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Ecological and climatological signals in tree-ring width and density chronologies along a latitudinal boreal transect

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ABSTRACT

Shifts in the climate sensitivity of trees throughout the twentieth century might indicate climate change effects in the boreal forest ecosystem. We here evaluated such potential changes by analyzing six tree-ring width (TRW) and maximum latewood density (MXD) chronologies from northern, central and southern boreal forests in Finland (60°N–69°N). Besides latitudinal effects, differing micro-sites (lakeshore and inland) were considered to evaluate the influence of ground water access on twentieth-century tree-ring formation and climate sensitivity. Overall, the boreal MXD chronologies appeared less affected by micro-site conditions compared to the TRW chronologies. Along the boreal transect, mean growth rates decrease with increasing latitude, but the ratio of earlywood-to-latewood (∼70%/∼30%) remains stable. However, latewood is slightly denser at the dry inland micro-sites. The correlations with climate data showed that TRW and MXD at all sites are positively related with summer temperature. The MXD chronologies are also negatively correlated with precipitation, a feature that is largely missing in TRW. A recent trend toward wetter and cloudier conditions in the study region coincides with a shift of the MXD signal from a distinct temperature limitation toward an additional sensitivity to precipitation, which in turn stimulated the trees' competition for sunlight.

Introduction

High latitude forest ecosystems not only appear to be sensitive to climatic changes (Wolf et al. 2008; Euskirchen et al. 2009), but changes in boreal vegetation composition and distribution might additionally stimulate multiple biosphere/atmosphere feedbacks (Pearson et al. 2013). In cold boreal environments, tree growth is mainly controlled by changes of ambient air temperatures, and summer warmth has been identified as the main limiting factor of tree-ring width (TRW) and maximum latewood density (MXD) variability of conifer trees (Schweingruber et al. 1988; Grudd 2008; Esper et al. 2014; Helama et al. 2014)

Boreal trees reveal a south-to-north gradient of increasing temperature signals, toward the arctic treeline, constituting the focus of dendroclimatic (Wilson and Luckman 2003; Kultti et al. 2006; McCarroll et al. 2013; Esper et al. 2014) and ecological studies (Schmitt et al. 2004; Seo et al. 2011; Düthorn et al. 2015) in this highly sensitive region. Further south, in the temperate zone, dendroclimatic studies mainly focus on the influence of precipitation on tree growth, and on drought reconstructions (e.g. Helama and Lindholm 2003; Drobyshev et al. 2011; Düthorn et al. 2014). Most of this research is based on TRW data and only some studies additionally use MXD for drought assessment (Helama et al. 2014). In comparison to TRW, MXD has a stronger link to summer temperature (Briffa et al. 2002), a less pronounced age trend (Frank and Esper 2005), reduced biological memory (Esper et al. 2015), and the capability of preserving millennial scale temperature variations (Esper et al. 2012).

Transect studies are an important tool to evaluate the influence of external drivers on wood formation and identify possible effects of changing environmental conditions on future forest ecosystems. Altitudinal transects have been studied in, for example, the Alps to describe elevational-dependent climate sensitivity patterns (Hartl-Meier et al. 2014a, 2014b) and identify sites and altitudes suitable for climate reconstruction (Kienast et al. 1987; Affolter et al. 2010). In a study from eastern North America, Martin-Benito and Pederson (2015) described the effects of changing precipitation and temperature on tree growth in relation to latitude. Similar effects are detailed by Helama et al. (2005) reporting strong July temperature and moderate May precipitation dependencies of Scots pine (*Pinus sylvestris* L.) TRW in northern Finland, but weaker relationships toward lower latitudes. An inconsistent connection of early summer precipitation and TRW chronologies was reported by Düthorn et al. (2014) for southern Finland. The generally more robust temperature signal in MXD (Esper et al. 2010), however, suggests this tree-ring parameter to reflect latitudinal changes more distinctly. In addition, the influence of different micro-site conditions (wet and dry) on MXD deviations and climate signals (Düthorn et al. 2013) has not yet been addressed.

As future warming and precipitation changes will likely have substantial influences on vegetation/atmosphere

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interactions, there is a need to estimate potential shifts in vegetation structure and climate sensitivity. Such potential changes are here studied considering a latitudinal transect of tree sites from southern to northern Finland, in combination with differences between locally wet lakeshore and locally dry inland micro-sites. These influences are assessed for both TRW and MXD data from the most common boreal species in northern Europe, *P. sylvetris*, to address:

(i) Are there differences in mean growth rate and cell wall formation (ratio between early- and latewood) along the boreal transect in Finland?
(ii) How different are the climate signals retained in TRW and MXD along the transect, and how do these signals change in wet and dry micro-sites?
(iii) What are the effects of recently increasing precipitation amounts on the climate sensitivity of Scots pine growth and density variations?

