Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes

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Great Basin bristlecone pine (*Pinus longaeva*) at 3 sites in western North America near the upper elevation limit of tree growth showed ring growth in the second half of the 20th century that was greater than during any other 50-year period in the last 3,700 years. The accelerated growth is suggestive of an environmental change unprecedented in millennia. The high growth is not overestimated because of standardization techniques, and it is unlikely that it is a result of a change in tree growth form or that it is predominantly caused by CO_2 fertilization. The growth surge has occurred only in a limited elevational band within ≈150 m of upper treeline, regardless of treeline elevation. Both an independent proxy record of temperature and high-elevation meteorological temperature data are positively and significantly correlated with upper-treeline ring width both before and during the high-growth interval. Increasing temperature at high elevations is likely a prominent factor in the modern unprecedented level of growth for *Pinus longaeva* at these sites.

climate change | dendrochronology | Great Basin | tree rings | treeline

Background. Bristlecone pine (*Pinus longaeva*) is notable for its individual trees that attain great age, for its use in the calibration of the radiocarbon timescale, and for its role in providing an element in millennial-scale multiproxy reconstructions of temperature. The ring-width chronologies from long-lived bristlecone pine are annually resolved and can reach back thousands of years, making these high-resolution multimillennial proxy records of climate a rare and valuable resource in paleoclimatology. Upper-treeline bristlecone pine site locations are cold for much of the year and can be extremely dry during the summer growing season. As a result, these high-elevation tree-ring series contain some information on moisture availability, but they also bear an important imprint of temperature variability, so that both types of signal may be present in records from the upper treeline (1–7). There are interannual responses to precipitation variations at all elevations, including some degree of high-frequency variability related to extreme drought conditions at the upper treeline (8), although the variability related to precipitation is more pronounced at lower elevations (1, 9). Conversely, the main decadal to multidecadal ring-width variability at treeline locations may be related more closely to temperature than to precipitation (10). Despite the challenges in using these natural archives of climate successfully, we argue that it is worthwhile to make considerable effort to achieve the best possible use of this concentration of long annual records.

Statement of the Problem. A strong upward trend in the ring widths in most upper- treeline bristlecone pines has existed since the mid-19th century. It is important to understand the extraordinary nature and potential causes of this trend to use bristlecone pine ring widths most effectively as a climate proxy. How unusual is this modern elevated rate of tree growth at high elevation? Is this rate of growth unique in a multimillennial context? If so, it would suggest a relatively recent, dramatic environmental change in the mountainous regions of western North America. Additionally, what are the causes of the trend? A non-climatic cause would suggest that calibration of these tree-ring records with instrumental climate data may not be possible. Potential causes of the increased growth rate are discussed in the following sections.

Statistical Methodology. The trend could be an artifact from the tree-ring chronology standardization process designed to remove age/size influences in tree-ring chronology development. Cook and Peters (11) show how a positive bias can be produced when dividing actual ring-width data by some fitted expected growth curve as it approaches zero, and Melvin and Briffa (12) demonstrate the existence of what they term “trend distortion” at the ends of chronologies as a result of the removal of non-climate-related variance.

Asymmetric Growth Habits. The trend could result from the irregular growth form of ancient bristlecone pine, in which partial cambial dieback results in what is referred to as “strip-bark morphology.” Radial growth that does not extend around the entire circumference of a tree may proceed over less surface area and therefore produce wider rings than those produced in the circular morphology of whole-bark trees. Growth differences between strip-bark and whole-bark trees have been noted in Great Basin bristlecone pine (13, 14) and in whitebark pine (*Pinus albicaulis*) from Montana (15). In bristlecone pine, Graybill and Idso (13) concluded that the modern increase in growth was greatest in trees with an irregular strip-bark growth form.

Atmospheric Pollution. The positive growth trend could be caused by increased atmospheric CO_2 concentrations (16). LaMarche et al. (17) proposed a hypothesis of fertilization at high elevation by increased atmospheric CO_2 concentrations through increased water-use efficiency (WUE) to explain the positive growth trend. Tang et al. (14) found increased WUE in both strip-bark and whole-bark bristlecone pines, whereas Graumlich (18) did not find evidence for a CO_2 fertilization effect as a cause for enhanced growth among subalpine conifers in the Sierra Nevada. It also should be noted that nitrogen inputs from human activity are enriching some western ecosystems (19), and long-term fertilization experiments suggest these inputs may be contributing to increases in tree growth (20).

