



# Resilience of Norway spruce (*Picea abies* (L.) Karst) growth to changing climatic conditions in Southwest Germany



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## ABSTRACT

Knowledge gaps still exist concerning the resilience of Norway spruce growth to changing climate conditions especially outside their natural range. We used a dendroecological approach to assess growth resilience of Norway spruce to changing moisture availability on different sites in southwest Germany near the xerothermic range limits of this species. We described the temporal and spatial variation of Norway spruce tree-ring width, comparatively assessed the response of tree-ring width to changes in moisture availability between different study sites and assessed the capacity of Norway spruce growth to absorb disturbance by drought. To assess the capacity, we applied the concept of resilience and the concept of early-warning signals to tree-ring width data. The results indicated no adequate short-term adaptive capacity to changing climate conditions for the respective Norway spruce trees within the study period. Furthermore the results showed an enhancement of growth synchronicity among the trees at each study site which is highly correlated with changes in moisture availability. Critical slow down, loss of buffering ability and simultaneous increase in spatial correlation are indicative of a loss in growth resilience of Norway spruce. We assume that the capacity of Norway spruce trees to absorb disturbance in terms of their growth response to moisture deficits decreased presumably as a consequence of a series of drought events in the more recent past.

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## 1. Introduction

Norway spruce (*Picea abies* (L.) Karst) in Central Europe is expected to be especially susceptible to anticipated climate changes (e.g. Kölling et al., 2007). Since the 16th century Norway spruce has been the preferred tree species to restore degraded and afforest new forests in Central Europe due to its superior growth potential, high timber quality, and limited requirements on site conditions. This preference resulted in an expansion of the area of Norway spruce far beyond the limits of its natural range (Spiecker, 2000; von Teuffel et al., 2003). The decision to cultivate Norway spruce outside its natural range, often was based on confident assumptions concerning growth potential and probability of survival. These assumptions were mostly derived from empirical evidence and encompass considerable uncertainties e.g. with respect to damage risks (Kölling et al., 2009). Knowledge gaps still exist concerning the resilience of Norway spruce growth to changing climate conditions especially at the limits and outside of their natural range. In an ecological context, resilience is defined as the property of a system to absorb disturbance and

reorganize while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks (Holling, 1973; Walker et al., 2004; van Nes and Scheffer, 2007). If there is only one stable state, the system will settle back to essentially the same state after a stochastic event. Some ecosystems however may occasionally change quite abruptly to a contrasting state due to a sufficiently severe perturbation (Holling, 1973; Scheffer et al., 2001). The likelihood of this depends not only on the perturbation, but also on the 'topography' around a state. Theoretical studies have suggested that such shifts may occur in ecosystems with alternative stable states in which the conditions approach a critical threshold (Scheffer and Carpenter, 2003). Ecosystems in the transition phase close to that critical threshold lose resilience, so that perturbations more likely push them into an alternative state.

Ecological resilience cannot be measured directly. In practice there is a need for assessable and measurable resilience indicators (Chrisholm and Filotas, 2009). It has recently been suggested that the shift of an ecosystem to a contrasting stable state may be announced in advance by generic leading indicators for critical transitions (Scheffer et al., 2009). Whether a system is getting close to a critical threshold is indicated by a phenomenon known in dynamical systems theory as 'critical slowing down' (Wissel,

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1984; Strogatz, 1994). Two decisive symptoms of critical slowing down are increased variance (Carpenter and Brock, 2006) and increased autocorrelation in the respective system process (e.g. Ives, 1995; Kleinen et al., 2003; Held and Kleinen, 2004; Scheffer et al., 2009; Dakos et al., 2012). In the context of ecological systems increased spatial correlation may in addition serve as an early-warning signal for approaching a critical transition (Dakos et al., 2010).

Climate conditions are considered as one of the main controlling factors of tree growth. The response of trees to weather conditions is modified by tree species, provenance, age, competition and site conditions (Spiecker, 2002). For explaining spatial and temporal patterns of tree growth variability series of tree-ring parameters provide important information and allow a retrospective analysis of climate-growth relationships over longer periods (e.g. Kahle, 1996; Kahle and Spiecker, 1996; Swetnam et al., 1999; Spiecker, 1999; Spiecker, 2002). Tree-ring parameters such as tree-ring width have long been recognized as indicators of climatic effects (e.g. Fritts, 1976; Cook and Kairiukstis, 1990) and have been used as a technique to explore the forest ecosystem response to climate conditions (e.g. Beck, 2009; Bolte et al., 2010).

Several studies revealed changes such as periodic fluctuations and level shifts in climatic factors relevant for tree growth in south-west Germany during past decades (Klein Tank and Können, 2003; Mayer et al., 2005). Regional climate models predict an increase in annual average air temperature for Central Europe of about 3 °C by 2100 (Christensen et al., 2007), and for the southern part of Central Europe up to about 2 °C within the next 40 years (Knoche and Forkel, 2004; Forkel and Knoche, 2006). A seasonal shift in the distribution of precipitation from summer to late winter and spring is predicted for parts of Europe including the southern part of Central Europe (Kunstmann et al., 2004). The increase in air temperature and simultaneous reduction in precipitation during the vegetation period are expected to cause an increase in the frequency and duration of intense summer droughts that will have severe effects on forest ecosystems (IPCC, 2001a,b; European Environmental Agency, 2004). However, there is still a considerable uncertainty regarding the future magnitude of climate changes and the probable impact of climate changes on tree growth.

Norway spruce was found to be a particularly drought-sensitive species (e.g. Eckstein et al., 1989; Schmidt-Vogt, 1991; Spiecker, 1991; Spiecker, 1995; Kahle and Spiecker, 1996; Andreassen et al., 2006; Pichler and Oberhuber, 2007; Lebourgeois, 2007; Lebourgeois et al., 2009; Bouriaud and Popa, 2009; van der Maaten-Theunissen et al., 2013), which makes this species in terms of tree-ring width especially susceptible to dry and warm summers in Central Europe (Kahle, 1994; Mäkinen et al., 2002). Several recent studies identified distinct growth depressions by the presence of narrow tree-rings during years with low moisture availability (e.g. Rolland et al., 2000; Utschig et al., 2004; Kohler et al., 2010). The projected increase in frequency and duration of intense summer droughts in central Europe (IPCC, 2001a,b; European Environmental Agency, 2004) may cause an increase in frequency and duration of severe growth depressions of Norway spruce in the future.