Material and methods

Sampling design and tree-ring measurements

Our study sites cover a latitudinal transect from northern to southern Finland, with each site being representative of a sub-field of the Finnish boreal forest ecosystem considering the classification of Ahti et al. (1986) (Figure 1). The northern site (Ailijärvi: 69.52°N, 28.56°E; hereafter: NB) is located close to the northern distribution limit of Scots pine. The southern boreal forest is represented by Melkuttimet (60.73°N, 24.05°E; hereafter: SB), and the transition zone between north and south is covered by the central Sotkamo site (64.11°N, 28.34°E; hereafter: CB). During fieldwork in 2012 we extracted 5 mm increment cores from 40 trees in each site, subdivided in 20 series from a lake shoreline (the "wet" micro-site) and 20 series from an inland ("dry") micro-site, according to Düthorn et al. (2013).

Different tree-ring parameters were quantified simultaneously including TRW, MXD, earlywood width (EW), latewood width (LW), latewood density (LWD) and earlywood density (EWD). The measurements were produced following a well-established approach detailed in Lenz et al. (1976) and Schweingruber et al. (1978). Increment cores were cut into 1.2 ± 0.02 mm thick laths using a twin blade saw (DENDROCUT – WALESCH Electronics), and organic extractives, for example, resin, were removed from the laths using 95% alcohol for 48 h. Before X-raying, the samples were acclimated for 24 h at 65% air humidity and 20°C air temperature. X-ray films (AGFA-Microvision Ci) were exposed for 55 min using a "BALTOGRAPHE" devise from Balteau, and grey values measured and transferred into g/cm^3 using the WALESCH "DENDRO 2003" densitometer at a resolution of ~10 μm. All tree-ring parameters, including TRW, MXD, EW, LW, EWD and LWD, were derived from the resulting high-resolution density profiles (details in Schweingruber et al. 1978).

Standardization and chronology development

Tree-ring age-effects were removed using Negative Exponential Curve Standardization with TRW, EW, and LW. Age trends in the density time series (MXD, LWD, EWD) were removed using Hugershoff Standardization enabling fit of initially
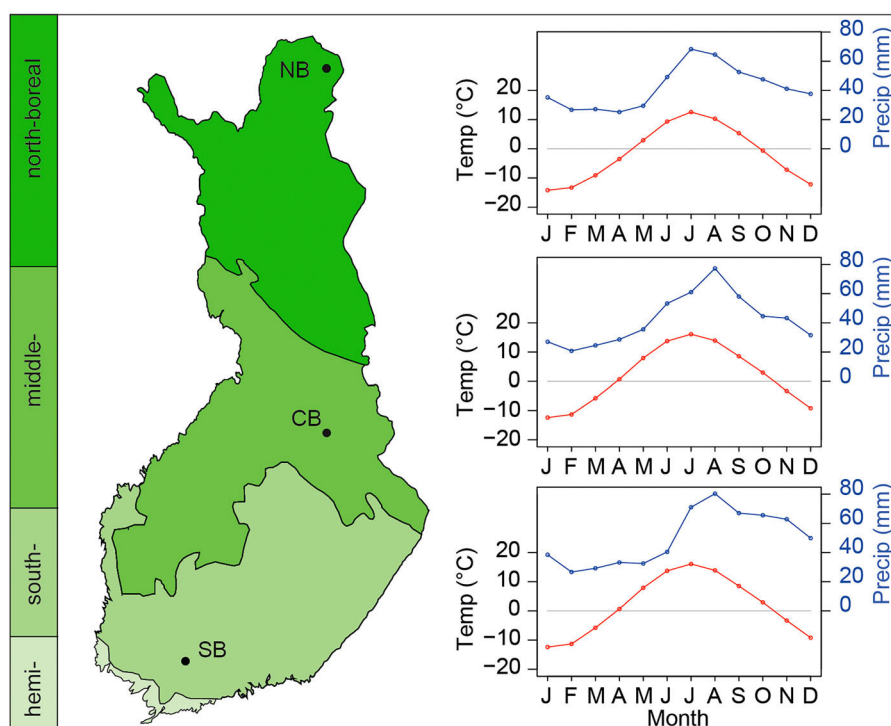

