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Impact of climatic variation on growth of Norway spruce and European beech in South-East Norway

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Abstract

The relationship of climate variation with growth of European beech and Norway spruce was investigated in beech-spruce forest stands in South-East Norway. In two study areas in total 81 pairs of beech and spruce trees were cored and for each tree species a chronology based on standardized year ring series was built. Climate data was gathered from nearby weather stations. The climate variables with the strongest influence on increment growth were identified with dendroclimatological methods and multiple linear regression models. The annual increment growth of Beech was related to previous year August temperature and current year June precipitation. Spruce growth is sensitive to previous year June and November temperature and previous year August precipitation. In both species growth was decreasing in the period from 1940 to 2013 with a stronger decrease in spruce growth. Under future climate conditions, competitiveness seems to become a regulatory factor for species composition and may thus favour beech at the expense of spruce. This could possibly lead to a narrowing of spruce distribution in South-East Norway.

Keywords: *Climate change, dendroclimatology, European beech, Norway spruce, competition, South-East Norway, TSAP-Win, multiple linear regression*

Sammendrag

Forholdet mellom klimavariasjon og vekst av bøk og gran ble undersøkt i bøk-gran-skog i Sør-Øst Norge (Vestfold). I to studieområder ble totalt 81 par av bøk og grantrær rørtråd. For hvert treslag ble det bygget en kronologi basert på standardiserte årring serier. Klimadata ble samlet inn fra nærliggende målestasjoner. Klimavariabler med sterkest innflytelse på tilveksten ble identifisert med dendroclimatologiske metoder og multiple lineære regresjonsmodeller. Den årlige tilveksten av bøk er relatert til august temperaturen året før og juni nedbør i det værende året. Gran vekst er sensitiv for juni og november temperatur og august nedbør året før. For begge arter er tilveksten avtagende i perioden 1940-2013 med en sterkere nedgang i gran. Under fremtidige klimaforhold synes konkurranseevne til å bli en regulerende faktor for artssammensetning som kan favorisere bøk på bekostning av gran. Dette kan muligens føre til en innsnevring av gran distribusjon Sør-Øst Norge.

Nøkkelord: *klimaendringer, dendroklimatologi, bøk, gran, konkurranse, Vestfold, TSAP-Win, multippel lineær regresjon*

1. Introduction

In the last decades the earth's surface temperature has been continuously increasing and the atmosphere and oceans have warmed successively (IPCC 2013). It is assumed that this rapid change of the climate system will have major impacts on today's ecosystems worldwide (Sarukhán & Whyte 2005) and trigger tree species migration (cf. Aitken et al. 2008; Giesecke et al. 2011; Prasad et al. 2013; Zhu et al. 2014).

In a Norwegian perspective, annual mean temperatures and precipitation are expected to increase considerably in the next 85 years (Hanssen-Bauer et al. 2009). In South-East Norway vegetation zones dominated by Norway spruce (*Picea abies* (L.) Karst.) are located in short distance to vegetation zones dominated by European beech (*Fagus sylvatica* L.) (Moen 1999). Recent projections of future distribution of potential natural vegetation zones suggest a northwards shift of the northern range limits of tree species by 300 to 500 km along with an expansion of European beech in southern Scandinavia (Hickler et al. 2012). European beech reaches its northern distribution limit here (Bolte et al. 2007; Jalas & Suominen 1972). It is assumed that trees on their latitudinal distribution limit are stressed by temperature during the growing season, and that this stress is recorded as growth response in tree ring width (Speer 2010). Climate variations influence tree growth and can be studied with dendrochronological methods (Fritts 1976). Dendrochronology and dendroclimatology have a long history in Fennoscandia and were used in many studies to investigate impact of climatic changes on trees (cf. Eckstein & Schweingruber 2009; Linderholm et al. 2010).

This study focuses on European beech (Fagus sylvatica L.) and Norway spruce (Picea abies [L.] Karst.), as these species represent the boreonemoral and boreal vegetation zone, respectively (Moen 1999). Beech and spruce are the key-stone species of their respective forest ecosystems and occupy the same habitat in the study region (Bradshaw & Lindbladh 2005). European beech requires an annual precipitation of 500 mm, July mean temperature < 19 °C, fewer than 141 frost days with a daily minimum temperature < 0 °C, a January mean temperature > -3 °C and more than 217 days with a daily mean temperature of 7 °C or more (Bolte et al. 2007). Norwegian spruce needs a minimum of 40 mm precipitation per month within the vegetation period. The species is vulnerable to wind throw, snow-break and insect attacks (Schlyter et al. 2006).

This study is part of the project “From spruce to beech forests - fundamental ecosystem transformation driven by climate change”, financed by the Norwegian Research Council (NFR). It investigates the relationship between climate variation and annual increment growth of beech and spruce at the distribution limit of beech in South-East Norway. I studied beech-spruce forest stands in order to (1) find relations between increment growth and climate variation, (2) to compare trends in annual increment growth among beech and spruce and (3) to discuss future growing conditions for the species based on my findings.

2. Materials and methods

2.1 Study area

The data for this study was collected from Brånakollane nature reserve and Dalaåsen nature reserve (Fig. 2.1). Both sites are located in Vestfold County in South-East Norway and belong to the Oslo Rift geological area, which is characterized by syenite, granite and monzonite bedrock with marine superficial deposits (Moen 1999; Solli & Nordgulen 2007). The region is part of the boreonemoral vegetation zone, which is characterized by coniferous and broad-leaved deciduous woodland and farm land (Moen 1999). The sites were selected because they provide beech-spruce forest stands relevant for my study. The stands represent a near-natural old growth beech-spruce forest (Fig. 2.2), while being located at the northern limit of beech distribution in Europe.

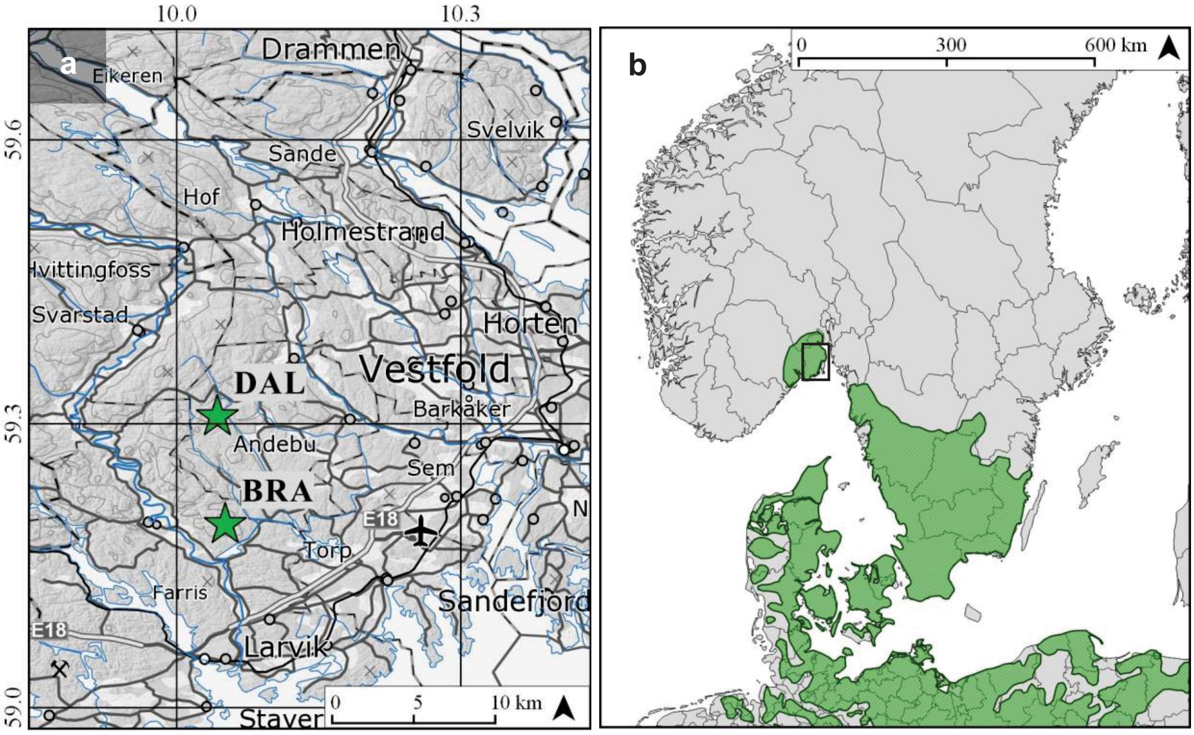

Fig. 2.1: Study sites in Vestfold, Norway (DAL = Dalaåsen; BRA = Brånakollane) *(a)* and natural distribution of European beech (green area; www.euforgen.org) *(b)*.

