

## Holocene Dynamics of Treeline Forests in the Sierra Nevada

Andrea H. Lloyd; Lisa J. Graumlich

*Ecology*, Vol. 78, No. 4 (Jun., 1997), 1199-1210.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9658%28199706%2978%3A4%3C1199%3AHDOTFI%3E2.0.CO%3B2-2>

*Ecology* is currently published by The Ecological Society of America.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [jstor-info@umich.edu](mailto:jstor-info@umich.edu).



## HOLOCENE DYNAMICS OF TREELINE FORESTS IN THE SIERRA NEVADA

ANDREA H. LLOYD<sup>1</sup> AND LISA J. GRAUMLICH

*Department of Ecology and Evolutionary Biology and Laboratory of Tree-Ring Research, The University of Arizona, Tucson, Arizona 85721 USA*

**Abstract.** We reconstructed a 3500-yr history of fluctuations in treeline elevation and tree abundance in the southern Sierra Nevada. Treeline elevation was higher than at present throughout most of the last 3500 yr. Declines in the abundance of live trees and treeline elevation occurred twice during the last 1000 yr: from 950 to 550 yr BP and from 450 to 50 yr BP. The earlier decline coincided with a period of warm temperatures (relative to present) in which at least two severe, multidecadal droughts occurred. This decline was apparently triggered by an increase in the rate of adult mortality in treeline forests. The more recent decline occurred during a period of low temperatures lasting for up to 400 yr and was apparently caused by a sustained failure of regeneration in combination with an increased rate of adult mortality. The apparent past importance of precipitation in controlling the position and structure of the treeline ecotone suggests that climatic controls over treeline may be more complex than previously thought. In the Sierra Nevada, responses of high-elevation forests to future warming may depend strongly on water supply.

**Key words:** *climate change; dendrochronology; foxtail pine; Holocene; paleoclimate; Sierra Nevada; stand dynamics; subalpine forests; treeline.*

### INTRODUCTION

Significant variation in global climate has occurred on decadal to centennial time scales during the last 3000 yr (Hughes and Diaz 1994, Briffa et al. 1995, Hughes and Graumlich 1996). Biotic responses to climate variation at these frequencies are not yet well understood. Modern ecological studies typically focus on biotic responses to inter- or intraannual climate variation (e.g., Pake and Venable 1995) and paleoecological studies, constrained by limits on temporal resolution, often emphasize ecological effects of millennial-scale climate variation (e.g., Gagnon and Payette 1981, Spear 1989, 1993, Moser and MacDonald 1990, Scuderi 1994, Kullman 1995b). The pace and pattern of biotic response to climate variation on scales of decades to centuries is highly relevant to understanding the potential ecological consequences of anthropogenically induced climate change. In the research reported here, we investigate decade-to-century scale changes in the position of the treeline ecotone and the structure of treeline forests in the southern Sierra Nevada during the late Holocene.

The late Holocene provides an excellent context in which to identify correlations between ecological change and climate variation at intermediate frequencies of decades to centuries, for two reasons. First, climate history for some regions, such as western North America, is especially well known for the late Holocene

and has been derived from both biological indicators (e.g., tree rings) and physical indicators (e.g., lake sediments). Paleoclimatic records for the last few millennia are generally well dated and often have enough resolution to discern annual (e.g., Briffa et al. 1992) and decadal-scale climate variation (e.g., Stine 1994, Hughes and Graumlich 1996). The multiple data sources used in reconstructions of late Holocene climate frequently allow climate history to be inferred independently of ecological history, and thus permit comparisons of independent records of physical environmental change and biotic change. Second, the high temporal resolution of late Holocene paleoecological records allows more reliable inference of ecological processes from reconstructed patterns (Payette and Gagnon 1985, Payette et al. 1985, 1989, Kullman 1986a, b, 1987, Jackson et al. 1988, Campbell and McAndrews 1993, Graumlich and Davis 1993, Payette and Morneau 1993). The wealth of largely independent climatic and ecological histories covering the late Holocene therefore provides an excellent, and largely unexploited, resource with which to explore how ecological change may be related to decadal- and centennial-scale trends in climate.

Patterns of plant population response to climate variation are most easily observed at climatically determined ecotones where the abiotic environment is the ultimate control over ecological processes (e.g., Delcourt and Delcourt 1992, Risser 1995). Altitudinal treeline is one such ecotone that has been particularly well studied to understand the sensitivity of plant populations to climate variation. Despite the complexities in determining proximal mechanisms of climatic control

Manuscript received 1 February 1996; revised 29 July 1996; accepted 31 July 1996; final version received 11 September 1996.

