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ORIGINAL PAPER

Similar growth responses to climatic variations in Norway spruce (*Picea abies*) and European beech (*Fagus sylvatica*) at the northern range limit of beech

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Abstract

In south-east Norway, in the hemiboreal vegetation zone, beech reaches its northern distribution limit and typically occupies the same type of sites as spruce. Under future climate change, this area is projected to fall within the temperate zone and beech to increase its distribution towards the north at the expense of spruce. However, such forecasts are based on very broad scale estimates and the knowledge of climatic adaptation and the competitive potential of the beech and spruce populations at these latitudes is scarce. Here, we use a dendrochronological approach to study the growth performance of neighbouring spruce and beech trees to climate variability over a period of 70 years. The two species responded quite similarly to variations in climate in the study area. Both showed increased incremental growth in response to high precipitation both in the previous and present year June, indicating that water is a limiting resource. In addition, beech showed a negative response to high temperatures in previous July and August, which is probably connected with growth reductions due to masting. Overall, spruce and beech in the hemiboreal zone show comparable responses to climatic variations as in the temperate zone. Due to the different drought-handling strategies of the two species, we suggest that the intensity of summer droughts and the variability between years are likely factors that would be decisive for which of them that will be more successful under future climatic conditions.

Keywords Tree-rings dendrochronology · Drought · Temperature

Introduction

Climate change is a key driver of species range shifts towards higher latitudes and higher altitudes (Chen et al. 2011; Steinbauer et al. 2018). Inevitably, such range shifts implicate competition among species that stand naïve when exposed to novel and previously unexperienced competitive interactions. The outcome of these interactions is determined by a multitude of abiotic- and biotic factors, and a key question is to what extent different species' growth and performance, and thereby their competitive ability, are being directly impacted by climate change. Here, we take the advantage of a dendrochronological approach to study the growth performance in two coexisting and competing late successional tree species in relation to climate variability over a period of 70 years. In our study area, European beech (*Fagus sylvatica*, hereafter "beech") meets its northern distribution limit, while Norway spruce (*Picea abies*, hereafter "spruce") is within its core area in Fennoscandia (Fig. 1). According to pollen records, both species established there in the 13–1400 s AD (Bjune et al. 2009 and 2013).

Recent projections of future climatic conditions in our study area predict temperature increases around 2.5 °C, increased winter precipitation, but also an increase in days with drought during the growing season (Hanssen-Bauer et al. 2015; Kausrud et al. 2022). In line with this, modelling of the future potential distribution of natural vegetation zones suggests a northward shift of the northern range limits of tree species by 300 to 500 km (Kramer et al. 2010; Saltré et al. 2015) and by the end of the century, our study area is expected to fall within the temperate vegetation zone

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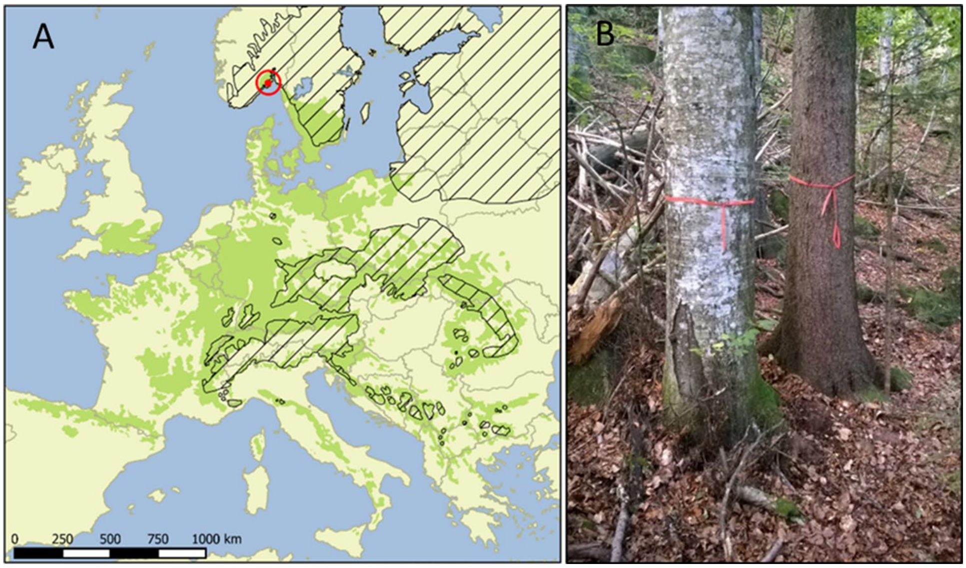