Brånakollane nature reserve (BRA) has a size of 19.2 ha and is located ca. 16 km north of Larvik (N 59.194067, E 10.049733). The site is characterized by rocky slopes covered with thin organic layers and partly decomposed litter. Mean annual precipitation is 1,029 mm, mean February temperature is -3.8 °C, and mean July temperature is 16.3 °C (normal values 1961-

1990 from weather station nr. 27450; eklima.met.no). European beech is the dominating tree species and forms a closed old-growth forest with natural regeneration. Other thermophilous tree species (e.g. lime) appear as mixed tree species. A recent study on the vegetation history of Brånakollane nature reserve found that small amounts of beech pollen occurred already 9100 cal B.P. in this area, but it is likely that today's beech forest established and expanded locally between 1300 and 1200 cal B.P. (Bjune et al. 2013). The area was protected by law in 1980 (Miljøverndepartementet 1980) and it is assumed that no significant forestry has taken place in the beech forest since the close-down of the regional iron industry in 1837 (Bjune et al. 2013). Brånakollane nature reserve is for the most part surrounded by managed spruce forest, which creates a clear border line between the spruce- and the more natural beech forest. Before the area was protected, it was used for some moderate grazing by livestock (Treschow 2014).

Dalaåsen nature reserve (DAL) has a size of 97.4 ha and is located ca. 28 km north of Larvik (N 59.30475, E 10.033733). The site characteristics are similar to Brånakollane nature reserve. The area was protected by law in 2009 (Miljøverndepartementet 2009). Before that, it was used for timber production and grazing (Gallis 2014). Relicts of a stall can be found in the southern part of the nature reserve.

Fig. 2.2: Beech forest in Brånakollane nature reserve. Stands on rocky and steep slopes *(a)* and on smooth slopes with deeper soil *(b)*.

2.2 Data collection

For this study 81 sample plots were established with 42 plots at Brånakollane nature reserve and 39 plots at Dalaåsen nature reserve. Every sample plot consists of a pair of beech and spruce trees located close to each other and thus representing the same growing conditions (see Fig. 2.3; maximum distance between trees in general < 5 m; some few up to 8 m apart). The plots were distributed over the site area according to these criteria. Only dominant or co-dominant individuals where selected to minimize the influence of tree size mediated competition, stand dynamics and thus to get a clearer climate signal (cf. Schweingruber 1988). All samples were taken in the period of May - October 2014, when in total 162 trees were cored.

Fig. 2.3: Examples for the sample plots consisting of a pair of beech and spruce trees. Trees were marked with degradable paper band.

In order to check the comparability of the trees in pairs and among pairs, several environmental variables were measured, i.e.: The number of tree species surrounding a plot was measured using a standard relascope (*l* = 60 cm, *f* = 1; Haglöf AB, Sweden). This gives an overview over the stand density, which could have an influence on annual increment growth through competition effects (Burschel & Huss 2003). The trees diameter at breast height (d.b.h.) was measured with a standard caliper (Haglöf AB, Sweden). The cardinal aspect of every single tree was measured using a standard trekking compass, and the slope was measured with a standard clinometer (Suunto, Finland). Geographic positions were obtained using a Garmin eTrex GPS device (Garmin Ltd., Switzerland).

Soil samples were taken in every sample plot with a small shovel. For every single tree, two soil samples (excluding litter layer) were taken near to the stem, each on opposite sides of the tree. These samples were mixed together and stored in labeled paper bags. The samples where dried in a drying chamber at 45 °C and then sieved trough a 2 mm mesh. In a glass tube, 10 ml soil material was mixed with 25 ml deionized water and stored at a dark place over night for sedimentation. The pH value of the so prepared probes where measured with a SenTix 81 pH electrode connected to a inoLab pH 720 benchtop meter (WTW GmbH, Germany).

Soil depth was measured for every sample plot by stabbing a thin metal bar vertically into the ground with moderate pressure until it was stopped by bedrock or stones. At least twelve samples per tree were taken with a radius of ca. 100 cm around the tree (Fig. 2.4 a, c).

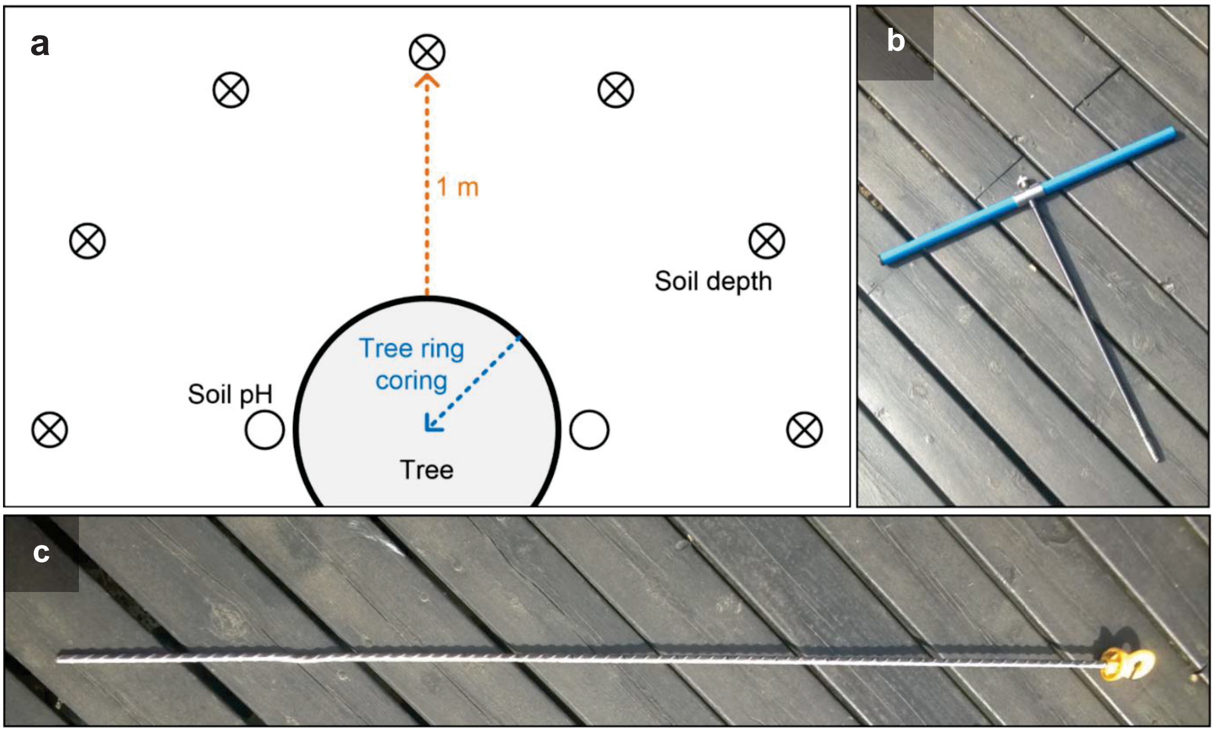

Fig. 2.4: Sample design *(a)*, increment corer *(b)* and the metal bar used for depth measurement *(c)*.

2.2.1 Tree ring samples

The trees were cored at breast height with a standard increment borer with a 5 mm diameter (Haglöf AB, Sweden; Fig. 2.4 b). The so obtained tree ring samples were stored in labeled paper straws and air-dried for ca. 14 days. The dried samples where mounted on wooden boards with ordinary wood glue and polished with sandpaper. The tree ring width (TRW) was visually measured with a LINTAB 6 tree ring measurement station (Rinntech e.K., Germany) and a Leica M50 microscope (Leica Microsystems GmbH, Germany) at a precision of 1/100 mm. This methods were used accordingly to common procedures (Fritts 1976; Grissino-Mayer 2003; Grundmann et al. 2011; Speer 2010).

2.2.2 Climate data

The climate data used in this study was obtained from different weather stations in Vestfold County via eklima.met.no. Since the records of the available stations are not complete and cover different time spans, temperature and precipitation data for my study could not be obtained from the same station. Precipitation data was obtained from Hedrum station (Stnr.: 27800; N 59.196, E 9.9641), whereas temperature data was obtained from Færder station (Stnr.: 27500; N 59.0272, E 10.5242). Since Færder station is located on an island on the coast of Vestfold County, the data was tested for correlation with available temperature data from the inland stations Melsom (Stnr.: 27450; N 59.23, E 10.3483; covered period: 1960-1993) and Holmestrand (Stnr.: 27080; N 59.4833, E 10.3333; covered period: 1913-1956). At both stations the correlation coefficient for each month is quite high with $r > 0.9$ and $r > 0.8$, respectively. The data consists of homogenized monthly mean temperature values in °C and monthly amount of precipitation in mm.

