

RESEARCH ARTICLE

10.1002/2017JG004196

Key Points:

- Cambial dieback is localized on the southern side of trees, suggesting a link between solar irradiance and stem injury
- Strip- and whole-bark trees have different radial growth trends, which can have implications for tree-ring reconstructions
- Radial growth of strip-bark trees increased rapidly in the early 20th century following extensive stem dieback in the 19th century

Supporting Information:

- Supporting Information S1
- Data Set S1
- Data Set S2
- Data Set S3

Correspondence to:

C. Leland,
cleland@ldeo.columbia.edu

Citation:








Leland, C., Cook, E. R., Andreu-Hayles, L., Pederson, N., Hessler, A., Anchukaitis, K. J., et al. (2018). Strip-bark morphology and radial growth trends in ancient *Pinus sibirica* trees from central Mongolia. *Journal of Geophysical Research: Biogeosciences*, 123. <https://doi.org/10.1002/2017JG004196>

Received 28 SEP 2017

Accepted 13 FEB 2018

Accepted article online 22 FEB 2018

Strip-Bark Morphology and Radial Growth Trends in Ancient *Pinus sibirica* Trees From Central Mongolia

Caroline Leland^{1,2} , Edward R. Cook¹ , Laia Andreu-Hayles¹, Neil Pederson^{1,3}, Amy Hessl⁴ , Kevin J. Anchukaitis⁵ , Oyunsanaa Byambasuren⁶, Baatarbileg Nachin^{1,6} , Nicole Davi^{1,7}, Rosanne D'Arrigo¹, Kevin Griffin^{1,8} , Daniel A. Bishop^{1,2}, and Mukund Palat Rao^{1,2} 

¹Tree-Ring Laboratory, Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, USA, ²Department of Earth and Environmental Sciences, Columbia University, New York, NY, USA, ³Harvard Forest, Harvard University, Petersham, MA, USA, ⁴Department of Geology and Geography, West Virginia University, Morgantown, WV, USA, ⁵School of Geography and Development and Laboratory of Tree Ring Research, University of Arizona, Tucson, AZ, USA, ⁶Department of Environmental and Forest Engineering, National University of Mongolia, Ulaanbaatar, Mongolia, ⁷William Paterson University, Wayne, NJ, USA, ⁸Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, NY, USA

Abstract Some of the oldest and most important trees used for dendroclimatic reconstructions develop strip-bark morphology, in which only a portion of the stem contains living tissue. Yet the ecophysiological factors initiating strip bark and the potential effect of cambial dieback on annual ring widths and tree-ring estimates of past climate remain poorly understood. Using a combination of field observations and tree-ring data, we investigate the causes and timing of cambial dieback events in *Pinus sibirica* strip-bark trees from central Mongolia and compare the radial growth rates and trends of strip-bark and whole-bark trees over the past 515 years. Results indicate that strip bark is more common on the southern aspect of trees, and dieback events were most prevalent in the 19th century, a cold and dry period. Further, strip-bark and whole-bark trees have differing centennial trends, with strip-bark trees exhibiting notably large increases in ring widths at the beginning of the 20th century. We find a steeper positive trend in the strip-bark chronology relative to the whole-bark chronology when standardizing with age-dependent splines. We hypothesize that localized warming on the southern side of stems due to solar irradiance results in physiological damage and dieback and leads to increasing tree-ring increment along the living portion of strip-bark trees. Because the impact of cambial dieback on ring widths likely varies depending on species and site, we suggest conducting a comparison of strip-bark and whole-bark ring widths before statistically treating ring-width data for climate reconstructions.

1. Introduction

Many of the oldest living trees in the world, and those most useful for climate reconstructions, persist under extremely cold and dry environmental conditions (LaMarche, 1969; Schulman, 1954). Ancient trees living near the margin of their environmental tolerances can be exceptionally slow growing and can have sinuous, stunted stems and limited foliage (Bailey, 1970; Kelly et al., 1992; Stahle, 1996; Swetnam & Brown, 1992). Strip-bark morphology, also known as partial cambial dieback, is another characteristic common among old trees growing in harsh environments. In contrast to whole-bark trees with a complete living cambium, strip-bark trees have discontinuous radial growth, exhibit strips of dead and living tissue along the stem, and have eccentric growth patterns (Esper, 2000; Schulman, 1954; LaMarche, 1969). Strip-bark morphology has been noted in *Pinus aristata* Engelm., *Pinus longaeva* Bailey, and *Pinus balfouriana* Grev. & Balf. in the Pinaceae family and some *Thuja* spp. and *Juniperus* spp. in the Cupressaceae family, among others (Matthes et al., 2002).

Strip-bark morphology is initiated by a localized disruption in resource transport, which ultimately results in cambial dieback along a vertical axis of the tree (Larson et al., 1993, 1994; Matthes et al., 2002; Matthes & Larson, 2009). Strip-bark *Thuja occidentalis* L., for example, has a sectorial radial architecture where shoot segments are directly connected to particular roots (Larson et al., 1993, 1994). These vertical segments are independent from other portions of the stem. Thus, root mortality might only result in death of the corresponding shoot segment while the remainder of the tree continues to grow. This type of physiology, in which only vulnerable portions of the cambium die, could allow trees to survive in adverse sites with spatially variable or transitory resources (Larson et al., 1993, 1994; Matthes et al., 2002).

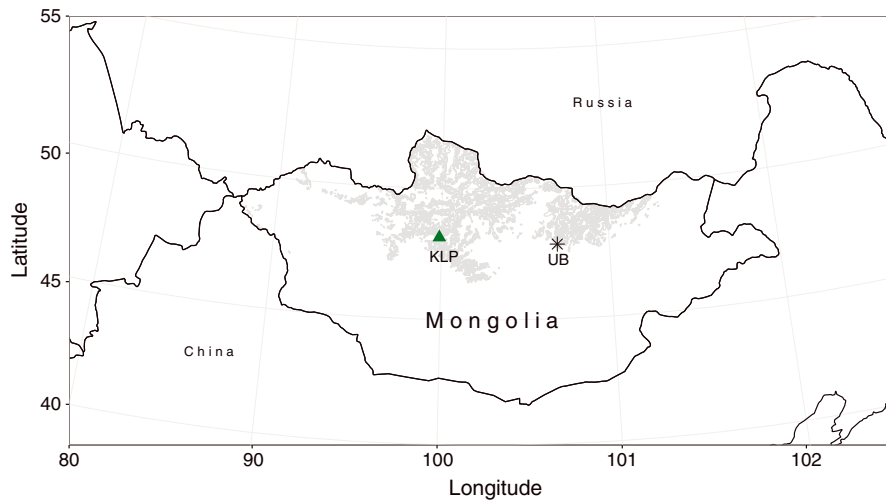


Figure 1. Map of Mongolia showing the Khorgo lava field study site (green triangle, “KLP”) and the capital Ulaanbaatar (“UB”) 530 km to the east of KLP. The light gray shading illustrates forest cover in Mongolia.

The factors initiating cambial dieback in trees likely depend on a suite of environmental hazards and physiological traits. Strong winds can cause localized injury to a stem via blowing ice or dirt particles that abrade leaves or shoots or more directly through tree swaying and root mortality (Beasley & Klemmedson, 1973; Boyce & Lubbers, 2011; LaMarche, 1969; Schauer et al., 2001). As a result, some high-elevation trees experience dieback along the side exposed to prevailing winds (Jacoby et al., 1996; Schauer et al., 2001). In cliff environments, rockfall and root exposure can cause root mortality and subsequent dieback along the spatially connected shoot system (Kelly et al., 1992; Larson et al., 1993; Matthes et al., 2002). However, experiments revealed that root loss may not always be required for sectorized bark stripping, suggesting that other factors could also trigger stripping events (Matthes & Larson, 2009). Tree age, size, and cellular structure are also cited as attributes that can predispose trees to bark stripping on particular individuals or species (Kelly et al., 1992; Matthes et al., 2002; Schauer et al., 2001). Earlywood tracheid pits were larger in mature *T. occidentalis* trees relative to young trees, indicating that older trees might be at a higher risk of drought-induced sapwood cavitation and stem stripping (Matthes et al., 2002). Wood anatomy of ancient *P. longaeva*, however, did not change as a function of age (Connor & Lanner, 1990). Although there are no universal factors that initiate partial cambial dieback across all sites and species, evidence suggests that strip bark is triggered by some degree of environmental and physiological stress.

The effect of localized cambial dieback on radial growth of the living portion of the stem, if any, remains uncertain across different species. Absolutely dated annual tree rings provide information on changes in radial growth rate through time and are valuable for reconstructing past climate when tree growth is limited by target climate variables (Cook & Kairiukstis, 1990; Fritts, 1976). Given that strip-bark trees can be found at sites targeted for dendroclimatic studies, there is a need to determine whether partial cambial dieback in trees can alter the trajectory of radial growth of the living stem subsequent to cambial dieback events and consequently alter estimates of past climate. Differences in radial growth rates between strip-bark and whole-bark trees could reflect morphological adjustments in strip-bark trees after dieback, where a reduction of operable stem circumference leads to higher growth rates along the remaining living axis. However, if the percentage of living cambium remains in proportion to the amount of foliage on the crown (Wright & Mooney, 1965) or if root-shoot carbon allocation is different in trees with partial cambial mortality (Graybill & Idso, 1993), the influence of dieback on annual growth of the remaining stem is uncertain.