Fig. 1 **a** Natural distribution of European beech *F. sylvatica* (green areas) and Norway spruce *P. abies* (striped areas) in western Europe. The red circle shows the location of the study area at the northern distribution limit for native beech forests in SE Norway. The distribution maps are adopted from the European Forest Genetics Programme http://euforgen.org. **b** pair of *F. sylvatica* (left) and *P. abies* (right)

(Kausrud et al. 2022). Beech is thus expected to increase its future distribution significantly towards the north due to climate warming (Hickler et al. 2012). However, future projections for beech and other trees at their northern range limits are uncertain due to the fact that the climate requirements of trees are highly site- and species-specific (Kramer et al. 2010). There are for instance large variations in dormancy release between provenances (e.g. Basler & Körner 2012) and the length of the wood formation period varies with latitudes (del Castillo et al. 2016). Further, the knowledge of how beech and spruce perform in coexistence under the current climate in northern Europe is scarce.

The growth of beech and spruce in relation to climate is well studied in central Europe, where beech has its core area and spruce is approaching its southern natural distribution limit. Increment growth of both species is negatively affected by drought, both in the growing season and the previous year (Gutiérrez 1988, Biondi 1993, Selås et al. 2002, Lebourgois et al. 2010, Andreassen et al. 2006, Piovesan et al. 2008). The negative correlation between tree growth and previous summer temperatures is often related to the allocation of resources between fruit set and vegetative growth. (Piovesan and Adams 2001, Drobyshev et al 2010; Selås et al. 2002). In a large dataset comparing the radial growth of the two species along a gradient from southern Germany to alpine Austria, Zang et al. (2014) showed that spruce in general is more vulnerable to drought than beech, especially at the warm-dry end of the climate gradient. Under extreme drought years like 1976 or 2003, both species suffered, but spruce showed a stronger growth decrease than beech (Pretzsch 2005; Pretzsch et al. 2014). In alpine areas of Europe (Büntgen et al 2006) and southern Sweden (Grundmann et al. 2011), spruce increment growth has changed lately from showing correlations with early summer precipitation to a larger sensitivity to late summer temperatures. This pattern was not detected in south-eastern Norway (Andreassen et al. 2006). Norway is at the cold–wet end of beech distribution, and it is thus unclear if spruce is more vulnerable to drought in relation to beech in these latitudes. Beech at higher altitudes in Europe responds differently to climatic variation than beech in the lowlands (Dittmar et al. 2003).

Our main aim was to provide insight into the growth of spruce and beech under variations in climate at their northwestern coexistence range limit, using tree-ring data. Such knowledge is a crucial for forecasting future performance under climate change and, as such, also for forest management strategies. Since both species are shown to be drought sensitive in central Europe, we hypothesize that both would be positively influenced by high levels of summer precipitation. Further, since our study area represents the northern distribution limit for beech, we hypothesize that beech should perform better than spruce in warm years.

Materials and methods

Study area

Our study area is located in the southern boreal vegetation zone (Moen 1999) and belongs to the Oslo Rift geological formation in SE Norway (Fig. 1). Here, the forest landscape consists of mixed and monospecific stands of coniferous and broad-leaved deciduous tree species, among which European beech and Norway spruce are most common. Two forest reserves with beech and spruce trees of about 100 years old (Table 2) were selected as study sites: Brånakollane Nature Reserve (N 59.19° E 10.05°, c.200 m a.s.l., 39.2 ha) and Dalaåsen Nature Reserve (N 59.30°, E 10.03°, c. 250 m a.s.l., 97.4 ha). The distance between the two sites is about 10 km, and both are characterized by rugged terrain, rather thin soils, and natural forest stand structures due to low logging activity. See Asplund et al. 2015; Ellingsen et al. 2017; Ohlson et al. 2017 for further information about vegetation conditions and forest disturbance history.

