Published in final edited form as:

Trees (Berl West). 2013 February ; 27(1): 61–69. doi:10.1007/s00468-012-0768-6.

Drought sensitivity of three co-occurring conifers within a dry inner Alpine environment

Roman Schuster and Walter Oberhuber*

Leopold-Franzens-University of Innsbruck, Institute of Botany, Sternwartestrasse 15, A-6020 Innsbruck, Austria

Abstract

We applied dendroclimatological techniques to determine long-term stationarity of climate-growth relationships and recent growth trends of three widespread coniferous tree species of the central Austrian Alps, which grow intermixed at dry-mesic sites within a dry inner Alpine environment (750 m asl). Time series of annual increments were developed from > 120 mature trees of *Picea abies*, *Larix decidua* and *Pinus sylvestris*. Calculation of response functions for the period 1911 – 2009 revealed significant differences among species in response to climate variables. While precipitation in May – June favoured radial growth of *Picea abies* and *Larix decidua*, *Pinus sylvestris* growth mainly depended on April – May precipitation. *P. abies* growth was most sensitive to May – June temperature (inverse relationship). Moving response function coefficients indicated increasing drought sensitivity of all species in recent decades, which is related to a decline in soil moisture availability due to increasing stand density and tree size and higher evapotranspiration rates in a warmer climate. While recent trend in basal area increment (BAI) of *L. decidua* distinctly declined implying high vulnerability to drought stress, moderately shade-tolerant *P. abies* showed steadily increasing BAI and quite constant BAI was maintained in drought adapted *P. sylvestris*, although at lowest level of all species. We conclude that synergistic effects of stand dynamics and climate warming increased drought sensitivity, which changed competitive strength of co-occurring conifers due to differences in inherent adaptive capacity.

Keywords

Basal area increment; Dendroclimatology; Inner Alpine valley; Radial growth; Moving response function; Tree-ring analysis

Introduction

Drought triggers temporary declines and mortality of susceptible or less competitive species in temperate forests (e.g., Bigler et al. 2006; Van Mantgem et al. 2009). In montane forests of inner Alpine dry valleys of the European Alps, species-specific seasonal differentiation of radial growth response to moisture availability and climate extremes were reported (Pichler and Oberhuber 2007; Weber et al. 2007). Battipaglia et al. (2009) and Bouriaud and Popa (2009) also found a clear difference in the response pattern to drought among sympatric coniferous species at a dry site in Southern Italy and in the Eastern Carpathian mountains, respectively. These and several other studies (see Bréda et al. 2006; Reyer et al. 2010) indicate interspecies differences in drought resistance, which will affect the development of

* Author for correspondence: Walter Oberhuber, Phone: +43-(0)512 507 5948, Fax: +43-(0)512 507 2715, Walter.Oberhuber@uibk.ac.at.

forest ecosystems under a changing climate regime by changing species composition and inducing shifts in forest distribution.

Radial growth indices are known to be valuable long-term measures of overall tree vigor (Dobbertin 2005) and dendroclimatological methods are frequently applied to identify the climatic factors most closely associated with variations in tree-ring parameters (Fritts 1976). Based on several dendroclimatological studies conducted within dry inner Alpine valleys, it is well established that radial growth of trees is primarily limited by spring precipitation (e.g., Oberhuber and Kofler 2002; Rigling et al. 2002) and severe drought during the growing season results in long-lasting growth reductions and increased tree mortality (Oberhuber 2001; Rebetez and Dobbertin 2004). Computer models of global climate change predict a significant warming during next decades, changes in seasonal precipitation pattern and an increase in both frequency and intensity of severe droughts in the future (IPCC 2007). Even if precipitation amounts increase slightly, conditions may become drier because higher temperatures lead to increased potential evapotranspiration. Furthermore, it has to be noted that in the Alpine area climate warming in the 20th-century was 2–3 times greater than the global average (Jungo and Beniston 2001). Concerns regarding effects on vegetation have been amplified, because Rebetez and Dobbertin (2004) reported that mortality rates of *P. sylvestris* within the Swiss Rhône valley substantially increased in recent decades and rates of change are expected to occur more rapidly than past successional processes (Overpeck et al. 1991). Hence, a better understanding of forest ecosystem functioning will improve mechanistic modelling of mixed coniferous stands under changing environmental conditions.

Dendroclimatological studies conducted by Büntgen et al. (2006) and Carrer and Urbinati (2006) revealed changes in tree-ring-climate relationships of Norway spruce (*Picea abies* (L.) Karst.) and European larch (*Larix decidua* Mill.), respectively, at high-elevation sites. Although non-stationary responses of tree-ring growth to climate variables in coniferous species might also occur at low altitude sites exposed to drought, comparable studies are still missing. To identify interspecies differences in climate-growth relationships and vulnerability to climate change, mixed species stands will have to be analysed, because topography and local edaphic conditions have frequently been shown to modulate tree response to climate (Orwig and Abrams 1997; Fekedulegn et al. 2003). Therefore, the focus of this study was to compare growth limiting climate variables, long-term stationarity of climate-growth relationships and recent growth trends of co-occurring *P. abies*, Scots pine (*Pinus sylvestris* L.) and *L. decidua*, which comprise major coniferous species in the Alps. Selected species show different successional and phenological traits, whereby evergreen *P. sylvestris* and deciduous *L. decidua* are light-demanding species dominating in early successional stages, while evergreen *P. abies* is a moderately shade-tolerant tree, which predominates in the late successional stage (Ellenberg and Leuschner 2010). We hypothesized that (i) interspecies differences in growth response to climate exist and (ii) climate warming causes increasing sensitivity to drought stress and competitive advantage of drought adapted *P. sylvestris* over *L. decidua* and *P. abies* in recent decades.