We used a dendroecological approach to assess growth resilience of Norway spruce to changing moisture availability on different study sites near the xerothermic range limits of this species. Our specific objectives were (1) to describe the temporal and spatial variation of Norway spruce tree-ring widths, (2) to comparatively assess the response of tree-ring width to changes in moisture availability between the study sites, and (3) to assess the capacity of Norway spruce growth to absorb disturbance by drought.

## 2. Material and methods

### 2.1. Study sites

The study sites are located in southwestern Germany (Baden-Wuerttemberg), they are distributed in the region as to cover a wide range of environmental conditions. The study sites belong to the Level II forest intensive monitoring network of the 'International Co-operative Programme on the Assessment and Monitoring of Air Pollution Effects on Forests (ICP Forests)'. This programme was launched by the European Commission in 1985 to monitor key ecological processes in forest ecosystems in Europe (<http://icp-forests.net/>). The study sites are similar with respect to stand establishment, stand composition (pure Norway spruce stands), and stand structure. With respect to their climatic, geological and pedological conditions the study sites are representative for most of the sites where Norway spruce can be found today in Baden-Wuerttemberg.

All study sites are located on slopes or plateaus in the submountainous and mountainous zone (350–835 m above sea level) (Table 1). Mean annual temperature at the study sites varies between 7.5 and 9.1 °C, mean annual precipitation sum from 950 to 1.280 mm. Available soil water capacity of the effective rooting depth varies distinctly between the sites (90–220 mm). All forest stands were planted and are dominated by Norway spruce. No severe stand disturbances were reported for the study sites, resulting in homogenous horizontal structure of the stands. In this coniferous dominated stands canopies are mono-layered.

### 2.2. Meteorological data

In order to extend the meteorological data set, time series of daily precipitation sum, daily mean air temperature and relative air humidity from six meteorological stations of the German National Meteorological Service (DWD) in the neighbourhood of the study sites have been included in the analyses (common period: 1954–2004). Additional data from other nearby meteorological stations were used as climatological reference stations to test the homogeneity of the respective data series (Schönwiese and Malcher, 1985).

Time-series of climatic water balance (WB) for the vegetation period (April–September) were calculated for each meteorological station based on the Haude model (Haude, 1955) for potential evapotranspiration (ETP). Similar investigations (Kahle, 1994) successfully used climatic water balance as index to quantify moisture availability and to describe drought intensity and duration. Daily ETP was calculated from the vapour pressure deficit at 2 pm, which is derived from the measured relative humidity and air temperature (Haude, 1955; Bormann et al., 1997). Monthly correction factors for spruce stands were used to account for other influential factors such as wind velocity (Häckel, 1999).

Climate data of neighbouring meteorological stations need to be carefully interpreted due to their limited representativeness for the situations in forest stands (König and Mayer, 1990; Flemming, 1993). To interpolate from the calculated monthly time-series of WB for the DWD meteo stations to the study sites, the mean monthly difference between the calculated WB for the study sites and the respective WB of the measurement station for the period 2000–2006 was used as correction factor.

### 2.3. Sampling, measurement and evaluation of tree-ring width

In 2004 at each study site 20 (pre-)dominant trees without visible signs of damage were selected as sample trees on the basis of a next-nearest neighbour approach. Two increment cores were taken

**Table 1**  
Summary information on site, climate, soil and forest stand characteristics of the six study sites.

Site	Conventwald	Ochsenhausen	Altensteig	Rotenfels	Esslingen	Heidelberg
Site acronym	<i>Con</i>	<i>Och</i>	<i>Alt</i>	<i>Rot</i>	<i>Ess</i>	<i>Hei</i>
Latitude (°)	48°0'	48°0'	48°35'	48°50'	48°76'	49°25'
Longitude (°)	8°0'	9°55'	8°40'	8°25'	9°43'	8°45'
Altitude (m asl)	835	680	520	575	350	510
Aspect	SE	S	SE	NE	NW	W
Temp <sub>ann</sub> (°C)	8.6	8.4	8.0	9.1	8.2	7.5
Prec <sub>ann</sub> (mm)	1290	1620	1250	1580	1160	1310
Temp <sub>veg</sub> (°C)	11.7	12.6	11.9	12.7	11.7	11.3
Prec <sub>veg</sub> (mm)	1160	1150	950	1280	980	1170
WB <sub>veg</sub> (mm)	520	460	220	370	260	370
Soil type	Cambisol	Luvisol	Spodic Gleysol	Dystric Cambisol	Dystric Cambisol	Dystric Cambisol
Soil texture	Sandy loam	Sandy clay-loam	Loamy sand	Loamy sand	Loamy sand	Loamy sand
AWC (mm)	115	220	110	50	90	140
Stand composition (%)	Pa (90), Fs (5), Aa (5)	Pa (60), Ld (20), Fs (20), Pm (5)	Pa (55), Ps (30), Aa (15)	Pa (85), Aa (15), Fs (5)	Pa (78), Pm (17), Ab (3), Fs (2)	Pa (100)

Temp<sub>ann</sub>: mean air temperature January–December (°C); Prec<sub>ann</sub>: precipitation sum January–December (mm); Temp<sub>veg</sub>: mean air temperature April–September; Prec<sub>veg</sub>: precipitation sum April–September; WB<sub>veg</sub>: climatic water balance April–September. All meteo data refer to on-site within stand measurements during 2000–2006 (stem flow is not included); AWC: available soil water capacity for effective rooting depth (mm); Pa: *Picea abies*; Fs: *Fagus sylvatica*; Ld: *Larix decidua*; Aa: *Abies alba*; Pm: *Pseudotsuga menziesii*.

from each tree at 1.3 m stem height at upslope side of the tree at right angles to slope direction in order to avoid compression wood. Tree-ring width was measured to an accuracy of nearest 0.01 mm using the measurement system WOODSCAN developed at Chair of Forest Growth, Albert-Ludwigs-University Freiburg. To detect measurement and cross-dating errors raw tree-ring width series of individual cores were plotted and cross-dated visually with the help of pointer years and additionally synchronized by applying an interval sign test (Gleichläufigkeit; Eckstein and Bauch, 1969).