2.3 Dendrochronological analysis

2.3.1 Retrieving the data

Tree ring samples were visually and statistically cross-dated using the TSAP-Win software (ver. 4.69h, incl. modules math and graphics; Rinntech e.K., Germany). By cross-dating, the year of growth of every year ring can be determined and the data can be compared to annual data like meteorological data (Speer 2010). All tree ring series were dated ending in 2013, the year before field work, as this was the youngest completed tree ring. To uncover possible mistakes in measurement or missing year rings in the time series, two often used methods are

Gleichlaeufigkeit (= slope equivalence) and t-values (Fritts 1976; Speer 2010). In this study I have used a combination of these two methods called Cross-Date Index (CDI) as recommended by Rinn (2011), in addition to visual inspection of time series and tree ring samples.

For the analysis of the mean annual tree ring width I used the complete data from beech and spruce (beech: 1819 - 2013; spruce 1843 - 2013). I cut off the year ring data earlier than 1913 AD for the analysis of growth response to climate, since the meteorological data for Vestfold County in the period before 1900 AD is sparse. This also removed a major part the fast growing early youth phase from the data (cf. Lamarche 1974). In this way I obtained tree ring series with a length of 101 years, starting in 1913 and ending in 2013.

2.3.2 Developing the chronologies

Two mean time series were developed for beech and spruce for each site, respectively. These time series show the mean TRW of all tree ring samples included. It also reveals years with outstanding narrow or wide tree rings common to all samples included in the series. I define such years as pointer years, a term which describes a year when many trees show similar growth reactions (common growth signal) simultaneously (Schweingruber et al. 1990). The final spruce chronology could be checked for analogy against an already existing spruce chronology including tree ring samples from south-east Norway built by Lie et al. (2009). For the beech population in south-east Norway, no reference chronology existed.

The two final chronologies for beech and spruce were stepwise generated from trees with matching pointer years and interval trends, as carried out by Grundmann et al. (2008). The match of the tree ring samples was defined visually and statistically according to their CDI-value. The procedure is shown in Fig. 2.5.

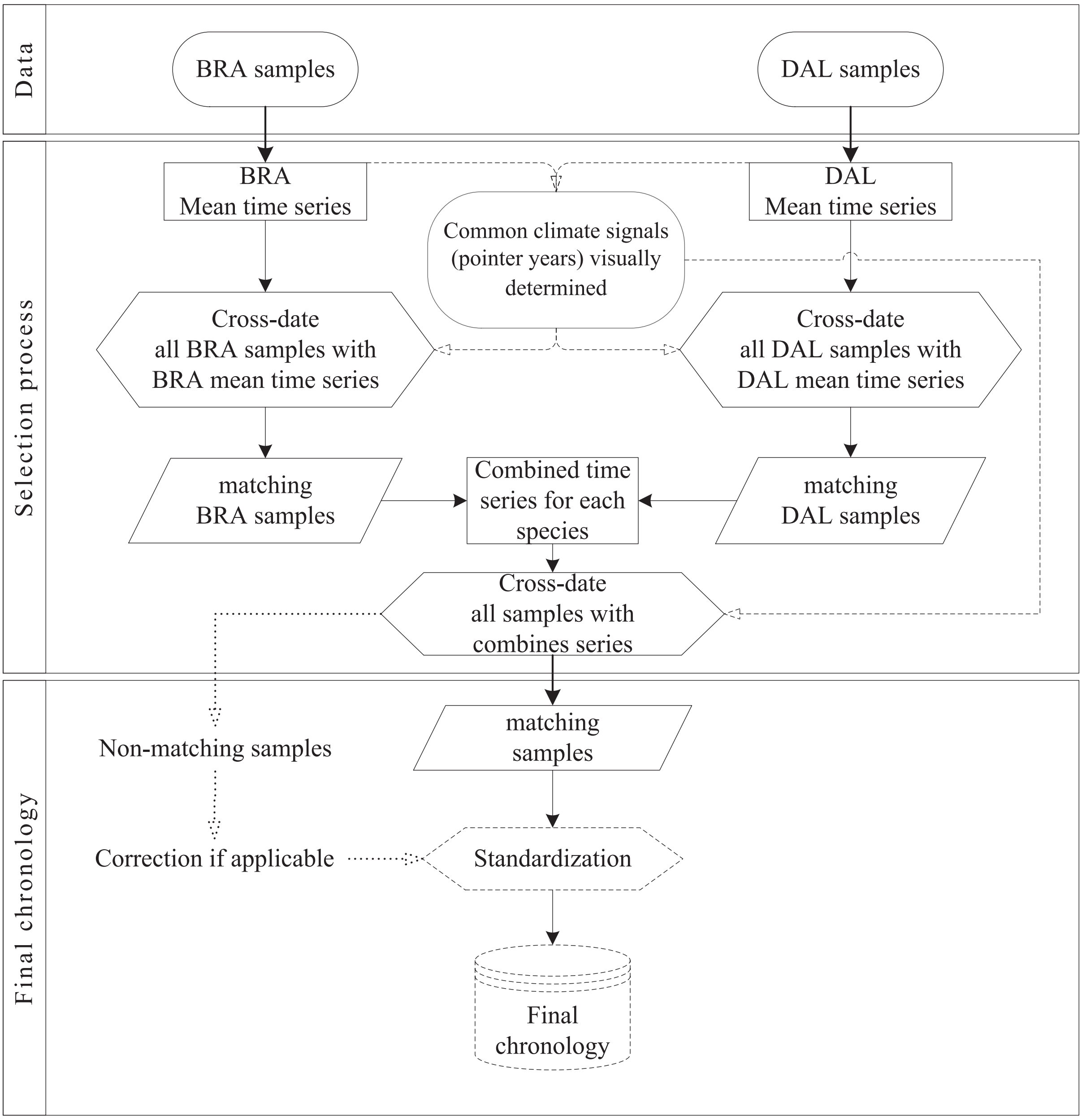

Fig. 2.5: Chronology development procedure used for both species separately.

2.3.3 Standardization

For further processing, I obtained unbiased climate signals from the tree ring samples by standardization of each sample which is used to build the chronology. Standardization (indexation) of tree ring data is an essential operation in dendrochronology which removes age-related growth trends, differences in growth between samples, heteroscedasticity and stand dynamic effects from tree ring series (Fritts 1976; Helama et al. 2004). In my study, I used an indexation method which computes ratios. To remove disturbing trends from the data, I used a moving-average method. For both of the selected methods, a suitable routine is provided by the TSAP-Win software. According to Rinn (2011), it fits a trend function of a specific length (bandwidth) to the time series, which moves stepwise forward along the series. The stiffness of the trend function can be adjusted by modifying the bandwidth. The moving-average method is recommended by Speer (2010) and is often used in dendrochronological studies (cf. Bolte et al. 2010; Drobyshev et al. 2013; Drobyshev et al. 2014). In order to find a bandwidth which removes noise from the data but keeps the climate signal, I compared four different modifications: 5, 15, 25 and 32 year moving averages. I decided to use a 25 year moving average, since this chronology showed the strongest relationship with climate data and also had a high correlation with the other options.

2.4 Statistical analysis

Statistical analyses were carried out with R-studio (ver. 0.98.1103; R ver. 3.1.2) and figures were generated with R-studio and the Veusz plotting package (ver. 1.22). For further processing, the data was checked for normality with the *qqnorm* function and the *shapiro.test* function. All data was further handled as parametric. The significance of differences for environmental data, soil pH, soil depth and annual mean growth between species and between study sites, were tested with the *t.test* function for paired data. Correlations between the weather stations were tested using the *cor* function.

2.4.1 Multiple linear regression models

In order to find the model which explains the relationship between annual tree ring growth and climate variables best, I built a multiple linear regression model with the final chronologies as response variables (see chap. 2.3.2) and the climate data as explanatory variables (see chap. 2.2.2). There was a large number of climate variables and several of the variables were correlated to each other (see Fig. 3.9). This brought up the issue of co-linearity between variables. To deal with this, I performed an initial pre-selection of climate variables to decrease the number of possibly co-linear variables to be included in the multiple regression model (cf. Halvorsen (2013) and citations therein). I built separate simple linear models for each monthly mean temperature and each monthly mean precipitation for the current year and the previous year (24 temperature variables and 24 precipitation variables) and tested them one by one against the chronology. Variables with a p-value > 0.1 were included in the full model. The temperatures of July and August came out significant and correlated strongly with each other. The mean temperature of these months were thus tested in an alternative full model as a single variable. The model was stepwise simplified by removing the least significant variables according to their p-value using the *drop1* function in R. This function also computes the Akaike information criterion (AIC) which compares the models fit before and after the removal of the specific variable (cf. Crawley 2007). These procedures were conducted for both species individually. The models with the July and August mean temperature did not turn out better than the models with separate temperatures. Hence, the models with the initial separate temperatures were preferred. With this procedure I identified the climate variables with significant influence on growth (see Tab. 3.5).

