

RESEARCH
PAPER



Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada, USA

Andrew G. Bunn*, Lindsey A. Waggoner and Lisa J. Graumlich

The Big Sky Institute, Montana State University,
PO Box 173490, 106 AJM Johnson Hall,
Bozeman, MT 59717–3490, USA

ABSTRACT

Aim Climate variability is an important mediating agent of ecosystem dynamics in cold, semi-arid regions such as the mountains of western North America. Climatologically sensitive tree-ring chronologies offer a means of assessing the impact of climate variability on tree growth across temporal scales of years to centuries and spatial scales of metres to subcontinents. Our goal was to bring practices from landscape ecology that highlight the impact of landscape heterogeneity on ecological pattern and processes into a dendroclimatic study that shows that the biophysical setting of target trees affects ring-width patterns.

Location This study was conducted at two sites near alpine treeline in the Sequoia National Park, USA (36°30′ 00′ N, 118°30′ 00′ W).

Methods We collected stand information and increment cores from foxtail pines (*Pinus balfouriana* Grev. et Balf.) for eight tree-ring chronologies in four extreme biophysical settings at two sites using proxies for soil moisture and radiation derived from a digital elevation model.

Results Biophysical setting affected forest age-class structure, with wet and bright plots showing high recruitment after 1900 AD, but had no obvious effect on immature stem density (e.g. seedlings). Biophysical setting strongly affected ring-width patterns, with wet plots having higher correlation with instrumental temperature records while dry plots correlated better with instrumental precipitation records. Ring-width chronologies from the wet plots showed strong low-frequency variability (i.e. hundreds of years) while ring-width chronologies from the dry plots showed strong variability on multidecadal scales.

Main conclusions There was a strong association between biophysical setting and age-class structure, and with ring-width patterns in foxtail pine. The mediation of ring widths by biophysical setting has the potential to further the understanding of the expression of synoptic-scale climate across rugged terrain. When combined with remotely sensed imagery, *a priori* GIS modelling of tree growth offers a viable means to devise first-order predictions of climatic impacts in subalpine forest dynamics and to develop flexible and powerful monitoring schemes.

Keywords

Biophysical setting, climate variability, dendrochronology, foxtail pine, landscape ecology, North America, *Pinus balfouriana*, potential relative radiation (PRR), topographic convergence index (TCI).

*Correspondence: The Woods Hole
Research Centre, PO Box 296; Woods Hole,
MA 02543–0296, USA.
E-mail: abunn@whrc.org

INTRODUCTION

Observational and palaeoclimatological studies of the earth's climate indicate that the Northern Hemisphere warmed sub-

stantially during the twentieth century (Mann *et al.*, 1998, 1999; IPCC, 2001). The impact of changes in precipitation on ecosystems during the 20th century remains less certain (Walsh *et al.*, 1998; Kattsov & Walsh, 2000; IPCC, 2001). It is evident, however,

that precipitation mediates forest dynamics, not only in deserts but also in cold, semiarid environments (Barber *et al.*, 2000). Given the impact of slowly evolving ocean–atmosphere interactions in controlling precipitation at decadal and longer time scales (Latif & Barnett, 1994; Mantua *et al.*, 1997; Minobe, 1999; Zhang *et al.*, 1997; Bond & Harrison, 2000), there is a clear need to develop long-term (i.e. multicentury) ecological records that can disaggregate the interactions between temperature and precipitation controls on ecosystem processes. Interest in disentangling the role of temperature and precipitation on forest dynamics is also driven by questions that arise in tracking the carbon cycle as evidence accumulates that twentieth century carbon accumulation in dry montane forests has profound implications for local to global carbon calculations (Schimel *et al.*, 2002).

The focus of this work is subalpine forests at treeline, the boundary between forest and tundra on high mountains. Alpine and arctic ecosystems are often presented as critical ecosystems for detecting and characterizing climate change (Billings & Bliss, 1959; Walker *et al.*, 1993, 1994; Henry & Molau, 1997; Graumlich *et al.*, 2004). The alpine treeline is a particularly rich system in which to investigate long-term dynamics because of the abundance of high-resolution palaeoecological records. Tree-ring chronologies, of up to several thousand years, associated with subalpine forest, particularly in western North America, are widespread spatially, climatically sensitive, and annually resolved (Graumlich *et al.*, 2004). While tree growth at alpine treelines is primarily temperature limited (Wardle, 1971, 1974), precipitation plays a strong role in controlling tree growth, recruitment, and mortality at alpine treelines in the Sierra Nevada (Lloyd & Graumlich, 1997; Bunn *et al.* 2005). Changes in temperature and the length of the growing season, in concert with precipitation variability, are predicted to have a substantial impact on tree growth and forest structure in high elevation forests (Scuderi, 1993; Cairns, 1998; McKenzie *et al.*, 2004). Furthermore, tree ring-width chronologies from long-lived conifers at or near alpine treelines in western North America have greatly informed our understanding of natural and anthropogenic climate change over the last millennium (LaMarche, 1974; Scuderi, 1993; Mann *et al.*, 1998, 1999; Crowley, 2000).

In this paper we focused on the biophysical setting as a mediating agent of subalpine forest structure. Although growth in alpine trees is generally limited by climate, which makes the trees good recorders of past climate (Graumlich *et al.*, 2004), there is no body of literature that incorporates the effect of biophysical setting at the scale of relatively small plots (< 1 ha) in determining treeline forest structure, ring-width patterns, and subsequent climate inference in western North America. A notable exception is Villalba *et al.* (1994), who showed the importance of topography in understanding species-specific response to climate in the Colorado Front Range.

Foxtail pine (*Pinus balfouriana* Grev. et Balf.) presents a rare opportunity to understand the effects of rugged topography on growth and recruitment because it inhabits a very narrow geographical area where it typically grows in monospecific stands occupying a severely cold climatic niche. Foxtail pine is

an uncommon tree that occurs in two disjunct areas: one in the Sierra Nevada near Sequoia National Park, and another about 500 km to the north in the Klamath mountains (Mastroguiseppe & Mastroguiseppe, 1980). Foxtail pine is known from the early Pleistocene (Bailey, 1970), and inhabits a very narrow biogeographical niche near alpine treeline where growth and reproduction are ostensibly limited by growing season temperature.

We hypothesized that the biophysical setting of the landscape ameliorates forest structure and annual growth (i.e. tree ring) pattern in two sites in the southern range of foxtail pine. We examined the impact of associations of proxies for soil moisture (topographic convergence) and solar radiation (potential relative radiation) with age class, seedling recruitment, and ring-width patterns in foxtail pine forests at two closely located sites. This study allowed us to demonstrate the impact of topography in growth and recruitment. We further hypothesized that trees in especially dry locations might exhibit water stress, which reduces tree growth and reproduction, and affects demography. This study provides a glimpse into the spatial heterogeneity of treeline forests in the Sierra Nevada and shows the need to account for biophysical setting in mediating tree growth and forest age class, as well as demonstrating methods to wed *a priori* geographical information system (GIS) modelling to sampling schemes, and monitoring protocols. Finally, we show how biophysical setting might be used as a primary variable in future process modelling efforts as a way of detecting and understanding vegetation dynamics.

METHODS

With elevations above 3000 m a.s.l. and slope gradients routinely in excess of 20%, the treeline ecotone of the eastern Sierra Nevada crest is both remote and extremely rugged. Given the difficulties of logistics and expense involved in transporting personnel and equipment to these back country field sites, we partitioned the treeline ecosystem in Sequoia National Park into manageable study units using GIS models (Urban, 2000). These models were based on topographic features most likely to influence tree growth – radiation and soil moisture – and allowed the sampling of eight plots at two sites to be done over the course of the summer field season in 2001 and provided data in disparate biophysical settings.

