Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco



Climate signal age effects—Evidence from young and old trees in the Swiss Engadin

Jan Esper^{a,b,*}, Rolf Niederer^a, Peter Bebi^c, David Frank^a

^a Swiss Federal Research Institute WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

^b Oeschger Centre for Climate Change Research, Erlachstrasse 9a, 3012 Bern, Switzerland

^c WSL Institute for Snow and Avalanche Research SLF, Flüelastrasse 11, 7260 Davos Dorf, Switzerland

ARTICLE INFO

Article history: Received 30 October 2007 Received in revised form 7 March 2008 Accepted 12 March 2008

Keywords: Growth trends Tree-rings Climate reconstruction European Alps Pinus cembra

ABSTRACT

A potential limitation of tree-ring based climate reconstructions is related to climate signal age effects (CSAE). CSAE may arise if the climatic response of young tree-rings differs from that of old tree-rings. This could mean that climatic signals become stronger (or weaker) with tree aging, or that the seasonality of signals or the sensitivity to a specific element (e.g., temperature, precipitation) changes over time. Such changes would affect the interpretation of dendroclimatic reconstructions, as the tree-rings included in these records are generally oldest at the end of a record (e.g., 21st century)—which is the time period generally used for calibration with instrumental data.

We here addressed this concern by analyzing young and old *Pinus cembra* trees from three high elevation sites in the central European Alps. Core and disc samples were collected in pre-defined plots to allow for a representative analysis of tree ages with tree-ring width (TRW) measurement series categorized into age classes (i) >1880, (ii) 1880–1939, and (iii) 1940–2002. Notably we report on the signal of the very young category (iii) not yet described in literature, and thus allow estimation of climate response and signal strength characteristics during the first years of the trees' lifespans.

Comparison of age classes (i)–(iii) revealed differences in TRW coherence and size, but little change in climatic signal. CSAE are in the order of the differences recorded among high elevation sites—a conclusion that holds for inter-annual to decadal scale TRW variations at near-treeline Swiss stone pine. Such data are typically included in regional and larger-scale temperature reconstructions; thus, our results add confidence to long-term climate estimates integrating a range of tree-ring age classes. Other findings, such as the reaction wood in juvenile tree-rings, and sensitivity of the climate signal to sample replication, suggest that comparisons of young and old age classes, and separate calibration of these categories against instrumental climate data might further the estimation of long-term uncertainty changes in tree-ring based climate reconstructions.

© 2008 Elsevier B.V. All rights reserved.

Forest Ecology and Management

1. Introduction

Tree-ring data from high elevation and northern environments are the most important proxy used to reconstruct climate variability over the past millennium (e.g., Briffa, 2000; Cook et al., 2004; D'Arrigo et al., 2006; Esper et al., 2002, 2004; IPCC, 2007). Some of these long-term records are composed of >1000year old living trees, such as the reconstructions from *Juniperus turkestanica* in central Asia (Esper et al., 2003b; Treydte et al., 2006), *Pinus longaeva* in southwestern USA (LaMarche, 1974), and *Cedrus atlantica* in northwestern Africa (Esper et al., 2007a). The majority of long-term climate reconstructions, however, are derived from a combination of samples from living trees with material from relict wood, such as preserved in moraine sediments and historical buildings, for example (e.g., Büntgen et al., 2005, 2006; Wilson et al., 2005; and references therein). Trees integrated in these composite records are generally younger – typically <200 years – and are combined into longer-term timeseries using a method known as crossdating, whereby the exact calendar year is assigned to each ring of all samples (Douglass, 1929).

Both types of chronologies, namely those composed of (a) living trees only, and (b) living trees and relict material, might be contaminated by climate signal age effects (CSAE). CSAE arise, if "juvenile" rings (i.e., those close to the pith) contain different climatic information than "adult" rings that are typically defined as being older than 50–100 years of cambial age. Climate reconstructions derived from mean chronologies integrating such data would

Corresponding author at: Swiss Federal Research Institute WSL, Zürcherstrasse
111, 8903 Birmensdorf, Switzerland. Tel.: +41 44 739 2510; fax: +41 44 739 2515.
E-mail address: esper@wsl.ch (J. Esper).

