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Article

Separating Trends in Whitebark Pine Radial Growth Related to Climate and Mountain Pine Beetle Outbreaks in the Northern Rocky Mountains, USA

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Abstract: Drought and mountain pine beetle (*Dendroctonus ponderosae* Hopkins) outbreaks have affected millions of hectares of high-elevation conifer forests in the Northern Rocky Mountains during the past century. Little research has examined the distinction between mountain pine beetle outbreaks and climatic influence on radial growth in endangered whitebark pine (*Pinus albicaulis* Engelm.) ecosystems. We used a new method to explore divergent periods in whitebark pine radial growth after mountain pine beetle outbreaks across six sites in western Montana. We examined a 100-year history of mountain pine beetle outbreaks and climate relationships in whitebark pine radial growth to distinguish whether monthly climate variables or mountain pine outbreaks were the dominant influence on whitebark pine growth during the 20th century. High mortality of whitebark pines was caused by the overlapping effects of previous and current mountain pine beetle outbreaks and white pine blister rust infection. Wet conditions from precipitation and snowpack melt in the previous summer, current spring, and current summer benefit whitebark pine radial growth during the following growing season. Whitebark pine radial growth and climate relationships were strongest in sites less affected by the mountain pine beetle outbreaks or anthropogenic disturbances. Whitebark pine population resiliency should continue to be monitored as more common periods of drought will make whitebark pines more susceptible to mountain pine beetle attack and to white pine blister rust infection.

Keywords: whitebark pine; *Pinus albicaulis*; mountain pine beetle; drought; tree rings; white pine blister rust; dendroclimatology

1. Introduction

Whitebark pine (*Pinus albicaulis* Engelm.) communities are highly sensitive to climate variability [1–8], with relatively small changes in temperature and precipitation having substantial effects on species productivity and community disturbance regimes [9,10]. Our understanding of how whitebark pine communities have responded to changing climate conditions in the past is therefore critical to understanding current widespread declines documented across the range of whitebark pine. Reconstructing climate and forest dynamics at multi-century scales provides insight into the resiliency of whitebark ecosystems in the Northern Rocky Mountains of the western United States. Dendroclimatological studies on whitebark pine have shown the complexity of climate-growth relationships within this species and demonstrated the importance of considering local environmental histories and microsite variation in developing climatically-sensitive whitebark pine chronologies [11,12].

In addition to directly affecting tree growth, climate variability also indirectly affects whitebark pine communities through influences on the dynamics and distributions of pests and pathogens. White pine blister rust (*Cronartium ribicola* J.C. Fischer) is driving declines in whitebark pine populations across much of the species range, with climate change likely to affect its future distribution and impacts [13]. Warming climate conditions, particularly rising winter minimum temperatures, will also expand the geographic range of mountain pine beetles (*Dendroctonus ponderosae* Hopk.) by increasing the area and length of season available for the beetles to complete their life cycle [14], resulting in more frequent beetle outbreaks during periods of warmer temperatures [15,16]. An increase in the number of infestations in formerly climatically unsuitable habitats indicates that mountain pine beetle populations have already expanded into high-elevation areas [17,18]. The overlapping effects of mountain pine beetle outbreaks and blister rust will likely intensify the overall decline of whitebark pine. The effects of climate change are important when assessing the resiliency of whitebark pine ecosystems and their potential to recover from mountain pine beetle outbreaks and other landscape-level disturbances [19]. Consequently, an urgency exists to understand the influence of climate change on the severity of mountain pine beetle outbreaks and white pine blister rust infections.

Dendroecological methods for detecting mountain pine beetle outbreaks in whitebark pine and lodgepole pine forests have relied mostly on growth release periods beginning almost a decade after the outbreak event [10,14,15,20–22]. We developed a new dendroecological approach for decoupling whitebark pine radial-growth signatures related to climate and the onset of the physiological impacts of mountain pine beetle infestations on tree growth. This method can be used to help determine which sites are best suited for further climate analysis and climate reconstruction in tree species where natural and anthropogenic disturbances are common.

In this study, we interpret radial growth patterns of six whitebark pine chronologies to differentiate the relative influence of climate response and mountain pine beetle outbreaks in whitebark pine populations in western Montana. The specific objectives of this study were to (1) determine which climate variables exert the greatest influence on whitebark pine radial growth; and (2) partition the growth response of whitebark pines to that caused by known mountain pine beetle outbreaks or climate over the 20th century.