Climatic Factors. The positive growth trend could be caused by a change in climatic conditions. LaMarche et al. (17) compared growth of high-elevation White Mountain bristlecone pine in eastern California with records from 2 high-elevation meteorological stations in the same mountain range for the period 1949 to 1980.

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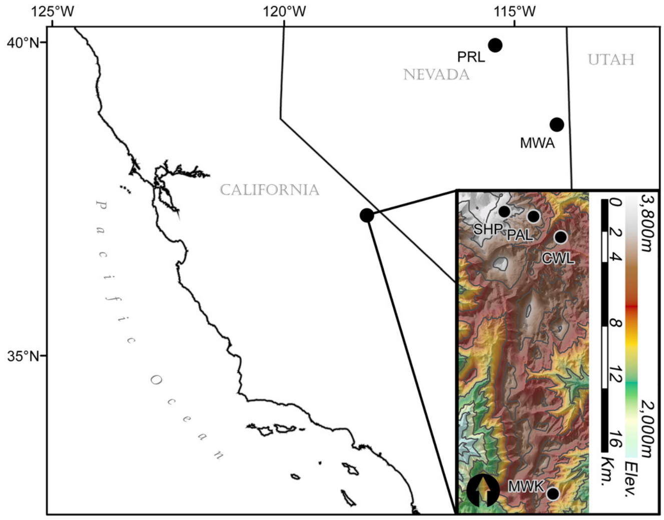

Fig. 1. Map of the study area shows locations of 3 upper forest border sites: Sheep Mountain, CA (SHP); Mt. Washington, NV (MWA); and Pearl Peak, NV (PRL). The inset includes the other sites used in the White Mountains, CA elevational transect: Patriarch Lower (PAL), Cottonwood Lower (CWL), and Methuselah Walk (MWK) (contour intervals = 200 m).

They reported that: "No climatic trends are apparent that might explain the positive trends in tree growth…." (p. 1019). However, contrary to this conclusion based on little more than 20 years of data from high-elevation stations, recent data sets of modeled high-elevation temperature (21) do reveal positive trends in climate over the last century that might explain the trends in tree growth (supporting information (SI) Fig. S1).

Our Approach to the Problem. We tested the unusual nature of modern growth by comparing the median ring-width values of consecutive 50-year intervals over 4,600 years using a data set of measured bristlecone pine ring width close to upper treeline (Fig. 1). We compared growth in regular (whole-bark) tree-ring chronologies with growth in irregular (strip-bark) chronologies to check if the modern trend is limited to trees with an irregular growth form. To help differentiate between unusual 20th-century growth caused either by atmospheric pollution or by climate, we compared growth patterns of closely spaced chronologies across an elevational transect (treeline and non-treeline) in the White Mountains of California. The transect chronologies were compared with each other and also with chronologies developed from bristlecone growing at treeline hundreds of kilometers away in Nevada. We used correlation analyses to investigate bristlecone growth response to modeled seasonal instrumental temperature and precipitation data, both along the White Mountain elevational transect and at the upper forest border in Nevada. Finally, we created a Great Basin regional upper-treeline chronology and compared it with both a density-based independent proxy record of temperature (22) and with modeled instrumental climate data (21).

Results

Unusual Modern Growth at High Elevation. The median ring width for the AD 1951–2000 period is the greatest (0.58 mm, $n = 8{,}910$) in the period of record and is rivaled only by 1 interval in the mid-second millennium BC (Fig. 2*A*, Table S1). In addition, the median ring widths of each of the 50 years between 1951 and 2000 are greater than the long-term median before AD 1951 (Fig. 2*B*). These results remain consistent when means rather than medians are used (Table S1). Ring widths for the 5-year period AD 2001–2005 are greater than for AD 1951–2000 (0.67 mm, $n = 406$) (Fig. 2*B*); however, existing data for the AD 2001–2005 period are incomplete, so conclusions based on the post-AD 2000 data are premature. When the ring-width measurements are separated into pre-AD 1951 and post-AD 1950 sets, the percentage of narrower rings is higher in the earlier time period (Fig. 2*C*). These results