Several studies have investigated radial growth rates of strip-bark and whole-bark trees over different time-scales. Ring widths of *T. occidentalis*, for example, drastically increased in the few years following cambial dieback events (Kelly et al., 1992). Over longer timescales, Bunn et al. (2003) found that the growth rate of strip-bark *Pinus albicaulis* Engelm. trees exceeded whole-bark trees starting around 1875. Graybill and Idso (1993) compared standardized chronologies of strip-bark and whole-bark *P. longaeva* trees and reported a more positive trend in the strip-bark chronology during the 20th century. However, using unstandardized

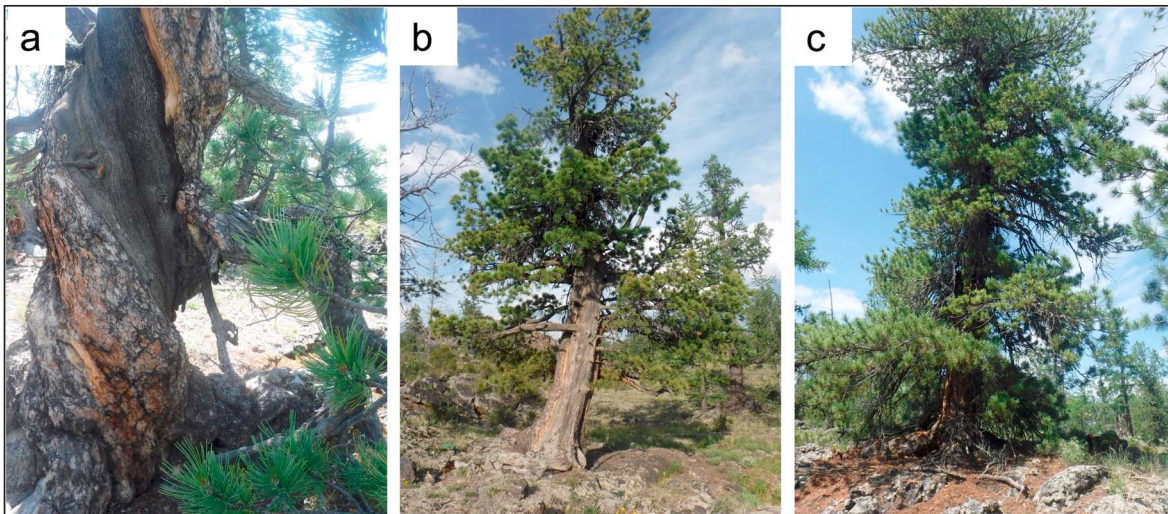


Figure 2. Examples of *P. sibirica* trees sampled from Khorgo. Trees with strip-bark morphology had spiral (a) or straight (b) growth forms. Whole-bark trees (c) often had large, full canopies.

(raw) ring-width data, Salzer et al. (2009) found that the 20th century trends between the two populations were the same. Standardization removes or reduces biological trends in the raw tree-ring data, but these data processing techniques can introduce differences in recent strip-bark and whole-bark trends that are not evident in raw ring-width data (Ababneh, 2006; Salzer et al., 2009). Despite similar growth rates and trends in the modern period, comparatively larger raw ring widths are evident in whole-bark *P. longaeva* trees in earlier centuries (Ababneh, 2006; Salzer et al., 2009), which can be due to younger trees comprising the whole-bark population (Salzer et al., 2009), leading to relatively steeper trends in strip-bark trees over the past several centuries. Other studies have also noted positive trends in raw ring-width data of strip-bark trees compared to whole-bark trees from the same site (Pederson et al., 2014; Yang et al., 2014).

The relationship between partial cambial dieback and radial ring width remains unclear, especially as it applies to different species or sites with different environmental stressors. Strip-bark morphology is a common feature in ancient Siberian pine (*Pinus sibirica* Du Tour) trees growing on the Khorgo lava field in central Mongolia (Figures 1 and 2). These drought-sensitive trees are valuable for reconstructions of past hydroclimate, and some appear to contain long-term positive growth trends that may be related to strip-bark morphology (Pederson et al., 2014). However, radial growth comparisons of strip-bark and whole-bark trees from this site have not been explicitly tested using living trees known to have a partial or full cambium. To better understand strip-bark morphology and its effect on ring widths, here we determine the timing and potential cause of cambial dieback events on the Khorgo lava field and compare radial growth rates and trends of living *P. sibirica* whole-bark and strip-bark trees. These findings will help improve our understanding of the environmental factors that stress long-lived trees, allow us to better identify morphology-related (non-climatic) signals in tree-ring data, and refine our reconstructions of past climate through reducing uncertainty in long-term radial growth variability and trends.

2. Materials and Methods

2.1. Field Collection

We collected increment cores and field data from trees growing on the Khorgo lava field located in the northern Khangai Mountains of central Mongolia (Figure 1; 48.16°N, 99.84°E, elevation: ~2,060 m asl). The sampled study area has complex microtopography and hydrology imposed by underlying basalt. The forest growing on Khorgo is dominated by widely spaced *P. sibirica* and *Larix sibirica* trees, many of which show classic old-growth characteristics, such as stunted and twisted (spiral grain) morphology, spiked tops, and strip bark (Swetnam & Brown, 1992; Pederson, 2010; Figure 2). Spiral grain due to cell reorientation is a common feature of old trees growing in rocky soils with heterogeneous resource supply and facilitates the distribution of sap and sugar to multiple parts of a tree (Kubler, 1991). In these spiral-grained individuals, dieback takes a

winding path from the base to the crown following the wood grain. Some trees at Khorgo grow directly on exposed lava rock, while others inhabit "islands" of soil development, likely self-created by litter accumulation and root action. Whole-bark trees tend to grow in areas with thicker soils and were often spatially clustered, whereas strip-bark trees were found in both environments.

We extracted increment cores from 45 strip-bark and 46 whole-bark *P. sibirica* trees. A tree was classified as strip-bark if cambial dieback could be traced along the entire vertical length of the stem extending to the crown. For each strip-bark tree, we took an "A" and "B" core from breast height of the living side near the axis of dieback and opposite the side of dieback, respectively. A "D" (for "dead") core was collected from the dead side of strip-bark trees only to estimate the year of cambial dieback along the sampled axis. The percentage of dead cambium along the circumference of each tree at breast height was estimated and recorded. Additionally, we noted the range of aspects showing dieback (dead stem) along the circumference at the base and breast height of each strip-bark tree. Dieback at both heights was documented to account for the spiral grain of some strip-bark trees (Figure 2a) and the possibility that environmental disturbances could initiate dieback along different heights of the stem. In terms of whole-bark trees, nearly all mature trees had some evidence of dead roots or isolated dieback at the crown; thus, trees were only classified as whole-bark if $\geq 95\%$ of the stem retained living cambium. We collected two cores per whole-bark tree, at opposing sides when possible, and perpendicular to the underlying slope of the terrain or lean of the tree (if present).

2.2. Laboratory Methods

Increment cores were prepared for analysis using standard dendrochronological methods in the laboratory (Stokes & Smiley, 1968). Cores were visually cross-dated, and the software program COFECHA was used to ensure accurate dating of each series (Holmes, 1983). Many whole-bark samples came from younger, fast-growing trees, so cores with < 315 rings (inner ring date after 1700 CE) were excluded from further analysis to reach a median tree series length comparable to the generally older strip-bark trees. All strip-bark trees were retained, including some cores with fewer than 315 rings; these cores came from trees that were visibly much older, but were rotten or hollow and thus were missing some inner growth rings. Some individual series were excluded due to gaps caused by rotten wood, the loss of outer rings during field collection, or in two cases, because extreme growth suppression precluded dating over several decades. However, for all excluded strip-bark series, there was another core from the same tree that was included in our analysis. Additional analyses were conducted using exclusively strip-bark and whole-bark cores with > 515 rings (at least back to 1500 CE) to evaluate growth patterns from the oldest trees.

In total, 45 strip-bark trees (78 series) and 35 whole-bark trees (60 series) were retained for analysis using the outlined criteria. The strip-bark series spanned the years 1022–2014 CE and retained a strong common signal back to 1215 (expressed population signal (EPS) > 0.85 using 50 year windows with overlapping 25 years; Wigley et al., 1984). The whole-bark series extended from 1297 to 2014 CE and had an EPS > 0.85 back to 1315. The median series lengths of the strip-bark and whole-bark chronologies were 491 and 407 years, respectively.

2.3. Analysis

To ascertain the potential causes of strip bark at Khorgo, we determined the cardinal direction and timing of cambial dieback across all trees. Estimated cambial death dates were plotted through time to determine if dieback events clustered around a similar time period, were randomly dispersed, and/or occurred during particular climatic events. Only approximate dieback dates could be determined due to erosion and decay on the dead side of the tree over time leading to potential loss of outer growth rings. Additionally, a gradual spreading of strip bark across the tree over time might result from multiple successive stripping events (Bunn et al., 2003). The former uncertainty implies that dieback estimates will predate the occurrence year, whereas the latter uncertainty suggests that dieback estimates will be related to the coring location. The "D" cores were taken wherever we could attain a quality sample from the strip of dead cambium, which ranged from the center of the dead strip to near the intersection with living cambium. These uncertainties preclude a direct year-to-year comparison between dieback dates and climate anomalies. Consequently, we analyze broader temporal associations between climatic conditions and large-scale dieback phenomenon. A June–July temperature reconstruction from the Ondor Zuun Nuruu site in Northern Mongolia (Davi et al., 2015) and a June–September self-calibrating Palmer Drought Severity Index (scPDSI) reconstruction derived

from a separate and independent set of samples from Khorgo trees (Pederson et al., 2014) were used to investigate the climatic conditions during dieback events from 1500 to 2005 CE. The scPDSI represents relative moisture availability, where negative (positive) values indicate drier (wetter) conditions (van der Schrier et al., 2013). The number of dieback events during a moving 30 year window was compared to the average reconstructed temperature and scPDSI for each corresponding window of time.