Study area and site selection

The study was conducted on the eastern crest of the Sierra Nevada in the Sequoia National Park at the alpine treeline (elev. c. 3300 m a.s.l.). Two study areas dominated by foxtail pine were chosen in the vicinity of Rock Creek and Mt. Tyndall (Fig. 1). This area is well known for extensive palaeoecological research that has demonstrated the dynamic nature of the foxtail pine ecotone with climate variability (Lloyd & Graumlich, 1997). The Rock Creek and Mt. Tyndall sites are similar in having abrupt treelines comprised of monospecific stands of foxtail pine with many ancient trees suitable for making palaeoclimate inference.

The regional distribution of subalpine forests is variable with trees absent from cooler microsites, some valley bottoms, and

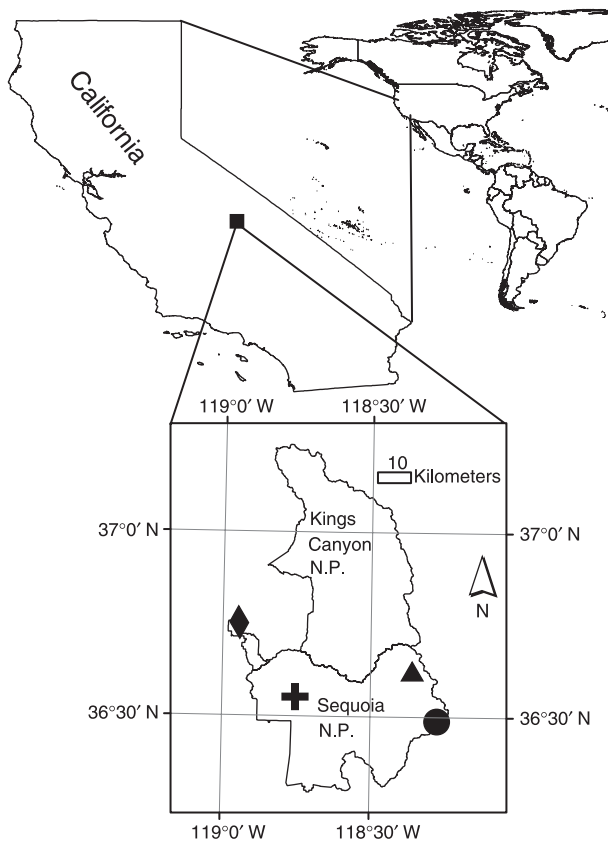


Figure 1 Study areas in Sequoia and Kings Canyon National Parks, California, USA are shown with a circle (Rock Creek) and a triangle (Mt. Tyndall). Weather stations used for climate-growth correlations are shown with a cross (Giant Forest) and a diamond (Grant Grove).

extremely steep slopes. Foxtail pine does not grow in a dwarfed krummholz form and therefore treeline tends to be an abrupt transition from forest to non-forest. Foxtail pine is an extremely long-lived species (a 1200-year-old specimen was found in this study) and the pattern of its annual growth rings has been found to be sensitive to both temperature and precipitation. Accordingly, this species has been used in numerous palaeoclimatic reconstructions and palaeoecological studies (Scuderi, 1987, 1993; Graumlich, 1991, 1993; Caprio & Baisan, 1992; Lloyd & Graumlich, 1997; Bunn *et al.* 2005).

Plot selection

A 10-m digital elevation model (DEM) was obtained from the National Park Service for Sequoia National Park (<http://www.nps.gov/gis>). Spurious sinks were filled to remove data anomalies using standard GIS procedures (Jenson & Domingue, 1988) in ArcInfo 8.2 (ESRI, 2002). A topographic convergence index (TCI) and a potential relative radiation index (PRR) were calculated from the DEM. TCI is a function of the upslope contributing area and the local slope, and measures the tendency of water to collect on the landscape (Moore *et al.*, 1991; Urban *et al.*, 2000; Bunn *et al.*, 2003). The index has high values in coves or streambeds, and lower values on drained areas such as ridge

tops. The PRR index uses measurements of the sun position over the course of a year and the hill-shading function common to most GIS packages to measure the relative amount of sunlight that a particular raster element received given the shading that its neighbourhood provided (Bunn *et al.*, 2003; Pierce *et al.* in press).

The top and bottom quartile for each index was calculated. Combining them pairwise resulted in 10-m cells that have high radiation and high convergence (HR/HC), high radiation and low convergence (HR/LC), low radiation and high convergence (LR/HC), or low radiation and low convergence (LR/LC). A map was produced of these cells and overlaid onto colour infrared digital orthophotos (with 1-m pixels) where treeline was easily discernable. The Rock Creek (3300 m a.s.l.) and Mt. Tyndall (3390 m a.s.l.) areas were chosen because of previous dendroclimatological research done in the area (Graumlich, 1991, 1993; Lloyd & Graumlich, 1997) and proximity to trail heads (c.10 km and 25 km, respectively). Study plots were randomly placed within the domain of possible plots (HR/HC, HR/LC, LR/HC, and LR/LC) using this map and the global positioning system. Four plots of 90 m by 90 m were chosen at each site of treelines that were HR/HC, HR/LC, LR/HC, and LR/LC. Plots were divided into nine, 30 m by 30 m subplots to facilitate data collection and analyses.

Forest demographic and time series data

Every stem was tallied in each of the eight plots (four plots at two sites) to allow for direct comparison of stem density across biophysical setting. All smaller stems were tallied, and for the purposes of this study, stems with diameters < 2 cm at breast height were designated as immature stems. An increment core was taken at breast height for trees with diameters at breast height (d.b.h. = 1.37 m) > 2 cm to explore the temporal pattern of stem establishment as well as climate-growth relationships. Cores were taken at breast height because of the logistical difficulties of coring ancient trees at ground level. Therefore, in subsequent age-class analysis we have used age-height regressions developed in nearby stands of foxtail pines (Lloyd, 1996) and have corrected the pith dates to germination dates. Cores were taken parallel to the slope contour to minimize the effects of slope pressure on wood formation. Although these forests are almost entirely foxtail pine stands, a small proportion (< 10%) of the trees on the plots were either lodgepole pine (*Pinus contorta* Dougl. ex Loud) or whitebark pine (*Pinus albicaulis* Engelm.). These trees tended to be at the lowest elevations within the plots. There was no relationship between species composition and plot type and the small proportion of these trees precluded dendrochronological analysis. They were therefore omitted from all analyses.

The cores were mounted, sanded, and measured using standard dendrochronological procedures (Stokes & Smiley, 1968). Samples were cross-dated using the program COFECHA (Holmes, 1983) and through visual examination of the rings to assign an exact calendar date to each ring. Existing foxtail pine chronologies developed at nearby sites were used to cross-date each chronology (Bunn *et al.* 2005). The chronologies were created by standardizing ring-width measurements by fitting

negative exponential curves or horizontal lines to the ring-width measurements. We used deterministic negative exponential curve standardization (NECS) in preference to stochastic standardization methods such as smoothing splines because NECS is an appropriate standardization method to use for preserving systematic signals in tree-ring series at these frequencies (Bunn *et al.* 2004). We also wished to avoid *ad hoc* model selection between series from different biophysical settings and risk filtering out information important to our study (Cook & Kairiukstis, 1990). Finally, these foxtail pine stands are robust indicators of climate signals and tend not to record stand dynamic events that might bias deterministic detrending (Lloyd, 1996). The standardized ring-width indices were then averaged to obtain mean chronologies at each plot (Fritts, 1976). Only series greater than one hundred years in length were included in the eight chronologies. All the chronologies were truncated at 1400 AD, which is where two of the plots reached a minimum reliable sample depth of five cores.