3. Results

3.1 Environmental data

The relascope measurements show just small differences between species. Both trees in a plot experience about the same stand density. At Brånakollane, the values are identical. At Dalaåsen, the difference is fairly small and non-significant ($t = 0.666$, df = 38, $p = 0.5094$). Over both study sites, there is a negligible non-significant difference ($t = 0.6685$, df = 80, $p = 0.5057$).

The diameter at breast height at Brånakollane differ significantly between beech and spruce ($t = -4.8559$, df = 41, $p < 0.001$). This applies also for Dalaåsen ($t = -2.2847$, df = 38, $p = 0.02801$) and over both sites ($t = -4.8897$, df = 80, $p < 0.001$).

Difference in slope values at Brånakollane and Dalaåsen is non-significant ($t = -1.5677$, df = 41, $p = 0.1246$ and $t = -1.5209$, df = 38, $p = 0.1366$, respectively). Over both sites, the difference is small but significant ($t = -2.1975$, df = 80, $p = 0.03088$). Tab. 3.1 summarises the measured data.

The data of cardinal aspect describes the topography of the study sites. Due to the very hilly area, the aspect differs even within the sample plots. Fig. 3.1 gives an overview for the species and the sites. It shows that Dalaåsen is directed more towards south than Brånakollane, while beech tends to have a more southward orientation than spruce.

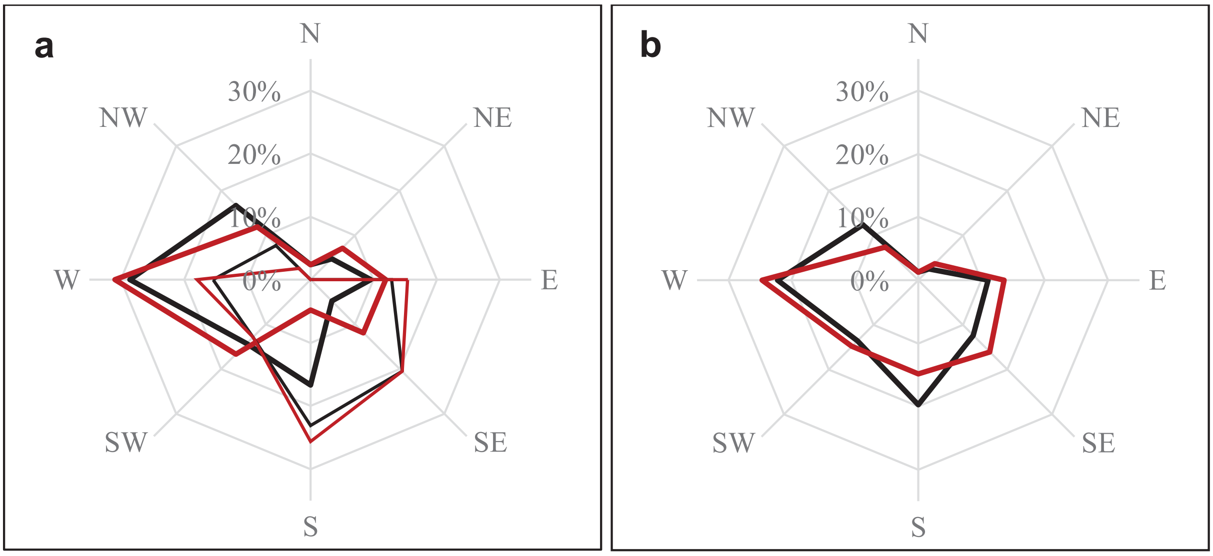

Fig. 3.1: Cardinal aspect for the tree species and sites *(a)* and for both sites combined *(b)*. The axis shows the respective percentage of beech (black) and spruce (red) for BRA (thick lines) and DAL (thin lines).

Tab. 3.1: Results of the environmental data measurements.

	Relascope (*n*)				d.b.h. (cm)				Slope (°)			
	Min	Mean	Max	SD	Min	Mean	Max	SD	Min	Mean	Max	SD
BRA						***						
Beech	20.0	30.6	44.0	6.0	20.5	36.0	55.0	7.8	0.0	10.9	31.0	7.1
Spruce	20.0	30.6	44.0	6.0	27.0	41.0	58.5	8.3	0.0	12.5	31.5	8.0
DAL						*						
Beech	14.0	25.3	41.0	5.5	24.0	38.3	58.0	8.1	0.0	18.5	42.0	10.5
Spruce	14.0	25.2	41.0	5.6	27.5	41.2	59.0	8.1	0.0	20.0	42.0	9.3
BRA+DAL						***				*		
Beech	14.0	28.0	44.0	6.3	20.5	37.1	58.0	7.9	0.0	14.5	42.0	9.6
Spruce	14.0	28.0	44.0	6.4	27.0	41.1	59.0	8.2	0.0	16.1	42.0	9.4

Significance levels: *** = $p < 0.001$; * = $p < 0.05$

3.2 Soil pH and depth

Soil pH under the trees differed slightly between and within the sites (Fig. 3.2, Tab. 3.2). The mean pH-value of beech soil is higher than spruce soil on both sites. At Brånakollane, the pH-value for beech is slightly but significantly higher than for spruce, 4.07 versus 3.92 ($t = 3.5766$, $p = 0.0009$, d.f. = 41). This also applies for Dalaåsen, yet the difference is smaller and non-significant ($t = 0.8748$, $p = 0.3872$, d.f. = 38). Over both study sites, beech soil pH is significantly higher than spruce soil pH ($t = 2.9446$, $p = 0.0042$, d.f. = 80).

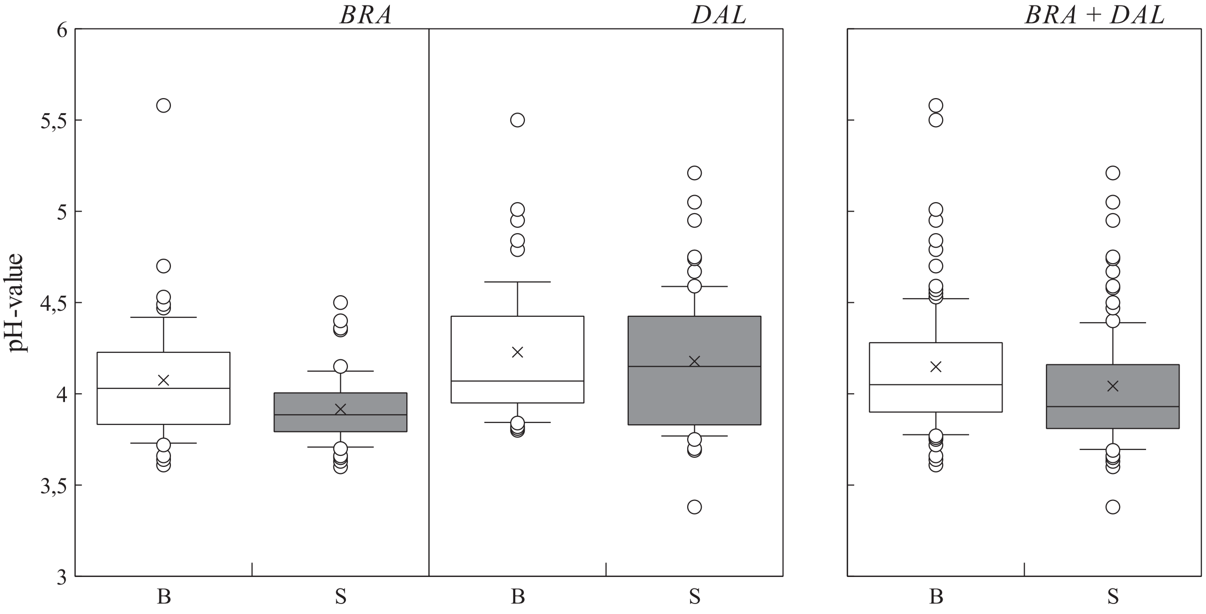

Fig. 3.2: Soil pH sorted by sites and tree species (x = mean, B = beech, S = spruce, error bars at ± 1SD).

There was no significant difference in mean soil depth under the trees between species and sites (Fig. 3.3, Tab. 3.2). At Brånakollane, the difference is non-significant (*t* = 1.3223, *p* = 0.1934, d.f. = 41). This also applies for Dalaåsen (*t* = 0.3613, *p* = 0.71992, d.f. = 38) and over both sites(*t* = 1.3402, *p* = 0.184, d.f. = 80). Even though there is no significant difference, beech soil depth shows a marginal trend to be lower than spruce soil depth.