Data collection

Beech and spruce trees were sampled in close pairs to secure that the trees were exposed to similar growing conditions. The distance between trees in pairs did not exceed 8 m. Only dominant or co-dominant trees of comparable size were selected to minimize the influence of tree size-mediated competition (Fig. 1b and Table 2). We sampled 42 tree pairs in Brånakollane, and 39 pairs in Dalaåsen, resulting in a total of 162 sampled trees. All samples were collected during the growing season in 2014.

To test the comparability of the trees in pairs and among pairs, several environmental variables were measured: The stand density surrounding each tree in a pair was measured using a standard relascope ($l=60$ cm, $f=1$; Haglöf AB, Sweden). The diameter at breast height (DBH, 1.3 m above the ground) of each tree was measured with a standard calliper (Haglöf AB, Sweden). For each tree, two samples of the organic soil (excluding the litter layer) were extracted near the trunk, on opposite sides of the tree. The pH value of the standard prepared soil samples was measured with a SenTix 81 pH electrode connected to an inoLab pH 720 benchtop metre (WTW GmbH, Germany).

Tree-ring samples

The trees were cored at breast height with a standard ø 5 mm increment borer (Haglöf AB, Sweden). The samples were stored in labelled paper straws and air-dried for ca. 14 days. The dried samples were mounted on wooden boards and polished with sandpaper. The tree-ring width was 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. Tree-ring series were visually and statistically cross-dated using standard procedures (Stokes & Smiley 1996, Fritts 2001, p. 1–23, Speer 2011, p. 96–109.). The statistical cross-dating was performed using TSAP-Win software (ver. 4.69 h, incl. modules math and graphics; Rinntech e.K., Germany).

Climate data

Monthly mean temperature data were obtained from Færder meteorological station (Stnr.: 27,500; N 59.0272, E 10.5242; 6 m a.s.l.; eklima.met.no) approximately 33 and 43 km from Brånakollane and Dalaåsen, respectively. Precipitation data consisted of the monthly mean values of stations in the area defined by the Norwegian Meteorological institute as "Østlandet" which is a larger part of south-east Norway surrounding the study site. Standardized Precipitation-Evapotranspiration Index (SPEI) was extracted from a global 1-degrees gridded SPEI database (https://spei.csic.es/).

Statistical analyses

Tree-ring series were detrended using a smoothing spline to remove long-term trends related to ageing and disturbances (Cook and Kairiukstis 1990). We used a spline with a 50% frequency cut-off at a frequency equal to two-thirds of each tree-ring series length. This is the default settings for method "spline" in the package dplR in R (Bunn et al. 2020; R core team 2020). Mean autocorrelation was calculated for raw and detrended tree-ring series (Table 1). First-order autocorrelation was identified in the detrended tree rings by visually inspection of PACF plots constructed in R. Standard and residual chronologies for spruce and beech were then constructed using the function "chron" in the package dplR (Bunn et al 2020).

The relationships between the yearly increment of each tree species and climate data were analysed by using the package "treeclim" in R (Zang and Biondi 2015). For each of the three climate variables precipitation, temperature and SPEI, we included monthly values for the previous year's June to October and the current year's April to September. The function "dcc" in "treeclim" is designed to address the problem of many correlated predictors in the analyses. We used the "dcc" function to analyse the relationships between yearly increments (residual and standard chronologies) and monthly climate conditions. Climate growth relationships were

Table 1 Mean first-order autocorrelation (AR1) of the tree-ring series, and mean series intercorrelation

	Beech, raw tree rings	Beech, detrended and standardized tree rings	Spruce, raw tree rings	Spruce, detrended and standardized tree rings
Mean (Std dev) of AR1 (Autoregressive Model of Order 1)	0.57 (0.15)	0.40 (0.11)	0.71 (0.12)	0.51 (0.12)
Mean (Std dev) series intercorrelation	0.56 (0.22)	0.58 (0.22)	0.51 (0.17)	0.53 (0.17)

There were 79 tree-ring series of each tree species. The series were 63 years long (1950–2012)

