

Vulnerability of Norway spruce to climate change in mountain forests of the European Alps

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ABSTRACT: Mountain forests offer a range of socio-economic and ecological services, e.g. providing wood harvest products, serving as hotspots of biodiversity and fulfilling protective functions. In the European Alps, where these environments are dominated by drought-sensitive Norway spruce, it has been questioned whether these services can be secured in the substantially warmer and drier climates predicted for the mid-to-late 21st century. Here, we compile a tree-ring width network of 500 spruce trees from the Northern Limestone Alps to assess growth reactions to drought events and evaluate the long-term impact of the recent temperature shift through analyses along elevational transects. Our dataset covers a larger region in the Northern European Alps extending 250 km from west to east and encompassing an altitudinal range of 1200 m (from 500 to 1700 m a.s.l.). Climate-growth analyses reveal spatially varying drought sensitivities within this spruce network, with elevation (along with associated hydrothermal changes) being the key drivers behind the varying responses. Trees at lower elevations are affected negatively by drought and high temperatures, but at higher altitudes, spruce benefits from warmer climatic conditions. However, despite a sharp temperature increase of ~1°C since the 1990s, we observed neither growth suppression at the lower elevation sites nor growth increase at higher elevation sites. These findings reveal the ability of mountain forests to adapt to an unprecedented temperature shift, suggesting that adaptation to forthcoming climate changes might not require a shift in tree species composition in the Northern Limestone Alps.

KEY WORDS: Drought · Extreme events · Tree-ring width · Dendroecology · Northern European Alps · *Picea abies*

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1. INTRODUCTION

Mountain forests cover over 9 million km² worldwide and compose 23% of the Earth's forest-covered surface (Price et al. 2011). These ecosystems fulfil a multitude of functions because they provide important goods, such as timber and fuelwood, and cultural services such as tourism (Bugmann et al. 2005, Mc

Morran & Price 2011). In addition, they provide ecological services, e.g. as a major terrestrial carbon pool, diversity hot-spots, and provision of fresh water through their function as a component of the fresh water cycle (Björnsen et al. 2005, Bugmann et al. 2005, Lindner et al. 2010). One of the fundamental ecosystem services is a protective function involving the attenuation of soil erosion and protection from

natural hazards (e.g. flooding, debris flow, landslides, rock falls and avalanches) (Schumacher & Bugmann 2006, Lindner et al. 2010). For example, the prime function of 20% of Austrian forests is protection against natural hazards, and in Bavaria (Germany), 63% of the forests are for prevention of soil erosion, and 42% are for protection against avalanches (Duguma & Gratzner 2011).

Mountains are fragile regions, and global change is likely to seriously impact these habitats, including effects on the protective function of mountain forests (Hofer 2005, Lindner et al. 2010). One aspect of global change is the atmospheric nitrogen and sulphur deposition that has been a major factor influencing forest growth over the last decades (Kahle et al. 2008, Elling et al. 2009). However, in recent years, more attention has been focused on the changes in climate. Climate change may exert indirect biotic effects, such as a higher frequency and intensity of insect outbreaks (cf. Esper et al. 2007, Seidl et al. 2008), and abiotic disturbances, such as changes in wind storm frequency and intensity (cf. Lindroth et al. 2009). The direct effects of rising CO₂ concentrations in the atmosphere (Lindner et al. 2010), as well as changes in temperature and precipitation, are likely to have major consequences for mountain forests in the European Alps (Schumacher & Bugmann 2006). In particular, a distinct temperature increase was observed in the Alps (1.2°C in the 20th century), with a pronounced warming in the last 30 yr (Auer et al. 2007), which doubled the global average temperature shift (Lindner et al. 2010). The projected continuing warming, in combination with more frequent and severe drought events, may play an important role in the future development of mountain vegetation (Engler et al. 2011). Anomalous meteorological conditions, such as those during the heat-wave of 2003, may occur more often (Luterbacher et al. 2004, Schär et al. 2004, Rebetez et al. 2006).

Thus, the question of whether mountain forests can adapt to climate change and maintain their protective functions is of pivotal interest. Due to their long lifespans and turnover times, trees and forests are considered to be particularly vulnerable to climate change, and not as readily adaptable as this occurs (Lindner et al. 2010). Water-limited sites with shallow soils on calcareous bedrock are the most sensitive, particularly in the montane elevation belt. Drought stress at such sites is expected to increase, followed by productivity losses and increased susceptibility to disturbances (Seidl et al. 2011). Furthermore, these sites are dominated by Norway spruce *Picea abies* (L.) Karst., a species described as particularly sensi-

tive to summer drought (Oberdorfer 2001, Zang et al. 2011). Norway spruce is the most prominent tree species in the European Alps (Ellenberg 1996), comprising ~60% of the Bavarian mountain forest area (Binder 2007) and ~52% of Austrian protection forest area (Niese 2011). Although it is predominantly indigenous to montane and subalpine forests (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006), spruce has also become the dominant species of the naturally mixed mountain forests in this region through human impact. Its presence there has been supported for centuries because spruce is economically the most important species (Ewald 1997).

Previous studies investigating the growth response of plants to the 2003 heat-wave indicated growth suppressions in montane forests and growth increases in high elevation sites in the Swiss Alps (Jolly et al. 2005). Similar findings were reported from tree-line environments in other regions of the European Alps (Rolland et al. 1998, Paulsen et al. 2000) and North America (Salzer et al. 2009). Savva et al. (2006) also concluded that rising temperatures will likely cause increased growth at high elevation Norway spruce sites in the Tatra Mountains but negative effects at lower elevation sites due to increased drought stress. Moreover, studies with different (i.e. dendroclimatological) approaches exist, which use tree growth as a proxy archive for temperature reconstructions (see Frank et al. 2010 for an overview). Trees from high latitudes and altitudes are used because growth in these environments is sensitive to temperature variations (Frank & Esper 2005). Several studies have, however, detailed a disassociation of mid-20th century tree growth and temperature trends, the so-called 'divergence phenomenon', where tree growth does not parallel the warming trend (D'Arrigo et al. 2008, Esper & Frank 2009 for an overview). Although this phenomenon is especially observed in tree line sites at high northern latitudes (Esper et al. 2010 and citations therein), Büntgen et al. (2008) did not identify unusual late 20th century divergence in the European Alps. Therefore, a growth enhancement at high elevation sites throughout the 20th century warming period is expected.

Common to all of the dendroclimatological studies mentioned above is a primary focus on singular events and/or on the tree growth–climate relationship. There is a lack of ecological interpretation in terms of the adaptability of species to future climate conditions.

