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Can microsite effects explain divergent growth in treeline Scots pine?

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Introduction

Northern treelines are expected to reflect a strong summer temperature signal as they are generally cold-limited. Ring width data from northern treelines, and in particular Scots pine (*Pinus sylvestris* L.) from Fennoscandia, have thus frequently been used to build long chronologies in order to reconstruct climatic conditions of the past centuries (Esper et al. 2002, Grudd et al. 2002, Linderholm & Gunnarson 2005, Helama et al. 2009, McCarroll et al. 2013, Lindholm et al. 2014). Studies on *Picea glauca* (Moench) Voss in North America, however, have revealed diverging growth response as well as a loss of sensitivity to summer temperatures, suggesting that e.g. temperature-induced drought stress/reduced water availability might lead to reduced tree growth at northern treelines (Lloyd & Fastie 2002, Wilmking et al. 2004, Wilmking & Juday 2005, Driscoll et al. 2005, D'Arrigo et al. 2008, Porter & Pisaric 2011). Although less prevalent, divergent growth of Scots pine has been found in some studies for Eurasia as well (e.g. Wilmking et al. 2005, Lloyd & Bunn 2007, Seo et al. 2011). Recently, DÜthorn et al. (2013, 2015) and Helama et al. (2013) have shown that a different response to climatic conditions as well as different growth rates among adjacent pine stands in Fennoscandia might be caused by different microsite conditions: Late spring snowmelt might shorten the growing period for wet-standing lakeshore / riparian trees due to water oversaturation and lower ground temperatures, especially for juvenile trees. Overall, chronologies built from individuals with inconsistent response to climate (e.g. from different microsities) may lead to a misinterpretation of past climatic conditions as well as of models for carbon storage and release in boreal forests (e.g. Barber et al. 2000).

In this preliminary study, we therefore further investigate the hypothesis that microsite differences (in terms of water availability) influence tree growth by addressing the questions whether and to what extent microsite conditions (dry, wet, both at a northern and a southern location near the treeline) cause differences in (i) growth performance, (ii) climate–growth relationships (we expect dry sites being correlated negatively with summer temperature or positively with summer precipitation) and (iii) stability of climate–growth relationships.

Materials and Methods

Study area

We analysed 82 individuals of Scots pine from two different locations in northern Finland. The southern stand is located just within the continuous distribution limits of Scots pine, near Laanila (68°30'N; 27°18'E, 260–280 m a.s.l.), while the northern stand is situated 135 km further north near lake Kenesjärvi (69°41'N; 27°6' E, 180–200 m a.s.l., about 10 km south of Kevo Subarctic Research Institute of the University of Turku), where islands of closed pine stands still occur. In each of the two stands, sampling was carried out in two differing microsities: Sites on lakeshores (Laanila) and large scale depressions (Kenesjärvi) were defined as wet sites (LW, KW), whereas adjacent well-drained south to south-west facing slopes were considered dry sites (LD, KD). Based on differences in topography and ground vegetation we assume that trees from wet sites have

permanent access to groundwater, while trees from dry sites might depend more on regular precipitation and snow melt.

Tree-ring data

Two cores per tree (A: 4.5 mm, B: 12 mm in diameter) perpendicular to each other were taken at breast height. After air drying, the surface of core A was cut using a WSL core-microtome (Gärtner & Nievergelt 2010) and scanned visually using a conventional scanner. Tree-ring width was measured from the optical images using Cybis CooRecorder (v. 7.7, Cybis Elektronik & Data AB) with 0.001 mm precision. Core B was glued to a sample holder and cut to a lath of 1.25 mm thickness using a two-bladed circular saw (Dendrocut 2003, Walesch Electronics). Resin and other soluble substances were extracted by boiling the laths in 96% ethanol for 24 hours. After letting the samples dry, they were x-rayed using an ITRAX Multiscanner (Cox Analytical Systems) with an exposure time of 25 ms, an intensity of 30 kV/50 mA, and in steps of 20 μm . Ring width, as well as density (not presented here), was subsequently measured on the grey-scale images obtained using WinDENDRO software v. 2014 (Regents Instruments Inc.). Visual cross-dating of core A and B was carried out with the software CDendro (v. 7.7, Cybis Elektronik and Data AB) and verified statistically using the dplR-package (Bunn 2008) of the R programming software v. 3.1.1 (R Foundation for Statistical Computing). The same package was used to detrend the series with a modified negative exponential curve or straight line to eliminate age trends. Standard chronologies of each microsite were built applying a biweight robust mean.

