Title

Geographical patterns in the radial growth response of Norway spruce provenances to climatic variation

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Abstract

Changing climate is expected to cause range shifts and reduced growth in Norway spruce (*Picea abies* (L.) Karst). In order to mitigate these changes, genetic variation between populations can be utilized in selecting alternative tree origins that are better suited to the new conditions. The aim of this study was to examine the intraspecific differences in the climatic drivers of radial growth in Norway spruce. We used tree-ring data from seven Norway spruce provenance experiments in Finland, located in different climatic conditions and including a large variety of provenances. The annual ring-width indices were studied with hierarchical clustering, correlation analysis with climate variables, pointer year analysis and linear models to identify the provenance differences in growth variation and its climatic control, and compare them on a latitudinal gradient. The cluster analysis revealed patterns of provenance differences in growth variation: north European and central European provenances were grouped in separate clusters within sites, although with some exceptions. Largest provenance differences in climate-growth responses were found in relation to winter and spring temperatures. In the southern provenances warm winters were typically associated with faster growth whereas for the northern provenances the correlations varied from non-significant to negative. In addition, the pointer year analysis showed negative growth anomalies only in the southern provenances for years with exceptionally cold winters. These patterns may reflect the physiological differences between the provenances relating to, for example, cold tolerance and the timing of spring phenology. As the climate warming in Europe is predicted to be strongest during the winter months, acknowledging the intraspecific growth responses to climate in Norway spruce becomes increasingly important.

**Keywords:** *Picea abies*, provenance experiment, tree-ring width, cambial growth, increment variation, growth variation
1. Introduction

In changing climate, rising temperature and increasing frequency and severity of drought are expected to have negative effects on forest production in many parts of Europe (Lindner et al., 2010). Norway spruce (Picea abies (L.) Karst.), a species with high economic and ecological importance, is found to be especially vulnerable (Lévesque et al., 2013; Zang et al., 2014) and the changes in climatic conditions are projected to lead to range shifts and reduced growth, resulting in substantial economic losses (Kellomäki et al., 2008; Hanewinkel et al., 2013). Even in northern Europe, where climate change is expected to increase overall forest productivity due to longer and warmer growing seasons (Lindner et al., 2010), conditions are expected to become less favorable for Norway spruce (Kellomäki et al., 2008; Ge et al., 2010; Ge et al., 2013).

In assessing the impacts of climate change, tree species are often treated as homogeneous groups with similar responses to environmental factors. However, since growth-limiting factors vary geographically (e.g. Mäkinen et al., 2002; Henttonen et al., 2014) and tree populations are adapted to the local conditions, the response to climate will also differ within a species. These differences can be utilized in strategies of climate change adaptation: information on population differences can be used to identify provenances suited to the new climatic conditions, and therefore maintain or even increase forest growth and wood production (Pedlar et al., 2012; Schueler et al., 2013; Williams & Dumroese, 2013). Additionally, considering within-species differences may improve the estimation of climate change impacts on future growth rates and distribution changes (O’Neill et al., 2008; O’Neill & Night, 2011).

Provenance experiments, in which trees originating from different geographical areas are grown in test sites with different climatic conditions, provide information on how the
environment and heredity interact in regulating tree growth (Matyas, 1994; Carter, 1996; Morgenstern, 1996). Tree-ring data from provenance experiments enable the examination of interannual growth variation and its determinants. In provenance studies linking climate and growth variation, focus has recently been on responses to drought events. For example, provenances well adapted to dry conditions have been identified for Scots pine (Pinus sylvestris L.) and Douglas fir (Pseudotsuga menziesii (Mirb.) Franco) (Jansen et al., 2012; Eilmann et al., 2013; Taeger et al., 2013).