^{0378-1127/\$ –} see front matter @ 2008 Elsevier B.V. All rights reserved. doi:10.1016/j.foreco.2008.03.015

be biased with tree age related noise. In case of type (a) chronologies, this bias would change systematically in time, as the age of rings from only living trees decreases steadily into the past. For type (b) chronologies, CSAE would be less systematic as tree-ring age is often balanced by the relict wood samples entering the chronology back in time. See Cook and Kairiukstis (1990) and Fritts (1976) for details on chronology types and consequences on age structure.

Evidence for CSAE is reported from France (Grav. 1982). Italy (Carrer and Urbinati, 2004), and North America (Ettl and Peterson, 1995; Szeicz and MacDonald, 1994, 1995), for example. Other work, however, revealed no significant CSAE in the US and Canada (Fritts, 1976; Colenutt and Luckman, 1991) and Morocco (Esper et al., 2007a), calling for more systematic analyses of this phenomenon, its prevalence and magnitude, and potential consequences for dendroclimatic reconstructions. While some of the differences reported in the literature may be related to the specific site ecologies and species considered in the various studies, differing sampling strategies, methodological approaches, focus on specific frequencies, and simply thresholds for what is considered CSAE, could also account for the range of conclusions. Further discrepancies may arise because relatively generous definitions of "young" age classes (i.e., <150 or even <200 years), occasionally low sample replications, and non-systematic sampling strategies are common to some previous studies.

We here mitigate some limitations of previous approaches, by studying a large Swiss stone pine dataset from near-treeline sites. All trees were sampled in pre-defined plots to include all age classes. For this dataset, we analyze inter-annual to decadal scale tree-ring width (TRW) variations and climatic signals. We split the data into various age classes, including a sub-sample composed of trees younger than 45 years, and use this setup to test for potential CSAE. Outcome from this approach will be of use to estimate CSAE in existent TRW-based climate reconstructions, but might also stimulate inclusion of all age classes in future sampling campaigns and testing for potential CSAE in newly developed records.

2. Material and methods

2.1. Tree-ring data and age class categorization

Three sampling plots (Muo, Tam, Sil), located at elevations between 2140 and 2180 m some 50–100 m below local treeline, in the Swiss Engadin in the central European Alps were defined (Fig. 1 and Table 1). Sampling sites are composed of *Pinus cembra* L. on north-to-southeast oriented and relatively steep (35–55%) slopes. Canopy cover ranges 30–40%, indicative for fairly open high elevation stone pine stands (Kulakowski et al., 2006). Temperature and precipitation in these sites are most closely reflected by the nearby Bernina Pass meteorological station at 2256 m (Ber in Fig. 1). Accordingly, monthly temperatures range from -7 °C in January to +10 °C in August with an annual mean of about 0 °C, and annual precipitation likely being >1000 mm.

To achieve a collection of Swiss stone pine representative of the sites, including their age structures, we took core and disc samples at breast height from all trees in pre-defined plots. Plot sizes were chosen so that about 60 trees per site were collected. Additionally,

Table	e 1

Site and	l data	characteristics
----------	--------	-----------------



Fig. 1. Map showing the tree-ring sampling sites (dots), and meteorological stations (triangles) in the Swiss Engadin south of Davos.



Fig. 2. Sample depths of the four Engadin pine sites, Tam, Sil, and Muo. White numbers indicate core sample replication per site.

at each site we sampled 20 old trees just outside each plot to ensure a solid sample replication in the older portion of chronologies. This way, a total of 488 TRW measurement series from about 250 trees were developed, crossdated, and quality checked (Fritts, 1976; Schweingruber, 1983). Sample replication per site ranges from 141 to 177 cores, with both the oldest tree (dating back to 1478) and highest mean series length (206 years) found in Tam (Table 1). In cases where neither core sample from a tree contained the pith, we used the curvature of the innermost rings to estimate pith offset (Esper et al., 2003a; Villalba and Veblen, 1997).

