

A dendroecological assessment of whitebark pine in the Sawtooth – Salmon River region, Idaho

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Abstract: Whitebark pine (*Pinus albicaulis* Engelm.) tree-ring chronologies of 700 to greater than 1000 years in length were developed for four sites in the Sawtooth – Salmon River region, central Idaho. These ring-width chronologies were used to (i) assess the dendrochronological characteristics of this species, (ii) detect annual mortality dates of whitebark pine attributed to a widespread mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) epidemic during the 1909–1940 period, and (iii) establish the response of whitebark pine ring-width growth to climate variables. Cross-dating of whitebark pine tree-ring patterns was verified. Ring-width indices had low mean sensitivity (0.123–0.174), typical of high-elevation conifers in western North America, and variable first-order autocorrelation (0.206–0.551). Mountain pine beetle caused mortality of dominant whitebark pine peaked in 1930 on all four sites. Response functions and correlation analyses with state divisional weather records indicate that above-average radial growth is positively correlated with winter and spring precipitation and inversely correlated with May temperature. These correlations appear to be a response to seasonal snowpack. Whitebark pine is a promising species for dendroclimatic studies.

Résumé : Des chronologies de cernes annuels du pin à blanche écorce (*Pinus albicaulis* Engelm.) couvrant une période de 700 à plus de 1000 ans ont été développées pour quatre sites situés dans la région de la rivière Sawtooth – Salmon dans le centre de l'Idaho. Ces chronologies de cernes annuels ont été utilisées pour (i) évaluer les caractéristiques dendrochronologiques de cette espèce, (ii) détecter les dates annuelles de mortalité du pin à blanche écorce due à une importante épidémie du dendroctone du pin ponderosa (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) survenue pendant la période allant de 1909 à 1940 et (iii) établir la réaction en croissance des cernes annuels du pin à blanche écorce en fonction des variables du climat. La contredatation des patrons de cernes annuels du pin à blanche écorce a été vérifiée. Les indices de largeurs de cernes avaient une faible sensibilité moyenne (0,123–0,174), typique des conifères croissant à haute altitude dans l'Ouest de l'Amérique du Nord, et une faible autocorrélation de premier ordre (0,206–0,551) entre les variables. La mortalité des pins à blanche écorce dominants, causée par le dendroctone du pin ponderosa, a atteint un sommet en 1930 dans les quatre sites. Des analyses de fonctions de réponse et de corrélation avec les données météorologiques de cette région de l'État indiquent qu'une croissance radiale supérieure à la moyenne est positivement corrélée avec la précipitation durant l'hiver et le printemps et négativement corrélée avec la température du mois de mai. Ces corrélations semblent être une réaction à l'accumulation saisonnière de neige. Le pin à blanche écorce est une espèce prometteuse pour des études dendrochronologiques.

[Traduit par la Rédaction]

Introduction

This research was initiated to evaluate whitebark pine (*Pinus albicaulis* Engelm.) tree-ring chronologies as a source of long-term information on the ecological and climatic processes affecting subalpine ecosystems. Our objectives were to assess the dendrochronological characteristics of

this long-lived pine, evaluate the timing of a mountain pine beetle (*Dendroctonus ponderosae* Hopkins (Coleoptera: Scolytidae)) epidemic that occurred in the early part of this century, and investigate the potential of whitebark pine for dendroclimatic research.

Whitebark pine is a slow-growing, long-lived, stone pine (subsection *Cembrae*) of high-elevation forests and timberlines of the northwestern United States and southwestern Canada. It occupies harsh, cold sites characterized by rocky, poorly developed soils and snowy, windswept exposures. Throughout its range whitebark pine may occur as an alpine species, including a krummholz form in communities above tree line, as a seral species, or codominant with subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) (Arno and Hoff 1989). Other common associates are lodgepole pine (*Pinus contorta* Dougl.), Engelmann spruce (*Picea engelmannii* Parry ex Engelm.), and mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) (Arno and Hoff 1989).

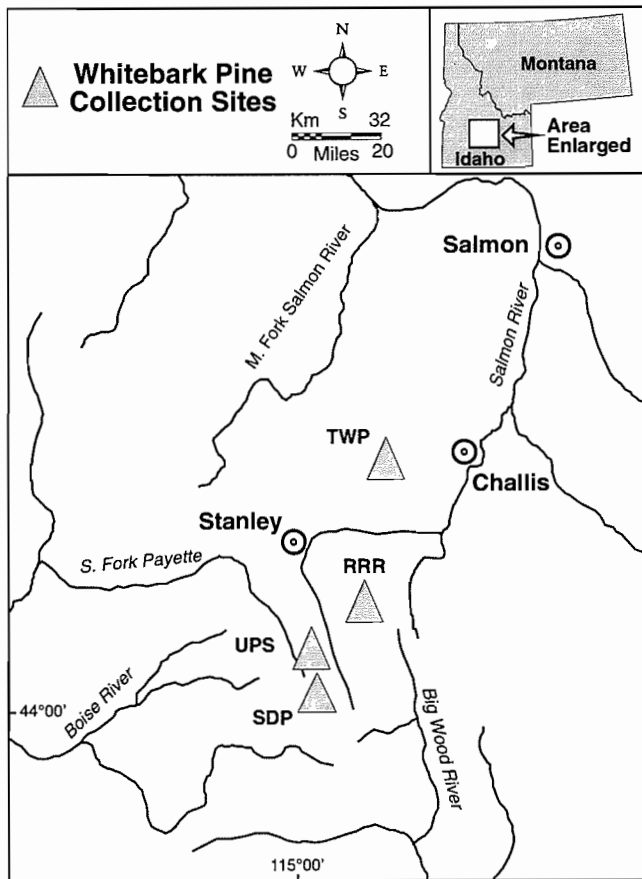
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Fig. 1. Whitebark pine study sites, Sawtooth – Salmon River region, Idaho. RRR, Railroad Ridge; SDP, Sandpass; UPS, Upper Sandpass; TWP, Twin Peaks.