Figure 1. Map of Finland with the boreal forest zones defined by Ahti et al. (1986). © Teuvo Ahti. Reproduced by permission of Teuvo Ahti. Notes: Dots represent the sampling sites of the TRW and MXD transect. On the right climate diagrams with mean temperature and precipitation sums (1961–1990) from interpolated data of the four nearest grid points to the sampling site are plotted.
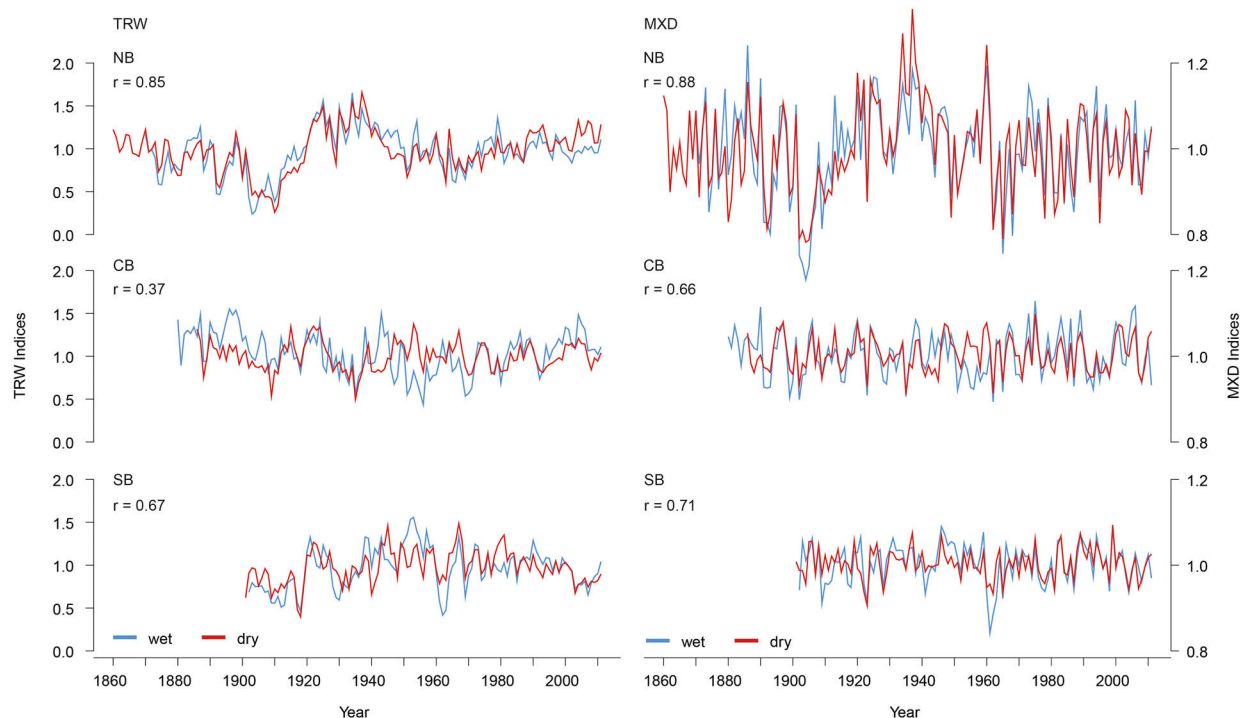
Figure 2. TRW (left) and MXD (right) micro-site chronologies for the northern, central and southern sampling site. Inter-chronology Pearson correlations are calculated over the 1902–2011 common period. Chronologies are truncated at $n < 3$.

increasing values typical to density data from juvenile rings (Bräker 1981; Cook and Kairiukstis 1990). Both standardization methods support emphasizing inter-annual to multi-decadal variability in mean chronologies. A data adaptive power transformation was applied to stabilize heteroscedastic variance, and residuals were calculated to obtain index time series (Cook and Peters 1997). Mean site and micro-site chronologies were produced using the biweight robust mean and the variance was stabilized using methods outlined in Frank et al. (2007). All chronologies were truncated at a minimum replication of three time series and, to further reduce effects of age-related biases, only tree-rings of an age from 5 to 120 years were used for calculating the mean growth or density chronologies (Esper et al. 2009; Figure 2).