Tree-ring width series for each tree were obtained by averaging the tree-ring width series of the two cores of the respective tree. The tree-ring width series were detrended on an individual tree basis by applying a smoothing spline function with a 50% frequency cutoff of 30 years using the R ad-on package dplR (Bunn, 2008). Tree-ring width index series were calculated as the ratio between the observed and the estimated values given by the spline function. Among other spline formulations and trend functions tested, the 30-year smoothing spline generated the highest mean interseries-correlation between the respective index series. Therefore the 30-year smoothing spline was used for detrending. Site chronologies were built by using the biweight robust mean of individual tree-ring width index series per study site (Fritts, 1976; Cook and Kairiukstis, 1990) and were truncated to only contain values with a sampling depth of more than five sample trees.

#### 2.4. Statistical analysis

Mean sensitivity (MS), standard deviation (SD), first order autocorrelation (AC1), inter-serial correlation (Inter-corr), expressed population signal (EPS) and first principal component loadings (PC1) were calculated to characterize the variability in tree-ring width series and to check the data quality prior to the dendroecological analyses (Fritts, 1976). MS is the mean percentage change between subsequent years and characterizes the intensity of year-to-year changes (Fritts, 1976; Riemer, 1994). SD estimates the variability of values and describes the magnitude of low- and medium-frequency variation (Fritts, 1976). Inter-corr is a measure of the high-frequency similarity among time-series. EPS is a function of mean inter-serial correlation and series replication and is a measure of how well single tree-ring width index series represent the theoretical population (Wigley et al., 1984; Briffa and Jones, 1990; Mérian and Lebourgeois, 2011). PC1 estimates the level of year-to-year tree-ring width variations shared by trees in the stratum.

#### 2.5. Response to moisture availability

For investigating tree growth response to changes in moisture availability with respect to study sites we used an analysis of covariance (ANCOVA). ANCOVA allows testing for differences in slopes and intercepts among linear regression lines by testing the effect of a categorical variable on a dependent variable while controlling the effect of a continuous co-variable. If the effect of the co-variable on the dependent variable depends on the categorical variable, the interaction effect between co-variable and the categorical variable is significantly different from zero (regression lines have different slopes). If the effect of the categorical variable itself is significant, but showing no interaction with the co-variable, the intercepts of the linear regression lines are different. Differences in intercepts are differences in magnitude but not in the rate of change. A difference in slope is a difference in the rate of change. In our study we tested the significance of the categorical variable 'study site' for four different time periods. Co-variable was mean WB for current vegetation period (Apr–Sep), dependent variable was site chronology. The test of stochastic trends in time series prior to linear regression is necessary to prevent from erroneous conclusions (Granger and Newbold, 1974). To avoid spurious regressions, we conducted the ANCOVA analysis with the differentiated WB series and site chronologies.

Regression models such as ANCOVA rest on four principal assumptions which justify the use of linear regression models: stationarity of the input series of dependent and independent variables (no trends exist in the data), normality of the relationship between dependent and independent variables (normality of regression residuals), independence of the regression residuals (no serial correlation), and homoscedasticity of the regression residuals. If one of these assumptions is violated, results of the regression model were inefficient or biased and may lead to erroneously high statistical significance and incorrect conclusions (Granger and Newbold, 1974).

A stationary time series is one whose statistical properties such as mean, variance, and autocorrelation are all constant over time (Cryer, 1986). Each site chronology and of WB was tested for stationarity using the augmented Dickey–Fuller (ADF) unit root test (Dickey and Fuller, 1979, 1981). Difference-stationary time series can be transformed into stationary series by differencing (Cryer, 1986). The first-order differences of the series  $X_t$  produce the stationary series  $W_t$  given by  $W_t = x_t - x_{t-1}$ , where  $t$  represents time. To maintain meaningful relationships between time series

of the dependent and the independent variable, both time series have to be differentiated. The second assumption of ANCOVA is the normality of the regression residuals. The error term of the ANCOVA should be a standard normal distribution if the functional part of the model is specified correctly. Since residuals after the ANCOVA model fitting approximate the actual errors, we checked the normality of the model residuals by using the Shapiro–Wilk (SW) test (Shapiro and Wilk, 1965). Serial independence of regression residuals were examined using the Durbin–Watson (DW) statistic (Durbin and Watson, 1951). The Durbin–Watson statistic provides a test for significant residual autocorrelation at lag 1. The Breusch–Pagan (BP) test was used to test for heteroscedasticity in the linear regression model of the ANCOVA. Breusch and Pagan (1979) derived this test for the null hypothesis of homoscedasticity versus the general alternative that the estimated variance of the residuals depend on the values of the independent variables.

## 2.6. Capacity to absorb disturbance

In the phase of ‘critical slowing down’ (Wissel, 1984) the intrinsic rates of change in a system tend to decrease, with the effect, that the state of the system at any given moment becomes more and more like its past state, which is characteristic for long-memory processes. The resulting increase in ‘memory’ of the system can be measured by the first order autocorrelation coefficient (AC1) (Held and Kleinen, 2004; Dakos et al., 2008), which can be directly interpreted as slowness of recovery in such natural perturbation regimes (Van Nes and Scheffer, 2007; Ives, 1995). Increased variance in the pattern of fluctuations is another possible consequence of critical slowing down (Carpenter and Brock, 2006).

To assess the capacity of growth of Norway spruce to absorb disturbance due to drought we investigated the temporal change in the early-warning signal AC1 and the amplitude of variance expressed as mean standard deviation (SD). We calculated AC1 and SD for site chronologies and for sub-periods of 25 years starting in 1954 and lagged onward in annual time steps.

Dakos et al. (2010) argued that an increase in spatial correlation may be indicative of an impending critical transition. To evaluate the spatial correlation of tree-ring width series between the sample trees at each study site, a principal component analysis was conducted for sub-periods of 25 years starting in 1954 and lagged onward in annual time steps. The temporal evolution of PC1 loadings expresses the varying share of the common signal among the tree-ring width index series of the study sites. For the same periods the expressed population signal (EPS) was calculated.

In order to assess the temporal stability in the coherency between tree growth and environmental conditions values of AC1, SD, PC1 and EPS were opposed to moisture availability anomalies

calculated as the relative deviation of climatic water balance for the respective sub-periods of 25 years compared to their 1954–2004 mean. Periods of 25 years were a compromise between statistical reliability and the aim to receive long enough time series.

