Date: January 28, 2010
Re: Final Report for RWO 81 Rocky Mountain Ungulates
To: CA Cooperative Research Unit
Attn: Kay Brisby, ASC
From: Erik S. Jules, Department of Biological Sciences, Humboldt State University

The following is a manuscript that is in preparation for submission the journal *Plant Ecology*. The paper represents the final report for this project. The paper is co-authored with our USGS collaborator Matthew Kauffman.

FINAL REPORT

RWO 81

Quantifying the influence of climate change on Rocky Mountain ungulate populations, migration and feedground use, and herbivory impacts on vegetation.

The relationship of climate and growth of quaking aspen (*Populus tremuloides*) in

Yellowstone National Park

Erik S. Jules[1], Allyson L. Carroll[1], and Matthew J. Kauffman[2]

[1]Department of Biological Sciences, Humboldt State University, Arcata, CA 95521, USA.

[2]US Geological Survey, Wyoming Cooperative Fish and Wildlife Research Unit, Zoology and

Physiology Department, University of Wyoming, Laramie, WY, 82071, USA.

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Abstract [<u>limit = 250 words</u>]

Quaking aspen is a widespread tree that is in decline across wide areas of western North America, and is predicted to experience a large range shift if future climate predictions are realized. The purpose of our study was to determine what climate factors have influenced aspen growth in Yellowstone National Park, USA, and to determine whether these climatic influences vary across a heterogeneous landscape. We extracted increment cores from 10-12 aspen in each of 16 stands spread across a 1,526 km^2 area. Using ring widths, we created a182-year standardized chronology from 1821 to 2003 A.D. composed of 151 series. We then assessed correlations of growth using instrumental records of temperature, precipitation, and the Palmer Drought Severity Index (PDSI) from 1932 to 2002, and records of maximum snow depth from 1949 to 2002. We found positive relationships between growth and springtime maximum snow depth, and negative relationships between growth and temperature and moisture stress (PDSI). Aspen were impacted by these factors from the previous growing season, suggesting a lag effect of climate. Variation in sensitivity to temperature and PDSI among our stands could not be explained by landscape variables, but sensitivity to the prior March maximum snow depth was greater at high elevations and on shallower slopes. High snow depth probably produces a long-lived water source at the beginning of the growing season. Our study demonstrates that aspen respond to variation in moisture related factors, and that changes in aspen growth due to future climate shifts will vary across small scales.

Introduction

  Quaking aspen (*Populus tremuloides* Michx.) is the most widespread of all North American tree taxa. Its range extends broadly from the permafrost boundary of Canada and Alaska southward to several disjunct, high-elevation sites in Mexico (Little 1971). In many ecosystems in which it is found, most especially conifer-dominated forest, sagebrush communities and grasslands of western North America, aspen are the only broadleaf deciduous tree (Mueggler 1985). While aspen often cover relatively small portions of these landscapes, several studies indicate that aspen stands contain disproportionally high levels of taxonomic diversity (e.g., Stohlgren et al. 1997, Chong et al. 2001). Aspen stands host a broad assemblage of herbivorous and predatory insects (Jones et al. 1985, Sheppard et al. 2006), provide habitat for numerous vertebrate species (Shepperd et al. 2006), and are an important winter food for ungulates (Debyle 1985). Because many of these functions are not provided by other plants, ecologists and managers alike consider aspen a critical resource.

  Declines of aspen health and abundance have been noted in several regions across North America (Shields and Bockheim 1981, Kay and Bartos 2000, White et al. 1998, Sheppard et al. 2006). Large-scale losses, including dramatic, rapid losses of aspen have been observed in some areas (Frey et al. 2004, Worral et al. 2008), while in other regions the decline has been gradual and often patchily distributed across the landscape (e.g., Bartos and Campbell 1998, Suzuki et al. 1999, Hogg et al. 2005, Brown et al. 2006). The cause of aspen declines are often unclear, and they differ between regions. For instance, the sudden dieback of aspen noticed during just the past decade in, for example, western Canada and southwestern Colorado, appears to be a combination of drought, insect damage, and damage to buds and roots by thaw-freeze events (Frey et al. 2004, Worral et al. 2008). In contrast, intense herbivory by elk and conifer

encroachment appear to be the most important factor leading to a continual decay of aspen stands in parts of the northern Rockies (Romme et al. 1995, Ripple and Larsen 2000).