Growth variability, independent of climatic influences, was assessed using regional curves in which the single raw series are aligned by their cambial age considering the sample pith offsets (i.e. the difference between the innermost ring on a core sample and the tree stem center at sampling height, details in Esper et al. 2003). The average of all age-aligned series represents the site- and species-specific growth-rate (or density, respectively) used to compare sites and micro-sites along the latitudinal boreal transect. The coherency among series within a chronology was assessed using the inter-series correlation (Rbar) among the detrended tree-ring series.

Climate data and response analysis

Climate-growth relationships were assessed by correlating monthly (April, May, June, July, August and September) and seasonal (April–September, June–August, July and August, July–September) climate data with the mean (TRW and MXD) site and micro-site chronologies. The relationship was

calculated by computing bootstrapped Pearsońs correlation coefficients ($p \leq .01$) over the common period 1902–2011 using the treeclim software (Zang and Biondi 2015). We used interpolated temperature and precipitation data derived from the four grid points nearest to our sampling sites (see the climate diagrams in Figure 1). The gridded data originate from CRU TS 3.21 (Mitchell and Jones 2005; Harris et al. 2014). Besides this, a multi-scalar drought index was considered to assess changes in the hydrologic water balance, using the standardized precipitation evapotranspiration index (SPEI) with a memory of 12 months (Vicente-Serrano et al. 2010). In order to evaluate the temporal robustness of climate signals, the MXD site chronologies were correlated against July and August (JA) temperatures and precipitation over three consecutive 37-year periods (early: 1901–1937, middle: 1938–1974, recent: 1975–2011).

Results

Chronology characteristics

The chronologies' common period (1902–2011) is limited by the relatively young trees from southern Finland (Figure 2 and Table 1). Generally, the Rbar values are similar between the micro-sites for both TRW and MXD. In TRW, Rbar is relatively consistent in all sites (0.27–0.46) indicating that there is high coherency among the series independent of latitude. In MXD, the Rbar values range from 0.14 to 0.50, revealing substantially changing internal coherency with latitude (Table 1). The inter-site correlation between wet and dry micro-sites is also higher for the MXD chronologies (1902–2011: $r_{NB} = 0.88$, $r_{CB} = 0.66$, $r_{SB} = 0.71$) compared to the correlation between TRW micro-sites (1902–2011: $r_{NB} = 0.85$, $r_{CB} = 0.37$, $r_{SB} = 0.66$).
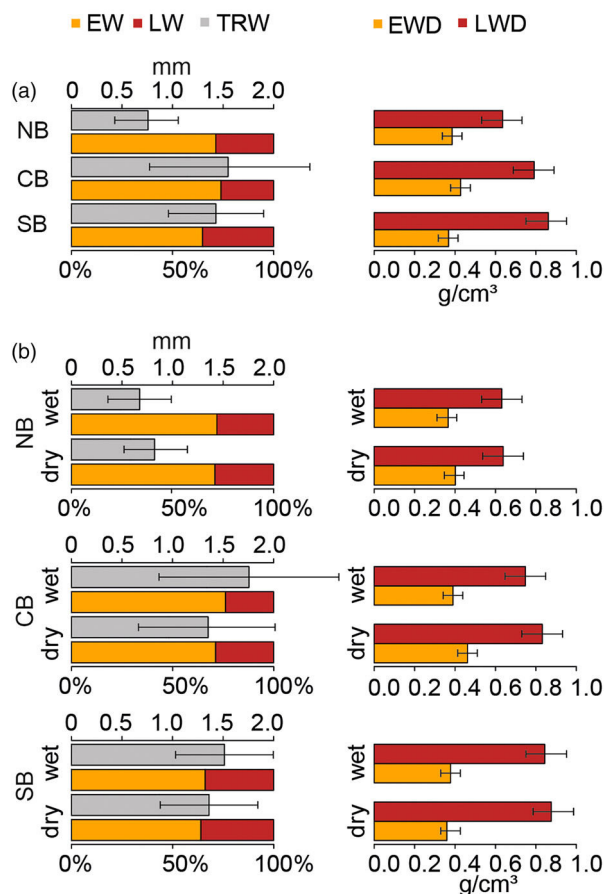
Figure 3. Comparison of the absolute and relative composition of the tree-rings for tree ages of 5–120 years. (a) Left panel shows the mean growth in grey and the relative composition of earlywood (EW) and latewood (LW) in orange and brown, respectively. Means of EWD and LWD are displayed in the right panel. (b) Same as (a) but the sites are grouped in "wet" and "dry" micro-sites. Note: Upper and lower error bars display the standard deviation of the mean values.