To study climate–growth associations, monthly temperature and precipitation measurements from 1927 to 2000 were obtained by updating the composite data used by Graumlich (1993) from Giant Forest (1927–68, 36°34' N, 118°46' W, 1940 m a.s.l.) and Grant Grove (1944–2000, 36°46' N, 118°58' W, 2005 m a.s.l.). We created two seasonal variables: summer temperature (mean June–August) and growing year precipitation (total of prior September–current August). These variables have been effective in capturing the climate–growth relationship of foxtail pine and are discussed by Lloyd (1996). Because all of the chronologies had highly significant first-order autocorrelation, climate–growth analyses were conducted for the calendar year prior to the growing season (i.e. a lag of one year). We used Pearson's product-moment correlation coefficients to describe the relationship between tree growth and climate by using a subset of the chronologies for the period of instrumental climate (1927–2000).

The temporal variance structure of the chronologies was evaluated with wavelet analysis. Wavelets are versatile tools of harmonic analysis that partition time series data into frequency components and then characterize the variance in each component with a resolution matched to its scale. Wavelets have advantages over traditional signal detection methods (e.g. Fourier and spectral analyses) in analysing data where the signal contains sharp spikes (Torrence & Compo, 1998). We performed a continuous wavelet transformation of the tree-ring chronologies using the non-orthogonal Morlet wavelet. The Morlet wavelet has been used successfully with tree-ring data to detect periodic patterns that might be driven by climate oscillations (Gray *et al.*, 2003;

Bunn *et al.* 2004). Transformations were done in the statistical software package R (Ihaka & Gentleman, 1996) with the R-wave contributed package (Carmona *et al.*, 1998; Carmona & Whitcher, 2002). Peaks in the wavelet power spectra were tested against a red-noise background assumption (a univariate lag-1 autoregressive AR [1] model of 0.70) using the methods of Torrence & Compo (1998). The hypothesis underlying the analysis was that peaks in the tree-ring wavelet power spectra that were significantly above the background spectrum were true features (Torrence & Compo, 1998 provide an excellent primer on wavelet analysis for time series).

RESULTS

The temporal pattern of stem recruitment, as reflected in the age–class structure of the plots, varied between sites and with biophysical setting (Table 1, Fig. 2). The bright and wet plots (HR/HC) showed a higher proportion of successful recruitment events after 1900 that was significantly greater than proportions generated using a bootstrapped uniform age–class distribution ($P \leq 0.0001$). The dark and dry plots (LR/LC), conversely, showed the lowest proportion of recruitment events after 1900: again this was significantly less than proportions generated using a bootstrapped uniform age–class distribution ($P = 0.0047$ and $P = 0.0437$ for Rock Creek and Mt. Tyndall, respectively). The higher proportion of successful recruitment events after 1900 in the bright and wet plots (HR/HC) suggested that the biophysical setting of these plots was favourable to tree establishment in the twentieth century.

The dark and dry plots (LR/LC) had fewer stems than the other plots (Fig. 2). The number of adult stems in the other biophysical settings varied and the number of immature stems per ha did not show a similar pattern between sites (Table 2). For instance, one of the dark (LR) plots at each site showed over 200 seedlings per ha while the dark and wet plot (LR/HC) at Rock Creek had only 27 seedlings per ha. The error associated with the immature stem data is large relative to the number of observations. The lack of obvious differences in the immature stems data, as well as the number of stems, surprised us and we discuss possible sampling bias or scaling issues below.

The common signal of the chronologies as described by three standard chronological statistics (i.e. mean interseries correlation, mean chronology sensitivity, and mean series autocorrelation) were similar at the eight plots and did not show obvious patterns by either site (Rock Creek vs. Mt. Tyndall) nor biophysical setting

	Percentage of stems recruited after 1900 AD	
	Rock Creek	Mt. Tyndall
Bright, wet (HR/HC)	59% ($n = 64$) $P < 0.0001$	56% ($n = 55$) $P < 0.0001$
Bright, dry (HR/LC)	10% ($n = 72$) NS	22% ($n = 69$) NS
Dark, wet (LR/HC)	12% ($n = 41$) NS	17% ($n = 48$) NS
Dark, dry (LR/LC)	6% ($n = 63$) $P = 0.0047$	10% ($n = 78$) $P = 0.0434$

Table 1 The percentage of stems successfully recruited after 1900 is greatest in the bright and wet plots (HR/HC) and lowest in the dark and dry plots (LR/LC). This pattern is evident in both sites and significantly different from a random expectation using 10,000 bootstrapped replications of a random age-class distribution (compare with Fig. 2)

Figure 2 The age-class structure of foxtail pine for all eight plots shows similarities between sites by biophysical setting. The leftmost portion of each bar represents the approximate germination date for each stem on the plot with a d.b.h. of > 2 cm. The most obvious similarity is between the high radiation and high convergence sites, which each show a high proportion of stems successfully recruited after 1900 AD. The low radiation and low convergence site has the lowest proportion of recruitment after 1900 AD (compare with Table 1).

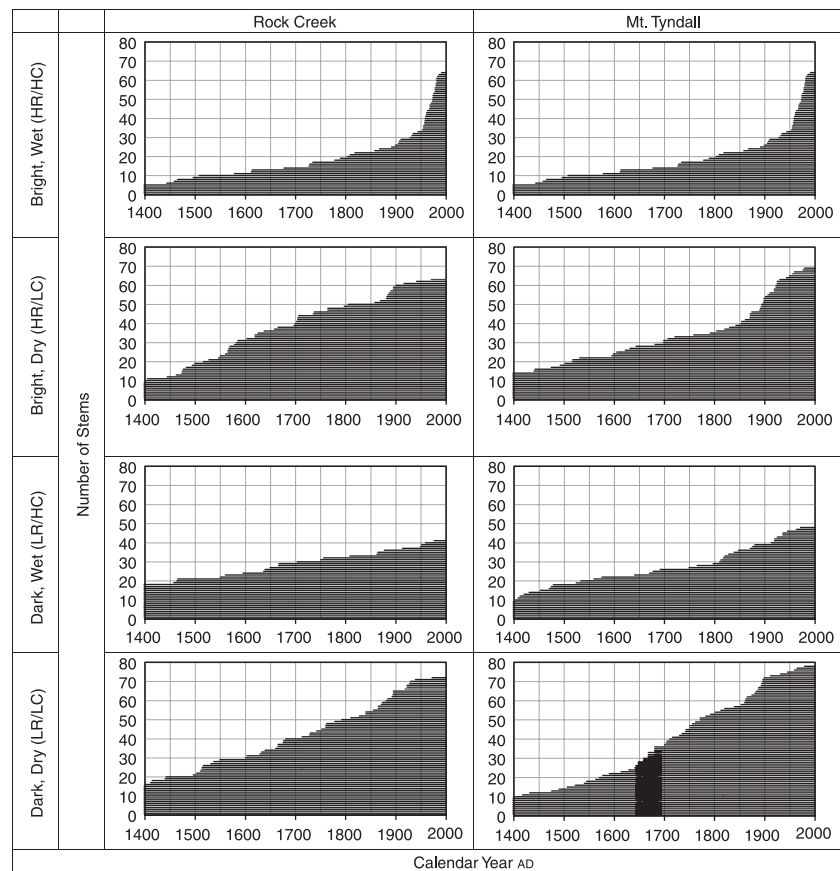


Table 2 Variability in the number of immature stems (d.b.h. < 2 cm) per ha. The number of stems does not show similarity within or between sites. One standard error of the sample, calculated from the 9 subplots, is shown in parentheses

