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3 **Title**

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

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17 Abstract

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

39 **Keywords:** *Picea abies*, provenance experiment, tree-ring width, cambial growth, increment
40 variation, growth variation

41 1. Introduction

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

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

63 Provenance experiments, in which trees originating from different geographical areas are
64 grown in test sites with different climatic conditions, provide information on how the

65 environment and heredity interact in regulating tree growth (Matyas, 1994; Carter, 1996;
66 Morgenstern, 1996). Tree-ring data from provenance experiments enable the examination of
67 interannual growth variation and its determinants. In provenance studies linking climate and
68 growth variation, focus has recently been on responses to drought events. For example,
69 provenances well adapted to dry conditions have been identified for Scots pine (*Pinus*
70 *sylvestris* L.) and Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Jansen *et al.*, 2012;
71 Eilmann *et al.*, 2013; Taeger *et al.*, 2013).

72 For Norway spruce, previous studies have analyzed the effects of provenance transfers on
73 tree height and volume increment (Beuker, 1994a; Schmidting, 1994; Gömöry *et al.*, 2012;
74 Kapeller *et al.*, 2012). Physiological differences in frost hardiness (Beuker *et al.*, 1998;
75 Westin *et al.*, 2000; Hannertz & Westin, 2005) and the timing of growth cessation (Krutzsch,
76 1992) and bud burst (Beuker, 1994b) have also been found between provenances. Genotypic
77 differences in the factors controlling interannual growth variation of Norway spruce have
78 been examined in a few studies but with inconsistent outcomes. Zubizarreta-Gerendiain *et al.*
79 (2012) found the effect of mean July temperature on ring-width to vary between Finnish
80 clones, whereas Burzyk and Giertych (1991) did not find differences in drought tolerance of
81 Polish provenances and King *et al.* (2013) concluded in their study in the Swiss Alps that
82 different responses to growing season temperature on altitudinal gradient are rather driven by
83 environment than heredity. However, these studies represent limited ranges of provenances
84 and conditions of the study sites. Thus, no clear understanding of intraspecific differences in
85 climate-growth responses of Norway spruce exists.

86 The aim of this study was (i) to investigate the provenance differences in the characteristics
87 of the Norway spruce radial growth variation, (ii) to analyze the provenance differences in
88 the climatic control of radial growth, and (iii) to compare these differences in seven
89 experiments with climatically varying conditions along a latitudinal gradient in Finland. To

90 achieve this, we used a tree-ring dataset from a provenance experiment series established in
91 the 1930s, including provenances from central Europe to the northern distribution limits of
92 the species.

93 2. Materials and methods

94 2.1 Provenance experiments

95 The study material was collected from Norway spruce provenance experiments established in
96 1931 and 1932 at seven sites in Finland. Seedlings from a total of 30 provenances from
97 central Europe to northern Finland (Fig 1.) were planted after being raised at nurseries for
98 five to six years. One plot per provenance was included at each site. The plot size and
99 planting density varied to some extent between the sites (see Table 1 for details). The
100 experimental sites represented different growing conditions: the difference in mean annual
101 temperature between the northernmost (latitude 66°28') and southernmost (60°05') site is c. 6
102 °C (Table 1). The site fertility decreases slightly from fertile soils in the south to relatively
103 fertile soils in the north. For a more detailed description of the sites and experiments see
104 earlier publications by Beuker (1994a, 1996).

105 2.2 Tree-ring data

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

115 On every sample tree, one increment core from the bark to the pith was taken at breast height
116 (1.3 m). The ring-widths were measured using a computer-aided system consisting of an

117 Olympus SZ51 stereo microscope (Olympus Corporation, Tokyo, Japan) connected to a
118 Heidenhein LS 303C transducer (Encoders UK Ltd., Birmingham, UK) with an accuracy of
119 0.01 mm (Table 3). The cross-dating of the ring-width series was done visually and verified
120 using the dplR package (Bunn *et al.*, 2013; cross-dating following Bunn, 2010) of the R
121 software (version 3.0.2, R Core Team, 2013). In each core three innermost rings were
122 removed from the data.

123 Detrending of the ring-width data was carried out in order to remove the long term trends
124 resulting from the effects of tree age and stand dynamics. The individual ring-width series
125 were detrended by fitting a spline function with a 50% frequency cutoff in 30 years, after
126 which the indices were calculated by dividing the ring-widths by the modelled spline curve
127 values (Cook & Peters, 1981; Speer, 2010). The resulting ring-width indices (RWI) represent
128 the year-to-year variability of the ring-widths with the long-term trends removed (Cook &
129 Kairiukstis, 1990). From these indices temporal autocorrelation was removed with first-order
130 autoregressive model (prewhitening). Finally, a mean chronology for each provenance at
131 each site was computed from the detrended and prewhitened RWIs of individual trees as
132 annual averages using Tukey's biweight robust mean. Only years with values from at least
133 three trees were included in the mean chronology, and only the common years of all
134 chronologies were used in the further analysis (1950-1991 for the A-G dataset and 1950-2013
135 for the B/E dataset). The reason for the late start of the time series is in the slow height
136 growth in northern Finland, especially in the case of southern provenances (Heikinheimo,
137 1949, see S1 for details), i.e., it took a longer time to reach the coring height.

138 *2.3 Weather data*

139 Daily weather data (daily mean temperature and precipitation sum) were obtained from the
140 Finnish Meteorological Institute. Weather stations with long measurement series were used in

141 order to cover the whole length of the ring-width chronologies (Fig. 1). In cases of missing
142 data, the gaps were filled using the interpolated 10 km weather data grid (years 1961-2000;
143 Venäläinen *et al.*, 2005). When this was not available, data from the nearest possible weather
144 station or from the next and previous days at the same weather station were used.

