FEEDBACK-DRIVEN RESPONSE TO MULTIDECADAL CLIMATIC VARIABILITY AT AN ALPINE TREELINE

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Abstract: The Pacific Decadal Oscillation (PDO) has significant climatological and ecological effects in northwestern North America. Its possible effects and their modification by feedbacks are examined in the forest-tundra ecotone in Glacier National Park, Montana, USA. Tree ring samples were collected to estimate establishment dates in 10 quadrats. Age-diameter regressions were used to estimate the ages of uncored trees. The temporal pattern of establishment and survival was compared to the pattern of the PDO. A wave of establishment began in the mid-1940s, rose to a peak rate in the mid-1970s, and dropped precipitously beginning ca. 1980 to near zero for the 1990s. The period of establishment primarily coincided with the negative phase of the PDO, but the establishment and survival pattern is not correlated with the PDO index. The pattern indicates a period during which establishment was possible and was augmented by positive feedback from surviving trees. Snow may be the most important factor in the feedback, but studies indicate that its effects vary locally. Spatially differentiated analyses of decadal or longer periodicity may elucidate responses to climatic variation. [Key words: alpine, ecotone, Pacific Decadal Oscillation, seedling establishment, snow, tree-rings.]

INTRODUCTION

Climate affects alpine forest-tundra ecotones (e.g., Tranquillini, 1979, Hansen-Bristow, 1986; Luckman and Kearney, 1986; Kullman, 1988, 2003; Lloyd, 1997; Lloyd and Graumlich, 1997; Pellatt et al., 1998; Daniels and Veblen, 2003; Pisaric et al., 2003). Treeline elevations seem to be correlated more strongly with temperature than with any other variable (Grace, 1989). The latitudinal gradient in alpine treeline elevation indicates that this is a global scale control (the suggested -40°C isotherm limit (Becwar et al., 1981) does not hold in the northern Rocky Mountains

and is probably coincidence in Colorado). Photosynthetic rates and carbon alloca-
tion of trees are influenced by leaf and root temperature (e.g., Korner, 1998). Tem-
perature also affects snowmelt and soil thaw, and the presence of late lying snow
influences photosynthesis (Lehner and Lutz, 2003). Alpine treelines also respond to
the availability of water (Grace, 1989; Hessl and Baker, 1997a; Lloyd, 1997) and
can be relatively dry environments. Alpine treelines are typically subject to high
wind velocities. Deformed and flagged trees and migrating tree islands demonstrate
the influence of wind on growth form (Marr, 1977; Holtmeier and Broll, 1992).
Wind affects the actual precipitation by redistributing snow, often removing it alto-
gether from treeline locations, and can increase evapotranspiration, thus exacerbat-
ing water shortages (Hiemstra et al., 2002). Snow may be the most important single
climatic factor at some treelines (Walker et al., 1993, 2001).

The role of treelines (here used for the ecotone) as indicators of climatic change
has been debated (e.g., Kupfer and Cairns, 1996; Didier and Brun, 1998). Several
factors weigh against this role. The interaction of many exogenous factors make it
difficult to assess what treeline change may indicate. A number of endogenous fac-
tors, including competition with tundra species and negative and positive feed-
backs between plants and microclimate can interfere with interpretation of climatic
signals (Malanson and Butler, 1994; Malanson, 1997; Korner, 1998; Alftine and
Malanson, 2004), the positive feedbacks introducing nonlinearity (Malanson, 1999,
2001; Lloyd et al., 2002; Cairns and Waldron, 2003).

Whether such effects are strong enough to have an effect on the use of treelines
as indictors, or simply on understanding the potential loss of tundra as a result of
the advance of trees, might be addressed by looking at advances in the recent past.
Our purpose is to assess the effect of recent climate variability on the potential inva-
sion of alpine tundra by tree species. We examined tree seedling establishment and
survival at the limit of tree species in relation to multidecadal climatic variation in
Glacier National Park, Montana. We appraised the effects of the Pacific Decadal
Oscillation (PDO) on treeline dynamics because it has been identified as an impor-
tant determinant of ecological processes in the mountains of the Pacific Northwest
and the northern Rockies (Fagre et al., 2003).