Our sampling strategy resulted in dendrochronologically uncommon replication diagrams, characterized by increases in sample depth well into the 20th century (Fig. 2). Twentieth century data distribution curves of Muo and Sil are steeper, as relatively few young (<50 years) *P. cembra* were found in Tam. This difference had an effect on the number of age classes per site, as too

Site	Elevation (m asl)	Aspect	Inclination (%)	Vegetation cover (%)	Number of cores	Mean series length (years)	Maximum length	Chronology length $(n > 4 \text{ series})$
Muo	2180	North	35	50	141	125	1662	1582
Tam	2180	Northwest	50	50	177	206	1478	1564
Sil	2140	Southeast	55	40	170	140	1603	1660

Table 2	
Age class categories of the sites Muo ($3\times$), Tam ($2\times$), and Sil ($3\times$)	

Site	Age class	Period	Number of cores	GLK (%)
Muo	Old	1662-1879	68	70
Tam	Old	1478-1879	128	73
Sil	Old	1603-1879	87	73
Muo	Middle	1880-1939	35	70
Tam	Middle	1880-2002	49	72
Sil	Middle	1880-1939	47	71
Muo	Young	1940-2002	36	71
Sil	Young	1940-2002	38	73

Separation was done according to the dating of the innermost rings of core samples (see Fig. 2). GLK is Gleichläufigkeit.

few juvenile data were available in Tam to create a young group. For age class categorization, we considered the date of the innermost ring on a core or disc sample plus pith offset, to signify a young, middle, and old class in Muo and Sil, and a middle and old class in Tam, according to the periods \geq 1940, 1880–1939, and <1880 (Table 2). These age classes were defined to yield equally replicated young and middle categories with no class containing fewer than 35 TRW series. Sample replication of the old age classes is larger (up to 128 in Tam), which might support climate calibration results (Wigley et al., 1984).

2.2. Coherence analysis and calibration trials

Growth characteristics for each site and age class were assessed by analyzing the Gleichläufigkeit (GLK) and low frequency growth trends. GLK is a measure of high-frequency coherence between tree-ring data (Esper et al., 2001) and allows an estimation of common signals within age class sub-samples. The raw TRW measurement series were also aligned by biological (cambial) age (Esper et al., 2003a), averaged for each site and age class using the arithmetic mean, and the resulting records smoothed to emphasize long-term growth trends. These timeseries are shown together with the site and age class sample replication curves to allow for a straightforward comparison of time-dependent growth characteristics.

For the comparison of common variance and climatic signals among age classes, TRW data were detrended using relatively stiff fixed splines to remove tree-age related trends from the raw measurement series (Cook, 1985). TRW timeseries were treated using a data-adaptive power transformation to minimize spread versus level relationships (the ratio between growth rate and interannual variance) in the measurement series (Cook and Peters, 1997). We then calculated residuals between the transformed records and fitted splines. Application of these, or similar, splines also reduces centennial scale fluctuations, so that inter-annual to multi-decadal scale wavelengths are emphasized in the final chronologies (Cook et al., 1995). Mean site and age class chronologies of the detrended TRW data were calculated using the bi-weight robust mean, and the chronologies' variance stabilized considering the sample size and interseries correlation (Rbar) information (MEANr correction as in Frank et al., 2007b). Rbar is a measure of the internal coherence of single (indexed) measurement series combined in a mean chronology. To estimate changes of this coherence through time, we calculated Rbar in 30year moving windows.

For climate/growth calibration we used mean temperature data from six nearby meteorological stations: Bernina Pass, Bever, Buffalora, Samendan, Sils Maria, and Station Maria (Fig. 1), and combined these measurements with gridded temperature data extending back to 1820 (Böhm et al., 2001). Calibration trials included the correlation of monthly and seasonal temperature means against tree-ring chronologies over 1820–1979, 1880–1939, and 1940–1999, to allow for both analyses of temperature signals though time and comparison among the old, middle, and young age classes. We also considered precipitation data for calibration, but do not report details here, as temperature variations are the primary forcing for high elevation *P. cembra* stem productivity.