Study Area

We sampled whitebark pine-dominated forests located on a north-south transect that extended from the U.S.-Canada border in northwestern Montana to the western side of Yellowstone National Park. We chose to sample along a north-south transect to evaluate landscape-level climate and mountain pine beetle outbreak trends. Our study sites were located in closed-canopy, whitebark pine forests that cover six peaks in western Montana (Table 1, Figure 1). The sites varied in elevation from 2040 m to 2535 m and were on south-facing slopes. Mean annual temperature ranges are similar among the sites. Soils are poorly developed Inceptisols at all sites.

Table 1. Locations of whitebark pine study sites located along a north-south transect in western Montana.

Study Site	National Forest	Elevation (m)	Latitude (Degrees N)	Longitude (Degrees W)
Hornet Peak	Flathead	2040	48.52.44	114.31.33
Mineral Peak	Lolo	2250	47.00.13	113.48.51
Morrell Mountain	Lolo	2370	47.11.53	113.21.25
Point Six	Lolo	2350	47.02.34	113.59.14
Ajax Peak	Beaverhead-Deerlodge	2535	45.20.25	113.42.57
Big Hole Pass	Beaverhead-Deerlodge	2255	45.31.14	113.48.16

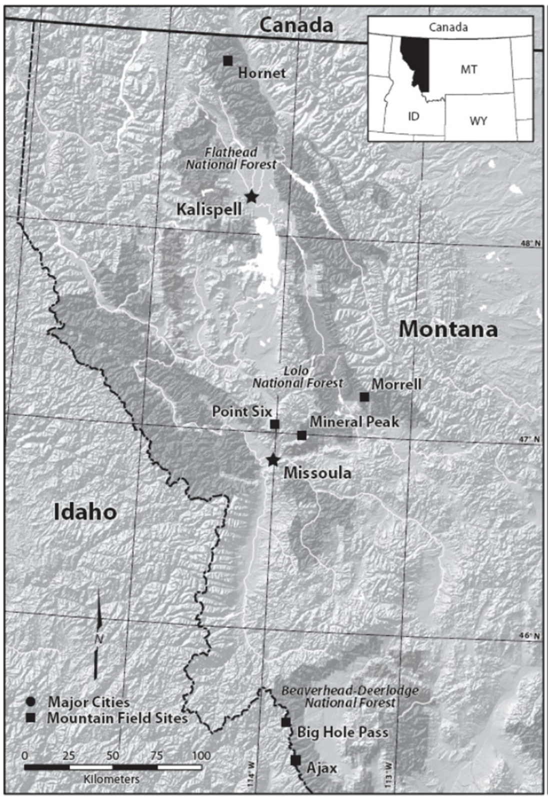

Figure 1. Terrain map of six study sites in western Montana. The Continental Divide is marked by a black dashed line.

Evidence of natural and anthropogenic disturbance were common at each site. Whitebark pine had experienced differing rates of mortality in each stand, predominantly from mountain pine beetle activity that we identified by the presence of J-shaped galleries on the boles of dead trees. We completed health surveys on 805 whitebark pine trees (diameter breast height (DBH) $\geq$ 5 cm) in our study area. Of the 805 whitebark pines examined, 30% (n = 238) were alive, 20% were declining (n = 159), and 50% (n = 408) were dead (Figure 2) [23]. We also observed several dead trees with what appeared to be old blister rust cankers (center of cankers were dark brown, rough, and broken) at the northern sites (Flathead National Forest) and central sites (Lolo National Forest). Blister rust was abundant at all sites, with living whitebark pine trees exhibiting open cankers or flagging (red needles due to the recent mortality of a branch or stem) in their upper canopies. Evidence of past logging and fires was common, especially in our central sites, with numerous whitebark pine trees displaying multiple fire scars at each site. Fire history data for the central sites indicated mixed-severity fire regimes with no widespread fires recorded during the 1900s [8,24]. Land-use history in the form of logging roads, fire towers, and ski resorts were most evident at the Morrell Mountain and Point Six sites, although roads were within ~2 km of all of our sites.