In addition, the distribution and abundance of aspen is forecasted to shift considerably if predicted levels of future climate warming are realized. The range of aspen is generally considered to be limited by low temperatures near the permafrost boundary in the north and by dry conditions in the south (Chen et al. 2002), and thus climate warming scenarios suggest large range contractions of aspen in southern portions of its range. For instance, Iverson and Prasad (2001) modeled the predicted distribution of 80 common trees species in the eastern deciduous forest of the United States based on their current distribution and five different scenarios of future climate change resulting from a doubling of carbon dioxide in the atmosphere. The average reduction in aspen cover predicted by the five models was >90% (see also Iverson and Prasad 1998, Hansen et al. 2001). Similar, though less dramatic predictions for aspen have been made for British Columbia (Hamann and Wang 2006; see also Leonelli et al. 2008). Other models of vegetation change under climate warming scenarios have suggested large-scale changes in tree distribution in places where aspen is considered an important vegetation type. For instance, Bartlein et al. (1997) described changes that are predicted in Yellowstone National Park (YNP) in the northern Rockies under conditions of doubling atmospheric CO_2 levels, which include, for example, significant declines of whiteback pine (*Pinus albicaulis*) and Engleman's spruce (*Picea engelmannii*), and increases in ponderosa pine (*Pinus ponderosa*) and *Thuja plicata* (western red cedar). Within YNP, aspen occur mainly in small, isolated stands surrounded by xeric shrub and grassland communities, or by conifer forest (citation). These aspen stands are presumably restricted by the presence of relatively high soil moisture resulting from seeps and springs or from topography that restricts drainage (citation). While the general

expected trend is for expansion of aspen forests along the permafrost boundary of Canada and Alaska, and contraction in the south, the expectation of shifts within smaller, intermediate regions, such as YNP, are less clear.

Understanding how particular taxa will respond to future climate changes will be enhanced by estimates of how those species have responded to past climatic fluctuations for which precise instrumental records are available. In particular, long-lived trees can provide useful models of plant-climate relationships, since their annual growth rings are often strongly correlated with records of, for instance, precipitation and temperature that have been measured for several decades or more (e.g., Douglass 1920, Graumlich, 1987, Carroll and Jules 2005). Climate responses, however, are not uniform across the range of any species (e.g., Abrams 1998, Brooks et al. 1998, Leonelli et al. 2008), and thus studies that characterize the spatial variation in responses can be particularly useful for predicting regions and/or habitats where the greatest change is likely to occur during periods of rapid climate change. The study we present here was intended to answer three questions. First, how sensitive is aspen growth to interannual differences in climatic factors? Second, how variable is that sensitivity across a relatively small, but heterogeneous landscape? Third, can the variation in sensitivity observed across our study landscape be attributed to any site variables, such as elevation, slope, aspect, and site productivity? To answer these questions, we studied 16 separate aspen population in YNP and compared their annual growth rings to instrumental records of temperature, precipitation, and snowpack starting in the 1930s. We use this information to discuss the types of environments in which future climate changes may result in the greatest impacts on aspen growth.

Methods

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Study area

We studied aspen-climate relationships on the Northern Range of YNP, a mid elevation (1,500–2,000 m), xeric landscape with a mix of grassland, shrub, and conifer habitat. The area receives approximately 25 cm of annual precipitation. To identify aspen stands, we divided the 1,526 km^2 Northern Range into four strata of approximately equal area and located four randomly selected points per stratum. The nearest aspen stand to each point that contained a minimum of 15 adult aspen was identified. In summer 2004, we extracted two increment cores per tree from a random sample of 10-12 large trees (> 6 cm DBH) per stand in each of the 16 stands. We recorded slope, elevation, and aspect for each stand. Aspect poses a unique problem for assessing relationships in that values of 0.0˚ are similar to seemingly large values, such as 350˚. Thus, we transformed our observed aspect (*A*) using the formula given by Beers et al. (1966), where the transformed value (*A'*) = cosine(45-*A*)+1. Here, warm, dry aspects are given low numbers, while cool, wet sites are given large values. We used a GIS to measure openness (see Boyce et al. 2003), where openness was estimated for each stand as the sum of non-forested cells within a 500 x 500 m moving window centered on each grid cell (range 0 [deep forest] − 289 [open grassland]).