145 *2.4 Flowering*

146 Flowering data were included in the analysis to account for growth reductions due to
147 intensive flowering and seed production (Pukkala, 1987; Koenig & Knops, 1998; Selås *et al.*,
148 2002). The intensity of flowering was obtained from Koski and Tallqvist (1978) and more
149 recent data from the Natural Resources Institute Finland (Tatu Hokkanen, unpublished). The
150 data contained seed counts at five stands in different parts of Finland (see S2 for more
151 details). These stands were selected on the grounds of having sufficiently long measurement
152 series. The seed crop measurements started in late 1950s or early 1960s depending on the
153 location. Since seed production of Norway spruce begins approximately at the age of 40
154 (Selås *et al.*, 2002) the growth in the early years was assumed to be unaffected by flowering.

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

161 In northern Finland seed production is infrequent due to the harsh climate (Koski & Tallqvist,
162 1978) and, thus, the number of intensive flowering years remains low. For site B in northern
163 Finland only year 1989 exceeded the threshold of 1200 seeds m⁻², whereas for site E in
164 central Finland seven years were classified as years of intensive flowering.

165 2.5 Statistical analysis

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

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

184 The tree-ring data were divided into groups of northern and southern provenances so that
185 central European provenances formed the southern group and northern European (mainly
186 Finnish) provenances the northern group (Table 2). Pointer year analysis was used to identify
187 years with abrupt common growth reactions within the provenance groups at each site. Based
188 on the raw ring-width measurements, the pointer years were identified using the method by
189 Cropper (1979; see also Neuwirth *et al.*, 2007). The method identifies years in which

190 majority of trees show abnormal growth compared to the neighboring years. This is done by
191 first calculating Z-scores for each tree within a five-year moving time window:

$$192 \quad Z_t = (x_t - \text{mean}[x_{t-2}, x_{t-1}, x_t, x_{t+1}, x_{t+2}]) / \text{st.dev}[x_{t-2}, x_{t-1}, x_t, x_{t+1}, x_{t+2}] \quad [1]$$

193 where x_t is the ring-width formed in year t . The Z-score shows, using the unit of standard
194 deviation, how much the ring-width differs from the mean of the five-year time window. If
195 over 50% of the trees in a provenance group have Z_t values higher than one, the year is
196 assigned as a positive pointer year. Similarly, if over 50% of trees show Z_t values lower than
197 -1 the year is assigned as a negative pointer year. Pointer years are shown starting from year
198 1950, from which there are at least seven trees included in all the provenance groups at each
199 site (for most groups the number of trees is clearly higher, for more details see S3).

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

208 To quantify and statistically test the effects of the mutually dependent weather variables, a
209 linear model was fit to the mean chronologies. The time periods for weather variables were
210 selected based on the correlation results so that time period with significant correlations with
211 several provenances at several sites were chosen. In the case of summer temperatures the
212 time period with strongest correlations with the RWI mean chronologies varied between the
213 sites. Therefore a longer period of two months was chosen to cover the important time

214 periods at different sites. To account for non-linear relationships, a log-transformation
 215 (natural logarithm) was applied to the weather variables, except for the winter temperature.
 216 The same provenances (1, 2, 4, 6, 8, 19 and 24) were used from all sites. In the A-G dataset
 217 sites A and F were excluded from the model due to their low number of provenances. Site
 218 and provenance were included as fixed categorical variables. Other independent variables
 219 were flowering intensity, temperature (winter and summer) and precipitation. Moreover,
 220 interaction terms between site and provenance with flowering, temperature variables, and
 221 precipitation were added to the model, to allow the responses of independent variables to
 222 vary between the sites and provenances. None of the three-variable interactions terms (e.g.
 223 site \times provenance \times precipitation) were significant and, therefore, they were excluded from
 224 the model.

225 The model was formulated as follows:

$$\begin{aligned}
 226 \quad RWI_{tij} = & \beta_0 + \beta_{1i} Site_i + \beta_{2j} Provenance_j & [2] \\
 227 & + \beta_3 Flower_{ti} + \beta_4 \log(TI_{ti}) + \beta_5 \log(PI_{ti}) + \beta_6 T2_{ti} \\
 228 & + \beta_{7i} Site_i Flower_{ti} + \beta_{8j} Provenance_j Flower_{ti} \\
 229 & + \beta_{9i} Site_i \log(TI_{ti}) + \beta_{10j} Provenance_j \log(TI_{ti}) \\
 230 & + \beta_{11i} Site_i \log(PI_{ti}) + \beta_{12j} Provenance_j \log(PI_{ti}) \\
 231 & + \beta_{13i} Site_i T2_{ti} + \beta_{14j} Provenance_j T2_{ti} \\
 232 & + \varepsilon_{tij}
 \end{aligned}$$

233 where RWI_{tij} is the ring-width index at year t (1950 to 1991 for the A-G dataset; 1950 to 2013
 234 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
 235 provenance j (1, 2, 4, 6, 8, 19, 24). *Site* and *Provenance* are dummy variables representing the
 236 site and provenance. *Flower* is the intensity of flowering (0, 1), *TI* is June-July mean
 237 temperature ($^{\circ}\text{C}$), *PI* is early summer precipitation sum (mm) (doy 165-195), and *T2* is mid-
 238 winter mean temperature ($^{\circ}\text{C}$) (doy 16-46). The error term is assumed to follow the normal

239 distribution $\varepsilon_{ij} \sim N(0, \sigma^2)$. Model (Eq. 2) parameters were estimated separately for A-G and
240 B/E datasets.