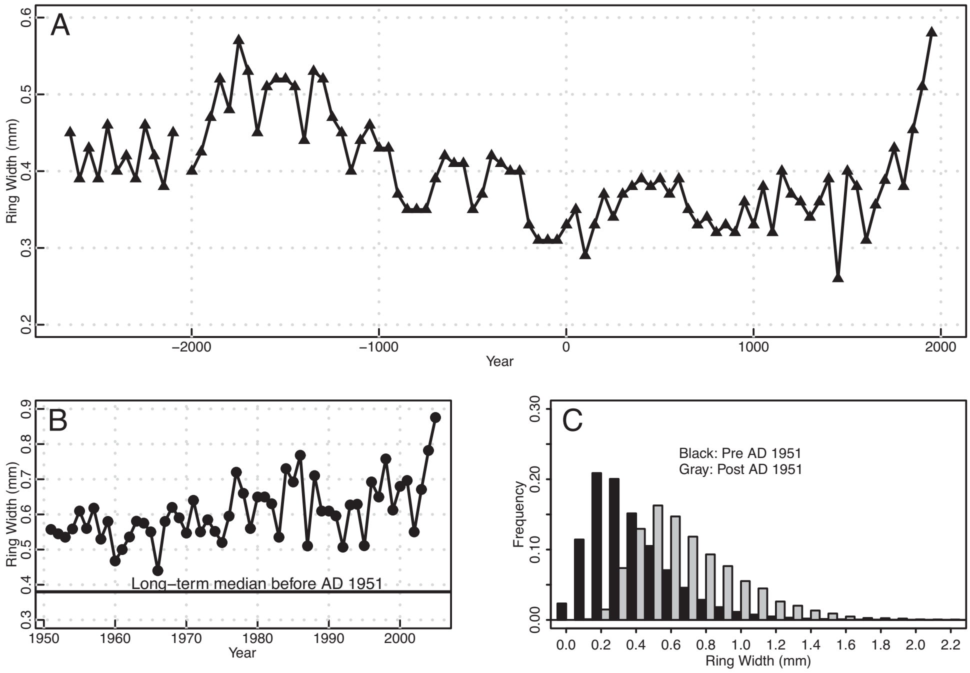

Fig. 2. Ring-width analysis of upper forest border *Pinus longaeva* from 3 sites (SHP, MWA, PRL) in western North America. (*A*) Ring-width medians for non-overlapping 50-year intervals plotted on first year of interval. (*B*) Annual ring-width medians for the period AD 1951–2005. The long-term median line is calculated for ring width before AD 1951. For comparison with Fig. 2*A*, the ring-width values for AD 2001–2005 have a median value of 0.67 mm (off the scale). The data for 2003–2005 are from SHP only. (*C*) Observed ring-width frequency distributions (SHP, MWA, PRL; $n = 310{,}922$ early, 9,316 late). Sites are separated into pre-AD 1951 (*black*) and post-AD 1950 (*gray*) sets.

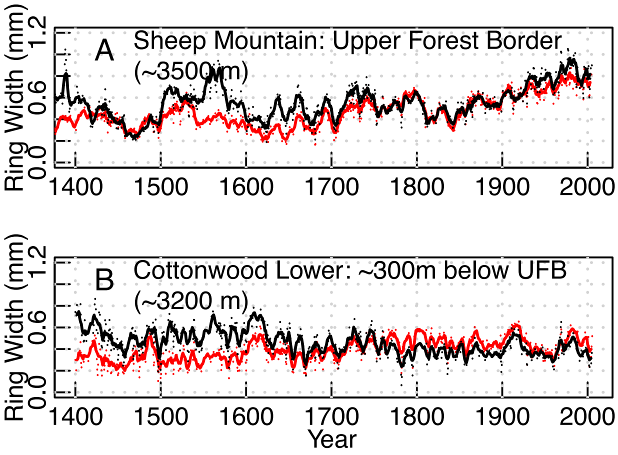

Fig. 3. Strip-bark and whole-bark ring-width chronologies from the White Mountains of California. Black chronologies are from whole-bark trees only; red chronologies are from strip-bark trees only. Note the similarity of whole-bark vs. strip-bark and the dissimilarity of the upper treeline (SHP) vs. the non-upper treeline (CWL). Smoothing was done with a 5-year moving average. (*A*) SHP (upper-treeline) ring-width chronologies. (*B*) CWL (non-upper-treeline) ring-width chronologies. SHP and CWL sites are separated by ≈3 km.

are consistent when the 3 sites are considered individually, indicating the pattern is not influenced unduly by a single anomalous site (Fig. S2).

Statistical Methodology. The unusually wide modern rings are, categorically, not a result of commonly applied statistical techniques applied to tree-ring data and designed to remove effects associated with the age or size of the tree. In this case, no such technique was used. We use simple, nonstandardized, raw ring-widths in all these analyses, a highly conservative approach that retains the original data and eliminates any data-transformation biases.

