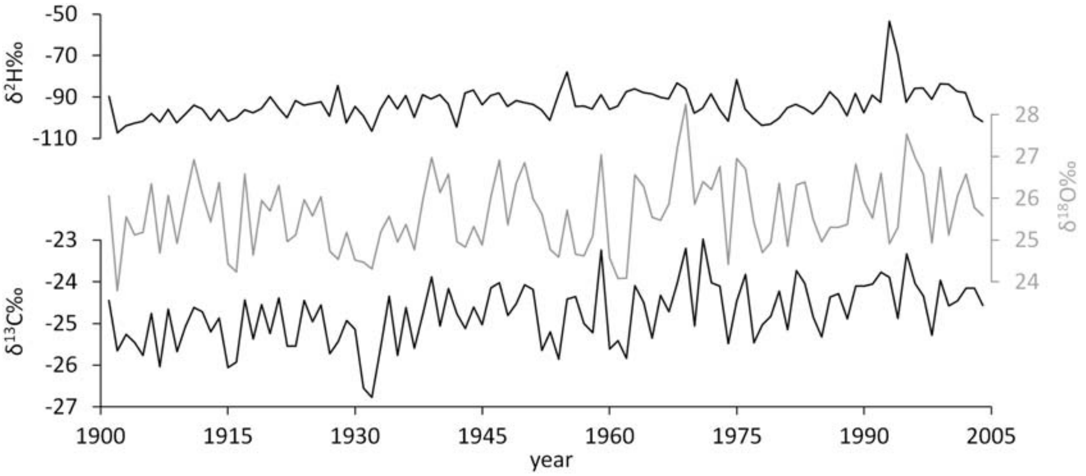

Figure 2. Isotope time series of hydrogen (δ^2H), oxygen (δ^{18}O) and carbon (δ^{13}C).

chronologies correlate significantly with the δ^2H chronology, although the correlation was weaker. The ERW, LRW and TRW chronologies correlated significantly with each other but not with isotope chronologies. PCA was calculated using the δ^{13}C, δ^{18}O, δ^2H and TRW$_{res}$ series. PC1 represented 51% of the variance and was most strongly associated with δ^{13}C and δ^{18}O, which also correlated with each other according to Pearson correlations (Table 3). PC2 represented 29% of the variance and was mainly associated with tree ring width. PC3 represented 15% of the variance and was associated with δ^{18}O, δ^2H and TRW$_{res}$. PC4 was associated with δ^{13}C and δ^{18}O. PCA analysis corroborates the result of the Pearson correlations analysis, which suggested that the TRW$_{res}$ and δ^{13}C and δ^{18}O chronologies have almost nothing in common (Figure 4). The δ^2H series contains some common features with both the TRW$_{res}$ and the other isotope chronologies.

Correlations with climate

Correlations between chronologies and climate during the growth period are presented in Figure 5. Both the δ^{13}C and δ^{18}O chronologies correlated significantly with all studied climate variables. The *r* values obtained for summer temperatures were positive, and *r* values obtained for cloud cover and precipitation were negative. The 30-day intervals when the *r* values were highest occurred approximately at the same time in each case, beginning in mid-July and ending in mid-August. For δ^2H, the *r* values were positive for temperature and negative for precipitation and cloud cover. However, the relationship was weaker in comparison with δ^{13}C and δ^{18}O. Furthermore, the period that correlated most strongly occurred slightly earlier. The *r* values obtained for ERW, LRW and TRW were low. The *r* values were significant and positive for precipitation and relative humidity. The highest *r* values occurred during longer periods of summer in comparison with what was observed for isotopes.

Correlation coefficients for averaged monthly climate variables are shown in Table 4. In addition, for each chronology the combination of months containing the strongest climate signal is given. Because of the detected autocorrelation, both the standard and residual ring-width chronologies were tested (TRW and TRW$_{res}$ or LRW and LRW$_{res}$, respectively). From the used climate variables, precipitation is the only one which correlates significantly with all of the chronologies. Temper-

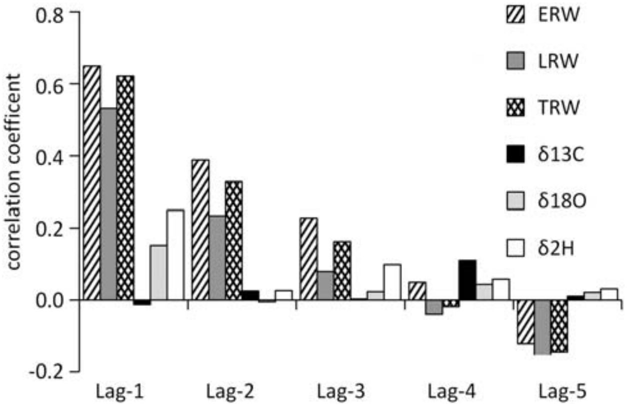

Figure 3. Autocorrelation in the time series. Linear trend has been removed from the isotope chronologies before the analysis.