	Immature stems per ha	
	Rock Creek	Mt. Tyndall
Bright, wet (HR/HC)	67 (20)	78 (16)
Bright, dry (HR/LC)	65 (70)	42 (15)
Dark, wet (LR/HC)	27 (20)	241 (51)
Dark, dry (LR/LC)	289 (61)	102 (46)

(Table 3). The differences between plots were reflected in their correlations with instrumental climate records (Table 4). Specifically, the ring widths at the wet plots (HC) had stronger correlations with temperature relative to the dry plots (LC) while the dry plots (LC) had stronger correlations with precipitation than did the wet plots (HC). These differences are slight but illustrated by the rank of the correlations by plot type (Table 4) and the annual tree-growth patterns, as reflected in the chronologies, showed obvious visual patterns of within site variability and between site similarities that might reflect topographic mediation of synoptic-scale climate forcings (Fig. 3). The bright and wet plot (HR/HC) at Rock Creek, for instance, showed strong low-frequency variation and suppressed growth from 1600 to

Table 3 The mean correlation between each series and the mean sensitivity (the relative change in ring width from one year to the next) does not show similar patterns between sites

		Mean inter-series correlation	Mean sensitivity	Mean autocorrelation
Rock Creek	Bright, wet (HR/HC)	0.620	0.211	0.681
	Bright, dry (HR/LC)	0.630	0.221	0.726
	Dark, wet (LR/HC)	0.666	0.188	0.759
	Dark, dry (LR/LC)	0.662	0.216	0.728
Mt. Tyndall	Bright, wet (HR/HC)	0.608	0.234	0.714
	Bright, dry (HR/LC)	0.701	0.283	0.620
	Dark, wet (LR/HC)	0.643	0.217	0.700
	Dark, dry (LR/LC)	0.632	0.213	0.671

Table 4 Pearson product moment correlations between the tree ring-width chronologies and instrumental climate records from Sequoia National Park (1927–2000) show similarity within and between sites. Temperature is mean previous summer temperature (June through August), and precipitation is the total precipitation from the previous year (September through August). Plot rank shows the relative order of the correlation by plot type

		Temperature	Plot rank	Precipitation	Plot rank
Rock Creek	Bright, wet (HR/HC)	0.326	1	0.334	4
	Bright, dry (HR/LC)	0.208	4	0.534	2
	Dark, wet (LR/HC)	0.311	2	0.480	3
	Dark, dry (LR/LC)	0.254	3	0.552	1
Mt. Tyndall	Bright, wet (HR/HC)	0.480	1	0.440	4
	Bright, dry (HR/LC)	0.238	3	0.564	2
	Dark, wet (LR/HC)	0.359	2	0.503	3
	Dark, dry (LR/LC)	0.190	4	0.602	1

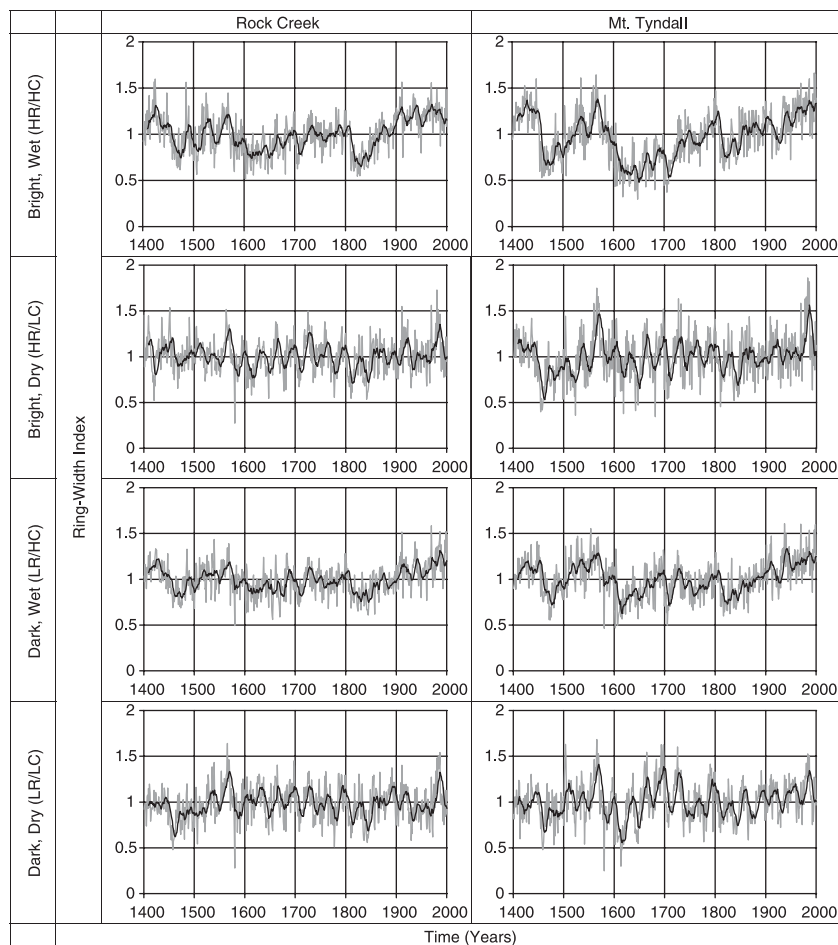


Figure 3 Four tree-ring chronologies from different physical settings (rows) are shown for each of two sites (columns). The x axis is marked in years and the y axis is tree growth shown as a dimensionless ring-width index. The grey line is the raw data and the thick black line shows a 10-year running average. All chronologies run 1400 AD to 2000 AD. Marked differences among the chronologies by biophysical setting are clearly visible. For instance, the bright and wet plots (HR/HC) (top) have different modes of temporal variation than the dark and dry plots (LR/LC) (bottom), and the wet plots (HC) show increased contemporary growth that is characteristic of many temperature-sensitive tree-ring chronologies.

1700 AD as compared to the dark and dry plot (LR/LC) (Fig. 3). There was a similar pattern for Mt. Tyndall. Only stems greater than 100 years in age were used to build the chronologies and when these (Fig. 3) are compared to the age-class diagrams (Fig. 2), the sample depth for the chronologies can be approximated.

The perspective of topographic mediation of synoptic-scale climate is supported by looking at the frequencies embedded in the time series, which also showed within and between site variability (Fig. 4). All eight plots showed secular (i.e. series length)

and high frequency (i.e. 2–4 years) periodicities. The low convergence plots (HR/LC and LR/LC) showed significant variation at the scale of multiple decades as well as showing more high frequency variability. We interpret the dominance of high and medium frequency variability in the dry plots to be an expression of precipitation variability. These periodicities were statistically significant ($P \leq 0.05$) as compared to a red-noise background suggesting that they are reflecting topographic mediation of synoptic-scale climate forcings.