In this study, we apply a dendroecological approach to a larger tree-ring width (TRW) network that integrates 500 spruce trees. Spruce is the domi-

nant conifer species, and economically the most important tree species in the Northern Limestone Alps. We hypothesize that spruce responds to increasing drought events and rising temperatures with a growth decline at lower elevations and growth increase at higher altitudes. TRWs were measured and subsequently detrended using different techniques to emphasize variance at lower to higher frequencies. The short-term impact of extreme climatic events is analysed with respect to site elevation. General growth–climate relationships are determined, and lower frequency growth trends are compared with temperature trends during recent decades. These assessments of higher and lower frequency covariance are considered for estimating the robustness of Norway spruce, and thus extrapolating the future vigour of the mountain forests in the Northern Limestone Alps.

2. DATA AND METHODS

2.1. Study design

Five hundred Norway spruce trees (2 cores per tree) were sampled at 50 sites (10 trees per site) in the Northern Limestone Alps. The 1000-series TRW network encompasses the Bavarian and Austrian Limestone Alps reaching from 11°01' to 14°28' E and 47°29' to 47°50' N (Fig. 1, Table 1). The study sites are typically comprised of stands on shallow soils with calcareous bedrock, predominantly on south-exposed slopes. Samples were taken at different altitudes between ~500 and 1700 m above sea level

(a.s.l.), thereby covering a region with a west–east extension of ca. 250 km and an altitudinal gradient of ~1200 m. The dataset was categorized into 4 elevational belts including lower montane (<950 m), montane (950 to 1200 m), altimontane (1200 to 1400 m) and subalpine (>1400 m).

2.2. Climate data

Monthly homogenized temperature and precipitation data representative of each site and elevation belt (see Table 2 for locations and annual means/sums) were obtained from the HISTALP database (Grid mode 2, 5' × 5' grid) (Auer et al. 2007, Böhm et al. 2009).

To identify 'drought events' in a precipitation-rich region like the Alps (see annual precipitation sums in Table 2), a region-specific humidity index was calculated derived from the mean precipitation and temperature of the vegetation period (May to September):

$$\text{Humidity index} = \frac{\text{Precipitation}}{(\text{Temperature} \times 10)} \quad (1)$$

Humidity index values < 1 represent warm and dry 'extreme events', equal to a temperature/precipitation factor of 1:10, similar to the climate diagram scheme by Walter & Lieth (1960–1967) (Fig. 2). Through this, 1947, 1992 and 2003 were identified as the 3 most extreme events in every region and elevation level.

The long-term climatic trends, i.e. mean temperatures and precipitation sums of the vegetation period, are expressed as anomalies with respect to the 1941–1970 mean.

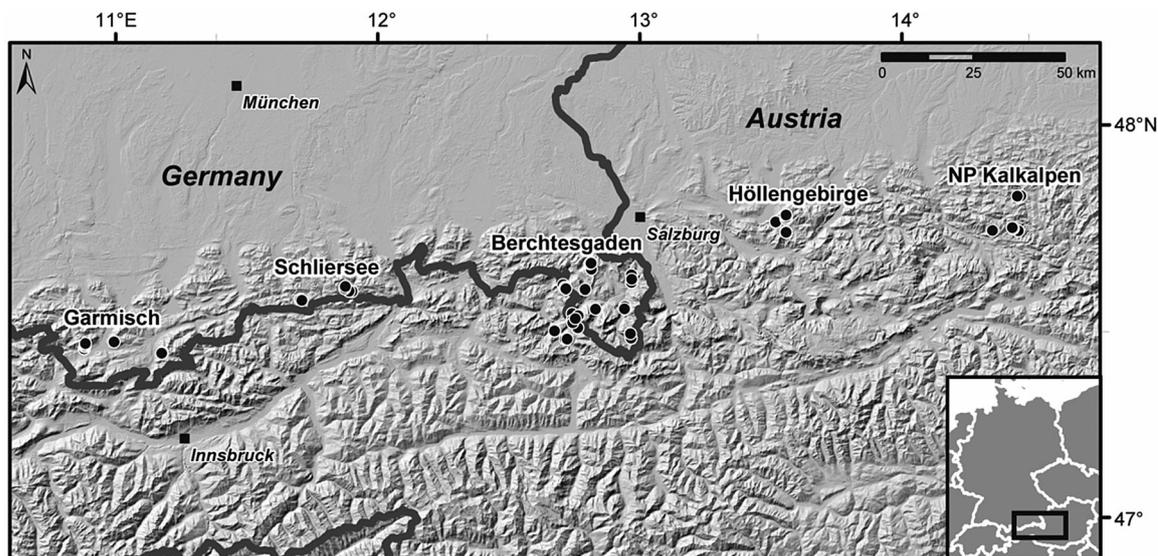


Fig. 1. Location of the 50 spruce sites in the Northern Limestone Alps

Table 1. Characteristics of the 50 spruce sites sorted by elevation within a region and statistics referring to RWI₆₇-chronologies. MSL: mean segment length (yr), AGR: average growth rate (mm), Rbar: inter-series correlation (calculated over 30 yr windows lagged by 15), EPS: expressed population signal (calculated over 30 yr windows lagged by 15), lag-1: first order autocorrelation