Materials and methods

Site description

The study site is part of a postglacial rock-slide area situated in the montane belt (c. 750 m asl) within the inner Alpine dry valley of the Inn River (Tyrol, Austria, 47° 14' 00" N, 10° 50' 20" E) and has a relatively continental climate with mean annual precipitation and temperature of 716 mm and 7.3 °C, respectively (long-term mean during 1911–2008 at Ötz, 812 m asl, 5 km from the study area). Daily precipitation records within the study area during 2007 – 2011 revealed that on 65.1 % of days with precipitation during April through

September the amount of rainfall was < 5 mm. The dominating plant community is an open Spring Heath-Pine wood (*Erico-Pinetum typicum*), which is widespread on dolomitic and calcareous parent material within inner Alpine dry valleys (Ellenberg and Leuschner 2010). On scattered dry-mesic sites, mixed stands composed of *P. sylvestris*, *P. abies* and *L. decidua* with c. 60, 20 and 20 % dispersion, respectively are developed, whereby all species occupy the dominant strata together (c. 70 % canopy coverage; stand height 12–15 m). Mean tree age is 150 yr with the exception of *P. abies*, which is splitted in a 138 yr (*P. abies-o*) and 90 yr age group (*P. abies-y*) (Table 1). Site topographic conditions include primarily hollows and north facing slopes (slope angle $5 - 20^\circ$), where a thick moss layer dominates the understory indicating moister conditions. Shallow soils of protorendzina type, i.e., rendzic leptosols according to the FAO classification system (FAO 2006), are developed and consist of unconsolidated, coarse-textured materials with low water holding capacity (soil depth 15 – 20 cm).

Field collection, sample preparation, chronology development and statistics Because chronology development was focused on establishing homogeneous and comparable age classes more than 45 dominant trees of each species, free of major stem or crown anomalies due to wind or snow breakage were sampled. We avoided stands disturbed by anthropogenic influences in order to be able to focus on differences in climate-growth relationships among co-occurring species. Diameter at breast height of sampled trees was 23 ± 6 cm (*P. abies-o*), 20 ± 9 cm (*P. abies-y*), 28 ± 5 cm (*P. sylvestris*) and 40 ± 13 cm (*L. decidua*). To minimize damage to living trees within the nature reserve, one core sample was extracted with an increment borer at 1.3 m of each tree. Cores were taken parallel to the contour line to avoid stem areas with reaction wood. In the laboratory increment cores were air-dried, glued in grooved wooden mounts and the surface prepared with a sharp razor-blade. Ring widths were measured to the nearest $1 \mu\text{m}$ under up to $60\times$ magnification using an incremental measuring table. The correct dating of tree ring series was checked using COFECHA (Grissino-Mayer 2001). Tree ring-series of each species from scattered mixed stands were averaged, a process which was justified by high cross-correlation among cores.

Climate-growth relationships were explored based on residual ring width chronologies, which were calculated using ARSTAN (Holmes 1994). Conservative detrending techniques (negative exponential curve or linear regression) were employed to remove non-climatic factors like tree aging and forest stand development in the tree-ring data (Fritts 1976). Dimensionless indices were formed by dividing the observed by the predicted ring width values. Residual chronologies were derived from first-order autoregressive modelling, with a robust mean value function applied to discount the effect of statistical outliers (Holmes 1994). Several statistics were calculated for the standardized chronologies, prior to autoregressive modelling. The standard deviation (SD) measures the variability of the measurements at all wave lengths. Mean sensitivity is a measure of the mean relative change between adjacent ring-widths and is calculated as the absolute differences between adjacent indices divided by the mean of the two indices (Fritts 1976). The first-order autocorrelation assesses relationships with previous growth. To estimate the signal strength, i.e. the amount of climatic information included in the developed chronologies, the signal-to-noise ratio (S/N ratio) and the expressed population signal (EPS; Wigley et al. 1984) were calculated. Though a specific range of EPS values cannot be given, Wigley et al. (1984) suggest a threshold of 0.85 as an acceptable statistical quality. Common variance in tree ring chronologies was estimated by the percentage of variance explained by the first component in principal component analysis (PCA). Higher common variance indicates a greater climatic influence on tree growth (Briffa and Jones 1990).