3. Results

3.1. Growth coherence

The GLK revealed fairly high and balanced results for all age classes (Table 2). GLK values \geq 70% are indicative of high levels of common variance, typical for alpine sampling sites (Frank and Esper, 2005a). Importantly, results of the young sub-samples (71 and 73%) were not poorer, as would perhaps be expected due to the increased mechanical stresses and potentially limited sensitivity to climatic constraints of young trees (see Section 4).

Average growth trends at sites Sil, Muo, and Tam are quite similar over the tree's full lifespans (Fig. 3A). TRW initially increases, reaching a maximum after about 50 years, and then decreases until about an age of 250 years, where site sample replications drop and growth curves become noisier. Growth at a cambial age of about 50 years is characterized by maximum differences among sites, with Sil possessing widest (1.63 mm), Muo medium (1.41 mm) and Tam minimum (1.26 mm) TRW. This range is, however, not extreme if compared with nearby lower elevation pines, which show a much earlier growth peak at about 20 years, and maximum TRW of only 0.84 mm (not shown).

Comparison of the age classes (Fig. 3B) indicated that the young trees at Sil grew much faster, at about 2.1 mm between 40 and 50 years, than the middle and old trees. This order was, however, not revealed in the other sites, in which either both the young and the middle (Muo), or only the middle sub-sample (Tam) indicate slower growth than recorded for the old class. These varying trends



Fig. 3. Growth trends in Sil, Muo, and Tam (A), and in the young, middle, and old age classes (B) except for Tam, where only two classes exist. Thin curves indicate growth trends; thick curves at the bottom of the panels are replication changes. All data aligned by biological age after consideration of pith offset.



Fig. 4. Site and age class chronologies and replication. (A) Tam, Sil, and Muo site chronologies spanning the past 3–4 centuries. Sample replication at the bottom of the panel. (B) Sample replication of the middle and young sub-samples, and age class chronologies back to 1880 at the bottom of the panel.

suggest that the high elevation pine data do not contain systematic, age-related growth difference indicative of CSAE. While growth rates of the young class at Sil were about twice that for Muo, growth of the old age classes is similar between these sites. Differences among mean site curves (Fig. 3A) are thus due to deviations in the young sub-samples in Sil and Muo, and overall slower growth of the middle and old classes in Tam.

The spline-detrended site chronologies showed quite similar variability, including common inter-annual (e.g., negative deviation in 1975) and decadal scale (e.g., the 1810s; Frank et al., 2007a) variations, over the past 300 years (Fig. 4A). Coherence between these records ranged from r = 0.71 (Sil–Muo) to r = 0.82 (Tam–Sil) over the well-replicated 1740–2002 period, and the most noticeable deviation was the recent negative trend seen in Sil since the late 1980s that is not reflected in Muo and Tam. Comparison of these site records with the age class chronologies (Fig. 4B) indicated slightly lower coherence among young, middle, and old data at each site, with correlations ranging from 0.50 to 0.73 over the 1940–2002 period. These reduced correlations, as well as the more substantial differences during earlier portions of the age class records – such as between the middle and old data at Sil – were likely affected by reduced sample replications (see top of panel 4B).

Evidence for small CSAE was reinforced through analyses of the variance retained in the decadal scale domain, indicating that inter-site and inter-age class coherences are similar (Fig. 5). The young, middle, and old records of the various sites, the running Rbar measurements, and the age class data averaged over the three sampling sites (Fig. 5A–C), all showed homogeneous and temporally stable coherency in most periods of the 20th century. Comparison of age class versus site chronologies (Fig. 5D) showed that decadal scale variations among the old, middle, and young records had comparable or even greater similarities than those among sites. While the age class records were characterized by an increased variability of the middle category before about 1940, a



Fig. 5. Decadal scale growth and temperature variations. (A) Growth trends of the old, middle, and young sub-samples in Tam, Sil, and Muo. (B) Thirty-year moving Rbar values. Horizontal dashed lines indicate correlations of 0.5. (C) Growth trends as in (A), but averaged over the three sampling sites. (D) Growth variations of the Tam, Sil, and Muo sites integrating all age classes. (E) Monthly and seasonal temperature timeseries. All data smoothed using a 7-year filter.

loss of coherence during the most recent period, largely caused by a (deviating) negative trend in Sil, is the most noticeable feature of the mean site curves.