Asymmetric Growth Habits. At both upper-treeline (Sheep Mountain: SHP) and non-upper-treeline (Cottonwood Lower: CWL) locations in the White Mountains, we found no differences in modern growth between the whole-bark and strip-bark trees that adequately explain the wide modern rings at the upper treeline (Fig. 3, Table S2). Thus, it is unlikely that the modern wide rings are a result of a change to the strip-bark growth form in recent centuries after partial cambial dieback. In the earlier part of these records (15th and 16th centuries), the whole-bark chronologies are composed of younger trees with wider rings (Fig. 3), but this difference is not maintained into the 20th century.

Atmospheric Pollution. Although our work showed little difference between the strip-bark and whole-bark chronologies, the chronologies across an elevational transect in the White Mountains exhibit conspicuous differences. In trees growing only ≈150 m below upper treeline, there is no modern high- growth period, but above this elevation, there is (Fig. 4*A*). The 3 chronologies at the lower elevations [CWL, Patriarch Lower (PAL), and Methuselah Walk (MWK)] are strongly correlated with each other and are weakly correlated with the chronology from the highest level (SHP) (Table S3). These patterns hold for the whole period since AD 1400 as well as for the period between 1400 and 1850 and for the period after 1850. It also is clear from Fig. 4*A* that the uppermost chronology varies differently on bidecadal and longer timescales than the 3 series from lower elevations and that the 3 lower-elevation series have strongly co-varied with one another since AD 1400. There also are strong similarities over large distances between chronologies from sites that are close to their upper elevational limit. The bidecadal-to-century-scale features of the upper forest border chronologies at SHP, MWA, and Pearl Peak, NV (PRL) exhibit