Computation of basal area index (BAI)

The use of ring width data to study long-term growth decline suffers from negative trend in ring series due to tree maturation (“age-trend”; Fritts 1976). Therefore, ring width was converted into BAI to remove variation in radial growth attributable to increasing circumference according to the formula:

$$BAI = \pi (R_n^2 - R_{n-1}^2),$$

where R is the radius of the tree inside bark and n is the year of tree ring formation. An estimate of bark thickness was used to estimate radius inside bark. Diameter at breast height (DBH) was measured at the time of core sampling. To examine the mean growth trend, BAI for each year was averaged over all individuals belonging to the same species. The BAI data were not standardized to preserve the long-term growth rate over the study period. Unlike in ring width series, age-related trends in BAI are generally positive and do not show a decreasing trend until trees begin to senesce (LeBlanc 1990). Hence, a negative trend in BAI can be regarded as a strong indication of a decline in tree growth (Pedersen 1998). To evaluate the effect of drought on tree growth, three drought years were selected based on long-term climate anomalies in April – June, i.e., the period which was found to be most limiting to radial stem growth of all species. Paired t -tests were used to compare BAI in drought years with BAI in prior year(s). Recovery after drought was analyzed by comparing BAI in year(s) before drought (pre-drought growth) with growth rate(s) after drought years (post-drought growth).

Climate-growth relationships

Climate-growth relationships were determined by applying the software package DENDROCLIM2002 (Biondi 1997; Biondi and Waikul 2004). Total monthly precipitation and mean monthly temperatures were collected at a meteorological station in Oetz (812 m asl; < 5 km from the study area) reaching back to 1911. Bootstrapped response coefficients were calculated for the period 1911 – 2009 and significantly influencing months were determined at $P = 0.05$. The climatic data set included mean monthly air temperature (°C) and total monthly precipitation (mm) from March of the year prior growth to October of the year of growth. We also combined rainfall and temperature into one single parameter representing a measure of precipitation effectiveness, the aridity index (AI) proposed by De Martonne (1926). The AI was calculated as $AI = P / (T + 10)$, where P is the sum of precipitation (mm) and T is mean air temperature (°C) of the periods April - June and July - August. AI indicates increasing aridity as indices diminish. Pearson correlations (r) were calculated for relationships between AI and residual ring width chronologies, whereby normal distribution of variables was tested. Temporal changes in climate-growth responses were evaluated by moving response function analyses (MRF), which are based on progressively shifting the period of a fixed number of years across time to compute the response coefficients. Predictors included March through July temperature and precipitation. To provide a sufficient number of degrees of freedom, the length of the calibration period was 35 yr. MRF produced a temporal set of coefficients for each monthly predictor, whereby statistical significance at $P = 0.05$ was tested using a bootstrap procedure (Biondi and Waikul 2004). MRF were arbitrarily plotted against the last year of the period.

Results

Chronology descriptive statistics

Four tree-ring chronologies of trees co-occurring in mixed stands were developed, whereby ring series of *L. decidua* and *P. sylvestris* showed a clear age-related exponential decrease in

ring width (Fig. 1a). Up to late 1930s radial growth of *L. decidua* was most intense compared to other species. In recent decades, however, ring widths of *L. decidua* were rather low, while those of *P. abies* gradually increased after about 1960. Residual ring width chronologies used for calculation of climate-growth relationships are depicted in Fig. 1b, whereby the period prior to 1911 was not considered in response functions analyses in order to match the length of the climate record used. Mean sensitivity ranged between 17 % (*P. sylvestris*) and 23 % (*L. decidua*). First-order autocorrelation indicate that radial growth of *L. decidua* was most strongly influenced by conditions in the preceding year. Principal component analyses on the individual samples from each chronology showed that the variance accounted for by PC1 varied between 38 % (*P. sylvestris*) and 57 % (*P. abies-y*). All chronologies showed EPS-values which clearly exceeded the suggested threshold of 0.85 indicating a strong climate signal in chronologies; high SNR values support this notion (Table 1).

Climate forcing of radial growth

Calculation of response functions revealed that the dominant climate factors controlling radial growth of *P. abies* were precipitation and temperature (direct and inverse relationship, respectively) in current May – June (Fig. 2). High precipitation in May – June also favoured growth of *L. decidua*. Incremental growth of *L. decidua* was also significantly limited by high temperatures in current February and June. Radial growth of *P. sylvestris* was favoured by moist conditions in April – May and low temperatures in May (Fig. 2). Significant precipitation coefficients in June (direct) and July (inverse) of the previous year were found for *L. decidua* and *P. sylvestris*, respectively. Furthermore, *P. abies-o* and *P. sylvestris* showed direct relationship with previous December temperature. Pearson correlations between chronologies and April – June AI revealed highly significant coefficients ($P < 0.001$) for all species, whereby coefficients for *P. abies-o*, *P. abies-y*, *P. sylvestris* and *L. decidua* were 0.595, 0.608, 0.554 and 0.515, respectively. No significant correlations were detected between AI and ring width series for the period July – August.