Tree Ring Analysis

The increment cores were mounted and sanded at the lab using standard dendrochronological methods (Stokes and Smiley 1968). Cores were measured to 0.001 mm precision using a Velmex measuring system (TA 4030H1-S6 Unislide, Bloomfield, New York). The ring series were cross-dated using visual techniques identifying marker years and patterns

and verified with the quality control program COFECHA (Holmes 1983). Series were omitted if they showed significant physical damage or could not be confidently cross-dated. The cores were initially cross-dated within individual stands and, then, proved to hold a common pattern among the entire study area.

Ring width measurements were standardized and chronologies developed using the ARSTAN method (Cook 1985; Cook and Kairiukstis 1990). Given the abundant number of cross-dated series (222 series from 166 trees from 16 stands), we selected the most appropriate series for the final chronology. Criteria for inclusion of a series were: (1) one core per tree, (2) time span of series, and (3) cross-dating strength. This resulted in 151 series from 151 trees. Standard detrending options were used in ARSTAN. Specifically, negative exponential curves or linear regressions were fit to the raw ring width data to remove trends due to age or stand dynamics. Visual confirmation using the interactive detrending option was employed to ensure appropriate fits. Chronologies were then created for each of the 16 stands separately using the same detrending options, with each stand having between 8 and 12 series. The residual chronology was chosen for the analysis of interannual climate response (Allyson -- citation). Rbar and expressed population signal (EPS) were used to describe the chronology quality. Rbar is independent of sample size and represents the mean correlation of all the growth series (Briffa 1995). EPS is a function of rbar and sample size and has a recommended cutoff for chronology confidence of 0.85 (Wigley et al. 1984).

Climate Data

Historical climate data was acquired from the National Climatic Data Center (NCDC) and the climate variables used were monthly mean temperature (MNTM), total monthly

precipitation (TPCP), total monthly snowfall (TSNW), and maximum snow depth (MXSD) for the month. The Tower Falls station within YNP (44°55'N / 110°25'W; elevation 1909.9 m) was selected because of its centrality among the 16 stands. For Palmer Drought Severity Index (PDSI) we used Wyoming Climate Division 01 (Yellowstone Drainage). PDSI is a standardized measure of soil moisture availability or drought conditions (Palmer 1965).

Climate Response Analysis

We assessed the relationship between annual aspen growth and climate using Pearson's correlation coefficients (r). A 20-month climate window from the prior-January to current August was used because annual ring growth can be influenced by climate from prior year(s) (Fritz 1976). Correlations were run for the period 1932 to 2002 for all climate variables except MXSD which had a period of 1949 to 2002. Correlations were not computed for months with only 0.0 values, such as July TSNW and July and Aug MXSD. Correlations of aspen growth and climate were calculated first using the full chronology. This analysis revealed three climate factors that showed a significant relationship with aspen growth (prior June temperature, prior July PDSI, and prior March MXSD; see *Results*), and we limited all subsequent analyses to these three factors. We then determined a second set of correlation coefficients (r) in which we compared growth and the three climate factors for each of the 16 populations separately. The resulting r values reflect to what degree trees respond to climate changes and thus were used as a measure of the "sensitivity" ("sensitivity index" from here on) of each aspen stand (e.g., Leonelli et al. 2008).

To assess how sensitivity to climate might vary across a the landscape, we tested for relationships between the sensitivity indices (r) and stand characteristics (slope, elevation,

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aspect, and openness) using multiple regression. Because site productivity may also influence

sensitivity of tree growth to climate factors (Leonelli et al. 2008), we calculated the annual Basal

Area Increment (BAI) for all trees, and then calculated the mean BAI among individuals for each

of the last 50 years of the series (1953-2003) for each stand. This mean BAI was included as an

explanatory variable in our multiple regression. We also assessed BAI to ensure that it was

independent of stand age (estimated using the oldest tree age) or average age of trees within the

stand using regression.

Results

We created a 182-year standardized chronology for YNP aspen on the Northern Range

from 1821 to 2003 A.D. composed of 151 series from 151 trees and 16 stands (Fig. 1). The

series intercorrelation was 0.547 and the average mean sensitivity was 0.282. While cross-dating

was confident throughout the chronology, sample size dropped below 50 series before 1880 (Fig.