No.	Site code	Lat. (N)	Lon. (E)	Elevation (m a.s.l.)	Period	MSL	AGR	Rbar	EPS	Lag-1
Oberammergau										
1	OGLD	47° 29.1'	11° 01.6'	838	1840–2010	146	1.43	0.22	0.84	0.81
2	OGLC	47° 29.4'	11° 01.7'	1020	1823–2007	165	1.12	0.24	0.85	0.79
3	OGLB	47° 29.7'	11° 01.8'	1220	1807–2010	181	1.11	0.28	0.89	0.83
4	TZSZ	47° 28.6'	11° 18.6'	1240	1954–2010	52	2.68	0.37	0.92	0.70
5	TZSB	47° 28.6'	11° 18.5'	1240	1814–2010	183	0.77	0.31	0.89	0.83
6	OGWB	47° 30.2'	11° 08.1'	1280	1804–2010	173	0.64	0.27	0.88	0.83
7	OGLA	47° 29.9'	11° 01.8'	1400	1797–2010	177	1.11	0.32	0.89	0.82
Schliersee										
8	SSHU	47° 37.8'	12° 00.0'	920	1813–2009	177	0.90	0.34	0.91	0.84
9	SLHB	47° 36.6'	11° 48.7'	1060	1851–2010	147	1.25	0.24	0.84	0.83
10	SLHI	47° 36.5'	11° 49.1'	1050	1835–2010	154	1.34	0.35	0.90	0.81
11	SLLS	47° 36.5'	11° 49.1'	1015	1853–2010	148	1.53	0.42	0.93	0.74
12	SSHO	47° 02.7'	11° 15.6'	1110	1825–2009	177	0.83	0.37	0.92	0.72
13	SSAK	47° 38.2'	11° 58.5'	1270	1932–2009	73	1.76	0.43	0.93	0.82
14	SSMS	47° 38.6'	11° 58.6'	1450	1874–2009	127	1.11	0.38	0.90	0.81
Berchtesgaden										
15	NGML	47° 35.0'	12° 59.7'	680	1901–2008	97	1.92	0.43	0.93	0.75
16	TSSW	47° 35.3'	12° 59.7'	690	1934–2008	62	2.95	0.40	0.92	0.68
17	SAGB	47° 31.9'	12° 44.3'	700	1874–2008	104	1.84	0.25	0.78	0.76
18	BGBS	47° 40.0'	13° 01.3'	760	1857–2008	128	1.36	0.24	0.85	0.81
19	BGOB	47° 38.9'	13° 01.2'	770	1880–2008	115	1.63	0.31	0.89	0.78
20	BGAA	47° 38.7'	12° 46.3'	920	1879–2010	126	1.26	0.45	0.94	0.79
21	NGEW	47° 34.4'	12° 48.2'	960	1870–2008	125	1.64	0.27	0.84	0.80
22	BGOA	47° 39.4'	13° 01.3'	1020	1882–2008	117	1.67	0.33	0.90	0.77
23	BGGP	47° 37.9'	12° 51.1'	1040	1885–2008	111	1.83	0.26	0.84	0.71
24	BGPA	47° 40.9'	12° 52.5'	1040	1926–2010	83	2.34	0.35	0.91	0.70
25	SAMA	47° 30.6'	12° 46.7'	1080	1879–2008	100	1.89	0.34	0.86	0.82
26	NGLS	47° 30.7'	13° 01.0'	1220	1820–2008	171	1.30	0.40	0.93	0.81
27	BGAB	47° 38.2'	12° 46.7'	1220	1761–2010	215	0.96	0.47	0.95	0.88
28	SAMG	47° 30.6'	12° 47.0'	1250	1871–2008	125	1.73	0.37	0.91	0.74
29	NGMW	47° 33.4'	12° 48.2'	1310	1794–2008	191	1.04	0.38	0.92	0.80
30	NGMK	47° 35.0'	12° 53.3'	1330	1849–2008	139	1.70	0.31	0.90	0.76
31	BGPB	47° 41.7'	12° 52.2'	1330	1815–2010	181	1.03	0.37	0.92	0.79
32	BGAC	47° 38.1'	12° 46.9'	1420	1781–2010	193	1.20	0.43	0.93	0.84
33	BGPC	47° 41.8'	12° 52.5'	1520	1830–2010	166	1.19	0.50	0.95	0.84
34	SAKK	47° 32.3'	12° 49.4'	1530	1851–2008	142	1.38	0.41	0.92	0.78
35	NGMA	47° 33.1'	12° 48.3'	1560	1879–2008	100	2.20	0.30	0.84	0.69
36	NGSB	47° 34.1'	12° 49.5'	1600	1684–2008	265	0.87	0.36	0.91	0.79
37	NGHS	47° 33.7'	12° 48.9'	1620	1848–2008	138	1.48	0.42	0.92	0.71
38	NGKS	47° 31.3'	13° 00.9'	1670	1836–2008	159	1.50	0.48	0.94	0.78
Höllengebirge										
39	MWSE	47° 47.5'	13° 33.1'	527	1826–2010	173	0.99	0.37	0.92	0.79
40	MWSD	47° 48.0'	13° 35.3'	791	1771–2010	212	0.88	0.38	0.92	0.79
41	MWSC	47° 48.1'	13° 35.5'	978	1770–2010	218	0.97	0.36	0.91	0.79
42	MWSB	47° 48.5'	13° 35.5'	1209	1782–2010	214	1.10	0.42	0.93	0.83
43	MWSA	47° 48.6'	13° 35.4'	1337	1797–2010	197	0.84	0.41	0.93	0.73
NP Kalkalpen										
44	NKZS	47° 50.3'	14° 26.7'	876	1781–2010	211	1.13	0.48	0.94	0.76
45	NKZP	47° 50.4'	14° 27.1'	894	1917–2010	88	2.03	0.29	0.89	0.68
46	NKZN	47° 50.4'	14° 26.3'	901	1838–2010	116	1.70	0.28	0.86	0.82
47	NKRB	47° 45.4'	14° 20.6'	950	1827–2009	162	1.17	0.37	0.92	0.79
48	NKSK	47° 45.2'	14° 26.3'	1150	1792–2009	188	0.98	0.38	0.92	0.84
49	NKGU	47° 45.6'	14° 25.2'	1350	1868–2009	124	1.53	0.36	0.91	0.87
50	NKGO	47° 45.7'	14° 25.0'	1460	1858–2009	146	1.29	0.43	0.94	0.84

Table 2. Annual temperature and precipitation from the gridded HISTALP dataset representative of regions and elevation belts in the study area from 1941 to 1970

Elevation belt	Lat. (N)	Lon. (E)	Temp. (°C)	Precip. (mm)
Oberammergau				
<950 m	47° 30.0'	11° 05.0'	7.2	1455
950–1200 m	47° 25.0'	10° 55.0'	5.9	1406
1200–1400 m	47° 30.0'	11° 10.0'	4.1	1468
>1400 m	47° 30.0'	10° 55.0'	1.7	1452
Schliersee				
<950 m	47° 45.0'	11° 55.0'	6.5	1494
950–1200 m	47° 45.0'	12° 00.0'	6.6	1425
1200–1400 m	47° 40.0'	12° 00.0'	6.7	1474
>1400 m	47° 40.0'	11° 55.0'	3.7	1542
Berchtesgaden				
<950 m	47° 35.0'	13° 00.0'	7.2	1703
950–1200 m	47° 35.0'	12° 50.0'	6.3	1739
1200–1400 m	47° 35.0'	12° 55.0'	6.5	1735
>1400 m	47° 35.0'	12° 45.0'	5.4	1750
Höllengebirge				
<950 m	47° 50.0'	13° 35.0'	6.7	1543
950–1200 m	47° 45.0'	13° 45.0'	5.0	1850
1200–1400 m	47° 40.0'	13° 40.0'	5.4	1759
>1400 m	47° 40.0'	13° 30.0'	4.2	1672
NP Kalkalpen				
<950 m	47° 50.0'	14° 30.0'	6.3	1458
950–1200 m	47° 45.0'	14° 35.0'	5.4	1497
1200–1400 m	47° 45.0'	14° 25.0'	4.8	1495
>1400 m	47° 40.0'	14° 25.0'	4.7	1451