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

244 3. Results

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

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

262 In the pointer year analysis differences between the provenance groups were found, for
263 example, in years with cold winters 1956, 1966 and 1985, which were all identified as pointer
264 years only in the southern provenance groups (Fig. 4, S3). Intensive flowering years, such as
265 1973 and 1989, were identified as negative pointer years both in the southern and northern
266 provenance groups. At all experimental sites with provenances from both groups the total
267 number of pointer years was higher in the southern provenance group than in the northern

268 provenance group (Fig. 4). This difference is statistically significant when tested with a two-
269 sided Wilcoxon signed rank test ($p=0.036$). The difference between the provenance groups
270 was not statistically significant when looking at the number of negative ($p=0.137$) or positive
271 ($p=0.098$) pointer years separately.

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

282 The results of the linear model (Eq. 2) were similar for the datasets A-G and B/E. Therefore
283 only the results of the latter dataset, containing a longer time series, are shown. The winter
284 temperature was the only independent variable with a significant interaction term with
285 provenance, i.e. the relationship between the RWIs and winter temperature varied between
286 the provenances. The site \times winter temperature interaction was also significant in the model,
287 suggesting different responses between the sites (Table 4). These differences were similar as
288 in the correlation analysis: The growth of southern provenances responded positively to
289 warmer winter temperatures in southern Finland. The northern provenances showed only
290 slightly positive response. In northern Finland, the southern provenances showed only a weak
291 response, but the northern ones responded negatively to mild winters (Fig. 6, S5, S6). The

292 model only accounted for a low proportion of the total variation (adjusted $R^2 = 0.204$ for the
293 B/E dataset).

294 4. Discussion

295 In this study, the largest provenance differences were found between the northern European
296 and central European provenances. This reflects the large geographic distances between these
297 provenances and is also in accordance with the genetic division of Norway spruce
298 populations in Europe. After the last ice age central European populations of Norway spruce
299 have dispersed from refugia in European mountain ranges whereas the populations in
300 Scandinavia originate from refugia located in present-day Russia (Lagercrantz & Ryman,
301 1990; Morgenstern, 1996; Vendramin *et al.*, 2000). However, the cluster analysis results did
302 not fully follow this division. At sites located in northern Finland (B and C) the southern
303 Finnish and the central European provenances were clustered together. This may reflect the
304 clinal variation within the Finnish populations of Norway spruce. Several features, including
305 required conditions of bud set in autumn and growth initiation in spring, show latitudinal
306 variation also among the north European populations of Norway spruce (Aitken & Hannerz
307 2001). This adaptation to different conditions is perhaps reflected to the growth variation so
308 that the growth variation of southern Finnish provenances in northern Finland resembles
309 more that of the genetically more distant central European provenances.

310 In the results concerning the climate effects on radial growth, the main provenance
311 differences were found in the correlations between the RWIs and temperatures during winter
312 and spring. In the southern provenances warm winters were associated with larger growth,
313 whereas in the northern provenances the correlations were sometimes even negative,
314 implying negative growth effects of warm winters. This negative growth response to mild
315 winters in northern Europe is in accordance with previous studies (Miina, 2000; Mäkinen *et*
316 *al.*, 2003; Andreassen, *et al.* 2006). However, to our knowledge provenance differences in
317 this pattern have not been reported earlier.

318 Previous studies on Norway spruce have shown provenance differences related to winter and
319 spring physiology that may explain the detected provenance differences in our results. For
320 example, provenances from southern parts of the species range are less adapted to cold
321 temperatures. When grown under similar conditions the southern provenances of Norway
322 spruce have shown a weaker tolerance to frost desiccation (Danusevicius *et al.*, 1999) and a
323 weaker and later induced autumn frost hardiness (Beuker *et al.*, 1998; Westin *et al.*, 2000;
324 Hannerz & Westin, 2005). Earlier studies from the experiments studied here detected more
325 damage in southern provenances after the exceptionally cold winters of 1939-1940
326 (Heikinheimo, 1949) and 1985 (Hagman, 1986). We also observed signs of growth reduction
327 associated with low winter temperatures. In the pointer year analysis, the three years with the
328 lowest winter temperatures (T2), 1956, 1966 and 1985, all showed negative growth
329 anomalies at several sites for southern provenance groups, but not for northern provenances.
330 In years 1956 and 1985 tree damage due to low winter temperatures has been reported also
331 previously (Raitio, 2000). These two years can be seen in figure 6f as outliers with low winter
332 temperatures and low growth in the Central European provenances (19 and 24), thus
333 evidently affecting the correlations and regression coefficients.

334 In addition, provenance differences in the timing of spring phenology may attribute to the
335 observed pattern in our results. As an adaptation to a short growing season, the temperature
336 requirements for the spring activation of the northern provenances are lower: they start
337 dehardening (Westin, 2000), bud burst (Beuker *et al.*, 1994b) and radial growth (Kalliokoski
338 *et al.*, 2012) earlier than the southern provenances. Because of this, the northern provenances
339 may be more vulnerable to frost damage if an abrupt temperature decline follows a warm
340 period that has lowered the hardiness level of tree tissues (Aitken & Hannerz, 2001). The
341 increased risk of frost damage due to an untimely activation during warm winters has been
342 suggested to be one reason for negative correlations between winter temperatures and growth

343 (Andreassen *et al.*, 2006). Southern provenances, which stay in winter dormancy longer, have
344 lower spring frost risk and may instead benefit from warm springs. The differences in spring
345 frost damage risk have been also previously identified as a cause of genotype \times environment
346 interactions of Norway spruce in Sweden (Karlsson & Högberg, 1998; Karlsson *et al.*, 2001;
347 Berlin *et al.* 2015). This effect may become increasingly important with the warmer winter
348 temperatures in future (Hänninen, 1991; Jönsson *et al.*, 2004).