## 3. Results

### 3.1. Temporal and spatial variation of tree-ring width

Mean tree age at sampling date ranged from 59 to 90 years (Table 2). At the age of 50 years the mean tree-ring width ranged from 2.27 mm to 4.05 mm with the highest value found for study site *Con*. The common period analysis (1954–2004) showed for all study sites except *Alt* slightly lower mean tree-ring width. SD increased with increasing tree-ring width ranging from 0.39 mm to 0.69 mm. MS showed the highest value for site *Hei* indicating the largest relative year-to year fluctuations in tree-ring width. AC(1) was for all sites around 0.3. Index series showed similar signal strength for all study sites with similar values for Inter-corr and variance expressed by PC1 and EPS. An exception is study site *Ess*, where Inter-corr, EPS and PC1 were slightly lower than for the other sites.

Tree-ring width site chronologies (solid line) showed rather synchronous annual variations (Fig. 1). Distinct growth depressions occurred on all sites in the years 1976, 1992, and 2003. Several year lasting periods with low tree-ring widths are noticeable for all sites in the mid-1960s, mid-1970s and early-1990s. These multi-year depressions were most pronounced for site *Ess*. With the exception of *Rot* the interquartile ranges at all sites were higher in the second half of the observation period. This indicates an increased annual variance of tree-ring width in recent years.

### 3.2. Response of tree-ring width to moisture availability

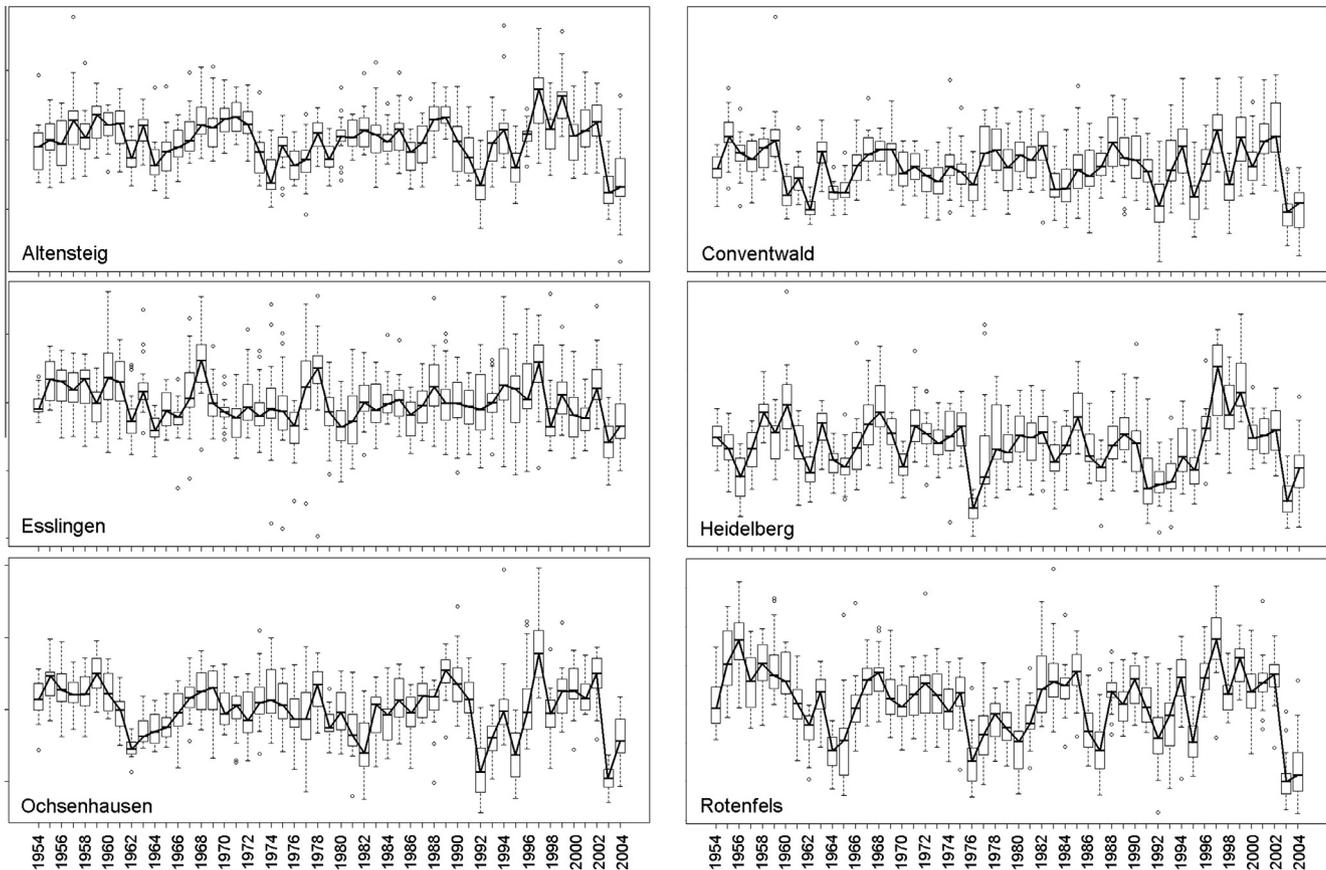
ADF tests were conducted on all site chronologies and series of WB to check for stationarity (Table 3). The null hypothesis of non-stationarity was not rejected for site chronology and WB series of study site *Rot*. For reasons of comparability each series was differenced in order to achieve stationary (verified by ADF test). All subsequent analyses were based on the differenced series.

The residuals are normally distributed (Shapiro–Wilk normality test,  $P < 0.05$ ) (Table 4). The DW test indicates no significant positive autocorrelation, in four out of six cases the statistics were slightly beyond the critical threshold, which is an indication of negative autocorrelation and could result in an overestimation of the level of significance. The BP test confirmed homoscedasticity at the 5% probability level.