Strip-bark and whole-bark radial growth patterns and rates were first compared using raw ring-width data. Analyzing raw ring-width data is a common approach for dendroecological studies seeking to evaluate radial growth patterns (Fritts & Swetnam, 1989; Bunn et al., 2003) while preventing standardization-related artifacts in trends of tree-ring data (Briffa & Melvin, 2011; Cook & Peters, 1997; Salzer et al., 2009). First, the means and 95% bias-corrected and accelerated (BCa) bootstrap confidence intervals (Efron, 1987) were computed for raw ring-width measurements of all strip-bark and whole-bark trees separately to compare radial growth rates between the two populations. This analysis was performed on all selected cores and a subset of cores with >515 rings from both groups (see section 2.2). Regional curves developed from age-aligned series (Briffa et al., 1992) were also produced for the strip-bark and whole-bark populations to compare growth trajectories with increasing cambial age. In this analysis, we only included cores that either reached pith or appeared to have rings with clear curvature nearing pith.

We conducted multiple analyses on the strip-bark trees alone to evaluate the range of ring-width variability within this population. First, strip-bark samples were divided into terciles based on the percentage of cambial dieback along the stem, and mean ring widths and 95% BCa bootstrap confidence intervals were compared among the three groups. Then, bootstrapped means and 95% confidence intervals were calculated for the "A" and "B" strip-bark cores separately to determine if the position along the stem (i.e., near to or distant from the dieback axis) influences mean ring widths. Strip-bark trees with only a narrow strip of active cambium along the stem required us to collect the "B" core nearly adjacent to the "A" core, so these trees ($n = 17$) were not included in this analysis.

We also compared whole-bark and strip-bark standardized chronologies to assess whether residual trends in the populations differ after removing the overall allometric radial growth trends from the individual series. All series were standardized using signal-free (SF) methods (Melvin & Briffa, 2008) with a time-varying spline (Melvin et al., 2007) with an initial stiffness of 50 years. This detrending method removes early allometric trends and stiffens through time to retain longer-term trends at the end of series, which theoretically should be related to climate. SF indices were estimated as residuals of the power-transformed ring widths from the fitted detrending curves (Cook & Peters, 1997), and final robust mean chronologies were produced using the RCSIgFree program (<http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>). The SF and residuals methods were selected to reduce the amount of bias and trend distortion that can occur as a result of standardization, particularly at the ends of tree-ring series (Cook & Peters, 1997; Melvin & Briffa, 2008). Trend distortion occurs when tree-ring variance related to climate affects the fitting of detrending curves used for removing nonclimatic variance and can therefore result in the distortion of some climate-related variance in the final tree-ring chronology (Melvin & Briffa, 2008). SF standardization iteratively removes the common chronology signal from tree-ring measurements to improve fitted standardization curves and produce a robust mean chronology with reduced trend distortion relative to traditional or standard methods (Melvin & Briffa, 2008).

A strip-bark and whole-bark chronology was computed using all series from each group, and we applied a nonparametric Mann-Whitney U test to determine whether there were significant differences in the indices over each century of analysis. Chronologies using a subset of series with >515 years from each group were also compared. Next, a dynamic linear regression using the Kalman filter (Kalman, 1960; Petris & An, 2010; Visser et al., 2010; Visser & Molenaar, 1988) was employed to assess the time-dependent relationship between the whole-bark chronology as a "target" predictor variable and the strip-bark chronology as the dependent variable. The whole-bark chronology, in this case, is assumed to be the control with no (or negligible) influence of physiological dieback on ring-width variability. Through estimating time-varying regression coefficients, this method tests how the index values of strip-bark and whole-bark chronologies change relative to one another through time and can be used to determine whether there are periods of time in which their trends diverge. Chronology comparison and the Kalman filter analysis were also applied to strip-bark and whole-bark chronologies developed from standard (i.e. not SF) methods, otherwise using the same standardization scheme, to compare with our SF results.

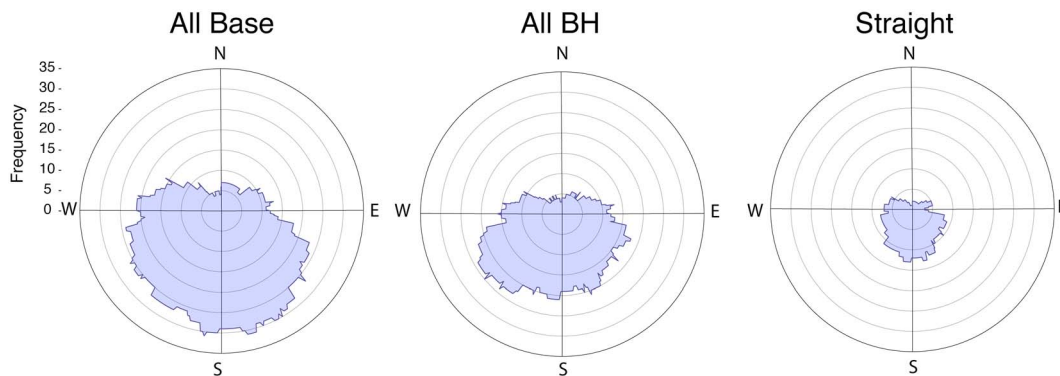


Figure 3. Polar plots showing the frequency of trees (out of 45 total trees) with evidence of strip-bark morphology along all compass directions. Dieback at the base (left) and breast height (middle) of all strip-bark trees, and only those with straight strip-bark morphology (right), are shown. Each nested circle, moving outward from the center, represents an incremental increase of five trees showing dieback.

3. Results

3.1. Cambial Dieback

Cambial dieback occurred along all aspects of strip-bark trees but was more frequent on the southern side of the stems (Figure 3). South-facing dieback was particularly dominant along the base of all strip-bark trees and for a subset of those with straight (i.e., not spiral-grained) strip-bark morphology. The breast-height measurements, which are different than basal measurements due to the spiral grain of some strip-bark trees, show more dieback along south and west-facing aspects (Figure 3). Approximate dieback dates were detectable for 40 of the 45 (89%) strip-bark trees studied. The remaining “D” (dead) cores had extremely suppressed rings at the modern end and could not be reliably dated. The dieback events were scattered throughout the 1500–2014 period; however, 45% of all cambial mortality events occurred in the 19th century (Figures 4a and S1a in the supporting information). This peak in dieback events is also apparent when controlling for declining sample depth through time (Figure S1b). The peak density of these events in the mid-1800s (Figure 4a) follows two of the coldest (Figure 4b; Davi et al., 2015) and one of the driest (Figure 4c; Pederson et al., 2014) nonoverlapping 30 year periods of summertime climate. Dieback events were more common during 30 year periods of below-average temperatures, but there was no consistent pattern with moisture conditions (Figure 4d, vertical and horizontal lines represent mean temperature and scPDSI, respectively, over the 1500–2005 common period).

3.2. Comparison of Mean Ring Width Trends

The mean ring-width chronologies of strip-bark and whole-bark trees are strongly coherent on interannual and decadal timescales from 1500 to 2014, but have differing centennial-scale trends. After prewhitening each chronology using the minimum Akaike information criterion to select the autoregressive (AR) model order (Akaike, 1974), the chronologies are strongly and significantly correlated on the interannual scale ($r = 0.90$, $p < 0.001$). However, the strip- and whole-bark chronologies have markedly different long-term growth trends from 1500 to 2014 (Figures 5a and 5b). The whole-bark chronology has a persistent decreasing trend not shared by the strip-bark chronology. The mean ring width of strip-bark trees oscillates around 0.3 mm/year across the entire record until the early 20th century when it suddenly increases and significantly exceeds the whole-bark mean ring-width chronology (Figures 5a and 5b). Moreover, when using series from older trees (with >515 rings), strip-bark trees significantly exceed whole-bark trees starting in the mid-1800s (Figure S2). Regarding age-aligned regional curves, based only on series reaching or nearing pith, both strip-bark and whole-bark trees show a decreasing allometric ring-width trend (Figure 5c). Strip-bark ring widths rapidly stabilize after a cambial age of ~ 200 years, whereas whole-bark trees have larger rings at a young cambial age and a more rapid ring-width decline that continues to decrease with increasing cambial age.