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

360 The main concern related to climate change effects on Norway spruce is the possibility of
361 more frequent and intensive drought events. Provenance differences in drought tolerance
362 could be expected because moisture conditions vary within the species' distribution area and
363 water availability is a growth limiting factor only in parts of its range (Mäkinen *et al.*, 2002;
364 Mäkinen *et al.*, 2003; Andreassen *et al.*, 2006). This is reflected to correlations between RWI
365 and growing season weather conditions. In moisture limited areas, unlike in the temperature
366 limited regions, RWIs are in general positively correlated with summer precipitation and
367 negatively correlated with summer temperature (e.g. Mäkinen *et al.*, 2003). In our results, no

368 signs of provenance differences in this respect were detected, as correlation of RWIs with
369 growing season precipitation and temperature did not differ between the provenances. This
370 may be partly explained by the conditions of the sites. Our experimental sites are situated
371 either in the temperature-limited region or in the transitional zone between temperature and
372 moisture-limited regions, and the data does not include a site with a low water holding
373 capacity. Therefore, different adaptation to dry conditions might not come up in our results.

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

387 The pointer year analysis also supports the higher year-to-year variability of radial growth in
388 the southern provenance group, as the number of detected growth anomalies was significantly
389 larger compared to the northern provenance group. Therefore, it seems that in favorable
390 conditions the southern provenances are able to better increase their growth (positive pointer
391 years), but they also show more distinct growth reductions during harsh years (negative
392 pointer years).

393 The provenance experiments included only one plot per a provenance at each experimental
394 site. Therefore, the risk that variation in growing conditions between the plots may affect the
395 results has to be taken into account. However, the patterns of provenance differences in our
396 results appeared to be consistent between the sites: the main provenance differences in, for
397 example, correlation analysis are found from winter temperatures at all sites. It would be
398 unlikely that variation in the growing conditions between plots would be similar in all sites,
399 which suggests that the observed patterns are in fact caused by actual provenance differences.

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

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

418 5. Conclusions

419 Our study found provenance differences in radial growth variation of Norway spruce and
420 identified winter and spring temperatures as important climatic variables causing different
421 growth responses between the provenances. The underlying processes behind the observed
422 differences between the provenances are linked to the adaptation of populations to different
423 environments: while the northern provenances are well-adapted to the cold temperatures, the
424 southern provenances are able to more effectively utilize warm conditions. The significance
425 of our results is further emphasized by the predicted change in the winter conditions related
426 to the ongoing climate change. Therefore, acknowledging the intraspecific growth responses
427 to climate becomes increasingly important in adaptation to climate change.

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656 **Supplementary material 1.** Mean heights of provenances at the age of 20 years. Data from
657 Heikinheimo 1949. Dashed line at the coring height (130 cm).

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

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

663 **Supplementary material 4.** Correlations between the ring-width chronologies and mean
664 temperature or precipitation sum in moving time windows of 31 days using the B/E dataset
665 (1950-2013).

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

668 **Supplementary material 6.** Model responses to the climate-related independent variables in
669 the linear model (Eq. 2) based on the A-G dataset (1950-1991). The model response lines
670 were calculated by assigning all other variables to their average values in the dataset, while
671 giving the predictor variable a sequence of values through its observed range in the data. The
672 provenances are marked with different colors and line types.

673

674 **Table 1.** Experiment details and the climatic conditions (1981-2010; Pirinen *et al.*, 2012) of the sites.

	A	B	C	D	E	F	G
Location	Rovaniemi	Rovaniemi	Muhos	Vilppula	Punkaharju	Tuusula	Tenhola
Latitude	66°28'	66°28'	64°52'	62°03'	61°48'	60°21'	60°05'
Longitude	26°39'	26°39'	26°04'	24°23'	29°18'	25°00'	25°00'
Altitude (m)	210	180	70	140	100	50	30
Planting spacing (m)	1.5 x 1.5	2 x 2	1.5 x 1.5	1.5-1.5	1.3 x 1.5	1.4 x 1.5	1.3 x 1.5
Plot size (m ²)	330-700	580-1200	1125-1575	500-855	1091-1568	400	1020-1500
Seedlings per plot	150-400	100-300	400-700	180-300	550-815	170-275	520-750
Planting year	1932	1932	1931	1931	1931	1931	1931
Mean annual temperature	-0.4	-0.4	2.0	3.3	4.2	5.9	5.6
Mean July temperature	14.5	14.6	16.0	16.5	17.6	17.8	17.6
Mean February temperature	-12.7	-12.8	-10.5	-8.5	-7.8	-4.7	-5.4
Mean annual precipitation	527	528	556	643	653	655	686*
Weather station used	Sodankylä	Sodankylä	Kajaani	Jyväskylä	Lappeenranta	Kaisaniemi	Salo/Kärkkä

*over period 1980-2000

676 **Table 2.** The the provenances and the sites in which each provenance was included. N and S
677 refer to the northern and southern provenance group, respectively, according to the cluster
678 analysis. See locations of the provenances in Figure 1.