For Norway spruce, previous studies have analyzed the effects of provenance transfers on tree height and volume increment (Beuker, 1994a; Schmidtling, 1994; Gömöry et al., 2012; Kapeller et al., 2012). Physiological differences in frost hardiness (Beuker et al., 1998; Westin et al., 2000; Hannertz & Westin, 2005) and the timing of growth cessation (Krutzsch, 1992) and bud burst (Beuker, 1994b) have also been found between provenances. Genotypic differences in the factors controlling interannual growth variation of Norway spruce have been examined in a few studies but with inconsistent outcomes. Zubizarreta-Gerendiain et al. (2012) found the effect of mean July temperature on ring-width to vary between Finnish clones, whereas Burzyk and Giertych (1991) did not find differences in drought tolerance of Polish provenances and King et al. (2013) concluded in their study in the Swiss Alps that different responses to growing season temperature on altitudinal gradient are rather driven by environment than heredity. However, these studies represent limited ranges of provenances and conditions of the study sites. Thus, no clear understanding of intraspecific differences in climate-growth responses of Norway spruce exists.

The aim of this study was (i) to investigate the provenance differences in the characteristics of the Norway spruce radial growth variation, (ii) to analyze the provenance differences in the climatic control of radial growth, and (iii) to compare these differences in seven experiments with climatically varying conditions along a latitudinal gradient in Finland.
achieve this, we used a tree-ring dataset from a provenance experiment series established in the 1930s, including provenances from central Europe to the northern distribution limits of the species.
2. Materials and methods

2.1 Provenance experiments

The study material was collected from Norway spruce provenance experiments established in 1931 and 1932 at seven sites in Finland. Seedlings from a total of 30 provenances from central Europe to northern Finland (Fig 1.) were planted after being raised at nurseries for five to six years. One plot per provenance was included at each site. The plot size and planting density varied to some extent between the sites (see Table 1 for details). The experimental sites represented different growing conditions: the difference in mean annual temperature between the northernmost (latitude 66°28’) and southernmost (60°05’) site is c. 6 °C (Table 1). The site fertility decreases slightly from fertile soils in the south to relatively fertile soils in the north. For a more detailed description of the sites and experiments see earlier publications by Beuker (1994a, 1996).

2.2 Tree-ring data

The tree-ring data consisted of two datasets. The dataset A-G, containing all seven experimental sites, was sampled in 1992 (Table 2). Up to ten dominant trees without visible damage were cored on the plots of selected provenances. Due to the number of remaining trees suitable for sampling and the quality of the sampled cores the final number of trees per plot ranged from six to ten (see Table 3 for exact numbers). In this dataset the included provenances differed between the sites. The dataset B/E, in which only sites B and E were included, was sampled in 2013. Eight dominant trees were cored from seven provenances, with the same provenances included at both sites (Tables 2 and 3). For the overlapping parts of the datasets (sites B and E 1950-1991) all data were used in the analyses.

On every sample tree, one increment core from the bark to the pith was taken at breast height (1.3 m). The ring-widths were measured using a computer-aided system consisting of an
Olympus SZ51 stereo microscope (Olympus Corporation, Tokyo, Japan) connected to a
Heidenhein LS 303C transducer (Encoders UK Ltd., Birmingham, UK) with an accuracy of
0.01 mm (Table 3). The cross-dating of the ring-width series was done visually and verified
using the dplR package (Bunn et al., 2013; cross-dating following Bunn, 2010) of the R
software (version 3.0.2, R Core Team, 2013). In each core three innermost rings were
removed from the data.

Detrending of the ring-width data was carried out in order to remove the long term trends
resulting from the effects of tree age and stand dynamics. The individual ring-width series
were detrended by fitting a spline function with a 50% frequency cutoff in 30 years, after
which the indices were calculated by dividing the ring-widths by the modelled spline curve
values (Cook & Peters, 1981; Speer, 2010). The resulting ring-width indices (RWI) represent
the year-to-year variability of the ring-widths with the long-term trends removed (Cook &
Kairiukstis, 1990). From these indices temporal autocorrelation was removed with first-order
autoregressive model (prewhitening). Finally, a mean chronology for each provenance at
each site was computed from the detrended and prewhitened RWIs of individual trees as
annual averages using Tukey’s biweight robust mean. Only years with values from at least
three trees were included in the mean chronology, and only the common years of all
chronologies were used in the further analysis (1950-1991 for the A-G dataset and 1950-2013
for the B/E dataset). The reason for the late start of the time series is in the slow height
growth in northern Finland, especially in the case of southern provenances (Heikinheimo,
1949, see S1 for details), i.e., it took a longer time to reach the coring height.