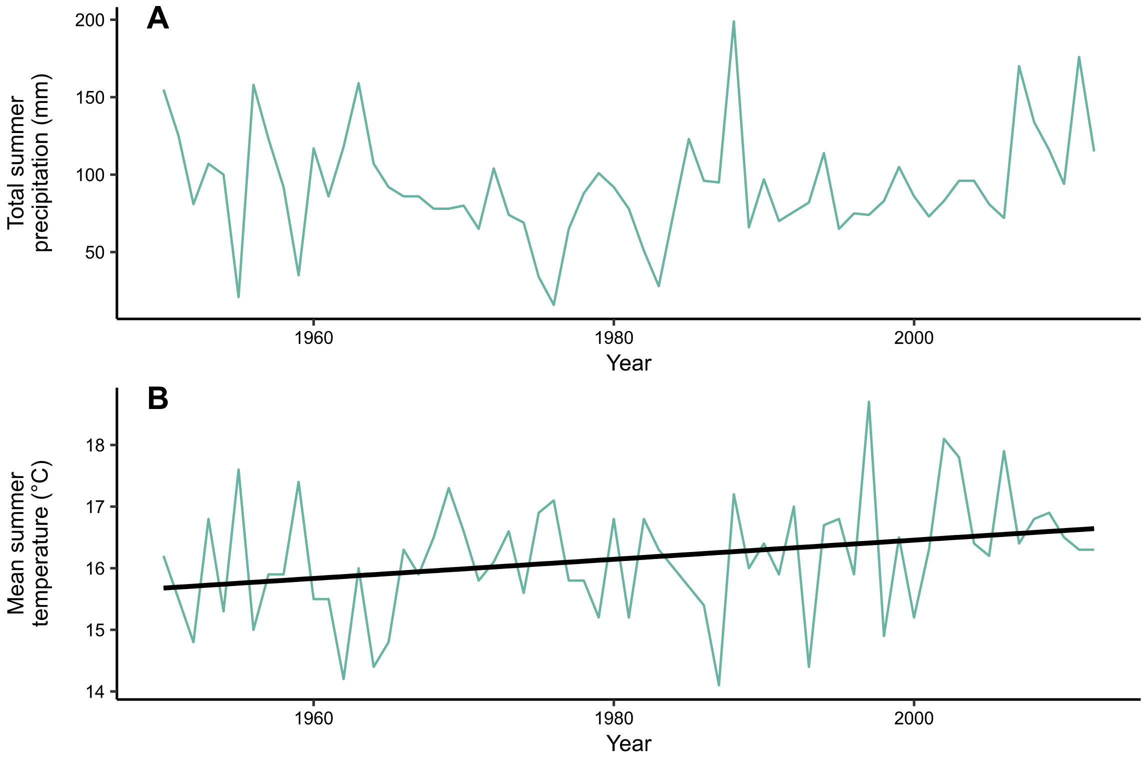


Fig. 2 Variation in **a** total summer precipitation and **b** mean summer temperature from 1950 to 2012

Table 2 Variables (mean ± S.E.) describing the beech–spruce pairs of the sampled trees and the immediate surroundings

Variable	Beech	Spruce	*V* (*P*)
Tree age (years)	108 ± 3.2	109 ± 2.6	1332.5 (0.769)
Diameter at breast height (cm)	**36.9 ± 0.90**	**41.4 ± 0.91**	**509.5 (< 0.001)**
Growth 1950–2012 (mean annual tree ring, 1/100 mm)	**171 ± 5.9**	**155 ± 7.4**	**1932.5 (0.015)**
Tree basal area around sampled trees (m^2 ha^{-1})	28 ± 0.72	28 ± 0.70	-
Soil pH	**4.1 ± 0.38**	**4.0 ± 0.35**	**1861 (< 0.001)**

V and *P* values are derived from Wilcoxon signed rank test. Statistically significant variables in bold

assessed for the period between 1950 and 2012 to avoid possible effects of logging, which took place in the period prior to 1950. The standard and the residual chronologies did not differ in the analyses, and we thus continued with the standard chronology in the climate analyses. We also performed separate analyses on chronologies from the two different study sites, but the results were the same in terms of statistical significance and correlation strength. We thus continued with the analyses based on one chronology for spruce and one for beech encompassing trees from both study sites. Differences in tree age, DBH, growth, tree basal area and soil pH between trees in the sampled pairs were tested with Wilcoxon signed rank test. Trends in summer (June, July and August) precipitation and mean temperature during the study period were analysed with a Mann–Kendall test and decadal change rates were calculating with nonparametric Sen´s slopes using the R package “wql”. We calculated resistance, recovery and resilience sensu Lloret et al. (2011) on raw tree width data of each tree using the R package pointRes with 4 years pre- and post-disturbance. We used linear mixed effects models to test how these indices varied between spruce and beech on the drought years (1955, 1959, 1975, 1976, 1983 and 2006) with tree pair nested within site as random effects. Response variables were natural log-transformed in order to comply with model assumptions of normality and homoscedasticity of residuals.