Growth rates and tree-ring formation

The composition of tree-rings reveals latitude-independent intra-annual wood formation processes, and latitude-dependent biomass production (Figure 3(a)). The ratio between earlywood and latewood is quite persistent throughout the transect at ~70% EW and ~30% LW. Similarly, mean EWD is fairly stable (0.39 g/cm³; SD = 0.06), but LWD decreases with increasing latitude. Slightly higher EWD (and LWD) values are also observed at the dry micro-sites.

The overall best growing conditions are recorded at the wet micro-site in central Finland (1.64 mm/year), and the harshest conditions are detected at the wet micro-site in the north where mean TRW is only 0.67 mm (Figure 3(b)). At CB and SB, the lakeshore trees grow faster, whereas in the north the trees at the dry micro-site show higher growth rates.

The age aligned growth curves, which are representative of the growth behavior at each site, reveal no clear pattern between wet and dry micro-sites (Figure 4). Age-related trends are overall more coherent among the TRW datasets, though the MXD data are additionally characterized by an increasing trend over the first 20–30 years revealed in all sites. The age trends are steep in CB TRW, and an initial increase is seen in SB TRW, as is otherwise characteristic for

MXD. On the other hand, the NB MXD trends appear anomalous revealing higher values with increasing tree age. In general, the growth rates are similar between micro-sites, though the wet trees grow faster and rings are less dense in CB and SB. Overall, MXD and TRW values increase with decreasing latitude.

Climate growth relationships

Bootstrapped correlation coefficients with temperature, precipitation and the SPEI-12 index help identifying seasons with significant ($p \leq .01$) impact on tree growth (Figure 5). In contrast to TRW, where only the northern and central sites respond significantly to July–August temperature changes ($r_{JA} = 0.49$), significant correlations (up to $r_{JA} = 0.69$ at NB) are characteristic to all MXD sites. An additional link to early growing season temperatures (April and May) could be detected for CB MXD.

In comparison, the TRW chronologies correlate overall weaker than their MXD counterparts, and in CB and particularly SB much fewer significant correlations are seen. Interestingly, while the TRW chronologies indicate only few significant correlations with precipitation and none with SPEI-12, the MXD chronologies show substantial inverse (negative) correlations with these climate parameters during the warm season. The negative correlation is strongest in SB during June, July and August (JJA), but July and July–August precipitation also seems important for CB MXD. The SPEI-12 signal is strongest in NB, though during the early vegetation period from April to May the southern trees also correlate positively with the drought index.

The micro-site chronologies react fairly similar and show no distinct differences between wet and dry habitats. However, there is a trend toward stronger correlations at the dryer micro-sites, especially in northern and southern Finland. This trend is seen in both tree-ring parameters, TRW and MXD.

An assessment of the temporal evolution of JJA temperature controls on MXD reveals decreasing correlations toward present (Figure 6). Simultaneously, a negative correlation with summer precipitation is evolving. NB shows the highest correlations with temperature during all periods (Figure 6(a)). The persistently lowest correlations are found in CB reaching a minimum of $r = .35$ during the most recent period. In CB and SB the correlations decrease gradually toward present, whereas in NB the highest correlation is attained during the middle period ($r = .78$). The correlation between MXD and precipitation is constantly negative and strengthens most substantially in SB toward present (Figure 6(b)).

Discussion

The boreal tree-ring growth patterns assessed here show that the EW/LW ratio is constant along a latitudinal gradient from 60°N to 69°N and among ecologically differing micro-sites. EW forms about 70% of the total ring. Schmitt et al. (2004) differentiated the pine growth vegetation period into a slow initiation phase, faster growth in the mid-season, and decreasing cambial activity toward growing season termination.

Table 1. Site description and characteristics of the site and micro-site chronologies.