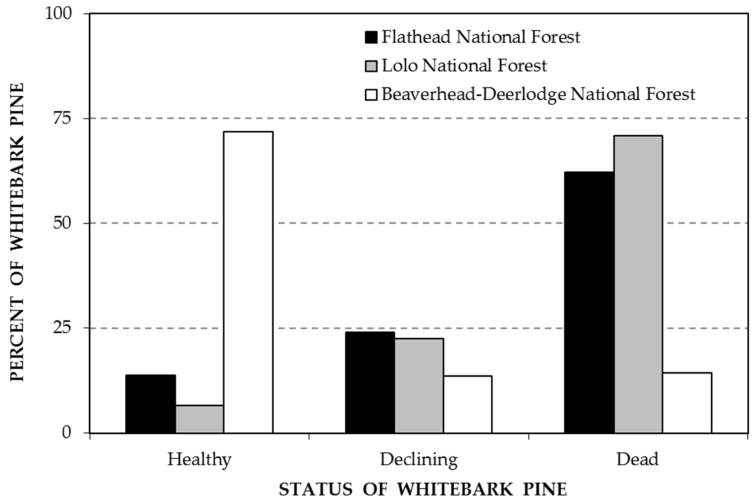

Figure 2. Comparing the health status of whitebark pine populations between national forests in western Montana. The Flathead National Forest is furthest north, the Lolo National Forest is in the middle, and the Beaverhead-Deerlodge National Forest is furthest south in the western Montana transect.

2. Materials and Methods

Whitebark pine tree-ring and health data were collected in four 0.05 ha fixed-radius plots on each of the six mountains included in this study ([24] overstory plots total). Increment cores were collected from all trees, living or dead, within each plot at or below 30 cm above the root collar and along the contour of the slope to minimize the effects of reaction wood on the growth patterns in each sample [25]. We used a chainsaw to collect 5 to 10 cross-sections from whitebark pine snags, stumps, and logs to extend the tree-ring information from the cores back in time, and examined cross-sections for fire and mountain pine beetle scars at each of the six mountain sites [26]. We visually examined each cross-section and noted the presence or absence of fire (i.e., internal fire scars), mountain pine beetle galleries, and blue-stain fungus on each sample. The 322 living and dead whitebark pine samples selected for dendroclimatological analysis included those affected by mountain pine beetle; samples that contained fire scars that resulted in distorted growth around the injury and diminished the strength of the overall climate signal were not included in our analyses (Table 2).

Table 2. Whitebark pine chronology information from six sites in western Montana.

Study Site	National Forest	Period of Record	Number of Samples	Interseries Correlation	Mean Sensitivity
Hornet Peak	Flathead	1682–2005	64	0.48	0.23
Morrell Mountain	Lolo	1489–2003	60	0.51	0.24
Point Six	Lolo	1581–2003	62	0.47	0.22
Mineral Peak	Lolo	1171–2003	76	0.47	0.21
Big Hole Pass	Beaverhead-Deerlodge	1778–2004	27	0.50	0.22
Ajax Peak	Beaverhead-Deerlodge	1832–2004	33	0.52	0.21

All samples were frozen at –40 °C for 48 h to kill any pathogens and/or insects that may have been transported with the samples. Cores and cross-sections were examined for blue-stain fungus in the outer tree rings, indicating mountain pine beetle presence. The 322 whitebark pine cross-sections and core samples were mounted, sanded, and processed following standard dendrochronological techniques [27,28].

We used visual and statistical crossdating to assign precise calendar years to the growth rings of the core and cross-section samples. Visual crossdating relied on recognition of characteristic patterns of wide and narrow rings common to each study site that were likely related to regional climate [25], and statistical crossdating was accomplished using ring-width measurements and the computer program COFECHA [29,30].

We measured the ring widths on all samples to 0.001 mm accuracy with a Velmex measuring stage coupled with MEASURE J2X software (version 4.0). We removed the age-related growth trend of each sample by dividing the width of each annual growth ring by the value of a negative exponential curve, linear regression with negative slope, or flat line through the mean fit to each series by the program ARSTAN [31]. The resulting indices were then averaged for each year across all series using a biweight robust mean to create a single index series for each site (Table 2). Shared variance among the measurement series likely related to climate was identified through autoregressive modeling and incorporated into each index series to produce what is referred to as an ARSTAN chronology for each site [31]. We used the ARSTAN chronologies to examine climate-tree growth relationships at our sites.

The climate-tree growth relationships for each of the six chronologies were identified by comparing the chronologies to divisional climate data obtained from the National Centers for Environmental Information [32] and site-specific climate data collected from the PRISM climate group [33]. PRISM data is a regression-based model that uses point data, a digital elevation model, and climate parameterization to generate repeatable estimates of annual, monthly, and event-based climate parameters for locations at any given point [33].

Correlation and response function analyses (RFA) were used to determine the strength of association between site-specific climate variables and the whitebark pine ARSTAN chronologies. Pearson correlation coefficients were calculated between growth indices and monthly climate variables (mean monthly temperature, total monthly precipitation, and Palmer's Drought Severity Index (PDSI; Palmer 1965)) for a 15-month period to include the previous and current summers (previous June–current August). PDSI is used by the National Weather Service to monitor drought and soil moisture conditions in the United States and is a measure of the moisture available for plant growth. For the Beaverhead-Deerlodge National Forest chronologies, we used climate data from National Oceanic and Atmospheric Administration (NOAA) Climate Division Montana 2 (Southwestern). For the Flathead and Lolo National Forest chronologies, we used climate data from NOAA Climate Division Montana 1 (Western).