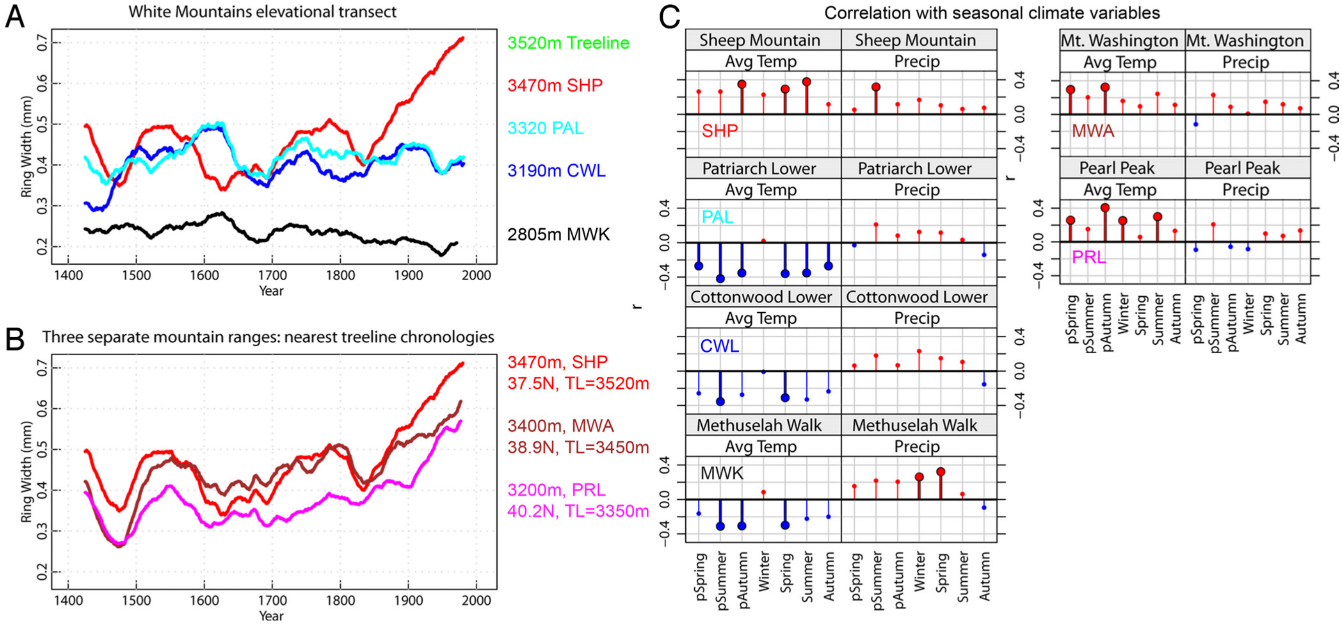

Fig. 4. *Pinus longaeva* mean ring-width chronologies smoothed with a 50-year moving average and correlations between the White Mountain chronologies (unsmoothed) and climate data. (*A*) Chronologies across an elevational gradient in the White Mountains, CA. Note the difference between the highest site (SHP, upper treeline) and the other 3 sites (PAL, CWL, MWK) and the similarity of the lowest 3 sites to each other. (*B*) Upper-treeline chronologies from SHP in the White Mountains, CA, MWA in the Snake Range, NV, and PRL in the Ruby Range, NV. Note the similarity between these chronologies despite the distances between sites (≈200–500 km). (*C*) Correlation of chronologies with PRISM (21) temperature data (SHP 1896–2005, PAL and CWL 1896–2006, MWK 1896–1996, MWA and PRL 1896–2002). Bolded symbols are significant at $P < 0.01$. Note the similar pattern in the response to temperature between SHP and the other upper-treeline sites (MWA, PRL) and the switch in pattern in the response to temperature between SHP (upper treeline) and the 3 non-treeline sites. Winter = December, January, February; spring = March, April, May; summer = June, July, August; autumn = September, October, November.

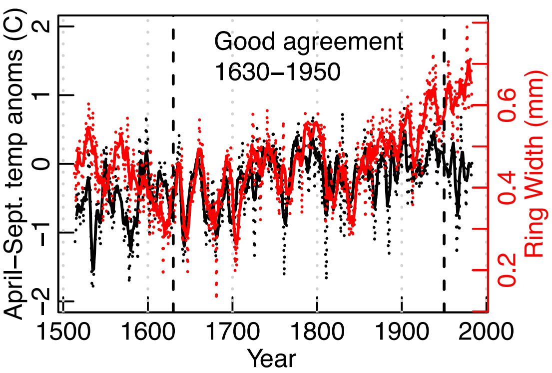

Fig. 5. Upper forest border regional ring width (*red*) compared with April-September temperature reconstructed from maximum latewood density (*black*) (22). The density series is an average of 2 grid points (37.5°N, 117.5°W; 37.5°N, 107.5°W) and was fitted with a 2-year moving average (t−1 and t) before plotting. Bold solid lines are center-plotted 5-year moving averages. The 2 series are completely independent.

obvious correspondence (Fig. 4*B*). Given the distance between sites (200–500 km) and the spatial coherence of temperature, this agreement suggests the existence of a common signal, as was argued by Hughes and Funkhouser (5). The PRL *Pinus longaeva* site at the upper forest border in the Ruby Mountains of north-central Nevada, at roughly 3,200 m and 40.2° N. latitude, is at an elevation similar to or lower than the 2 "relatively low" White Mountain chronologies CWL and PAL (Fig. 4*A*). However, PRL (Fig. 4*B*) still conforms more closely to the "high-elevation pattern," presumably because of its more northern latitude and thus closer proximity to local treeline (Fig. 1).

Climatic Factors. There is a striking change in the pattern of correlation between seasonal climate and ring-width chronologies (Fig. 4*C*). The chronologies closest to the upper tree limit (SHP, MWA, PRL) show strong positive association with temperature and markedly weaker, mostly positive, association with precipitation. The 3 non-treeline chronologies (PAL, CWL, MWK) show a stronger positive association with precipitation but a negative association with temperature. These results were obtained in an ordinary least squares standard linear model where the P-value was calculated against the effective number of samples (23). The pattern remains consistent using a generalized least squares approach (24) that explicitly models autocorrelation (Table S4).

Upper-Treeline Ring Width Variability and an Independent Temperature Proxy. We compared the upper-treeline mean ring-width chronology (GBR3) with a proxy record of April-September temperature reconstructed from tree-ring maximum latewood density (22) that is completely independent from the GBR3 ring-width record (Fig. 5). There is more persistence in the ring-width series than in the density series, and there is a lagged correspondence wherein ring width may reflect more than 1 year of past temperature, possibly because of needle retention over multiple years (10, 25, 26). Therefore, we used a 2-year moving average on the density series that effectively equalized the first-order autocorrelation in both series. We found significant correspondence ($r = 0.48$, $n = 321$, $N_{\mathrm{eff}} = 133$, $P < 0.001$) between an average of the density values from 2 grid points averaged over 2 years (t−1 and t) and upper-treeline bristlecone pine ring width from year t over the interval AD 1630–1950. There was no correspondence before AD 1630 ($r = -0.11$, 1514–1629), perhaps because of low sample depth in the density data at these grid points. There also was no correspondence in the period after 1950 ($r = -0.03$, AD 1951–1983). However, the GBR3 variability and reconstructed temperature anomalies co-vary in their decadal-scale frequencies for much of the past 400 years (Fig. 5). It is worth emphasizing again that these 2 records are completely independent and were developed from different species of trees and different sites at different elevations; one is based on maximum latewood density, and the other is based on ring width.