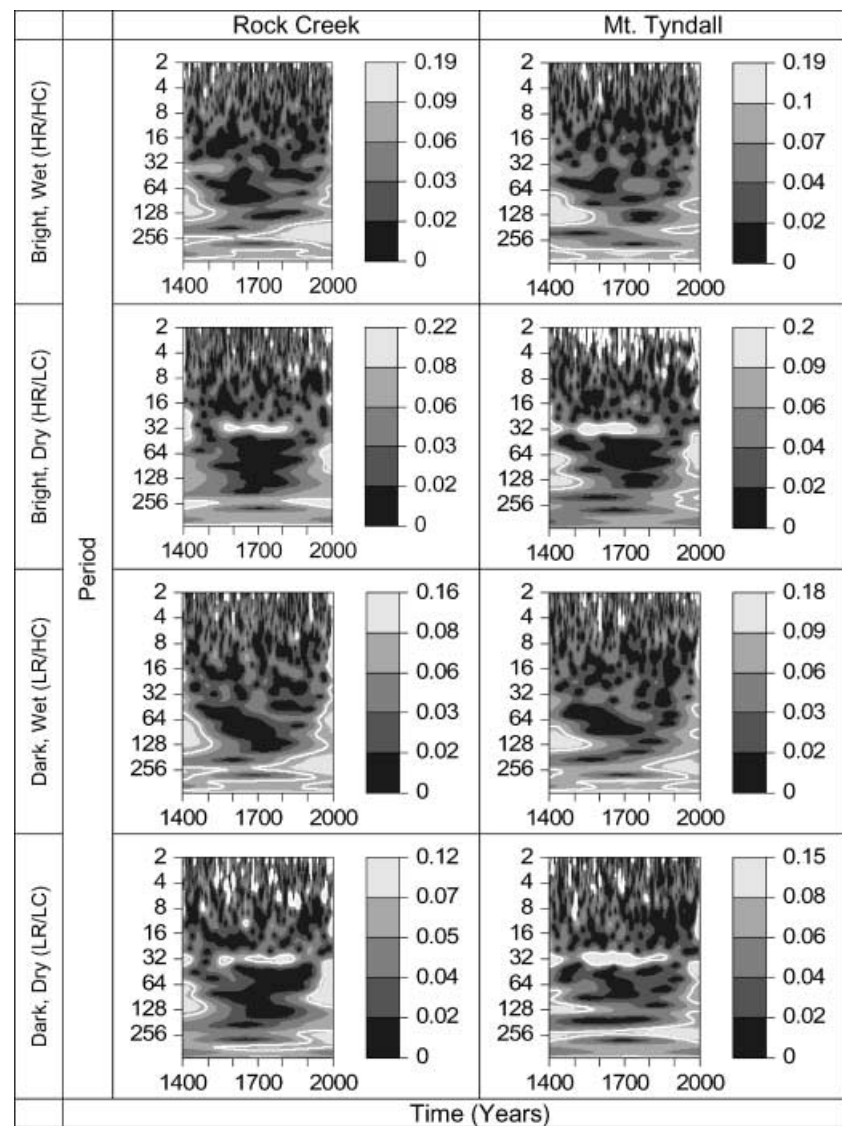


Figure 4 Continuous wavelet power spectra density estimates for each of the eight chronologies are shown and allow the variance of each time series to be studied as a function of the frequency of the variation. Time is on the *x* axis in years, and period (inverse frequency) is shown in years on the *y* axis. From dark to light the greyscale contour intervals show 0–25%, 25–50%, 50–75%, 75–95%, and 95–100% of the wavelet power measured as ring-width index squared — thereby capturing periods of high and low growth. The white contour encloses a 95% confidence interval using a red-noise background spectrum. Important peaks in power occur at similar wavelengths in sites depending on physical setting. Especially interesting are the decadal signals in the dry plots (LC). It is also interesting that the Mt. Tyndall site shows higher overall power (in ring widths) than the Rock Creek site.

DISCUSSION

Our study comprised four types of biophysical setting at two sites similar in forest composition and structure near the alpine treeline in the Sierra Nevada. The expense of collecting and analysing the data in this study was substantial. We would need many more replicates to make strong statistical inference about the consistency of the patterns we noticed among and between sites. Although we were unable to make strong deductive inference about these results because of the low sample size, we are gratified to see similar qualitative and quantitative patterns between and within the sites, which are discussed below.

This study showed that the age–class structure and the climate–growth association in approximately one hectare stands of foxtail pine varied with biophysical setting and supports three principles of ecological theory. Palaeoecological research has demonstrated the effect of multiple climate factors on vegetation dynamics at times scales from years to centuries (Brubaker, 1986; Delcourt & Delcourt, 1987; Graumlich, 1993; Lloyd & Fastie,

2002). Similarly, gradient analysis (the study of species or ecosystems along continua of physical conditions) has a long and influential history, from Merriam (1898) to the classic studies by Whittaker (1956, 1967), and Peet (1978), and has demonstrated the important role of multiple limiting factors on community development (Urban *et al.*, 2002). Finally, the influence of spatial scale on observed pattern is increasingly well understood (Urban *et al.*, 1987; Levin, 1992; Turner *et al.*, 2001). Our results emphasized these three ecological principles for a single species of tree in the Sierra Nevada, California.

In this study, we attempted to disaggregate two of the most critical abiotic influences on plant growth — soil moisture and radiation — across a rugged alpine landscape. Soil moisture, as represented by topographic convergence, was the most critical variable for modifying fine-scale patterns in climate–growth relations of foxtail pine, while the effect of radiation on tree growth was less clear. Using temperature loggers and soil moisture probes, PRR and TCI predictions can improve estimates of plant-available soil water in mountainous terrain at the scale of

metres (Lookingbill & Urban, 2003, 2004). Soil water supply and demand estimates across environmental gradients in mountains have the ability to account for species distribution at the scale of kilometres (Stephenson, 1990; Urban *et al.*, 2000). We discuss the potential benefits of using the TCI and PRR proxy in ecological sampling and modelling below.

The effect of radiation on vegetation dynamics was most apparent when the age-class structure of the plots was examined (Fig. 2). The higher proportion of successful recruitment events after 1900 in the HC/HR plots suggests that the conditions in these plots have been amenable to tree establishment, as the climate became relatively warmer and wetter after the so-called 'Little Ice Age' (Graumlich, 1991). The opposite might be true of the dark and dry plots (LR/LC), which showed the lowest proportion of successful recruitment events after 1900. We do not know if this pattern is stationary in time, but related work (Lloyd & Graumlich, 1997) has shown the dynamic nature of population processes in these subalpine forests over the last three millennia. The climate niche that allows successful recruitment from immature stem to adult tree is likely found in the HR/HC, which are warmer and wetter than the other plots. Relatively warmer and wetter conditions might promote the establishment of the root system, which is deep and spreading in foxtail pine (Arno, 1973) and allows for a considerable storage effect (Lloyd, 1996; Chesson & Huntley, 1997). Furthermore, total growing season carbon uptake has been found to be strongly correlated with springtime soil moisture in high mountain systems (Schimel *et al.*, 2002), which might result in increased recruitment in the relatively warm and wet climate of the twentieth century.

Identifying the physical niches for different life stages is an important challenge in forest ecology and a necessity when modelling forest dynamics in complex terrain. Unfortunately, in this study, immature stem densities showed no trend with biophysical setting within or between sites (Table 2), which implied that the patterns of recruitment (i.e. high recruitment in the bright and wet plots) seen in the age class of the mature life stages of the trees were not applicable to immature stems at the same scale. It is possible to reconcile this observation with the increased recruitment in the bright and wet plots (HR/HC), if the abundance of microhabitats available for seedling establishment was not captured by this sampling design, which was based on 10-m cells of a DEM. Patterns of seedling distribution at a finer grain, however (using a 0.5 m DEM and a 50 m × 50 m plot), have shown seedling presence/absence to be linked to TCI (Bunn, unpublished data). If our study design did not capture the abundance of microhabitats available for seedling establishment then we are likely seeing a classic scaling issue, where seedlings are more abundant in wet microsites at the scale of the organism (metres), but not more abundant in the wetter biophysical settings at the scale of tens of metres used in this study (Wiens, 1989). Further speculation about scale effects regarding tree growth and establishment is difficult without research that investigates the growth and reproduction niches for different life history stages (seedlings vs. adult trees). For instance, adult trees can withstand interannual periods of poor growing conditions that will be fatal to seedlings.

