average annual temperature in GTNP is increasing, while the annual amounts of both overall precipitation and snowfall are decreasing (Figure 1). It has been suggested that only a slight increase in global atmospheric temperature (4.5° C) would completely remove whitebark pine from the Greater Yellowstone Area and GTNP ecosystems (Schrag et al. 2008) (Figure 1).

Figure 1. The current range and distribution of whitebark pine in GTNP and GYA (left), and the predicted range and distribution of whitebark pine in GTNP and GYA given a projected 4.5°C temperature increase (right). From Schrag et al. 2008.

Whitebark pine is considered to be a keystone species of the particular ecological niche it occupies in the United States for three reasons. First, more than one hundred animal species, including the endangered grizzly bear (*Ursus arctos horribilis)*, depend on its high-energy seeds for survival (Felicetti et al. 2003). If whitebark pine should vanish from its niche, endangered species would be forced to lower elevations in search of food, thus increasing the potential for contact with humans and human-caused casualties. Second, the presence of whitebark pine in subalpine ecosystems helps to slow the melting of accumulated snow, resulting in reduced flooding occurrences. And third, by slowing the melt of snow, whitebark pine provides a high quality source of water to plants and animals during the summer melting season (Keane and Parsons 2010).

In addition to its importance as a keystone species, whitebark pine also has value as a recreational resource. Whitebark pine has many aesthetic qualities that make it a potential attraction to park visitors. Tree species that thrive at high altitudes generally have unusual morphological characteristics resulting from the harsh conditions provided by high altitude conditions. One of the most striking characteristics of high altitude species, including whitebark pine, is the twisted formations of trunks and branches. Additionally, whitebark pine has value as a recreational resource because communities tend to form very open, park-like forests ideal for adventurous hikers (Keane and Parsons 2010). Lastly, whitebark pine forests offer value as a recreational resource for avid birdwatchers. Whitebark pine is the only species of pine in North America that does not disperse its seeds utilizing wind. Rather, whitebark pine relies on a mutualistic relationship with a bird – the Clark’s nutcracker – to disperse its seeds. In the late summer and fall, Clark’s nutcrackers harvest seeds from the whitebark pinecones and carry them up to ten kilometers away and bury them (Tomback 1982). The nutcrackers will eventually return for the seed stocks, but those seeds left unclaimed will eventually begin to germinate (Tomback et al. 2001). This mutualistic relationship with the Clark’s nutcracker would provide avid birders the opportunity to see this high-altitude bird in action during the summer and fall months that, without the presence of whitebark pine, they would likely never see.

We have conducted preliminary research on the history of whitebark pines in Paintbrush Canyon. We reconstructed a long paleoecological record of 8,000 years from a 1.5 meter sediment core obtained from Whitebark Moraine Pond (by Sarah Spaulding, Alex Wolfe, and Jill Baron). We analyzed the sediment core for pollen, charcoal, and macrofossils to reconstruct Holocene-scale vegetation and fire history records. Our data indicate that the site has predominately been occupied by whitebark pine with brief periods of vegetation dominated by non-arboreal taxa, and that the site historically experienced frequent, low-intensity fire episodes. However, fire episodes have been decreasing in frequency and increasing in intensity towards the present. In addition to sedimentary data, we collected a set of increment cores from whitebark pine trees at the site in 2013 to identify how climate has impacted the growth of the modern stand. The average age of establishment for the 20 trees we cored in this stand is, with the oldest individual dating to 1300 C.E. Our dendrochronogical results indicate that increasing growing season temperatures are correlated with a recent decline in whitebark growth, thereby highlighting the need for further dendrochronological studies examining the role of climate on the growth and survival of whitebark pine stands in GTNP.

Obtaining additional increment cores from the higher-elevation Holly Lake site (Figure 2) and oxygen isotope data from annual tree rings at both study sites has provided two key pieces of evidence. First, by obtaining a complementary set of increment cores from whitebark pine at Holly Lake, we have made comparisons regarding establishment dates and site-specific responses to climate between the two study sites. Because the study sites vary primarily in elevation, we examined how relatively small shifts in elevation affect annual growth of whitebark pine trees.

Second, results from the oxygen isotope analysis portion of this study would identify the type of precipitation utilized by whitebark pine for the 700 years of the dendrochronological record. This, in turn, would allow for inferences to be made about how precipitation source influences the growth and stability of whitebark pine populations. As both precipitation quantity and type (snow vs. rain) are predicted to shift in the future, it is important to know how whitebark pine has responded to past precipitation variability. By understanding how two different populations of whitebark pine responded to past climate change, park ecologists can formulate more effective conservation and management plans to prevent the disappearance of whitebark pine from GTNP with current and future climate change.