Site	Location	Lat (°N)	Lon (°E)	Elevation (m asl)	Samples (wet/dry)	MSL (years)/SD	July temperature (°C) 1961–1990	July precipitation (mm) 1961–1990
NB	Ailijärvi	69.52	28.57	120	17/19	141/65	12.58	68.30
CB	Sotkamo	64.12	28.34	148	20/20	106/24	16.08	61.00
SB	Melkuttimet	60.73	24.06	120	18/20	87/19	16.00	71.08

Site	Standard deviation (wet/dry)[a]	rbar (wet/dry)	Autocorrelation lag-1 (wet/dry)	Mean density (wet/dry)[a]	Standard deviation (wet/dry)[a]	rbar (wet/dry)	Autocorrelation lag-1 (wet/dry)	Mean growth (wet/dry)[a]
NB	**0.12/0.12**	0.50/0.47	0.30/0.44	**0.75/0.74**	0.29/0.34	0.35/0.46	0.62/0.74	0.67/0.77
CB	**0.11/0.11**	0.18/0.14	0.36/0.36	**0.85/0.94**	1.04/0.75	0.27/0.27	0.65/0.66	1.64/1.27
SB	**0.09/0.1**	0.30/0.32	0.35/0.30	**0.96/1**	0.58/0.49	0.40/0.42	0.70/0.53	1.47/1.32

Note: Bold values represent MXD measurements.
[a]Only tree-rings of an age of 5–120 years are included.

The timing and length of these phases are adjusted to the overall duration of the vegetation period and therefore the relative composition of EW/LW is not affected by latitude.

In higher latitudes, growing season temperatures are the limiting factor of cell division and enlargement, and the number of "degree days" reaching temperatures adequate for pine growth decreases toward the arctic treeline. At the same time, summer day length and sunshine hours increase toward north, partly compensating the degree day reduction.

The positive correlation of TRW chronologies with summer temperature reflects the dependency of photosynthetic and cambial activity on warm season conditions (Figure 5). Due to the larger fraction of EW (70%) of the total ring, early- and mid-season temperatures are dominating ring formation. In late summer, when secondary wall formation is the dominating process, the proportion of lumen shrinks and wood density increases (Butterfield 2003; Rossi et al. 2015). Besides the seasonality of cell formation, cell wall development also depends on latitude and micro-habitat. In the moderate, southern Finish sites both EW and LW density increase, a finding that coincides with the altitudinal studies of Schweingruber (1983) revealing a direct association between wood density and growing degree days. High temporal resolution studies showed that the duration of latewood formation is closely related with cell wall thickness, and that extended formation periods result in higher maximum densities (Rossi et al. 2006). These differences substantiate the importance of late summer temperatures and changing season length on the density of Scots pine tree-rings along the boreal transect in northern Europe.

As TRW is dominated by EW formed at the beginning of the growing season, this tree-ring parameter is influenced by carry-over effects of the previous-year and the harsh conditions during winter time (Fritts 1976; Kagawa et al. 2006; Büntgen et al. 2010). It has been argued that these memory effects, on top of the current-year growing season influence, cause a reduced climate sensitivity compared to MXD (Büntgen et al. 2010). This conclusion is supported by the higher lag-1 autocorrelation for TRW compared to MXD (Table 1). Ecotone tree growth in high latitudes and elevations is mainly controlled by one limiting factor. Besides the widely recognized temperature signal in high latitudes (Fritts 1976; Schweingruber et al. 1978; Büntgen et al. 2010; McCarroll et al. 2013; Esper et al. 2014; Helama et al. 2014), some studies also point to precipitation variations as a secondary effect affecting densities (Briffa et al. 2002). However, until now mainly TRW data are used as proxy for precipitation and drought variability (Cook and Jacoby 1977; Casty et al. 2005; Wilson et al. 2005; Drobyshev et al. 2011).