The PDO describes a mode of North Pacific sea surface temperature variability
on a multidecadal time scale (Mantua et al., 1997; Zhang et al., 1997; see Mantua,
2004, for complete and updated information). The PDO index is calculated using
the difference between monthly observed values of Pacific sea surface temperatures
north of 20°N in relation to the monthly mean for 1900–1993 (Zhang et al., 1997).
The PDO is calculated The PDO index from 1900–2000 shows one major negative
phase (from the late 1940s to the late 1970s, the end reported as 1977; Fig. 1). Con-
siderable variation exists within the multidecadal trends. Analyses of PDO focus on
the contrast between its positive and negative phases. Mantua (2002) reported a
number of climatic effects that are ecologically important. The PDO may have
widespread climatic correlations (e.g., Gedalof et al., 2002; Hidalgo and Dracup,
2003) but they are strongest in the Pacific Northwest and northern Rocky Mountains
(Zhang et al., 1997; Wallace et al., 1996; Gershunov and Barnett, 1998), where
cooler winters and wetter springs are found when the index is negative. Snowfall is
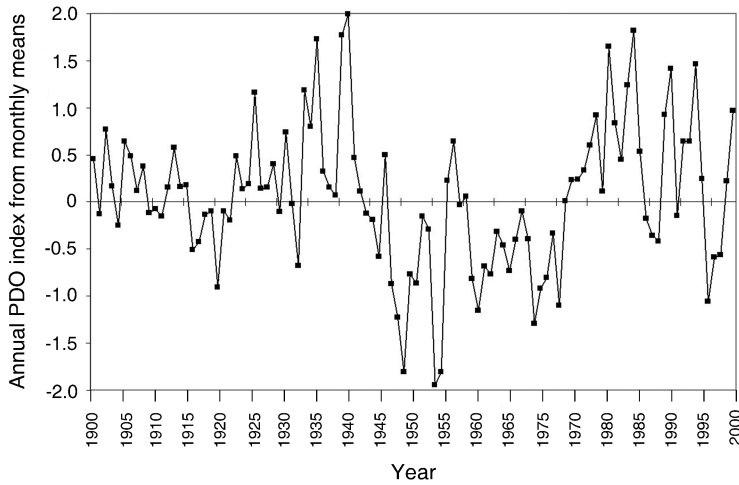one of the key factors negatively correlated with the PDO (Moore et al., 2002;

Fig. 1. PDO signal from 1900 to 2003. *Source*: Mantua, 2004.

Selkowitz et al., 2002; Kovanen, 2003). Of most relevance here, the negative phase of the PDO has been linked to increased snow in the region of Glacier National Park; Selkowitz et al. (2002) reported that for 5-yr. moving averages the October–March PDO index accounted for 70.4% of the variability in the April 1 snow-water equivalent for 1950–2001.

The PDO has regional ecological impacts in the Pacific Northwest. It affects Pacific salmon production (Mantua et al., 1997; Hare and Mantua, 2000; Drake et al., 2002), forest growth (Kadonaga et al., 1999; Peterson and Peterson, 2001; Peterson et al., 2002), and forest fire regimes (Heyerdahl et al., 2002) in northwestern North America. Ecological responses of trees, extending south into Mexico, and tropical coral have been used to develop a PDO chronology (Gedalof et al., 2002). Ecological impacts at a distance are expected given the nature of teleconnections (Panagiotopoulos et al., 2002).