No.	Country	Provenances				Sites						
		Location	Lat	Lon	Altitude	A	B	C	D	E	F	G
1	Finland	Muonio	67°55'	23°30'	200-300	N	N*	N	N	N*		N
2	Finland	Sodankylä	67°30'	26°30'	200	N	N*	N	N	N*	N	N
3	Finland	Rovaniemi1	66°30'	25°26'	180							N
4	Finland	Rovaniemi2	66°25'	26°30'	250	N	N*	N	N	N*	N	N
5	Finland	Simo	65°44'	25°5'	20							N
6	Finland	Kajaani	64°15'	27°50'	150-200	N	N*	N	N	N*		N
8	Finland	Pieksämäki	62°20'	27°15'	150		N*	N	N	N*	N	N
10	Finland	Elimäki	60°40'	26°30'	40-60		N					N
15	Estonia	Perawald	58°0'	27°30'	30-35							N
19	Germany	Schmiedefeld	50°38'	10°49'	600		S*	S	S	S*		S
21	Germany	Carlsfeld B	50°24'	12°35'	900							S
22	Germany	Carlsfeld C	50°24'	12°35'	900							S
23	Germany	Schilbach	50°24'	12°18'	400-600							S
24	Germany	Bavaria	48°57'	13°25'	750-800		S*	S	S	S*	S	S
26	Hungary	Köszeg	47°20'	16°30'	200-300							S
27	Switzerland	Higher alt.	46°40'	7°45'	1300							S
29	Switzerland	Middle alt.	46°40'	7°45'	800							S

* included in the B/E dataset

679

680 **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
 681 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.

Prov.*	A	B	C	D	E	F	G
1	0.92±0.29 (9)	1.32±0.21 (10+8)	1.70±0.31 (10)	1.85±0.16 (9)	1.96±0.29 (10+8)		1.60±0.32 (9)
2	0.98±0.22 (9)	1.29±0.27 (10+8)	1.90±0.45 (9)	1.70±0.23 (10)	1.75±0.31 (7+8)	1.03±0.19 (9)	1.79±0.38 (8)
3							1.62±0.29 (9)
4	1.02±0.21 (9)	1.33±0.30 (10+8)	1.45±0.43 (9)	1.84±0.29 (10)	2.13±0.47 (10+8)	1.43±0.37 (9)	1.93±0.52 (9)
5							1.60±0.31 (8)
6	1.16±0.17 (10)	1.59±0.33 (10+8)	1.60±0.30 (10)	1.99±0.31 (10)	2.61±0.50 (9+8)		1.85±0.20 (8)
8		1.41±0.23 (10+8)	1.54±0.44 (10)	1.74±0.31 (10)	1.87±0.29 (10+8)	1.52±0.42 (10)	1.82±0.15 (9)
10		1.76±0.21 (8)					1.76±0.15 (9)
15							1.48±0.21 (9)
19		1.56±0.26 (9+8)	2.06±0.53 (10)	2.04±0.36 (10)	2.31±0.49 (10+8)		1.49±0.33 (8)
21							1.70±0.31 (9)
22							1.60±0.24 (9)
23							1.60±0.24 (9)
24		1.78±0.41 (10+8)	1.95±0.44 (10)	2.52±0.27 (9)	2.37±0.39 (10+8)	1.94±0.42 (7)	1.90±0.57 (6)
26							1.73±0.33 (8)
27							1.56±0.25 (9)
29							1.65±0.30 (10)

*The provenances are introduced in Table 2.

682

683 **Table 4.** The analysis of variance (type 3) for the linear model from the B/E dataset (1950-
684 2013) with all explanatory variables and interaction terms.

	Sum Sq	Df	F value	Pr(>F)
Intercept	0.002	1	0.116	0.734
Site	0.015	1	0.733	0.392
Provenance	0.102	6	0.833	0.544
Flower	0.260	1	12.761	< 0.001
log(T1)	0.113	1	5.540	0.019
log(P1)	0.039	1	1.921	0.166
T2	0.038	1	1.886	0.170
Site : Flower	0.028	1	1.365	0.243
Provenance : Flower	0.105	6	0.857	0.526
Site : log(T1)	0.003	1	0.129	0.720
Provenance : log(T1)	0.062	6	0.511	0.800
Site : log(P1)	0.001	1	0.064	0.801
Provenance : log(P1)	0.049	6	0.405	0.876
Site : T2	0.761	1	37.391	< 0.001
Provenance : T2	0.309	6	2.526	0.020
Residuals	17.423	856		
Multiple R-squared	0.239			
Adjusted R-squared	0.204			