<sup>1</sup> Present address: Department of Biology, Middlebury College, Middlebury, Vermont 05753 USA.

over treeline position, the overriding influence of climate on tree growth and survival at treeline is indicated at physiological, population, and landscape scales (Klikoff 1965, Schulze et al. 1967, Wardle 1968, Marr 1977, Tranquillini 1979, Black and Bliss 1980, Hasler 1982, Hadley and Smith 1983, 1986, Kullman 1986a, Earle 1993). Seedling establishment above treeline and the formation of upright stems on shrubby, prostrate krummholz trees at a number of sites coincide with late 20th-century warming, adding to the evidence that temperature may exert direct control over treeline position (Griggs 1934, Brink 1959, Patten 1963, Bray 1971, Franklin et al. 1971, Gorchakovskiy and Shiyatov 1978, Payette and Filion 1985, Kullman 1986b, Magee and Antos 1992). The sensitivity of treeline forests to climate is also suggested by paleoecological studies that demonstrate that millennial-scale fluctuations in the elevation of treeline often coincide with millennial-length trends in temperature (Bryson et al. 1965, LaMarche and Mooney 1967, Denton and Karlen 1977, Spear 1989, Moser and MacDonald 1990, Elias et al. 1991, Kullman 1995a).

Shifts in the position of ecotones are easily documented from paleoecological records because they can be reconstructed with presence/absence data. However, ecotonal shifts ultimately result from environmental influences on population-level and physiological processes. Changes in the position of an ecotone can be decomposed into two linked processes: changes in abundance and changes in distribution of individuals. The history of abundance variation at marginal sites may provide a more complete record of the pace and pattern of biotic response to climate variation than does the history of distributional changes. However, evidence of changing abundance is poorly preserved in paleoecological records, so opportunities to examine these more subtle changes in vegetation structure over long time spans are few.

In the Sierra Nevada of California, dead trees at high elevations are preserved in situ for millennia. Dead trees located above current treeline testify to the dynamic behavior of treeline in the recent past. Recent seedling establishment above the current elevational limit of adult trees at these same sites suggest ongoing change at the ecotone (A. H. Lloyd, *unpublished manuscript*). The paleoecological record preserved in dead trees in the southern Sierra Nevada is highly resolved spatially and temporally, providing a unique opportunity to reconstruct fine-scale changes in the structure of treeline forests and the position of this treeline ecotone. Abundant paleoclimatic information from the Sierra Nevada (Graumlich and Lloyd 1996), allows comparison of ecological history with an independent history of climate. In this research, we investigated three questions. (1) How has the abundance of trees beyond the current distributional limits of subalpine forests changed over the last few millennia? (2) How do changes in tree abundance relate to changes in levels

of recruitment and mortality? (3) How has the position of the treeline ecotone changed over the last few millennia?

## METHODS

### *Study area*

We conducted this study on the eastern crest of the Sierra Nevada in Sequoia National Park, California, United States (Fig. 1). Treeline elevation is between 3300 and 3500 m. Trees are frequently absent from valley bottoms and east-facing and north-facing slopes at elevations >3100 m. Treeline forests here are monospecific stands of foxtail pine (*Pinus balfouriana* Gräv. & Balf.). Because foxtail pine does not generally adopt the krummholz growth form characteristic of many high-elevation tree species, treeline is an abrupt boundary in this area. The forests are open and have a low density of trees (50–100 trees/ha) with a sparse herbaceous understory. Herbaceous plants above treeline are scarce, occurring in densities considerably less than 1 plant/m<sup>2</sup>.

High elevation and the rain-shadow effect from the western peaks of the Sierra Nevada create a cold and dry climate at treeline in the eastern Sierra Nevada. Snowpack varies greatly from year to year. Average maximum snowpack ( $\pm 1$  SD) ranges from  $157.6 \pm 74.8$  cm at our northernmost sites to  $140.0 \pm 68.3$  cm at our southernmost sites (1948–1994 data; State of California Department of Water Resources, *unpublished data* 1996).

### *Sampling*

We selected five study sites at which to reconstruct past changes in tree abundance and treeline position along the eastern ridge of the southern Sierra Nevada (Fig. 1). We systematically selected sites at upper treeline that had similar topography (Table 1) and evidence of past movements of treeline, as indicated by the presence of dead wood above current treeline. We avoided areas such as landslide chutes where position of dead trees may have been substantially altered. However, some downslope movement of trees may have occurred at our sites, so elevations reported here are minimum estimates of the elevation at which each tree grew.

All study sites were located in areas that are currently treeless. All but one are immediately adjacent to forested areas (Table 1). Three study sites were located at altitudinal treeline (Fig. 1, Upper Treeline 1, 2, and 3). We sampled other topographic expressions of treeline at two additional study sites (Fig. 1, East Slope and Meadow). The East Slope site is an area where there is a forest edge associated with a change from a south-facing to east-facing slope. The Meadow site is an area where there are dead trees within a now-treeless, flat valley bottom. The five sites are clustered into a southern group, consisting of Upper Treeline 1 and 2, and a northern group, consisting of the remaining three