Table 2. Correlation coefficient between chronologies. Significance indicated with asterisks.

Chronology	$\delta^{13}C$	$\delta^{18}O$	$\delta^{2}H$	TRW	LRW
$\delta^{18}O$	0.79***				
$\delta^{2}H$	0.43***	0.30**			
TRW	0.12	0.08	−0.10		
LRW	0.10	0.06	−0.18	0.98***	
ERW	0.10	0.09	0.04	0.82***	0.70***

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

ature correlates significantly only with isotope chronologies and with the PC1 and PC3. $\delta^{18}O$ exhibits the highest correlation coefficients with climatic variables and $\delta^{13}C$ the second highest. The strongest relationship is detected between cloud cover and $\delta^{18}O$.

Also, correlation coefficients for the winter half of the year (previous October–April) were calculated, but only weak correlations between LRW and previous October temperature ($r = 0.26$, $P < 0.05$) and $\delta^{2}H$ and previous October precipitation ($r = 0.26$, $P < 0.05$) were detected. Significant correlations were not found between agro-climatic indices (CDD-15 and FAF-2) and isotope series or tree ring-width series.

Discussion

We assumed that tree ring characteristics of a species at its northern limit would primarily depend on either summer or winter temperatures, since these factors should be limiting. However, in spite of the northern location, the temperature signal was not significant for TRW or for LRW. In contrast, the detected dependences, positive correlations with precipitation, relative humidity and cloud cover relate to water availability of the trees. In accordance with our study, significant signals for June–July rainfall but not for temperature were observed by Robertson et al. (1997) in Turku less than 100 km away. They, in addition, did not find differences between dry and humid sites. Similarly, Helama et al. (2009) found that summer moisture was the most pervasive factor influencing the radial growth of oak in the Helsinki area. Also in nearby Sweden, the growth has been found to be controlled by summer precipitation (June–July), at least during climatically non-extreme years (Drobyshev et al. 2008). Although it has been recently hypothesized (Repo et al. 2008) that short summers, cold winters and autumns and consequent frost damage may limit the distribution of oak in Fennoscandia, our data suggest that cold autumns and winters do not have much influence on growth. The short-summer hypothesis would assume that growth is limited by spring and summer temperatures since warm temperatures tend to increase the rate of growth and cell maturation, but this was not supported by our data. In addition, we did not detect significant relationships between calculated agro-climatic indices and ring growth, which indicates that inadequate cold hardening or winter frost damage does not have a regular effect on annual growth variations. Furthermore, data from Sweden on the mortality of oaks do not support high mortality after cold summers or cold autumns. However, Drobyshev et al. (2007) discuss a possible association between oak mortality and summer drought.

Table 3. PCA analysis.

PCA axes	Variance explained (%)	Correlation with chronologies			
		$\delta^{13}C$	$\delta^{18}O$	$\delta^{2}H$	TRW_{res}
PCA 1	51	−0.93	−0.88	−0.64	0.03
PCA 2	29	0.18	0.20	−0.50	0.91
PCA 3	15	0.08	0.32	−0.58	−0.40
PCA 4	5	0.32	−0.28	−0.08	−0.04

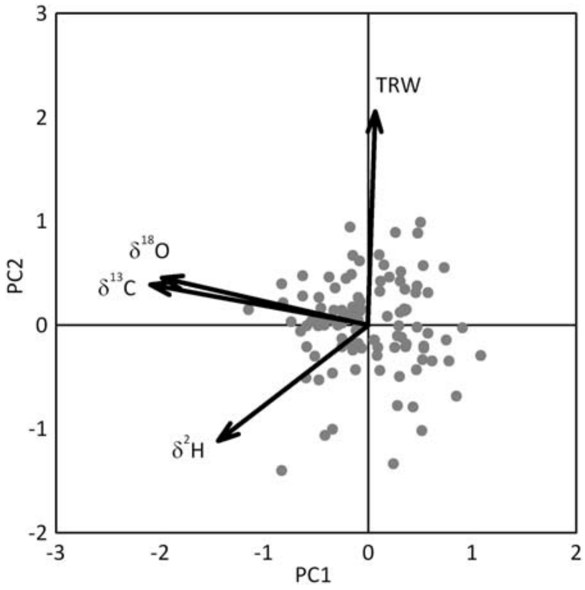

Figure 4. PCA analysis. Different years are represented by gray points.