1). Using the common period of 1880 to 2003, the chronology statistics were strong with rbar of

0.250 and EPS of 0.932 (Table 1). The 16 separate chronologies for the natural stand included

an average of 9.4 series (trees) per stand (min. = 7, max. 12) and spanned an average of 132

years. These stands had rbars ranging from 0.146 to 0.557 and EPSs ranging from 0.722 to

0.932 (Table 1).

Standardized aspen growth over the period 1932-2002 (70 years) recorded in the master

chronology was significantly negatively correlated with temperature during the previous

summer, most especially June temperatures (r = -0.419, Fig. 2). In addition, growth during the

period 1949-2002 (53 years) was strongly positively correlated with MXSD in spring.

Correlations were significant both for the March at the beginning of the growing season (r =

0.277), and the previous March ($r = 0.345$). No significant correlations were found between aspen growth and precipitation (Fig. 2). Lastly, aspen growth was positively correlated with PDSI in the previous growing season, with the strongest correlation found during July ($r = 0.336$, Fig. 2). A high PDSI value indicates higher levels of soil moisture. The correlations of aspen growth with June temperatures and MXSD in the previous March were the strongest correlations we found between aspen growth and climatic factors.

When analyzed separately from one another, the 16 stands showed variation in the degree to which their growth was correlated with climatic factors (i.e., their sensitivities), some of which could be explained by site characteristics associated with individual stands. Multiple regression showed that none of the site factors nor BAI explained variation in sensitivity indices for prior June temperature or prior July PDSI. However, aspen were more sensitive to prior March MXSD at higher elevations ($t = 0.0002$, d.f. $= 15$, $P = 0.089$) and on shallow slopes ($t = -0.0069$, d.f. $= 15$, $P = 0.054$). Our measure of stand productivity (BAI) was independent of stand age; average BAI was not related to either stand age (regression using age of oldest tree; $R^2 = 0.068$, d.f. $= 15$, $P = 0.329$) or average age of individuals within each stand ($R^2 = 0.007$, d.f. $= 15$, $P = 0.758$). None of the variables we used in our multiple regression were correlated with one another, except for slope and BAI; productivity was higher on shallow slopes ($r = -0.501$, $P = 0.048$).

Discussion

We found strong correlations of aspen growth on the Northern Range of YNP with several climatic factors, including temperature, snow depth, and the PDSI drought index. Aspen grew more when the previous summer was cooler and experienced relatively low drought stress

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(Fig. 2). In addition, aspen grew better when there was greater maximum snow depth (MXSD) in both the spring of the current growing season and the previous growing season (Fig. 2). The three factors that influenced aspen the most (specifically, prior June temperature, prior July PDSI, and prior March MXSD) show significant covariance; for example, July PDSI shows a modest positive relationship with March MXSD ($r = 0.247$, $P = 0.105$) and a modest negative relationship with June temperature ($r = -0.245$, $P = 0.110$). Thus, these climate factors are unlikely to act independently in influencing aspen growth. Our study also demonstrates that the degree to which aspen are sensitive to these climatic factors varies between sites within YNP and appears to be governed by the elevation and slope of the site.

That all three of the important factors influencing aspen growth in our study were of the previous growing season is in accordance with other studies of aspen (Hogg et al. 2005, Leonelli et al. 2009), as well as studies of other tree taxa (Peterson and Peterson 2001, Allyson – insert 2-3 references). For example, Leonelli et al. (2009) found that aspen growth was positively correlated with precipitation and negatively correlated with both temperature and the Canadian Drought Code (CDC) during the previous growing season. This relationship, as Leonelli et al. (2009) note, most likely suggests that aspen growth depends heavily on stored reserves (found in branches, stems, and roots), and/or that years with optimal climates produce wood vessels that are still active during the subsequent year. In either case, it appears that the best predictor of aspen growth is the moisture and temperature regimes found the year before a particular growing season. The role of snow depth was not assessed by Leonelli et al. (2009), and Hogg et al. (2005) found no relationship of snow depth and aspen growth, though our study suggests it may play an important role for many aspen stands. Higher snow depth in the spring months is likely to result in a longer-lasting source of water during the early part of the growing season. On the

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other hand, higher snow depth may delay how quickly soils reach a temperature high enough for roots to become active. Our study indicates the positive effects of snow depth outweigh any negative effects for aspen growth.