Results

The 1950 to 2012 mean (± SE) summer (June–August) precipitation and temperature were 278 ± 13 mm and 16.2 ± 0.12 °C, respectively. The driest summer was in 1976 with only 48 mm precipitation, while 1988 was the wettest summer with 597 mm precipitation (Fig. 2a). In our study period, 1997 was the warmest summer, with a mean temperature of 18.7 °C and the 1987 summer was the coldest (14.1 °C; Fig. 2b). Mean summer temperature increased with 0.15 °C per decade during the study period ($S = 398$, $P = 0.018$, Mann–Kendall), while precipitation showed no trend ($S = -29$, $P = 0.868$, Mann–Kendall).

The wilcoxon signed rank test showed that the chosen tree pairs were comparable in terms of tree age (Table 2). Spruce trees were on average larger than beech trees, but there was no difference in tree age. The soil was more acidic below the spruce trees than below the beech trees (Table 2), even though the trees were growing just a few metres apart.

Beech and spruce increment growth were positively influenced by June precipitation and SPEI in the previous year and the growing season. (Figs. 3 and 4). The beech tree-ring width correlated negatively with summer temperatures of July and August of the previous year.

Based on climate data (Fig. 2) and the standardized tree chronologies (Fig. 4), we looked closer at the responses of spruce and beech to six significant drought years, 1955, 1959, 1975, 1976, 1983 and 2006. Beech had a higher recovery (i.e. growth increase after four year relative to the minimum growth during the dry episode) than spruce from the droughts in 1959, 1975, 1976 and 1983, while spruce