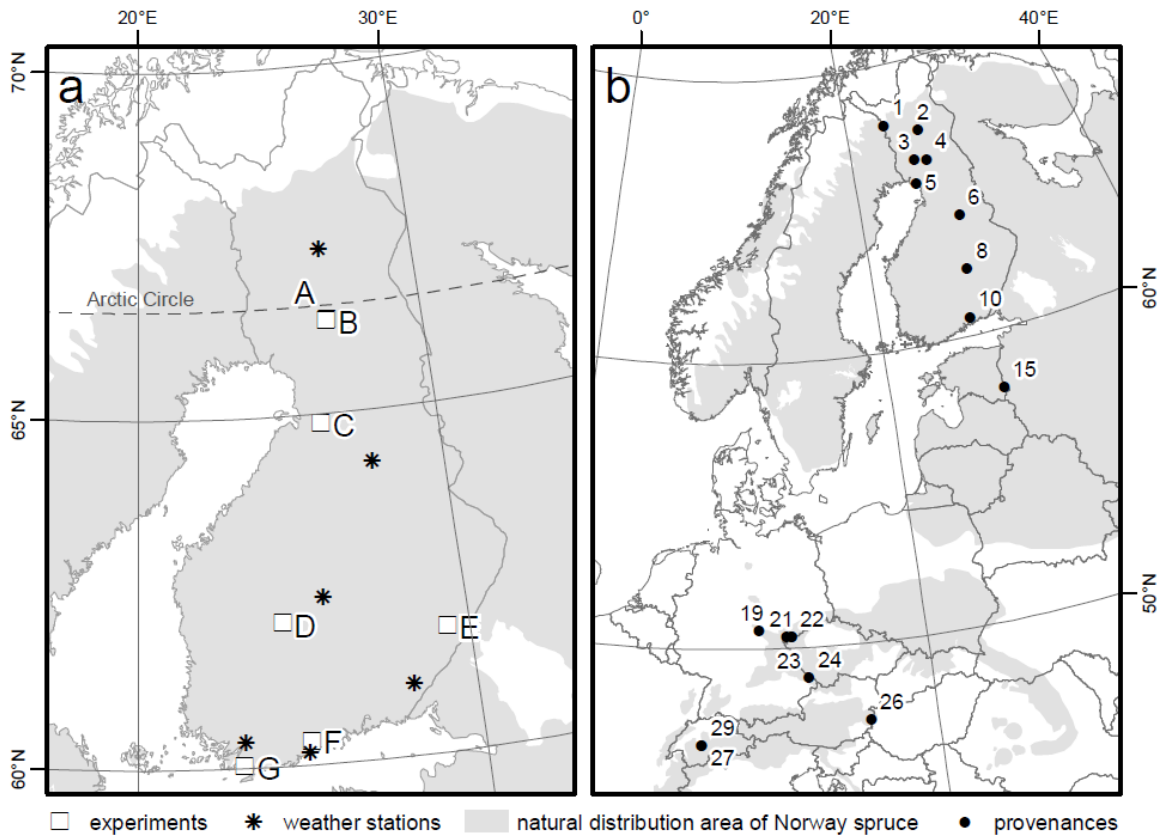
Flower - intensity of flowering

T1 - mean temperature (June-July)

P1 - precipitation sum (doy165-195)

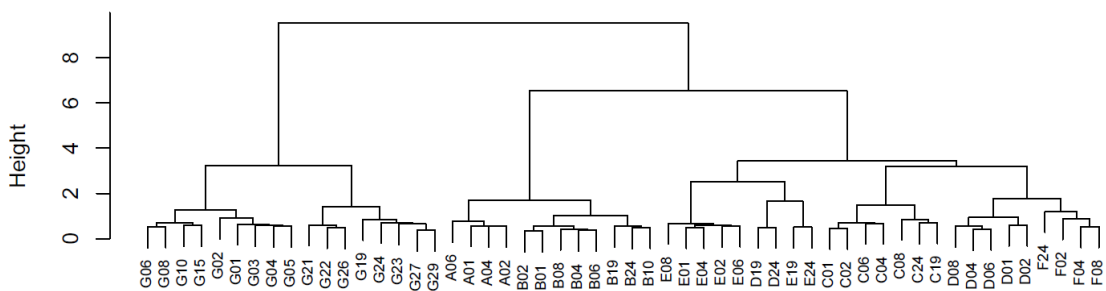
T2 - mean temperature (doy 16-46)

685



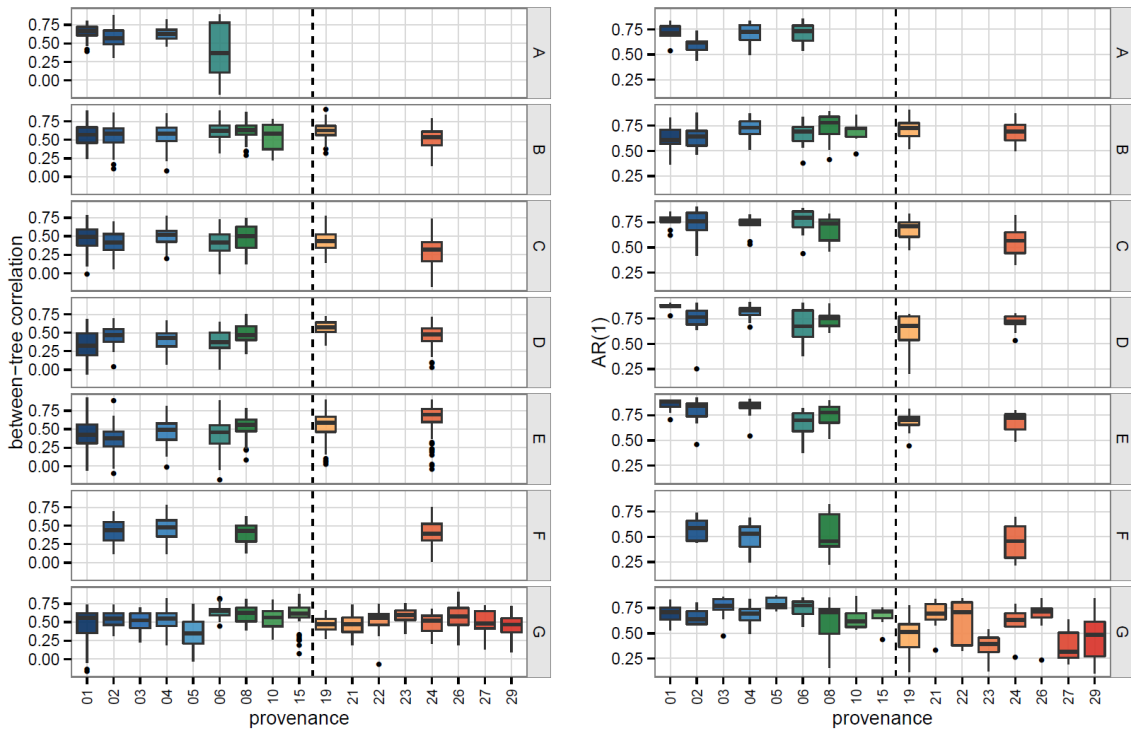
687 **Figure 1.** Locations of the experiments and weather stations (a), the provenances (b), and the
 688 natural distribution area of Norway spruce (EUFORGEN 2009).