2.3 Weather data

Daily weather data (daily mean temperature and precipitation sum) were obtained from the
Finnish Meteorological Institute. Weather stations with long measurement series were used in
order to cover the whole length of the ring-width chronologies (Fig. 1). In cases of missing
data, the gaps were filled using the interpolated 10 km weather data grid (years 1961-2000;
Venäläinen et al., 2005). When this was not available, data from the nearest possible weather
station or from the next and previous days at the same weather station were used.

2.4 Flowering

Flowering data were included in the analysis to account for growth reductions due to
intensive flowering and seed production (Pukkala, 1987; Koenig & Knops, 1998; Selås et al.,
2002). The intensity of flowering was obtained from Koski and Tallqvist (1978) and more
recent data from the Natural Resources Institute Finland (Tatu Hokkanen, unpublished). The
data contained seed counts at five stands in different parts of Finland (see S2 for more
details). These stands were selected on the grounds of having sufficiently long measurement
series. The seed crop measurements started in late 1950s or early 1960s depending on the
location. Since seed production of Norway spruce begins approximately at the age of 40
(Selås et al., 2002) the growth in the early years was assumed to be unaffected by flowering.

For each experimental site one or two most closely located seed measurement sites were
chosen. To identify the intensive flowering years, a threshold of 1200 seeds m\(^{-2}\) was defined
based on the 90\(^{th}\) quantiles of seed production in the southern stands and visual inspection of
the density distributions of the seed data (S2). If the seed crop exceeded this threshold the
previous year was marked as an intensive flowering year (1) while the other years were coded
as normal years (0).

In northern Finland seed production is infrequent due to the harsh climate (Koski & Tallqvist,
1978) and, thus, the number of intensive flowering years remains low. For site B in northern
Finland only year 1989 exceeded the threshold of 1200 seeds m\(^{-2}\), whereas for site E in
central Finland seven years were classified as years of intensive flowering.
2.5 Statistical analysis

Hierarchical clustering is a method of forming clusters iteratively, starting with each object in its own cluster and then proceeding by combining the most similar pairs of clusters step by step, thus forming a hierarchy of clusters (e.g. Everitt et al., 2011). We performed hierarchical clustering on the mean chronologies in the A-G dataset (1950-1991), using Euclidean distance as a measure of similarity and Ward’s minimum variance method as the clustering method. Alternative methods for clustering (complete and average linkage) and distance (Pearson’s correlation coefficient, distance being 1 - $r_p$) were tested with similar outcomes.

In order to characterise the growth variation of the provenances we calculated first-order autocorrelation (AR(1)) for each tree using the raw ring-width measurements, and between-tree correlations ($r_p$) within provenances using the detrended RWIs. First-order autocorrelation describes the linkage of current year growth with the previous year’s growth. Autocorrelation can be caused, for example, by resources from the previous year – such as increased leaf area after a summer with favourable conditions – affecting the growth in the following year (Fritts, 1976). The between-tree correlations were computed as the correlations of pairs of trees within a provenance at a site. Thus, it describes how similar the growth variation is between the trees. AR(1) and between-tree correlation were compared between the provenances at each site.

The tree-ring data were divided into groups of northern and southern provenances so that central European provenances formed the southern group and northern European (mainly Finnish) provenances the northern group (Table 2). Pointer year analysis was used to identify years with abrupt common growth reactions within the provenance groups at each site. Based on the raw ring-width measurements, the pointer years were identified using the method by Cropper (1979; see also Neuwirth et al., 2007). The method identifies years in which
majority of trees show abnormal growth compared to the neighboring years. This is done by first calculating Z-scores for each tree within a five-year moving time window:

\[
Z_t = \frac{(x_t - \text{mean}[x_{t-2}, x_{t-1}, x_t, x_{t+1}, x_{t+2}])}{\text{st.dev}[x_{t-2}, x_{t-1}, x_t, x_{t+1}, x_{t+2}]}
\]  

[1]

where \( x_t \) is the ring-width formed in year \( t \). The Z-score shows, using the unit of standard deviation, how much the ring-width differs from the mean of the five-year time window. If over 50% of the trees in a provenance group have \( Z_t \) values higher than one, the year is assigned as a positive pointer year. Similarly, if over 50% of trees show \( Z_t \) values lower than -1 the year is assigned as a negative pointer year. Pointer years are shown starting from year 1950, from which there are at least seven trees included in all the provenance groups at each site (for most groups the number of trees is clearly higher, for more details see S3).

