

IOPscience

Home

Search Collections Journals About Contact us My IOPscience

Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps

This content has been downloaded from IOPscience. Please scroll down to see the full text. 2014 Environ. Res. Lett. 9 104021 (http://iopscience.iop.org/1748-9326/9/10/104021) View the table of contents for this issue, or go to the journal homepage for more

Download details:

IP Address: 109.52.142.76 This content was downloaded on 29/10/2014 at 16:51

Please note that terms and conditions apply.

Winter precipitation effect in a mid-latitude temperature-limited environment: the case of common juniper at high elevation in the Alps

Elena Pellizzari, Mario Pividori and Marco Carrer

Università degli studi di Padova, dip. TeSAF, Agripolis, I-35020 Legnaro, PD, Italy

E-mail: elena.pellizzari.4@studenti.unipd.it

Received 16 May 2014, revised 25 September 2014 Accepted for publication 25 September 2014 Published 27 October 2014

Abstract

Common juniper (Juniperus communis L.) is by far the most widespread conifer in the world. However, tree-ring research dealing with this species is still scarce, mainly due to the difficulty in crossdating associated with the irregular stem shape with strip-bark growth form in older individuals and the high number of missing and wedging rings. Given that many different species of the same genus have been successfully used in tree-ring investigations and proved to be reliable climate proxies, this study aims to (i) test the possibility to successfully apply dendrochronological techniques on common juniper growing above the treeline and (ii) verify the climate sensitivity of the species with special regard to winter precipitation, a climatic factor that generally does not affect tree-ring growth in all Alpine high-elevation tree species. Almost 90 samples have been collected in three sites in the central and eastern Alps, all between 2100 and 2400 m in elevation. Despite cross-dating difficulties, we were able to build a reliable chronology for each site, each spanning over 200 years. Climate-growth relationships computed over the last century highlight that juniper growth is mainly controlled by the amount of winter precipitation. The high variability of the climate-growth associations among sites, corresponds well to the low spatial dependence of this meteorological factor. Fairly long chronologies and the presence of a significant precipitation signal open up the possibility to reconstruct past winter precipitation.

S Online supplementary data available from stacks.iop.org/ERL/9/104021/mmedia

Keywords: Juniperus communis, tree-ring, climate-growth response, winter precipitation, snow cover

1. Introduction

Trees growing at their uppermost or northernmost limits have long attracted scientists. Indeed, these areas usually offer a clear representation of the activity of an environmental driver, namely temperature, which is able to set a limit to growth and distribution of the tree life form. This feature, together with other peculiarities such as the presence of a relatively undisturbed area with respect to sites at lower elevation the presence of more long-lived individuals, contributes to *treeline* being a key topic with a very rich literature and longstanding research history in plant ecology (Körner 2012). In the last decades, the discussion on global change has further increased the attention of the scientific community on these temperature-limited ecosystems. Indeed, they are highly sensitive to even minor temperature variation related, for example, to climate variability (Körner 2012) or

Content from this work may be used under the terms of the Creative Commons Attribution 3.0 licence. Any further distribution of this work must maintain attribution to the author(s) and the title of the work, journal citation and DOI.

microtopographical settings (Bunn *et al* 2011, Bunn *et al* 2005, Carrer and Urbinati 2001) and play a major role in various feedback mechanisms within the climate system with significant effects at global scale *e.g.* the treeline advance (Grace *et al* 2002, Devi *et al* 2008, Harsch *et al* 2009) or the change in the terrestrial albedo (Bonan *et al* 1995).

The Alps are one of the most studied areas for high elevation forests and their relationships with climate (Holtmeier 2009, Tranquillini 1979); the most investigated species are conifer trees (Larix decidua, Pinus cembra, Picea abies, *Pinus sylvestris*, *Abies alba*). In this area tree species usually have the typical erect life form, once they reach 2-4 m in height they become closely coupled to prevailing atmospheric conditions and for this reason temperature is generally the key limiting factor for tree growth (Carrer and Urbinati 2004, Büntgen et al 2005, Frank and Esper 2005, Carrer and Urbinati 2006). In the Alps, as in most of the high-latitude regions (St George 2014), precipitation, and specifically winter precipitation, is rarely a limiting factor for tree growth if we exclude some special cases where a mechanical action, linked to avalanches or slow mass movement, is involved (Holtmeier and Broll 2010, Smith et al 2003, Casteller et al 2007). This is why in the Alps almost no investigations found the clear presence of a tree growth sensitivity to precipitation or, within a long-term perspective, no clear precipitation signal has ever been detected in high elevation treering sequences (Büntgen et al 2008, Carrer et al 2007, Frank and Esper 2005). Nonetheless, in many regions snow cover emerged as an important driver of tree and shrub growth by providing a constant cover and protection against frosts during the early growing season (Wipf et al 2009, Rixen et al 2010), and increasing the nutrient supply (Hallinger et al 2010). In contrast, massive snowpack could delay the onset of the growing season (Kirdyanov et al 2003, Schmidt et al 2006, Vaganov et al 1999), reducing the duration of cambial activity.