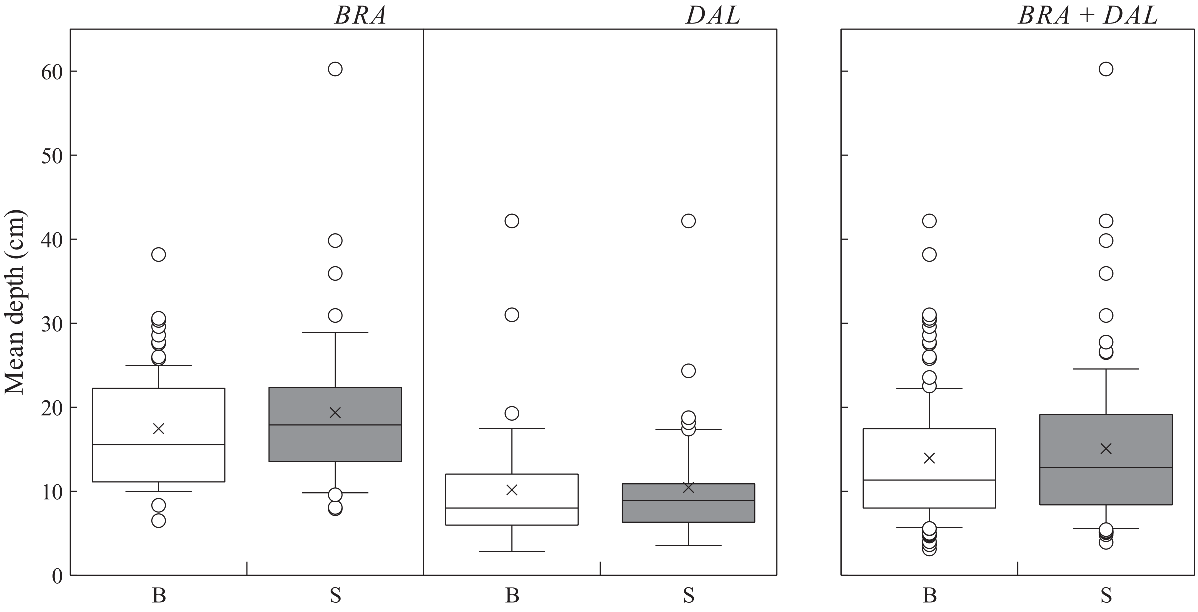

Fig. 3.3: Mean soil depth. Sorted by sites and tree species (x = mean, B = beech, S = spruce, error bars at ± 1SD).

Tab. 3.2: Soil pH and depth.

	pH				Depth (cm)			
	Min	Mean	Max	SD	Min	Mean	Max	SD
BRA		**						
Beech	3.61	4.07	5.58	0.35	6.50	17.46	38.17	7.60
Spruce	3.60	3.92	4.50	0.21	7.92	19.36	60.25	9.66
DAL								
Beech	3.80	4.23	5.50	0.39	3.13	10.16	42.17	7.41
Spruce	3.38	4.18	5.21	0.41	3.92	10.45	42.17	6.98
BRA+DAL		**						
Beech	3.61	4.15	5.58	0.37	3.13	13.94	42.17	8.31
Spruce	3.38	4.04	5.21	0.35	3.92	15.07	60.25	9.54

Significance levels: ** $p < 0.01$

3.3 Mean tree ring width

The measurement of tree ring width covers the complete available length from the tree ring samples (see Tab. 3.3). At Brånakollane, the difference between beech and spruce growth is significant (t = -3.2346, df = 41, p = 0.00241). This is not the case at Dalaåsen (t = -0.4523, df = 38, p = 0.6536). Over both sites, the mean tree ring width is significantly different (t = -2.6354, df = 80, p = 0.01009), with beech showing a lower mean annual TRW than spruce. Note that the unit for TRW is 1/100 mm. This gives a difference in mean TRW over both sites of 0.167 mm.

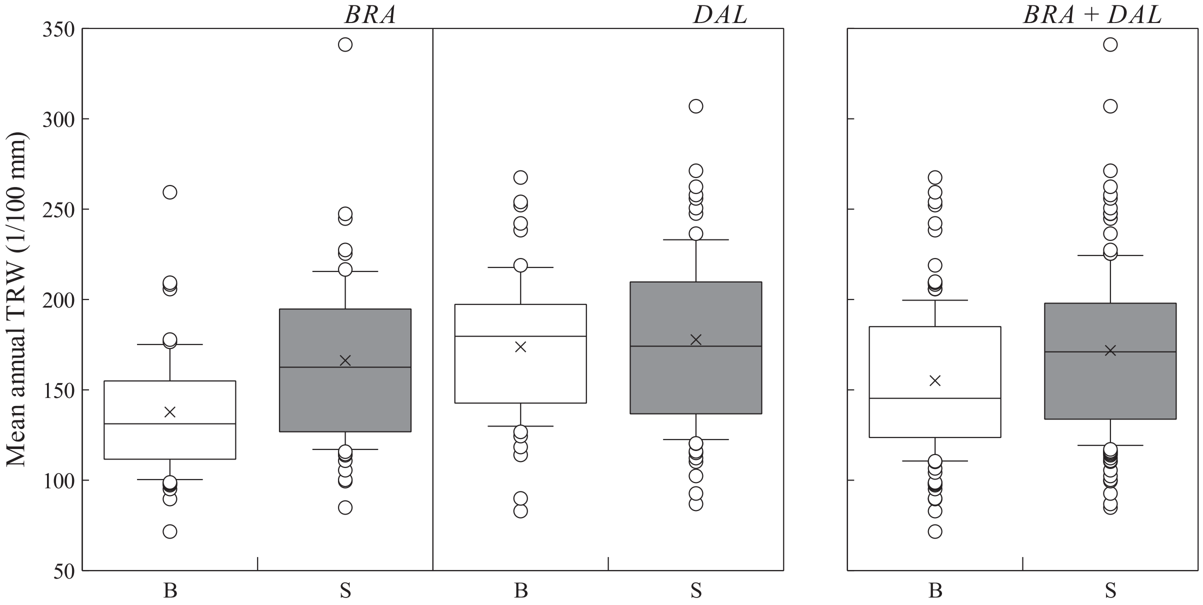

Fig. 3.4: Mean tree ring width sorted by sites and tree species (x = mean, B = beech, S = spruce, error bars at ± 1SD).

Tab. 3.3: Mean annual tree ring width and differences among species and sites.

	TRW (1/100 mm)				Sample length (years)		
	Min	Mean	Max	SD	Min	Mean	Max
BRA		**					
Beech	71.6	137.7	259.4	37.8	83	119	195
Spruce	84.9	166.3	341.1	49.8	37	111	171
DAL							
Beech	82.9	173.8	267.5	44.5	64	101	179
Spruce	86.9	177.8	307.0	56.0	60	105	157
BRA+DAL		*					
Beech	71.6	155.1	267.5	44.8	64	110	195
Spruce	84.9	171.8	341.1	52.9	37	108	171

Significance levels: ** = $p < 0.01$; * = $p < 0.05$ (tested by t-test)

Even though beech has a lower mean annual TRW than spruce over the complete time series, beech TRW shows a faster increase in growth compared with spruce. Fig. 3.5 shows a contrast in linear growth trends for both species between different periods.