2.3. Tree-ring data

TRW was measured with a LINTAB 6 (RINNTECH, Heidelberg) system and TSAP-Win Scientific software (Rinn 2003). The TRW series were cross-dated visually and confirmed statistically using the software COFECHA (Holmes 1983). For further analyses, non-climatic trends related to age and size trends, stand dynamics and internal and external disturbances were removed from the raw ring widths (Fritts 1976). Ring width indices (RWI) were obtained using 3 different detrending techniques: (1) A cubic smoothing spline with a frequency cut-off of 50% at 67 yr (RWI_{67}) to preserve inter-annual and multi-decadal scale variability, (2) a stiffer spline with a frequency cut-off of 50% at 300 yr (RWI_{300}) to preserve centennial scale variability (Cook & Peters 1981), and (3) regional curve standardization (RCS) to retain potential multi-centennial variance in the resulting chronologies (RWI_{RCS}). RCS was applied on a site-by-site basis and considering the pith offset of each sample (see Esper et al. 2003 for details).

The site chronologies were obtained by averaging the detrended single series using a robust mean (Mosteller & Tukey 1977). Chronologies were corrected for lag-1 autocorrelation and truncated at a minimum sample replication of 5 series. Standard parameters, such as the inter-series correlation (R_{bar}) and expressed population signal (EPS), were calculated for RWI_{67} using 30 yr windows, lagged by 15 yr, over the common 1900–2004 period (shorter period for 6 sites, see Table 1) to estimate the internal

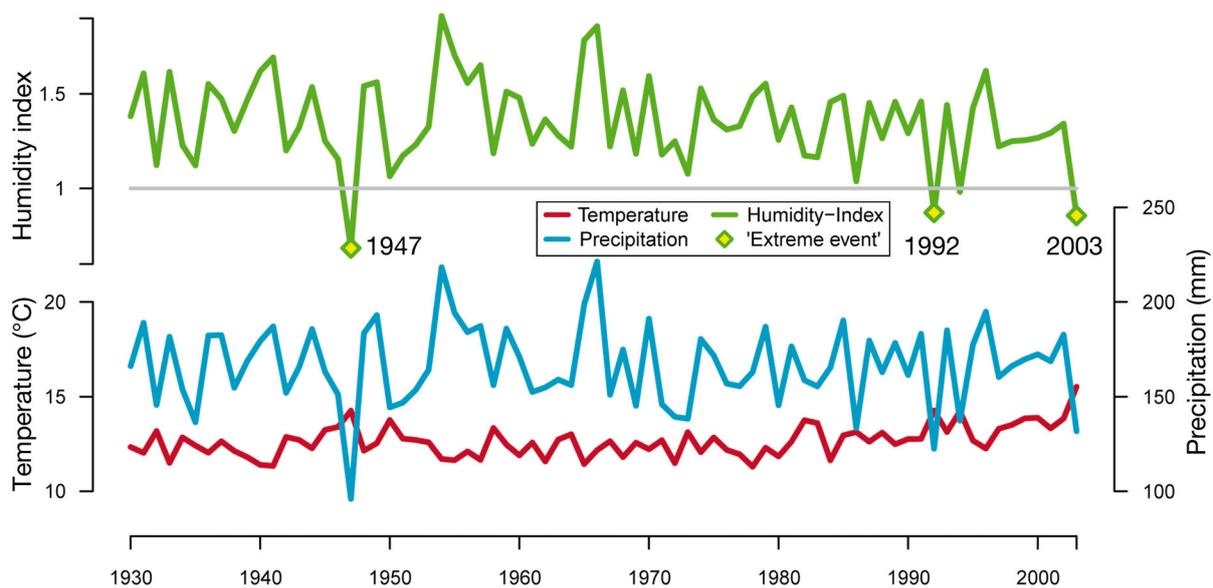


Fig. 2. Vegetation period (May to September) temperature, precipitation and humidity index averaged for the entire study

coherence of the site chronologies (Table 1) (Wigley et al. 1984). Furthermore, the mean segment length (MSL, i.e. an estimate of mean tree age within 1 chronology), average growth rate and lag-1 autocorrelation (raw ring widths) are presented in Table 1 for the different sites.

2.4. Statistical analyses

The short-term impact of relative drought events on the radial growth of Norway spruce was analysed by calculating the percentage growth reaction. Here, the RWI_{67} data were used, because the inter-annual variability was the primary interest when calibrating against the humidity index. The growth in warm and dry years was related to the average growth of the 5 previous years:

$$\text{Growth Reaction} = \left(\frac{1}{3} \sum_k \frac{RWI_{67k}}{\frac{1}{5} \sum_j^5 RWI_{67k-j}} - 1 \right) \cdot 100; \quad (2)$$

with $k = 1947, 1992, 2003$

The growth reaction was calculated for each individual series and then summarized at the site level.

To investigate the influence of climate elements on tree growth, Pearson's correlation coefficients (r) were computed between the RWI_{67} site chronologies and the mean temperatures and precipitation sums of the vegetation period over the common 1900–2003 period (shorter for 6 sites, see Table 1). The relationship between elevation and growth/climate response was represented by a generalized additive model (GAM) using a penalized thin plate regression spline as the spline base (Wood 2006).

To study the response of Norway spruce to 20th century climate trends, particularly the long-term increase in temperature, we calculated the relative growth change of each individual series to a reference period (1941 to 1970) for every tree-ring in the year i and each detrending procedure separately as follows:

$$\text{Growth Change}_i = \left(\frac{RWI_i}{\frac{1}{30} \sum_{j=1}^{30} RWI_{m+j}} - 1 \right) \cdot 100; \text{ with } m = 1940 \quad (3)$$

The results of the individual series were combined for each site and elevation belt using a robust mean.

Associations between climate and growth change were assessed using moving 31 yr correlations calculated between the elevational belt growth change

curves and temperature, precipitation and humidity index anomalies. All statistical procedures were performed using R 3.0.1 (R Development Core Team 2013) and the packages `dplR` (Bunn et al. 2012) and `mgcv` (Wood 2006).