Our results do not indicate that the climate signal in growth indices becomes simpler when approaching the species distribution limit. It has been well known that extreme conditions and limiting factors, as they occur close to the tree line, often lead to clear signals in tree ring chronologies (Fritts 1976, Schweingruber et al. 1990). It has been implicitly assumed that a single limiting factor also explains the growth of trees near the distribution limits. However, our results and other studies (Brewer et al. 2002, Fang and Lechowicz 2006, Bolte et al. 2007, Morin et al. 2007) indicate that the limitations to temperate species close to northern distribution limits are not necessarily that clear. The mean sensitivity observed in our study was slightly lower than what is reported from central Europe (Eilmann et al. 2006, van der Werf et al. 2007, Friedrichs et al. 2009). The climate signals observed resemble studies reported from elsewhere in Europe, where ring growth is complex and affected mostly by drought conditions, water supply, summer precipitation and air humidity (Siwecki and Ufnalski 1998,

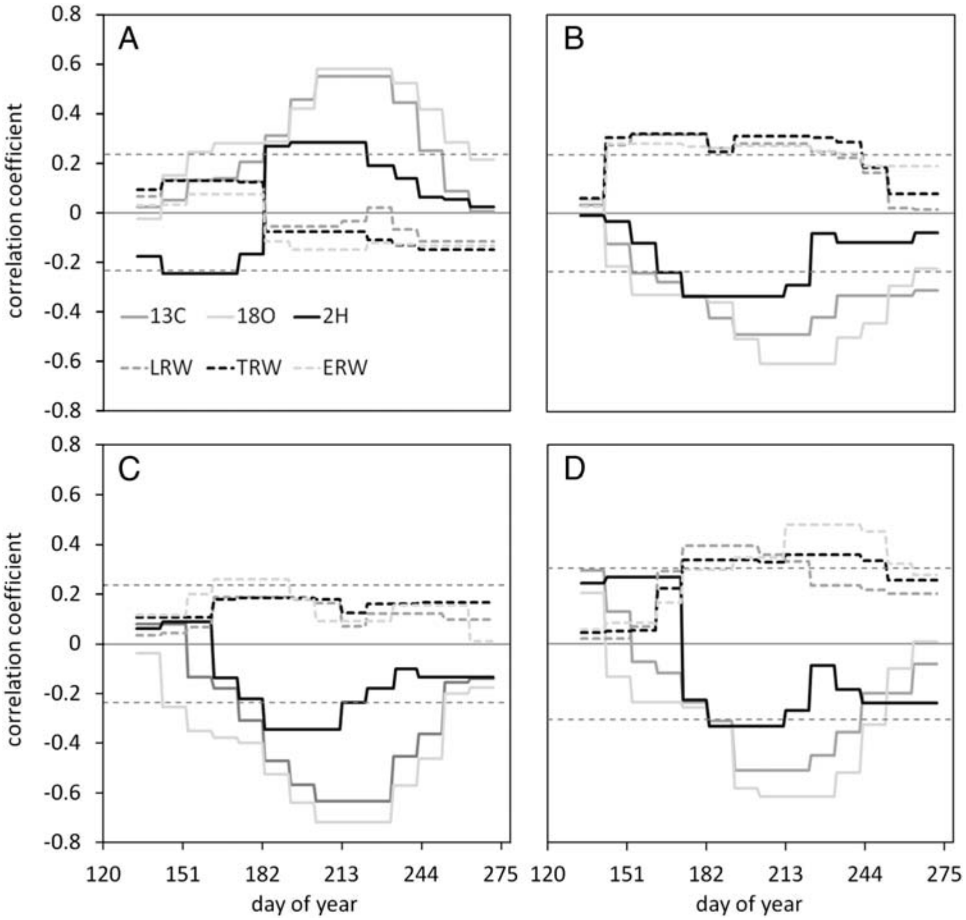

Figure 5. Correlation between time series and temperature (A), precipitation (B), cloud cover (C) and relative humidity (D) of shifting temporal windows of 30 days' duration. The periods are shifted in 10-day intervals. Correlations for temperature, precipitation and cloud cover are calculated for years 1936–2004 and relative humidity for years 1964–2004. Dashed line represents $P < 0.05$.

Kelly et al. 2002, Etien et al. 2008*a*, Friedrichs et al. 2009, K.T. Rinne et al., in preparation).