**Table 2**  
Descriptive statistics for raw data and indices of Norway spruce radial growth.

Site	<i>Alt</i>	<i>Con</i>	<i>Ess</i>	<i>Hei</i>	<i>Och</i>	<i>Rot</i>
Age	90	59	83	73	73	90
Time span	1930–2004	1952–2004	1937–2004	1940–2004	1938–2004	1923–2004
$i_r$ 50 (SD <sub>50</sub> )	2.27 (0.77)	4.05 (1.25)	2.67 (1.03)	2.63 (0.9)	2.85 (0.83)	3.02 (0.91)
$i_r$ (SD)	2.31 (0.39)	3.71 (0.69)	2.35 (0.41)	2.41 (0.5)	2.55 (0.55)	2.61 (0.66)
MS	0.190	0.201	0.206	0.225	0.204	0.187
AC(1)	<b>0.332</b>	0.259	<b>0.338</b>	<b>0.324</b>	<b>0.361</b>	<b>0.37</b>
EPS	0.938	0.940	0.875	0.954	0.954	0.965
PC1	48.6	47.9	30.2	53.5	53.9	60.7
Inter-corr	<b>0.60</b>	<b>0.54</b>	<b>0.48</b>	<b>0.55</b>	<b>0.66</b>	<b>0.79</b>

Age (years): age in breast height in 2004; time span: period covered by all trees;  $i_r$  50: mean tree-ring width at cambial age 50 (referred to breast height); SD<sub>50</sub>: mean tree-ring width standard deviation at cambial age 50. The following data refer to the maximum common overlap period 1954–2000;  $i_r$ : mean tree-ring width (mm); SD: mean tree-ring width standard deviation (mm); MS: mean sensitivity of tree-ring width index series; AC(1): mean first order autocorrelation of tree-ring width index series; EPS: expressed population signal of tree-ring width index series; PC1: first principal component loadings of tree-ring width index series (%); Inter-corr: mean series inter-correlation coefficients of tree-ring width index series. Bold type indicates statistical significance at the 5%-level.



**Fig. 1.** Box-and-Whisker plots of tree-ring width indices of the sample trees versus calendar year for the six study sites. Each box (thin solid line) represents the interquartile range and the whiskers (dotted lines) extend to the 5th and 95th percentiles. The thick black solid line in the centre of the box shows the mean. Outliers are shown as points beyond the whiskers. The solid black line represents the site chronology.

**Table 3**  
Results of ADF test for stationarity of the site chronologies and WB series.

	Site chronologies		WB series	
	ADF original data	ADF 1st difference	ADF original data	ADF 1st difference
Alt	<b>-3.78</b>	<b>-3.65</b>	<b>-4.89</b>	<b>0.01</b>
Con	<b>-3.77</b>	<b>-3.84</b>	<b>-5.95</b>	<b>0.01</b>
Ess	<b>-3.91</b>	<b>-6.70</b>	<b>-4.81</b>	<b>0.01</b>
Hei	<b>-3.89</b>	<b>-4.43</b>	<b>-4.88</b>	<b>0.01</b>
Och	<b>-4.00</b>	<b>-4.30</b>	<b>-5.21</b>	<b>0.01</b>
Rot	-3.49	<b>-4.04</b>	<b>-4.97</b>	<b>0.01</b>

Bold denotes the rejection of null hypothesis of non-stationarity at 5% level. The critical value of ADF at the 5% level of significance is  $-3.50$ . Parameter  $k$  has been set to 3. The parameter  $k$  is a truncated lag parameter used in the non-parametric correction for serial correlation and is set according the sample size.

In the ANCOVA model site chronology was modelled as a function of WB as co-variable and study site as categorical variable (Table 5).

The summary showed a highly significant effect of WB (positive relationship) for the entire study period 1954–2004, and a significant effect for the subperiod 1988–2004. The effect of study site was highly significant for both periods 1954–2004 and 1988–2004. This result suggested differences in level of the regression lines of the respective study sites for those two periods. No interaction effect between the co-variable and the categorical variable is indicated by the ANCOVA analysis. This result suggests that the slope of the regression lines between site chronology and WB were similar for all study sites in all time periods.

The ANCOVA results for the first differences confirmed a close relationship between site chronology and WB for all sites indicated

by highly significant values for subperiod 1988–2004 and the entire study period 1954–2002.

### 3.3. Capacity to absorb disturbance

AC(1) and SD values were calculated for subperiods of 25 years starting in 1954 and shifted in 1 year steps to examine temporal changes in both parameters. The average periodic moisture anomalies highlight a consistent trend of significantly decreasing moisture availability for all study sites (Fig. 2). With the exception of sites *Alt* and *Och* the sites show minimum moisture availability in most recent years.

For the study sites *Alt*, *Con*, *Ess*, *Och* and *Rot* the decrease in AC(1) is accompanied by an increase in SD and paralleled by a decrease in WB (significant for *Och* and *Rot*). For study site *Hei* the

**Table 4**  
Validation statistics for ANCOVA.

	SW	DW	BP
<i>Alt</i>	0.9849	2.704	1.484
<i>Con</i>	0.9810	2.811	0.145
<i>Ess</i>	0.9909	2.344	0.152
<i>Hei</i>	0.9826	2.623	2.671
<i>Och</i>	0.9476	2.669	1.351
<i>Rot</i>	0.9814	2.393	0.011

The critical value of SW test at the 5% level of significance is 0.9463; The lower and upper bound of the DW test at the 5% level of significance is for positive and negative autocorrelation 1.494 and 1.585, and 2.415 (=4–1.585) and 2.506 (=–4–1.494) respectively (explanatory variables: 1; number of values: 49). Between both bounds the test statistic is inconclusive. The test statistic becomes smaller as the serial autocorrelation increases; the critical value of BP test at the 5% probability level is 65.156.

correlation was negative (Table 6). The increase in SD is inversely correlated with moisture availability (significant except for study site *Alt*). For all study sites the point where the increase of SD accelerates coincides with the time when moisture availability fell below average. A different result can be found for study site *Hei*: here not only SD but also AC(1) values increase when moisture availability fell below average. Correspondingly AC(1) and SD showed a negative relationship to WB (Table 6).

The growth variance of tree-ring width indices common to the trees at each study site together with EPS showed a slight decrease for the early periods, followed by an increase to the end of the observation period (Fig. 3). The period of increasing common variance is closely synchronized with changes in moisture availability. PC1 loadings and EPS started to increase at the point when moisture availability fell below average.