Upper-Treeline Ring Width Variability and Instrumental Climate Data. Mean GBR3 ring width and a regional average high-elevation temperature record we created from PRISM (21) climate data, referred to here as PRISM3 (see *Methods*), are significantly correlated over the AD 1896–2002 interval ($r = 0.48$, $n = 107$, $N_{\mathrm{eff}} = 89$, $P < 0.001$). Many of the main decadal-scale features evident in the PRISM3 temperature series also are evident in the GBR3 series, including the troughs in the second and fifth decades of the 20th century and the overall positive trend (Fig. 6).

Discussion

Ring Width and Tree Age. The unprecedented wide rings of the second half of the 20th century, unique in the record extending for more than 3,500 years, suggest a relatively recent environmental change in these mountainous regions of western North America that is unmatched during the last 3.5 millennia. We are confident that the large widths of the 20th century rings are not the result of juvenile growth. Young trees typically grow wider rings than old trees, and at these sites the rings are largest in the first few centuries of a tree's life and become narrower as the tree ages (Fig. S3) (25). In our data set, there are more than 20,000 rings from more than 200 series that contribute to the large median values for the periods after AD 1900. The vast majority of these rings are old rings that are not from the juvenile period of the trees' lives. Despite these circumstances, the observed frequency distribution of upper-treeline ring width for the interval after AD 1950 is decidedly skewed toward wider rings when compared with earlier periods (Fig. 2*C*). We are not able to make any firm statements about the cambial ages of the rings from the period of large rings in the late second millennium BC, because these very old pieces of remnant wood often have weathered and fractured extensively. Rings from exposed portions of these samples are regularly worn away, frequently including the pith area, and many hundreds of rings could be missing as a result of this erosion. Without the pith, we are unable to determine if the remaining portion of the sample includes large rings associated with the juvenile periods of the trees' lives. Thus, these early wide rings may reflect a larger proportion of young trees in the overall sample, whereas the modern wide rings decidedly do not.

"Strip-Bark" vs. "Whole-Bark" Trees. The lack of a substantial difference in ring width between our strip-bark and whole-bark groups in the modern period appears to contradict the finding of Graybill and Idso (13) for the same species in the same mountain range. In fact, when their raw ring widths are plotted in the same manner as our Fig. 3, there is little difference between their strip-bark and whole-bark groups in the modern period (Fig. S4*A*). The apparent divergence of their strip- and whole-bark chronologies from the mid-19th century to the late-20th century is the result of the standardization scheme they used (Fig. S4*B*). When compared in an appropriate manner, without artifacts introduced by standardization, recent growth rates of strip-bark and whole-bark trees from the same environment are very similar. In light of these results, the suggestion that strip-bark pines should be avoided during analysis of the last 150 years (27) should be reevaluated.

Treeline and Non-Treeline Chronologies. The differences between treeline and non-treeline ring-width patterns are suggestive of a different primary climatic control on growth at treeline and non-treeline sites. The elevation changes in the White Mountain transect are relatively small (Figs. 1 and 4*A*). Such large differences in growth patterns across relatively small elevation changes (≈150 m) in the same mountain range would not be expected from changes

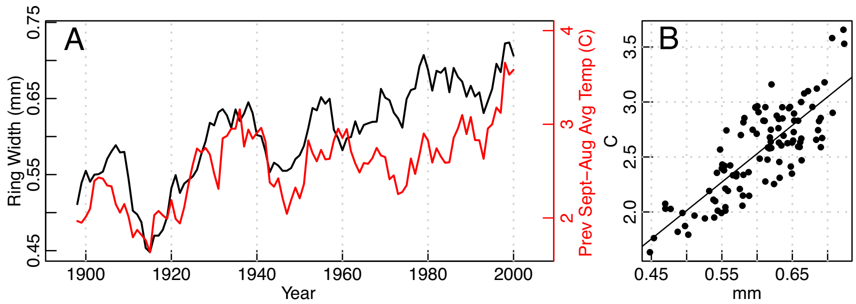

Fig. 6. Upper forest border regional ring width compared with regional high-elevation PRISM3 (21) temperature data. (*A*) Time-series plot of smoothed ring width (*red*) and temperature (*black*). Series were smoothed with a center-plotted 5-year moving average. Ring-width series is GBR3. Temperature series is PRISM3, previous September-August mean of 3 pixels closest to SHP, MWA, PRL sites. (*B*) Scatterplot of the same 2 variables. The 3 points in the upper-right corner are the 3 most recent 5-year periods.