While our 16 stands varied in how sensitive there were to climate variation, only one sensitivity index (that of March MXSD) could be explained by any of the site factors that we measured. Sites at higher elevations responded more to interannual changes in snow depth, as did sites that were on shallower slopes (Fig. 3). Because the elevations and slopes of our stands were not correlated, it appears these two factors both influenced climate sensitivity. Stand productivity, as measured by BAI, was not related to the sensitivity index for snow depth when we included it in our multiple regression ($t = 0.0007$, d.f. $= 15$, $P = 0.622$). We acknowledge that our site variables probably influence site productivity, so including BAI in our multiple regression may be redundant. Nonetheless, removing BAI from the regression does not produce qualitatively different results. Additionally, simple linear regression of the sensitivity index on BAI alone shows a weak positive relationship ($R^2 = 0.152$, d.f. $= 15$, $P = 0.135$). This finding is similar to that found by Leonelli et al. (2009), however they found a much stronger, positive relationship between productivity and climate sensitivity.

The increase in sensitivity to interannual variation in snow depth at higher elevations and on shallower slopes may be the result of patterns of snow accumulation. Aspen stands found on shallow slopes may experience greater accumulations of snow due to the protective nature, and thus reduced wind speed, of their topographic position (M.J.K, personal observation). Likewise, higher elevation sites should retain their snow longer into spring, when snow appears to have the greatest impact on aspen (Fig. 2). More snow pack in spring should allow individual aspen to maintain low moisture stress longer into the growing season and so respond more strongly than

at other sites. Thus, our finding of a strong correlation between the MXSD sensitivity index and site factors is likely a result of significant variation in snow depth among sites, rather than a direct impact of the site factor. Because we do not have separate estimates of snow pack for each of the 16 aspen stands, we cannot test this hypothesis directly.

Our work confirms what previous authors have suggested (Leonelli et al. 2009): that aspen stands vary in their sensitivity to climate change. In addition, our work demonstrates that this variation can occur across small spatial scales. Leonelli et al. (2009) studied 15 aspen stands that spanned across several 100 km of British Columbia, and Hogg et al. (2005) studied 72 stands across >1500 km of the western interior of Canada. In contrast, our 16 sites were found within a relatively small 1,526 km^2 area. This suggests that the way aspen will respond to future climate changes will be variable, even within small regions like the Northern Range of YNP.

Models of future climate suggest that YNP will experience higher summer and winter temperatures, greater winter precipitation, and slightly less summer precipitation (Bartlein et al. 1997). Greater winter precipitation may result in higher snowpack in spring, while higher summertime temperatures may lower PDSI (i.e., increase moisture stress). While speculative, our work suggests that these climate changes may have different, and contrasting, effects on aspen growth in YNP. Higher snowpacks should increase aspen growth, especially in stands found at high elevation or on gentle slopes. Higher summertime temperatures should lead to reduced aspen growth, and this impact may be experienced more uniformly across the landscape. Our work, however, cannot dissect which climate changes will have the greatest influence on aspen.

Lastly, our chronology of aspen growth reveals an interesting and marked reduction in growth in 1989. This year experienced the least growth of any year in our chronology (tree ring

index = 0.235; Figure 1). None of our climate factors provides an easy explanation for this observation. The 1988 June temperatures were normal and, while the 1988 July PDSI was low, PDSI had been low from 1983 until 1987 though only 1989 produced such small tree rings. March MXSD in 1988 was less than half the average snowpack since 1948, but similar snowpacks have not produced the same reduction in growth. We posit that the observed reduction in aspen growth is the result of the large fires that burned across ~400,000 hectares in YNP in 1988 (Despain et al. 1989). Our aspen stands were not burned during the fire, though fires burned extensively the areas surrounding our stands. The marked reduction we observed the following year is likely a result of damage and/or reduced growth from smoke that occurred during 1988, reducing the energy stored that would facilitate 1989 growth. Alternatively, the fires may have been a cue for adult aspen to shift energy allocation toward sexual reproduction the following year. Aspen reproduce more frequently by asexual ramet production than by seeds, yet large numbers of seedlings were found in YNP in 1989 (Romme et al. 2005). These seedlings presumably came from seeds produced prior to 1989, and they do not explain the reduction we found. Nonetheless, 21% of the aspen that Romme et al. (2005) found in burned areas had germinated in 1990 and were found many kilometers from the nearest adult aspen.