The absence of a precipitation signal in the Alps with the consequent impossibility to adopt tree-ring sequences as a proxy to infer past precipitation conditions still represents a gap in our knowledge. Indeed, short- and long-term water cycle dynamics in a densely populated mountain area such as the Alps could have major social and environmental effects, from the collapse of the glaciers mass balance (Haeberli and Beniston 1998, Beniston 2012), to freshwater resource management (Viviroli et al 2011) or the permanence of a winter snow pack fundamental for many alpine plant species but also for winter tourism and related activities (Elsasser and Burki 2002, Morrison and Pickering 2013). To fill this gap, we directed our attention on a different species that grows at the same elevation as or higher than the other conifer species, but which could be sensitive to winter precipitation: common juniper (Juniperus communis L.).

The species has a wide distribution in the Alps, as in the whole northern hemisphere, and its slow growth, associated with high longevity, are the main reasons for considering the possibility of applying dendrochronological techniques to find a reliable climatic signal within ring-width sequences.



Figure 1. Location of the study sites. CDL: Croda da Lago; VIN: Vinschgau-Val Venosta; VEN: Ventina.

Our underlying hypothesis refers to the height of the species at high elevation, no taller than 0.5 meters, and therefore usually beneath the snow cover during wintertime. Since juniper does not start growing until it is free of the snowpack (Hantemirov *et al* 2000), we will test the hypothesis that shrub growth is linked to winter precipitation, based in snowpack depth. The objectives of the study are twofold: (i) to assess the possibility of building reliable juniper ring width chronologies in the Alps; (ii) verify the sensitivity of the species to precipitation, and especially to winter snowfalls.

2. Material and methods

2.1. Study area

Juniper ring chronologies were built for three sites in the central and eastern Alps (figure 1). The study areas were: Ventina (VEN, 46° 18'N, 9° 46'E, 2200 m a.s.l.), Vinschgau-Val Venosta (VIN, 46° 38'N, 10° 31'E, 2300 m a.s.l.) and Croda da Lago (CDL, 46° 28'N, 12° 07'E, 2150 m a.s.l.). The substrate differs at the sites, with dolomite and limestone with shallow rendzic leptosols at CDL, and igneous, volcanic and metamorphic silicates (i.e. granite, porphyry, gneiss and phyllite) with spodosols and podzols at VEN and VIN. Annual (and winter) precipitation also varies, with 608 (327) mm in Vinschgau, 1068 (615) mm in Croda da Lago and 1196 (681) mm in Ventina (figure S1). In our study winter was defined as the period from October through May, when precipitation normally falls as snow at our research sites.

2.2. Ring width measurements and crossdating

Most samples were collected above the treeline, between 2100 and 2400 m a.s.l., by randomly selecting the shrubs



Figure 2. The typical prostrate growth form of common juniper at high elevation.

(figure 2) and saw-cutting one of the main stems that depart from the root collar to obtain a disk. During summer 2012 we collected and measured a total of 91 samples both dead and alive, at the three sites: 22 in VIN, 27 in CDL and 42 in VEN. At the same sites we also collected cores from larch (*L. decidua*) at the timberline-treeline belt (2000–2200 m) to compare juniper growth to that of a typical high elevation tree species often used in dendroecological investigation. We sampled 121 larches, 23 in VIN, 70 in CDL and 28 in VEN, collecting two cores per tree.

At the lab, disks and cores were sanded with progressively finer gridded sandpaper for a clear visualization of the rings and measured to the nearest 0.01 mm using a sliding stage micrometer interfaced with a personal computer (Aniol 1987). Juniper stems have a typical lobate form resulting from irregular growth. For this reason, to obtain a more reliable representation of ring width, we measured two to four radii per disk. In some cases, to enhance the visibility of the ring -width sequences, we applied microscopic sample preparation through (i) cutting the disks into small pieces (3-5 cm); (ii) cutting thin sections (ca. 20 nm) with a microtome; (iii) staining them with safranin and permanently fixing with balsam (Gärtner and Schweingruber 2013). We then measured the rings as for the normal samples.