Much of the high-elevation wildlife and scenery in GTNP exist because of whitebark pine as a keystone species. Understanding how climate change has affected, and continues to affect, this threatened and disappearing species will help park conservationists develop new strategies for maintaining and restoring the current stands of whitebark pine. This increased conservation effort would ultimately lead to both an enhanced recreational and educational experience for park visitors. Our proposed research will provide information critical to the survival of whitebark pine stands by using the long-term paleoecological perspective to gain new insight on the resilience or vulnerability of whitebark pine to past climate change.

✦ STUDY AREA

Holly Lake, a glacially moraine dammed lake, is an ideal comparison site to Whitebark Moraine Pond (Figure 2) because of its similar vegetation composition, relative proximity, and higher elevation. The purpose of choosing site locations in Paintbrush Canyon is to match high-resolution dendrochronological records with the previously-mentioned sediment record of fire and vegetation history for the area.

The modern vegetational ecosystem of the study area can be characterized as a subalpine conifer forest. Canopy species dominate the watershed and consist primarily of whitebark pine (*Pinus albicaulis*) and subalpine fir (*Abies lasiocarpa*).

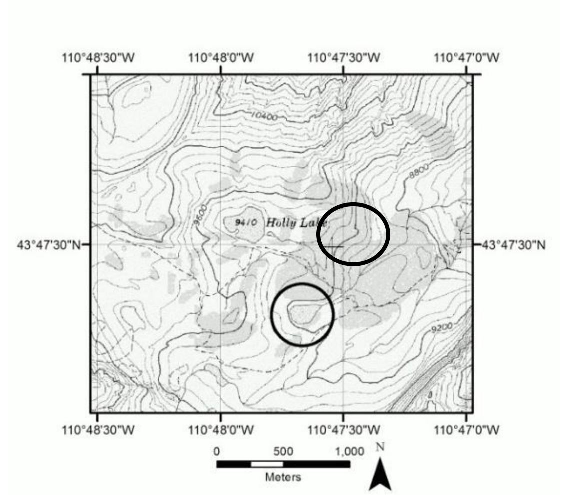

Figure 2. Topographic map with study sites circled in black. Holly Lake is located to the north, while Whitebark Moraine Pond is the site located to the south.

✦ METHODS

Where necessary, project methods have been approved by the respective permitting authority or oversight committee.

Increment cores and response to modern climate

A subset of 20 living whitebark pine trees were cored to establish ages and dates of establishment in the watershed surrounding Holly Lake. Cores from 20 trees were taken using standard dendrochronological techniques with a 5.15 mm diameter increment borer 30 cm above the soil surface (Elliot 2011). Diameter at breast height (dbh) was also recorded. GPS coordinates of all trees were recorded to assess the role of microsite and topography in placement of whitebark pine trees. Once the cores were in a laboratory setting, they were sanded and scanned, and rings on each individual core were counted to establish chronologies, using cross-dating protocols and software (Coo Recorder, C Dendro). Pith estimators and age-to-coring-height equations were applied as in Elliot (2011).

Ring widths were analyzed to understand the magnitude of climate change events experienced by each cored tree, as well as how climate change events impacted the growth and stability of each tree on a local scale. Methods generally followed those of a larger study of climate and local-scale factors on upper treeline in the Rocky Mountains (Elliot 2012). Because climate stations are rare at higher elevations in the Rocky Mountains, Precipitation-elevation Regressions on Independent Slopes Model (PRISM) data was used to make inferences regarding how the trees responded to past climates (Daly et al. 2008). This climate analysis allows for comparisons to be made between climate conditions in the past and the current climates in order to predict the response of the current stand of whitebark pine. We sampled, processed, and analyzed tree cores from Whitebark Moraine Pond in 2013 using the same methods outlined here.

Role of historical precipitation

To assess the history of precipitation source in the Holly Lake and Whitebark Pine Moraine watersheds, we measured the composition of the carbon and oxygen isotopes in the wood for at least 200 years of the dendrochronological record on a decadal temporal scale. Briefly, a chemical digestion procedure was used to purify the wood into □-cellulose at the University of Arizona, and the stable oxygen and carbon isotopic composition was then analyzed using standard mass spectrometry techniques at Washington State University. To calibrate the wood □^{18}O proxy, we sampled snow, ice, and water from the two watersheds for preliminary interpretations (Anderson 2011).

✦ PRELIMINARY RESULTS

Demography of current stands

The average date of establishment for the current stand of whitebark pine at Whitebark Moraine Pond is 1751 C.E. (Figure 3), while the average date of establishment for the current stand of whitebark pine at Holly Lake is much younger, with the majority of trees averaging a date of establishment around 1895 C.E. Older trees located at Holly Lake appeared to be significantly affected by mountain pine beetle infestations. No trees at the Whitebark Moraine Pond site were affected by pine beetles.