MRF provided a dynamic perspective on the evolution of growth response to key climate variables (Fig. 3). Strong and largely stable climatic signals of *P. abies* growth (both age classes) were an inverse response to June temperature and direct response to May precipitation. The strength of the direct relationship between June precipitation and ring width series of *P. abies* increased in recent decades and became significant when the calibration interval ended in the early 1980s. April precipitation significantly influenced radial growth of *P. sylvestris*, when the calibration interval ended around 1970. The strength of the negative relationship between June temperature and *P. sylvestris* ring series increased in recent decades and became finally significant. Influence of May precipitation on growth of *L. decidua* increased, while significant coefficients of June temperature were scattered up to mid 1970s and in recent years.

Long-term anomalies in April – June precipitation, temperature and AI are depicted in Fig. 4. While air temperature remarkably deviated from 1961 – 1990 mean (11.2 ± 0.8 °C) around 1950 and showed an increasing warming trend since early 1990s, precipitation showed only short-term deviations from 1961 – 1990 mean (203 ± 39 mm), while a clear long-term trend is not obvious. During 1911 – 2009 AI was lowest in 1941, 1952 and 2004 showing a deviation of -45.0 , -47.2 and -54.3 %, respectively, compared to 1961 – 1990 mean.

Long- and short-term basal area growth

Basal area growth (BAI) was highest for *L. decidua* and showed a fluctuating pattern with a sharp decline after early 1980s (Fig. 5). In contrast, BAI of both age classes of *P. abies* was

consistently and strikingly increasing after early 1960s. BAI of *P. sylvestris* increased slightly from 1900 to 1960, but remained quite constant in recent decades. In comparison to mean BAI 3-yr prior drought, BAI in all drought years was reduced, whereby growth reduction in 1952 and 2004 was not significant for *P. abies*-y (Table 2). *P. sylvestris* showed significant growth reduction in all drought years, irrespective whether compared to BAI of prior year or mean of three previous years. Although April – June precipitation was lowest in 2004, BAI decline was less than in 1952 in all species. On the other hand, BAI recovered most strongly from drought which occurred in 1952, whereby mean BAI 3-yr post-drought increased between 13 and 42 % compared to 3-yr growth prior to drought. Growth decline after 1941 drought recovered within 3 years in all species. Growth comparison before and after drought years revealed that all species did not recover following the drought in 2004 ($P < 0.01$).

Discussion

Species growth responses to climate

At xeric sites in inner Alpine valleys of the European Alps several studies revealed that drought occurring during the growing season has a strong impact on radial stem growth of coniferous and deciduous trees (Oberhuber and Kofler 2002; Zweifel et al. 2006; Eilmann et al. 2009). In this study we also found that precipitation is the primary growth-limiting factor for all three conifer species growing intermixed at dry-mesic sites. Statistics of ring width series revealed quite lower values of mean sensitivity and common variance accounted for by the first EV of *P. sylvestris* compared to *L. decidua* and *P. abies*, which is indicative of a lower climatic influence on radial growth of the former species. This finding suggests that *P. sylvestris* is better adapted to temporary drought at dry-mesic sites. Because climate-growth relationships revealed significant differences among species in response to year-to-year variability of climate, results confirm our first hypothesis that differences in phenological and successional traits induce species-specific growth responses to climate variability. While precipitation in May – June favoured radial growth of *P. abies* and *L. decidua*, *P. sylvestris* growth mainly depended on April – May precipitation. Significant negative response coefficients found between temperature in May and June and annual increments suggest that *P. abies* growth is most strongly limited by high temperatures. Since high temperatures stimulate evapotranspiration rates, water availability is further constrained within the study area, which is characterized by low soil water content of shallow and stony soils. This is in agreement with other studies in temperate forests at low elevation, which found that above average temperatures induce negative growth responses (Battipaglia et al. 2009; Linares and Tíscar 2010).

Climate-growth response patterns also denote the influence of climate conditions during the previous year on current year growth. In *L. decidua*, previous June precipitation might favour carbon storage, root growth or bud development, while the inverse relationship with previous July precipitation and *P. sylvestris* growth could result from a delay in the switch from growth to storage due to favourable environmental conditions. While we are not aware of a physiological explanation of previous December temperature (direct relationship) on next year radial growth of *P. sylvestris* and *P. abies* when considering mean air temperature in December of -1.85 ± 1.8 °C (long-term mean 1911 - 2009), inverse relationship with current temperature in February (-1.06 ± 2.5 °C) and growth of *L. decidua* might be related to respiration of stored carbon and/or early snow melt, which might decrease carbon availability and soil moisture content, respectively, at start of the growing season.