in available CO_2 and intrinsic WUE or from increased nitrogen deposition alone, which should affect most of these sites similarly (14, 28, 29). The high-elevation pattern of rapid growth in recent decades at PRL (Fig. 4*B*) and the lack of this pattern at CWL and PAL (Fig. 4*A*) suggests that the cause of the pattern has less to do with actual elevation and, for example, partial pressure of CO_2, than it does with the ecotonal position of the trees near their upper limit of distribution. In addition, although the differences in the relatively low-elevation vs. the relatively high-elevation chronologies are most obvious in the modern period, there also are differences in the earlier parts of the chronologies. Some striking differences exist between the higher-elevation and lower-elevation chronologies before the industrial revolution that cannot be attributed to the onset of increases in atmospheric CO_2. The differences between our relatively low-elevation and relatively high-elevation chronologies, and the similarity of distant treeline chronologies indicate the influence of temperature as a major factor in the modern high rate of growth at the upper treeline in Great Basin bristlecone pine.

Divergence. The agreement between GBR3 ring width and reconstructed temperature anomalies from maximum latewood density does not deteriorate noticeably after 1850, as might be expected with a strong CO_2/WUE effect and as previously suggested by Graybill and Idso (13); rather, it is sustained at least until 1950. After 1950 there is no agreement between the 2 proxy records. However, the bristlecone ring widths (Fig. 6), and the density-based reconstruction (Fig. S5 and Table S5) both track PRISM (21) temperature data at their respective elevations to their particular end points. Thus, the post-1950 divergence between the 2 tree-ring data sets (upper-treeline ring width and density, Fig. 5) may be related to an amplification of temperature trends with elevation (30) rather than to any divergence effect in which a proxy record ceases to behave as a reliable recorder of climate, as has been noted elsewhere (31, 32).

Temperature vs. Precipitation. Although the positive associations with temperature data and with a temperature proxy support our claim that high-elevation increases in temperature play a major role in the modern growth surge, the weaker positive association with precipitation suggests that precipitation increases may contribute to the recent growth trend. However, the decadal-scale relationship between upper-treeline ring width and temperature is relatively strong (Fig. 4*C* and Fig. 6), but for these sites no such clear relationship with precipitation emerges. The nature of the transition in the properties of the ring-width chronologies and their associations with climate between 3,320 m and 3,470 m is suggestive of a threshold in environmental control of tree-ring growth as seen near treeline in the Alps where the climatic response of trees includes a temperature-threshold component (33).

The Role of Temperature. Körner (34) hypothesized that the upper treeline is created by the temperature limitation of trees' ability to form new tissue (sink inhibition) rather than by a shortage of photosynthate (source limitation). This global model of treeline suggests a narrow range of growing-season temperatures of treelines at different elevations around the globe and supports a common minimum temperature limit of tree growth (35). Recent direct observations of xylogenesis (wood formation) coupled with soil, air, and stem temperatures provide strong corroboration for temperature-limited growth in alpine and boreal conifers (36). The reported critical value of mean daily temperature for the onset of wood formation is 8 to 9 °C, a value that usually is not reached until mid to late June at treeline in the White Mountains. Maximum mean daily temperatures at SHP (11 °C) commonly are not reached until late July and are only slightly greater than the minimum reported for wood formation. It follows that tree establishment, survival, and growth at upper treeline requires that temperatures at critical times of year consistently equal or exceed this general minimum temperature for wood formation. Even with sufficient moisture to support growth, tissue formation (ring growth) could not occur if the threshold temperature was not met for a sufficiently long period. Clearly, this reasoning may be extended to fluctuations of temperature and growth from year to year, or from decade to decade, as well as along elevational gradients. Consideration should be given to the possibility that ring growth close to the upper treeline is limited by temperature control of xylogenesis as part of the environmental control of the development of tissue (34). The influence of temperature on xylogenesis provides an alternative or complement to the paradigm of growth limited by the availability of photosynthate, at least close to treeline.