3. RESULTS

3.1. Long-term climatic trends

Vegetation period climate data reveal a long-term temperature increase but no clear change in precipitation compared to the 1941–1970 reference period (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/c060p119_supp.pdf). The average temperature rise is similar across the study region, i.e. since the 1990s, temperatures are 0.97 to 1.08°C higher than the 1941–1970 reference period. Some precipitation differences were observed between the sub-regions, the western section indicating increased (+13 to 31 mm) and eastern section decreased (–52 mm) vegetation period rainfall since the 1990s.

3.2. Chronology characteristics

The EPS values exceed the widely accepted threshold of 0.85 (Wigley et al. 1984), indicating sufficient internal signal strength in most sites (except for Site 17). EPS reaches 0.84 in Sites 1, 9, 21, 23 and 35 (Table 1). R_{bar} values range from 0.22 (Site 1) to 0.50 (Site 33), indicating substantially changing internal coherences among the chronologies. Lag-1 autocorrelation fluctuates between 0.68 (Sites 16 and 45) and 0.88 (Site 27), and the average growth rate varies between 0.64 mm (Site 6) and 2.95 mm (Site 16) (Table 1). Ring widths over the common first 60 yr of the tree's lifespan do not significantly decrease with elevation, but growth rates over the entire chronology lengths correlate with the MSL ($r^2 = 0.75$, $p < 0.001$), indicating that distinct age trends are inherent to the data (see Fig. S2 in the Supplement).

3.3. Short-term impact of drought events

The impact of relative drought events on tree growth resulted in distinct growth reductions at 43 of 50 sites (Fig. 3). The strongest decline was recorded at low-elevation Site 16 in the Berchtesgaden region, with 42.6% less growth compared to the 5 yr preceding the drought event. Nine sites exhibited an in-

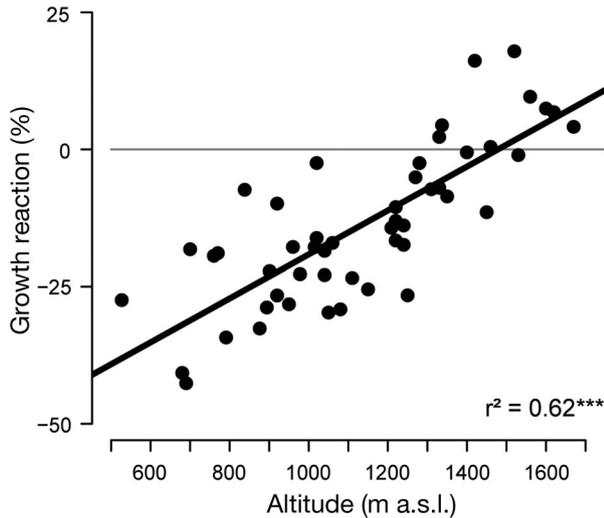


Fig. 3. Relationship between altitude and the percentage growth reaction of spruce to drought events (** $p < 0.001$)

crease in growth. The strongest increase of 17.9% was detected at a high elevation Site 33 in the Berchtesgaden region. The subalpine sites at 1400 m and higher predominantly displayed growth releases during warm and dry years. In contrast, all sites below 1300 m a.s.l. showed a growth decline, so that overall a significant association between growth decline and elevation in warm and dry years was observed that can be approximated by a linear regression model explaining 62% ($p < 0.001$) of the variance (Fig. 3).

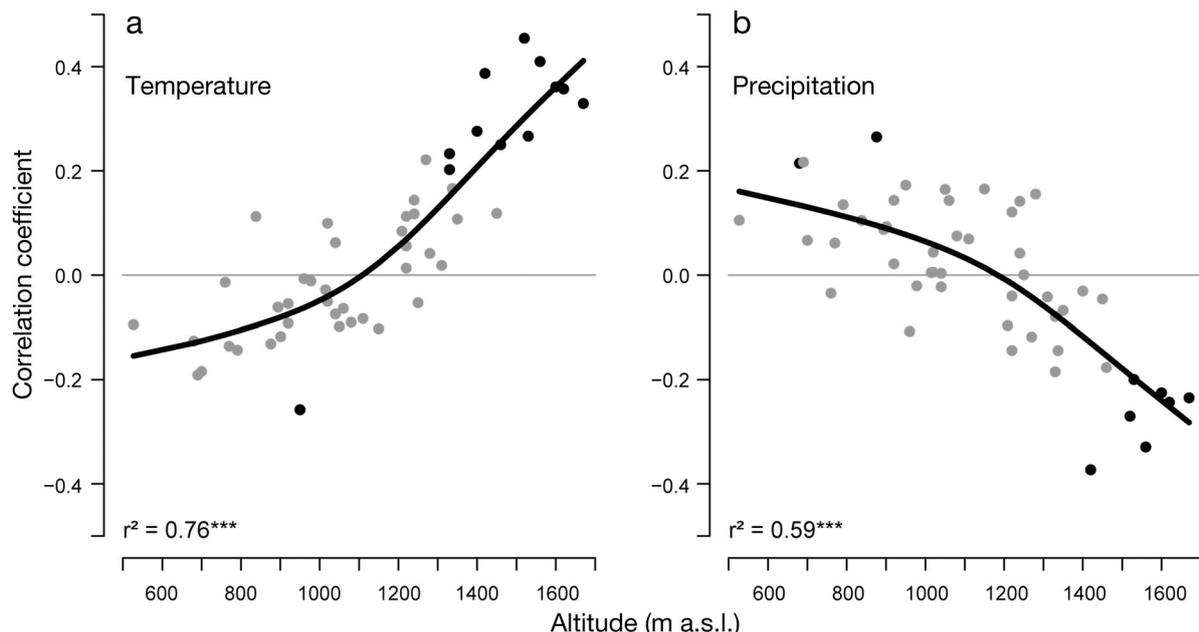


Fig. 4. Comparison of seasonal correlations as a function of elevation for RWI_{67} -chronologies and (a) temperature and (b) precipitation. Black dots indicate significant correlations ($p \leq 0.05$). Non-linear fits and adjusted r^2 (** $p < 0.001$) are based on generalized additive models

3.4. Growth–climate response

Spruce growth and temperature during the vegetation period are consistently negatively correlated at the lower elevation sites; in contrast, at the high elevation sites, growth is significantly ($p \leq 0.05$) positively correlated with temperature (Fig. 4a). An altitude of ~ 1200 m a.s.l. seems to be a turning point from predominantly negative to positive growth/temperature correlations. A trend along the altitudinal gradient was observed, where the effects of high temperatures on radial growth gradually changed from negative to positive with increasing elevation. This relationship can be represented by a GAM explaining 76% ($p < 0.001$) of the temperature response variance (Fig. 4a). An inverse pattern was observed for precipitation (Fig. 4b). Whereas positive correlations between tree growth and vegetation period precipitation are predominant at lower altitudes, this association weakens and turns negative toward the higher elevation belts. The turning point for precipitation is less obvious, compared to temperature, but might lie between 1300 and 1500 m a.s.l., where correlations turn negative and reach significance ($p \leq 0.05$). The general association between precipitation signal and elevation is less tight, but the GAM function still explains 59% of the variance ($p < 0.001$; Fig. 4b). The overall highest absolute r values were observed at the higher elevation belts for both temperature and precipitation (Fig. 4).