Long-term non-stationarity of climate-growth relationships

MRF indicate that sensitivity to precipitation of all species increased in recent decades, although a decreasing trend in April – June precipitation or increasing aridity is not obvious within the study area. Voelker (2011) reported age-dependence of radial growth rate to precipitation for tree ages less than 50 yr, which the author explained by changes in rooting depth during first few decades of a tree's life. These early growth stages found to be sensitive to precipitation were not included in our MRF-analyses. MRF were determined during the last century of c. 150 yr old *P. sylvestris* and *L. decidua* (cambium age at breast height). Furthermore, both age classes of *P. abies* showed increasing sensitivity to June precipitation and temperature, indicating that in our study age related effects on instability of climate-growth relationships can be excluded. However, we refrain from arguing that higher sensitivity to precipitation and temperature is solely caused by recent warming trend, which might have increased water loss by stimulating evapotranspiration, because trends in temperature and sensitivity to climate variables are offset in time by several decades. Rather, increasing competition for scarce water and nutrients with increasing stand density and enlarging tree size might explain higher sensitivity to precipitation and temperature of all species in recent decades. This is consistent with findings of Mérian and Lebourgeois (2011) in a multi-species analysis of size-mediated climate-growth relationships. Authors report that generally larger trees were more sensitive to drought than smaller trees especially under xeric climate, which might be explained by increase in hydraulic constraints and nutrient limitation as trees grow taller (Anfodillo et al. 2006; Ryan et al. 2006; Martínez-Vilalta et al. 2007). In this regard, the step-wise increase of growth sensitivity of *L. decidua* and *P. abies* to precipitation in May and June, respectively, may suggest the presence of threshold-controlled mechanisms, which were reported to occur in high-altitude (Carrer and Urbinati 2006) and boreal species (Wilmking et al. 2004). Higher sensitivity of *P. sylvestris* growth to April precipitation might indicate earlier start of the growing period due to climate warming. This is supported by findings of Swidrak et al. (2011), who reported a minimum air temperature threshold for onset of xylem growth in *P. sylvestris* under drought and e.g., Studer et al. (2005) reporting earlier onset of phenological phases in spring due to global warming.

Growth response to climate extremes and interspecific competition

Significant growth decline in selected drought years indicate that irrespective of environmental conditions in prior years, radial stem growth of all species is sensitive to drought during current April – June. Moist conditions after the spring drought event in 1952 caused a short-term growth recovery, whereby *P. abies* was most responsive. Because lag-effects of drought stress extending 3 yr are not apparent after 1941 and 1952 drought, it can be assumed that trees within the study area respond immediately to favourable climate. We explain long-term growth reductions seen after most intense drought in 2004 by surpassing of a physiological threshold, whereby the heat-wave of summer 2003 (Beniston 2004) might have negatively preconditioned trees. This interpretation is in agreement with results reported by Bigler et al. (2006), who found that single drought years had a reversible effect on growth, while multi-year drought caused prolonged growth decreases. That growth of *P. abies* of both age classes decreased least and recovered most after 1952 and 2004 drought events indicates competitive strength of this late successional species.

Although climate-growth relationships show increasing sensitivity to precipitation and temperature of all species, trend in BAI is strikingly different among species. Because no apparent influence of pathogens or insects on *L. decidua* trees are known within the study area, we suggest that recent successive loss of vigour in *L. decidua* trees is caused by high vulnerability to drought stress aggravated by increasing temperature. *L. decidua* is known to have a less efficient water-use compared to sympatric evergreen conifers (Gower and

Richards 1990) and influence of precipitation on growth of *Larix* sp. was also reported by Oleksyn and Fritts (1991) and Dulamsuren et al. (2010). Latter authors found that recent increase in aridity in Mongolia caused strongly decreasing annual increments in *Larix sibirica*. Similarly, Eilmann and Rigling (2012) reported that *L. decidua* lacks the ability to recover from drought years and seems to be maladjusted to dry conditions. Furthermore, increasingly denser stands are more favourable to moderately shade-tolerant *P. abies*, which may have imposed a further competitive stress on light demanding *L. decidua*.

Surprisingly, climate-growth relationships and long-term growth dynamics revealed no competitive advantage of drought adapted *P. sylvestris* compared to *P. abies*, forcing us to reject our second hypothesis. Results rather suggest that the superficial root system of *P. abies* might be more efficient in exploiting small rain events, which primarily increase soil water content in upper soil layers, and therefore improved competitive status of late successional *P. abies* compared to early successional (pioneer) conifers. Furthermore, micro-site heterogeneity of edaphic conditions, which were found to exert influence on susceptibility of trees to climatic stresses within the study area (Oberhuber and Kofler 2000) might exist and contribute to higher productivity of *P. abies*. Although a shift in tree-species composition of mixed coniferous stands is also indicated by scattered natural regeneration restricted to *P. abies* (data not shown), a successional shift to a forest dominated by *P. abies* is unlikely, because competition acts in the long term and *P. sylvestris* will benefit from declining water availability at dry-mesic sites due to high adaptability to drought-prone conditions and dominance at xeric sites within the study area. Hence, we presume that the observed recent growth increase of *P. abies* constitutes a temporary effect.