Concern over whitebark pine decline caused by exotic white pine blister rust (*Cronartium ribicola* J.C. Fisch.), infestations of mountain pine beetle, fire suppression, and subsequent succession by shade-tolerant conifers (Arno and Hoff 1989; Keane et al. 1990; Morgan and Bunting 1989; Keane and Arno 1993) has stimulated research on whitebark pine populations. Widespread mortality of whitebark pine and potential successional replacement by other tree species suggest changes in distribution and abundance of whitebark pine in the northern Rockies. Research on this species has concentrated in the intermountain region of western Montana and in the Greater Yellowstone ecosystem (Arno 1986; Arno and Hoff 1989; Keane et al. 1990). In northwestern Montana, environmental conditions favorable to the propagation of blister rust have resulted in severe pine mortality and reduced whitebark pine cone crops (Keane and Arno 1993; Kendall and Arno 1990; Mattson and Jonkel 1990).

The Sawtooth – Salmon River region, near the southern edge of whitebark pine distribution (Arno and Hoff 1989), represents a large geographic gap in whitebark pine research and in current tree-ring chronology networks. Schulman (1956) sampled 1600-year-old limber pines (*Pinus flexilis* James) near Ketchum, Idaho, but no other sites with 1000-year tree-ring chronologies have been developed for the northern Rockies in the United States. Whitebark pine ring-width

series are known to cross-date, and chronologies have been produced from the Canadian Rockies, eastern Oregon, and California (Luckman 1993, 1994; Peterson 1990; M.L. Parker and L.J. Graumlich, unpublished data). This species, however, has been infrequently used in dendrochronological studies, and dendrochronological characteristics and response to temperature and precipitation variables in Idaho have not been described.

Whitebark pine in the Sawtooth – Salmon River region have thus far not sustained major blister rust damage, but stands have sustained widespread mortality from bark beetle infestations. High-elevation whitebark pine forests in this area are composed of large-diameter, old whitebark pine snags mixed with stands of live whitebark pine and subalpine fir. Mass mortality of mature age-class trees has been attributed to a mountain pine beetle outbreak transmitted from lower-elevation lodgepole pine forests to high-elevation stands of whitebark pine (Arno and Hoff 1989; Bartos and Gibson 1990). This outbreak reached epidemic proportions from 1920 to 1940 and was reported from southern Canada to Wyoming (Arno and Hoff 1989; Ciesla and Furniss 1975). However, timing and patterns of mortality within and between whitebark pine stands are largely unknown, raising specific questions: Did the numerous dead overstory trees within stands succumb in a short period of a few years, or did they die over longer periods? Are mortality events synchronous among stands in the region? We demonstrate the utility of tree-ring chronologies for answering these questions.

The semiarid conditions of homogeneous, open-canopied, high-elevation stands in central Idaho favor the dendroecological study of whitebark pine. The high-elevation forests are relatively free of human disturbances such as logging and fuelwood collection. Living, dead, and subfossil wood in situ is available for sample collections. This area is influenced by North Pacific weather patterns and is located in a transition zone between continental and inland-maritime climates (Arno and Hammerly 1984). The variability of continental atmospheric patterns likely affects ecophysiological requirements of whitebark pine and mountain pine beetle. The dynamical feedbacks among these variables, i.e., trees, beetles, and climate, are important for understanding changing environments. In particular, assessment of natural disturbance patterns and climatic factors affecting whitebark pine is essential to provide base-line reference for current and future changes in these subalpine habitats.

We establish the potential of whitebark pine for producing millennial length tree-ring time series and demonstrate the ability to date dead trees killed by mountain pine beetle using these chronologies. Finally we investigate climatic correlates of annual growth and establish whitebark pine as a species of dendroclimatic interest.

Study area

Four whitebark pine study sites were selected in central Idaho in the geographic region north of the headwaters of the Salmon River, south of the Middle Fork of the Salmon River, west of the East Fork of the Salmon River, and east of the North Fork of the Boise River (Fig. 1). Two sites, Sandpass (SDP) and Upper Sandpass (UPS), are within the Sawtooth Wilderness

Table 1. Whitebark pine site descriptions.

	Sandpass	Upper Sandpass	Twin Peaks	Railroad Ridge
Lat. (N)	43°58'15"	43°58'28"	44°36'03"	44°08'25"
Long. (W)	114°58'06"	114°58'02"	114°27'46"	114°33'07"
Elev. (m)	2800	2800	2800	2930
Aspect	S-SE	WSW-W	S	S-E
Slope (degrees)	5-30	20-35	15-30	5-30
Soil	Granite	Granite	Rhyolite	Granite
Area (ha)	3.0	2.2	1.5	4.0

area on the windward (west) side of the northwest-trending Sawtooth Mountains. The Railroad Ridge site (RRR) is in the lee (east side) of the northwest-trending White Cloud Mountains, and the Twin Peaks site (TWP) is on the east flank of the Salmon River Mountains, in the southeastern region of the Frank Church River of No Return Wilderness near Challis, Idaho.

Whitebark pine stands in this region are typical of light-demanding conifers near timberline. They show increasing stand openness with elevation, often lack sharp stand boundaries, and occur in an uneven mosaic pattern (Walter 1968; Tranquillini 1979). Because mountain peaks are under 3300 m (11 000 ft) in elevation, tree distribution at the study sites appears to be limited by edaphic factors and wind rather than elevational constraints and associated temperature limitations typical of tree-line ecotones. Ground cover is virtually nonexistent on Sandpass, Upper Sandpass, and Twin Peaks. The broad flat ridgetop of the Railroad Ridge site has ground cover composed primarily of *Artemisia tridentata* (Nutt.) and *Carex geyeri* (Boott). Habitat types are the PIAL/ABLA or PIAL series according to Steele et al. (1981).