3.5. Impact of 20th century climatic trends

To quantify a potential long-term impact of the observed temperature increase on tree growth, the percentage growth change of the RCS detrended data, in which lower frequency variance is preserved (Esper et al. 2003), is considered. Extremely similar growth changes within the different altitudinal belts were observed, especially since 1900 and independent of the location of the site (e.g. west or east, Bavaria or Austria) (see Fig. S3 in the Supplement). R_{bar} values range from 0.45 in the lower montane and montane belts to 0.46 in the altimontane and 0.48 in the subalpine belts. Overall, no clear pattern of negative or positive growth change trends was observed, either in the lower or in the higher elevational belts (Fig. S3).

To evaluate potential influences of the detrending technique on the results, the elevational mean growth change curves of the different detrendings are juxtaposed to each other (Fig. 5). The different detrending procedures yielded approximately equivalent trends. Whereas the RWI_{67} chronology indicates smaller values during recent decades, the RWI_{300} chronology indicates increased growth toward the present. The RWI_{RCS} curve lies in most cases between the other detrendings. Distinct growth fluctuations over the entire period were found for all detrendings and elevation belts (Fig. 5). Some periods indicate negative growth patterns, e.g. at the end of the 1940s until the 1950s. In the 1990s and in the mid-2000s, no negative growth pattern was observed except for a downward trend compared to previous years. These periods of growth decline can be compared to the identified drought events in 1947, 1992 and 2003 (grey dashed lines in Fig. 5). The results confirm the findings of the short-term impact assessment: trees at the subalpine elevation belt respond positively in these extreme years, but growth reactions below 1400 m are negative. Furthermore, an after-effect of these events becomes apparent, suggesting that drought influences spruce growth over multiple years.

3.6. Temporal variability of climate signals

To assess the temporal patterns of climate–growth change associations, moving 31 yr correlations were calculated. Consistently positive growth–temperature-change relationships since 1900 were observed at the subalpine elevation belt (Fig. 6a). The growth change correlates clearly with the temperature

change, though the growth trend does not entirely track the rising temperatures after 1990. In contrast, the lower montane belt exhibited changing correlation coefficients and no clear relationship with temperature (Fig. 6b). A distinct negative relationship since the 1980s that suggested an increase in a temperature-driven growth reduction could not be confirmed. Spruce growth in the subalpine belt also revealed no clear relationship with precipitation (see Fig. S4a in the Supplement). The coefficients are negative from 1900 to 1960 and fluctuate around zero thereafter. In the lower montane belt, spruce growth correlates positively with precipitation before 1900, but this association weakens thereafter (Fig. S4b). Comparison with the humidity index data indicates that cool and moist conditions negatively affected growth since 1900 in higher altitudes (Fig. S5a). In the lower montane belt, the correlation coefficients did not stabilize and adjust to zero with time (Fig. S5b). This indicates that even in the lower elevation belts, cool and moist (warm and dry) conditions do not exert distinct positive (negative) effects on tree growth.

4. DISCUSSION AND CONCLUSIONS

We compiled a TRW network of 500 Norway spruce trees from the Northern Limestone Alps covering a region extending 250 km from west-to-east and including an altitudinal gradient of ~1200 m. We performed this investigation to assess the impact of climate change on mountain forests and to estimate the performance of these forests and the persistence of their protective function. As ring width has been identified as a key parameter to assess a tree's vitality (Dobbertin 2005), we used this parameter to evaluate the species vulnerability. Because Norway spruce is the dominant species in the Alps (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006) and is among the most drought-sensitive mountain forest species (Kölling 2007), it was chosen in our dendroecological approach.

Our findings suggest that the growth reaction of spruce to drought depends on altitude. An elevation of ~1400 m seems to be the break point between growth decline and increase. Plants at higher elevations benefit from exceptionally warm and dry conditions but suffer at lower elevations. These findings confirm results of a study on the 2003 drought event in the Swiss Alps (Jolly et al. 2005). Comparable dependencies were also reported in other studies on annual extremes from the Swiss and French Alps