3.2. Climate signals

Calibration against regional climate data demonstrated that growth of high elevation stone pine is largely controlled by temperature variations. TRW data from Muo, Tam, and Sil showed responses to previous year fall and current year summer temperatures, with July and JJA being most influential (Fig. 6).



Fig. 6. Monthly and seasonal climate/growth correlations for the Muo, Tam, and Sil mean site chronologies. Results over three periods (1820–1879, 1880–1939, 1940–1999) are shown.

While this seasonal pattern was similar among the high elevation sites, assessment over three distinct periods since 1820 revealed substantial alterations through time, including changes from significant to non-significant correlations and vice versa. Correlations at Sil were overall slightly lower, particularly for the early (<1880) and late (>1939) periods (e.g., JJA).

In comparison to these site-by-site correlation results, the separation of data into age classes and calibration over distinct periods supports the conclusion of small CSAE in these pine data (Fig. 7). Again, the seasonal pattern including positive association to previous year fall and current year summer was found to be similar among the various sub-samples. Temporal alterations between the two calibration periods were much larger, and again included changes from non-significant to significant correlations and vice versa. Examples include the correlation decline with June temperatures at all sites, and the increasing response to July temperatures at Muo and Tam. Importantly, these temporal modifications and the differences among age classes were in the order of variance typically



Fig. 7. Climate/growth correlations over two periods (1880–1939, 1940–1999) and for different age classes (old, middle, young).

found among tree sites (Fig. 6) and are not systematic. We did not find decay in climate response from old to young data, and, except for the June and JJA post-1940 results at Sil, no systematic tendencies were found between the early (1880–1939) and late (1940–1999) calibration periods.

As much of the climate signal in TRW data is typically retained in the decadal scale frequency domain (Frank and Esper, 2005b), analysis of the smoothed site and age class data together with the relevant temperature records allowed further estimation of potential CSAE (Fig. 5E). This comparison indicated the importance of warmth around 1970, which is reflected in all sites and age classes. This deviation is, however, only weakly developed in the July and JJA timeseries, but striking in the smoothed October temperatures. The negative trend since the late 1980s as seen in Sil, is not recorded in the July, JJA, and annual data, but pronounced in the SON and October means, perhaps indicating a seasonal shift in the climate response of this sampling site or drought stress. A similar feature is missing in the age class data though.

4. Discussion

To estimate CSAE in long-term tree-ring records, we analyzed growth variations and climate response in age class-categorized P. cembra TRW data from the Swiss Engadin. Overall, our results indicate little evidence for CSAE. Differences among age class records are in the same order as those among site records, adding some confidence to long-term temperature estimates derived from tree-ring material of changing age. Age class differences in our data were similar or even smaller than aspect-effects in high elevation P. cembra sites (Urbinati et al., 1997; Carrer et al., 2007), species differences within the Alps (Frank and Esper, 2005a; Frank et al., 2005), and within and between various species in other mountain systems (Büntgen et al., 2007; Esper et al., 2007b; Wilson et al., 2005). The results derived herein from high elevation *P. cembra* in the Alps, are not necessarily indicative for other species, site ecologies, or other tree-ring parameters, such as maximum latewood density (Büntgen et al., 2006) and stable isotopes (Trevdte et al., 2006, 2007). We recommend testing to confirm or refute the general applicability of these results.

Our analysis revealed minimal CSAE in trees younger than 60 years. This finding is surprising as the climatic signal of these young trees is most prone to reaction wood contamination resulting from snow, geomorphic, and wind stresses (Fig. 8).



Fig. 8. Disc sample of a 21-year *Pinus cembra* L. from the Engadin including sequences of compression wood rings; a common feature in young tree-ring material.

However, as these anatomical indicators of increased mechanical stresses were frequent in young tree-rings, and quite sizeable (though non-systematic) growth rate differences were recorded between young and old trees, we still recommend caution for potential CSAE in palaeoclimatology. Sampling both old and young trees in field campaigns and checking for CSAE in existing chronologies should be considered, whenever feasible.