689



690

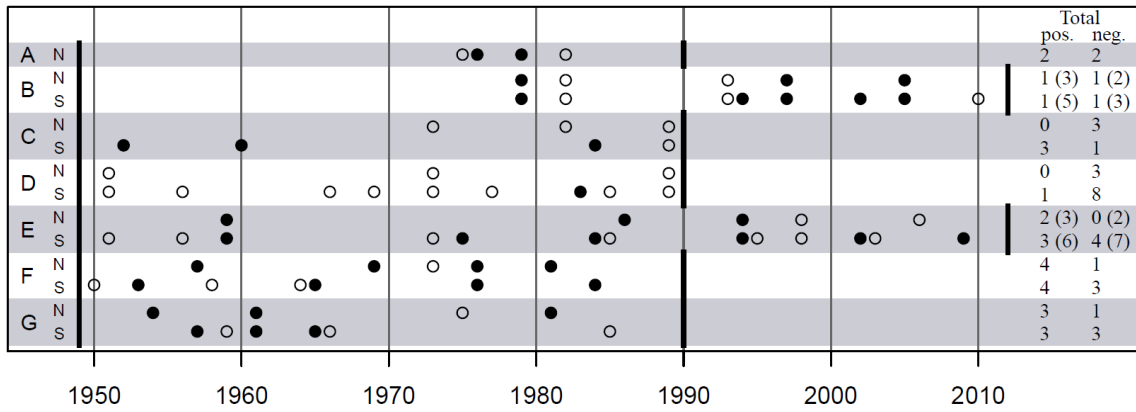
691 **Figure 2.** Hierarchical clustering of the chronologies in dataset A-G (1950-1991), using the
 692 Euclidean distance and Ward's minimum variance clustering method. The letter in the
 693 chronology name refers to the site (Table 1) and the number to the provenance (Table 2)



694

695 **Figure 3.** Boxplots of between-tree correlation and first-order autocorrelation (AR(1)) for A-
 696 G dataset (years 1950-1991). The dashed line shows the division to northern and southern
 697 provenance groups. In the boxes, the black horizontal line denotes the median, the upper and
 698 lower level of the box show the first and third quartiles, and the vertical lines are the
 699 minimum and maximum values within the range of 1.5 times the interquartile distance from
 700 the median. Black dots mark outliers. The provenances are presented with the same colors as
 701 in figures 5 and 6.