The combination of temperature and precipitation as controls on alpine treeline growth has been successfully exploited in reconstructing climate variability in the Sierra Nevada (Scuderi, 1987; Caprio & Baisan, 1992; Graumlich, 1993; Scuderi, 1993). The ways in which stands of climate-sensitive trees are selected by analysts are typically *ad hoc* (e.g. searching for the oldest trees) and have not been modelled using the methods above. These results show the importance of considering soil water as well as growing season temperature in a system where tree growth is considered temperature-limited. We found it interesting that the tree-ring chronologies from the different biophysical plots showed such similar qualitative growth patterns within and between sites despite the lack of obvious differentiation by common tree-ring chronology statistics (Table 3).

Our results showed that landscape position influenced tree-ring width in a manner that corresponds with foxtail pine physiology. Specifically, ring-width in the high convergence plots correlated more strongly with temperature while the low convergence plots correlated more strongly with precipitation. Adult foxtail pines are able to maintain photosynthetic activity in an extremely dry environment because they have a deep root system, high tracheid density, and they retain needles for several years, which reduces the need for moisture and nutrients (Mastroguiseppe & Mastroguiseppe, 1980). Given the wide distribution of foxtail pine on the cold and dry eastern crest of the Sequoia National Park, it is interesting that the growth patterns of trees respond to an abiotic proxy for soil moisture. Temperature-induced drought stress on tree growth has been shown in boreal Alaska (Barber *et al.*, 2000) and might be reflected in our data where trees in the wetter parts of the landscape show higher correlations with temperature. The trees in the drier plots might lose the ability to grow in warm temperatures if insufficient soil water leads to drought stress. We are also intrigued by the concept of mountain carbonsheds, where flows of water and air in sloping terrain make it possible to model the accumulation of respired carbon as a function of relief (Schimel *et al.*, 2002). By explicitly modelling tree growth and topography, our results might support the proposal of Schimel *et al.* (2002) of coupling hydrology and carbon exchange to characterize system respiration and ecological patterns.

These correlations with instrumental data from weather stations represent very simplistic climate-growth models. Better fits between the climate data and the ring widths can be built, for instance, by using multiple predictors across seasons, but for the sake of clarity we have chosen to highlight the simplest results. The simplicity of the climate-growth correlations highlights the strong association between topography and tree growth. We expect that it is possible to improve mechanistic understanding of foxtail pine growth using this type of approach by explicitly modelling growth as a function of soil water and temperature. TCI and PRR have been successfully interpolated to soil water (Lookingbill & Urban, 2004) and soil and air temperatures (Lookingbill & Urban, 2003) in rugged terrain using arrays of relatively inexpensive sensors. Moving toward a process-based understanding of foxtail pine growth has strong implications for improving both palaeoclimate reconstructions of growth and global change monitoring efforts using this species.

The wavelet analysis indicated that topographic factors strongly influence the response of foxtail pine to climate variability through time. In our simple presentation of climate–growth relationships, these trees sometimes show lower correlations with temperature than precipitation despite being ultimately limited by temperature (Körner, 1999) (Table 4). This association has been pointed out by Graumlich (1993) and is interesting in light of the results of the wavelet analysis as understanding the frequencies in the different chronologies might yield information about underlying physical mechanisms. In a classic paper, LaMarche (1974) found that lower frequencies dominated the temporal variance of growth with alpine treeline from bristlecone pine (*Pinus longaeva* D.K. Bailey) while higher frequencies were dominant at lower treeline. From correlation analysis of frequency-stratified components of variability, LaMarche determined that the low-frequency variations reflected temperature fluctuations, and the high-frequency fluctuations precipitation variations, and linked the low frequency response to climate to extreme needle longevity in this closely related congener. Graumlich (1993) found that foxtail pine chronologies were attenuated to low frequency temperature variability but that nonfrequency-stratified analysis of growth and temperature yielded low correlations because of the short length of the instrumental record and problems with degrees of freedom. Despite this, the significant wavelet signals in the tree-ring chronologies matched the instrumental climate correlations (e.g. chronologies that correlated well with precipitation showed significant interannual and multidecadal periodicities while the temperature-sensitive chronologies showed strong low frequency signals). This corresponds to the current understanding of climate periodicities.

Oscillatory and quasi-oscillatory modes of climate have been shown on multiple time scales — from interannual events like El Niño, to multidecadal patterns such as the Pacific decadal and North Atlantic oscillations (see review by Wang & Schimel, 2003). The concentration of power in growth in the very low frequencies (corresponding to > 100-year periods) in the wet (HC), temperature-sensitive settings is consistent with the longer oscillatory mode of temperature variability (Jones *et al.*, 1998; Moore *et al.*, 2002). Similarly, the concentration of power in the multidecadal periods seen in the dry, precipitation-sensitive plots (LC) matches current understanding of precipitation variability which is driven by slowly evolving earth–ocean interactions (e.g. Cayan *et al.*, 1998; Dettinger *et al.*, 1998; McCabe & Dettinger, 1999; Biondi *et al.*, 2001; Gedalof & Smith, 2001). The patterns of significant power by plot type were displayed between sites comprised of the same species, removing the potential for observed differences to be related to species-specific responses (e.g. as a function of species-specific physiology). The wavelet power spectra are continuous and allowed for the examination of various periodicities at specific times. The dry plots (LC) show significant multidecadal variability from 1600 to 1800 AD, implying a precipitation regime that switches between persistent (e.g. > 20 years) wet and dry events across both sites during that time. The correlation of precipitation and growth in the dry plots (LC) enhances understanding of the 20-year and 50-year positive precipitation anomalies extracted by Graumlich (1993) at vari-

ous points during that period. Similarly, the dry plots showed a much higher number of long lived El Niño-like events (that last from four to eight years) than do the relatively wetter plots, adding further support for the ability of low convergence tree-ring chronologies to record the temporal modes of precipitation.

There are at least two implications of these results for future process modelling efforts and general understanding of foxtail pine forest dynamics. The first is that *a priori* modelling of the biotic response to biophysical setting is both possible and desirable using simple models of tree biology based on biophysical setting. Physical models, such as the one described here, can be used in sampling design and when designing field efforts to improve data collection that is logistically difficult and expensive (*sensu* Urban, 2000).

The second implication is that the combination of remotely sensed imagery and GIS models can provide greater spatial understanding of biotic indicators of climate variability and stand dynamics over large spatial extents. By classifying IKONOS satellite imagery of the Mt. Tyndall site, for instance, it is possible to locate the lowest density foxtail pine forest (Bunn, 2004; Lawrence *et al.*, 2004). Low-density forests have the strongest climate signal as a result of low turnover and competition (Fritts, 1976). Mapping relative forest density of foxtail pine together with TCI and PRR allows visualization of covariates potentially important for studying subalpine forest dynamics in order to document the population response to climate change and better reconstruct palaeoclimate (Fig. 5). We propose that in this cold and dry climate,

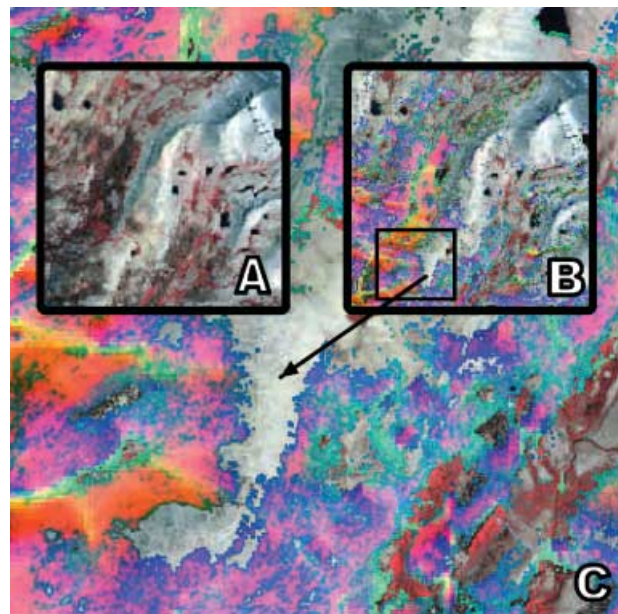


Figure 5 A false-colour composite of tree sensitivity for Mt. Tyndall shows some of the implications of topographic mediation for process modelling. Red colours are tree density derived from classified IKONOS imagery; green colours are TCI; and blue colours are PRR. All variables increase with the intensity of the colour. For instance, lime green pixels are moderately forested, wet (HC), and are average brightness. Panel A shows the raw imagery in a 7.5 km by 7.5 km area. Panel B shows the same area as a false-colour composite, and panel C shows the false-colour composite zoomed in to 2 km by 2 km.