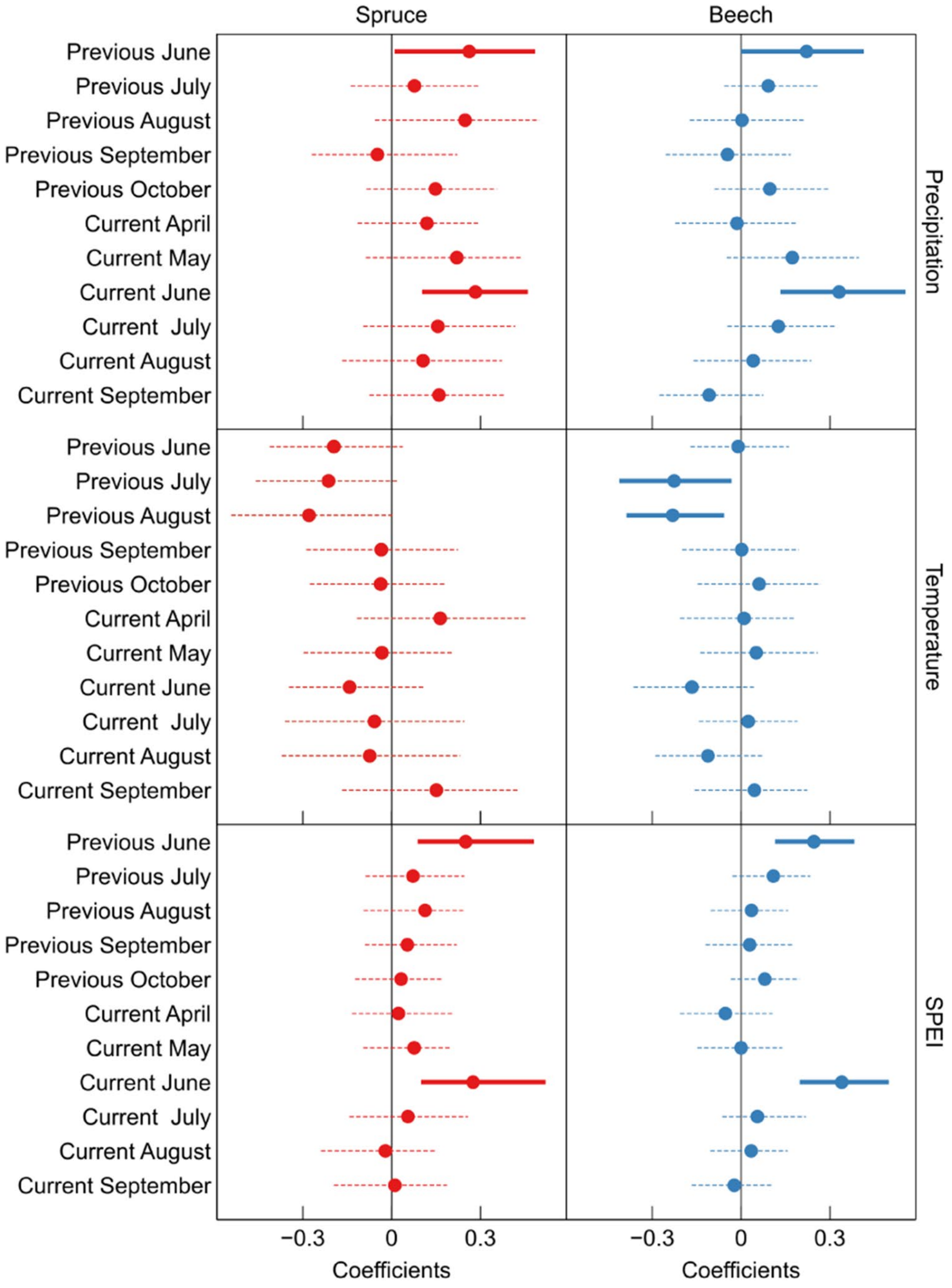


Fig. 3 Climatic variables influencing yearly tree-ring growth of *Fagus sylvatica* and *Picea abies*. Monthly values of total precipitation, mean temperature and the Standardized Precipitation-Evapotranspiration Index (SPEI) for June to October of the previous year and April to September of the current year were included. Thick solid confidence intervals denote significant responses

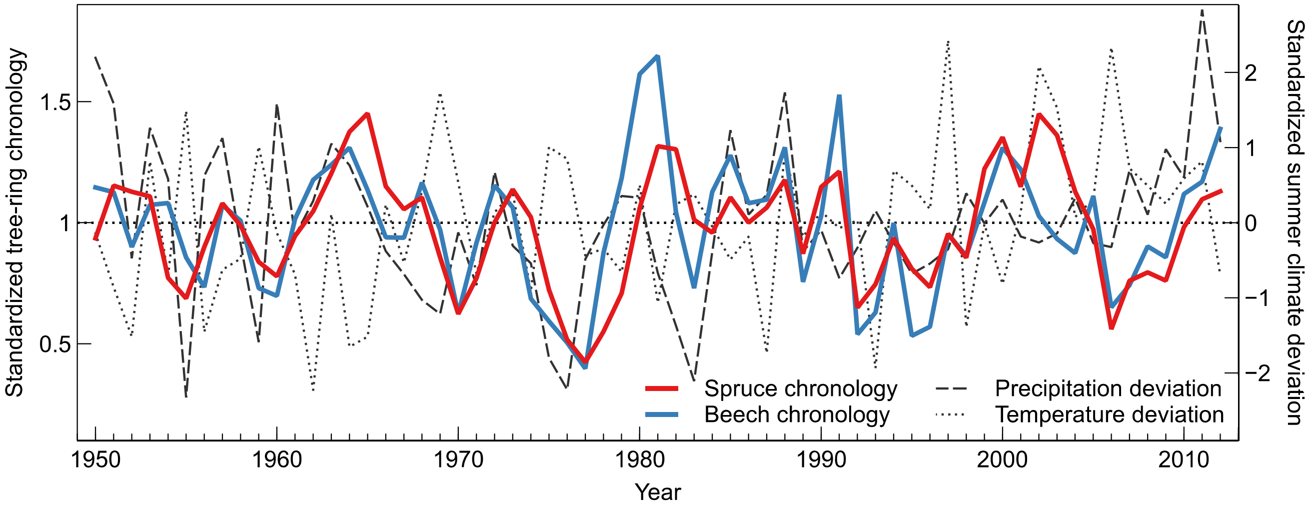


Fig. 4 Standardized tree-ring chronologies and standardized deviation, from the 1960–1991 normal, in summer precipitation and temperature (climate data from eklima.no, summer months: June–August)

had a higher recovery after the 1955 drought (Fig. 5a, Supplementary Table 1). Resistance, defined as growth in the drought year relative to pre-drought (4 years) levels, was higher for beech in 1955 and 2006 but higher for spruce in 1975 and 1983 (Fig. 5b, Supplementary Table 1). Resilience, the capacity to reach pre-drought growth levels (i.e. growth four years prior to the event divided with four years after the event), was higher for beach in 1959, 1975, 1976 and 2006, but slightly higher for spruce in 1983 (Fig. 5c, Supplementary Table 1).