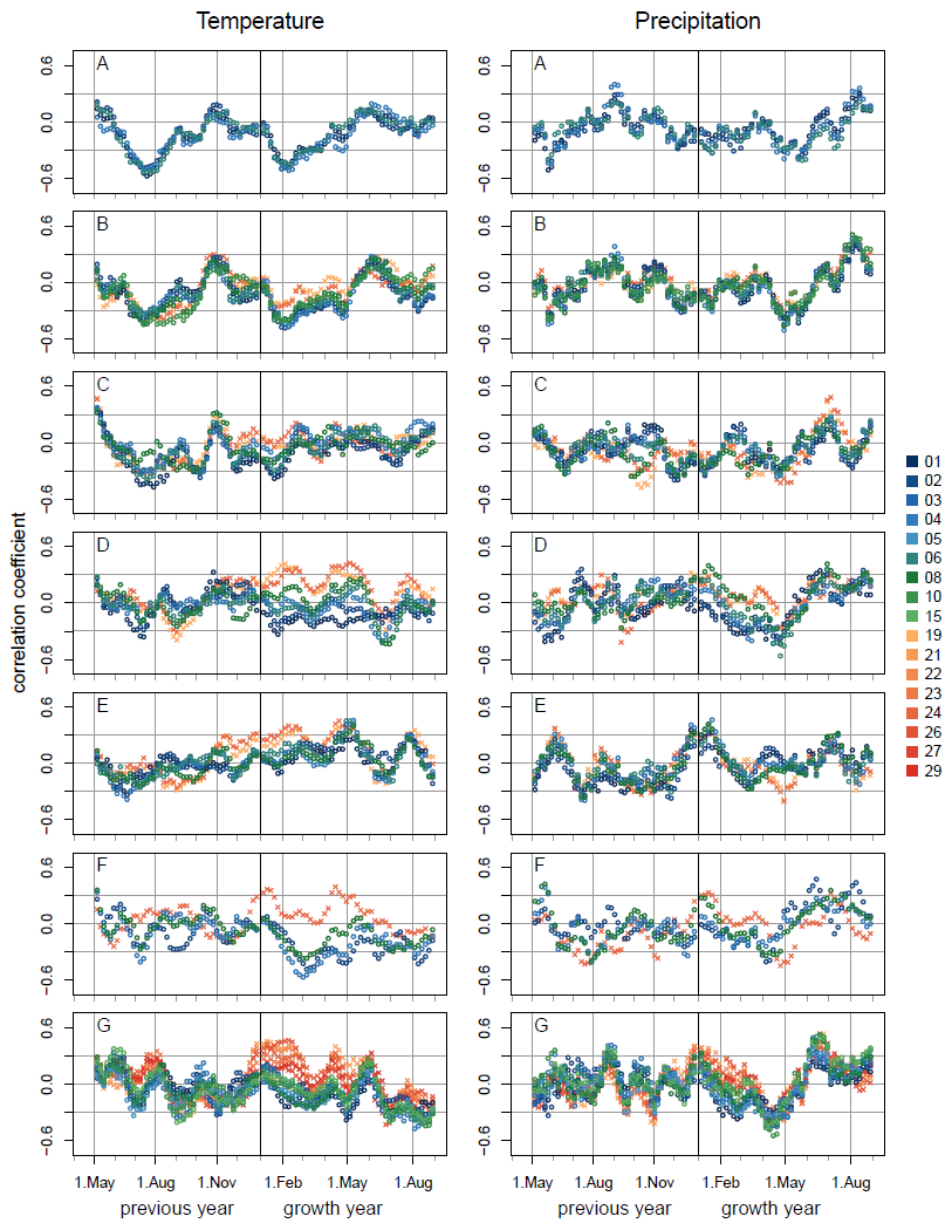
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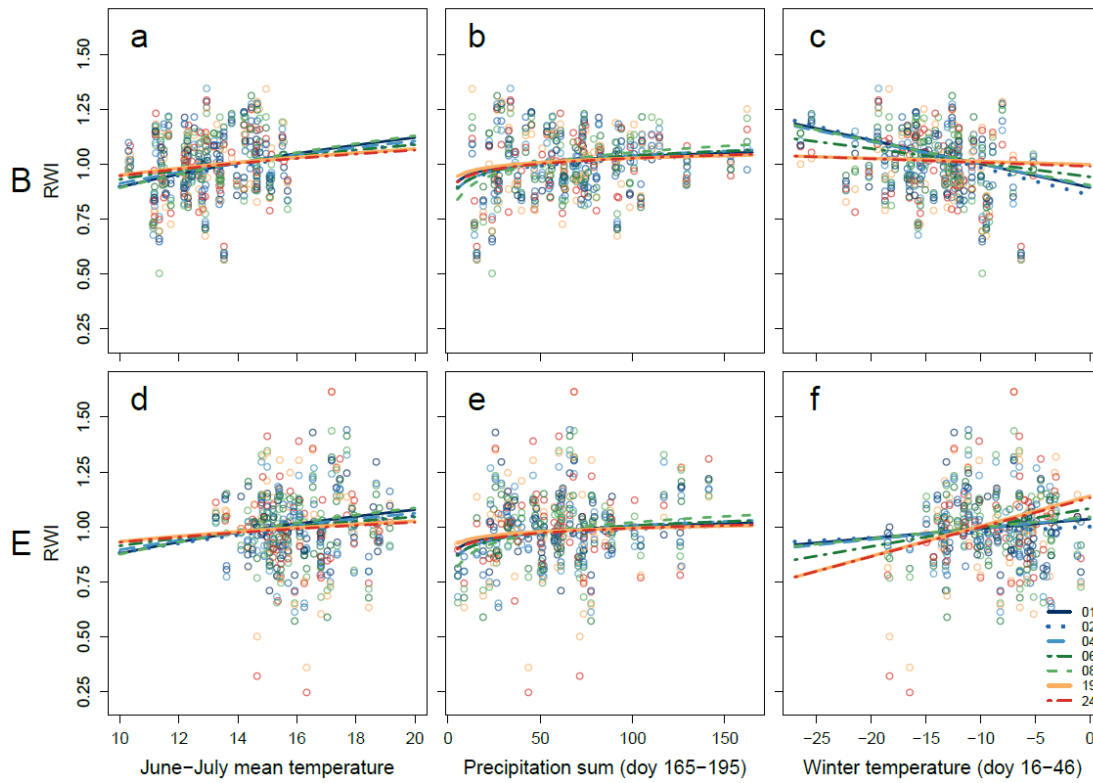
704 **Figure 4.** Pointer years of the northern (N) and southern (S) provenance group in each site
 705 (A-G). The black dots and empty circles represent positive and negative pointer years,
 706 respectively. Black vertical bars show the time frame where calculations were done at each
 707 site. Total counts of positive and negative pointer years are shown for 1950-1989. For sites B
 708 and E counts for the whole time period (1950-2011) are shown in parenthesis.

709



710

711 **Figure 5.** Correlation coefficients between the RWI mean chronologies and mean
 712 temperature (left) and precipitation sum (right) in moving time windows of 31 days using the
 713 A-G dataset (1950-1991). The provenances are separated by color and the provenance groups
 714 by symbols: southern provenance group is marked with x's and northern provenance group
 715 with circles. The x-axis is the central day the time window used to calculate the climate
 716 variables (axis ticks show first day of each month). Gray horizontal lines show significance
 717 limit of correlations.



718

719 **Figure 6.** Model (Eq. 2) responses of ring-width indices (RWI) to the temperature and
 720 precipitation variables, and the observed ring-width indices in sites B (a-c) and E (d-f). The
 721 model response lines were calculated by assigning all other variables to their average values
 722 in the dataset, while giving the independent variable in question a sequence of values through
 723 its observed range in the data. The provenances are marked with different colors and line
 724 types.