the bright and wet (HR/HC) locales on the landscape show the strongest response to twentieth century forcings and these locations are where change is rapid, significant, and detectable. We further propose that the dark and dry plots (LR/LC) are the places where precipitation forcing is maximally observable for this ecosystem and that multiple plots based on these biophysical settings within a single site are needed to understand issues of global change monitoring at the treeline. Analysis of these data shows that < 1% of this 7.5 km by 7.5 km landscape is in the bottom quartile of tree density, TCI, and PRR. Our results have shown that forest pattern in response to climate processes was not ubiquitous or even, and these are the locations that are likely to be the most sensitive for monitoring precipitation variability. This makes them attractive places, for instance, for instrumentation such as permanent weather stations to help improve understanding of climate–growth relationships.

CONCLUSIONS

Long tree-ring chronologies from treeline forests provide critical data on climate, especially temperature variability. We have shown that there are simple techniques that can tease apart expressed temperature and precipitation signals in foxtail pine treeline forests. Our results showed the importance of considering the biophysical setting, as it related to soil moisture and radiation, of a forest stand and that biophysical setting affected forest age-class structure, ring-width patterns, and subsequent climatic inference, especially for detection of multidecadal and centennial trends. In this (ostensibly) temperature-limited ecosystem, precipitation acted as a mediating agent of forest patterns at the scale of hectares. The *a priori* GIS models we applied in this study have the potential to greatly enhance future climate reconstructions, by disaggregating temperature and precipitation signals, as well as laying a blueprint for monitoring this critical climate change resource. Most importantly, we showed that understanding biophysical impacts on forest growth and structure is useful for looking backward to understand climatic signals in palaeoclimatic records. It might also be of use in looking forward in ecological forecasting of when, where and how climatic variability will affect subalpine forests.

ACKNOWLEDGEMENTS

This work was funded by the Sierra Nevada Global Change Project under UGSG BRD contract CA99WRAG0026 (Graumlich) and the Canon National Parks Science Scholars Program (Bunn). G. Bellante, G. Buppert, C. Caruso, S. Gobbs, S. Hill, B. Peters, and A. Toivola, assisted in collecting or analysing the tree-ring data.

REFERENCES

- Arno, S.F. (1973) *Discovering Sierra trees*. Yosemite Association, Yosemite National Park, CA.
- Bailey, D.K. (1970) Phytogeography and taxonomy for *Pinus* subsection *Balfourianae*. *Annals of the Missouri Botanical Garden*, **57**, 210–249.
- Barber, V.A., Juday, G.P. & Finney, B.P. (2000) Reduced growth of Alaskan white spruce in the twentieth century from temperature-induced drought stress. *Nature*, **405**, 668–673.
- Billings, W.D. & Bliss, L.C. (1959) An alpine snowbank environment and its effects on vegetation, plant development, and productivity. *Ecology*, **40**, 388–397.
- Biondi, F., Cayan, D.R. & Gershunov, A. (2001) North Pacific decadal climate variability since 1661. *Bulletin of the American Meteorology Society*, **14**, 5–9.
- Bond, N.A. & Harrison, D.E. (2000) The Pacific decadal oscillation, air–sea interaction and central north Pacific winter atmospheric regimes. *Geophysical Research Letters*, **27**, 731–734.
- Brubaker, L.B. (1986) Responses of tree populations to climatic change. *Vegetatio*, **67**, 119–130.
- Bunn, A.G. (2004) *Temporal and spatial patterns at alpine treeline in the Sierra Nevada USA: Implications for global change*. PhD Dissertation. Montana State University, Bozeman, MT.
- Bunn, A.G., Graumlich, L.G. & Urban, D.L. (2005) Interpreting the climatic significance of trends in twentieth-century tree growth at high elevations. *The Holocene*, in press.
- Bunn, A.G., Lawrence, R.L., Bellante, G.J., Waggoner, L.A. & Graumlich, L.J. (2003) Spatial variation in distribution and growth patterns of old growth strip-bark pines. *Arctic, Antarctic, and Alpine Research*, **35**, 323–330.
- Bunn, A.G., Sharac, T.J. & Graumlich, L.J. (2004) Using a simulation model to compare methods of tree-ring detrending and to investigate the detectability of low-frequency signals. *Journal of Tree-Ring Research*, in press.
- Cairns, D.M. (1998) Modelling controls on pattern at alpine treeline. *Geographical and Environmental Modelling*, **2**, 43–63.
- Carmona, R., Hwang, W.L. & Torresani, B. (1998) *Practical time frequency analysis: Gabor and wavelet transforms with an implementation in S*. Academic Press, San Diego, CA.
- Carmona, R. & Whitcher, B. (2002) *Rwave version 1.20*. R package. <http://www.r-project.org>
- Cayan, D.R., Dettinger, M.D., Diaz, H.F. & Graham, N.E. (1998) Decadal variability of precipitation over western North America. *Journal of Climate*, **11**, 3148–3166.
- Chesson, P. & Huntley, N. (1997) The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist*, **150**, 519–553.
- Crowley, T.J. (2000) Causes of climate change over the past 1000 years. *Science*, **289**, 270–277.
- Delcourt, P.A. & Delcourt, H.R. (1987) Late-Quaternary dynamics of temperate forests: applications of paleoecology to issues of global environmental change. *Quaternary Science Reviews*, **6**, 129–146.
- ESRI (2002) *ArcGIS™ Redlands*, CA, ESRI.
- Fritts, H.C. (1976) *Tree rings and climate*. Academic Press, New York City, NY.
- Graumlich, L.J. (1991) Subalpine tree growth, climate, and increasing CO₂: An assessment of recent growth trends. *Ecology*, **72**, 1–11.
- Graumlich, L.J. (1993) A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research*, **39**, 249–255.