Crossdating was accomplished following the standard procedure (Stokes and Smiley 1968): first by visual comparison of the 2-4 radii within each sample, then comparing radii from different samples. In this phase the presence of event rings, i.e. rings with a conspicuous feature within a limited section of the radius (Kaennel and Schweingruber 1995) assisted in finding the correct match among the series. Lastly, after computing the individual mean growth curve, dating and measurement errors were checked using the COFECHA program (Holmes 1983). Ring-width site chronologies were obtained from the crossdated ring-width series using the ARSTAN program (Cook and Holmes 1997) that was specifically developed to remove any biologically induced age-trends and transient disturbance pulses present in raw tree-ring series and to enhance the high-frequency year to year variability often associated to climate. In both species we applied a rather conservative detrending using a spline function with 50% frequency cut-off at 100 years. Individual series were therefore standardized by fitting the spline function to measured data series and dividing observed by expected values. Several statistical parameters were calculated to compare the chronologies: (i) mean sensitivity (MS), a measure of the relative difference in ring width between consecutive years, adopted to assess the high frequency variability of the series, (ii) first order autocorrelation (ac), a measure of the influence of previous year's condition on ring formation (Fritts 1976), (iii) the variance explained by the first principal component (PC1), and (iv) the mean correlation between samples (rbar) and the 'expressed population signal' (EPS) (Wigley et al 1984) to estimate the level of year-byyear growth variations shared by samples in the same site. Higher values of PC1 and rbar indicate higher synchronization in the annual growth patterns among samples and better common signal strength in the mean growth chronologies, while EPS is commonly adopted as a criterion for assessing mean chronology reliability.

2.3. Climate-growth association

Rather than take records from the closest weather stations, which may not be totally representative in a mountain area, we used the HISTALP gridded dataset (Auer et al 2007). This dataset, valid for the Greater Alpine Region, is based on precipitation and temperature data from hundreds of weather stations firstly subjected to homogeneity tests and relative adjustments regarding elevation and changes of instrument position and type, then gridded on a $1^{\circ} \times 1^{\circ}$ network and finally expressed as anomalies with respect to the 20th century mean (Auer et al 2005, Böhm et al 2001). We selected the climate data from the closest grid points to each study site and computed the growth/climate analyses over the 1876-2005 period. We investigated climate-growth associations by correlating each site chronology with monthly precipitation and temperature data from June of the previous year (t-1) to September of the current year (t). Seasonal data were also taken into account by considering the period from October to May (POM, TOM) when, at this elevation, precipitation mainly occurs as snow and the months from June to September (PJS, TJS) considered as the growing season. The bootstrap approach (Efron 1979) was applied to test the stability and significance of the outcomes. After 100 000 replications, each correlation was deemed significant at the 95% level if the ratio between the correlation coefficient (r) and the standard deviation of the bootstrap replications (s) was higher



Figure 3. (A) and (B) Samples of common juniper having 401 and 180 rings respectively. (C) Microscopic image of a microtome slice taken at $40 \times$ showing many wedging rings induced by uneven cambial activity.

Table 1. Site location and chronology statistics for Juniperus communis and Larix decidua (shaded).

Site	Lat	Long	Period	Series length (years) (max- mean-min)	N	MS	AC (Indexed)	PC1	Rbar (Indexed)	Missing rings (%)	Frost rings (%)
CDL-JC	46.28	12.07	1749-2012	263-177-75	15	0.32	0.59 (0.45)	0.36	0.16 (0.18)	19 (0.73)	20 (0.77)
VEN-JC	46.18	9.46	1611-2012	402-167-94	17	0.28	0.69 (0.51)	0.33	0.19 (0.19)	14 (0.48)	33 (1.14)
VIN-JC	46.38	10.31	1765-2012	232-115-43	14	0.32	0.64 (0.49)	0.32	0.17 (0.15)	3 (0.18)	89 (5.45)
CDL-LD	46.29	12.06	1452-2009	557-270-84	70	0.39	0.66 (0.36)	0.66	0.59 (0.64)	86 (0.22)	n.d.
VEN-LD	46.18	9.46	1496-2012	514-360-234	28	0.35	0.71 (0.50)	0.57	0.41 (0.55)	29 (0.22)	n.d.
VIN-LD	46.43	10.38	1668-2004	403-220-36	23	0.34	0.73 (0.46)	0.78	0.76 (0.76)	39 (0.39)	n.d.

Note: chronology statistics include mean ring width (MRW), mean sensitivity (MS) and first-order serial autocorrelation (ac) computed on the raw (indexed) ring-width series, the variance explained by the first principal component (PC1) and the mean interseries correlation (Rbar) computed on the raw (indexed) ring-width series. Site codes CDL, VEN, VIN correspond respectively to Croda da Lago, Ventina, and Vinschgau-Val Venosta respectively.

than |2| (Guiot 1991). Analyses were performed on the complete 130-year period as well as on two 65-year subperiods (1876–1940 and 1941–2005).