The advance of treelines depends first on seedling establishment (Smith et al., 2003; see Malanson et al., 2001; Vostral et al., 2002; Li et al., 2003; and Butler et al., 2004 for seedbed, geomorphic and microsite limits), but often reflects survival for greater than a decade; this transition reflects the scale of tree ring and other pale-oecological data. Rochefort et al. (1994) summarized the implications of paleoecological studies of treeline change. Where they had a temperature signal, they reported that advances were always associated with higher temperatures and retreats with lower temperatures. The precipitation signal was not so clear, but higher treelines were associated with lower precipitation twice as often as the reverse, which occurred in some of the driest climates (LaMarche, 1973; Carrara et al., 1991). Relevant climate-vegetation studies of seedling establishment and survival during the past century have tended to focus on high elevation meadow invasion (e.g., Franklin et al., 1971; Agee and Smith, 1984; Butler, 1986; Rochefort and

Peterson, 1996). These studies, particularly those in the Pacific Northwest, found invasion associated with warmer, drier climate. In more exposed locations, but still not among tree islands, Daly and Shankman (1985) found a spatial association with wind, and Hessl and Baker (1997b) reported recent establishment in cooler periods within a long term warming trend. More recent paleoecological work has associated advance of trees with higher snowfall at treeline sites in the Sierra Nevada (Lloyd, 1997).

Some of these studies may not be directly comparable to ours. Weisberg and Baker (1995) reported different establishment in various environments within the ecotone (but general influence of soil moisture). We examine establishment and survival at the extreme limit of tree species growth, which is the leading edge of any advance. Meadow invasions may differ because the microclimates may differ from regional climate in a different direction from that at the extreme tree limit. Of those that do examine the same area, some do not rely on tree rings; Hattenschwiler and Smith (1999) and Germino et al. (2002), directly observing seedlings, found that seedlings were more likely to establish and survive in protected locations with moderate snow cover in years with above average precipitation and to be inhibited by dry conditions, higher temperatures, and more sunlight in Wyoming. In this same area Moir et al. (1999) reported better seedling establishment in places with less snow cover, but only one of their three sites were in comparable tundra; the other two were in meadow, and they did not have much temporal information.

METHODS

Study Area

We examined an advancing treeline in the northern Rocky Mountains, Montana, USA. Lee Ridge in Glacier National Park, MT is a wind-exposed, northwest-facing slope encompassing subalpine forest, alpine-tundra transition and tundra habitat at 2000–2100 m elevation. As in other areas of the Rockies, tree-island formation and distorted tree growth forms are apparent at this treeline. Treeline structures vary from tree islands at upper sites that appear to be krummholz but consist of short upright (ca. 1 m) stems creating a dense canopy of ca. 20 cm depth; to dwarfed trees found in fingers (ca. 2 × 10–50 m islands or extensions from forest) at lower elevations; to individual seedlings, samplings, and small trees in coves between fingers and near tree islands. There is no understory among the trees islands or fingers. Tundra is thin, usually consisting of a mat of *Arctostaphylos uva-ursi* or *Dryas octopetala* on the steeper portions of solifluction terraces, where its depth is <5 cm (Fig. 2). Regional changes in treeline have been reported to be minor (Butler et al., 1994; Klasner and Fagre, 2002).

The elevation and relative topography prevented Pleistocene glaciation. Inactive solifluction terraces across most of Lee Ridge created stripes of vegetated areas separated by rocks that have been expelled by freeze-thaw processes; the vegetation patterns do not directly correspond to these features (Malanson et al., 2001; Walsh et al., 2003). The uppermost surface is erosional, but soil is developing; depth is greater than 50 cm, clay is accumulating, and no charcoal was found in recent soil

Fig. 2. Trees establish in tree islands or fingers in sparse tundra on the relict solifluction lobes of Lee Ridge, Glacier National Park, Montana.

pits dug in and near the high elevation krummholz (Ginger Schmid, Ph.D. candidate, Department of Geography, Texas State University, pers. comm., March 1, 2003). Soil under the tree and krummholz canopies often consisted of an indurated layer of duff. Other landscape disturbance factors that may preclude upslope movement of treeline, such as snow avalanche and debris flows, are not evident.