We conducted forward evolutionary interval analysis (FEI) in DendroClim 2002 [34] to provide a complementary assessment of temporal stability for significant monthly climate-radial growth relationships. Our objective for this analysis was to elucidate temporal variability in the relationships identified between climate and whitebark pine radial growth (Biondi and Waikul 2004). FEI begins with the earliest year in common to all variables, from which forward evolutionary intervals are progressively enlarged by adding one year to a base interval length at each iteration [34]. The FEI base interval length was double the number of monthly climate variables (30 years), thus the period of results from the correlation analysis was 1925–2005. Stable relationships between monthly climate variables and radial growth during the 20th century would further substantiate the results of correlation analysis and suggest the suitability of whitebark pine tree-ring data for use in dendroclimatic reconstructions at each of the six sites. Changing correlation results over time would indicate shifting climate-growth relationships or disturbance impacts on radial growth.

We used the PRECON program version 5.17 [35] to develop 100-year time series plots that incorporated the results from a bootstrapped, stepwise regression using the six whitebark pine chronologies and 30 monthly variables: 15 variables for mean monthly temperature and 15 variables for monthly total precipitation. The 15 months began with the June of the previous growing season and ended with August of the current growing season. The bootstrapped, stepwise regression used the months with significant climate effects to show those periods during the 20th century when tree growth was above or below that modeled from the observed climate variables. Declines in growth not associated with climate could be caused by large-scale disturbances, such as mountain pine beetle outbreaks, that contribute to the mortality of mature whitebark pines within a stand. Smaller-diameter whitebark pines that survived the periodic mountain pine beetle outbreaks were expected to show an increase in growth within a decade following the outbreak [15,22]. The mountain pine beetle outbreaks between 1920 and 1940 and between 1970 and 1980 were expected to influence whitebark pine radial growth, thus reducing the strength of the overall climate signal immediately following those events. We used PRECON to create residual chronologies (actual tree growth minus predicted tree growth) during the 20th century to distinguish the separate influences of mountain pine beetle outbreak periods and climate in whitebark pine radial growth. Creating the residual chronologies also allowed us to infer mountain pine beetle outbreak trends along a latitudinal transect through western Montana. These analyses could be performed in other software programs, however, we chose to use PRECON because it was developed specifically for tree-ring analyses [35].

3. Results

3.1. Climate Response

The correlation analysis indicated a strong response between whitebark pine radial growth and precipitation and temperature from 1895 to 2005 (Table 3). However, none of the sites exhibited stable radial growth-climate relationships between 1925 and 2005 (Figure 3). The months during which precipitation and temperature exhibited the strongest relationship with whitebark pine radial growth varied by site along the north-south transect (Table 3). Whitebark pine showed different climate responses at each site, but results from the RFA showed that monthly climate variables were less important to whitebark pine growth than prior summer growth (data not shown). We also analyzed site-specific PRISM climate parameter data and found the correlations between our chronologies and PRISM data were weaker than with the divisional climate data from NOAA (data not shown).

Table 3. Strongest relationships between whitebark pine radial growth and mean monthly temperature and total monthly precipitation in western Montana.

Study Site	Period	Climate Variable	Month	Correlation Coefficient
Hornet Peak	1895–2005	Precipitation	June	0.29 *
Morrell Mountain	1895–2003	Precipitation	Previous June	0.27 *
Point Six	1895–2003	Precipitation	January	−0.32 **
Mineral Peak	1895–2003	Temperature	April	0.34 **
Big Hole Pass	1895–2004	Precipitation	Previous July	0.45 ***
Ajax Peak	1895–2004	Temperature	Previous July	−0.24 *

* $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Hornet Peak (northern site), Morrell Mountain (central site), and Big Hole Pass (southern site) had the strongest positive correlations between radial growth and June, previous June, and previous July precipitation, respectively (Table 3). The positive correlations in the previous summer indicate that an increase in precipitation in the previous year's summer results in increased radial growth during the current growing season. Of the three sites, Morrell Mountain whitebark pines had the weakest precipitation relationship (Figure 3). The relationships at most sites weakened between 1957 and 1977. Big Hole Pass whitebark pines had the strongest correlation with previous July precipitation but radial growth had periods of non-significant climate relationships between 1945 and 1961. We found a strong negative relationship between radial growth and precipitation at Point Six (central site) during January when precipitation is in the form of snow and snowpack levels are high.