3. Results

3.1. Ring-width measurements and crossdating

The irregular and lobate growth form of juniper stems frequently induces the presence of wedging (figure 3) and missing rings (i.e. rings that are absent in a sample due to failure of cambial activity Kaennel and Schweingruber 1995). To reduce the crossdating complexity we usually selected the least problematic and most representative radii, where the rings did not wedge out. Nonetheless, almost half of the samples collected (45 samples) could not be successfully crossdated. On the 46 dated disks (17 for VEN, 14 for VIN and 15 for CDL), we selected and measured an average of 2.4 radii per disk, for a total of 210 radii and 7146 rings. Within these samples we detected 142 frost rings (i.e. distorted xylem tissue damaged by freezing in the growing season Kaennel and Schweingruber 1995) corresponding to 0.77% in CDL, 1.14% in VEN and 5.44% in VIN and 36 missing rings, which correspond to ca. 0.73%, 0.48% and 0.18% for CDL, VEN and VIN respectively. Chronology length is 402 years for VEN (from 1611 to 2012), 247 years for VIN (from 1765 to 2012), and 263 years for CDL (1749-2012) (table 1, figure S2). The larch chronologies were all longer, reaching up to 557 years for CLD, with the typical high mean sensitivity and common signal statistics of the species (Carrer and Urbinati 2006). The PC1 and rbar values of the juniper chronologies are lower than those of the larch. In juniper the expressed population signal often results as lower than the threshold level of 0.85 (figure 4).

3.2. Climate-growth association

Two of the stations, VEN and CDL, show significant negative correlations between precipitation and ring growth with r/scoefficients lower than -2. Winter months, from September to January in VEN and from November to January in CDL show the most significant correlations. With winter precipitation (POM), we obtained a much higher and significant association (figures 5, 6). Splitting the time period in two, precipitation and especially the winter seasonal sum, confirmed the previous outcomes, being always significant although with less variability (figure S3). At the third site, VIN, juniper ring widths were not related to either precipitation or temperature. We found that temperature is not a key factor for juniper growth; indeed it shows no significant coherent correlation with growth apart from for a few isolated months, corresponding to the late previous and current growing season. We found the opposite for larch, where precipitation



Figure 4. Raw and indexed ring-width chronologies. Smoothed lines are 20-year low-pass filter. Top-inset graph represents the 30-year running EPS with the 0.85 threshold highlighted.

seems to play a negligible role both at monthly and seasonal level, whereas temperature has a highly significant effect that is clearly homogeneous among sites (figure 5).

4. Discussion

High elevation and high latitude are considered to be the areas most sensitive to climate change (IPCC 2007, 2013). Indeed, climate is the major environmental driver of conifer growth at high altitude, where the limiting effect of temperature on tree growth is reflected in the prevailing significant correlation between tree-ring parameters and summer temperatures (Carrer and Urbinati 2004, Büntgen et al 2005, Frank and Esper 2005, Carrer and Urbinati 2006). At high altitude in the Alps tree growth seems not to be sensitive to precipitation, however, our study demonstrates that growth of a shrub conifer, J. communis, growing at the same or higher elevation, is influenced by winter precipitation. Many researchers investigated other species of the same genus (Juniperus thurifera, J. excelsa, J. occidentalis, etc) and the most common outcomes were a positive correlation between juniper growth and summer temperatures or precipitation when the species grew in temperature- (e.g. Tibetan plateau, Northern Scandinavia) or water- (e.g. Ethiopia and Oregon) limited environments (Sass-Klaassen et al 2008, Liang et al 2012, Knapp et al 2004, Hallinger et al 2010). Hallinger et al (2010) reported a positive effect of snow cover on J. nana at high latitude. In these regions (Northern Scandinavia), in contrast to our sites, higher snow accumulation would increase the insulation with warmer soil temperature promoting microbial activity. Shrub growth would benefit from a resulting increase in nutrient supply. Given the growing interest in the water cycle and the consequent effects at environmental level (Haeberli and Beniston 1998, Beniston 2012), this study adds a valuable contribution, by providing the first example at midlatitude across Eurasia (St George 2014) of a long-living plant limited in growth by winter precipitation. We highlight a

5

potential new proxy that could be useful in the Alps, an area where summer temperature has so far been the only climate signal detected in tree-ring chronologies.