Pearson’s correlation coefficients were calculated between the RWI mean chronologies (for each provenance at each site) and weather variables. In order to find the most important time periods, mean temperature and precipitation sum were calculated for moving time-windows of 15, 21, 31, 41 and 51 days for each site. The start date of the interval was moved forward at the resolution of one day, i.e., every date between day of year (doy) 121 (1 May) of the previous year and doy 204 (28 August) of the current year was used as the median date for the averaging for each window length. The correlations were calculated separately for the A-G (1950-1991) and the B/E datasets (1950-2013).

To quantify and statistically test the effects of the mutually dependent weather variables, a linear model was fit to the mean chronologies. The time periods for weather variables were selected based on the correlation results so that time period with significant correlations with several provenances at several sites were chosen. In the case of summer temperatures the time period with strongest correlations with the RWI mean chronologies varied between the sites. Therefore a longer period of two months was chosen to cover the important time
periods at different sites. To account for non-linear relationships, a log-transformation (natural logarithm) was applied to the weather variables, except for the winter temperature. The same provenances (1, 2, 4, 6, 8, 19 and 24) were used from all sites. In the A-G dataset sites A and F were excluded from the model due to their low number of provenances. Site and provenance were included as fixed categorical variables. Other independent variables were flowering intensity, temperature (winter and summer) and precipitation. Moreover, interaction terms between site and provenance with flowering, temperature variables, and precipitation were added to the model, to allow the responses of independent variables to vary between the sites and provenances. None of the three-variable interactions terms (e.g. site × provenance × precipitation) were significant and, therefore, they were excluded from the model.

The model was formulated as follows:

\[
RWI_{tij} = \beta_0 + \beta_{1i} Site_i + \beta_{2j} Provenance_j
+ \beta_3 Flower_{ti} + \beta_4 \log(T1_{ti}) + \beta_5 \log(P1_{ti}) + \beta_6 T2_{ti}
+ \beta_7i Site_i Flower_{ti} + \beta_8j Provenance_j Flower_{ti}
+ \beta_9i Site_i \log(T1_{ti}) + \beta_{10j} Provenance_j \log(T1_{ti})
+ \beta_{11i} Site_i \log(P1_{ti}) + \beta_{12j} Provenance_j \log(P1_{ti})
+ \beta_{13i} Site_i T2_{ti} + \beta_{14j} Provenance_j T2_{ti}
+ \epsilon_{tij}
\]

where \(RWI_{tij}\) is the ring-width index at year \(t\) (1950 to 1991 for the A-G dataset; 1950 to 2013 for the B/E dataset), site \(i\) (B, C, D, E, G for the A-G dataset; B, E for the B/E dataset), and provenance \(j\) (1, 2, 4, 6, 8, 19, 24). Site and Provenance are dummy variables representing the site and provenance. Flower is the intensity of flowering (0, 1), \(T1\) is June-July mean temperature (°C), \(P1\) is early summer precipitation sum (mm) (doy 165-195), and \(T2\) is mid-winter mean temperature (°C) (doy 16-46). The error term is assumed to follow the normal
distribution $\epsilon_{ij} \sim N(0, \sigma^2)$. Model (Eq. 2) parameters were estimated separately for A-G and B/E datasets.

The statistical analyses were done using the statistical software R except for the calculation of the moving time window correlations, which was performed in the SAS software, version 9.3 (SAS Institute Inc., 2011).
3. Results

The results of the cluster analysis (Fig. 2) showed that the mean chronologies were grouped primarily by the site and secondarily by the provenance. For most sites a separate cluster was formed, and the northern and southern provenances formed sub-clusters within each site. Exceptions from this pattern were sites D and E that did not form site-specific clusters. However, also for these sites the southern provenances were clustered separately from the northern provenances. The division of northern and southern provenances in the cluster analysis was mainly between central European and northern European provenances, and therefore this division was also used for the provenance groups used in the pointer year analysis (Table 2). However, for the sites B and C, located in northern Finland, also some southern Finnish provenances were grouped together with the central European provenances.