Two of the six whitebark pine sites had a stronger response to temperature than precipitation. Mineral Peak (central site) whitebark pines responded favorably to warm April temperatures, but not consistently until 1970. Ajax Peak (highest elevation and most southern site) had a weaker, negative relationship with radial growth and previous July temperature, which indicates that high temperatures during the previous summer negatively impact whitebark pine radial growth during the current year.

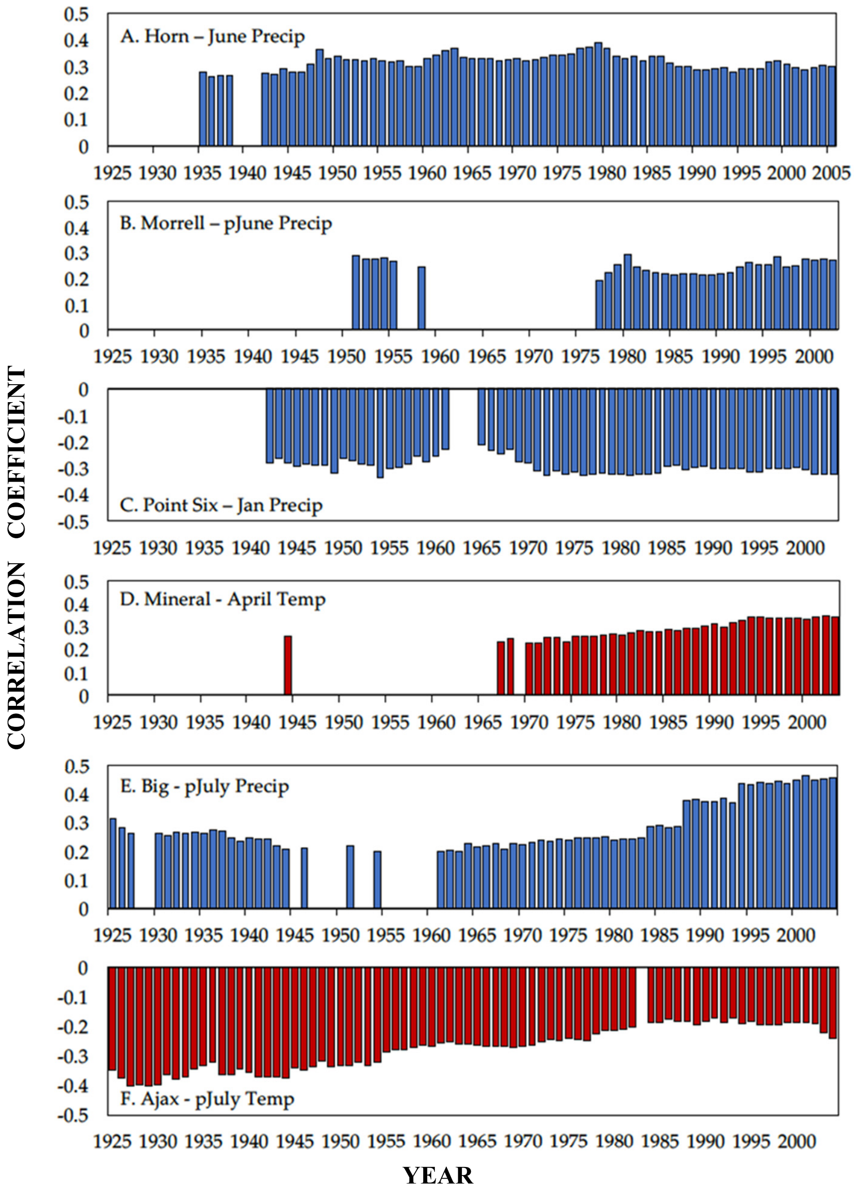

Figure 3. Forward evolutionary interval analysis (1896–2005) between whitebark pine site chronologies and the monthly climate variables exhibiting the strongest correlation coefficients over time (**A**–**F**). The last years of the forward intervals are listed on the *X*-axis (30-year base interval). Significant ($p < 0.05$) correlations are blue (precipitation) and red (temperature). Variables preceded by "p" represent months from the previous year.