Climate data

Temperature and precipitation data were obtained from the CRU TS 3.22 0.5°x0.5° gridded dataset for the period 1901–2013 (Harris et al. 2014). Based on these data, mean annual temperature and annual precipitation are -2.5°C and 509 mm in Kenesjärvi, and -1.5°C and 442 mm in Laanila, respectively. At both locations, July is the warmest and wettest month ($12.3^{\circ}\text{C}/69$ mm in Kenesjärvi and $13.6^{\circ}\text{C} / 70$ mm in Laanila, respectively). Calculating a 30-years running mean (1 year lag) for July mean temperature and July precipitation sums identifies the coldest (1942–1971) as well as the warmest phase (1913–1942) of the observed period for both Kenesjärvi (lowest mean: 11.9°C , highest mean: 12.8°C) and Laanila (lowest mean: 13.3°C , highest mean: 14.1°C) (Fig. 1). The beginning of the 20th century (1921–1950 for Kenesjärvi and 1901–1930 for Laanila) comprises the driest years for July (55 mm / 62 mm), while July precipitation has been clearly increasing over the past decades (mean of 78 mm in 1982–2011 in Kenesjärvi and in 1984–2013 in Laanila).

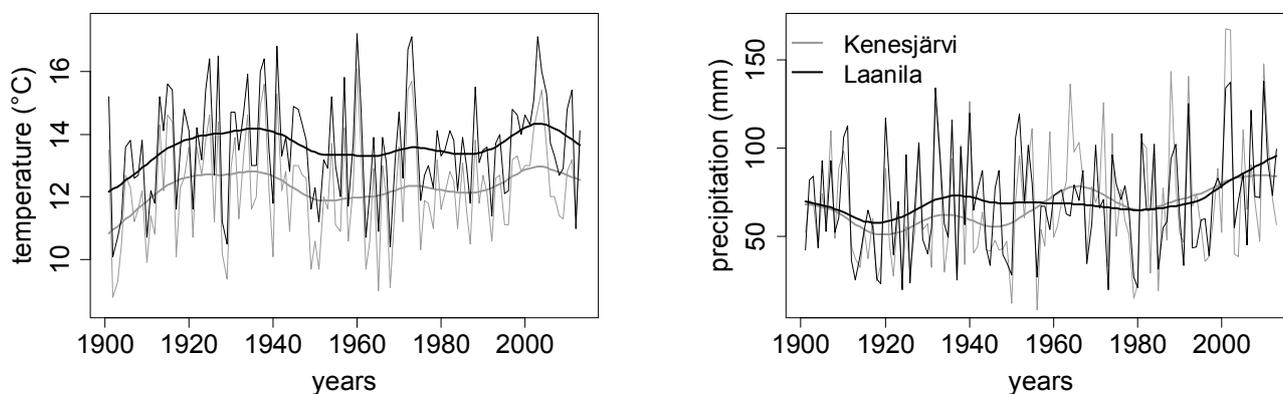


Figure 1: July mean temperature (left) and July precipitation sums (right) for the period 1901–2013 according to the CRU TS 3.22 dataset. Smoothed curves highlight long-term trends.

Statistical analysis

To calculate climate–growth relationships for each microsite, standard chronologies were correlated with monthly mean temperature and monthly precipitation sums of the period 1901–2013, including all months from June of the year prior to growth up to September of the current year. To test the stability of the climate–growth correlations, a moving window analysis was performed for the relevant months (May to August of the current year) over the same period with a step-size of one year and a windows length of 25 years. All climate–growth analyses were carried out using the R-package treeclim (Zang & Biondi 2015), applying stationary bootstrapping in static and moving correlation functions. Confidence interval was set to 95%.