## 4. Discussion

### 4.1. Temporal and spatial variation of tree-ring width

The common period analysis showed that the growth data of all study sites was of high statistical quality for investigations of climate-growth relationship: the tree-ring width index series reflected a strong signal of exogenous influences common to all trees per study site. This can be confirmed by high values of Inter-corr and PC1 loadings. Inter-corr coefficients were in the same range as in previous studies carried out in Baden-Wuerttemberg with the same species (Kahle et al., 2008). Judged from EPS values, the tree-ring width index series were very reliable. Wigley et al. (1984) reported values over 0.85 to be satisfactory for dendroclimatological analysis. According to Mérian and Lebourgeois (2011) the sample size that yielded the EPS value of 0.85 on average for Norway spruce was 27 trees. For this study the sample size was 20 trees per study site, however the EPS values are well above 0.85 and gave accurate estimation of the common signal. For study

site *Ess* Inter-corr, EPS and PC1 were slightly lower than for the other sites. This indicates that tree-ring width varied more among the trees at *Ess* than at the other sites. All mean tree-ring width index series except for study site *Con* possess a significant AC(1) indicating that previous year tree-ring width affected current year tree-ring width. The magnitude is similar to that found in other previously reported studies (Kahle, 1996). MS values also were similar as those reported by Kahle (1994) for Norway spruce in the southern Black Forest; but lower than in other investigations (Koprowski and Zielski, 2006). Low MS values are indicative of complacent growth behavior of Norway spruce on our study sites. The calculated statistics did not show any distinct altitudinal, latitudinal, or longitudinal trend.

The marked growth depressions in the years 1976, 1992 and 2003 and the subsequent years were in accordance with other investigations. Several studies have shown that these drought years caused growth depressions of Norway spruce on many sites in Central Europe (e.g. Rolland et al., 2000; Utschig et al., 2004; Kohler et al., 2010). The higher interquartile ranges in the second part of the observation period were surprising, because potential effects due to ageing or changing growth dynamics should have been eliminated by the detrending and no severe stand disturbances affected the growth of the sample trees in the past.

### 4.2. Response of tree-ring width to moisture availability

Based on the ANCOVA model (Table 3) a significant effect of WB on the tree-ring chronologies could be identified. It could be shown, that the slopes of the regression lines between site chronologies and WB were similar for all study sites in each time period. This means that the effect of changing moisture conditions on tree-ring width does not depend on the specific site. WB variations had the same effect on the tree-ring width on all study sites for the studied time periods. Furthermore the model showed significantly different values for the intercepts of the regression lines for the last subperiod and the entire study period. A high level of moisture availability during the vegetation period is accompanied by a high level of tree-ring width and vice versa. By comparing the results for the subperiods, it became obvious that the effect of WB and study site became more significant with time. On all study sites moisture availability decreased with time, during 1988–2004 average moisture availability was lower than for the reference period 1954–2004. This may partly be due to an accumulation of extreme years, such as 2003. Previous investigation showed that Norway spruce trees are adapted to the local average water availability (Kahle, 1994). Consequently for the study sites a reduction of relative moisture availability will lead to drought stress and growth depressions.

Similarities and differences in the tree-ring width response of Norway spruce to moisture availability among the study sites may be affected by a combination of many factors including climate conditions, site characteristics, and competitive interactions

**Table 5**

Results of analysis of covariance (ANCOVA) for WB (degree of freedom (DF) = 1), WBxsite interaction (DF = 5), and site (DF = 5) using site chronologies (dependent variable), mean WB of current vegetation period (co-variate) and study site (categorical variable) for four time periods. Left side: original data; right side: data differenced.

	1954–2004	1954–1970	1971–1987	1988–2004	1955–2004	1955–1970	1971–1987	1988–2004
WB	7.10**	0.03 ns	1.84 ns	6.22*	17.99***	1.80 ns	4.55 ns	13.90***
WBxsite	0.66 ns	0.44 ns	0.33 ns	0.07 ns	1.56 ns	1.34 ns	0.54 ns	0.34 ns
Site <sup>a</sup>	3.83**	0.48 ns	1.48 ns	3.32**	0.03 ns	0.04 ns	0.04 ns	0.02 ns

Codes for associated probability: >0.5 = ns.

\* Between 0.01 and 0.05.

\*\* Between 0.001 and 0.01.

\*\*\* Between 0 and 0.001.

<sup>a</sup> F-value of second ANCOVA model without the interaction to test for significant differences in intercept.