To determine whether whitebark pine in this region had sufficient climatic sensitivity to display a common response in ring-width pattern, we selected sites with steep exposed slopes, open-grown stands, coarse well-drained soils, and southerly aspects. In dendrochronology, these physical characteristics are considered "classic" site attributes that maximize climatic responsiveness of ring-width chronologies, while minimizing the influence of within-stand dynamics, such as competition and interference (Douglass 1941; Schulman 1956; Fritts 1976). We also selected these sites because of the standing dead component that could be attributed to mountain pine beetle infestation.

Site elevations range from 2800 to 3000 m. Site areas range from 1.5 to 4.0 ha. The SDP and UPS sites occur on the divide between the Payette River and Salmon River basins on the granitic contact between the Sawtooth and Idaho batholiths. These two sites are subject to the prevailing westerly weather patterns. The substrate at the Twin Peaks site is rhyolitic, and that at the Railroad Ridge site is granitic. Physical site characteristics are summarized in Table 1.

This region is semiarid with 30–80 cm of precipitation a year, most of which falls as snow and rain during winter and spring. At elevations above 2700 m, most precipitation falls as snow. Precipitation may range from lows of 20 cm in the valleys to over 150 cm on mountain peaks (Steele et al. 1981). Annual temperatures range from average minima of -8°C to average maxima of 10°C . Extreme cold temperatures of -34 to -47°C are recorded from December through February. Winds redistribute snow around whitebark pine trees to form snowdrifts that may linger until July and occasionally August. In open areas, near clumps of trees and associated snowdrifts, remnant dead and subfossil wood is abundant. The semiarid nature of this region precludes rapid decay of these fallen trees.

Field collections

Ring-width chronologies

Field collections were made to develop master ring-width chronologies on each of the four sites using standard dendrochronological procedures (Fritts 1976; Swetnam et al. 1985). Fifteen to 30 live and (or) dead trees were sampled on each site during the 1992 and 1993 growing seasons. At least two cores were extracted from each tree using a 51-cm (20-in.) increment borer.

Mortality and stand structure

A sampling strategy based on distance methods (Pollard 1971; Smeins and Slack 1978) was used to determine the relative frequency of trees killed by mountain pine beetle and to characterize stand structure. Relative frequency, F_i , is expressed as $F_i = (n_i/n) 100$, where n_i is the number of occurrences of the phenomena of interest (size or mortality class) and n is the total number of occurrences (total trees sampled). Transects were systematically established on 61-m (200-ft) topographic contours (level curves) across each site. On each transect, plot centers were located at random distances. From each plot center we recorded the mortality and size class of the nearest two trees. Snags and down logs were included.

Mortality patterns were described by recording whether the tree was live (L), dead by an unknown cause (U), or dead due to beetle kill (B). The latter was determined if adult mountain pine beetle galleries, which appear as distinctive, vertically aligned, J-shaped marks (Wood 1982), were observed on the bole. These galleries were constructed in the phloem tissue under the bark during the year of infestation (Wood 1982). Dead trees and subfossil wood without beetle galleries were coded unknown dead (U). At least two increment cores were extracted from all beetle-killed trees to obtain the outermost tree ring for dating purposes.

To describe stand structure patterns, we recorded diameter at breast height (DBH), estimated height, and coded cohorts according to the following criteria: seedling (s), those trees less than 1 in. (2.54 cm) in DBH and under 1 ft (30.5 cm) tall; sapling (S), less than 1 in. (2.54 cm) to 4 in. (10.2 cm) DBH and greater than 1 ft (30.5 cm) tall; intermediate (i), 4–8 in. (10.2–25.8 cm) DBH; codominate (c), 8–19 in. (25.8–48.3 cm) DBH; and dominant (d), greater than 19 in. (48.3 cm) DBH. Although this categorization scheme is not exhaustive, all trees observed on our sites fall into these categories.

Laboratory analysis

Chronology development and assessment

Increment cores were mounted in wooden holders and surfaced with sandpaper to reveal ring boundaries and diagnostic ring structures (Stokes and Smiley 1968; Swetnam et al. 1985).

Table 2. Whitebark pine chronology statistics.

	Sandpass	Upper Sandpass	Twin Peaks	Railroad Ridge
Length of chronology (years)	1037	783	1028	1267
Number of trees	19	28	12	11
Number of cores	37	52	29	22
Mean ring width (mm)	0.46	0.33	0.39	0.49
Interseries correlation	0.63	0.56	0.62	0.57
Mean sensitivity	0.17	0.12	0.17	0.17
First-order autocorrelation	0.55	0.29	0.21	0.48

Measurements of ring widths were made with a sliding-stage micrometer interfaced with a microcomputer (Robinson and Evans 1980).

Cross-dating consisted of combined traditional techniques of skeleton plotting, a graphical technique of ring-width comparison (Stokes and Smiley 1968; Swetnam et al. 1985), and the use of a quality control cross-dating program, COFECHA, to ensure measured series were accurately dated (Holmes 1983). Cross-dating is the fundamental principle of dendrochronology. It is the property that cores sampled from different trees within a stand, and cores from the same tree, share a common pattern of wide and narrow annual rings or other diagnostic structures such as frost rings. The synchronicity of these patterns allows assignment of an exact calendar year to each tree ring. (Douglass 1941; Fritts 1976). The COFECHA algorithm calculates running correlation coefficients between a single series and the master composite that excludes the series being tested. Cross-dating was confirmed if the highest significant correlation occurred at the dated position. If COFECHA suggested an alternative position, the core was visually examined to confirm the suggested repositioning. After cross-dating was assured by the above methods, each series was standardized to remove biological age and stand-related (endogenous) trends (Fritts 1976; Cook 1985).