We note that our findings are not fully in line with other studies on CSAE in stone pine (Carrer and Urbinati, 2004) and other species (Ettl and Peterson, 1995; Gray, 1982; Szeicz and MacDonald, 1994, 1995), as we did not find systematic decreases in climatic sensitivity in younger trees. In fact, the analyses carried out here revealed common variance independent of age, and most importantly the absence of systematic patterns in growth or climate response related to age. This differing conclusion is most likely related to sample replication that was fairly high in our analysis; i.e., >35 radii in all age class sub-samples, and our consideration of natural between-site variability. If correct, this notion would suggest that CSAE are replication-sensitive in a way that more data are required from young trees to reach comparable signal strengths than contained in old trees-or that above a certain replication threshold CSAE diminish. Even though our study alone does not support this hypothesis, some systematic analysis of possible replication effects seems advisable.

Potential physiological causes for CSAE (see Carrer and Urbinati, 2004, for a comprehensive overview) include reduced hydraulic resistances (Ryan and Yoder, 1997) and increased photosynthetic rates (Hubbard et al., 1999) in younger, i.e., smaller, trees. Sizerelated hydraulic constraints typically affect water supply necessary for transpiration, which in turn influences stomatal conductance (Bond, 2000; Kolb and Stone, 2000). For young trees, these hydraulic constraints are smaller, resulting in overall higher photosynthetic rates (Yoder et al., 1994), larger TRW, and potentially reduced climatic sensitivity. While fewer constraints and increased photosynthesis are good arguments for faster juvenile growth (besides geometric reasons), they do not necessarily apply as arguments for less sensitive juvenile tree-rings, however. If the juvenile rings were less climatically sensitive, we would expect a reduced inter-annual variance-a condition not observed. In fact, it appears more likely that increased mechanical stresses superpose the climatic signal in juvenile tree-rings-an assumption, in line with the non-complacent but noisy juvenile TRW sequences. As this noise is largely random the timing and extent of reaction wood vary from tree to tree - its influence on mean timeseries is likely decreasing with increasing sample replication, and diminished above a certain threshold as applied in this current study.

An unexpected but noticeable component in the analysis of high elevation *P. cembra* trees was the negative growth trend recorded over the most recent decade in the south-exposed site Sil, a feature not revealed in the other sites analyzed here, and also uncommon if related to evidence from other valleys in the European Alps (Frank and Esper, 2005a). This deviating trend was likely affected by a weakening of the climatic signal and/or shift in response seasonality, a conclusion supported by the climate correlation results and comparison of smoothed growth and temperature data. While achievement of a more conclusive answer on the cause of this trend divergence requires further research, our analysis clearly showed that similar deviations of this magnitude are not observed between differently old trees.

Acknowledgements

We thank Ulf Büntgen, Daniel Nievergelt, and Kerstin Treydte for discussion. Supported by the EC project Millennium (Grant No. 017008), and the SNSF through the National Centre for Competence in Climate Research (NCCR-Climate).