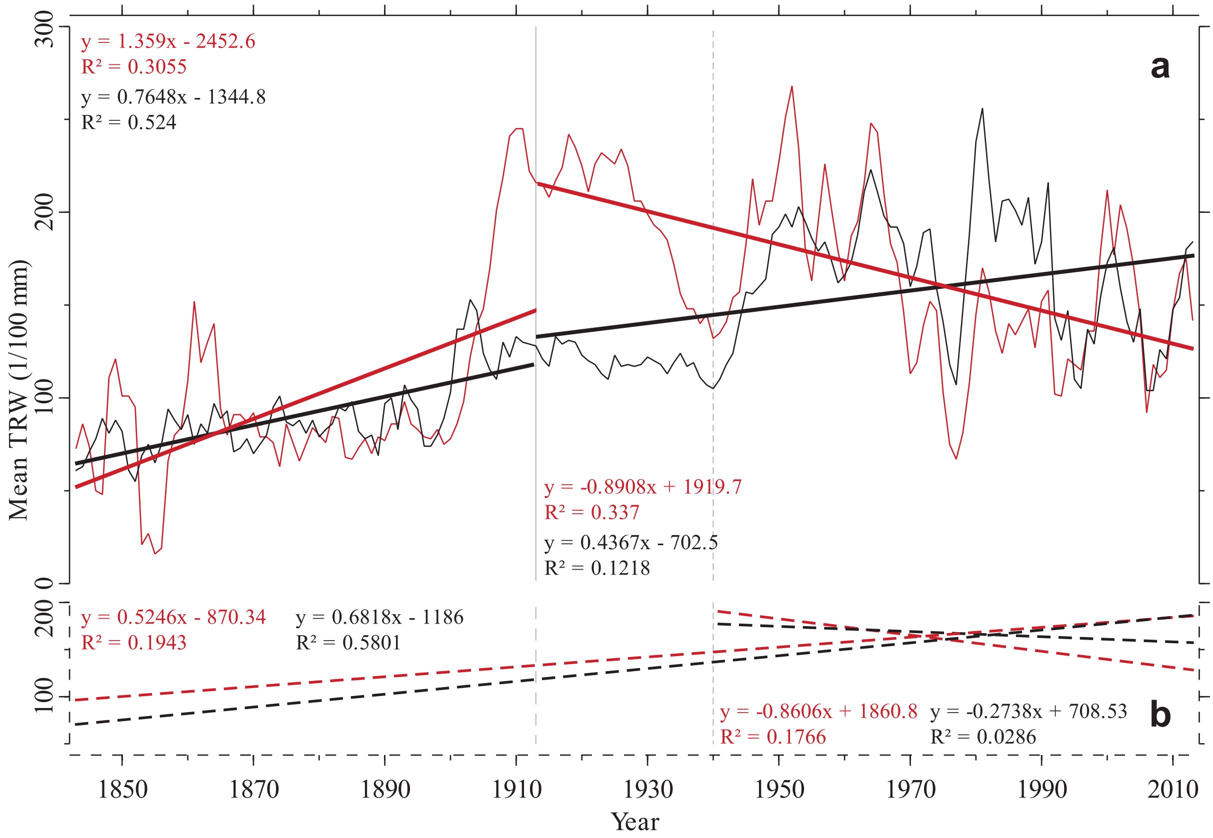

Fig. 3.5: Mean annual tree ring width for beech (black) and spruce (red) for the complete overlapping data (1843 - 2013), separated in study period (1913 - 2013) and the preceding period (1843 - 1913), with the respective linear trends for TRW separated by periods (*a*), and for the complete time series (solid) and the period with natural growth dynamics (assumed 1940 - 2013; dashed) (*b*).

3.4 Chronologies

After conducting the necessary dendrochronological procedures, a final chronology for each tree species could be developed (Fig. 3.6). They show the variation in increment growth represented by indexed values (ratios). Both chronologies show clear peaks reflecting the respective climate conditions. They show similar trends for the most part of the studied period. However, they sometimes differ considerably in minimum/maximum values. These chronologies were used to reveal interactions between climate and annual increment growth.

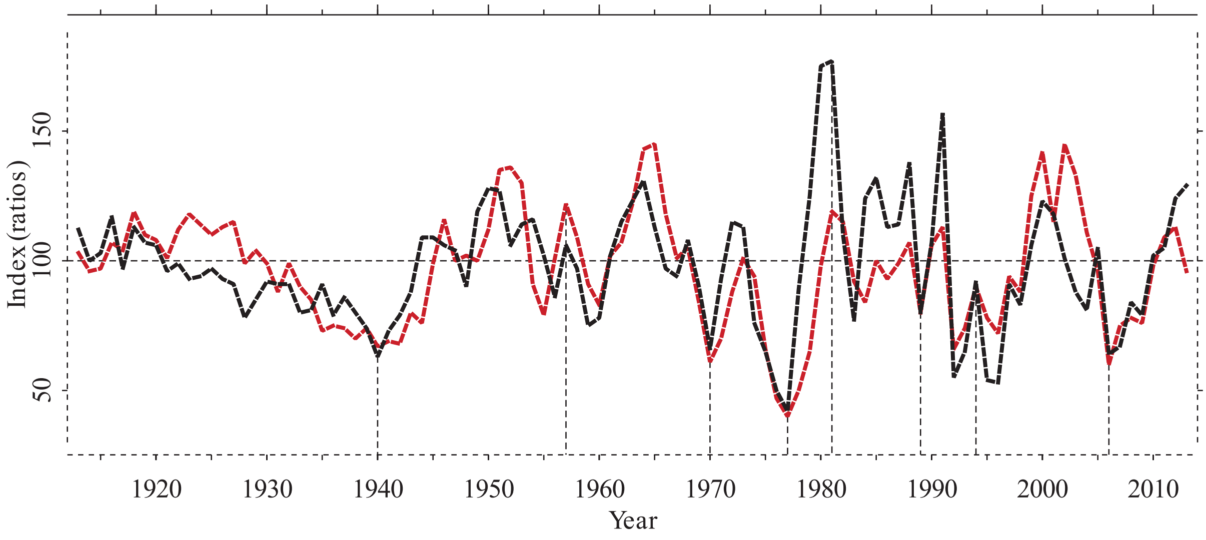

Fig. 3.6: Chronologies of beech (black) and spruce (red) with clear common climate signals in 1940, 1957, 1970, 1977, 1981, 1989, 1994 and 2006 (dashed lines).

Tab. 3.4: Internal statistics for the indexed chronologies.

Chronology	Sample density (*n*)			Indices			SD	Glk	AC (1)	MS (%)	TC (%)
	Min	Mean	Max	Min	Mean	Max					
Beech	29	48	51	42	98	177	23.7	67	0.53	17	51
Spruce	46	70	75	40	97	145	21.8	66	0.73	14	55

TRW = tree ring width; Glk = internal gleichlaeufigkeit; AC(1) = autocorrelation (lag = 1); MS = mean sensitivity; TC = tendency changes

3.5 Growth response to climate

After testing all climate variables against the chronology for each tree species one by one, the following variables showed significant influence on growth variation (Tab. 3.5). Through model simplification, the number of variables could be further reduced to two climate variables for beech and three climate variables for spruce (bold type in Tab. 3.5).

The strongest climate signal in beech growth is related to high temperatures in previous year August, followed by precipitation in June of the current year. Spruce growth correlates strongest with previous year August precipitation, followed by a somewhat weaker correlation with June and November temperature of the previous year (Fig. 3.7).

Tab. 3.5: Climate Variables explaining a significant part of variation in tree ring widths.

Beech		Spruce	
Temperature	*Precipitation*	*Temperature*	*Precipitation*
January^1*	**June****	June .	June*
July^1**	January^1*	**June^1***	August .
August^1***	August^1*	July^1.	**August^1****
		August^1*	
		November^1*	

^{1} = previous year; signif. levels: *** = $p < 0.001$; ** = $p < 0.01$; * = $p < 0.05$; **.** = $p < 0.1$

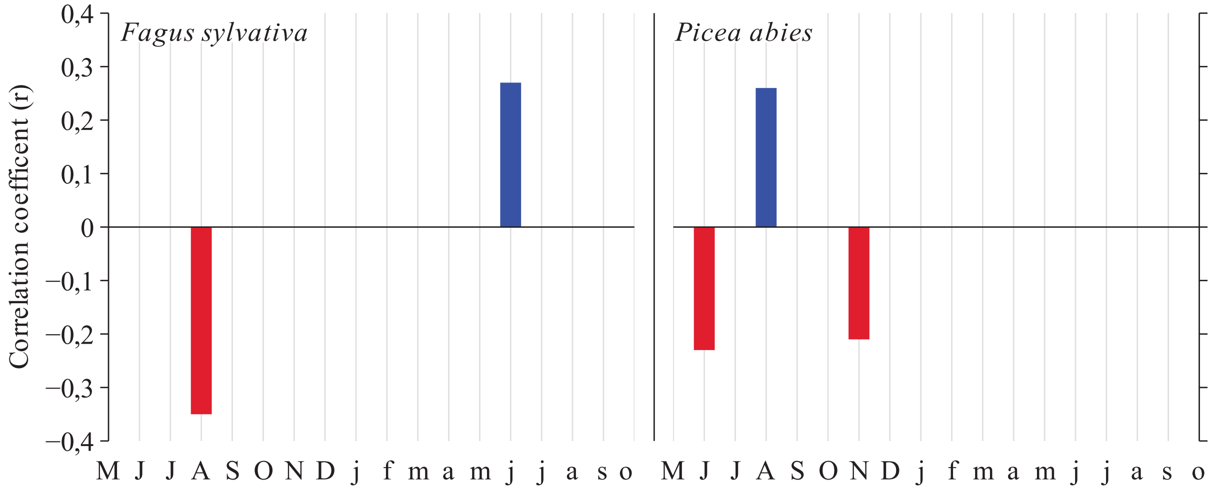

Fig. 3.7: Correlation coefficients between the chronology and temperature (red) and precipitation (blue) variables from previous March (M) to current October (o), divided by tree species.