Ring widths and modern climate

Average yearly ring widths at Whitebark Moraine Pond ranged from 1.23 mm in 1950 to 0.60 mm in 2011 for the period of available climate data (1895-2012) (Figure 4A). A breakpoint analysis confirmed the presence of change point at 1949 (±4.5 years) and further indicated that average ring widths increased until 1949, and then began to decline to their current widths.

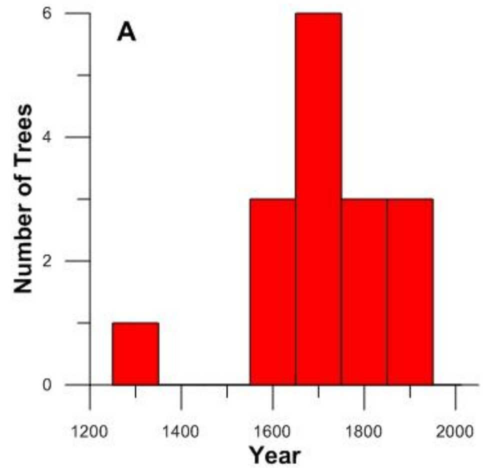

Figure 3. Trends in estimated dates of establishment for all cored trees at Whitebark Moraine Pond.

Average July minimum temperature (Tmin) was identified as the most statistically significant variable affecting annual ring widths ($p < 0.001$) (Figure 4B). Other temperature and precipitation variables had no significant effect on the growth of whitebark pine at this site. Until 1991 (±2 years), average July Tmin values experienced no significant variation and remained relatively constant through time. A maximum value of 37.38 F was reached in 1945, with a spread in data of 8.07 F. After 1991, however, average July Tmin values exhibited more variability and increased to temperatures higher than any other time during the record. Values reached a maximum in 2011 with an average July Tmin of 45.7 F with a spread of 13.34 F from 1991-2011.

Average July Tmin values were plotted against average annual ring widths to determine the effect of climate on tree growth (Figure 4C). Analyses indicated that average July Tmin values were a significant ($p < 0.001$) predictor of whitebark pine growth. The resulting relationship between the two variables reveals that the modern decline in whitebark pine growth at the study site can be attributed to increasing July minimum temperatures.

Increasing July minimum temperatures have aided in the displacement of whitebark pine by subalpine fir. The initial onset of declining ring widths around 1949 may have been triggered by an unknown ecological event which subsequently increased the stand's sensitivity to later temperature changes beginning in 1991, thereby amplifying its effect on the population. *Abies* and *Picea*, competitors of whitebark pine, are better adapted to survive in warmer climates than whitebark pine. While July minimum temperatures were discovered as the most significant variable at this site, Perkins and Swetnam (1996) observed a significant inverse relationship between ring widths and May temperatures in the Sawtooth-Salman River region of Idaho. This discrepancy in climate variables may be caused by the geographic difference in site locations. In both cases, increased growing season temperatures have resulted in altered subalpine conifer communities by allowing warm temperature-adapted species to invade the niche normally occupied by whitebark pine. Because subalpine fir tends to grow much faster than whitebark pine, it acts as a competitor for resources and ultimately restricts the growth of whitebark pine by out-shading.

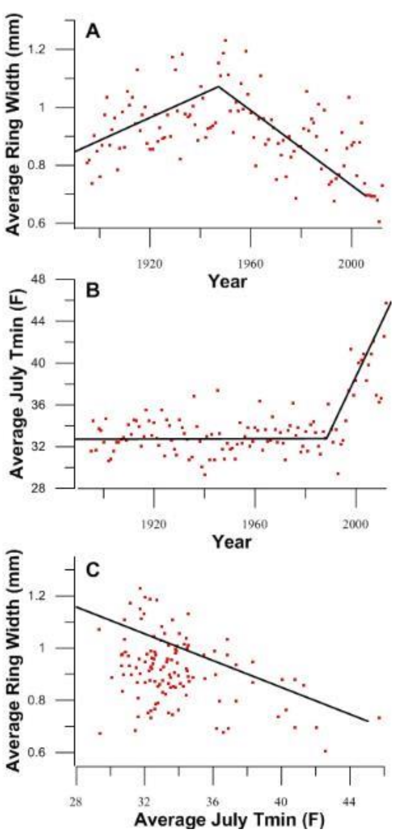

Figure 4. (A) Average ring widths by year. (B) Average July minimum temperatures by year. (C) Relationship between ring widths and July minimum temperatures (p<.001).