Conclusions

At 3 sites in western North America close to the upper-elevation limit of tree growth, Great Basin bristlecone pine (*Pinus longaeva*) showed radial growth in the second half of the 20th century that was greater than any time in the last 3,700 years. We have shown several new lines of evidence that suggest that at the upper forest border bristlecone pine ring widths have responded to temperature in the past and continue to do so. (*i*) The unique 20th-century increase in ring width is specific to the upper forest border and is not associated with a particular elevation. The link to upper treeline rather than to a specific elevation is not consistent with the WUE hypothesis of indirect fertilization by CO_2 or fertilization by nitrogen deposition. (*ii*) The strong modern trend in growth observed at the upper forest border is not the product of any preprocessing or standardization of the data—there was none. (*iii*) The modern trend is not related to the difference between strip-bark and whole-bark growth forms. Both forms show the same levels of growth in the 20th century when samples are collected at similar elevations and when no distortions are introduced by standardization. (*iv*) There is a marked transition in the nature of the climate associations of bristlecone pine ring-width chronologies in the White Mountains over ≈150 vertical meters. Above the transition elevation (≈3,320 m to 3,470 m in the White Mountains), ring width is strongly positively associated with temperature and also is weakly positively associated with precipitation. Below the transition elevation, ring width is strongly negatively associated with temperature and also is strongly positively associated with precipitation. (*v*) Strong spatial correspondence in growth patterns in upper-treeline chronologies over relatively long distances (hundreds of kilometers) is seen in chronologies that also share similar positive associations with temperature. (*vi*) There is significant correlation between upper-treeline ring widths and an independent proxy temperature reconstruction over 321 years (AD 1630–1950). (*vii*) Significant correlation is observed between upper-treeline ring widths and local PRISM temperature data from high elevations over 107 years. (*viii*) Ring width at our treeline sites may be limited by low temperature that reduces the ability of the tree to create tissue; this idea is consistent with a treeline hypothesis that emphasizes sink inhibition as result of low temperature (34). These findings suggest an important role for temperature in controlling bristlecone pine ring widths at these upper-treeline sites on decadal-to-multicentury time scales. They also point to a prominent role for temperature as a cause of the rapid acceleration of ring growth in these trees in the 20th century. This notion further suggests that multimillennial bristlecone pine ring-width time series at the upper forest border are a potentially valuable resource for information regarding past variability in temperature. The unprecedented growth observed in upper-treeline chronologies of the Great Basin over the last century is unmatched in millennia and is suggestive of dramatic environmental changes, most likely linked to increases in temperature.

Materials and Methods

We created multimillennial annual time series of bristlecone pine ring widths from 3 upper-treeline sites at ≈3,200–3,600 m and from 37.50° to 40.25° N. latitude within 150 m of altitudinal treeline (Fig. 1). Treeline is coarsely defined as a line connecting the highest patches of forest within a given slope or series of slopes of similar exposure. Increment cores were taken from living trees, and cross-sections or cores were taken from remnant wood. Core samples were mounted, and all samples were sanded using increasingly fine sandpaper grits. Individual rings on samples were dated to the calendar year using both graphical and statistical methods according to standard methods (37). Rings were measured to the nearest 0.01 mm. For Fig. 2, the records extend back more than 4,600 years at each of the 3 sites. Bins before 2650 BC were not considered because they did not meet our minimum number of 250 rings for a 50-year bin. This limitation also was the reason for the missing data point at 2050–2001 BC, where $n = 248$. For the elevational transect, 2 non-treeline chronologies (PAL and CWL) were developed, and we used data from a third previously developed chronology (MWK) (Fig. 4). In all cases, we chose not to standardize to tree-ring indices to avoid any potential data-transformation biases that might be introduced by standardization. The absence of standardization does not affect our ability to interpret tree-growth anomalies in terms of climate over these time scales, because the vast majority of our hundreds of samples are old rings that are not from the juvenile period of the trees' lives. There is little, if any, age-related change in ring width in such old rings (see Fig. S3). We have used the PRISM gridded data set of monthly surface temperature and precipitation at 4-km resolution (21) for the period AD 1895–2006 for comparison with bristlecone growth along the White Mountains elevational transect and at the upper forest border in the Snake (MWA) and Ruby (PRL) ranges in Nevada (see *SI Text* for more information about PRISM). The upper-treeline mean ring-width chronology (GBR3) is an average of the 3 chronologies of mean ring-width from the collections at each of the 3 upper-treeline bristlecone pine sites: SHP, MWA, and PRL (Fig. 1 and 4*B*). The PRISM3 record of mean monthly temperature anomalies is an average of data from the 3 pixels geographically closest to the SHP, MWA, and PRL sites, each seasonalized to a previous-September-to-August mean. This seasonal window allows the inclusion of the previous autumn temperatures, thought to be important in some species for late-season photosynthesis and for influencing the next year's growth through food storage processes (25), and the current-year summer temperature, expected to be important for radial growth at the upper forest border.

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