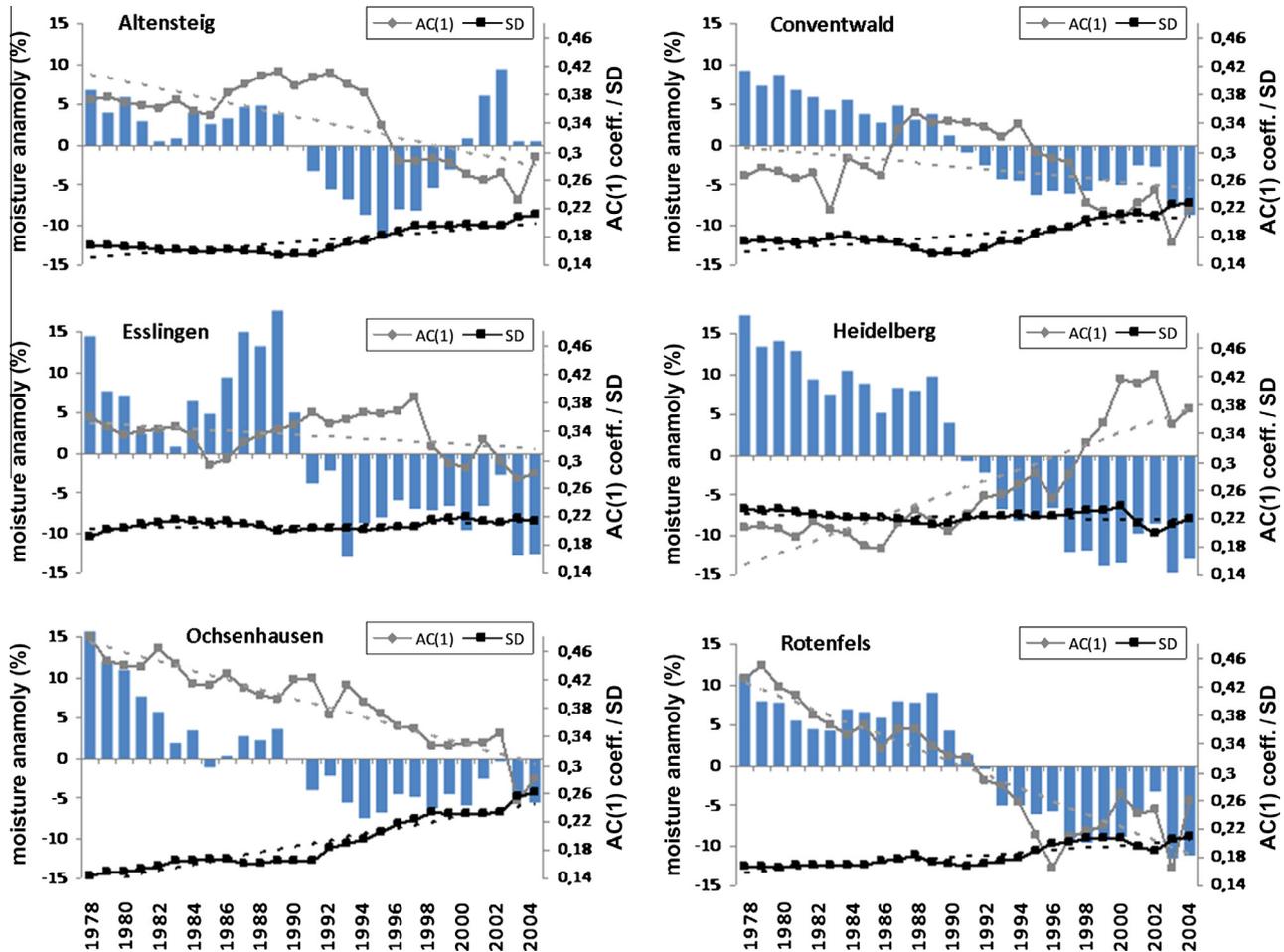


Fig. 2. Time series of first order autocorrelation (AC(1); black line) and mean standard deviation (SD; grey line) of the tree-ring width index series for the preceding 25 years. Blue bars represent average moisture anomalies (reference period 1954–2004) for the preceding 25 years. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 6

Pearson correlation coefficients between series of AC(1), SD and WB.

	AC(1)–SD	AC(1)–WB	SD–WB
Alt	<b>-0.76</b>	0.06	0.19
Con	-0.31	0.25	<b>-0.94</b>
Ess	0.16	0.13	<b>-0.64</b>
Hei	<b>0.78</b>	<b>-0.82</b>	<b>-0.85</b>
Och	<b>-0.80</b>	<b>0.71</b>	<b>-0.88</b>
Rot	<b>-0.80</b>	<b>0.85</b>	<b>-0.88</b>

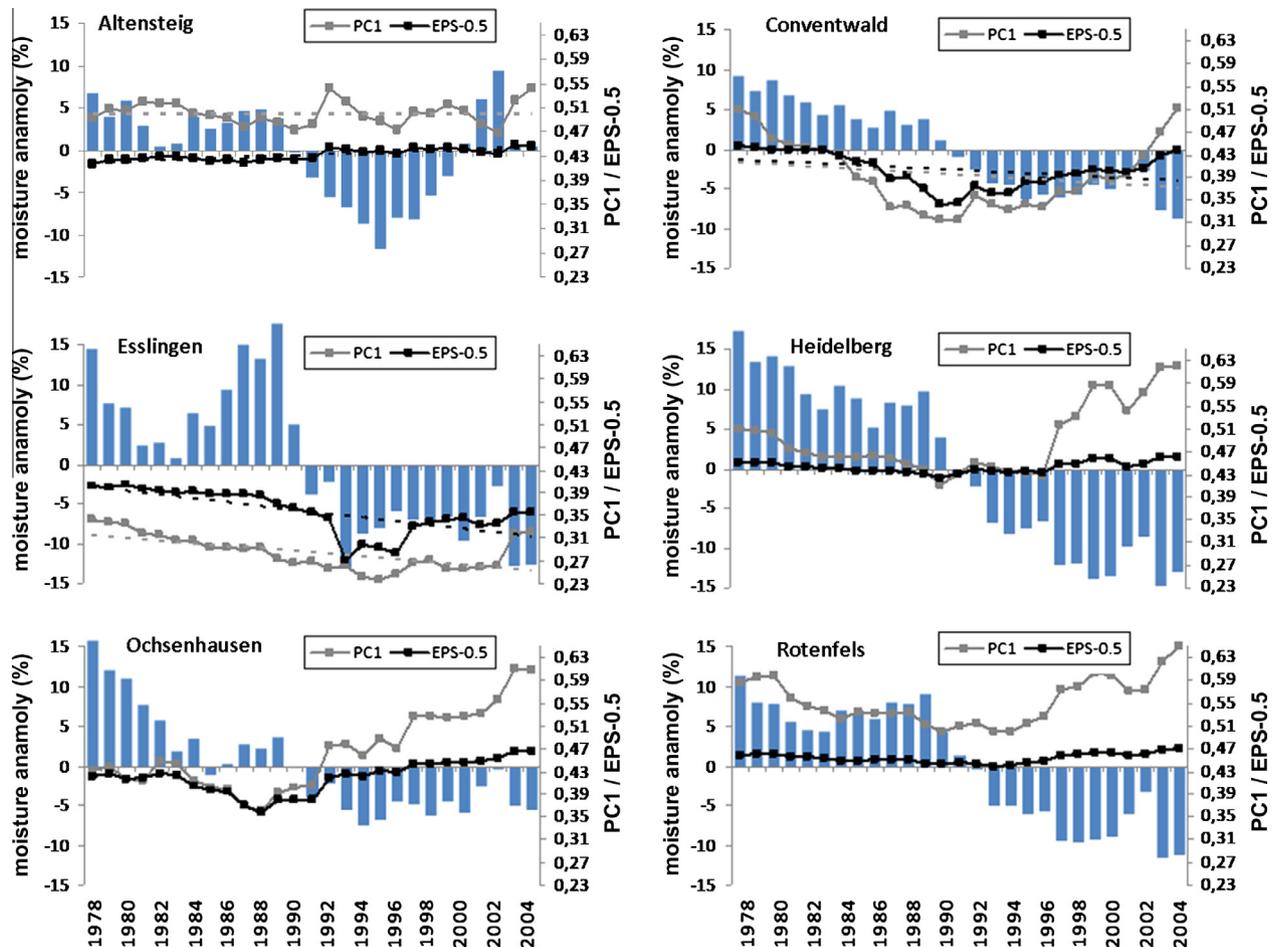
The critical value of Pearson correlation at the 5% level of significance is 0.381 (significant values bold). Due to the calculation series of AC(1), SD and WB were autocorrelated. An adjustment of the sample size for autocorrelation was not conducted, because of a low number of independent samples after adjustment.

with neighbours or stand history (Fritts, 1976). Due to the fact that forest stand history and stand structure on all Level-II plots are comparable, and that study sites were different in their site characteristics but showed similar responses to moisture availability and similar growth synchrony characteristics, we conclude for the material we studied that similarities or differences in tree-ring width response were mainly driven by climatic conditions expressed as WB.