The climate of Glacier National Park has the spatial variability typical of mountain landscapes (Finklin, 1986). Average annual precipitation ranges from 585 to 2500 mm. At the moderate elevation SNOTEL site at Flattop Mountain, 60% of the precipitation is as snow. Average January minimum temperatures range from -3° to -6°, but these do not include the high elevation interior; average July maximums range from 24° to 27°. Glacial retreat indicates long-term climatic change (Hall and Fagre, 2003). At Lee Ridge, a temporary weather station was maintained by the USGS from summer 1999 to fall 2001 for research and then removed because of NPS restrictions. Data were recorded hourly. The station had some missing data as a result of power problems, so we report only indicators here.) Lee Ridge had a mean August temperature of 14.2°, definitely lower than the 16.9° recorded 20 km to the southwest at Babb (1310 m) where the long term average is 15.4° (Western Regional Climate Center, 2004). Babb has a mean frost free summer period of 68 days, while Lee Ridge had 31 and 64 days over the two full summers of record. Average hourly wind speed recorded on Lee Ridge for the entire period was 16 km/hr.

Lee Ridge is similar to many of the convex uplands just east of the Continental Divide in the northern Rocky Mountains from Wyoming to southern Alberta.

Fig. 3. Snow accumulates in the tree islands and fingers and their immediate lee, but is blown clear on the tundra so that the total precipitation available for plant growth is spatially limited; Lee Ridge, Glacier National Park, Montana. Photo courtesy of Karen Holzer, USGS, March 2002.

Although the slope aspect is northwesterly, the slope is relatively dry. Much of the precipitation as snow blows clear of the ridge except where held by patches of krummholz and small trees (Fig. 3; Christine Geddes, graduate student, and Daniel Brown, associate professor, School of Natural Resources and Environment, University of Michigan, pers. comm., July 9, 2003). The findings here may not be generally applicable to this region, because our sample is on this one ridge, which we find has an unusual combination of species; we do not expect the limiting factors to have the same weights as in other climatic situations.

Field Methods

Within the tree to tundra transition zone of Lee Ridge, an area of 1200 × 150 m, we located ten 50 × 50 m quadrats using randomly selected UTM coordinates and navigating to these points using GPS. With this point as a center, we ran two perpendicular transects along the cardinal directions. We carefully examined every 1/4 m^2 of the quadrat and recorded each tree by species and diameter at base. We recorded the location of individual trees to the nearest 0.5 m on the transects; trees found in tree islands or fingers were not individually recorded, but these patches were mapped and inventoried. Each 0.25 m^2 was mapped as tree or tundra. Because of the erosional surface and thin tundra cover, we believe that we were able to locate all individuals in our quadrats. Seedlings on the order of >5 yrs. age

should be readily visible given our methods and we also did not find dead seedlings. The sample necessarily reflects individuals that survived.

Most of the quadrats were dominated by lodgepole pine (*Pinus contorta* var. *latifolia*), as is the nearby forest, but subalpine fir (*Abies lasiocarpa*), Engelmann spruce (*Picea engelman*), and whitebark pine (*Pinus albicaulis*) were also present. Whitebark pine was found on exposed sites, usually at the windward edge of tree islands.

We estimated dates of tree establishment from tree rings counted on increment cores and basal disks. We took increment cores from every tree greater than 3.5 cm in diameter at the base, with the exception of trees that were found in larger patches. In these, the area was divided into 5-m sections, the trees were grouped into three size classes based on basal diameter, and one core was taken from each size class in each section. For trees that were less than 3.5 cm in diameter, we sampled 33 basal disks. The number of tree rings is not equal to the age of the tree, but we cored at the lowest possible point on the trees; because of the erosional nature of the surface, our coring point was close to where the seedling first emerged from the ground. We collected 339 cores and disks. We processed the samples by standard dendrochronological procedures (Stokes and Smiley, 1968). We did not measure ring widths, and we did not cross date the samples as a result of the young age of the trees and the inherent problems in cross dating alpine treeline samples (Colenutt and Luckman, 1995). We counted the rings in each sample twice and accepted the highest count as the age of the tree. For those cores that did not contain pith, we geometrically estimated the number of missing rings (Applequist, 1958).