Annual growth trends of the whitebark pine stand at Holly Lake show an altogether different growth trend. Whitebark pine trees at Holly Lake showed a definite cyclical growth trend not observed at Whitebark Moraine Pond, as well as an overall increase in annual growth towards present (Figure 5); however, annual growth has declined in the last five years. Similar to Whitebark Moraine Pond, Growth trends observed at Holly Lake also show a statistically significant relationship with minimum growing season temperatures, particularly during time periods of growth decline. It is important to note that the overall increasing growth trend at Holly Lake may be an artifact of the relatively young age of trees sampled due to a high mortality resulting from pine beetle infections.

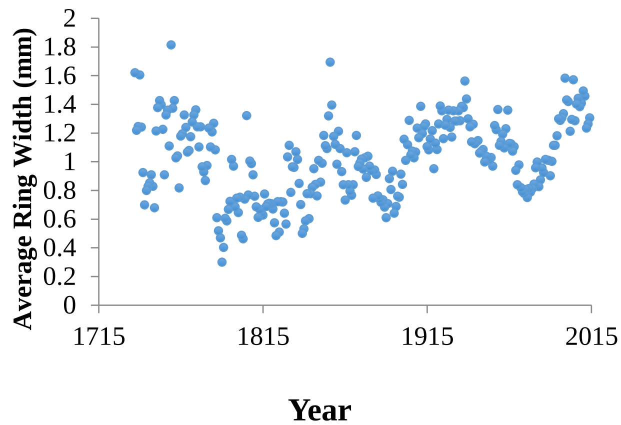

Figure 5. Ring width results from the Holly Lake stand of whitebark pine trees showing the cyclic nature of the data. Comparable to Figure 4.A.

Historical precipitation

Oxygen isotope data were analyzed from snow, lake water, and stream water in Paintbrush Canyon in an effort to aid in the interpretation of oxygen data resulting from processed tree rings (Figure 6). There did not appear to be a pattern related to the elevation at which water and snow samples were collected, but there was an observable difference in the isotopic signatures of snow vs. liquid water when compared to the global meteoric water line (GMWL) which will aid in our interpretation of final tree ring isotopic data.

Purified alpha-cellulose samples are currently being processed at Washington State University's Stable Isotope Lab and final isotopic data are expected to be received during the summer of 2015. We suspect that we will be able to use collected snow and water samples to interpret these results and determine, quantitatively, the role that different moisture sources play in the growth trends of whitebark pine trees at these two sites.

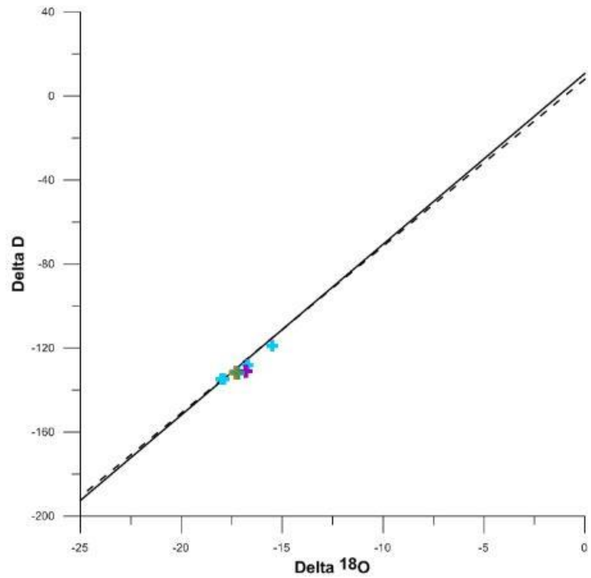

Figure 6. Preliminary oxygen isotope data collected from snow, lake water, and stream water. Solid line indicates the global meteoric water line and the dashed line indicates the local meteoric water line. Different colors represent different elevations the samples were collected at, though this shows no significant trend.

✦ MANAGEMENT IMPLICATIONS

Our results indicate that whitebark pine populations are decreasing in GTNP as a direct result of warming growing season temperatures. This modern decline of whitebark pine poses several management and conservation challenges. The fundamental risk associated with the loss of this species centers around whitebark pine's role as a keystone species. Because the endangered grizzly bear depends so heavily on whitebark pine seeds for survival, the disappearance of whitebark pine has the potential to increase human-bear mortality events as bears are forced to lower elevations in search of alternative food sources.

The central challenge associated with mitigating this modern decline of whitebark pine is that climate change (the main driver of this decline) is not an environmental problem with a simple solution. Climate change is a global phenomenon acting on a long timescale. Because this driver of whitebark pine decline is not easily managed, the best management option will be to focus on more locally-driven processes contributing to the decline, such as fire suppression.

✦ ACKNOWLEDGEMENTS

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