#### 4.3. Capacity to absorb disturbance

In this study we applied the concept of resilience and the concept of early-warning signals (AC(1), SD and spatial correlation) on tree-ring width data of Norway spruce. A decrease in tree-ring

width paralleled by an increase in AC(1) may be interpreted as an early-warning signal indicating the critical slowing down before a transition (e.g. Dakos et al., 2012). However, we found an increase in AC(1) just for study site Hei, the other study sites showed a decreasing AC(1). A decrease in tree-ring width associated with increased variation (SD) may as well be indicative of a critical slowing down before a transition (Carpenter and Brock, 2006). We found a temporal increase of SD on all study sites, the increase of SD accelerated around the time when moisture availability becomes below average. A major statistical challenge in applying early-warning signals in natural systems is to accurately estimate variance and autocorrelation in the face of limited data availability (Dakos et al., 2012). Accurate estimates of AC(1) require long time-series. We used annual time-series of 25 year periods which is a compromise between long enough time series and the data which is available for the period 1954–2004. This may be the reason, why an increase in AC(1) could not be detected for our study sites except Hei. Other authors have found as well no rising AC(1) prior to transition under strong noise conditions (Dakos et al., 2012). Another reason why we could not find an increase in AC(1) may be due to the ability of trees to buffering against climatic stress factors. It is concluded that the deteriorating effect of changing climate conditions on Norway spruce trees will result in a loss of their buffering ability in terms of growth response to drought stress (c.f. Beck and Müller, 2007). From a biological perspective the autocorrelation of a series of tree-ring width may be



**Fig. 3.** Time series of PC1 loadings and expressed population signal (EPS) calculated for 25 year periods starting in year 1954 and shifted in 1 year steps. Blue bars represent average moisture anomalies (reference period 1954–2004) for the preceding 25 years. For graphical reasons EPS values were reduced by a factor of 0.5. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

interpreted as an expression of the biological inheritance in terms of tree-ring formation. The decrease in  $AC(1)$  in our study material may therefore be indicative of a loss of buffering ability. In consequence this result indicated no adequate short-term adaptive capacity in tree-ring growth to changing climate conditions for the respective Norway spruce trees during the study period. Further research is necessary concerning the reliability of  $AC(1)$  as early-warning signal for tree-ring data.

Most research work on early-warning signals for critical transitions has focussed on simple models and controlled experiments (Scheffer et al., 2009). Some investigations into highly complex real systems found that some signals are robust in the sense that they arise despite high complexity and noisiness (e.g. Alley et al., 2003; Dakos et al., 2008). Generally, a shift that is caused by an abrupt and permanent change of external conditions may not be indicated by early-warning signals, the same may hold if the perturbation regime changes over time (Scheffer et al., 2009).

The use of spatial information may help to improve the diagnosis of early warning signals (Dakos et al., 2011). It could be shown that spatial correlation could provide a stronger warning signal than temporal autocorrelation (Dakos et al., 2010). We analysed the spatial correlation of PC1 loadings and EPS among the sample trees of each study site. Our results showed an enhancement of growth synchronicity among the trees of each study site which is highly correlated to changes in moisture availability. It is concluded that the decreasing water availability from around the period '1965–1989' onwards has increasingly limited tree-ring

formation at all study sites. This is indicated by the well corresponding starting point of enhancement of growth synchronicity. However at the beginning of the study period some study sites showed as well high values for PC1 and EPS. In times of favourable growing conditions in terms of moisture availability, the trees may tend as well to grow more synchronous. By exclusively considering spatial correlation as indicator for shifts this effect could lead to false conclusions.

In conclusion, early-warning signals appeared for our study material in combination with signs of a loss of buffering ability and an increase in spatial correlation. Therefore we assume that presumably due to the sequence of more severe climatic events the buffering ability of Norway spruce and the capacity to absorb disturbance in terms of their growth response to respective moisture conditions decreased for our study period. The loss of growth resilience made Norway spruce more fragile in the sense that it can more easily be tipped into a contrasting state, through stochastic events such as drought. As Spiecker (1995) showed, there exists a significant relation between drought stress induced growth depressions and mortality of Norway spruce in Southwestern Germany. The growth reactions were rather similar on all sites even so the climatic water balance of the study sites varied. Therefore we conclude that Norway spruce trees were able to adapt to average site conditions on the different study sites. Growth reaction was similar especially when exposed to extreme climatic events. In the long run Norway spruce may be as well able to adapt to changing average conditions, but the adaptive capacity to sudden

changes such as higher frequency of more severe droughts is rather limited.

The negative trend in moisture availability is expected to amplify in the future (Spekat et al., 2007). The study confirmed that Norway spruce is a drought sensitive species. Even a moderate change in hydro-climatic conditions leading to reduced water availability is expected to increase the risk of growth depressions and mortality in those areas outside the natural range of Norway spruce. Anticipated accompanying changes in disturbance regimes such as storms, insects and pathogens will most probably have further contributing and/or triggering effects on already predisposed Norway spruce.

We showed for our study material a loss of growth resilience and stress response of Norway spruce in terms of their growth response to respective moisture conditions. Only by short-term adaptation and plasticity Norway spruce trees are able to counteract the threat of growth depressions and mortality under less suitable climate conditions (Lindner et al., 2010). But those natural processes alone are too slow to cope with the intensity and frequency of extreme drought events. Extreme events may weaken Norway spruce on sites representative for most of the sites where Norway spruce can be found today. Understanding the resilience is crucial for further management of Norway spruce stands, as inherent adaptive capacity can be supported with planned adaptation measures (Lindner et al., 2010). Stochastic events are difficult to predict or to control. Therefore, building and maintaining resilience of Norway spruce stands by sustaining stability is likely the most pragmatic and effective way to manage these stands in the face of increasing environmental change.

Further management efforts are necessary to either maintain this economically important species outside its natural range or to support the regeneration of more adapted species. At individual tree level, thinning could be used to increase tree resistance to drought stress (Mission et al., 2003). In the recent past several authors already recommended transformation by stabilising Norway spruce stands grown under narrow spacing (Hanewinkel, 1996; Schütz, 1999; Spiecker, 2000). Diversity in forest structures and silviculture may support the adaptive capacity and resilience of those vulnerable Norway spruce stands.

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