Conclusions

Quaking aspen is strongly influenced by climatic factors for which we have precise instrumental records. In particular, the aspen of YNP appear to be most influenced by moisture and moisture stress, and the best predictor of growth is the climate regime in the year prior to growth. In addition, the sensitivity of aspen to climate is not uniform across the landscape. Instead, aspen stands at higher elevations and on flatter slopes will respond more to changes in

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climate. Future changes in aspen productivity that may result from global climate change are expected to be variable, even across small areas.

Acknowledgements

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Table 1. Summary statistics and landscape variables for the Yellowstone Northern Range aspen chronology. Data for the full chronology uses all trees sampled from the sixteen natural study stands. See text for details on landscape and chronology variables.

Site	First year of chronology	Last year of chronology	Chronology length (yrs)	No. of trees (series)	rbar (between trees)	EPS	Slope (°)	Openness	Elevation (m)	Aspect (°)
FULL	1821	2003	182	150	0.250	0.932				
YC1	1875	2003	128	12	0.146	0.894	5.59	288.31	2056.13	123.83
YC3	1872	2003	131	8	0.457	0.855	11.23	288.90	1807.93	84.42
YC4	1894	2003	109	10	0.404	0.844	7.81	289.00	2259.78	49.76
YC5	1884	2003	119	8	0.374	0.807	20.57	124.09	2344.23	220.05
YD1	1869	2003	134	9	0.385	0.814	15.46	151.98	1864.27	241.74
YD3	1865	2003	138	9	0.447	0.879	9.14	162.17	2237.74	223.56
YD4	1900	2003	103	9	0.545	0.878	11.38	151.38	2268.33	259.01
YD5	1834	2003	169	10	0.302	0.796	4.96	108.83	2020.04	52.71
YE3	1847	2003	156	9	0.448	0.867	13.23	109.51	2051.21	320.32
YE4	1853	2003	150	7	0.337	0.780	5.23	265.87	2016.29	51.13
YE6	1821	2003	182	12	0.434	0.874	7.00	200.44	2242.94	161.32
YE7	1899	2003	104	10	0.382	0.861	6.31	156.32	1927.97	318.48
YF1	1875	2003	128	10	0.391	0.865	14.94	232.93	2142.37	148.69
YF3	1861	2003	142	8	0.255	0.732	8.72	81.89	2117.62	160.94
YF4	1900	2003	103	9	0.342	0.722	1.31	196.50	2013.33	195.95
YF5	1874	2003	129	10	0.557	0.919	8.90	52.64	2095.02	110.92

Fig. 1. Aspen standardized tree-ring chronology from 1821 to 2003 for the Northern Range, Yellowstone National Park, USA. The chronology is standardized around the mean of 1.0.

Fig. 2. Pearson correlation coefficients (r) between tree-ring width index and (A) mean monthly temperature (MNTM), (B) monthly mean temperature (MNTM), (C) maximum monthly snow depth (MXSD), and (D) the Palmer Drought Severity Index (PDSI). See text for details on climate data. The horizontal line indicates critical r values ($\alpha = 0.05$), which is 0.235 for all but MXSD ($r = 0.279$).