Analysis

We linearly regressed the number of rings on the diameter for the samples within species. We used these regression equations to calculate an age for trees not cored. The temporal pattern of establishment must be used with caution for four reasons. First, we were unable to cross date the rings; missing or double rings may occur, but within 50 yrs. they are probably few (Matthew Bekker, assistant professor, Department of Geography, Brigham Young University, pers. comm., July 18, 2003; Greg Pederson, Ph.D. candidate, Department of Land Resources and Environmental Sciences, Montana State University, pers. comm., July 14, 2003). Second, we do not know the interval between germination and our ring counts; given that we cored or cut at the base, it is likely that the interval is less than 5 yrs. Third, for some samples we made a geometric correction; given the variability in growth rates for seedlings in this environment, error is introduced. Fourth, we used all of the trees observed on the plots by calculating an age based on diameter through regression so that we would not misrepresent young individuals too small to core. Given these limitations, we can interpret only general patterns, but this is the resolution we need; most importantly, we are not correlating to any specific year or short interval. A measure of contagion as a percentage of the maximum value possible (Li and Reynolds, 1993) was calculated from the tree-tundra maps.

Table 1. Regression of Number of Tree-Rings on Diameter Used to Extend the Sample to All Trees

Species total trees	Regression equation[a]	R^2	Trees cored	Coefficient standard error	p
Abies lasiocarpa, 306	$y = 10.20 + 5.34x$	.26	9	3.60	.1907
Picea engelmanii, 420	$y = 23.59 + 1.90x$	.19	55	0.54	.0010
Pinus albicaulis, 597	$y = 12.51 + 3.22x$	.53	50	0.44	<.0001
Pinus contorta, 881	$y = 14.09 + 2.34x$	.46	229	0.17	<.0001

[a]y = age, x = basal diameter.

RESULTS

Because of the low number of trees sampled and consequent high standard error (Table 1) we excluded subalpine fir from further analyses. The tree ring data collected for this study showed that 90% of the trees found at treeline have established within the last 40 yrs. (Fig. 4). The calculations show only eight trees in the range greater than 100 yrs. These data suggest that recent seedling establishment has recently occurred on Lee Ridge. They contrast with older reports of minimal recent seedling establishment above treeline in the Rocky Mountains (Billings, 1969; Butler et al., 1994) but are more similar to some recent studies (Hattenschwiler and Smith, 1999; Germino et al., 2002). However, the decline in establishment after 1980 differs here.

Establishment and survival began in the 1930s, increased during the 1940s and ended during the 1980s. The latter part of this period coincides with the negative phase of the PDO (Fig. 1). The establishment began prior to the negative phase and persisted through short positive periods within it. Given that our quadrats were located at the leading edge of the ecotone, it is possible that the establishment represents part of a longer-term establishment that we would have captured had we sampled additional down-slope quadrats where a continuous advance since the end of the Little Ice Age might be found. The observed steep decline in establishment following the end of the negative phase of the PDO, however, tends to support the connection between the PDO and tree establishment and survival. By contrast, a Spearman correlation coefficient ($r = .056$) between seedling establishment and mean PDO from 1940 to present in the 5-yr. intervals shown in Figure 4 indicates that no direct relationship exists.