3.2. Separating Disturbance Events and Climate Response

Extensive mountain pine beetle outbreaks in the Northern Rocky Mountains occurred between 1925 and 1935, 1970 and 1985, and more recently in the 2000s [24,26,36]. The series of outbreaks that occurred from 1925 to 1935 in Idaho and Montana killed an estimated 1.4 billion lodgepole pines and vast numbers of whitebark pines [36–39]. A massive infestation, extending over 12 million hectares, also devastated lodgepole and whitebark pine stands in the Northern Rocky Mountains and in central British Columbia in the 2000s [36]. Mountain pine beetle outbreaks caused anomalous growth patterns in our whitebark pine chronologies and influenced the strength of the climate response (Figure 4). Radial growth outliers were related to mountain pine beetle outbreaks in the western United States during the period from 1940 to 2005. The whitebark pine chronologies at Morrell Mountain and Point

Six showed below-average growth from 1970 to 1975 while precipitation was relatively high during the early 1970s. Mineral Peak showed an inverse relationship in the early 2000s, with whitebark pine growth declining during a period of increased precipitation.

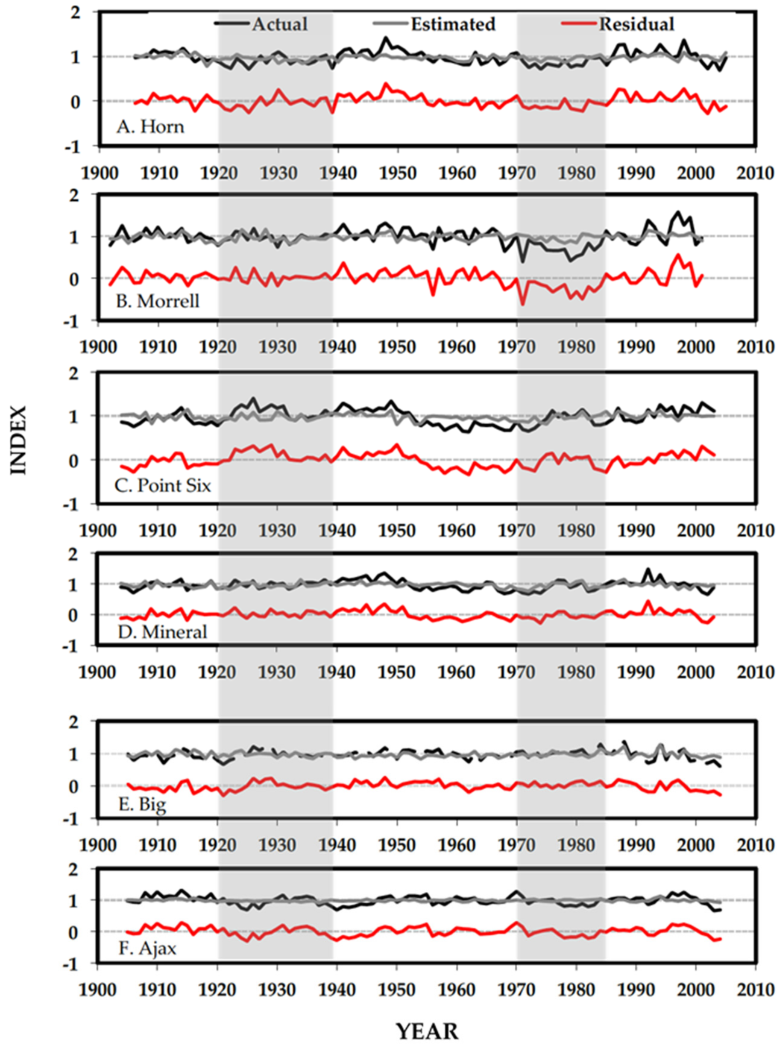

Figure 4. PRECON results for most significant monthly climate variables and actual, estimated, and residual indices of whitebark pine chronologies at six sites (**A**–**F**). "Actual" (black) indicates the whitebark pine radial growth, "estimated" (gray) indicates the predicted annual whitebark pine growth based on the significant monthly climate variables, and "residual" (red) is the difference between the actual and estimated chronologies from 1905 to 2005. The gray bars highlight mountain pine beetle outbreak periods.