Along our boreal tree-ring transect, the highest correlations with summer temperature were found in the density data. In addition, the MXD chronologies are significantly anti-correlated with summer precipitation and the SPEI-12 drought-index (Figure 5), a finding that is less consistent in the TRW data throughout the transect. The anti-correlation indicates that trees react with reduced wood density to increasing precipitation sums (Cook et al. 2015). This effect seems to be more pronounced at NB where also the SPEI-12 index is negatively associated. A closer look at the micro-sites reveals
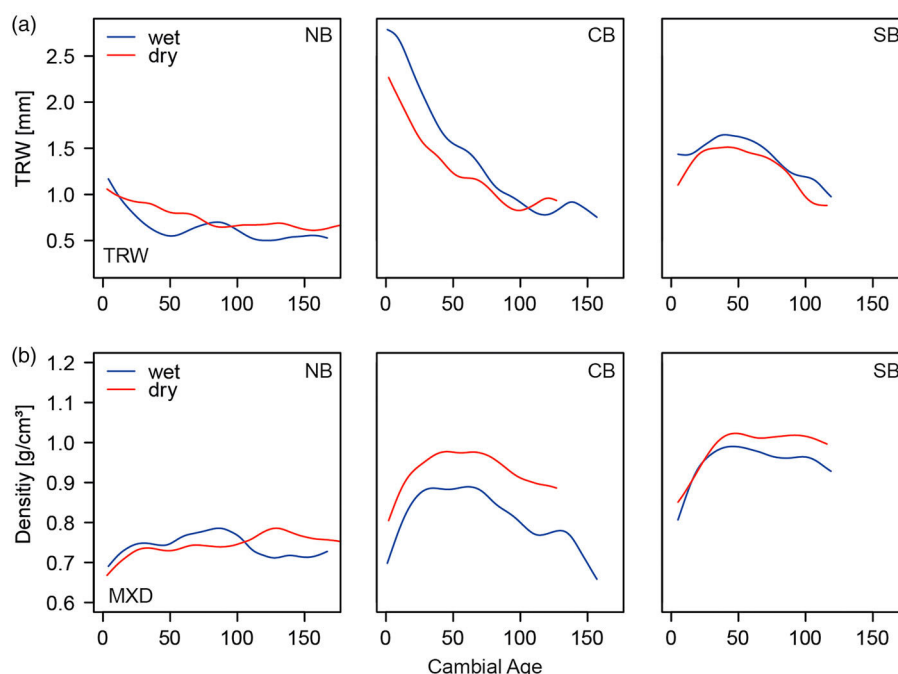
Figure 4. Smoothed (40-years) age-aligned regional growth curves of wet and dry micro-sites for (a) TRW and (b) MXD.

no striking difference between the different habitats. The slightly stronger correlations of the dry micro-sites might indicate an increased sensitivity to moist atmospheric conditions in this locally drier "inland" environment. Briffa et al. (2002) defined this signal as a besides effect, as summer temperature and precipitation are coupled through cloud cover and radiation changes.

Our results indicate that the inland trees are slightly more stressed by moist atmospheric conditions, but run-off and percolation at these micro-sites, situated on the slopes surrounding the lakes, might limit the buildup of tailwater. Lower growth rates at the dry micro-sites in CB and SB also imply a more restricted tree growth. Depending on the prevailing atmospheric regime, increased cloud coverage impedes the passing of sunlight and also forces precipitation

(Schneider et al. 2014). Messier et al. (1999) discussed the aspect of increasing competition for sunlight in closed canopy forests, particularly during the growing season (Nemani et al. 2003). Competition for sunlight among trees at dry sites, where forests are typically characterized by a closed canopy structure, is higher than at wet sites, which are typically dominated by open canopy structures and increased diffuse and direct sunlight from the lakeside.

The climate correlations also reveal that the differentiation into wet and dry micro-site is less important for MXD compared to TRW. This finding indicates that climate reconstructions derived from MXD data should be less affected a mixture of samples from wet (sub-fossil material from lakes) and dry (living tree) samples, compared to TRW composite chronologies. Whereas for MXD significant responses to
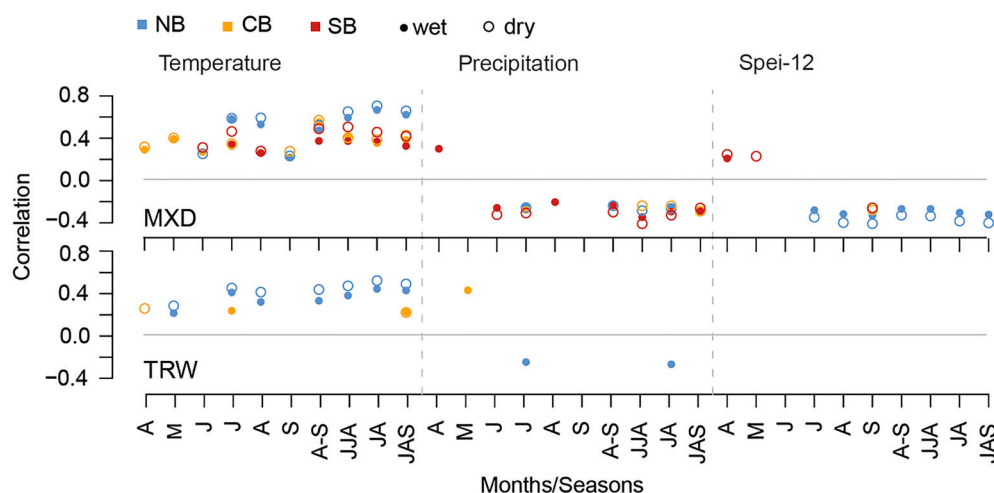