Whereas TRW and LRW show relatively low levels of climatic sensitivity, the isotope chronologies reveal a strong relationship with climate. Our study conforms to the results of Robertson et al. (1997), who suggested that δ^{13}C is superior to ring width as a climate proxy in oaks in Southern Finland. However, since δ^{18}O also correlated well with climate and since fewer trees were needed to fulfill the EPS criteria, our results suggest that δ^{18}O would be best suited for palaeocli-

Table 4. Correlation coefficients for chronologies and PC1 and PC2 with current year mean monthly environmental variables of strongest correlation. Correlations for temperature, precipitation and cloud cover are calculated for years 1936–2004 and relative humidity 1964–2004. The month or combination of months is indicated, JA = July–August JJA = June–July–August. Significant values are indicated with asterisks.

Chronology	Temperature		Precipitation		Cloud cover		Relative humidity	
δ^{13}C	0.45***	JA	−0.52***	JA	−0.56***	JA	−0.33*	JA
δ^{18}O	0.52***	JJA	−0.62***	JJA	−0.70***	JJA	−0.44**	JA
δ^{2}H	0.27*	July	−0.35**	July	−0.34**	July	−0.28	July
TRWstd	0.12	June	0.40***	JJA	0.20	JA	0.41**	JA
TRWres	0.07	June	0.29*	JJA	0.16	JA	0.37*	July
LRWstd	0.15	June	0.37**	JJA	0.18	JA	0.35*	JA
LRWres	0.09	June	0.25*	JJA	0.12	JA	0.31*	July
PC1	−0.52***	JA	0.62***	JJA	0.65***	JA	0.43**	JA
PC2	0.23	June	0.25**	July	0.14	July	0.31*	July
PC3	0.24*	JJA	−0.33**	JJA	−0.39***	JJA	−0.37*	June

*$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

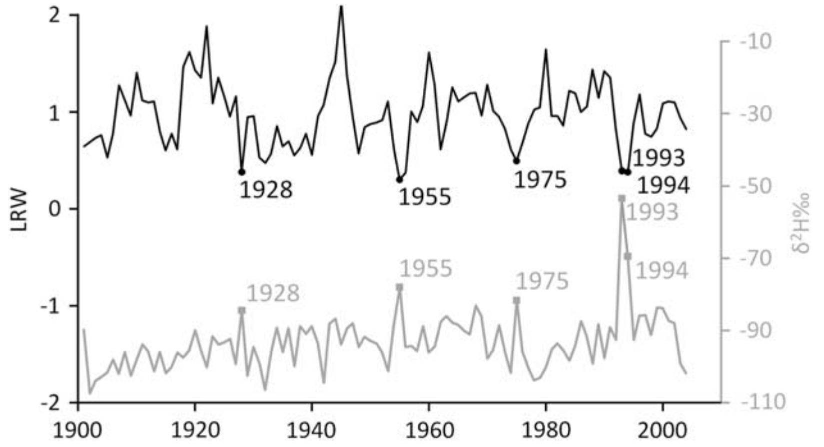

Figure 6. Latewood ring width and δ^2H series. Common years of exceptional value are indicated.

mate research. This finding is also in line with several other recent studies on European oaks which have found δ^{18}O to be the most suitable climate proxy (Szczepanek et al. 2006, Etien et al. 2008*a*, Loader et al. 2008, Weigl et al. 2008, K.T. Rinne et al., in preparation). Contrary to TRW and LRW, δ^{13}C and δ^{18}O did not correlate with previous year values but were sensitive to current year climate conditions, which further argues for their potential. δ^{13}C and δ^{18}O chronologies exhibited significant correlations with all tested climate variables. Correlations with cloud cover were the strongest for both of them, indicating that when used as a climate proxy these isotopes would best reflect variations in cloud cover. Unfortunately, the relative humidity time series was much shorter than the other climate time series and can thus not be directly compared in Table 4 and Figure 5. However, when calculated for the same period (1964–2004), cloud cover, temperature and precipitation still all exhibit higher correlations with δ^{13}C and δ^{18}O than relative humidity. Maximum temperatures alone, which sometimes have been found to correlate well with isotope series (Etien et al. 2008*a*), did not give better results than the average temperatures with our data.