Separating the strip-bark trees into terciles based on percentage of cambial dieback yields low (7–23%; $n = 26$ series), medium (23.1–40%; $n = 26$ series), and high (40.1–81%; $n = 26$ series) dieback groups. High dieback trees have larger mean ring widths across some periods of time, particularly in the early 1600s and mid-to-

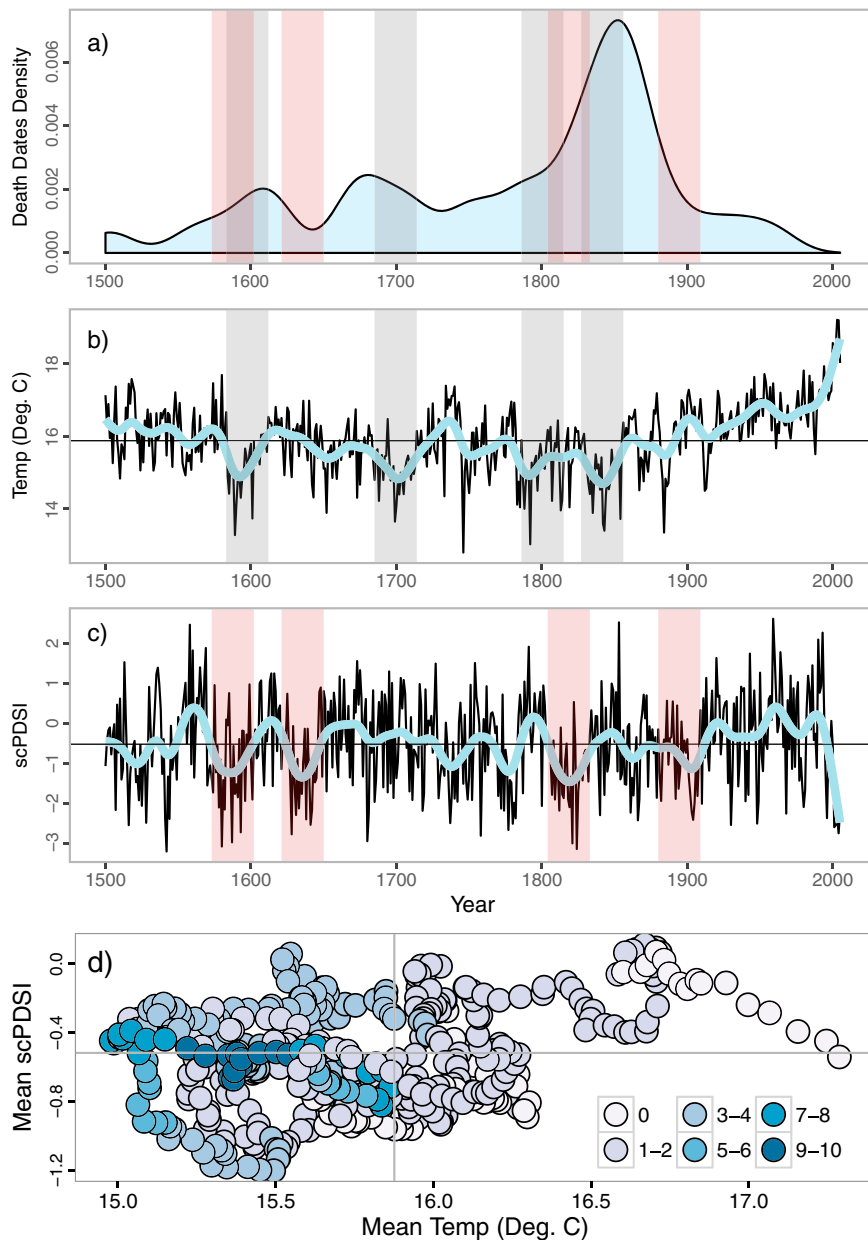


Figure 4. Comparison of death date estimates with climate. (a) Density of dieback dates from strip-bark trees over time; (b) June-July temperature reconstruction from Ondor Zuun Nuruu (OZN) in Northern Mongolia (Davi et al., 2015) with a 50 year smoothing spline in blue; gray bars highlight the four coldest 30 year periods based on nonoverlapping windows. (c) June-September scPDSI reconstruction derived from independent Khorgo trees (Pederson et al., 2014), and a 50 year smoothing spline in blue; pink bars represent the four driest 30 year periods based on nonoverlapping windows. Panel (d) shows the number of death dates occurring in each 30-year moving window, plotted against the mean temperature and drought index for each corresponding period. Vertical and horizontal gray lines in panel (d) represent the long-term common period (1500–2005) mean for temperature and scPDSI, respectively.

late 1900s, followed by the medium and low dieback trees, although these differences are not consistent (Figure 6a). In comparing “A” and “B” cores of strip-bark trees (Figure 6b), the “A” cores near the region of cambial dieback have a higher positive slope from 1500 to 2014 ($\beta = 0.00028$, in units of mm/year, $p < 0.001$) relative to the “B” cores ($\beta = 0.00007$, $p < 0.001$). The “A” cores had smaller mean ring widths than “B” cores until the 20th century, although the 95th percentile confidence interval of “A” cores also exceeded the same confidence limit for “B” cores during the early 1600s. Even though the “B” cores had a smaller positive slope than “A” cores, the mean ring widths of “B” cores alone still significantly exceeded whole-bark ring widths starting in the 20th century ($p < 0.05$, Figure S3).

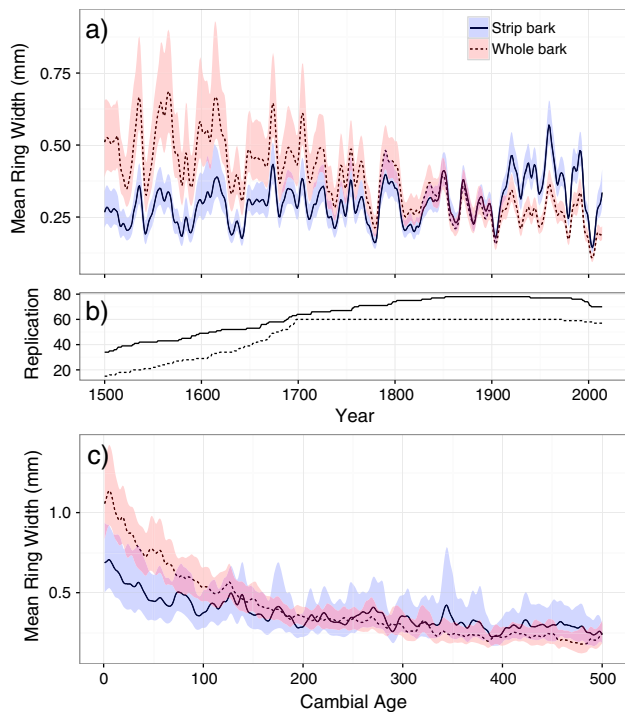


Figure 5. Mean ring-width comparisons of strip-bark and whole-bark trees. (a) A 10 year spline of strip-bark (solid line) and whole-bark (dashed line) mean ring-width chronologies from 1500 to 2014. The 95% BCa bootstrap confidence intervals around the mean are shown in blue and pink for strip-bark and whole-bark trees, respectively. (b) The number of strip-bark (solid) and whole-bark (dashed) series over time corresponding to (a). (c) Age-aligned regional curves for strip bark ($n = 22$) and whole bark ($n = 25$) series, shown with 95% BCa bootstrap confidence intervals.

3.3. Comparison of Standardized Chronologies

The SF standardized chronologies of strip-bark and whole-bark trees show differing trends over the past several centuries. The strip-bark standardized chronology has lower or equivalent index values relative to the whole-bark standardized chronology until the mid 19th to early 20th century (Figure 7a). The strip-bark and whole-bark chronologies have significantly different index values only in the 16th ($W = 4,027$; $P_{Wilcox} = 0.0180$) and 20th ($W = 7,047$; $P_{Wilcox} < 0.0001$) centuries (Table S1). Further, the strip-bark chronology has a higher slope over the full 1500–2014 period relative to the whole-bark chronology ($\beta = 0.00093$ and 0.00019 , in units of index value/year, respectively). Results are similar when using standard chronologies developed with traditional methods rather than SF methods; the strip-bark chronology slope is higher than that of whole-bark trees ($\beta = 0.00061$ and 0.00005 , respectively; Figure S4c). However, differences between strip-bark and whole-bark standard indices are significant only in the 20th century ($W = 6,713$; $P_{Wilcox} < 0.0001$; Table S1).

There is an overall positive trend in dynamic regression slope between strip-bark and whole-bark SF chronologies from 1500 to 2014 (Figure 7b), indicating that strip-bark indices are steadily increasing relative to whole-bark trees. However, this general trend is punctuated by periods of rapid increases, steady plateaus, and short-term decreases in the coefficients through time. Notably, the early 1600s, mid-1800s, and early 1900s, following cold and dry periods (Figures 4b and 4c), show a rapid increase in regression coefficients, indicating a sudden surge in the strip-bark chronology compared to the whole-bark chronology. While there is a particularly sudden and steep increase in regression coefficients during the early 20th century when using all cores to develop the chronologies (Figure 7b), this effect is more gradual when only including the longest cores (>515 rings; Figures S4a and S4b). These temporal patterns of dynamic regression coefficients between strip-bark and whole-bark chronologies are also evident with standard chronologies (Figures S4c and S4d).

4. Discussion

In this study, we investigate the cause and timing of partial cambial dieback in *P. sibirica* trees from central Mongolia and evaluate whether dieback can affect tree-ring widths on the remaining portion of stems. Our results indicate that cambial dieback was most abundant on the southern side of stems and occurred most frequently during the 19th century, when there were periods of unusually cold (and sometimes dry) growing season conditions. Following this period, ring widths of strip-bark trees significantly exceeded whole-bark trees, indicating a potential link between tree morphology and radial growth trends. These findings have important implications for the use of *P. sibirica*, or other trees with morphology-related growth trends, in climate reconstructions.

4.1. Proposed Cause and Timing of Dieback

The causes of cambial dieback leading to strip-bark morphology are not well understood across a range of different tree species and environments. Trees on the Khorgo lava field in central Mongolia are exposed to a number of environmental hazards throughout the year, many of which could cause cambial dieback. The predominance of cambial dieback on the southern side of trees suggests that the primary environmental drivers of strip bark are unidirectional. One key driver might be solar radiation, which can cause the sunlit (southern) side of the tree to warm several degrees more than the northern side of the tree during midday (Harvey, 1923; Sakai, 1966), particularly in locations such as Khorgo, where trees are exposed and have little relief from direct sun.