The mathematical standardization function that has the most widespread application for semiarid open-grown conifers is the decreasing exponential function, $y = a e^{-bx} + k$ (Fritts et al. 1969). For each series, $x = x(t)$ is the observed ring width in a given year, t . The constants a , b , and k are estimated for each series, and y is the expected ring width in year t . Each series is normalized by dividing each ring width by y .

A partial theoretical justification for this detrending method is that a decreasing exponential function idealizes the addition of wood volume to a cylinder, which biologically reflects the geometric growth of a tree bole (Fritts et al. 1969). All series with this type of monotonically decreasing growth trend were standardized in this manner. When the coefficients b and a were negative, then a line was fitted to the series.

For series with oscillatory growth trends, we chose a 100-year smoothing spline (Cook and Peters 1981; Reinsch 1967) that preserves 50% of the amplitude frequency response at the 100-year wavelength. Generally this detrending method removes the interdecadal to subcentury length trends in the ring-width series caused by nonclimatic endogenous stand dynamics (Cook and Peters 1981; Cook 1985). For instance, growth releases following the creation of canopy gaps after insect attack or fire are usually removed by this type of detrending. As a result of this detrending method, our series are unlikely to contain centennial-length climatic variation. All standardization methods are designed to remove the nonstationary time domain trend (Cook 1987). Sandpass and Upper Sandpass were standardized with a combination of the decreasing exponential, linear, or 100-year smoothing spline, and all series at the Twin Peaks and Railroad

Ridge sites were standardized with the the 100-year smoothing spline.

Division of the observed ring-width values by the expected values calculated from the selected detrending function produced the index value for the series. The series were then averaged to produce a master index chronology for the site. Selection of the detrending options and development of the final master chronologies were performed with procedures in the computer program ARSTAN (Cook 1985).

Correlation analyses and standard descriptive statistics, i.e., mean ring width, length of series, first-order autocorrelation, and mean sensitivity (Douglass 1936; Fritts 1976), were used to compare dendrochronological characteristics between whitebark pine master chronologies for the four sites.

For correlation analyses both prewhitened, i.e., autocorrelation effects removed (Cook 1985), and standard chronologies were used. The new chronologies were also compared with other chronologies on sites with the same or similar species type, similar site elevation, and geographic proximity. These included a Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) chronology from near Ketchum, Idaho, a Douglas-fir chronology near Salmon, Idaho, three whitebark pine chronologies from near Joseph, Oregon, and one Rocky Mountain juniper (*Juniperus scopulorum*) chronology near Jarbidge, Nevada. A fast Fourier transform (FFT) algorithm (Press et al. 1988), which preserves the spectral trends of time series, was derived for each chronology and overlain on the master chronology for visual comparison of trends. The interval chosen for this analysis was 8 years.

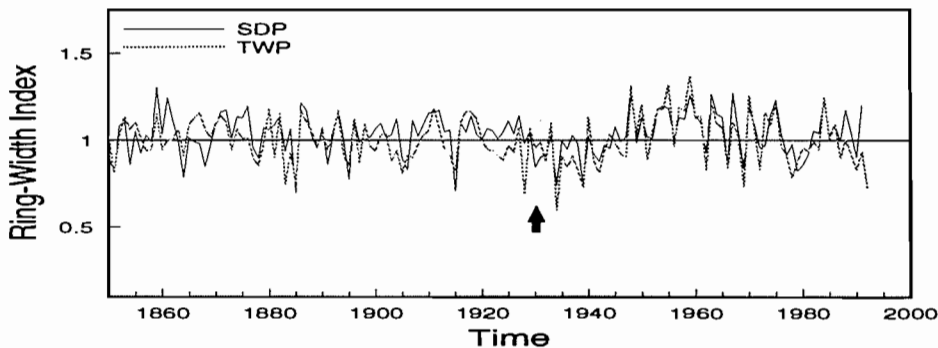
Mortality assessment

Increment core samples from the trees killed by mountain pine beetle were skeleton plotted and visually cross-dated with the master chronologies. Two criteria were considered to record the year of mortality of a whitebark pine: (i) observed adult beetle galleries on the bole and (ii) dating of outer ring of against cross-dated series and chronology. Measured ring widths were processed through the program COFECHA to verify cross-dating and the outside ring date.

Dendroclimatic assessment

Simple correlations and response functions (Fritts et al. 1971, 1976) were calculated to assess whitebark pine annual ring growth response to monthly average temperature and total precipitation factors. Response function analysis regresses principal components (eigenvectors) of climate variables upon the master index chronology to calculate a set of coefficients (weights) that correspond to the original set of climate variables. A bootstrap method provides confidence intervals for the response coefficients (Guiot 1990). Meteorologic data for the central mountain region of Idaho, division 1004, from the National Climatic Data Center, Asheville, North Carolina, were used for this analysis. These data were a composite, based on

Fig. 2. SDP and TWP master chronologies for 1850–1991. Arrow indicates peak of mountain pine beetle kill in whitebark pine.



homogeneity of weather patterns, for the 95-year time period 1896–1991. Divisional data were selected because nearby weather stations were scarce and situated at low elevations, and data sets had many missing values. High-elevation climate data were available (Finklin 1988), but they were short and primarily from north and east of the study area. Divisional climate data are often a better climate variable for tree growth – climate analysis because they integrate the large-scale climate variation better than single-site meteorological data (Fritts 1976, 1991). Monthly total precipitation and monthly average temperature values for a 14-month period starting in July through the following August were selected as the climatic variables. Three years of prior growth was also used to assess autocorrelation effects (Fritts 1976).