In summary, results revealed increasing drought sensitivity of all species, which differently influenced competitive strength of co-occurring conifers at a drought-prone inner Alpine site. The *P. abies*'s competitive strength on dry-mesic sites is most likely related to synergistic effects of shade-tolerance, efficient uptake of small rainfall events by fine roots distributed primarily in upper soil layers and high water use efficiency. Because influence of provenance on drought resistance of *P. abies* trees was reported by Grabner et al. (2010), the occurrence of a drought adapted provenance within the study area has to be considered. This issue and species-specific limitation of radial stem growth by insufficient carbon supply and/or occurrence of tree water deficit during drought will have to be assessed through detailed ecophysiological studies.

Acknowledgments

This work was supported by the Austrian Science Fund (FWF Project No. P22280-B16 "Conifer radial stem growth in response to drought"). We thank Julia Mennel for help with measurement of tree-ring width and Sergio Rossi for discussion. We greatly acknowledge Hydrographischer Dienst, Innsbruck, for providing us the climate data.

References

- Anfodillo T, Carraro V, Carrer M, Fior C, Rossi S. Convergent tapering of xylem conduits in different woody species. *New Phytol.* 2006; 169:279–290. [PubMed: 16411931]
- Battipaglia G, Saurer M, Cherubini P, Siegwolf RTW, Cotrufo MF. Tree rings indicate different drought resistance of a native (*Abies alba* Mill.) and a nonnative (*Picea abies* (L.) Karst.) species co-occurring at a dry site in Southern Italy. *For Ecol Manage.* 2009; 257:820–828.
- Beniston M. The 2003 heat-wave in Europe: a shape of things to come? An analysis based on Swiss climatological data and model simulations. *Geophys Res Lett.* 2004; 31:2022–2026.
- Bigler C, Bräker OU, Bugmann H, Dobbertin M, Rigling A. Drought as an inciting mortality factor in Scots pine stands of the Valais, Switzerland. *Ecosystems.* 2006; 9:330–343.
- Biondi F. Evolutionary and moving response functions in dendroclimatology. *Dendrochronologia.* 1997; 15:139–150.

- Biondi F, Waikul K. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. *Comp Geosci*. 2004; 30:303–311.
- Bouriaud O, Popa I. Comparative dendroclimatic study of Scots pine, Norway spruce, and silver fir in the Vrancea Range, Eastern Carpathian Mountains. *Trees*. 2009; 23:95–106.
- Bréda N, Huc R, Granier A, Dreyer E. Temperate forest trees and stands under severe drought: a review of ecophysiological responses, adaptation processes and long-term consequences. *Ann For Sci*. 2006; 63:625–644.
- Briffa, KR.; Jones, PD. Basic chronology statistics and assessment. In: Cook, ER.; Kairiukstis, L., editors. *Methods of dendrochronology*. Kluwer, Dordrecht: 1990. p. 137–153.
- Büntgen U, Frank DC, Schmidhalter M, Neuwirth B, Seifert M, Esper J. Growth/climate response shift in a long subalpine spruce chronology. *Trees*. 2006; 20:99–110.
- Carrer M, Urbinati C. Long-term change in the sensitivity of tree-ring growth to climate forcing in *Larix decidua*. *New Phytol*. 2006; 170:861–872. [PubMed: 16684244]
- De Martonne E. L'indice d'aridité. *Bulletin de l'Association des Géographes Français*. 1926; 9:3–5.
- Dobbertin M. Tree growth as indicator of tree vitality and of tree reaction to environmental stress: a review. *Eur J For Res*. 2005; 124:319–333.
- Dulamsuren C, Hauck M, Leuschner C. Recent drought stress leads to growth reductions in *Larix sibirica* in the western Khentey, Mongolia. *Glob Change Biol*. 2010; 16:3024–3035.
- Eilmann B, Zweifel R, Buchmann N, Fonti P, Rigling A. Drought-induced adaptation of the xylem in Scots pine and pubescent oak. *Tree Physiol*. 2009; 29:1011–1020. [PubMed: 19483185]
- Eilmann B, Rigling A. Tree-growth analyses to estimate tree species' drought tolerance. *Tree Physiol*. 2012; 32:178–187. [PubMed: 22363071]
- Ellenberg, H.; Leuschner, C. *Vegetation Mitteleuropas mit den Alpen in ökologischer, dynamischer und historischer Sicht*. Ulmer; Stuttgart: 2010.
- FAO. *FAO, World Soil Resources Reports*. Vol. 103. Rome: 2006. World reference base for soil resources.
- Fekedulegn D, Hicks RR Jr, Colbert JJ. Influence of topographic aspect, precipitation and drought on radial growth of four major tree species in an Appalachian watershed. *For Ecol Manage*. 2003; 177:409–425.
- Fritts, HC. *Tree rings and climate*. Academic Press; London: 1976.
- Gower ST, Richards JH. Larches: deciduous conifers in an evergreen world. *Bioscience*. 1990; 40:818–826.
- Grabner, M.; Karanitsch-Ackerl, S.; Schüler, S. The influence of drought on density of Norway spruce wood. In: Kúdela, J.; Laga a, R., editors. *Wood structure and properties '10. Proceedings of the 6th IUFRO Symposium on "Wood structure and properties '10"*. Podbanské; Slovakia: 2010.
- Grissino-Mayer HD. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. *Tree-Ring Res*. 2001; 57:205–221.
- Holmes, RL. *Dendrochronology program library user's manual*. Laboratory of Tree-Ring Research University of Arizona; Tucson, USA: 1994.
- IPCC. Working group I: Contribution to the fourth assessment report of the Intergovernmental panel on climate change. Cambridge University Press; Cambridge: 2007. *Climate Change 2007: the physical science basis*.
- Jungo P, Beniston M. Changes in the anomalies of extreme temperature anomalies in the 20th Century at Swiss climatological stations located at different latitudes and altitudes. *Theor Appl Clim*. 2001; 69:1–12.
- LeBlanc DC. Relationships between breast-height and whole-stem growth indices for red spruce on Whiteface mountain, New York. *Can J For Res*. 1990; 20:1399–1407.
- Linares JC, Tíscar PA. Climate change impacts and vulnerability of the southern populations of *Pinus nigra* subsp. *salzmannii*. *Tree Physiol*. 2010; 30:795–806. [PubMed: 20522420]
- Martínez-Vilalta J, Vanderklein D, Mencuccini M. Tree height and age-related decline in growth in Scots pine (*Pinus sylvestris* L.). *Oecologia*. 2007; 150:529–544. [PubMed: 16983553]
- Mérian P, Lebourgeois F. Size-mediated climate-growth relationships in temperate forests: A multi-species analysis. *For Ecol Manage*. 2011; 261:1382–1391.