We explored whitebark pine growth without the influence of climate to examine the mountain pine beetle outbreak periods in the chronologies more closely. The residual chronologies were developed to examine the periodicity of departures from the mean, independent of climate, which showed disturbance patterns at each site during the 20th century (Figure 4). We used a residual chronology percent growth change of (+/−) 25% sustained for at least 5 years to examine suppression and release trends in growth related to disturbance. The percent growth change parameters were developed to quantify the radial growth changes associated with disturbances from climate and are comparable to metrics used in other studies of forest canopy disturbances [40]. The time series plot for our most northern site, Hornet Peak, indicated that actual whitebark pine growth agreed relatively well with predicted growth, although positive departures (indicating non-climate growth releases) were found in the 1940s and 1980s, a decade after known mountain pine beetle outbreaks. The three central sites showed different patterns of growth unrelated to climate during the past 100 years (Figure 4). The Mineral Peak time series plot revealed a close relationship between actual and predicted whitebark pine growth, but the residual chronology showed peaks in growth in the 1940s and 1990s. The Morrell Mountain and Point Six time series plot showed that the predicted whitebark pine growth deviated from actual growth between 1965 and 1980. This 15-year growth suppression indicated disturbances such as white pine blister rust or anthropogenic land-use influences on radial growth. Following the growth suppression, whitebark pines at Morrell Mountain showed a release from 1982 to 1986.

Our southern sites also showed asynchronous growth patterns, similar to the central sites (Figure 4). In comparison to the other sites, whitebark pines at the highest-elevation site, Ajax Peak, were the least responsive to temperature and precipitation during the 20th century (Table 3, Figure 4). Therefore, more periodic positive and negative growth departures were evident at this site. Ajax Peak experienced growth suppressions in the 1920s, 1940s, and the 1980s. Growth releases at Ajax Peak occurred in 1970 and in the late 1990s. Conversely, the time series plot for Big Hole Pass indicated that the actual whitebark pine growth closely matched the predicted growth (climate), with only one growth suppression period in the 1920s.

4. Discussion

4.1. Climate Response

Whitebark pine radial growth is responsive to temperature and precipitation and its seasonal distribution, but to varying degrees along the latitudinal transect in western Montana. Aspect and slope position could also impact forests' temperature response and moisture availability [25]. Temperature exerted less of an influence on whitebark pine radial growth at our sites than did precipitation, likely due to our sites being largely in closed-canopy forests, and below treeline [41]. Wet conditions from precipitation and snowpack melt in the previous summer months enhance whitebark pine growth during the following growing season. Previous year's precipitation affects water and nutrient storage, and the initiation of growth in the current growing season [25]. In the Northern Rocky Mountains, climate-response models typically explain 30–55% of the variance in ring-width indices [5,42], which is comparable to our results.

The strongest, positive relationship between whitebark pine growth and precipitation occurred during the previous July at Big Hole Pass (southern site). The northern and central sites (Hornet Peak, Morrell Mountain, and Point Six) responded to precipitation during different periods throughout the year, indicating microsite conditions may influence the amount of available moisture for tree growth. Hornet Peak is the lowest in elevation of the study sites and therefore may experience an earlier snowpack melt, which could explain the strong positive correlation to current June precipitation. Morrell Mountain whitebark pines responded favorably to snowmelt in the previous June.

Point Six had a significant negative response to precipitation during January, indicating that winter snowpack conditions are also important for understanding tree growth at these sites. Point Six is dissected by ski runs and artificial snow is blown early during the ski season which contributes to snowpack accumulation throughout the winter. Snow was still on the ground in late June when we sampled this site during our field seasons, indicating that heavy snow accumulation persists into the growing season and likely causes an extended dormant period [25,43]. Tree growth in any year in high-elevation, moisture-stressed trees is often related to a climatic window that includes part of the previous and current summers [44]. Therefore, if the June–September growing season is further shortened due to high accumulations of snowpack, the window for whitebark pine photosynthesis is narrower [45]. Although precipitation in the form of snow occurs throughout the year at Point Six, the water is not available to whitebark pines until the summer when temperatures are warmer and snowpack begins to melt. The longer snowpack period at Point Six contributes to the inverse relationship between tree growth and January precipitation. Point Six is an example of the important influence of land-use history on climate-growth response in whitebark pine forests. During the winter season, when available moisture is low due to water contained in the snowpack, whitebark pines may favor respiration over photosynthesis. When low precipitation and soil moisture levels occur, trees experience water stress which results in decreased photosynthesis. Water stress causes lower amounts of carbohydrate storage and lower amounts of growth hormones to be produced, which causes a reduction in cambial growth and results in the formation of a narrow ring [25]. If favorable precipitation and snowmelt conditions occur in the previous summer, the carbohydrate reserves are available for the current year's growth [25]. The fluctuations in precipitation and drought also reflect the fluctuations in snowpack. Snowpack variability is a central force that limits tree growth at high-elevation sites [46], therefore the timing of snowpack melt is important in understanding growth conditions in whitebark pine forests across the six sites.