Figure 5. Significant correlations ($p \leq .01$) between micro-site chronologies and climate data over the 1902–2011 common period. Upper (lower) panel shows correlations with MXD (TRW) series for single months and seasonal means (A-S: April to September, JJA: June, July and August, JA: July and August, JAS: July, August and September) of the growing season. On the left the relationship with temperature is plotted, the middle climate parameter is precipitation and on the right correlations with the 12 months SPEI index are computed. Blue dots represent NB, orange CB and red SB. Filled dots (circles) symbolize the wet (dry) sites.
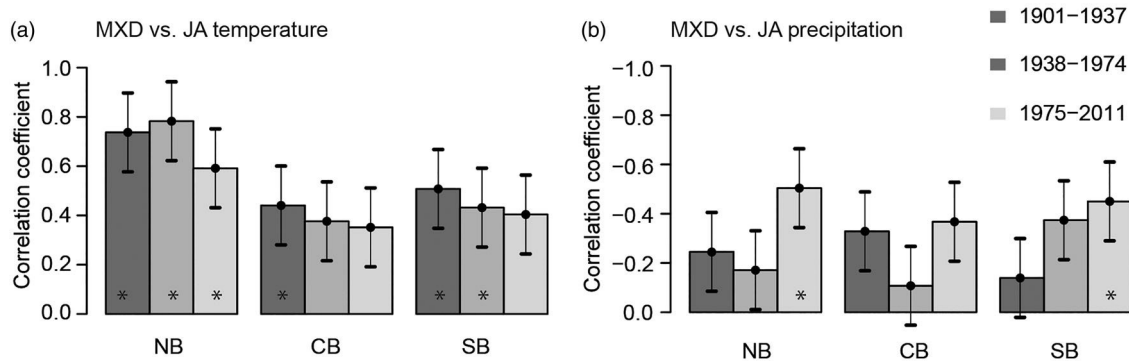
Figure 6. Correlation patterns with (a) JA temperatures and (b) JA precipitation over different time periods (1901–1937, 1938–1974, 1975–2011). Notes: Upper and lower error bars display the standard deviation. Asterisks mark significant correlations with $p \leq .01$.

temperature and precipitation were found in both micro-sites, this is not the case for TRW. For instance, TRW shows a stable relationship to summer temperatures in NB, but the precipitation signal appears only at the wet NB micro-site. This indicates that the lakeshore trees are stressed by high precipitation sums, while inland trees are less affected (Düthorn et al. 2015).

In addition to the micro-sites, also the period of correlation with climate data matters. Splitting the calibration period into three equally long segments revealed enhanced precipitation sensitivities toward present (Figure 6(b)). This increase is connected with higher precipitation sums suggesting increased cloud coverage during recent decades. Furthermore, Cook et al. (2014) predicted wetter twenty-first-century conditions for the Scandinavian Peninsula, whereas other regions including the Mediterranean area might face increased drought stress. In Scandinavia, the increasing precipitation and cloud cover will likely diminish the amount of direct sunlight, likely affecting the plants' metabolism and photosynthetic productivity (Stine et al. 2013).

The boreal forest ecosystem is sensitive to changing external forcings. During the growing season, higher precipitation sums and more clouds negatively affect tree growth. In contrast to earlier studies (Düthorn et al. 2013), differing micro-sites do not reveal a clear pattern of growth rates between wet and dry sites along a boreal gradient from 60°N to 69°N. Interestingly, the MXD data are not affected by the separation into inland and lakeshore trees. This is in accordance with Wilson and Luckman (2003) stating that site-specific factors are less important to the common signal of MXD chronologies. In contrast, sampling different micro-sites influences the TRW data, supporting the importance of considering such differences in tree-ring sampling campaigns and the development of long chronologies for climate reconstruction purposes (Düthorn et al. 2015). However, the inconsistent regional TRW curves obtained here for different micro-sites along a latitudinal transect suggest that further research including more sampling sites is needed to disentangle the full impact of such differences on dendroclimatological results.

In conclusion, tree growth and climate signal differences are overall larger along the latitudinal boreal transect than between micro-sites. Micro-site effects are less pronounced in MXD compared to TRW, and they seem to decrease with increasing latitude. Indeed if the effects of the micro-sites are overall small, the insights in ecological issues for assessing tree growth under future climatic conditions, for example, increasing precipitation (Cook et al. 2014), are substantial.

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