Results

Growth performance

Age did not differ significantly between dry and wet microsities in Kenesjärvi or Laanila while growth did (Table 1): On average, trees on dry sites are taller and have a larger crown in both northern and southern sites. In Laanila, trees differ significantly also in breast-height diameter (dbh) and average growth rate among the two microsities. Overall, trees from Laanila are notably older and taller than trees from Kenesjärvi, while their average growth rate is smaller. Trees from Laanila wet site (LW) are the smallest in average growth rate, dbh, crown area, and crown volume.

Table 1: Selected metadata (mean values) for all microsities. Crown area and volume were calculated based on formulas for a circle (the mean of two radii perpendicular to each other was used) and a cone, respectively. Significant differences among wet and dry microsities within one location are marked with an asterisk ($p < 0.05$). Site abbreviations: K = Kenesjärvi; L = Laanila; D = dry; W = wet.

site	ø age	ø growth rate (mm)	dbh (cm)	height (m)	crown base height (m)	crown area (m ²)	crown volume (m ³)
KD	190	0.91	41.2	13.3*	2.3	38.7*	147.0*
KW	192	0.84	38.5	11.4*	2.0	31.3*	98.3*
LD	302	0.70*	49.6*	21.1*	3.5	40.7*	240.8*
LW	261	0.57*	34.8*	13.2*	3.3	23.0*	86.6*

As climate data is available only from 1901 on, we concentrate on the 20th and beginning of the 21st century for radial growth. Site chronologies are well replicated back to 1840 though (at least 15 trees are available for each microsite), which is reflected in high values of GLK, rbar and EPS (clearly above 0.85 in the period investigated, Tab. 2) and thus emphasizes the strong common signal of trees per microsite (Wigley et al. 1984).

Table 2: Standard-chronology statistics. Site abbreviations: see Table 1.

site	n	period	glk	rbar	EPS < 0.85 before
KD	26	1779–2014	0.72	0.52	-
KW	19	1751–2014	0.72	0.52	1814
LD	20	1547–2014	0.68	0.41	1714
LW	17	1545–2014	0.68	0.50	1789

Overall, trees from all microsities show similar relative growth rates since the beginning 20th century (Figure 2): A period of reduced growth during the first 10–15 years of the 20th century is followed

by a phase of enhanced growth until around 1940. Since that time, growth rates first decreased until about 1960 and then remained more or less stable until today. At high frequency, slight differences in various periods become apparent between the microsites:

Trees grow better in wet than in dry sites in the period 1940–1950. Recently, growth performance splits up between northern and southern sites: Trees from Laanila grow better than trees from Kenesjärvi from the late 1970s until the early 1990s, while this relation inverses since around 2000.

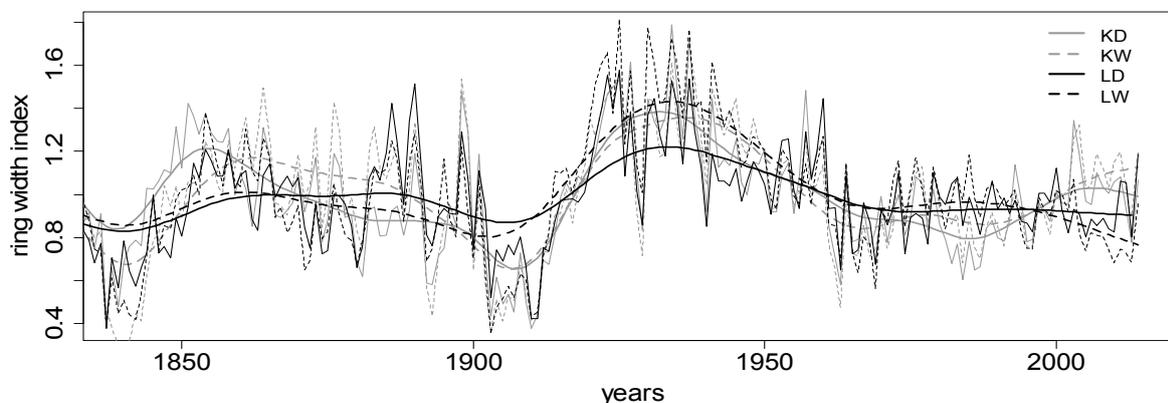


Figure 2: Standard chronologies of all microsites. The series are truncated at 1840 (sample depth falls below 15 in KW and LW beyond this point). Smoothed curves highlight long-term trends.