There are several ways in which differential radiation and warming could result in physiological damage and subsequent dieback on the southern side of stems. Freeze-thaw dynamics can cause severe and localized

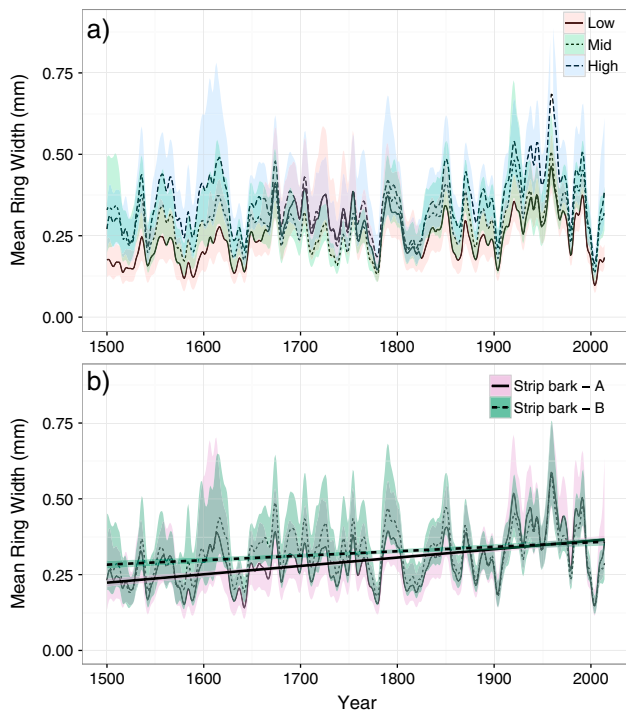


Figure 6. Mean ring-width comparisons between and within strip-bark trees. (a) Mean ring width of all series for trees with a low (7–23%), medium (23.1–40%), and high (40.1–81%) percentage of cambial dieback, with 95% BCa bootstrap confidence intervals (pink, green, and blue, respectively). (b) Mean and 95% BCa bootstrap confidence intervals for “A” (solid, purple) and “B” (dashed, green) cores from strip-bark trees. “A” cores were taken near the dead strip, and “B” cores were taken opposite of the dead strip.

physiological injuries to trees. For example, in the eastern United States, freeze-thaw dynamics, in combination with direct sublimation or evaporation from xylem units, were shown to result in localized emboli formation on the southern side of *Acer saccharum* trees during the winter (Sperry, Donnelly, & Tyree, 1988). While conifers have anatomical features that can increase resistance to xylem cavitation relative to some woody angiosperms, often resulting in lower rates of embolism (Sperry, Hacke, & Pittermann, 2006; Sperry & Sullivan, 1992), severe freeze-thaw embolism has been reported in many coniferous species, particularly under severe drought conditions (Mayr et al., 2002, 2003) or during periods with reduced insulating snow cover (Beier et al., 2008). If warmer localized temperatures initiate earlier cambial reactivation of trees (Begum et al., 2008; Oribe, Funada, & Kubo, 2003; Oribe & Kubo, 1997) and earlier cambial division on the southern side of stems, this region could be even more vulnerable to cavitation and hydraulic disruption. Many conifers can sufficiently recover from wintertime hydraulic stress via tracheid refilling (Mayr et al., 2014; Sperry et al., 1994); however, concurrent drought conditions or high embolism rates might make recovery more difficult.

Sunscald is another unidirectional and sun-related injury where cambium and bark can separate from the wood (Sakai & Larcher, 1987). Solar radiation can warm and prematurely dehydrate the southern side of trees in early spring, effectively decreasing the freezing tolerance of tissues (Harvey, 1923; Kramer & Kozłowski, 1979; Sakai & Larcher, 1987). If refreezing occurs, cambial death on the south side of trees can follow, and phloem tissue can be damaged; this blocks sugar translocation along the stem, and bark peeling and exposure can introduce pathogens, which can lead to additional deterioration on the injured side of the stem (Kramer & Kozłowski, 1979). Therefore, it is possible that injuries related to solar radiation and direct heating of the southern side of stems could have initiated localized mortality and strip-bark morphology on the *P. sibirica* stems studied here.

The peak of dieback events occurred during the 19th century, when central Mongolia experienced extremely cold conditions in addition to some severe droughts (Davi et al., 2015; Pederson et al., 2014). We can only comment on past summer climatic conditions because the tree-ring based reconstructions estimate June–July temperature and June–August scPDSI. However, the June–August period represents the vast majority of the growing season in this region (Davi et al., 2006; De Grandpré et al., 2011). Although we do not have paleoclimatic information specifically for the earliest portion of the growing season, when trees might be especially susceptible to freezing injuries, we hypothesize that trees during the 19th century were exposed more often to inhospitable temperatures during all periods of radial growth. If cold temperatures were combined with dry (and possibly sunny) conditions, as identified during some periods of the 1800s, trees might have been at a higher risk of unidirectional stem injury. In contrast to the high dieback rate in the 1800s, there were only three of 40 recorded dieback events in the 20th century, a period of relatively warmer and wetter climatic conditions (Davi et al., 2006; Pederson et al., 2014).

Although variation in solar radiation and climate could have contributed to the strip-bark phenomenon due to the prevalence of south-facing dieback, some trees experienced dieback exclusively on other sides of the stem indicating that other environmental factors could be important as well. In particular, some of the spiral-grained trees had dieback along south-west facing aspects at breast height. Spiral-grain morphology leads to an additional complication when determining cause of dieback initiation because ribbons of dieback migrate around the stem with height. It is possible that blowing ice particles and dust from surface winds, which arrive primarily from the west at Khorgo (Figure S5; Molod et al., 2015; Rienecker et al., 2011), could have contributed to west-facing dieback near breast height on some of these stems. Differing local and/or seasonal wind directions could have affected other sides of some trees as well. Jacoby et al. (1996) noted partial cambial dieback on the northern side of Siberian pines from a tree-line site in the Tarvagatay Mountains of

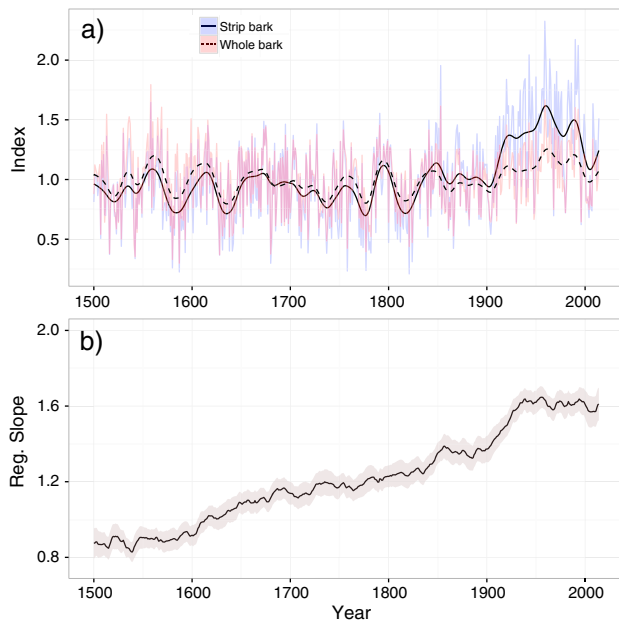


Figure 7. Standardized chronologies of strip-bark and whole-bark trees and their relationship over time. (a) Strip-bark (blue with solid 30 year spline) and whole-bark (pink with dashed 30 year spline) signal free “SF” chronologies for all cores. (b) Dynamic regression coefficients for a model relating Khorgo strip-bark and whole-bark chronologies, with gray shading representing a 95% confidence interval. The increase in regression slope through time indicates a gradual increase in the index values of strip-bark trees relative to whole-bark trees.

growth trend, is due to the geometry of trees in which a similar volume of wood is placed around an ever-increasing cylinder (Fritts, 1976). Allometric radial growth trends are prominent in trees growing under open-canopy conditions, free of direct tree-to-tree competition, such as those at Khorgo. In contrast, this allometric growth trend was not apparent in the mean ring-width strip-bark chronology. However, the regional curves of age-aligned series, based only on tree-ring series reaching or nearing pith, illustrate that the allometric growth trend is present but relatively muted in strip-bark trees compared to whole-bark trees. Strip-bark ring widths stabilized with increasing cambial age, and strip-bark trees had a lower initial growth rate than whole-bark trees at young cambial ages. Slow early growth rates indicate that strip-bark trees might have been disadvantaged from a juvenile stage, due to either the microsite environment or genetics, and such disadvantages might have predisposed these trees to dieback events. The stabilization of strip-bark radial growth over time suggests that these trees can reduce their biomass to a sustainable level for continued radial growth (Matthes et al., 2002), perhaps allowing them to live under and adapt to unfavorable conditions for longer periods of time.

The prominent growth increase starting around the beginning of the 20th century in the strip-bark chronology was largely absent in the whole-bark mean chronology. A similar pattern was observed in *P. albicaulis* from Montana, where strip-bark and whole-bark trees had similar growth rates until about 1875, after which the strip-bark trees showed a step-change increase compared to whole-bark trees (Bunn et al., 2003). While strip-bark and whole-bark *P. longaeva* trees from the White Mountains in California have similar growth rates and trends over the industrial period, the strip-bark trees have steeper increasing linear trends in mean ring widths relative to whole-bark trees over several centuries (Ababneh, 2006; Salzer et al., 2009). This steeper trend may occur because strip-bark trees were older and initially slower growing, similar to the trees analyzed in our study, but showed the same modern growth rate increase as whole-bark trees (Salzer et al., 2009).