Results and discussion

These chronologies constitute the first 700-year chronologies constructed from the northern Rocky Mountain region in the United States. The discovery of the oldest living whitebark pine known in North America was made in the Sawtooth – Salmon River region during this study. This tree exceeds 1270 years in age. The innermost ring of an increment core that did not include the pith was AD 726. Whitebark pine is now eleventh on the longest-lived tree species list, after Douglas-fir (Brown 1996). The largest whitebark pine on the National Register of Big Trees also occurs in this region; it exceeds 840 cm (331 in.) circumference at 1.37 m above the ground (Cannon 1996). Discovery of ancient trees and the presence of abundant well-preserved logs and snags indicate that it is possible to develop millennia-length chronologies for this species and region.

Cross-dating characteristics

Cross-dating of these trees was problematic, but successful. Narrow-ring signature years common to most sites aided cross-dating efforts, but lack of high-frequency variation of ring widths made cross-dating difficult on some cores. Old, large-diameter trees cross-dated well with each other and comprise the master chronologies. On all sites, the cross-dating of the intermediate and codominant trees with the dominant and old trees was poor.

The strength of cross-dating among these trees was highest for the two south-facing sites Sandpass and Twin Peaks as reflected by an interseries correlation above 0.6

(Table 2). The synchronous ring-width patterns punctuated by narrow ring marker years 1885, 1895, 1915, 1928, 1934, 1939, and 1969 are evident in Fig. 2. Upper Sandpass and Railroad Ridge had interseries correlations slightly lower, but above 0.5. Trees with interseries correlations near and below 0.43 were problematic to cross-date and were not included in the master ring-width chronologies.

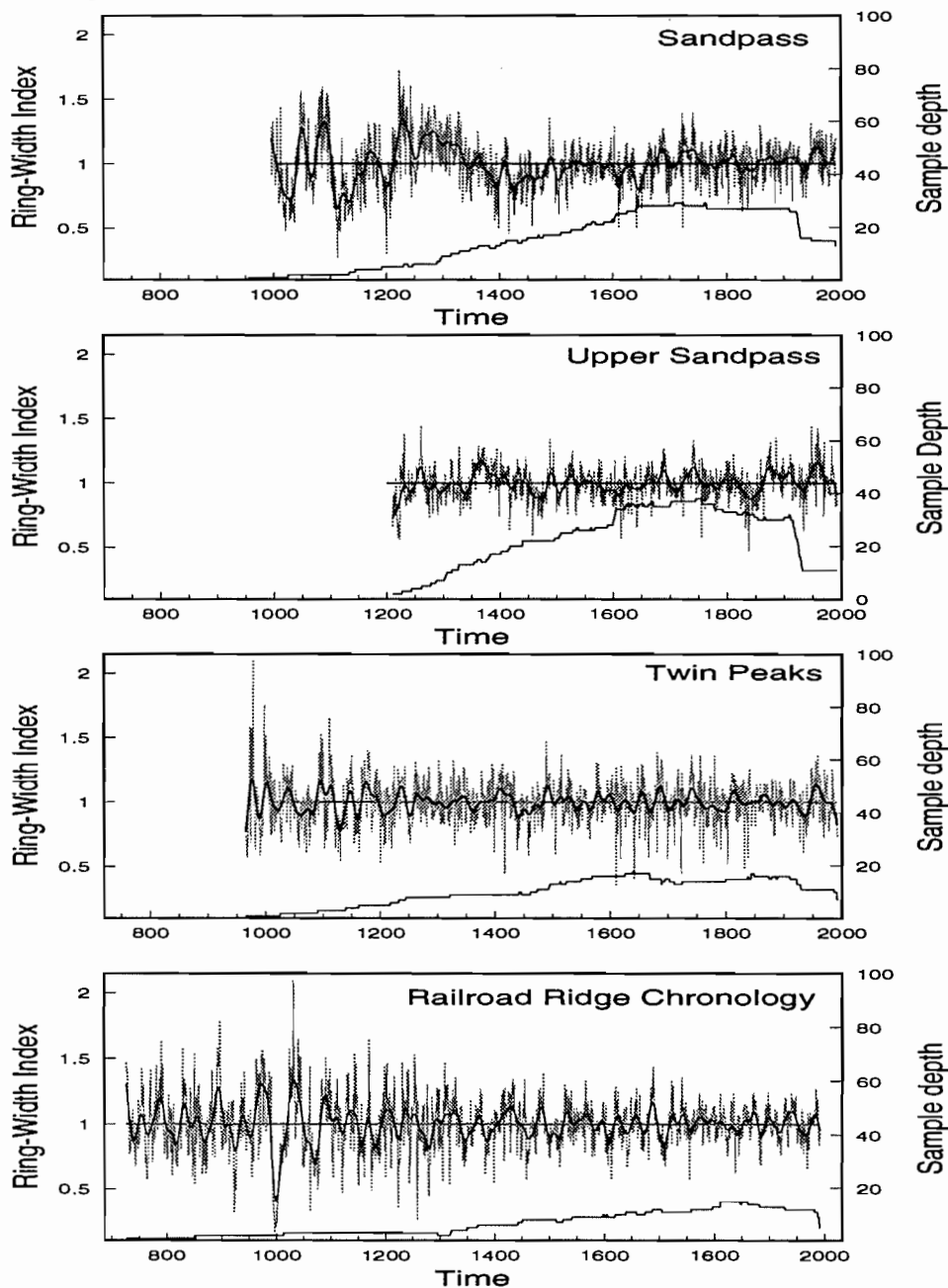
The complacent nature of many segments of the ring-width series, the occurrence of heart rot, and the low sample depth before AD 1300 prevented us from including some live, some standing dead, and several remnant fallen and dead samples in the master ring-width chronologies. Sample depth, the number of trees or series included in the chronology in a given calendar year, dropped off rapidly before AD 1300 and after 1930 (Fig. 3). Increased sampling efforts, particularly of dead and remnant wood, may allow future development of chronologies with good sample depth in the period AD 700 to 1300.