Hydrogen isotope chronology differed from the δ^{13}C and δ^{18}O chronologies, although more similar variation to δ^{18}O would have been expected from the presented theoretical models. According to the models, both of the isotopes should be affected by source water, with which the isotopes are known to be highly correlated, and by evaporation effects in leaf, which vary as a result of changing air humidity. The correlations with climate variables were, however, much weaker for δ^2H than for δ^{18}O. δ^2H also correlated with climate slightly earlier in summer than δ^{18}O or δ^{13}C (Figure 5). Mayr et al. (2003) compared oak latewood and earlywood isotopic composition and found earlywood δ^2H value to be on average 17 ‰ higher than latewood δ^2H value. Robertson et al. (1995) found similar results for *Quercus petraea*, but the difference between earlywood and latewood was even higher, more than 20 ‰. If our samples were contaminated from earlywood or from previous year photosynthates, this contamination would be significant during years of very narrow growth. This kind of contamination seems possible, when the years containing the narrowest latewood growth and the highest δ^2H are compared (Figure 6). Five of the six (1928, 1955, 1956, 1975, 1993 and 1994) narrowest latewood rings are reflected in the δ^2H time series as exceptionally high values. However, it cannot explain all of the observed enrichment in δ^2H, especially concerning the year 1993. Other possible reasons for low correlation values can be found from the recent works of Augusti et al. (2006, 2008). Their studies imply that a likely explanation for the difficulties encountered in δ^2H-based climate reconstructions in recent studies around Europe (Waterhouse et al. 2002, Etien et al. 2008*b*, Loader et al. 2008) lies in fractionations happening within the tree which are traditionally assumed to be constant. These enzymatic fractionations that alter the isotopic composition of the metabolites compared with the source and leaf water can vary, reflecting alternative biosynthetic pathways or changes in the regulation of enzyme reactions caused by changing metabolic fluxes (Schleucher 1998, Schleucher et al. 1999). Therefore, our results suggest that δ^2H at this site as such cannot be used to create reliable climate reconstructions.

The observed negative association between radial growth and water availability points to limitations due to stomatal conductance and consecutive reductions in carbon assimilation during dry periods. This conclusion is supported by the isotopes. Oxygen isotopes enrich in the leaves when air relative humidity is low. Carbon isotopes, on the other hand, enrich in the photosynthates either when stomatal conductance is reduced or when the photosynthetic rate is increased. Because trees try to avoid loss of water and reduce transpiration by closing stomata, the covariance of δ^{13}C and δ^{18}O suggests that the leaf internal concentration of CO_2 is controlled by stomatal conductance. This is not contradictory to the fact that at this site the climate variable correlating most strongly with δ^{13}C is cloud cover. Cloud cover is closely related to available irradiance and, thus, if correlated with δ^{13}C, can be used to argue for photosynthetic rate limitation (Young et al. 2010). However, at this site, cloud cover correlates strongly with both precipitation and temperature (cloud cover and precipitation: r= 0.72, cloud cover and temperature: $r = -0.75$, precipitation and temperature $r = -0.42$), and therefore high correlation between cloud cover and δ^{13}C is expected.

It has also been shown that in large old oaks increasing path length and the reduction in hydraulic conductance of the conducting tissues can limit photosynthesis (Rust and Roloff 2002). As well as being in line with other expectations, this phenomenon could explain the observed increasing trend found in δ^{13}C and δ^{18}O time series during the study period. This trend is otherwise difficult to explain with only climatic factors, since cloud cover has increased and precipitation has not decreased during the studied period (Tuomenvirta 2004). However, this trend can be caused by factors specific to the site, e.g., changing stand density. It is also noteworthy that all our isotope data showed significant trends over time. This kind of long-term trend has been observed previously for ^{13}C and could lie in changes in stomatal conductance with CO_2 or other pollutants (e.g., Berninger et al. 2000).

Altogether, our study and other studies (Robertson et al. 1997, Helama et al. 2009) show that moisture regime is more important than temperature for the growth of oak at its northern distribution limit in Finland as in Sweden (Drobyshev et al. 2008). Although oak is known to have extended its range further to the north than today during climatically warmer periods in the past (Donner 1995, Huldén 2001), our results suggest that the current limit might not only be due to low summer temperatures or short summers. Based on observations on existing oak plantations, Ollinmaa (1952) and Hämet-Ahti et al. (1992) speculated that the limit of oaks' natural distribution without competition would lie more than 100 km to the north of the current range. Also, Rainio (1977) suggests that the distribution in the north is affected by the combined effect of human exploitation and competition with spruce. Our study supports these results in the sense that it shows that current summer temperatures could permit more northerly growth of oak. Therefore, we hypothesize that either competitive replacement from fertile sites or failure to regenerate limits the distribution of oak in Southern Finland.

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