References

- Böhm, R., Auer, I., Brunetti, M., Maugeri, M., Nanni, T., Schöner, W., 2001. Regional temperature variability in the European Alps: 1760–1998 from homogenized instrumental time series. Int. J. Climatol. 21, 1779–1801.
- Bond, B., 2000. Age-related changes in photosynthesis of woody plants. Trends Plant Sci. 5. 349–353.
- Briffa, K.R., 2000. Annual climate variability in the Holocene-interpreting the message from ancient trees. Q. Sci. Rev. 19, 87–105.
- Büntgen, U., Esper, J., Frank, D.C., Nicolussi, K., Schmidhalter, M., 2005. A 1052-year tree-ring proxy for Alpine summer temperatures. Clim. Dyn. 25, 141–153.
- Büntgen, U., Frank, D.C., Nievergelt, D., Esper, J., 2006. Summer temperature variations in the European Alps, A.D. 755-2004. J. Clim. 19, 5606–5623.
- Büntgen, U., Frank, D.C., Kaczka, R.J., Verstege, A., Zwijacz-Kozica, T., Esper, J., 2007. Growth/climate response of a multi-species tree-ring network in the Western Carpathian Tatra Mountains, Poland and Slovakia. Tree Phys. 27, 689–702.
- Carrer, M., Urbinati, C., 2004. Age-dependent tree-ring growth responses to climate in *Larix decidua* and *Pinus cembra*. Ecology 85, 730–740.
- Carrer, M., Nola, P., Eduard, J.L., Motta, R., Urbinati, C., 2007. Regional variability of climate–growth relationships in *Pinus cembra* high elevation forests in the Alps. J. Ecol. 95, 1072–1083.
- Colenutt, M.E., Luckman, B.H., 1991. The dendrochronological characteristics of alpine larch. Can. J. For. Res. 25, 777–789.
- Cook, E.R., 1985. A Time Series Analysis Approach to Tree-ring Standardization. Lamont-Doherty Geological Observatory, New York.
- Cook, E.R., Kairiukstis, L.A., 1990. Methods of Dendrochronology–Applications in the Environmental Science. Kluwer, Dordrecht.
- Cook, E.R., Peters, K., 1997. Calculating unbiased tree-ring indices for the study of climatic and environmental change. Holocene 7, 361–370.
- Cook, E.R., Briffa, K.R., Meko, D.M., Graybill, D.A., Funkhouser, G., 1995. The 'segment length curse' in long tree-ring chronology development for palaeoclimatic studies. Holocene 5, 229–237.
- Cook, E.R., Esper, J., D'Arrigo, R., 2004. Extra-tropical Northern Hemisphere temperature variability over the past 1000 years. Q. Sci. Rev. 23, 2063–2074.
- D'Arrigo, R., Wilson, R., Jacoby, G., 2006. On the long-term context for late twentieth century warming. J. Geophys. Res. 111, D03103.
- Douglass, A.E., 1929. The secret of the Southwest solved by talkative tree rings. Nat. Geogr. Mag. 56, 736–770.
- Esper, J., Neuwirth, B., Treydte, K., 2001. A new parameter to evaluate temporal signal strength of tree ring chronologies. Dendrochronologia 19, 93–102.
- Esper, J., Cook, E.R., Schweingrüber, F.H., 2002. Low-frequency signals in long treering chronologies for reconstructing past temperature variability. Science 295, 2250–2253.
- Esper, J., Cook, E.R., Peters, K., Schweingruber, F.H., 2003a. Tests of the RCS method for preserving low-frequency variability in long tree-ring chronologies. Tree-Ring Res. 59, 81–98.
- Esper, J., Shiyatov, S.G., Mazepa, V.S., Wilson, R.J.S., Graybill, D.A., Funkhouser, G., 2003b. Temperature-sensitive Tien Shan tree ring chronologies show multicentennial growth trends. Clim. Dyn. 8, 699–706.
- Esper, J., Frank, D.C., Wilson, R.J.S., 2004. Temperature reconstructions—low frequency ambition and high frequency ratification. EOS 85 (113), 120.
- Esper, J., Frank, D.C., Büntgen, U., Verstege, A., Luterbacher, J., Xoplaki, E., 2007a. Long-term drought severity variations in Morocco. Geophys. Res. Lett. 34, doi:10.1029/2007GL030844.
- Esper, J., Frank, D.C., Wilson, R.J.S., Büntgen, U., Treydte, K., 2007b. Uniform growth trends among central Asian low and high elevation juniper tree sites. Trees 21, 141–150.
- Ettl, G.L., Peterson, D.L., 1995. Extreme climate and variation in tree growth: individualistic response in subalpine fir (*Abies lasiocarpa*). Glob. Change Biol. 1, 231–241.
- Frank, D., Esper, J., 2005a. Characterization and climate response patterns of a highelevation, multi-species tree-ring network for the European Alps. Dendrochronologia 22, 107–121.
- Frank, D., Esper, J., 2005b. Temperature reconstructions and comparisons with instrumental data from a tree-ring network for the European Alps. Int. J. Clim. 25, 1437–1454.
- Frank, D., Wilson, R., Esper, J., 2005. Synchronous variability changes in alpine temperature and tree-ring data over the last two centuries. Boreas 34, 498–505.
- Frank, D., Büntgen, U., Böhm, R., Maugeri, M., Esper, J., 2007a. Warmer early instrumental measurement versus colder reconstructed temperatures: shooting at a moving target. Q. Sci. Rev. 26, 3298–3310.
- Frank, D., Esper, J., Cook, E.R., 2007b. Adjustment for proxy number and coherence in a large-scale temperature reconstruction. Geophys. Res. Lett. 34, doi:10.1029/ 2007GL030571.
- Fritts, H.C., 1976. Tree Rings and Climate. Academic Press, New York.
- Gray, B.M., 1982. Comment on transfer functions. In: Hughes, M.K., Kelly, P.M., Pilcher, J.R., LaMarche, V.C. (Eds.), Climate from Tree Rings. Cambridge University Press, Cambridge, pp. 56–58.
- Hubbard, R.M., Bond, B.J., Ryan, M.G., 1999. Evidence that hydraulic conductance limits photosynthesis in old *Pinus ponderosa* trees. Tree Phys. 19, 165–172.