Climate–growth relationships

Tree-ring width (TRW) in all sites shows a strongly significant ($p < 0.05$) positive correlation with July temperature and a weaker negative correlation with July precipitation of the current year (July temperature, KD: $r = 0.48$, KW: $r = 0.50$, LD: $r = 0.44$; LW: $r = 0.42$; July precipitation, KD: $r = -0.23$, KW: $r = -0.25$, LD: $r = -0.16$, LW: $r = -0.17$). Other significant correlations exist between TRW and August temperature (KD: $r = 0.34$, KW: $r = 0.31$, LD: $r = 0.19$) and precipitation in May of the current year (KD: $r = 0.16$, KW: $r = 0.21$, LD: $r = 0.25$). All sites except LW are significantly positively correlated with previous year's summer and autumn temperatures, but these are not further examined here.

The stability test showed correlations with July temperature being more or less stable for both microsites of Kenesjärvi, but not of Laanila (Fig. 3): Since the 1980s, the strength of July temperature correlations is decreasing continuously and is turning insignificant recently. July precipitation starts to lose its negative influence clearly in the middle of the century in both Kenesjärvi sites, while at the same time May precipitation becomes a significant positive influence. In LD, however, May precipitation has become less influential recently.

Discussion

Growth performance

The generally better tree growth (average growth rates, dbh, height, crown volume) on dry microsites is most likely due to site differences, as age was excluded as the driving factor (no significant difference in age between microsites). This is in line with findings of previous studies (Düthorn et al. 2013, 2015; Helama et al. 2013). The lower dbh, height and crown values of Kenesjärvi trees in comparison to LD trees can likely be explained by their younger age and the latitudinal difference with lower temperatures and shorter growing season in the northern location. LW site trees show reduced growth in almost all parameters even when compared to KW site trees, possibly due to excess water stress. This results in colder soils with decreased root functioning, thus hampering tree growth at the lakeshore to a certain extent, similarly to what has been reported for Scots pine by e.g. Linderholm et al. (2002), Moir et al. (2011), and Helama et al. (2013).