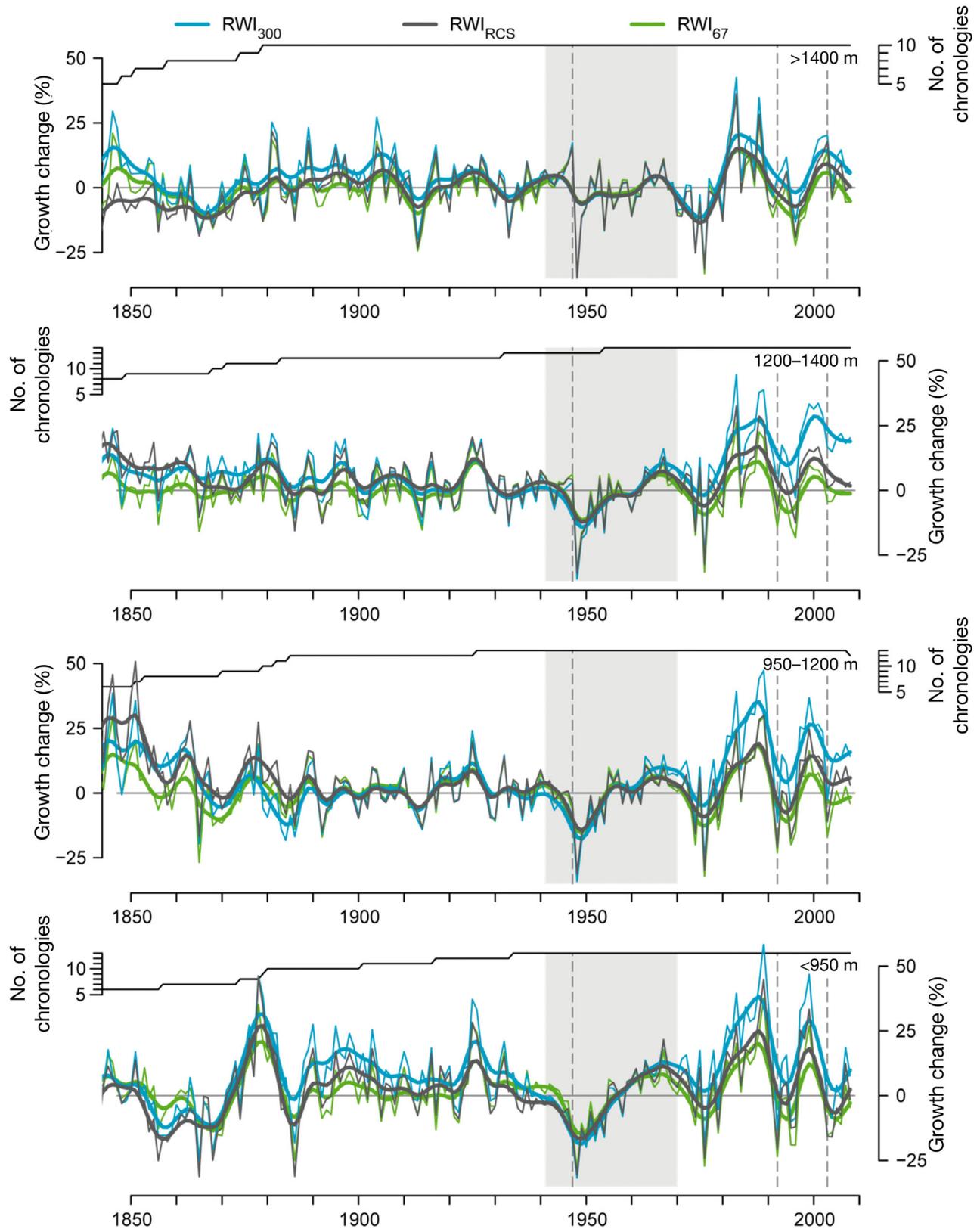


Fig. 5. Comparison of mean percentage growth change curves (with reference to 1941–1970, grey bar) based on different de-trending techniques (blue = RWI₃₀₀, grey = RWI_{RCS}, green = RWI₆₇) for different elevation belts. Smoothed curves are 45 yr low-pass filters. The dashed lines mark relative drought events in 1947, 1992 and 2003

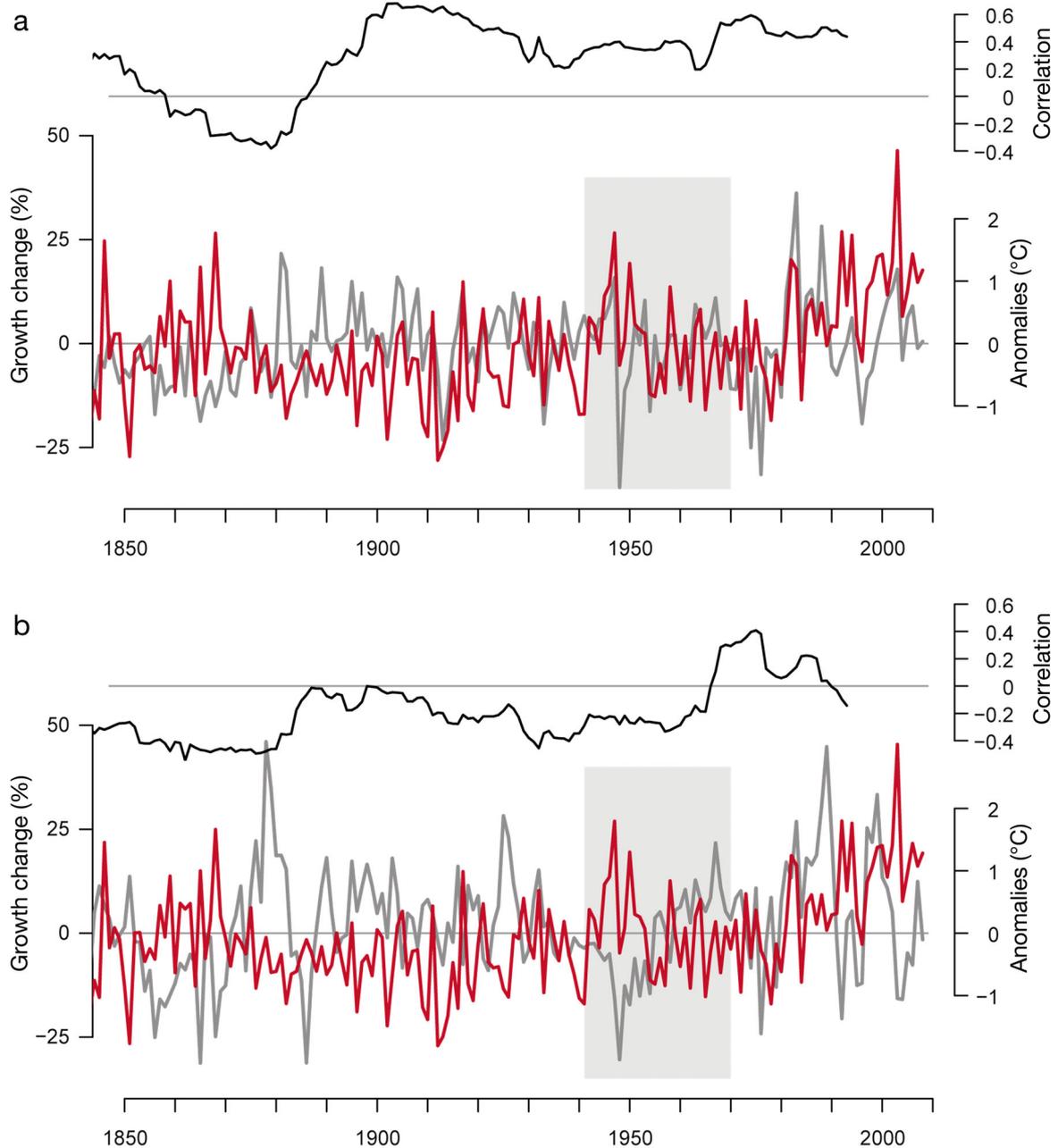


Fig. 6. Comparison of the RCS-detrended percentage growth change (grey curves) and temperature anomalies (red curves), both with reference to 1941–1970 (grey bars), in the (a) subalpine and (b) lower montane belts. Top panels show running 31 yr correlations (black lines) between the tree-ring and instrumental data

(e.g. Desplanque et al. 1999, Neuwirth et al. 2004). Although we observed a distinct growth decline at lower elevations (max. ~40%), this is a minor reduction compared to the reaction in lowland spruce sites in southern Germany (up to ~60%; Zang et al. 2011, Zang 2012), indicating that an extended transect would further emphasize the elevational dependence of drought signals in this species.