As visualized in Fig. 3.8, high previous year August temperatures show an opposite trend compared with increment growth in beech, while the curve for current year June precipitation tend to follow the growth trend. Due to low correlation, the curve of previous year June precipitation differs somewhat more from the indexed beech chronology. Fig. 3.10 shows the relations of spruce growth with climate variables. Opposite trends for temperature and similar trends for precipitation data can be seen here as well. Beech growth correlates with previous August temperature, while spruce growth correlates with precipitation of the same month. The relation between temperature and precipitation in previous August are shown in Fig. 3.9. This relation is also shown for previous November, where spruce growth is correlated with temperature.

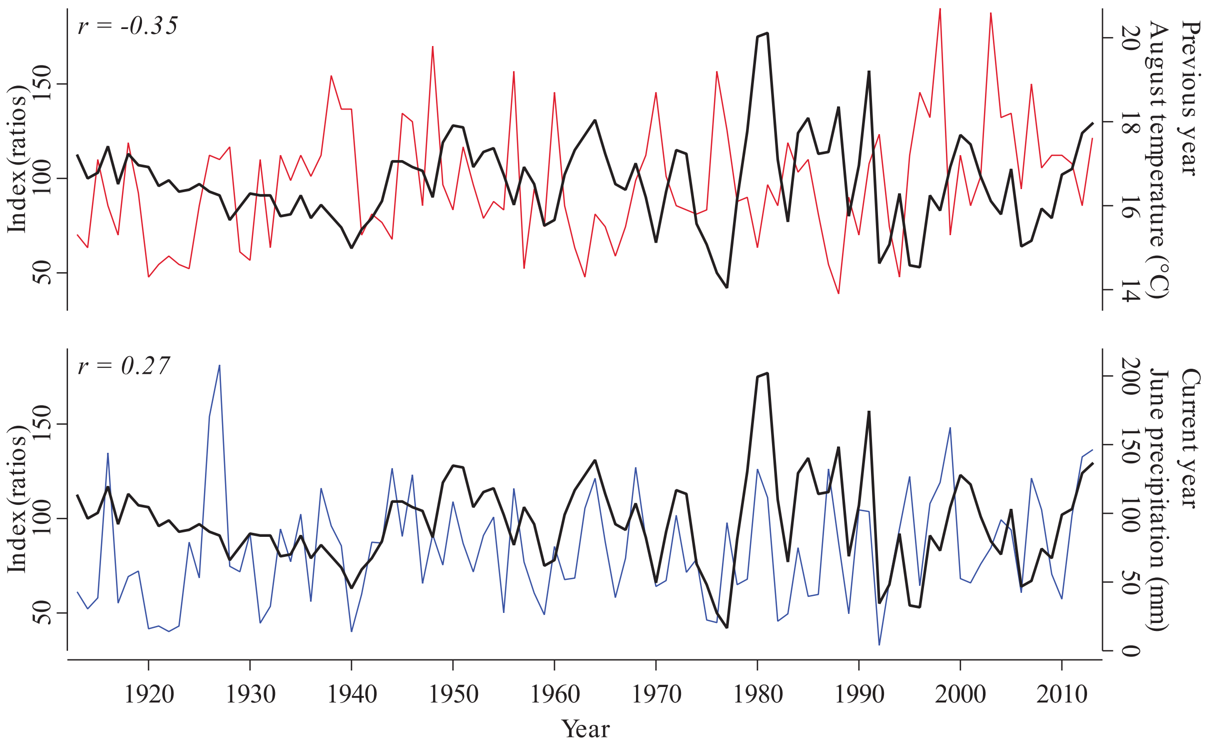

Fig. 3.8: Beech chronology (black) compared with significant climate variables in order of their correlation (*r* = correlation coefficient).

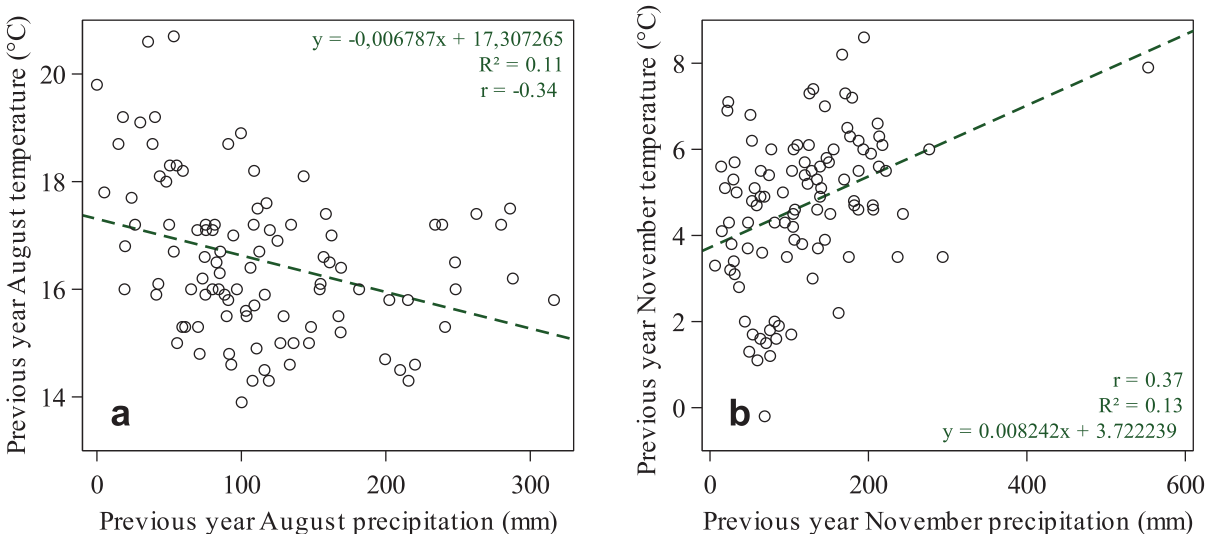

Fig. 3.9: Relationship between temperature and precipitation for previous year August (*a*) and previous year November (*b*) with respective linear trends (green).

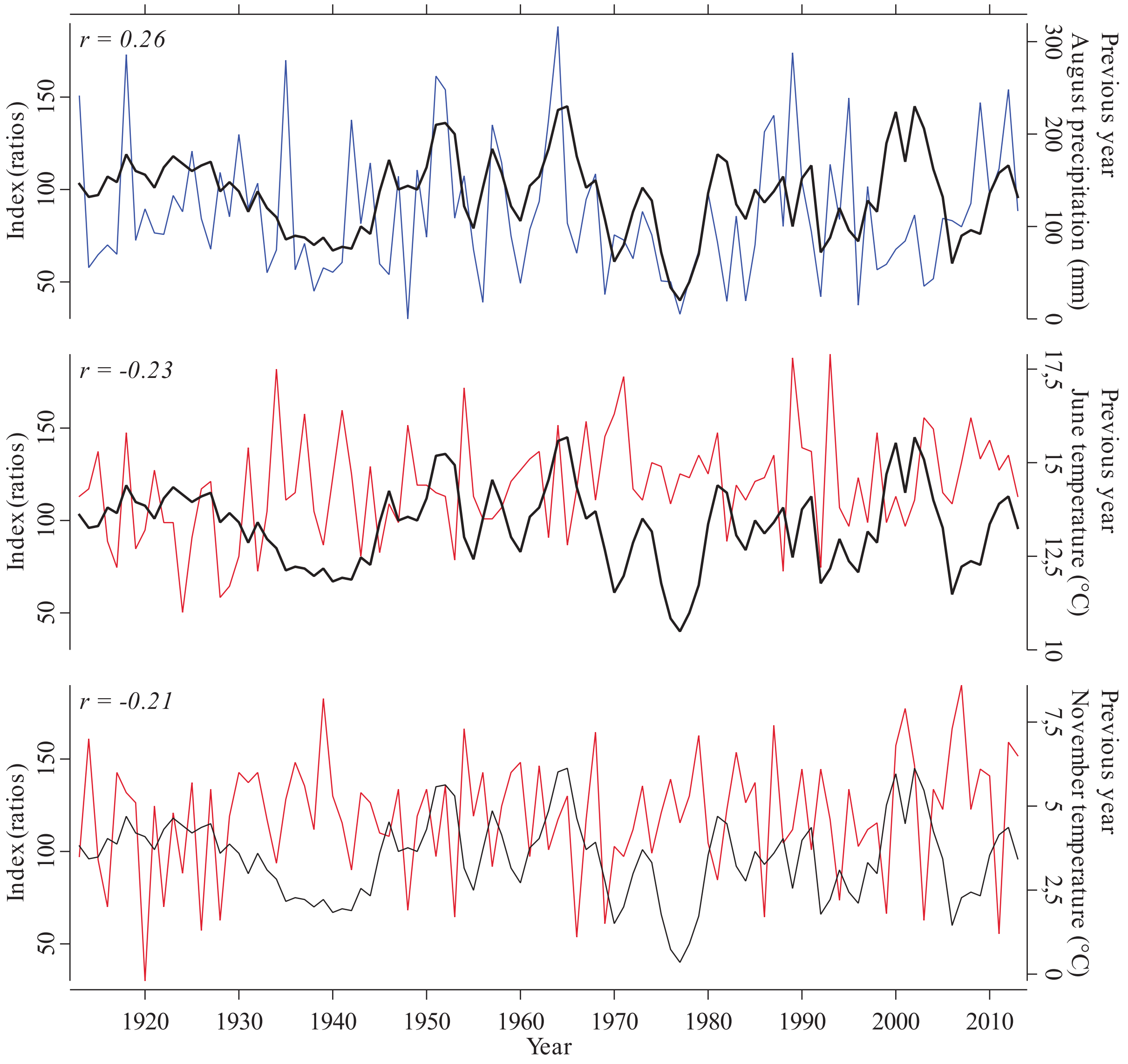

Fig. 3.10: Spruce chronology (black) compared with significant climate variables in order of their correlation (*r* = correlation coefficient).