- Graumlich, L.J., Waggoner, L.A. & Bunn, A.G. (2004) Detecting global change at alpine treeline: coupling paleoecology with contemporary studies. *Global change and mountain regions: a state of knowledge overview* (ed. by U. Huber, H. Bugmann and M. Reasoner), pp. 405–412. Springer, Dordrecht, The Netherlands.
- Gray, S.T., Betancourt, J.L., Fastie, C.L. & Jackson, S.T. (2003) Patterns and sources of multidecadal oscillations in drought-sensitive tree-ring records from the central and southern Rocky Mountains. *Geophysical Research Letters*, **30**, 1316–1319.
- Henry, G.H.R. & Molau, U. (1997) Tundra plants and climate change: the International Tundra Experiment (ITEX). *Global Change Biology*, **3**, 1–10.
- Holmes, R.L. (1983) Computer-assisted quality control in tree-ring dating and measurement. *Tree-Ring Bulletin*, **43**, 69–78.
- Ihaka, R. & Gentleman, R. (1996) R: a language for data analysis and graphics. *Journal of Computational and Graphical Statistics*, **5**, 299–314.
- IPCC (2001) Contribution of working group I to the third assessment report of the intergovernmental panel on climate change. *Climate change 2001: the scientific basis* (ed. by J.T. Houghton, Y. Ding, D.J. Griggs, M. Noguer, P.J. van der Linden and D. Xiaosu), Cambridge University Press, Cambridge, UK.
- Jenson, S.K. & Domingue, J.O. (1988) Extracting topographic structure from digital elevation data for geographic information analyses. *Photogrammetric Engineering and Remote Sensing*, **54**, 1593–1600.
- Jones, P.D., Briffa, K.R., Barnett, T.P. & Tett, S.F.B. (1998) High-resolution palaeoclimatic records for the last millennium: interpretation, integration and comparison with General Circulation Model control-run temperatures. *The Holocene*, **8**, 455–471.
- Latif, M. & Barnett, T.P. (1994) Causes of decadal climate variability over the north Pacific and North America. *Science*, **266**, 634–637.
- Lawrence, R.L., Bunn, A.G., Powell, S. & Zambon, M. (2004) Classification of remotely sensed imagery using stochastic gradient boosting as a refinement of classification tree analysis. *Remote Sensing of the Environment*, **90**, 331–336.
- Levin, S.A. (1992) The problem of pattern and scale in ecology: the Robert H. MacArthur award lecture. *Ecology*, **73**, 1943–1967.
- Lloyd, A.H. (1996) *Patterns and processes of treeline forest response to late Holocene climate in the Sierra Nevada, California*. PhD Dissertation. University of Arizona, Tucson, AZ.
- Lloyd, A.H. & Fastie, C.L. (2002) Spatial and temporal variability in the growth and climate response of treeline trees in Alaska. *Climatic Change*, **52**, 481–509.
- Lloyd, A.H. & Graumlich, L.J. (1997) Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, **78**, 1199–1210.
- Lookingbill, T. & Urban, D.L. (2003) Spatial estimation of air temperature differences for landscape-scale studies in montane environments. *Agricultural and Forest Meteorology*, **114**, 141–151.
- Lookingbill, T. & Urban, D.L. (2004) An empirical approach towards improved spatial estimates of soil moisture for vegetation analysis. *Landscape Ecology*, **19**, 417–433.
- Mann, M.E., Bradley, R.S. & Hughes, M.K. (1998) Global-scale temperature patterns and climate forcing over the past six centuries. *Nature*, **392**, 779–787.
- Mann, M.E., Bradley, R.S. & Hughes, M.K. (1999) Northern hemisphere temperatures during the past millennium: inferences, uncertainties, and limitations. *Geophysical Research Letters*, **26**, 759–762.
- Mantua, N.J., Hare, S.R., Zhang, Y., Wallace, J.M. & Francis, R.C. (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society*, **78**, 1069–1079.
- Mastroguspe, R.J. & Mastroguspe, J.D. (1980) A study of *Pinus balfouriana* Grev. et. Balf. (Pinaceae). *Systematic Botany*, **5**, 86–104.
- McCabe, G.J. & Dettinger, M.D. (1999) Decadal variations in the strength of ENSO teleconnections with precipitation in the western United States. *International Journal of Climatology*, **19**, 1399–1410.
- Minobe, S. (1997) A 50–70 year climatic oscillation over the North Pacific and North America. *Geophysical Research Letters*, **24**, 683–686.
- Minobe, S. (1999) Resonance in bidecadal and pentadecadal climate oscillations over the north Pacific: role in climatic regime shifts. *Geophysical Research Letters*, **26**, 855–858.
- Moore, I.D., Grayson, R.B. & Ladson, A.R. (1991) Digital terrain modelling: a review of hydrological, geomorphological, and biological applications. *Hydrological Processes*, **5**, 3–30.
- Moore, G.W.K., Holdsworth, G. & Alverson, K. (2002) Climate change in the north Pacific region over the past three centuries. *Nature*, **420**, 401–403.
- Peet, R.K. (1978) Latitudinal variation in southern Rocky Mountain forests. *Journal of Biogeography*, **5**, 275–289.
- Schimmel, D., Kittel, T.G.F., Running, S., Monson, R., Turnipseed, A. & Anderson, D. (2002) Carbon sequestration studied in western US mountains. *EOS, Transactions, American Geophysical Union*, **83**, 445–456.
- Scuderi, L.A. (1987) Late-Holocene upper timberline variation in the southern Sierra Nevada. *Nature*, **325**, 242–244.
- Scuderi, L.A. (1993) A 2000-year tree ring record of annual temperatures in the Sierra Nevada Mountains. *Science*, **259**, 1433–1436.
- Stephenson, N.L. (1990) Climatic control of vegetation distribution: the role of the water balance. *American Naturalist*, **135**, 649–670.
- Stokes, M.A. & Smiley, T.L. (1968) *An introduction to tree ring dating*. The University of Chicago Press, Chicago, IL.
- Torrence, C. & Compo, G.P. (1998) A practical guide to wavelet analysis. *Bulletin of the American Meteorological Society*, **79**, 61–78.
- Turner, M.G., Gardner, R.H. & O'Neil, R.V. (2001) *Landscape ecology in theory and practice: Pattern and process*. Springer-Verlag, New York City, NY.

- Urban, D.L. (2000) Using model analysis to design monitoring programs for landscape management and impact assessment. *Ecological Applications*, **10**, 1820–1832.
- Urban, D.L., Goslee, S., Pierce, K. & Lookingbill, T. (2002) Extending community ecology to landscapes. *Ecoscience*, **9**, 200–212.
- Urban, D.L., Miller, C., Halpin, P.N. & Stephenson, N.L. (2000) Forest gradient response in Sierran landscapes: the physical template. *Landscape Ecology*, **15**, 603–620.
- Urban, D.L., O'Neill, R.V. & Shugart, H.H. (1987) Landscape ecology. *Bioscience*, **37**, 119–127.
- Villalba, R., Veblen, T.T. & Ogden, J. (1994) Climatic influences on the growth of subalpine trees in the Colorado Front Range. *Ecology*, **75**, 1450–1462.
- Walker, D.A., Halfpenny, J.C., Walker, M.D. & Wessman, C.A. (1993) Long-term studies of snow–vegetation interactions. *Bioscience*, **43**, 287–301.
- Walker, M.D., Webber, P.J., Arnold, E.H. & Ebert-May, D. (1994) Effects of interannual climate variation on aboveground phytomass in alpine vegetation. *Ecology*, **75**, 393–408.
- Wardle, P. (1971) An explanation for alpine timberline. *New Zealand Journal of Botany*, **9**, 371–402.
- Wardle, P. (1974) Alpine timberlines. *Arctic and alpine environments* (ed. by J.D. Ives and R.G. Barry), pp. 371–402. Methuen, London, UK.
- Whittaker, R.H. (1956) Vegetation of the Great Smoky Mountains. *Ecological Monographs*, **26**, 1–80.
- Whittaker, R.H. (1967) Gradient analysis of vegetation. *Biological Reviews*, **49**, 207–264.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Zhang, Y., Wallace, J.M. & Battisti, D.S. (1997) ENSO-like interdecadal variability: 1900–93. *Journal of Climate*, **10**, 1004–1020.

BIOSKETCHES

Andrew G. Bunn is an ecologist with research interests in late Holocene climate variability and the implications of Anthropocene climate change impacts on ecosystem structure and function.

Lindsey A. Waggoner was a tree-ring analyst and field technician for the Big Sky Institute at the time of this research. She is currently pursuing graduate work on land use controls of water quality in the developing world.

Lisa J. Graumlich is the executive director of the Big Sky Institute and Professor of Environmental Science at Montana State University. She is an ecologist with career-long interest in climate variability and treeline forests.