Within strip-bark trees alone, we found notable variability in growth rates where there is a positive association between dieback extent and mean ring width. Across much of the record, a higher percentage of cambial dieback occurring on a stem results in higher mean ring widths on the remainder of the living

central Mongolia and suggested that northerly winds were the likely driver of dieback on these trees, which were growing on a north-facing slope. Prevailing surface wind was also found to be a dominant contributor to dieback in *P. aristata* trees from other environments (Boyce & Lubbers, 2011; Schauer et al., 2001). Regardless, the preponderance of dieback on the southern base of trees with and without spiral grain suggests that the dominant stressor affects primarily the south-facing side of trees. Further, the clustering of dieback events through time might indicate that temporally variable environmental factors, such as climate, are likely important contributors of dieback.

Microsite characteristics on the lava, such as underlying soil conditions or topography, or variation in snow depth or relative moisture, may put particular individuals at risk of cambial mortality. Initial observations at Khorgo suggest that strip-bark trees tend to grow on more stressed microsites, with thinner soil development. Bunn et al. (2003) found that the topographic convergence index (a soil moisture proxy) can explain some of the spatial patterning of strip-bark *P. albicaulis* trees; however, they suggest that strip-bark trees might cluster on wet sites because these individuals might not survive on more adverse sites. Future research should further evaluate the microsite conditions of strip-bark and whole-bark trees at Khorgo and other locations to determine the extent to which local abiotic characteristics are related to tree morphology.

4.2. Differences in Radial Growth Trends

Our study shows that strip-bark *P. sibirica* trees in central Mongolia have different long-term growth trends than trees with a fully active cambium. The whole-bark mean (raw) ring-width chronology has a clear and persistent decline over time. This decline, referred to here as the allometric

stem. These findings, in addition to our comparison of strip-bark and whole-bark trees, support the notion that strip-bark events and subsequent morphological changes can directly cause an increase in radial growth rate along the living part of a stripped tree. Drastic short-term growth increases have been reported after strip-bark events in *T. occidentalis* trees (Kelly et al., 1992); however, we did not see a clear association between specific dieback events and growth rates of individual trees (results not shown). This might be due to inherent error in estimates of dieback dates, or the ability to capture only one of many possible dieback events through time (Bunn et al., 2003). However, we observed a combination of multiple step changes and gradual growth increases in individual strip-bark series, suggesting that multiple dieback events can occur across the bole of a tree and continually influence growth rates of strip-bark trees.

In addition to between-tree variability, we document pronounced within-tree differences in ring-width trends between two cores of the same strip-bark tree. Cores taken near the axis of cambial dieback ("A" cores) displayed marginally slower growth rates before the 20th century than those distant from strip ("B" cores) and thus had a steeper positive trend in ring width through time. Physical injuries to tree stems can have an important impact on ring-width variability across the stem, which is useful for identifying past geomorphic or ecological processes (Stoffel & Bollschweiler, 2008). Features such as overgrowing callus tissue and distorted tree rings near the injured axis can contribute to eccentricity and different ring-width trends along the stem. Based on observations in the field, lobate protrusions of the stem near the axis of dieback were common. Lobate growth morphology in other species prone to partial cambial dieback has also been reported (Esper, 2000; Kelly et al., 1992). As such, larger modern ring widths near the strip were not particularly surprising and indicated that cambial injury might have a more dramatic impact on ring-width patterns nearest the injured region.

After detrending all tree-ring series using an age-dependent spline, the gradual positive trend, and the sudden increase in tree-ring indices particularly near the beginning of the 20th century remained in the strip-bark standardized chronology. This further supports a significant distinction between radial growth trajectories of strip-bark and whole-bark *P. sibirica* trees at Khorgo, even after removing biological trends related to tree allometry. However, it is important to note that the standardization method applied to tree-ring series can influence the relative difference between recent trends of strip-bark and whole-bark standardized chronologies (Salzer et al., 2009; see section 4.4).

4.3. Linking the Mechanisms and Timing of Strip-Bark Growth Trends

The large increase in radial growth rate of strip-bark trees starting around the early 20th century, in both the mean ring-width and standardized chronologies, follows a high proportion of cambial dieback events identified in the 19th century. Frequent dieback events during that time, perhaps due to unfavorable climatic conditions, might have reduced the area of active cambium across many individual trees on the landscape and affected subsequent growth rates on the remaining part of the stems. Following the late 1500s, another cold and dry period, there is a small jump in dynamic regression coefficients between strip-bark and whole-bark trees, and cores taken near the cambial injury have a sudden growth increase relative to those taken from farther away. However, there are fewer estimated dieback dates during the 16th and 17th centuries, and the sample size of living trees is much lower during that time.

The mechanisms behind increasing ring widths of strip-bark trees after cambial dieback events are not well understood. The sectorized radial architecture of some strip-bark trees suggests that xylem units are independent; the loss of functioning on one side of the tree, due to catastrophic environmental hazards and loss of resource acquisition, would not necessarily impact other sides of the tree (Larson et al., 1993). Wright and Mooney (1965) similarly noted that the amount of living stem on *P. longaeva* seems in proportion to that of the living crown. Under these conditions, decreasing photosynthetic capacity of the crown might be matched by a decrease in nonphotosynthetic stem tissue. A proportional equilibrium between photosynthetic and nonphotosynthetic tissue in a tree might suggest that ring widths on the independent, living portion of the stem would not necessarily change as a function of dieback given acquisition of other resources remains proportional.

A prevailing theory is that strip-bark trees might grow wider annual rings as a similar amount of growth is applied to a decreasing area of active stem (Salzer et al., 2009). Thus, a change in tree geometry, but not necessarily carbon allocation and total growth along the stem, would cause changes in ring widths on the

remaining living axis of the stem. Considering a “pool” of resources available to a strip-bark tree could also explain why a persistent growth increase could be evident after the loss of part of the tree. In a conceptual model of stem stripping, Matthes et al. (2002) discuss how a sudden decline in resource pool size (e.g., physical damage to part of a tree such that some resources can no longer be accessed) would result in stem stripping on one side of the tree; death along one axis allows the living remainder of the plant to maintain growing conditions despite a net reduction in resources. This model explains why strip-bark trees are able to survive in sites with spatially heterogeneous resources (Matthes et al., 2002). However, if a portion of the tree dies, additional resources within a common below-ground pool might become available to the living remainder of the plant. For example, if a severe drought reduces water availability particularly for one axis of a tree, resulting in unidirectional dieback, a return to wet conditions would mean the living part of the tree would directly benefit from the loss of the other side and have more resources available to it (i.e., resources become available to a smaller region of active growth in strip-bark trees). This hypothetical mechanism could explain the larger ring widths we identified in the strip-bark trees during the relatively wet (Pederson et al., 2014) and warm (Davi et al., 2015) 20th century in Mongolia following inhospitable climate and frequent dieback events in the 19th century.

Previous reports have suggested that changes in water-use efficiency (WUE) could also play an important role in radial growth increases seen in strip-bark individuals (Bunn et al., 2003; Graybill & Idso, 1993). Graybill and Idso (1993) argued that the physiological response of trees to increasing atmospheric carbon dioxide might be more apparent in radial growth rates of strip-bark trees relative to whole-bark trees. They proposed that the two growth forms might have different allocation strategies, where strip-bark trees direct new carbon primarily to cambial growth, while whole-bark trees allocate more carbon to a larger root system, reproduction, and foliage (Graybill & Idso, 1993). Bunn et al. (2003) suggested that an increase in relative strip-bark *P. albicaulis* growth rates only after 1875, despite evidence of cambial dieback well before that period, could indicate that increased WUE due to increased atmospheric CO₂ is a driver of these changes, although it was not explicitly tested. In contrast, Tang et al. (1999) found similar increases in WUE for both strip-bark and whole-bark *P. longaeva* trees over the past two centuries. Detailed physiological (including $\delta^{13}\text{C}$ and intrinsic WUE) and allometric measurements will be necessary to fully understand the factors causing the increasing ring-width trends identified in strip-bark trees at Khorgo.

4.4. Considerations for Dendroclimatic Interpretations

The distinct long-term growth trends in *P. sibirica* trees due to stem morphology have important implications for climate reconstructions using both strip-bark and whole-bark trees. Based on our strip-bark and whole-bark chronology comparison for Khorgo and knowledge of the drought sensitivity of these trees (Davi et al., 2006; Leland et al., 2013; Pederson et al., 2014), we can infer that a hydroclimatic reconstruction using the standardization methods and strip-bark chronology presented here would indicate a wetter 20th century and a more positive trend in moisture through time, relative to a reconstruction derived from the whole-bark chronology. While morphology-related growth trends may not be present at other sites or with other species prone to strip-bark, we recommend several precautionary steps before using strip-bark trees for climate reconstruction. First, we recommend taking thorough notes in the field regarding the presence or absence of strip bark. Researchers might take samples from documented living strip-bark and whole-bark trees to determine whether differences in radial growth or trends occur between the growth forms at their particular study sites. Further, if a larger biological effect on ring widths occurs near the zone of injury, as supported by our results, tree-ring samples should be taken as far away from the injury as possible to avoid any additional bias.