Master chronologies

Master chronologies for the time period AD 760 to 1991, overlain with the FFT-smoothed curve, revealed low frequency variation from AD 1300 to the present (Fig. 3). The large amplitude of ring-width variations between 970 and 1300 was likely a consequence of few samples and juvenile growth patterns. (Fig. 3). Generally, as young trees mature, annual ring increment increases to a maximum, then decreases exponentially to an asymptotic ring-width level.

Mean sensitivity, defined as the average absolute difference between two adjacent ring-width measurements divided by their mean measurement (Douglass 1936), ranges from 0.12 on the UPS site to 0.17 on TWP, RRR, and SDP sites and is representative of the low year to year variance typical of Rocky Mountain conifers at high-elevation sites (LaMarche and Stockton 1974; Fritts and Shatz 1975). First-order autocorrelation coefficients are variable and range from 0.21 at the Twin Peaks site to 0.55 at the Sand Pass site. This is a measure of the average dependence of a ring-width value at year t relative to the ring-width value at year $t - 1$. High autocorrelation coefficients are typical of high-elevation tree-ring chronologies (LaMarche and Stockton 1974; Fritts and Shatz 1975). Sandpass and Railroad Ridge sites are moderate in this response, whereas Upper Sandpass and Twin Peaks are less autocorrelated (Table 2).

Fig. 3. Whitebark pine master ring-width chronologies, scaled to a common interval and overlain with a fast Fourier transform smoothing function to accentuate interdecadal trends. Sample depth, the number of series represented in the chronology at a particular year, is plotted on the right-hand axis.



Visual comparisons of master skeleton plots and correlation analysis with Idaho Douglas-fir, Oregon whitebark pine, and Nevada Rocky Mountain juniper chronologies revealed no cross-dating with the exception of one whitebark pine chronology, from near Joseph, Oregon (CHJOE2). Possible explanations for lack of cross-dating include site differences (e.g., elevation, substrate, aspect), differential species response to climate variables, and spatial climatic pattern variation.

Moderate to strong positive correlations among the four Sawtooth – Salmon River region whitebark pine chronologies for the period AD 1300–1991 and positive association with the eastern Oregon chronology (M.L. Parker, unpublished data, AD 1543–1964) are shown in a correlation matrix (Table 3). The two south-facing sites, SDP and TWP, are approximately 80 km (50 mi) distant from each other, yet exhibited the strongest correlation. This is surprising because the UPS site is only 0.6 km from the SDP

Table 3. Correlation matrix for whitebark pine tree-ring chronologies, central Idaho and eastern Oregon.

	SDP	UPS	TWP	RRR	CHJOE2
SDP	1.0				
UPS	0.64 (0.67)	1.0			
TWP	0.65 (0.72)	0.59 (0.64)	1.0		
RRR	0.48 (0.52)	0.51 (0.60)	0.46 (0.54)	1.0	
CHJOE2	0.38 (0.46)	0.32 (0.54)	0.35 (0.51)	0.47 (0.58)	1.0

Note: Time periods for comparison are 1300–1991, except for correlations with the eastern Oregon site, CHJOE2, which were 1543–1964. Correlations in parentheses are for prewhitened chronologies. All correlations are significant at $p \leq 0.01$.

Table 4. Whitebark pine stand structure summary.

	SDP	UPS	TWP	RRR
Number of plots	47	25	18	35
Number of trees inventoried	94	50	36	71
Live trees	73 (78)	32 (64)	23 (64)	47 (66)
Dead trees	21 (22)	18 (36)	13 (36)	24 (34)
Live trees				
Seedlings	27 (29)	4 (8)	8 (22)	7 (10)
Saplings	32 (34)	19 (38)	11 (30)	24 (34)
Intermediates	10 (11)	5 (10)	4 (14)	9 (13)
Codominants	3 (3)	1 (2)	0	6 (8)
Dominants	1 (1)	3 (6)	0	1 (1)
Subset of dead trees				
Beetle-killed trees	4 (20)	11 (61)	9 (70)	14 (58)
Unknown dead	17 (80)	7 (39)	4 (30)	10 (42)

Note: Trees killed by mountain pine beetle had distinct J-shaped adult galleries on the stem. Trees were coded unknown dead when galleries were not observable. Numbers in parentheses are relative frequencies of occurrence (%).

site. A feasible explanation for the lower correlates between the two neighbor sites may be that west-facing UPS trees show a differential growth response to the feedbacks among westerly pressure gradients, radiation loads, and soil moisture availability. RRR is the least well correlated with the other Idaho sites but shows the highest correlation with the CHJOE2 site in eastern Oregon. Competition of trees with understory plants on the RRR site may explain lower correlates with the rocky understoried Idaho sites. A credible explanation for the positive correlations within the study area and with the eastern Oregon site includes a regional-scale response of trees to climate and similar site characteristics (Table 1).