The seasonal growth–climate response also demonstrated a significant relationship with altitude. In lower montane and montane elevations, tree growth correlated negatively with temperature but positively with precipitation during the vegetation period, indicating these sites may be sensitive to drought. At higher altitudes, the coefficients were inverse; hence, warm and dry conditions have a pos-

itive effect on tree growth, while cold and wet conditions have a negative influence. The dependency of the growth–climate relationship on elevation has been demonstrated in other studies of Norway spruce (e.g. Dittmar & Elling 1999, Wilson & Hopfmüller 2001, Mäkinen et al. 2002, Frank & Esper 2005, Savva et al. 2006, Leal et al. 2007). The switch from negative to positive correlation coefficients at ~1200 m a.s.l. as revealed here differs from thresholds reported in previous studies based on fewer spruce sites: ~800 m a.s.l. in Dittmar & Elling (1999), ~900 m a.s.l. in Wilson & Hopfmüller (2001) and ~1500 m a.s.l. in Frank & Esper (2005). However, a direct comparison of critical altitudes for this conversion is difficult due to the varying seasons of the growth–climate relationships as well as the differing regions in the European Alps and Southern Germany considered in these studies.

The growth–climate relationship showed a significant sensitivity of spruce to temperature, particularly at higher altitudes, thus confirming the ‘common knowledge’ of distinct temperature signals at high elevations (and latitudes) (Babst et al. 2013). However, the growth change trends do not follow the temperature increase. To examine this disassociation in more detail, long-term climate data were combined with growth change results. We identified relatively stable (and since ~1900, consistently positive) relationships between the temperature change and growth change at the subalpine elevation belt. Previously, the coefficients were negative, similar to the results of the June growth–temperature relationship demonstrated by Büntgen et al. (2006). Nonetheless, Büntgen et al. (2006) observed a recent decreasing growth–temperature response that we could not confirm in our study. Indeed, no direct tracking of the rising temperatures could be observed in the growth change data; instead spruce growth seemed to remain constant. In contrast to the higher altitudes, the temporal stability of the relationship between the temperature change and growth change at the lower montane belt is much lower, as could be expected for the generally weaker connections between tree growth and climate at this elevation. At the lower montane belt, the precipitation signal appeared more stable. The humidity index represents a fairly good combination of temperature and precipitation conditions and illustrates that a cool and wet climate negatively affects growth at higher sites but has a rather positive effect at lower elevations.

Although the growth change pattern does not indicate a positive or negative effect of rising temperatures, the effect of drought events is more apparent.

The spruce growth pattern contains fluctuations connected to drought events, at least at the lower elevation sites. After a drought event, we observed downwards growth trends over several years, which, after about 5 to 10 yr, changed toward wider rings again. In southern Germany, prolonged growth suppression after drought events was also reported for spruce by Zang et al. (2011). However, our results also reflect the ability of Norway spruce to successfully recover from drought, indicating this tree species to be resilient to recent temperature changes.

Since we did not observe a growth increase associated with rising temperatures at subalpine elevations, our results could be interpreted as evidence for the divergence phenomenon. However, Büntgen et al. (2008) did not find an unusual divergence in growth in the European Alps. Because we dedicated special care to the detrending of tree-ring series in the present study, we can exclude a divergence phenomenon detection by mistake. For the northern latitudes, Esper et al. (2010) demonstrated that the preservation of low-frequency variance in tree-ring series can prevent the spurious detection of divergence phenomena. In addition, studies from the European Alps (Rolland et al. 1998, Paulsen et al. 2000) and North America (Salzer et al. 2009) identified positive growth trends at high elevation sites. A possible explanation may be that our study does not comprise trees from tree-line sites (at ~1800 to 1900 m in the Northern Alps; Ellenberg 1996). Even trees from the subalpine sites were growing in closed canopy conditions, and the tree temperature sensitivity studied is generally weaker in these sites. Higher temperatures are also expected to extend the growing season (Lindner et al. 2010), which could potentially lead to increased tree growth at higher elevations. Cornelius et al. (2013) observed, in a phenological study of our investigation area, that trees were less sensitive to temperature changes than herbs; thus, the tree response to climate change should be less pronounced. However, Hasenauer et al. (1999) observed an incremental increase in Norway spruce growth in the 1980s in the Austrian Alps and explained this as being the result of warmer climatic conditions and the associated prolonged vegetation period. We also identified above-average growth in this period, but a growth decline occurred thereafter due to the drought events in 1992 and 2003. At lower elevations, the missing growth suppression might be due to the general climatic conditions of the Northern Limestone Alps, where the precipitation sums are commonly high (between 740 and 980 mm for 1941–1970 in the vegetation period only), so the tempera-

ture trend may actually have a small effect. Furthermore, despite the temperature shift of 1°C, all of the study sites are still in the recognized Norway spruce climate envelope (Kölling 2007).

Spruce is the dominant species of mountain forests (Ellenberg 1996, Oberdorfer 2001, Büntgen et al. 2006), but mountain forests also contain other species, so it is not possible to assess the vulnerability of these forests in their totality from other results. Although spruce is regarded as being sensitive to summer drought (Oberdorfer 2001), it displayed a high potential to successfully recover from a growth decline after drought events; nevertheless, lag effects can occur in the years following an event. Additionally, if drought events appear more often, and with a higher intensity, the lower elevations might be negatively affected in the long term. In addition to this pattern, the effects of climate change are not restricted to temperature and precipitation. A higher frequency and intensity of wind storms (Lindroth et al. 2009) and insect outbreaks (Seidl et al. 2008) can also occur. Norway spruce is again considered the most vulnerable species of the mountain forests to such disturbances, and it would be ecologically valuable to mix other species with deeper roots, especially in the montane elevation belts.

Our results suggest that up to the present climate change has not had an adverse effect on Norway spruce in the European Alps. Norway spruce is still robust in the existing conditions, and can thrive in the mountain forests of the Northern Limestone Alps; however, our hypothesis of increased growth at high elevations and growth suppression in low elevation sites could not be verified. The mountain forests of the Northern Limestone Alps seem to have the capability to respond and adapt to unprecedented temperature shifts.

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