- Oberhuber W, Kofler W. Topographic influences on radial growth of Scots pine (*Pinus sylvestris* L.) at small spatial scales. *Plant Ecol.* 2000; 146:231–240.
- Oberhuber W, Kofler W. Dendroclimatological spring rainfall reconstruction for an inner Alpine dry valley. *Theor Appl Climatol.* 2002; 71:97–106.
- Oberhuber W. The role of climate in the mortality of Scots pine (*Pinus sylvestris* L.) exposed to soil dryness. *Dendrochronologia.* 2001; 19:45–55.
- Oleksyn J, Fritts HC. Influence of climatic factors upon tree rings of *Larix decidua* and *L. decidua* x *L. kaempferi* from Pulawy, Poland. *Trees.* 1991; 5:75–82.
- Orwig DA, Abrams MD. Variation of radial growth responses to drought among species, site, and canopy strata. *Trees.* 1997; 11:474–484.
- Overpeck JT, Bartlein PJ, Webb T III. Potential magnitude of future vegetation change in eastern North America: comparisons with the past. *Science.* 1991; 254:692–695. [PubMed: 17774796]
- Pedersen BS. The role of stress in the mortality of Midwestern oaks as induced by growth prior to death. *Ecology.* 1998; 79:79–93.
- Pichler P, Oberhuber W. Radial growth response of coniferous forest trees in an inner Alpine environment to heat-wave in 2003. *For Ecol Manage.* 2007; 242:688–699.
- Rebetez M, Dobbertin M. Climate change may already threaten Scots pine stands in the Swiss Alps. *Theor Appl Clim.* 2004; 79:1–9.
- Reyer C, Lasch P, Mohren GMJ, Sterck FJ. Inter-specific competition in mixed forests of Douglas-fir (*Pseudotsuga menziesii*) and common beech (*Fagus sylvatica*) under climate change – a model-based analysis. *Ann For Sci.* 2010; 67:805. doi: 10.1051/forest/2010041.
- Rigling A, Bräker OU, Schneiter G, Schweingruber FH. Intra-annual tree-ring parameters indicating differences in drought stress of *Pinus sylvestris* forests within the Engadina in the Valais (Switzerland). *Plant Ecol.* 2002; 163:105–121.
- Ryan MG, Phillips N, Bond BJ. The hydraulic limitation hypothesis revisited. *Plant Cell Environ.* 2006; 29:367–381. [PubMed: 17080592]
- Studer S, Appenzeller C, Defila C. Inter-annual variability and decadal trends in alpine spring phenology: a multivariate analysis approach. *Clim Change.* 2005; 73:395–414.
- Swidrak I, Gruber A, Kofler W, Oberhuber W. Effects of environmental conditions on onset of xylem growth in *Pinus sylvestris* under drought. *Tree Physiol.* 2011; 31:483–493. [PubMed: 21593011]
- Van Mantgem PJ, Stephenson NL, Byrne JC, Daniels LD, Franklin JF, Fulé PZ, Harmon ME, Larson AJ, Smith JM, Taylor AH, Veblen TT. Widespread increase of tree mortality rates in the western United States. *Science.* 2009; 323:521–524. [PubMed: 19164752]
- Voelker, SL. Age-dependent changes in environmental influences on tree growth and their implications for forest responses to climate change. Size- and age-related changes in tree structure and function. In: Meinzer, FC.; Lachenbruch, B.; Dawson, TE., editors. *Tree Physiology*. Vol. 4. Springer; New York: 2011. p. 455–479.
- Weber P, Bugmann H, Rigling A. Radial growth responses to drought of *Pinus sylvestris* and *Quercus pubescens* in an inner-Alpine dry valley. *J Veg Sci.* 2007; 18:777–792.
- Wigley TM, Briffa KR, Jones PD. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. *J Clim Appl Meteor.* 1984; 23:201–213.
- Wilmking M, Juday GP, Barber VA, Zald HSJ. Recent climate warming forces contrasting growth responses of white spruce at treeline in Alaska through temperature thresholds. *Glob Change Biol.* 2004; 10:1724–1736.
- Zweifel R, Zeugin F, Zimmermann L, Newbery DM. Intra-annual radial growth and water relations of trees—implications towards a growth mechanism. *J Exp Bot.* 2006; 57:1445–1459. [PubMed: 16556628]