Mountain pine beetle caused mortality

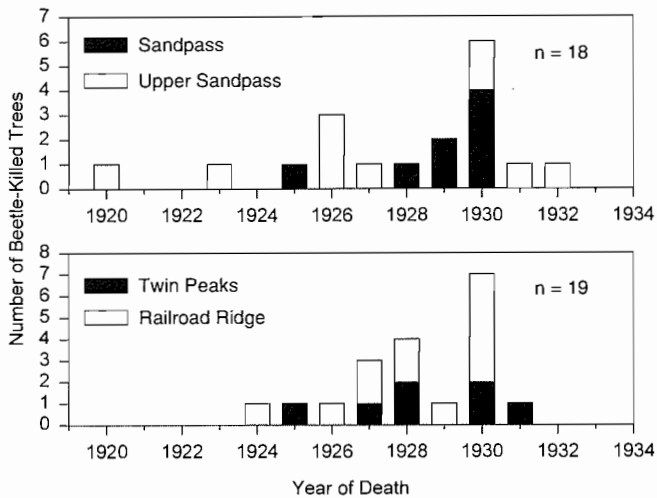
The magnitude of the early 20th century mountain pine beetle epidemic is apparent by examining the relative frequency of occurrence of the dominant and codominant trees (Table 4). On all four sites, live codominant and dominant trees composed less than or equal to 9% of the total sample. These results seem to indicate that beetles prefer the large diameter size class whitebark as they do in the more common host, lodgepole pine (Cole and Amman 1969; Amman 1977). From the dead tree subset, the relative

frequency of beetle-killed trees ranged from 20% on SDP to 70% on TWP. The ratio of beetle-killed snags to all large diameter size class snags was 67% on SDP, 57% on UPS, 100% on TWP, and 52% on RRR.

Calendar dates were determined for the mountain pine beetle outbreak of the early 20th century. The distribution of cross-dated beetle-killed trees starts in the early 1920s and clusters around a single peak maximum at 1930 on all four sites (Fig. 4). These observations were made independently of historical documentation of mountain pine beetle infestation in central Idaho. In a 1929 letter to the District Forester in Ogden, Utah, the Challis Forest Supervisor reports that infestation reached epidemic stage in lodgepole pine, in the summer of 1926. He noted that although the chief host was lodgepole pine, whitebark pine and limber pine were also infected and appeared less resistant to beetle attack than lodgepole pine (Renner 1929).

Laboratory analysis of all trees with adult mountain pine beetle galleries revealed the presence of blue stain fungus (*Ophiostoma clavigerum*) in the outer sapwood. This fungus is associated with several species of bark beetles (Harrington 1987) and is not a sufficient criterion alone to indicate mountain pine beetle presence. Blue stain fungus, however, may be viewed as a secondary indicator

Fig. 4. Cross-dated death dates of 37 whitebark pine killed by mountain pine beetle. Mortality reaches a maximum at 1930.



of bark beetle presence. In addition to the beetle-killed tree mortality dates shown in Fig. 4, two other dead trees with blue stain fungus looked like probable beetle-killed trees in the field. Death dates were 1730 and 1887. The weathering of the bole prevented us from confirming the presence of adult galleries on these trees. One tree on the UPS site died in 1819 and had observable mountain pine beetle galleries on the stem. This is the only tree in our sample base that we suggest was killed by mountain pine beetle before the 20th century epidemic.

The decrease of dominant whitebark pine trees ca. 1930 (see sample depth lines in graphs in Fig. 3) and synchronous cross-dated beetle-killed dates over the Sawtooth – Salmon River region (Fig. 4) exemplify the great magnitude and scope of the mid-1920s to early 1930s mountain pine beetle epidemic. This infestation occurred at the start of the longest sustained low growth period for the last 200 years (Fig. 2) and is concurrent with the documented 1920's and 1930's drought (Finklin 1988). These results suggest some association with poor growing conditions for trees and may support the plant drought stress hypothesis (Mattson and Haack 1987), which states that insect outbreaks may be predisposed in stressed plant populations. However, lack of replication and understanding of mechanism limits further interpretation. The duration of the epidemic in whitebark pine was approximately 8–12 years (Fig. 4) and was typical of the range of infestation in the most common host, lodgepole pine (Roe and Amman 1970; Cole and Amman 1980).

A provisional explanation for the increase in annual ring width of trees that survived the epidemic was a growth release from reduced competition for resources (Fig. 2). The relative frequency of young living trees (Table 4) may be evidence of gap phase recruitment following the epidemic.

Climate – tree growth relationships

Whitebark pine is a promising species for dendroclimatic studies of the transitional climate zone of the northern Rockies. All four sites showed the same response to climate

variable analysis. However, Sandpass and Twin Peaks ring-width chronologies revealed significant correlations at the $p < 0.05$ level. Results for those sites are reported here (Fig. 5).

Response functions for the Sandpass standard chronology revealed that 51% of the variance (r^2 adjusted) in ring width was explained by climate variables and 3% was explained by prior growth, giving a total of 54% explained by the measured abiotic and biotic components of this system (Fig. 5).