The between-tree correlations were in general high, i.e. the trees with the same provenance had similar growth variation (Fig. 3). No clear patterns of provenance differences were detected in the magnitude of the between-tree correlations. However, AR(1) varied between the provenances (Fig. 3). On average, the southern provenances had somewhat lower AR(1), but the differences were not consistent across the sites. For example, no provenance differences in AR(1) were detected at site B and at site G only some southern provenances had low autocorrelations.

In the pointer year analysis differences between the provenance groups were found, for example, in years with cold winters 1956, 1966 and 1985, which were all identified as pointer years only in the southern provenance groups (Fig. 4, S3). Intensive flowering years, such as 1973 and 1989, were identified as negative pointer years both in the southern and northern provenance groups. At all experimental sites with provenances from both groups the total number of pointer years was higher in the southern provenance group than in the northern
provenance group (Fig. 4). This difference is statistically significant when tested with a two-sided Wilcoxon signed rank test ($p=0.036$). The difference between the provenance groups was not statistically significant when looking at the number of negative ($p=0.137$) or positive ($p=0.098$) pointer years separately.

In the correlation analysis the largest provenance differences were found in the correlations between the RWI mean chronologies and the winter and spring temperatures (Fig. 5, S4). For southern provenances these correlations were mostly positive or non-significant whereas for the northern provenances they were negative or non-significant. The provenance differences in the correlations were slightly larger for the four southern sites (D-G) than for the northern sites (B and C). The correlations between RWIs and precipitation were similar between the provenances: negative correlations in spring and, for the southern sites, positive correlations during summer. Only results based on a 31-day time window and the A-G dataset are shown (Fig. 5), as the results for B/E dataset (shown in supplementary material S4) and the other time window lengths were similar.

The results of the linear model (Eq. 2) were similar for the datasets A-G and B/E. Therefore only the results of the latter dataset, containing a longer time series, are shown. The winter temperature was the only independent variable with a significant interaction term with provenance, i.e. the relationship between the RWIs and winter temperature varied between the provenances. The site × winter temperature interaction was also significant in the model, suggesting different responses between the sites (Table 4). These differences were similar as in the correlation analysis: The growth of southern provenances responded positively to warmer winter temperatures in southern Finland. The northern provenances showed only slightly positive response. In northern Finland, the southern provenances showed only a weak response, but the northern ones responded negatively to mild winters (Fig. 6, S5, S6). The
model only accounted for a low proportion of the total variation (adjusted $R^2 = 0.204$ for the B/E dataset).
4. Discussion

In this study, the largest provenance differences were found between the northern European and central European provenances. This reflects the large geographic distances between these provenances and is also in accordance with the genetic division of Norway spruce populations in Europe. After the last ice age central European populations of Norway spruce have dispersed from refugia in European mountain ranges whereas the populations in Scandinavia originate from refugia located in present-day Russia (Lagercrantz & Ryman, 1990; Morgenstern, 1996; Vendramin et al., 2000). However, the cluster analysis results did not fully follow this division. At sites located in northern Finland (B and C) the southern Finnish and the central European provenances were clustered together. This may reflect the clinal variation within the Finnish populations of Norway spruce. Several features, including required conditions of bud set in autumn and growth initiation in spring, show latitudinal variation also among the north European populations of Norway spruce (Aitken & Hannerz 2001). This adaptation to different conditions is perhaps reflected to the growth variation so that the growth variation of southern Finnish provenances in northern Finland resembles more that of the genetically more distant central European provenances.