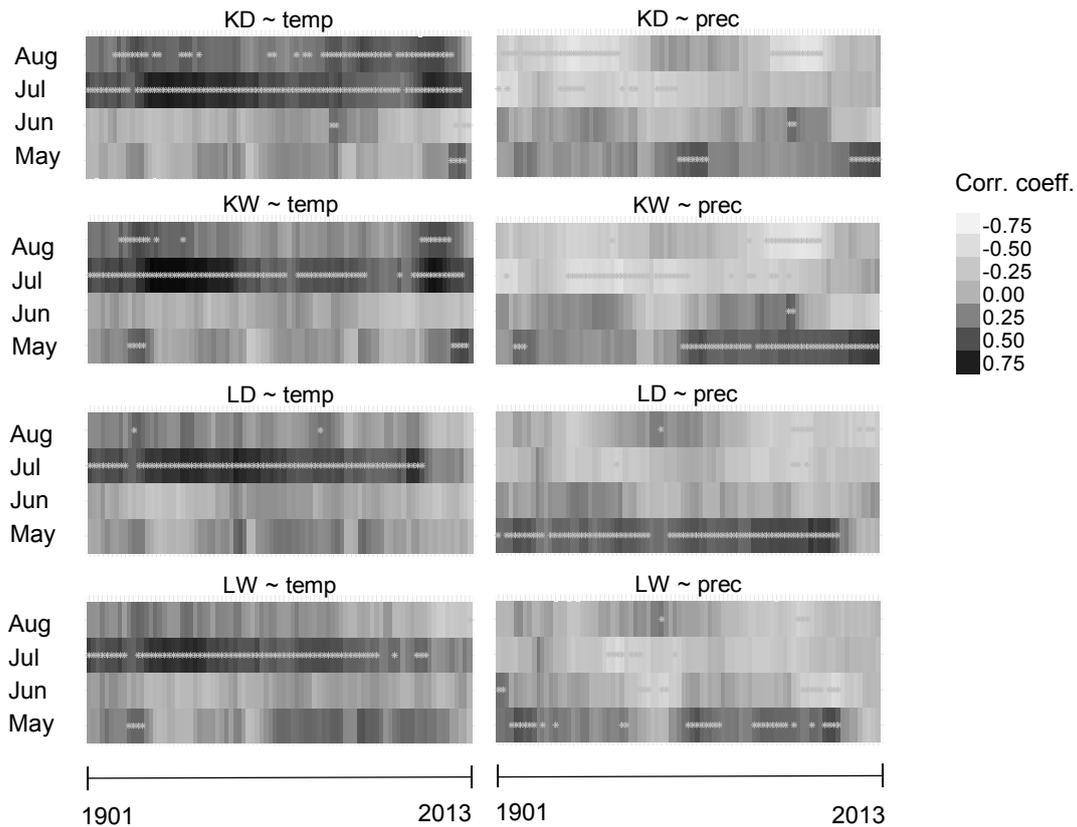


Figure 3: Moving window climate–growth relationships (windows length: 25 years, step-size: 1 year) for all microsites with mean monthly temperature (left) and precipitation sums (right), respectively. White colouring indicates negative, black colouring positive correlation. Grey asterisk indicates that the correlation is significant ($p < 0.05$).

The congruent long-term growth trend of all chronologies, showing reduced growth in the beginning 20th century and enhanced growth in the decades thereafter clearly reflects the dominant climatic conditions of the larger area, which has also been reported from other studies in Fennoscandia (e.g. Tuovinen 2005, Büntgen et al. 2011, McCarroll et al. 2013, Lindholm et al. 2014, DÜthorn et al. 2015).

Climate–growth relationships

All sites reflect the same temperature (positive with July) and precipitation (negative with July) signals of the current year. In terms of diverging growth response we were thus not able to identify differences among dry and wet microsites by calculating ‘common’ climate–growth relationships over the entire period. The weaker response of LW trees to climate supports the assumption that trees at the lakeshore are influenced by water table level in addition to climate and thus the interpretation of their climate–growth relationships is challenging, as reported e.g. for Scots pine in Sweden (Linderholm et al. 2002) and Finland (Smiljanić et al. 2014). Overall, if the individuals investigated here were susceptible to drought conditions, we would have expected a divergent growth response to climate, namely dry site trees showing a negative response to elevated summer temperatures, as e.g. reported by Wilmking et al. (2005) and Seo et al. (2011) for certain groups of individuals, while at the same time reacting positively to summer precipitation (e.g. D’Arrigo et al. 2008).

When focusing on the stability of climate–growth relationships over time, however, a striking difference between northern and southern locations becomes apparent. To make this point more evident, we plotted smoothed curves of the standard chronologies and the corresponding mean

temperature / precipitation values on top of each other, after having performed a z-transformation of both (Fig. 4):

Both Kenesjärvi chronologies follow the July temperature trend constantly (albeit at different levels), and thus seem to benefit from past and current favourable summer temperatures. In contrast, Laanila growth rates have remained at the same level since the late 1960s and LW growth rates even show a clear decreasing trend since the 1990s despite simultaneously increasing July temperature. This is supported by the findings of Seo et al. (2011) from the same Laanila area, in clearly younger trees though.

One possible explanation of this contrasting evolution concerning sensitivity might be the difference in tree height and crown volume that exists between the two locations. The taller shape of LD trees presumably leads to a potentially higher evapotranspiration, yet strengthened by the fact that Laanila receives the same absolute amount of summer precipitation as Kenesjärvi, while absolute summer temperatures are higher. Hence, LD trees might begin to show signs of drought stress earlier as do trees from the north. However, if due to the factors mentioned here reduced water supply was growth limiting, according to our theory we would have expected only LD trees to grow worse, while LW trees still should show a stable positive temperature response.