IPCC, 2007. Climate Change 2007-the Physical Science Basis. University Press, Cambridge.

- Kolb, T.E., Stone, J.E., 2000. Differences in leaf gas exchange and water relations among species and tree sizes in an Arizona pine-oak forest. Tree Phys. 20, 1–12.
- Kulakowski, D., Rixen, C., Bebi, P., 2006. Changes in forest structure and in the relative importance of climatic stress as a result of suppression of avalanche disturbances. For. Ecol. Manag. 223, 66–74.
- LaMarche Jr., V.C., 1974. Paleoclimatic inferences from long tree-ring records. Science 183, 1043–1048.
- Ryan, M.G., Yoder, B.J., 1997. Hydraulic limits to tree height and tree growth. BioScience 47, 235–242.
- Schweingruber, F.H., 1983. Der Jahrring-Standort, Methodik, Zeit und Klima in der Dendrochronologie. Haupt, Bern.
- Szeicz, J.M., MacDonald, G.M., 1994. Age-dependent tree-ring growth responses of subarctic white spruce to climate. Can. J. For. Res. 23, 120–132.
- Szeicz, J.M., MacDonald, G.M., 1995. Dendroclimatic reconstruction of summer temperatures in northwestern Canada since A.D. 1638 based on age-dependent modeling. Q. Res. 44, 257–266.

- Treydte, K., Schleser, G.H., Helle, G., Frank, D.C., Winiger, M., Haug, G.H., Esper, J., 2006. Millennium-long precipitation record from tree-ring oxygen isotopes in northern Pakistan. Nature 440, 1179–1182.
- Treydte, K., et al., 2007. Signal strength and climate calibration of a European treering isotope network. Geophys. Res. Lett. 34, doi:10.1029/2007GL031106.
- Urbinati, C., Carrer, M., Sudiro, S., 1997. Dendroclimatic response variability of *Pinus cembra* L. in upper timberline forests of Italian eastern Alps. Dendrochronologia 15, 101–117.
- Villalba, R., Veblen, T.T., 1997. Determination of total tree ages using increment core samples. Ecoscience 4, 534–542.
- Wigley, T.M.L., Briffa, K.R., Jones, P.D., 1984. On the average value of correlated time series, with applications in dendroclimatology and hydrometeorology. J. Clim. Appl. Meteorol. 23, 201–213.
- Wilson, R.J.S., Luckman, B.H., Esper, J., 2005. A 500-year dendroclimatic reconstruction of spring-summer precipitation from the lower Bavarian forest region, Germany. Int. J. Climatol. 25, 611–630.
- Yoder, B.J., Ryan, M.G., Waring, R.H., Schoettle, A.W., Kaufmann, M.R., 1994. Evidence of reduced photosynthetic rates in old trees. For. Sci. 40, 513–527.