4.1. Ring-width chronologies characteristics

The genus Juniper includes many long-living species (Brown 1996) in which ring-width chronologies have been shown to contain strong climatic signals (Treydte et al 2006, Knapp et al 2001, DeSoto et al 2012). As the other species of the same genus, J. communis in the Alps has proved to register a climatic signal at least in two sites out of three. We detected the presence of frost rings in the ring-width sequences. Juniper is considered rather vulnerable to frost damage due to its thin bark, yet the presence of frost rings does not decrease with age (Hantemirov et al 2000, 2004) as observed in other tree species. The total number of these event rings we recorded is low, probably because the significant snow cover and late melting at high elevation delay the onset of cambial growth reducing the chance of being injured by an abrupt freeze (Hantemirov et al 2000). This is likely why the highest number of frost rings are observed at VIN. This site has the lowest amount of winter precipitation, which implies a shallower snow cover that melts faster in spring increasing the chance of late frost damage. Furthermore, VIN sampling area is subjected to constant strong winds that blow away the snow cover (Whiteman and Dreiseitl 1984), in some cases leaving the shrubs with a higher probability of being exposed to frosts (Bokhorst et al 2009). As reported by other authors, although not always confirmed (Bär et al 2008), shrub growth is largely influenced by microenvironmental variability or local topography (Kivinen et al 2012, Hantemirov et al 2000, 2004) that can differ between and within the same sites, inducing a corresponding variability between individual ring-width chronologies. Some of the chronology statistics, namely rbar and to a lesser extent EPS, mirror this ring-width variability dominated by individual rather than population variability. However, the fairly low values of these statistics are likely not species- or sitespecific as similar values have been reported by many authors working on the same genus (Liang et al 2012, Hallinger et al 2010, Sass-Klaassen et al 2008, Zhu et al 2008). Still, despite the difficulties in crossdating and the high individual variability (figure S2), the three site chronologies we built allowed us to compute reliable climate-growth associations. This represents a fundamental step for investigating how juniper reacts to winter precipitation.

4.2. Climate—growth association

The VEN and CDL sites demonstrate a significant negative correlation between accumulated winter precipitation and juniper ring width together with a weaker correlation with monthly precipitation. There are several reasons for the importance of using a seasonal correlation along with examining correlations with monthly data. We are dealing with a meteorological parameter, precipitation, which tends to accumulate over the winter months. Once juniper is covered



Figure 5. Climate-growth associations between the three ring-width site chronologies and total monthly precipitation and mean monthly temperatures for the previous (June–December) and current (January–September) year plus the seasonal precipitation sum and temperature mean from previous October to current May and from current June to September. Standardized coefficients were obtained by dividing the mean correlations by their standard deviations after the bootstrap replications. They express the significance of monthly parameters. Values above |2| are significant at p < 0.05.



Figure 6. Comparison between the cumulative winter precipitation from October to May (blue lines) and ring-width indexed chronologies of Croda da Lago (CDL) and Ventina (VEN), the two sites that show a significant association with this precipitation parameter. The second *Y* axis related to precipitation sum has been reversed for a better visualization. Pearson correlation coefficients (*r*) are also shown, both are significant at P < 0.001.

by the first snowfalls in October/November, there is no direct effect from the amount of precipitation during the winter rest period. The negative correlation indicates that the higher the amount of winter precipitation is, the thicker the snowpack is and the narrower the rings are in the following growing season. This is supported by the fact that cambial activity does not start until after snowmelt (Hantemirov *et al* 2000). In fact, a thicker snowpack usually takes longer to melt thus delaying the onset of cambial activity and shortening the growing season, with the resulting narrower ring formation. Late-persisting snow could also have a detrimental effect on growth through cooler soil temperature which can delay the onset or slow down the first phases of the growing season (Schmidt et al 2006, Kirdyanov et al 2003, Vaganov et al 1999, Peterson and Peterson 1994). In our study larch trees did not show any sign of this negative effect. This is further confirmation that the most plausible reason for the negative precipitation correlation in juniper is the physical effect of the snow cover that filters the incoming solar radiation blocking photosynthesis, rather than the collateral reduction in soil temperature. The only area with no significant growth-climate correlation for either precipitation or temperatures is VIN. The possible reason is the rather low quality of the common signal among the ring-width series highlighted by the low EPS value of the chronology. The VIN site is a zone exposed to strong wind, as is most of the high Vinshaug valley (Whiteman and Dreiseitl 1984) and due to this, the snow falling during winter is blown away, leaving the ground almost bare. A lack of snow cover implies a potential earlier start of cambial activity, with the consequence of no correlation with winter precipitation. The higher presence of frost rings due to late frosts could also be evidence of an earlier onset of cambial activity: the probability of freezing injuries is higher with an earlier start to the growing season. Temperature did not affect ring-width formation at any of our sites, which confirms, although surprisingly, the weak influence of this factor on juniper growth. Indeed, it is well-known that temperature is the key limiting factor for tree growth at high elevation, as confirmed by our comparison with larch growing in the same areas. This is likely due to the fact that trees are more closely coupled to air temperature. A similar result, has been recorded on another prostrate shrub, Salix arctica, in Greenland (Schmidt et al 2006). Even if other investigations at high-latitudes report that temperature, and especially summer temperature, is the key environmental factor driving shrub growth (Bär et al 2008, Buchwal et al 2013, Weijers et al 2013, Buras et al 2012, Hallinger and Wilmking 2011), at mid-latitude, at least in the Alps, common juniper is seemingly less affected than trees by air temperature. Indeed, with its prostrate growth form juniper grows within the boundary layer and is likely more influenced by soil temperature. Furthermore, the topography, aspect and landscape heterogeneity influence the persistence of snow at local level (Kivinen et al 2012) and this also explains to some extent the high variability between samples. However, despite this high individual and spatial variability the winter precipitation signal seems to be fairly stable in time as it is significant for both the subperiods analyzed (figure S3). The increasing or decreasing of this winter precipitation signal could likely be connected with the not uniform climate data quality and with the corresponding variability in time of the common signal as shown by the running EPS values (figure 4).