The maps of tree-tundra cells indicate clumping (contagion: mean = .716; standard deviation = .189); although though is no standard test for the significance of contagion, O'Neill et al. (1999) reported that a random arrangement has a contagion of about .58 and an aggregated distribution has a contagion of about .70 (from their Fig. 2 for two cover types). Using those numbers and the standard deviation, a t-test shows our aggregation to be nonrandom ($p < .01$).
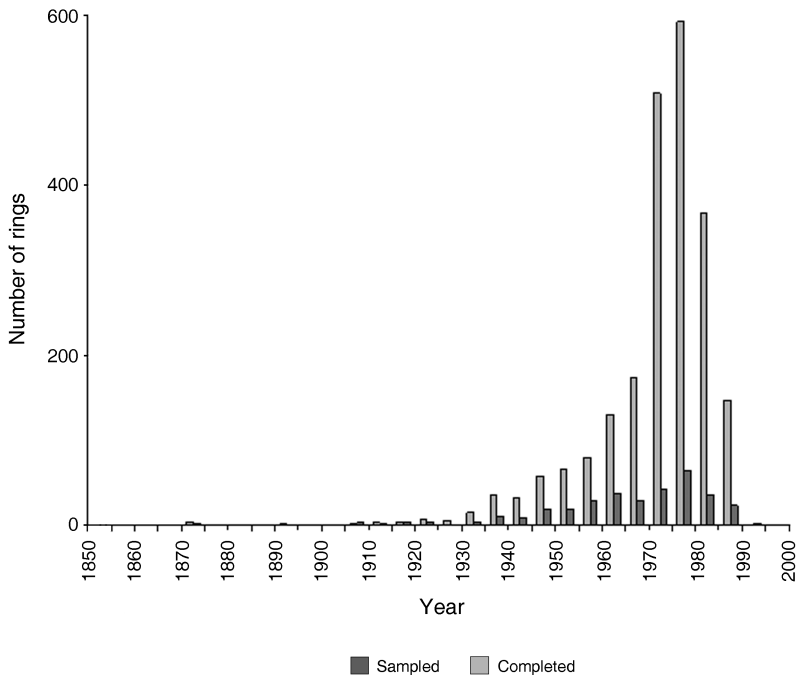
Fig. 4. The number of trees established. The sampled data are the ring-counts of the trees cored or cut; the computed values are from age-diameter regressions of the sample used to calculate an age for all of the trees in the study. *Abies lasiocarpa* is excluded as a result of the small number sampled and the high standard error. The counts are grouped into 5-yr. intervals.

DISCUSSION

Treeline advance in Glacier National Park is not directly influenced by the PDO. The PDO index is rather uniform across the period, and does not show a rise to a peak and sudden drop after 1980 as do the tree ring data—thus the low correlation. We interpret the temporal establishment pattern to be indicative of a positive feedback, also supported by the spatial aggregated spatial pattern.

Positive feedback is likely to have an effect on establishment and survival in patches or tree islands at high, exposed sites (e.g., Smith et al., 2003). Reports of recent establishment also show that seedlings tend to establish near extant trees (Daly and Shankman, 1985; Hattenschwiler and Smith, 1999; Erschbamer et al., 2001; Germino et al., 2002). Once the climate becomes more favorable to establishment and survival, the actual rate of establishment accelerates as established trees modify their surroundings and improve the conditions for continued establishment. Thus, once the conditions for establishment become even slightly favorable, the rate will begin to increase through time; when the basic conditions are no longer favorable, the positive feedback is unable to maintain the process. Because we are able to observe only one full cycle of the PDO in our data period and our

dates are not precise, our results should be taken as a newly generated hypothesis rather than a conclusion.