If distinct strip-bark and whole-bark trends in ring-width data are identified, researchers should proceed with informed and cautious statistical data treatment and should compare standardized strip-bark and whole-bark chronologies prior to combining them for climate reconstruction. For example, a common detrending method is to use a fitted linear or exponential curve that is constrained to be negative or have a slope of zero in order to conservatively remove only the expected allometric growth trend (Cook & Kairiukstis, 1990). In the case of this study, such a method could retain positive morphology-related trends unique to strip-bark trees. A few studies have recognized the uncertainty associated with strip-bark morphology on growth trends and took steps to avoid bias in climate reconstructions due to tree morphology. Using independent living and dead trees from the same site as this study, Pederson et al. (2014) allowed for straight-line detrending with

positive slopes and found no significant difference between chronologies of living and dead trees inferred to have strip and whole-bark forms. Yang et al. (2014) also noted strip-bark forms in ancient *Juniperus przewalskii* Kom from the northeastern Tibetan Plateau and thus allowed for increasing Regional Curve Standardization (RCS) curves for trees older than 1,500 years; no strip-bark bias was found in trends of indices over the past 1000 years. These methods, or more flexible detrending curves, can effectively reduce or remove the potential influence of tree morphology on ring-width trends and better isolate long-term climate variability in tree-ring data.

The use of SF versus traditional methods should also be further explored to determine the extent to which these two forms of standardization, when applied to raw tree-ring data, might influence trends in the chronologies of strip-bark and whole-bark populations. In both cases, we found here that the strip-bark chronology had a higher positive slope relative to the whole-bark chronology. However, the slope difference between the two chronologies was slightly greater when using the SF approach. This larger discrepancy between strip-bark and whole-bark chronologies might suggest that the SF method can retain more non-climatic, common morphological trends in the data, however, more analysis is required to understand the impact of these standardization methods on strip-bark trees. Future research should focus on testing different standardization and detrending methods on trees with morphology-related growth trends in order to reduce potential bias in climate reconstructions.

Acknowledgments

We would like to thank Khashaa Eldevochir, Jennie Zhu, and Byambagerel Suran for their help in collecting samples in the field and Jeffery Benjamin and Javier Martin-Fernandez for their laboratory assistance. We would additionally like to thank all members of the Climate and Ecology of the Mongol Empire (CEME) group for their contributions and suggestions. The field data and tree-ring chronologies used in this study are included in the supporting information. The authors acknowledge the support from the National Science Foundation award BCS-1210360. L.A.H., N.D., and M.P.R. acknowledge the National Science Foundation award OPP-1737788. Lamont-Doherty Earth Observatory contribution number 8193.

References

- Ababneh, L. N. (2006). *Analysis of radial growth patterns of strip-bark and whole-bark bristlecone pine trees in the White Mountains of California: implications in paleoclimatology and archaeology of the Great Basin* (PhD Thesis). The University of Arizona. Retrieved from The University of Arizona Campus Repository.
- Akaike, H. (1974). A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, *19*(6), 716–723. <https://doi.org/10.1109/TAC.1974.1100705>
- Bailey, D. K. (1970). Phytogeography and taxonomy of *Pinus* subsection Balfourianae. *Annals of the Missouri Botanical Garden*, *57*(2), 210–249. <https://doi.org/10.2307/2395110>
- Beasley, R. S., & Klemmedson, J. O. (1973). Recognizing site adversity and drought-sensitive trees in stands of bristlecone pine (*Pinus longaeva*). *Economic Botany*, *27*(1), 141–146. <https://doi.org/10.1007/BF02862228>
- Begun, S., Nakaba, S., Bayramzadeh, V., Oribe, Y., Kubo, T., & Funada, R. (2008). Temperature responses of cambial reactivation and xylem differentiation in hybrid poplar (*Populus sieboldii* × *P. grandidentata*) under natural conditions. *Tree Physiology*, *28*(12), 1813–1819. <https://doi.org/10.1093/treephys/28.12.1813>
- Beier, C. M., Sink, S. E., Hennon, P. E., D'Amore, D. V., & Juday, G. P. (2008). Twentieth-century warming and the dendroclimatology of declining yellow-cedar forests in southeastern Alaska. *Canadian Journal of Forest Research*, *38*(6), 1319–1334. <https://doi.org/10.1139/X07-240>
- Boyce, R. L., & Lubbers, B. (2011). Bark-stripping patterns in bristlecone pine (*Pinus aristata*) stands in Colorado, USA. *The Journal of the Torrey Botanical Society*, *138*(3), 308–321. <https://doi.org/10.3159/TORREY-D-11-00045.1>
- Briffa, K. R., Jones, P. D., Bartholin, T. S., Eckstein, D., Schweingruber, F. H., Karlén, W., et al. (1992). Fennoscandian summers from AD 500: Temperature changes on short and long timescales. *Climate Dynamics*, *7*(3), 111–119. <https://doi.org/10.1007/BF00211153>
- Briffa, K. R., & Melvin, T. M. (2011). A closer look at regional curve standardization of tree-ring records: Justification of the need, a warning of some pitfalls, and suggested improvements in its application. In M. K. Hughes, T. W. Swetnam, & H. F. Diaz (Eds.), *Dendroclimatology* (pp. 113–145). Dordrecht: Springer. Retrieved from http://link.springer.com/chapter/10.1007/978-1-4020-5725-0_5
- Bunn, A., Lawrence, R., Bellante, G., Waggoner, L., & Graumlich, L. (2003). Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic, and Alpine Research*, *35*(3), 323–330. [https://doi.org/10.1657/1523-0430\(2003\)035%5B0323:SVIDAG%5D2.0.CO;2](https://doi.org/10.1657/1523-0430(2003)035%5B0323:SVIDAG%5D2.0.CO;2)
- Connor, K. F., & Lanner, R. M. (1990). Effects of tree age on secondary xylem and phloem anatomy in stems of Great Basin bristlecone pine (*Pinus longaeva*). *American Journal of Botany*, *77*(8), 1070–1077. <https://doi.org/10.1002/j.1537-2197.1990.tb13602.x>
- Cook, E. R., & Kairiukstis, L. A. (1990). *Methods of dendrochronology: Applications in the environmental sciences*. Berlin: Springer Science & Business Media. <https://doi.org/10.1007/978-94-015-7879-0>
- Cook, E. R., & Peters, K. (1997). Calculating unbiased tree-ring indices for the study of climatic and environmental change. *The Holocene*, *7*(3), 361–370. <https://doi.org/10.1177/095968369700700314>
- Davi, N. K., D'Arrigo, R., Jacoby, G. C., Cook, E. R., Anchukaitis, K. J., Nachin, B., et al. (2015). A long-term context (931–2005 C.E.) for rapid warming over Central Asia. *Quaternary Science Reviews*, *121*, 89–97. <https://doi.org/10.1016/j.quascirev.2015.05.020>
- Davi, N. K., Jacoby, G. C., Curtis, A. E., & Baatarbileg, N. (2006). Extension of drought records for Central Asia using tree rings: West-central Mongolia. *Journal of Climate*, *19*(2), 288–299. <https://doi.org/10.1175/JCLI3621.1>
- De Grandpré, L., Tardif, J. C., Hessler, A., Pederson, N., Conciatori, F., Green, T. R., et al. (2011). Seasonal shift in the climate responses of *Pinus sibirica*, *Pinus sylvestris*, and *Larix sibirica* trees from semi-arid, north-central Mongolia. *Canadian Journal of Forest Research*, *41*(6), 1242–1255. <https://doi.org/10.1139/x11-051>
- Efron, B. (1987). Better bootstrap confidence intervals. *Journal of the American Statistical Association*, *82*(397), 171–185. <https://doi.org/10.1080/01621459.1987.10478410>
- Esper, J. (2000). Long-term tree-ring variations in *Juniperus* at the upper timber-line in the Karakorum (Pakistan). *The Holocene*, *10*(2), 253–260. <https://doi.org/10.1191/095968300670152685>
- Fritts, H. C. (1976). *Tree rings and climate*. London, UK: Academic Press.
- Fritts, H. C., & Swetnam, T. W. (1989). Dendroecology: A tool for evaluating. *Advances in Ecological Research*, *19*, 111. [https://doi.org/10.1016/S0065-2504\(08\)60158-0](https://doi.org/10.1016/S0065-2504(08)60158-0)
- Graybill, D. A., & Idso, S. B. (1993). Detecting the aerial fertilization effect of atmospheric CO₂ enrichment in tree-ring chronologies. *Global Biogeochemical Cycles*, *7*(1), 81–95. <https://doi.org/10.1029/92GB02533>