In the results concerning the climate effects on radial growth, the main provenance differences were found in the correlations between the RWIs and temperatures during winter and spring. In the southern provenances warm winters were associated with larger growth, whereas in the northern provenances the correlations were sometimes even negative, implying negative growth effects of warm winters. This negative growth response to mild winters in northern Europe is in accordance with previous studies (Miina, 2000; Mäkinen et al., 2003; Andreassen, et al. 2006). However, to our knowledge provenance differences in this pattern have not been reported earlier.
Previous studies on Norway spruce have shown provenance differences related to winter and spring physiology that may explain the detected provenance differences in our results. For example, provenances from southern parts of the species range are less adapted to cold temperatures. When grown under similar conditions the southern provenances of Norway spruce have shown a weaker tolerance to frost desiccation (Danusevicius et al., 1999) and a weaker and later induced autumn frost hardiness (Beuker et al., 1998; Westin et al., 2000; Hannerz & Westin, 2005). Earlier studies from the experiments studied here detected more damage in southern provenances after the exceptionally cold winters of 1939-1940 (Heikinheimo, 1949) and 1985 (Hagman, 1986). We also observed signs of growth reduction associated with low winter temperatures. In the pointer year analysis, the three years with the lowest winter temperatures (T2), 1956, 1966 and 1985, all showed negative growth anomalies at several sites for southern provenance groups, but not for northern provenances. In years 1956 and 1985 tree damage due to low winter temperatures has been reported also previously (Raitio, 2000). These two years can be seen in figure 6f as outliers with low winter temperatures and low growth in the Central European provenances (19 and 24), thus evidently affecting the correlations and regression coefficients.

In addition, provenance differences in the timing of spring phenology may attribute to the observed pattern in our results. As an adaptation to a short growing season, the temperature requirements for the spring activation of the northern provenances are lower: they start dehardening (Westin, 2000), bud burst (Beuker et al., 1994b) and radial growth (Kalliokoski et al., 2012) earlier than the southern provenances. Because of this, the northern provenances may be more vulnerable to frost damage if an abrupt temperature decline follows a warm period that has lowered the hardiness level of tree tissues (Aitken & Hannerz, 2001). The increased risk of frost damage due to an untimely activation during warm winters has been suggested to be one reason for negative correlations between winter temperatures and growth.
Southern provenances, which stay in winter dormancy longer, have lower spring frost risk and may instead benefit from warm springs. The differences in spring frost damage risk have been also previously identified as a cause of genotype × environment interactions of Norway spruce in Sweden (Karlsson & Högberg, 1998; Karlsson et al., 2001; Berlin et al. 2015). This effect may become increasingly important with the warmer winter temperatures in future (Hänninen, 1991; Jönsson et al., 2004).

The linear model results showed site-wise differences in the trend between the RWIs and winter temperature. At the sites in northern Finland negative growth responses to warm winters appeared to be more common whereas positive growth responses were found more often in sites located in southern Finland. This might be a result of different winter conditions along the latitudinal gradient. For example, a thicker and more consistent snow cover at northern part of the gradient affects the soil frost conditions (Repo et al., 2011). The risk of spring frost damage has also been shown to be smaller at the latitudes of northern Finland (Jönsson et al., 2004). Although the pointer year analysis and the correlations suggested smaller provenance differences at the northern sites, the differences in the provenance effects between the sites were not significant in the linear model (three-variable interactions not shown).

The main concern related to climate change effects on Norway spruce is the possibility of more frequent and intensive drought events. Provenance differences in drought tolerance could be expected because moisture conditions vary within the species’ distribution area and water availability is a growth limiting factor only in parts of its range (Mäkinen et al., 2002; Mäkinen et al., 2003; Andreassen et al., 2006). This is reflected to correlations between RWI and growing season weather conditions. In moisture limited areas, unlike in the temperature limited regions, RWIs are in general positively correlated with summer precipitation and negatively correlated with summer temperature (e.g. Mäkinen et al., 2003). In our results, no
signs of provenance differences in this respect were detected, as correlation of RWIs with
growing season precipitation and temperature did not differ between the provenances. This
may be partly explained by the conditions of the sites. Our experimental sites are situated
either in the temperature-limited region or in the transitional zone between temperature and
moisture-limited regions, and the data does not include a site with a low water holding
capacity. Therefore, different adaptation to dry conditions might not come up in our results.