Where PDO and tree growth have been shown to be associated, the sign differs depending on situation. Peterson and Peterson (2001) and Peterson et al. (2002) reported that growth responses of mountain hemlock (*Tsuga mertensiana*) and subalpine fir at cold limited sites were negatively impacted by snow depth associated with the cool phase of the PDO while lower, drier sites had a positive response. Thus the effect is likely to operate through snow accumulation, which is affected by the plants themselves in a positive feedback. Patches of trees hold snow, and open areas melt out and dry out earlier in the summer. This is a key hypothesized positive feedback for alpine treeline (Walker et al., 1993; Lloyd, 1997). Snow-shrub interactions in the Arctic indicate other positive associations such as warmer winter soil temperatures leading to increased nutrient availability (Sturm et al., 2001). Because windswept tundra is a dry environment, new tree seedling establishment could be dependent on increased snow. Other feedbacks probably also operate, but snow emerges as an important factor. The negative phase of the PDO has been linked to increased snow in the region of Glacier National Park (Selkowitz et al., 2002).

The positive association of establishment and survival with snowfall appears to contradict some earlier studies, and our results may be particular to relatively dry sites, often east of the continental divide in this region. Earlier studies of meadow invasion (e.g., Franklin et al., 1971; Agee and Smith, 1984; Butler, 1986; Rochefort and Peterson, 1996; Moir et al., 1999), even if close to treeline, probably are not comparable. Even at slightly lower elevations in Glacier National Park increased snow is likely to reduce conifer seedling establishment in subalpine meadows, where snow deposition shortens the growing season, although the associated ribbon forest pattern is created initially by geomorphic differences, not by feedback as suggested by Billings (1969; Butler et al., 2003). The difference hinges upon what wind does with snow in the two settings. In subalpine meadows, snow accumulates in the meadows in the lee of trees. At the limits of tree growth, wind scours snow from tundra, leaving snow banks within small tree and krummholz patches. Some treeline studies that have reported advances during drier climates may also be focusing on evidence from less extreme sites where more trees are able to fill the spaces between the real pioneers.

In both meadow and extreme tundra environments, spatial variation may reverse the effect of snow at a fine scale. On Lee Ridge, conditions that favor establishment in the open, within patches, or near them may differ. Within-patches desiccation should be decreased because of reduced wind, while snow depth may reduce the length of the growing season. Establishment near a patch, but not in one, may be favored by increased snow.

Moreover, the setting in which trees established will have changed during the course of the past century. The initial trees in the current patches would have been established in more open settings, as some recent trees are doing. This spatial variation can be seen as part of a hierarchy of scale effects (Reiners and Lang, 1979; Walker et al., 1993).

The multiplicity of exogenous factors and the nonlinearity introduced by endogenous factors make problematic the interpretation of alpine treelines as indicators

of climatic change (Kupfer and Cairns, 1996; Malanson, 1999, 2001; Lloyd et al., 2002; Cairns and Waldron, 2003). To the extent that our tree ring data can resolve a decadal scale, however, a treeline can show definitive responses to climatic variability. The recent treeline advance coincided with the recent negative phase of the PDO, during which Glacier National Park tended to experience increased snow pack (Selkowitz et al, 2002) that may in turn have provided needed soil moisture (Lloyd, 1997). Even when the PDO index becomes positive, either for a short period as around 1960 or for a longer cycle as in 1977, positive feedback may help sustain establishment or seedling survival. The effect of a climatic oscillation such as the PDO must be added to other potential teleconnections, such as ENSO, in order to assess their effects on the interpretation of human-caused climatic change. What may have looked like global-change driven establishment and survival on Lee Ridge during the negative phase of the PDO now looks like a temporary pulse within the post–Little Ice Age environment. It may yet be, however, that the PDO and ENSO will be modifiers or multipliers of a global phenomenon. Detection of annual scale advances will require more careful analysis of the spatial variation in microclimates.

We can speculate that treeline advances in response to future climatic change will show pulses associated with climate oscillations. While the results here are specific to eastern GNP, the speculations have implications throughout the interior western United States in that snow and moisture probably play a role, even if that role varies, in all alpine treeline locations in the region. This work is germane to the National Park Service Inventory and Monitoring Program (National Park Service, 2004). Managers should be concerned that significant changes may be occurring, but their temporal variability needs to be accounted for in the design of monitoring programs.

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