Discussion

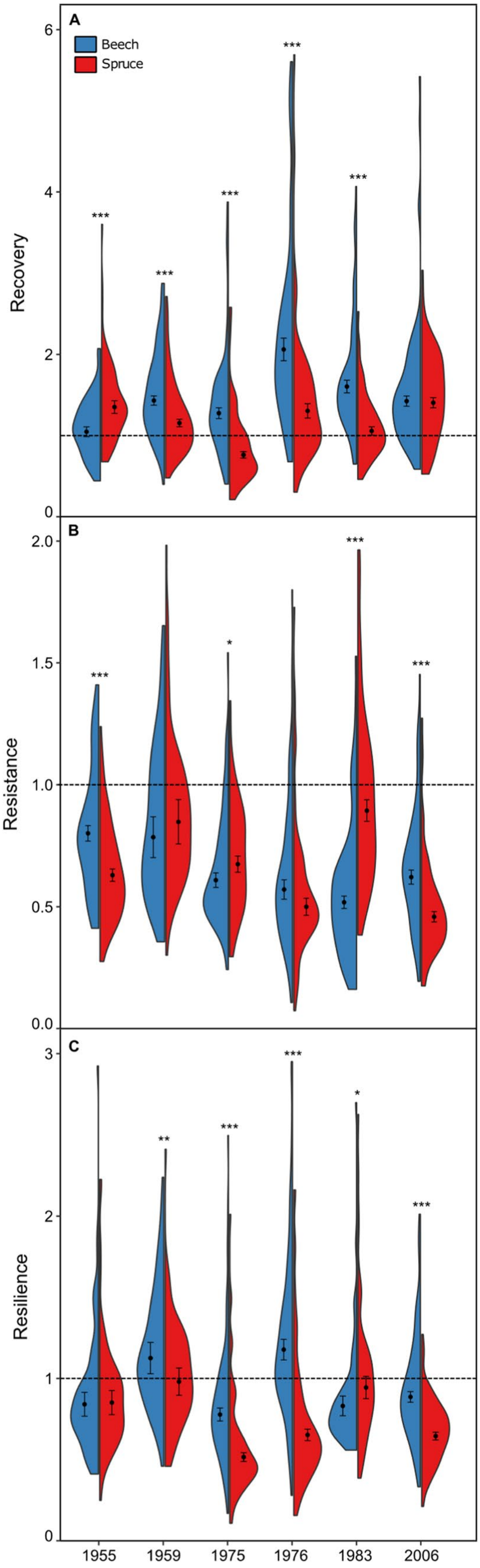
Spruce and beech are both late successional species, with their main distributions in different bioclimatic zones. The growth and interaction between the two have been widely studied in the temperate zone, where beech has its main domain and spruce is its margin. However, we know much less about their performance in areas where beech reaches its northern range limit, like in the hemiboreal zone in southern Norway. This study explores unique data from near-natural forests in this area.

Responses to climatic variations between years may be harbingers of what can be expected under future climatic conditions. Soil moisture influences the water flux through the tree and thereby the carbon assimilation and transport of nutrients (Breda et al. 2006, Backes and Leuschner 2000, Pretzch et al. 2014). Tree growth is thus highly dependent on soil water content, and the positive impact of precipitation on spruce and beech increment is thoroughly documented in central Europe (Lebourgeois et al. 2010, Mund et al. 2010). In line with this, the tree-ring data supported our first hypothesis that high levels of summer precipitation would increase incremental growth. Both species reacted positively to precipitation in June in the present and previous years. Present year June has also been shown to be the most important month in terms of increment growth for both species at higher altitudes in central Europe (Kraus et al. 2016). Further, stored carbohydrates contribute to growth in spring (Skomarkova et al. 2006; Sohn et al. 2012) and thus the climate of the previous season influences the formation of early wood (Rossi et al. 2008).