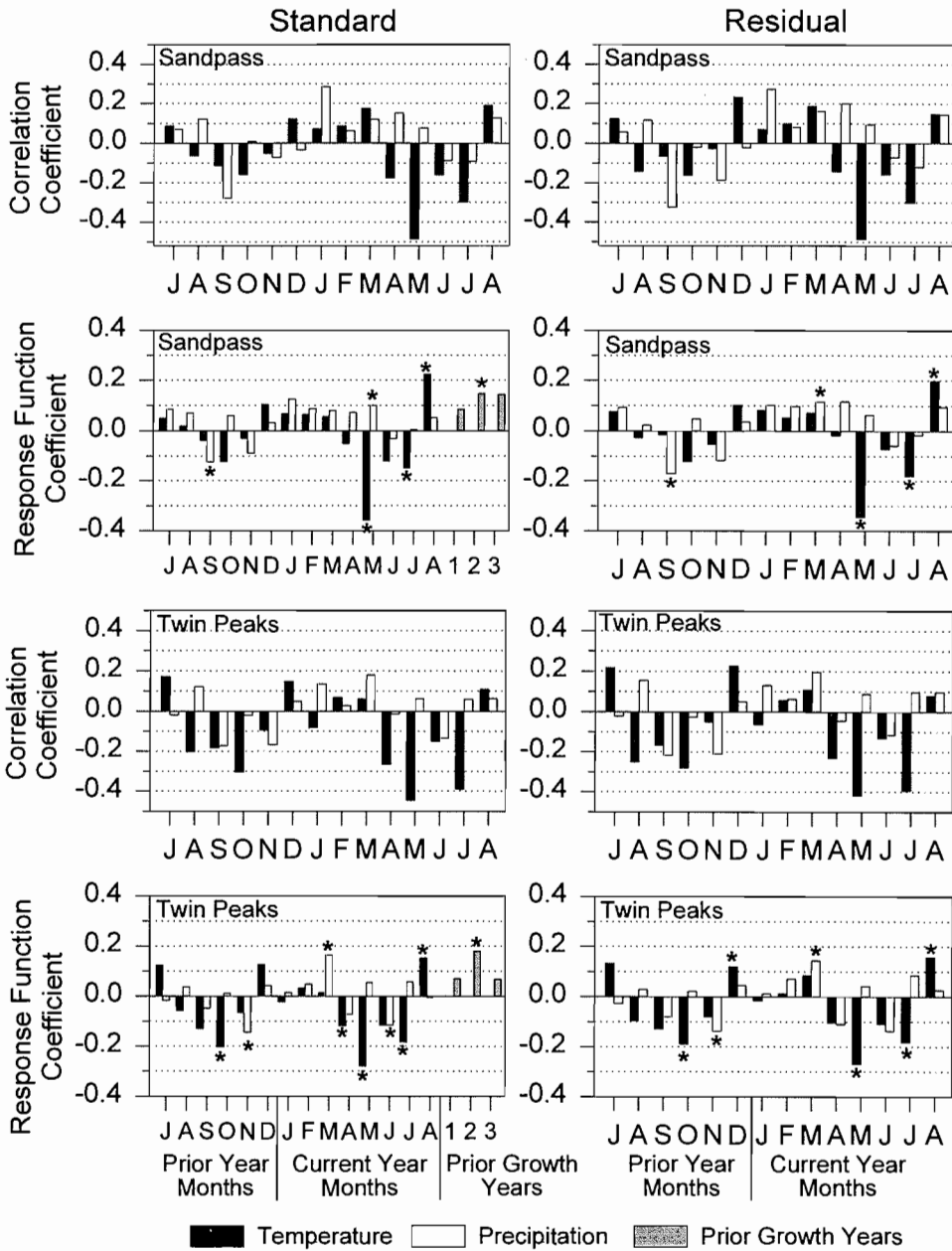
In the Twin Peaks standard chronology, 52% of the variance in ring width was explained by climate variables and 4% was explained by prior growth, for a total explained variance of 56% (Fig. 5). The second year's previous growth was significant on both SDP and TWP sites (Fig. 5). This is a low contribution by previous growth relative to most other tree-ring chronologies used in dendroclimatic work (Fritts 1991), particularly high-elevation conifers (LaMarche 1974; LaMarche and Stockton 1974). The low importance of autocorrelation in these results was confirmed by computing correlation and response functions using chronology residuals from autoregressive models (i.e., whitened series) (Fig. 5). Residual chronologies revealed that 52% of the variance was explained by climate for both Sandpass and Twin Peaks.

Correlation and response function analyses revealed ring-width growth was positively correlated with winter and spring precipitation, and inversely correlated with May and July temperatures (Fig. 5). This response implies above-average growth with abundant snowpack and cool spring (through early summer) temperatures. Under these conditions, persistent snowpack gradually melts in early summer and favors optimal soil moisture for tree growth. On high-elevation sites in North America, correlations of tree growth with climate variables typically respond positively to winter and spring precipitation and summer temperature (Kienast and Schweingruber 1986; Graumlich and Brubaker 1986; Peterson et al. 1990; and others). Whitebark pine was similar in this response, with positive correlations with winter and spring precipitation variables. August temperature was also positively correlated and statistically significant ($p < 0.05$) on both sites (Fig. 5). The feedbacks among spring precipitation and temperature variables likely produce nonlinear interactions affecting snowpack. Results from this work suggest that increased sampling of open-grown stands of high-elevation living whitebark pine and further time series analysis are needed to clarify relationships between climate and whitebark pine tree-growth variables.

Conclusions

Attempts to understand processes governing forest ecosystems are plagued by short data sets and compounded by the long generation time of trees. Preliminary dendroecological analysis of high-elevation whitebark pine stands on classic dendroclimatic sites generated time series greater than 700 years. These chronologies have filled a large geographic gap in the North American tree-ring network, particularly of high-elevation sites. We have shown that whitebark pine tree-ring chronologies reveal patterns associated with the biotic and abiotic factors affecting their growth.

Fig. 5. Correlation and response function coefficients for Sandpass and Twin Peaks. Monthly climatic means are from Idaho Divisional data 1004. Correlation coefficients are significant at $p < 0.05$ for $|r| = 0.210$. Response function coefficients are significant at $p < 0.05$ as indicated by asterisks.



These long time series are essential for investigating the dynamics of disturbance events and are candidates for dendroclimatic research. As such, whitebark pine tree rings may serve as a type of subalpine clock recording changes in the time domain.

The southern Idaho semiarid climate favors preservation of high-elevation remnant wood. Therefore increased sample size and replication in earlier time periods included in our current chronologies could extend ecological and climatic investigations back into the first millennium AD. The observation of the 19th century (1819) beetle-killed tree

with galleries preserved in the sapwood is encouragement to look further for evidence of pre-20th century infestations.

The ability to map a mountain pine beetle epidemic in the time domain was demonstrated. A logical continuation of this research would generate spatial maps of the mountain pine beetle outbreak using the methods established here. Decay and loss of sapwood may limit the accurate dating of time of death to subsets of trees and sites. The potential to expand this sampling to other locations could resolve spatial and temporal patterns of mountain pine beetle infestations on stand level to regional scales.

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