Future snowpack conditions will directly influence the relationship between whitebark pine growth and available moisture. Climate change will reduce the depth, duration, and distribution of snowpack in the Northern Rocky Mountains [47,48]. Snow cover has already significantly decreased every month (except November and December) from 1966 to 2013 in western North America [49]. Continued warming will cause snowpack to melt earlier during the year, which may lengthen the whitebark pine growing season. Photosynthesis and transpiration by whitebark pine and other high-elevation plant species will remove the available soil moisture earlier in the summer and will therefore experience drought stress later in the summer, causing increased moisture stress in many trees. Large snowpack reductions will also eliminate the insulation that prevents soil from freezing during winter cold waves in high elevations [47,48], which will further negatively affect whitebark pine growth.

Our temperature and precipitation analyses are suggestive of the preconditioning effects of drought on disturbance events at our study sites [50]. For example, Hornet Peak and Morrell Mountain experienced a drought in the 1970s, during a mountain pine beetle outbreak. Hornet Peak, Point Six, Ajax Peak, and Big Hole Pass also had a drought period in the mid-1920s that may have caused the whitebark pines to be more susceptible to the mountain pine beetle outbreak that occurred from 1920 to 1940.

Whitebark pines at Big Hole Pass had the strongest response to climate and the least amount of influence from mountain pine beetle outbreaks of the six sites. Whitebark pines at Big Hole Pass are the most climatically sensitive in our study because the site is located on the Continental Divide in a semiarid region with an open, grassy understory, and little competition from competing shade-tolerant species. This would be an ideal site for further dendroclimatological studies using whitebark pine in the Northern Rocky Mountains. Further dendroclimatological research should be conducted on sites where the mountain pine beetle influence appears to be minimal.

4.2. Separating Disturbance Events and Climate Response

Asynchronous patterns between radial growth and expected climate response in the time series plots, particularly in Hornet Peak, Morrell Mountain, Point Six, and Ajax Peak, are most likely due to mountain pine beetle outbreaks. The departure from expected whitebark pine growth during the 1970s and 1980s is clearly seen at these sites and is interpreted here as an indication of the landscape-level mountain pine beetle outbreak. An earlier mountain pine beetle outbreak from 1920 to 1940 affected whitebark pine growth at most of our sites. Hornet Peak and Ajax Peak were the only two sites that exhibited growth departures from both mountain pine outbreaks during the 20th century.

In addition to mountain pine beetle outbreaks, other landscape-level patterns in the whitebark pine chronologies were evident. The whitebark pine chronologies showed a sharp growth decline in the study sites from 1998–2005. This decrease in radial growth is likely related to a combination of drought, mountain pine beetle outbreaks, and white pine blister rust infections. Although both white pine blister rust and mountain pine beetle were present at each site, the drought from 1999 to 2008 has also impacted these sites [51]. Over 50% of the United States experienced moderate to severe drought conditions during the early 2000s, with record or near-record precipitation deficits throughout the western United States [52]. Severe drought conditions have continued to affect the western United States through 2008 [47]. Droughts restrict biological activity in whitebark pine and change processes within the whitebark pine ecosystem. Drought conditions are critical during the previous growing season. Moisture conditions late in the previous year's growing season may affect the current year's bud break and the initiation of growth more than climate during the current year's growing season. Dry conditions have previously been associated with mountain pine beetle outbreaks [53,54]. Continued periods of drought will likely stress whitebark pines and make them more susceptible for mountain pine beetle attack and white pine blister rust infection [19].

5. Conclusions

Whitebark pine radial growth in western Montana is influenced by temperature and precipitation patterns during the previous summer, current spring, and current summer. Tree growth is clearly responsive to temperature and precipitation and its monthly distribution but may vary by site depending on the site disturbance history. Wet conditions from precipitation and snowpack melt in the previous summer and spring enhance whitebark pine growth during the following growing season.

By using both the PRECON and DendroClim 2002 programs, we were able to distinguish the relationship between whitebark pine radial growth and climate with mountain pine beetle outbreaks. We used a new method to explore divergent periods in the residual chronologies after mountain pine beetle outbreaks at six sites in Montana. Our understanding of how whitebark pine radial growth responds to both changing climate conditions and mountain pine beetle outbreaks is critical in understanding the current decline of whitebark pine throughout its range.

The results of this study substantiate the importance of site disturbance history and drought in whitebark pine communities. We suggest that the increase in drought frequency and severity predicted to result from continued climate change may amplify existing threats to whitebark pine populations by changing biological processes, reducing whitebark pine productivity, and increasing stress, collectively reducing whitebark pine resiliency to mountain pine beetle infestations and white pine blister rust infections.

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