Overall, the two species seemed to respond quite similarly to variations in climate in the study area, as demonstrated by the rather small and non-consistent species differences in resistance to drought. On the other hand, beech showed higher recovery and resilience to drought than spruce in most of the serious drought years. This is supported by several other dendrochronological studies (Löw et al 2006; Van der Werf et al 2007; Pflug et al 2018). However, Pretzch et al. (2013) found beech to recover slower than spruce from the 1976 drought in southern Germany.

Strategies to cope with drought are known to differ between the species. For example, the isohydric spruce closes its stomata in periods of drought and may risk carbon starvation, whereas the anisohydric species beech keeps its stomata open and may risk xylem embolism (Pretzch et al. 2014). Although beech experiences a risk of hydraulic failure due to cavitation, its gas exchange and photosynthesis remain active under drought conditions (McDowell et al. 2008; Klein 2014). Spruce, on the other hand, is known to be susceptible to insect and fungal attacks after stress episodes like a serious drought (Breda et al. 2006). This is likely a consequence of a weakened defence capacity resulting from

Fig. 5 Violin plots of **a** recovery, **b** resistance and **c** resilience of ▸ beech (blue) and spruce (red) for six drought years. The filled areas represent the distribution of values measured per tree, and the black dots are the estimated marginal means (± SE; back-transformed from the log scale). Dotted lines are at value 1. For recovery this means that growth four years after the event is equal to the growth level during the event. Trees with resistance value 1 grew equally fast during the event as they did four years prior to it. For resilience it means that post-event growth levels equal the pre-event levels. Asterisks denote significant differences between the two tree species at * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.0001$



carbon starvation when photosynthesis stops. Following the drought summers of the seventies there were several summers with large bark beetle populations in Norway that killed many spruce trees (Bakke 1983). Moreover, studies from mixed forests in Germany (Nikolova et al. 2020) showed that also belowground strategies could be part of the explanation for contrasting responses of the two species after a severe drought event: beech produced thin, non-mycorrhizal fine roots enabling effective resource exploitation, while spruce increased root suberization instead of growth.

In the temperate zone, the temperature is thought to be secondary to soil water, as high temperatures mainly increase the negative effects of low levels of soil water (Breda et al. 2006) but have less impact if there is sufficient soil water. However, being in the colder parts of its distribution, we hypothesized that beech would benefit more from warm years than spruce in our study area, similarly to the improved growth of beech found at high elevations in central Europe (Pretzch et al. 2020). In contrast, we found no effects of temperature on increment in the present growing season for either of the species, indicating that temperature is less important when there is enough precipitation, also at higher latitudes. Instead, there was a negative effect of the previous year's July–August temperature on beech tree-ring growth. Beech starts bud set in July and high temperatures in July–August have been related to the allocation of resources to the fruit set (Drobyshev et al. 2010; Müller-Haubold et al. 2013). The negative relationship between late summer temperature and beech increment might thus be related to masting, but unfortunately, there are no records of this from the study area. Spruce also shows masting behaviour, with positive relationships between previous summer temperatures and fruit set (Selås et al. 2002) and negative correlations between seed production and tree-ring growth (Koening and Knops 1998). However, the negative effect of temperature in the previous year on increment growth was barely not statistically significant in our data set. At high altitudes in both Germany and Czech Republic, spruce seems to benefit from high summer temperatures (Obladen et al. 2021; Altman et al. 2017).

In conclusion, precipitation seems to limit the growth of both spruce and beech also at the northern range limit of their coexistence. For forest management, this implies that other species should be chosen where there is a risk of summer drought or thinning from above could be an option in younger stands. Although the two species show the same level of resistance to drought, beech seems to have somewhat higher recovery and resilience, but this varied between drought years. Due to the different strategies of the two species, both above and belowground, the intensity of summer droughts and the variability between years are likely factors that would be decisive for which of them would be more suitable under the climatic conditions expected in the decades to come.

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Author contributions MHL planned and did fieldwork, analysed the data and wrote the manuscript. JA supervised fieldwork, analysed the data and took part in writing the MS. MG planned and did fieldwork, as well as taking part in discussions about the MS. MO participated in planning the study and preparation of the MS. LN planned and did fieldwork and played a major part in preparation of the MS. All authors reviewed the manuscript.

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Declarations

Conflict of interest The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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