Fig. 3 The relationship of elevation (A) and slope (B) with climate sensitivities for 16 aspen stands. Climate sensitivities shown are correlation coefficients (r) between aspen growth and March maximum snow depth (MXSD).
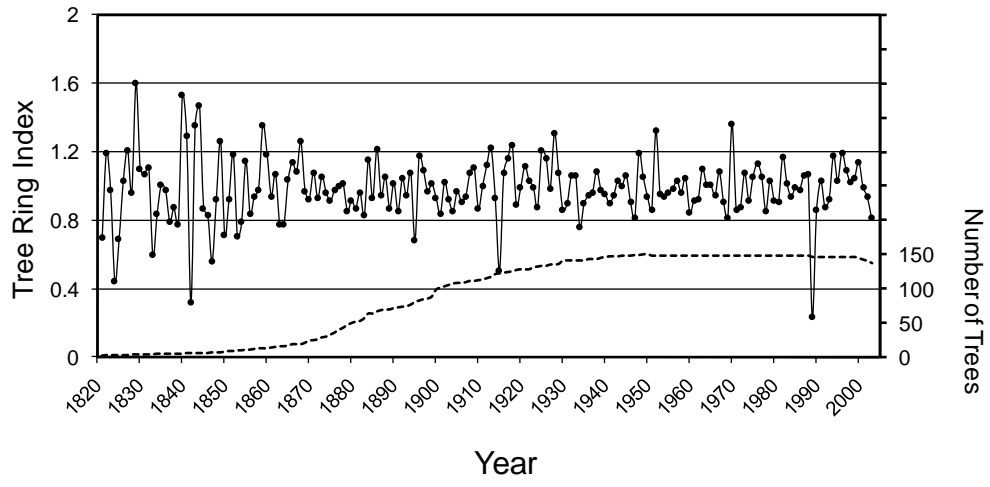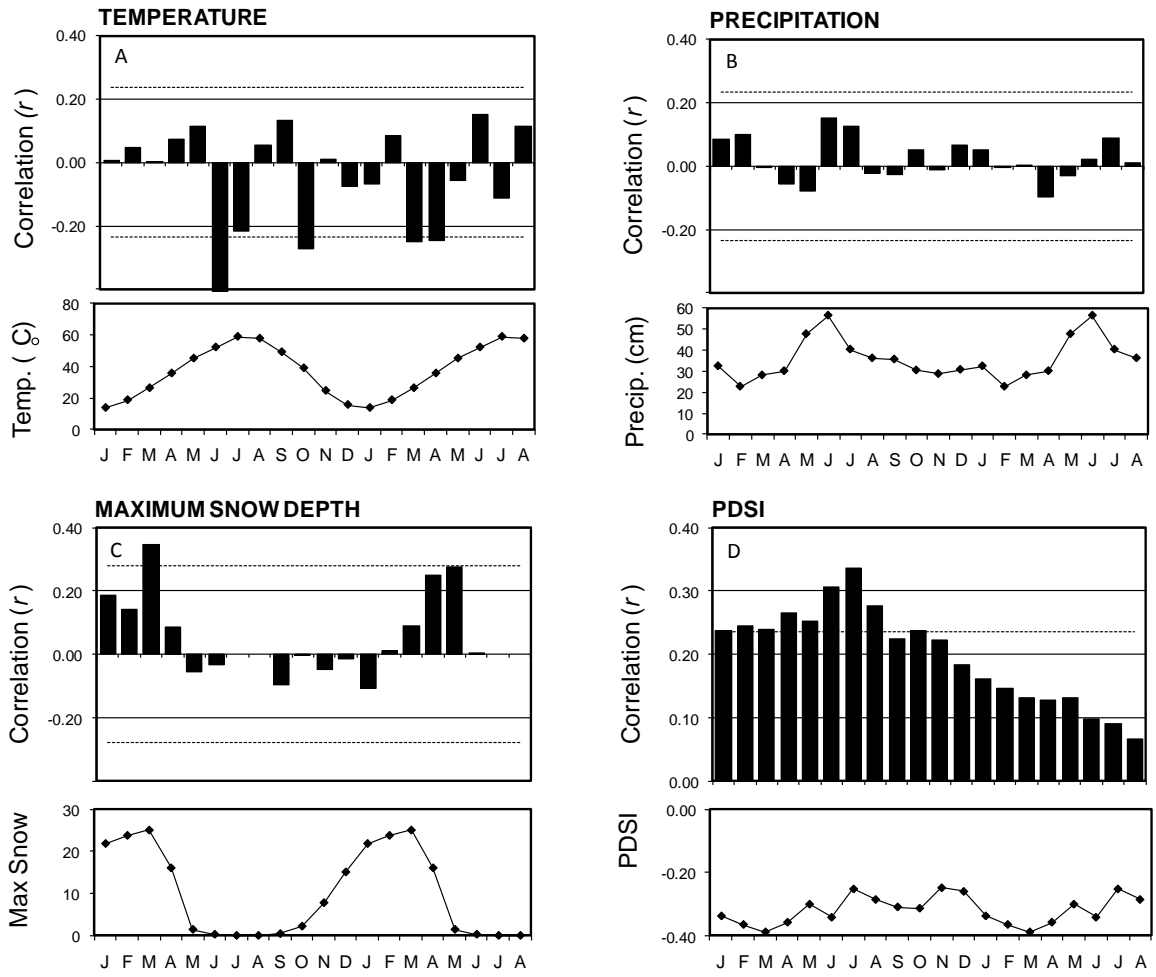
Figure 1

Figure 2

TEMPERATURE

PRECIPITATION

MAXIMUM SNOW DEPTH

PDSI

Figure 3