- Harvey, R. B. (1923). Cambial temperatures of trees in winter and their relation to sun scald. *Ecology*, 4(3), 261–265. <https://doi.org/10.2307/1929049>
- Holmes, R. L. (1983). Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, 43(1), 69–78.
- Jacoby, G. C., D'Arrigo, R. D., & Davaajamts, T. (1996). Mongolian tree rings and 20th-century warming. *Science*, 273(5276), 771–773. <https://doi.org/10.1126/science.273.5276.771>
- Kalman, R. E. (1960). A new approach to linear filtering and prediction problems. *Journal of Fluids Engineering*, 82(1), 35–45. <https://doi.org/10.1115/1.3662552>
- Kelly, P. E., Cook, E. R., & Larson, D. W. (1992). Constrained growth, cambial mortality, and dendrochronology of ancient *Thuja occidentalis* on cliffs of the Niagara escarpment: An eastern version of bristlecone pine? *International Journal of Plant Sciences*, 153(1), 117–127. <https://doi.org/10.1086/297013>
- Kramer, P. J., & Kozlowski, T. T. (1979). *Physiology of woody plants*. New York: Academic Press.
- Kubler, H. (1991). Function of spiral grain in trees. *Trees-Structure and Function*, 5(3), 125–135.
- LaMarche, V. C. Jr. (1969). Environment in relation to age of bristlecone pines. *Ecology*, 50(1), 53–59. <https://doi.org/10.2307/1934662>
- Larson, D. W., Doubt, J., & Matthes-Sears, U. (1994). Radially sectored hydraulic pathways in the xylem of *Thuja occidentalis* as revealed by the use of dyes. *International Journal of Plant Sciences*, 155(5), 569–582. <https://doi.org/10.1086/297195>
- Larson, D. W., Matthes-Sears, U., & Kelly, P. E. (1993). Cambial dieback and partial shoot mortality in cliff-face *Thuja occidentalis*: Evidence for sectored radial architecture. *International Journal of Plant Sciences*, 154(4), 496–505. <https://doi.org/10.1086/297133>
- Leland, C., Pederson, N., Hessel, A., Nachin, B., Davi, N., D'Arrigo, R., & Jacoby, G. (2013). A hydroclimatic regionalization of central Mongolia as inferred from tree rings. *Dendrochronologia*, 31(3), 205–215. <https://doi.org/10.1016/j.dendro.2012.11.003>
- Matthes, U., Kelly, P. E., Ryan, C. E., & Larson, D. W. (2002). The formation and possible ecological function of stem strips in *Thuja occidentalis*. *International Journal of Plant Sciences*, 163(6), 949–958. <https://doi.org/10.1086/ijps.2002.163.issue-6>
- Matthes, U., & Larson, D. W. (2009). Can stem strips be induced? An experimental investigation of cliff-face *Thuja occidentalis*. *International Journal of Plant Sciences*, 170(9), 1109–1119. <https://doi.org/10.1086/592014>
- Mayr, S., Gruber, A., & Bauer, H. (2003). Repeated freeze-thaw cycles induce embolism in drought stressed conifers (Norway spruce, stone pine). *Planta*, 217(3), 436–441. <https://doi.org/10.1007/s00425-003-0997-4>
- Mayr, S., Schmid, P., Laur, J., Rosner, S., Charra-Vaskou, K., Damon, B., & Hacke, U. G. (2014). Uptake of water via branches helps timberline conifers refill embolized xylem in late winter. *Plant Physiology*, 164(4), 1731–1740. <https://doi.org/10.1104/pp.114.236646>
- Mayr, S., Wolfschwenger, M., & Bauer, H. (2002). Winter-drought induced embolism in Norway spruce (*Picea abies*) at the Alpine timberline. *Physiologia Plantarum*, 115(1), 74–80. <https://doi.org/10.1034/j.1399-3054.2002.1150108.x>
- Melvin, T. M., & Briffa, K. R. (2008). A “signal-free” approach to dendroclimatic standardisation. *Dendrochronologia*, 26(2), 71–86. <https://doi.org/10.1016/j.dendro.2007.12.001>
- Melvin, T. M., Briffa, K. R., Nicolussi, K., & Grabner, M. (2007). Time-varying-response smoothing. *Dendrochronologia*, 25(1), 65–69. <https://doi.org/10.1016/j.dendro.2007.01.004>
- Molod, A., Takacs, L., Suarez, M., & Bacmeister, J. (2015). Development of the GEOS-5 atmospheric general circulation model: Evolution from MERRA to MERRA2. *Geoscientific Model Development*, 8(5), 1339–1356. <https://doi.org/10.5194/gmd-8-1339-2015>
- Oribe, Y., Funada, R., & Kubo, T. (2003). Relationships between cambial activity, cell differentiation and the localization of starch in storage tissues around the cambium in locally heated stems of *Abies sachalinensis* (Schmidt) Masters. *Trees*, 17(3), 185–192.
- Oribe, Y., & Kubo, T. (1997). Effect of heat on cambial reactivation during winter dormancy in evergreen and deciduous conifers. *Tree Physiology*, 17(2), 81–87. <https://doi.org/10.1093/treephys/17.2.81>
- Pederson, N. (2010). External characteristics of old trees in the Eastern Deciduous Forest. *Natural Areas Journal*, 30(4), 396–407. <https://doi.org/10.3375/043.030.0405>
- Pederson, N., Hessel, A. E., Baatarbileg, N., Anchukaitis, K. J., & Cosmo, N. D. (2014). Pluvials, droughts, the Mongol empire, and modern Mongolia. *Proceedings of the National Academy of Sciences*, 111(12), 4375–4379. <https://doi.org/10.1073/pnas.1318677111>
- Petris, G., & An, R. (2010). An R package for dynamic linear models. *Journal of Statistical Software*, 36(12), 1–16.
- Rienecker, M. M., Suarez, M. J., Gelaro, R., Todling, R., Bacmeister, J., Liu, E., et al. (2011). MERRA: NASA's modern-era retrospective analysis for research and applications. *Journal of Climate*, 24(14), 3624–3648. <https://doi.org/10.1175/JCLI-D-11-00015.1>
- Sakai, A. (1966). Temperature fluctuation in wintering trees. *Physiologia Plantarum*, 19(1), 105–114. <https://doi.org/10.1111/j.1399-3054.1966.tb09080.x>
- Sakai, A., & Larcher, W. (1987). *Frost survival of plants: Responses and adaptation to freezing stress*, *Ecological Studies* (Vol. 62). Berlin: Springer. <https://doi.org/10.1007/978-3-642-71745-1>
- Salzer, M. W., Hughes, M. K., Bunn, A. G., & Kipfmüller, K. F. (2009). Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proceedings of the National Academy of Sciences*, 106(48), 20,348–20,353. <https://doi.org/10.1073/pnas.0903029106>
- Schauer, A. J., Schoettle, A. W., & Boyce, R. L. (2001). Partial cambial mortality in high-elevation *Pinus aristata* (Pinaceae). *American Journal of Botany*, 88(4), 646–652. <https://doi.org/10.2307/2657064>
- Schulman, E. (1954). Longevity under adversity in conifers. *Science*, 119(3091), 396–399. <https://doi.org/10.1126/science.119.3091.396>
- Sperry, J. S., Donnelly, J. R., & Tyree, M. T. (1988). Seasonal occurrence of xylem embolism in sugar maple (*Acer saccharum*). *American Journal of Botany*, 75(8), 1212. <https://doi.org/10.2307/2444104>
- Sperry, J. S., Hacke, U. G., & Pittermann, J. (2006). Size and function in conifer tracheids and angiosperm vessels. *American Journal of Botany*, 93(10), 1490–1500. <https://doi.org/10.3732/ajb.93.10.1490>
- Sperry, J. S., Nichols, K. L., Sullivan, J. E. M., & Eastlack, S. E. (1994). Xylem embolism in ring-porous, diffuse-porous, and coniferous trees of northern Utah and interior Alaska. *Ecology*, 75(6), 1736–1752. <https://doi.org/10.2307/1939633>
- Sperry, J. S., & Sullivan, J. E. (1992). Xylem embolism in response to freeze-thaw cycles and water stress in ring-porous, diffuse-porous, and conifer species. *Plant Physiology*, 100(2), 605–613. <https://doi.org/10.1104/pp.100.2.605>
- Stahle, D. W. (1996). Tree rings and ancient forest relics. *Arnoldia*, 56(4), 2–10.
- Stoffel, M., & Bollschweiler, M. (2008). Tree-ring analysis in natural hazards research? An overview. *Natural Hazards and Earth System Sciences*, 8(2), 187–202. <https://doi.org/10.5194/nhess-8-187-2008>
- Stokes, M. A., & Smiley, T. L. (1968). *An introduction to tree-ring dating*. Chicago, IL: The University of Chicago Press.
- Swetnam, T. W., & Brown, P. M. (1992). Oldest known conifers in the southwestern United States: Temporal and spatial patterns of maximum age. *Old growth forests in the southwest and rocky mountain regions*. *USDA Forest Service General Technical Report RM-213*, 24–38.
- Tang, K., Feng, X., & Funkhouser, G. (1999). The $\delta^{13}\text{C}$ of tree rings in full-bark and strip-bark bristlecone pine trees in the White Mountains of California. *Global Change Biology*, 5(1), 33–40. <https://doi.org/10.1046/j.1365-2486.1998.00204.x>

- van der Schrier, G., Barichivich, J., Briffa, K. R., & Jones, P. D. (2013). A scPDSI-based global data set of dry and wet spells for 1901–2009. *Journal of Geophysical Research: Atmospheres*, *118*, 4025–4048. <https://doi.org/10.1002/jgrd.50355>
- Visser, H., Büntgen, U., D'Arrigo, R., & Petersen, A. C. (2010). Detecting instabilities in tree-ring proxy calibration. *Climate of the Past*, *6*(3), 367–377. <https://doi.org/10.5194/cp-6-367-2010>
- Visser, H., & Molenaar, J. (1988). Kalman filter analysis in dendroclimatology. *Biometrics*, *44*(4), 929–940. <https://doi.org/10.2307/2531724>
- 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. *Journal of Climate and Applied Meteorology*, *23*(2), 201–213. [https://doi.org/10.1175/1520-0450\(1984\)023%3C0201:OTAVOC%3E2.0.CO;2](https://doi.org/10.1175/1520-0450(1984)023%3C0201:OTAVOC%3E2.0.CO;2)
- Wright, R. D., & Mooney, H. A. (1965). Substrate-oriented distribution of bristlecone pine in the White Mountains of California. *American Midland Naturalist*, *73*(2), 257–284. <https://doi.org/10.2307/2423454>
- Yang, B., Qin, C., Wang, J., He, M., Melvin, T. M., Osborn, T. J., & Briffa, K. R. (2014). A 3,500-year tree-ring record of annual precipitation on the northeastern Tibetan Plateau. *Proceedings of the National Academy of Sciences*, *111*(8), 2903–2908. <https://doi.org/10.1073/pnas.1319238111>