5. Conclusion

We demonstrated that, despite the challenging crossdating, it is possible to built centuries-long chronologies with common juniper. In addition, we found a significant winter precipitation signal in the ring-width chronologies of two of our three research sites. As a prostrate shrub J. communis seems better coupled with the soil surface rather than the air temperature. This is probably one of the reasons why the influence of air temperature on ring-width formation seems less significant. This study is just a pilot investigation. Future research will be directed to (i) enlarging the sample size, paying attention to collecting more sections along the stem to obtain a more reliable representation of plant growth and to reduce the risk of losing any information due to missing rings (Wilmking et al 2012); (ii) extending back in time the ring-width series, considering the high potential to generate longer chronologies than these with additional collections including also dry dead wood remains; and (iii) extending the sites network across the Alps. If the climatic signal we detected is confirmed, this will provide a baseline for a possible reconstruction of past winter precipitation variability in the region. Our results suggest that J. communis ring width chronologies may serve as a winter precipitation proxy in the Alps.

Acknowledgements

The authors would like to thank Paola Nola and Renzo Motta for providing the larch series from the Ventina (VEN) site and the two anonymous reviewers for their helpful comments and suggestions on the earlier version of the manuscript.

References

- Aniol R W 1987 A new device for computer assisted measurement of tree-ring widths *Dendrochronologia* **5** 135–41
- Auer I *et al* 2005 A new instrumental precipitation dataset for the greater alpine region for the period 1800-2002 *Int. J. Climatol.* 25 139–66
- Auer I, Bohm R, Jurkovic A, Lipa W, Orlik A, Potzmann R, Schoner W, Ungersbock M, Matulla C and Briffa K 2007 HISTALP–historical instrumental climatological surface time series of the greater alpine region *Int. J. Climatol.* 27 17–46
- Bär A, Pape R, Bräuning A and Löffler J 2008 Growth-ring variations of dwarf shrubs reflect regional climate signals in alpine environments rather than topoclimatic differences *J. Biogeogr.* 35 625–36
- Beniston M 2012 Is snow in the Alps receding or disappearing? Wiley Interdiscip. Rev.-Clim. Change 3 349–58
- Böhm R, Auer I, Brunetti M, Maugeri M, Nanni T and Schoner W
 2001 Regional temperature variability in the European Alps:
 1760-1998 from homogenized instrumental time series *Int. J. Climatol.* 21 1779–801
- Bokhorst S F, Bjerke J W, Tømmervik H, Callaghan T V and Phoenix G K 2009 Winter warming events damage sub-Arctic vegetation: consistent evidence from an experimental manipulation and a natural event *J. Ecol.* **97** 1408–15
- Bonan G B, Chapin F S III and Thompson S L 1995 Boreal forest and tundra ecosystems as components of the climate system *Clim. Change* 29 145–67
- Brown P M Oldlist. A database of maximum tree ages ed J S Dean, D M Meko and T W Swetnam *Tree Rings, Environment and Humanity: Proc. Int. Conf. (17–21 May 1994 Tucson, AZ) Radiocarbon* **1996** 727–731
- Buchwal A, Rachlewicz G, Fonti P, Cherubini P and Gaertner H 2013 Temperature modulates intra-plant growth of Salix polaris from a High Arctic site (Svalbard) *Polar Biol.* 36 1305–18
- Bunn A G, Hughes M K and Salzer M W 2011 Topographically modified tree-ring chronologies as a potential means to improve paleoclimate inference *Clim. Change* 105 627–34
- Bunn A G, Waggoner L A and Graumlich L J 2005 Topographic mediation of growth in high elevation foxtail pine (*Pinus* balfouriana Grev. et Balf.) forests in the Sierra Nevada, USA Glob. Ecol. Biogeogr. 14 103–14
- Büntgen U, Esper J, Frank D C, Nicolussi K and Schmidhalter M 2005 A 1052-year tree-ring proxy for alpine summer temperatures *Clim. Dyn.* 25 141–53
- Büntgen U, Frank D, Wilson R, Carrer M, Urbinati C and Esper J 2008 Testing for tree-ring divergence in the European Alps *Glob. Change Biol.* 14 2443–53
- Buras A, Hallinger M and Wilmking M 2012 Can shrubs help to reconstruct historical glacier retreats? *Environ. Res. Lett.* 7 044031
- Carrer M, Nola P, Eduard J L, Motta R and Urbinati C 2007 Regional variability of climate-growth relationships in *Pinus cembra* high elevation forests in the Alps J. Ecol. 95 1072–83
- Carrer M and Urbinati C 2001 Spatial analysis of structural and treering related parameters in a timberline forest in the Italian Alps *J. Veg. Sci.* **12** 643–52
- Carrer M and Urbinati C 2004 Age-dependent tree-ring growth responses to climate *Larix decidua Pinus Cembra Ecol.* **85** 730–40
- Carrer M and Urbinati C 2006 Long-term change in the sensitivity of tree-ring growth to climate forcing *Larix decidua New Phytol.* **170** 861–71
- Casteller A, Stöckli V, Villalba R and Mayer A C 2007 An evaluation of dendroecological indicators of snow avalanches in the Swiss Alps *Arctic Antarct. Alpine Res.* **39** 218–28