Fig. 1. (a) Ring width chronologies, (b) residual chronologies used as predictand in response functions and (c) sample depth (= number of trees included in chronologies), which is 5 for the period shown

Fig. 2. Response function analysis between residual chronologies and monthly precipitation and monthly mean temperature for the period 1911 – 2009. Symbols indicate significant relationships at $P = 0.05$

Fig. 3.

Moving 35-year response functions between key climate variables and residual chronologies for the period 1911 – 2009 (P = precipitation, T = temperature). For clarity, non-significant response functions of April precipitation and temperature for (a) *Picea abies*-o, (b) *Picea abies*-y and (d) *Larix decidua* are not shown. Symbols indicate significant relationships at P 0.05

Fig. 4.

Time-series plots of April – June (a) precipitation sum, (b) mean air temperature and (c) De Martonne aridity index (anomalies relative to the 1961 - 1990 average). Data were smoothed based on fast Fourier transform low-pass filter, whereby the number of points was set to five. Years 1941, 1952 and 2004, when April – June aridity was highest are indicated

Fig. 5. Mean annual basal area increment of co-occurring coniferous species (sample depth = 5 for the period shown, cf. Fig. 1). Data were smoothed based on fast Fourier transform low-pass filter, whereby the number of points was set to ten

Table 1

Statistics of developed ring-width chronologies (Autocorr = first-order autocorrelation, MS = mean sensitivity, SD = standard deviation, SNR = signal to noise ratio, EPS = expressed population signal, EV = eigenvector)

	Trees ^a (n)	Age ^b (years)	Ring width (μm)	Autocorr ^c	MS ^c	SD ^c	SNR ^c	EPS ^c	Variance first EV ^c (%)
<i>Picea abies-o</i>	21	138 $\pm$ 20	659 $\pm$ 191	0.33	0.19	0.17	22.5	0.96	55.8
<i>Picea abies-y</i>	20	90 $\pm$ 19	834 $\pm$ 252	0.17	0.20	0.17	17.1	0.95	57.1
<i>Pinus sylvestris</i>	42	152 $\pm$ 17	695 $\pm$ 180	0.23	0.17	0.14	23.2	0.96	38.1
<i>Larix decidua</i>	39	150 $\pm$ 17	911 $\pm$ 378	0.48	0.23	0.20	32.1	0.97	49.4

^aEach tree was cored radially and parallel to the contour line

^bCambial age at circa 1.3 m above ground

^cCalculated on the basis of standardized chronologies

Table 2

Growth decline and recovery (percent change in BAI) in response to April – June drought in 1941, 1952 and 2004 (cf. Fig. 5). Statistically significant differences of mean changes in BAI (paired *t*-test) are indicated (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$).

Species	Drought year vs.				Drought year vs.				Pre-drought vs.				3-yr pre-drought vs.			
	3-yr pre-drought				prior year				post-drought				3-yr post-drought			
	1941	1952	2004		1941	1952	2004		1941	1952	2004		1941	1952	2004	
<i>Picea abies</i> -o	-20**	-17***	-16*		-31***	-21*	+2		-19***	+8	-29***		-4	+36***	-15***	
<i>Picea abies</i> -y	-15**	-11	-12		-27***	-18**	0		-12**	0	-32***		+1	+42***	-16*	
<i>Pinus sylvestris</i>	-10**	-32***	-24***		-9*	-34***	-13**		-10**	0	-29***		-4	+13**	-37***	
<i>Larix decidua</i>	-23***	-36***	-14*		-37***	-26***	-7		-40***	+23**	-58***		-3	+29***	-33***	

Calculation of percent growth changes in BAI:

Drought year vs. 3-yr pre-drought (%) = $(BAI1 - BAI3)/BAI3 * 100$

Drought year vs. prior year (%) = $(BAI1 - BAI2)/BAI2 * 100$

Pre-drought vs. post-drought (%) = $(BAI4 - BAI2)/BAI2 * 100$

3-yr-pre-drought vs. 3-yr post-drought (%) = $(BAI5 - BAI3)/BAI3 * 100$

where, BAI1 = BAI in drought year, BAI2 = BAI 1 year prior drought; BAI 3 = average BAI of 3 years prior drought; BAI 4 = BAI 1 year after drought year; BAI 5 = average BAI of 3 years after drought.