Temporal first-order autocorrelation of growth (AR(1)), i.e. how much the growth of the
previous year accounts for the growth of the following year, is often higher in northern
latitudes. This is because trees living in cold conditions are assumed to follow a more
conservative growth strategy (Loehle, 1998). For example, needle life span is longer in
northern areas (Weidman, 1939; Ewers & Schmid, 1981), which reduces the variation in
photosynthetic needle area between years and can therefore reduce abrupt growth differences
between years (Fritts 1976, Speer 2010). In our results the southern provenances indeed had a
somewhat lower AR(1) than the northern provenances. The results imply that the processes
causing autocorrelation in growth are not solely driven by environmental conditions but also
partly by inherited properties. On the other hand, Reich et al. (1996) showed that needle
longevity is mainly a phenotypic response to environmental conditions. Thus, the patterns of
autocorrelation in our results were likely caused by a mixture of genetic and environmental
factors.

The pointer year analysis also supports the higher year-to-year variability of radial growth in
the southern provenance group, as the number of detected growth anomalies was significantly
larger compared to the northern provenance group. Therefore, it seems that in favorable
conditions the southern provenances are able to better increase their growth (positive pointer
years), but they also show more distinct growth reductions during harsh years (negative
pointer years).
The provenance experiments included only one plot per a provenance at each experimental site. Therefore, the risk that variation in growing conditions between the plots may affect the results has to be taken into account. However, the patterns of provenance differences in our results appeared to be consistent between the sites: the main provenance differences in, for example, correlation analysis are found from winter temperatures at all sites. It would be unlikely that variation in the growing conditions between plots would be similar in all sites, which suggests that the observed patterns are in fact caused by actual provenance differences.

We did not have data about seed production at the provenance experiments. Therefore, we assumed the annual variation in flowering intensity to be similar for all provenances. In reality, provenance differences may exist in flowering. For example, Nikkanen and Ruotsalainen (2000) found differences in flowering abundance between Norway spruce clones from northern Finland, although also in their study the most intensive flowering years were common for all clones. Our results did not suggest major differences in flowering, at least in the most intensive flowering years, since in the linear model the interaction of flowering with provenances was not significant.

Information about provenance differences is needed in identifying provenances suitable for future conditions. Currently, in northern Europe, short distance transfers of provenances northward are made to increase productivity (for example, Estonian provenances are used in southern Finland), but transfers too far north lead to higher damage occurrence and mortality (Persson, 1994; Vasiliaskas et al., 2001; Napola, 2014). The predicted effects of climate change in northern Europe are strongest during winter and spring (IPCC, 2014; Mikkonen et al., 2014) and warmer winters may therefore enable the use of southern, more productive provenances at higher latitudes than before. However, since low winter temperatures are predicted to occur also in future, only less frequently (Ruosteenoja et al., 2013), they will still pose a risk to provenances with a low cold tolerance.
5. Conclusions

Our study found provenance differences in radial growth variation of Norway spruce and identified winter and spring temperatures as important climatic variables causing different growth responses between the provenances. The underlying processes behind the observed differences between the provenances are linked to the adaptation of populations to different environments: while the northern provenances are well-adapted to the cold temperatures, the southern provenances are able to more effectively utilize warm conditions. The significance of our results is further emphasized by the predicted change in the winter conditions related to the ongoing climate change. Therefore, acknowledging the intraspecific growth responses to climate becomes increasingly important in adaptation to climate change.
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Supplementary material 1. Mean heights of provenances at the age of 20 years. Data from Heikinheimo 1949. Dashed line at the coring height (130 cm).

Supplementary material 2. Additional information about the seed data: details on the measurement stands and distributions of the seed count data as density plots.

Supplementary material 3. Details of the pointer year analysis for provenance groups: number of trees, number of trees above chosen threshold of $Z$, mean and standard deviation of $Z$.

Supplementary material 4. Correlations between the ring-width chronologies and mean temperature or precipitation sum in moving time windows of 31 days using the B/E dataset (1950-2013).

Supplementary material 5. Model coefficients of the linear model (Eq. 2) based on the dataset B/E (1950-2015).

Supplementary material 6. Model responses to the climate-related independent variables in the linear model (Eq. 2) based on the A-G dataset (1950-1991). The model response lines were calculated by assigning all other variables to their average values in the dataset, while giving the predictor variable a sequence of values through its observed range in the data. The provenances are marked with different colors and line types.
Table 1. Experiment details and the climatic conditions (1981-2010; Pirinen et al., 2012) of the sites.