On the other hand, the higher age of Laanila trees might be the trigger of reduced response to July temperatures. Carrer & Urbinati (2004), e.g., found an increasing sensitivity to climatic conditions of treeline European larch (*Larix decidua* Mill.) when aged above 200 years, likely connected with hydraulic limitations. However, when Seo et al. (2011) compared tree-ring widths of clearly younger trees from Laanila and Rovaniemi (250 km south of Laanila), Laanila trees also showed divergence around 2000 and thereafter while Rovaniemi trees did not, suggesting that higher age might not be the cause for the loss of sensitivity to temperature in Laanila. A test of age cohorts is needed to assess age effects ultimately for our study.

Different growth rates might finally also arise from a recent temperature- or moisture-induced change in soil nutrient availability as e.g. found for White spruce (*P. glauca*) in Alaska by Sullivan et al. (2015). Pollution, e.g. by nitrogen, however, does not seem to affect our study sites as this area has the lowest (and stable) values compared to the rest of Europe for the period 2005–2010 (Harmens et al. 2015).

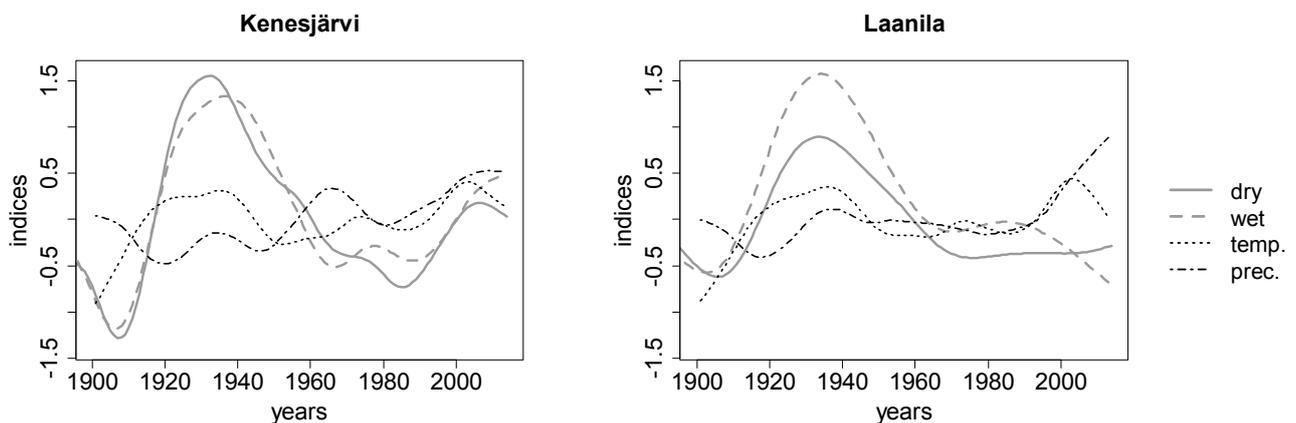


Figure 4: Smoothed curves of the standard chronologies and the corresponding mean July temperature (left) and July precipitation sum (right) curves for the period 1901–2013. Both standard chronologies and climatic data were z-transformed.

Concluding remarks

Preliminary results suggest that differences in growth performance exist among the investigated dry, wet, northern and southern sites. When calculated over the entire period, main climate–growth correlations are similar between all microsites. But only in the northern sites, stable climate–growth correlations exist (July temperature). Our results concerning growth performance seem to be

explicable through varying (micro-)site conditions, while the main trigger for the fading climate–growth relationships remains unclear for now. However, these differences require further investigation (e.g. test of age cohorts), also taking into account additional environmental factors and methodological aspects (D'Arrigo et al. 2008), as well as additional tree-ring proxies (density, anatomy). These analyses are planned in the future.

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