- Cook E R and Holmes R L 1997 *The International Tree-Ring Data Bank Program Library, version 2.1, user's Manual* ed H D Grissino Mayer *et al* (Tucson, AZ, USA: University of Arizona Laboratory of Tree-Ring Research) pp 75–92
- DeSoto L, Camarero J J, Olano J M and Rozas V 2012 Geographically structured and temporally unstable growth responses of *Juniperus thurifera* to recent climate variability in the Iberian Peninsula *Eur. J. Forest Res.* **131** 905–17
- Devi N, Hagedorn F, Moiseev P, Bugmann H, Shiyatov S, Mazepa V and Rigling A 2008 Expanding forests and changing growth forms of Siberian larch at the polar urals treeline during the 20th century *Glob. Change Biol.* 14 1581–91
- Efron B 1979 Bootstrap methods: another look at the jackknife *Ann. Stat.* **7** 1–26
- Elsasser H and Burki R 2002 Climate change as a threat to tourism in the Alps *Clim. Res.* **20** 253–7
- Frank D and Esper J 2005 Characterization and climate response patterns of a high-elevation, multi-species tree-ring network in the European Alps *Dendrochronologia* **22** 107–21
- Fritts H C 1976 Tree Rings and Climate (London, UK: Academic)
- Gärtner H and Schweingruber F H 2013 Microscopic Preparation Techniques for Plant Stem Analysis (Remagen: Kessel)
- Grace J, Berninger F and Nagy L 2002 Impacts of climate change on the tree line *Ann. Bot.* **90** 537–44
- Guiot J 1991 The bootstrapped response function *Tree Ring Bull.* **51** 39–41
- Haeberli W and Beniston M 1998 Climate change and its impacts on glaciers and permafrost in the Alps *Ambio* 27 258–65
- Hallinger M, Manthey M and Wilmking M 2010 Establishing a missing link: warm summers and winter snow cover promote shrub expansion into alpine tundra in Scandinavia *New Phytol.* 186 890–9
- Hallinger M and Wilmking M 2011 No change without a cause why climate change remains the most plausible reason for shrub growth dynamics in Scandinavia New Phytol. 189 902–8
- Hantemirov R M, Gorlanova L A and Shiyatov S G 2000 Pathological tree-ring structures in Siberian juniper (*Juniperus sibirica* burgsd.) and their use for reconstructing extreme climatic events *Russ. J. Ecol.* **31** 167–73
- Hantemirov R M, Gorlanova L A and Shiyatov S G 2004 Extreme temperature events in summer in northwest Siberia since AD 742 inferred from tree rings *Palaeogeogr. Palaeoclim. Palaeoecol.* 209 155–64
- Harsch M A, Hulme P E, McGlone M S and Duncan R P 2009 Are treelines advancing? A global meta-analysis of treeline response to climate warming *Ecol. Lett.* **12** 1040–9
- Holmes R L 1983 Computer-assisted quality control in tree-ring dating and measurement *Tree Ring Bull.* **43** 69–78
- Holtmeier F-K and Broll G 2010 Wind as an ecological agent at treelines in North America, the Alps, and the European Subarctic *Phys. Geogr.* **31** 203–33
- Holtmeier F K 2009 Mountain Timberlines: Ecology, Patchiness, and Dynamics (Berlin: Springer)
- IPCC 2007 Climate Change 2007: The Physical Science Basis Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change ed S Solomon et al (Cambridge: Cambridge University Press) p 996
- IPCC 2013 Climate Change 2013: The Physical Science Basis Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change ed T Stocker et al (Cambridge: Cambridge Univ Press) p 1535
- Kaennel M and Schweingruber F H 1995 Multilingual Glossary of Dendrochronology (Berne: Wsl/Fnp Birmensdorf, P. Haupt Pub)
- Kirdyanov A, Hughes M, Vaganov E, Schweingruber F and Silkin P 2003 The importance of early summer temperature and date of snow melt for tree growth in the Siberian Subarctic *Trees-Struct. Funct.* **17** 61–9