<table>
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<tr>
<th>Location</th>
<th>A</th>
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<th>D</th>
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*over period 1980-2000
Table 2. The provenances and the sites in which each provenance was included. N and S refer to the northern and southern provenance group, respectively, according to the cluster analysis. See locations of the provenances in Figure 1.

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* included in the B/E dataset
### Table 3.
Mean ring-width (mm), its standard deviation and number of trees cored (in parentheses) for the provenances in each site in the A-G dataset (1950-1991). For the plots that were sampled twice the number of trees is written as trees in 1992 sampling + trees in 2013 sampling.

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<th>C</th>
<th>D</th>
<th>E</th>
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<td>1.70±0.31 (10)</td>
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<td>6</td>
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*The provenances are introduced in Table 2.
Table 4. The analysis of variance (type 3) for the linear model from the B/E dataset (1950-2013) with all explanatory variables and interaction terms.

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<td>Site : Flower</td>
<td>0.028</td>
<td>1</td>
<td>1.365</td>
<td>0.243</td>
</tr>
<tr>
<td>Provenance : Flower</td>
<td>0.105</td>
<td>6</td>
<td>0.857</td>
<td>0.526</td>
</tr>
<tr>
<td>Site : log(T1)</td>
<td>0.003</td>
<td>1</td>
<td>0.129</td>
<td>0.720</td>
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<tr>
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<td>0.062</td>
<td>6</td>
<td>0.511</td>
<td>0.800</td>
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<tr>
<td>Site : log(P1)</td>
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<td>0.801</td>
</tr>
<tr>
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<td>0.876</td>
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<tr>
<td>Site : T2</td>
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<td>&lt; 0.001</td>
</tr>
<tr>
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</tr>
<tr>
<td>Residuals</td>
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<td>856</td>
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</tr>
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</table>

Multiple R-squared 0.239
Adjusted R-squared   0.204

Flower - intensity of flowering
T1 - mean temperature (June-July)
P1 - precipitation sum (doy165-195)
T2 - mean temperature (doy 16-46)
Figure 1. Locations of the experiments and weather stations (a), the provenances (b), and the natural distribution area of Norway spruce (EUFORGEN 2009).

Figure 2. Hierarchical clustering of the chronologies in dataset A-G (1950-1991), using the Euclidean distance and Ward’s minimum variance clustering method. The letter in the chronology name refers to the site (Table 1) and the number to the provenance (Table 2).
Figure 3. Boxplots of between-tree correlation and first-order autocorrelation (AR(1)) for A-G dataset (years 1950-1991). The dashed line shows the division to northern and southern provenance groups. In the boxes, the black horizontal line denotes the median, the upper and lower level of the box show the first and third quartiles, and the vertical lines are the minimum and maximum values within the range of 1.5 times the interquartile distance from the median. Black dots mark outliers. The provenances are presented with the same colors as in figures 5 and 6.
**Figure 4.** Pointer years of the northern (N) and southern (S) provenance group in each site (A-G). The black dots and empty circles represent positive and negative pointer years, respectively. Black vertical bars show the time frame where calculations were done at each site. Total counts of positive and negative pointer years are shown for 1950-1989. For sites B and E counts for the whole time period (1950-2011) are shown in parenthesis.
Figure 5. Correlation coefficients between the RWI mean chronologies and mean temperature (left) and precipitation sum (right) in moving time windows of 31 days using the A-G dataset (1950-1991). The provenances are separated by color and the provenance groups by symbols: southern provenance group is marked with x’s and northern provenance group with circles. The x-axis is the central day the time window used to calculate the climate variables (axis ticks show first day of each month). Gray horizontal lines show significance limit of correlations.
Figure 6. Model (Eq. 2) responses of ring-width indices (RWI) to the temperature and precipitation variables, and the observed ring-width indices in sites B (a-c) and E (d-f). The model response lines were calculated by assigning all other variables to their average values in the dataset, while giving the independent variable in question a sequence of values through its observed range in the data. The provenances are marked with different colors and line types.