4. Discussion

The evaluation of the environmental data shows a sufficient similarity of the environmental factors of beech and spruce. Even though there were significant differences between the species variables, these differences were moderate. Relascope measurements revealed that both species experienced the same competitive pressure from the surrounding forest stand. Based on these findings, I assume that the choice of trees for the pairwise plots were appropriate and that beech and spruce trees experienced comparable environmental conditions. The depth measurements did not differ significantly and therefore supported this assumption. Yet, the measuring method for soil depth didn't seem to be entirely suitable, since it depended strongly on the respective ground structure. The stony ground of the study sites most probably prevented the detection of the actual soil depth. I assume that the real soil depth accessible to the trees is higher than the one that was measured.

Soil pH data showed that mean soil pH for beech is slightly but significantly higher than for spruce. This difference between the two species was also found by a study dealing with old-growth beech-spruce stands (Scheu et al. 2003). This could be due to an effect of a difference in litter quality. Albers et al. (2004) found that beech litter decomposed significantly slower than spruce litter although beech litter contained more microbial biomass (decomposing organisms), while Binkley and Valentine (1991) reported an acidifying effect of spruce on soil pH. At Dalaåsen soil pH is relatively high for both species and showed no significant difference. I assume that the bedrock here is more calcareous and therefore buffers the soil pH. The shallow ground on this site could facilitate that effect. The limy conditions are indicated by *Galium odoratum* and *Hepatica nobilis*, both species occurring in typical beech forest communities on calcareous soil with sufficient water supply (e.g. Hordelymo-Fagetum) (Fischer 2003).

The analysis of the raw growth data (mean tree ring width / year) showed an increasing growth for both species over the last 171 years. However, beech growth accelerated and reached a slightly higher mean annual growth compared to spruce in 2013. The separation of the TRW data into different periods revealed an interesting disparity in growth trends. While spruce growth exceeded beech growth in the early period (1843 - 1912), this relation is reversed in the later periods (1913 - 2013 and 1940 - 2013). Spruce focused forestry in the early period could have caused better conditions for spruce growth, while beech coexisted as suppressed or understory trees. The TRW data showed an increase in spruce growth around 1895 AD. This could be due to controlled thinning which improved light availability, lowered competitive pressure and lead to a dominance of spruce for the next 40 to 50 years. The ability of beech to immediately react to thinning (Burschel & Huss 2003) could be found in the data. Yet, beech growth did not outrun spruce growth and stagnated on a lower range (see period between 1895 and 1940 in Fig. 3.5.). The theory that these differences in growth are not caused by climate variation is supported by the fact that they disappeared in the chronologies after standardization. Both the raw TRW data and the indexed chronologies show a change in growth patterns towards a higher level of variation after 1940. This most probably marks the end of logging activity in the study area. After that, the forest stands could develop more natural growth and stand dynamics. Since the forest was mainly undisturbed after 1940, the indexed time series show very clear climate signals after that date, e.g. a severe drought event in 1977 (Spiecker 2000). After 1940 both species showed a negative growth trend. This was also reported by Grundmann et al. (2011) for the period after the 1950s. However, I found that spruce growth is decreasing faster than beech growth since 1940. This could be due to greater efficiency of beech in occupation of canopy space compared to spruce (Pretzsch & Schütze 2005) and its ability to adapt to belowground competition by spruce (Bolte & Villanueva 2006).

In my study, the major climate signal in beech growth was negatively related to late summer temperature (August) of the previous year and positively related to early summer precipitation (June) of the current year. This relation was also reported by other authors (Di Filippo et al. 2007; Drobyshev et al. 2010; Grundmann et al. 2008; Grundmann et al. 2011) and seems to describe a common climate-growth relationship of beech inside its distribution limits. Spruce growth showed negative relationships with temperature in early summer (June) and late autumn (November) of the previous year and a positive relationship with late summer precipitation (August) of the previous year. The negative relationship of spruce growth with previous year November temperatures could arise from a negative effect of high autumn temperatures on the development of frost hardiness in spruce, which can increase sensitivity to frost events in the following winter moths (Fritts 1976). I found no significant relationships with climate of the current year for spruce. These findings contradict the results of other studies that found strong relationships to current year summer conditions (Bosela et al. 2014; Seidling et al. 2012). However, Selas et al. (2002) emphasised that strong relations of spruce growth in the current year with growing conditions during the previous year are characteristic for spruce biology and reported a decrease in sensitivity to current year summer temperatures since at least 1971. Furthermore, Grundmann et al. (2011) described a recent shift of spruce sensitivity from current June precipitation to previous year late summer temperatures in southern Sweden and suggested that this could indicate a shift of its distribution range. A further investigation on my data could possibly identify such sensitivity shifts and allow a determination of such events. Future increase in summer temperature and a simultaneous decrease in precipitation could cause higher seed production in spruce, which has a negative effect on growth (Selas et al. 2002). Drobyshev et al. (2010) found a similar growth-reproduction relationship in beech. It could also cause disturbances like wildfires and storm events, which are supposed to have an impact on increment growth in trees (Schlyter et al. 2006). The mentioned impacts may be reflected in the chronologies, but were not further investigated of this study.

Hanssen-Bauer et al. (2009) projects an increase in annual mean temperature (2.3 to 4.6 °C) and precipitation (5 to 30 %) for Norway in general, and for the specific region of my study an increase in mean summer (JJA) temperature from 1.5 to 3.8 °C and in summer precipitation from -21.0 to 9.4 % in particular, until the year 2100. This probably results in a decrease in summer precipitation. She further predicts the highest increase of these variables for the winter months and the lowest for summer. The correlations between the climate variables showed negative correlations between summer temperature and precipitation, with the strongest negative correlation for August (see Fig. 3.9). In consideration of this, higher summer temperature combined with lower summer precipitation would have negative consequences for both species, since growth was negatively related to these variables. A general increase in annual mean precipitation would, on the one hand, promote growth as long as it would not cause a critical oversaturation of soil (cf. Fritts 1976).

The expected increase in winter temperature could have opposite effects on the two tree species. Bolte et al. (2010) defines the short growing season, low mean air temperatures, extended frost periods and cold winter temperatures as limiting factors for beech growth at its northern distribution limit. According to this, the projected warming and the extension of the growing season in Norway (Hanssen-Bauer et al. 2009) could facilitate beech growth in the future. Whereas spruce, which showed a negative growth response with a warmer November, could experience unfavourable growing conditions in the future. The detected sensitivity to November temperature could interfere considerably with the hardening process of spruce and cause severe frost damage. Changing climate conditions may trigger other factors that could have influence on species growth and distribution, e.g. increasing bark beetle populations threatening spruce (Økland & Wollebæk 2014), Phythophthora infections of beech (Jung 2009) and wildfires (Ohlson et al. 2011).

5. Conclusion

In South-East Norway the weather conditions are expected to become warmer and dryer within the next 85 years (Hanssen-Bauer et al. 2009). My findings suggest that this will have a negative impact on both beech and spruce growth. However, beech seems to have a higher competitive vigour under these circumstances (Bolte et al. 2010; Grundmann et al. 2011). This could lead to an advance in beech growth and an increase in dominance of the species as compared to spruce. Based on these assumptions, I agree with other studies that future climate change could favour beech at the expense of spruce and possibly lead to a future narrowing of spruce distribution and an expansion of beech in south-east Norway (Bolte et al. 2010; Grundmann et al. 2011; Hickler et al. 2012). Under changing climate conditions competitiveness seems to be the regulatory factor for species composition in the studied beech-spruce forest ecosystem.

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