- Kivinen S, Kaarlejärvi E, Jylhä K and Räisänen J 2012 Spatiotemporal distribution of threatened high-latitude snowbed and snow patch habitats in warming climate *Environ*. *Res. Lett.* 7 034024
- Knapp P A, Soule P T and Grissino Mayer H D 2001 Detecting potential regional effects of increased atmospheric CO_2 on growth rates of western juniper *Glob. Change Biol.* **7** 903–17
- Knapp P A, Soule P T and Grissino-Mayer H D 2004 Occurrence of sustained droughts in the interior pacific Northwest (AD 1733-1980) inferred from tree-ring data J. Clim. 17 140–50
- Körner C 2012 Alpine Treelines: Functional Ecology of the Global High Elevation Tree Limits (Basel: Springer)
- Liang E, Lu X, Ren P, Li X, Zhu L and Eckstein D 2012 Annual increments of juniper dwarf shrubs above the tree line on the central Tibetan Plateau: a useful climatic proxy *Ann. Bot.* **109** 721–8
- Miles D and Worthington M 1998 Sonora Pass junipers from California USA: construction of a 3500-year chronology Dendrochronology and Environmental Trends. Proc. of the Int. Conf. pp 17–21
- Morrison C and Pickering C M 2013 Perceptions of climate change impacts, adaptation and limits to adaption in the Australian Alps: the ski-tourism industry and key stakeholders *J. Sustainable Tourism* **21** 173–91
- Peterson D W and Peterson D L 1994 Effects of climate on radial growth of subalpine conifers in the North Cascade Mountains *Can. J. Forest Res.* **24** 1921–32
- Rixen C, Schwoerer C and Wipf S 2010 Winter climate change at different temporal scales in Vaccinium myrtillus, an Arctic and alpine dwarf shrub *Polar Res.* 29 85–94
- Sass-Klaassen U, Couralet C, Sahle Y and Sterck F J 2008 Juniper from Ethiopia contains a large-scale precipitation signal *Int. J. Plant Sci.* 169 1057–65
- Schmidt N, Baittinger C and Forchhammer M 2006 Reconstructing century-long snow regimes using estimates of High Arctic Salix arctica radial growth Arctic Antarct. Alpine Res. 38 257–62
- Smith W K, Germino M J, Hancock T E and Johnson D M 2003 Another perspective on altitudinal limits of alpine timberlines *Tree Physiol.* **23** 1101–12
- St. George S 2014 An overview of tree-ring width records across the Northern Hemisphere *Quat. Sci. Rev.* **95** 132–50
- Stokes M A and Smiley T L 1968 Introduction to Tree-Ring Dating (Chicago, IL: University of Chicago Press)
- Tranquillini W 1979 *Physiological Ecology of The Alpine Timberline* vol 31 (Berlin: Springer)
- Treydte K, Schleser G H, Helle G, Frank D, Winiger M, Haug G H and Esper J 2006 The twentieth century was the wettest period in northern Pakistan over the past millennium *Nature* **440** 1179–82
- Vaganov E A, Hughes M K, Kirdyanov A V, Schweingruber F H and Silkin P P 1999 Influence of snowfall and melt timing on tree growth in subarctic Eurasia *Nature* 400 149–51
- Viviroli D *et al* 2011 Climate change and mountain water resources: overview and recommendations for research, management and policy *Hydrol. Earth Syst. Sci.* **15** 471–504
- Weijers S, Wagner-Cremer F, Sass-Klaassen U, Broekman R and Rozema J 2013 Reconstructing High Arctic growing season intensity from shoot length growth of a dwarf shrub *The Holocene* 23 721–31
- Whiteman C D and Dreiseitl E 1984 Alpine Meteorology: Translations of Classic Contributions ed A Wagner, E Ekhart and F Defant p 129
- Wigley T M L, Briffa K R and Jones P D 1984 On the average value of correlated time series with applications in dendroclimatology and hydrometeorology *J. Clim. Appl. Meteorol.* 23 201–13

- Wilmking M, Hallinger M, Van Bogaert R, Kyncl T, Babst F, Hahne W, Juday G P, de Luis M, Novak K and Vollm C 2012 Continuously missing outer rings in woody plants at their distributional margins *Dendrochronologia* **30** 213–22
- Wipf S, Stoeckli V and Bebi P 2009 Winter climate change in alpine tundra: plant responses to changes in snow depth and snowmelt timing *Clim. Change* **94** 105–21
- Zhu H, Zheng Y, Shao X, Liu X, Xu Y and Liang E 2008 Millennial temperature reconstruction based on tree-ring widths of Qilian juniper from Wulan, Qinghai Province, China *Chin. Sci. Bull.* 53 3914–20