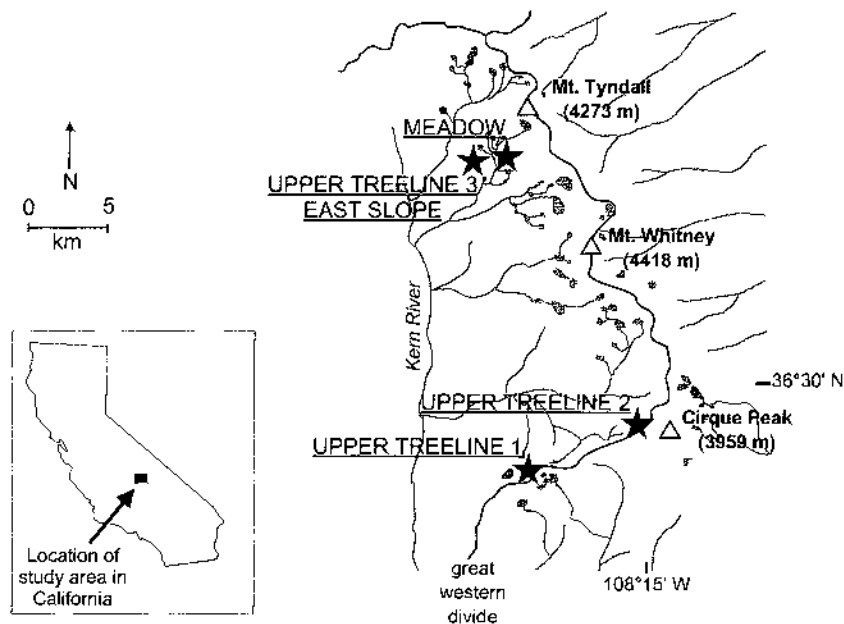


FIG. 1. Location of study sites in Sequoia National Park. The inset shows the location of the study area in California. River drainages are indicated by the light gray lines. The Great Western Divide, indicating the major crest of the Sierra Nevada, is indicated by the solid black line. Major peaks in the area are indicated by triangles. Stars show the position of sites. Upper Treeline 3 and the East Slope sites are <1 km apart, so are indicated by a single symbol.

sites. The two clusters of sites are separated by  $\approx 20$  km. With the exception of Upper Treeline 3 and East Slope, all sites are separated by a minimum of 1 km.

We located a single plot (1–4 ha) at each site. A site is therefore our sampling unit, and within each site a complete sample was conducted. The density of dead trees at each site varies from 10 to 70 trees/ha (Table 1). Except at the Meadow site, plots directly abutted current treeline. The plots extended to the maximum elevation, or at the East Slope site to the eastern extent, at which dead wood was found. Within each plot, we mapped the position of all dead wood and removed at

least one increment core from each piece that was sound enough to be cored. We noted degree of decay (presence of sapwood, surface texture, color, extent of center rot) of each sampled tree. We examined each specimen prior to coring in order to select the radius most likely to contain the maximum number of rings. We obtained increment cores from >90% of all dead trees at each site.

#### Data analysis

To determine the calendar year of each tree's inner and outer ring, we measured ring widths in each in-

TABLE 1. Sequoia National Park study plot characteristics.

Site	Elevation (m)	Aspect (degrees)	Plot size (ha)	Dead tree density (trees/ha)	Distance from current to maximum paleo-treeline (m)	Elevational change from current to maximum paleo-treeline (m)
Upper Treeline 1	3 420	270°	3.6	24.16	180	54
Upper Treeline 2	3 560	230°	5.6	10.89	280	94
Upper Treeline 3	3 510	210°	3.0	54.6	150	51
East Slope	3 490	80°	1.6	68.75	320	N/A
Meadow	3 445	N/A	1.025	47.8	$\approx 500$	N/A

*Note:* Elevation, except for the Meadow site, is the elevation of the lowest edge of the plot. No aspect is indicated for the Meadow plot, because it is on a flat valley bottom. The distance from current to maximum paleo-treeline is the distance to the nearest living forests. At the meadow site, there is no evidence that the sampled area was ever contiguous with the nearest living forests. Maximum paleo-treeline is defined as the elevation of the highest dead tree in the plot and is assumed to represent the highest elevation of treeline during the mid to late Holocene.

TABLE 2. Results of crossdating.

Site	Number of samples	% dated	Range of outer ring dates (yr BP)
Upper Treeline 1	88	60	4925–present
Upper Treeline 2	61	67	5046–85
Upper Treeline 3	164	53	5182–124
East Slope	110	72	1951–234
Meadow	49	57	3552–564

Note: Total numbers of samples from which we obtained increment cores are given. Dated samples are those to which we could confidently assign an inner and outer ring date by crossdating. The range of outer ring dates is expressed as calendar-years before present and is based on the corrected outer ring dates.

crement core and crossdated those ring widths against foxtail pine and bristlecone pine (*Pinus longaeva* D. Bailey) chronologies from nearby sites (LaMarche 1974; D. Graybill and G. Funkhouser, unpublished data, A. H. Lloyd and L. J. Graumlich, unpublished data). Crossdating was accomplished using the computer program Cofecha (Holmes 1995), which statistically matches undated samples against samples for which exact dating has been established. Dates obtained with computer crossdating were subsequently confirmed by visually comparing undated and dated samples (Stokes and Smiley 1968). In this manner, we were able to date 53–72% of samples at all sites (Table 2). From calibrated decay classes, we determined that the majority of undated samples predated the period of this reconstruction (data not shown), and are therefore unlikely to cause a systematic error in our interpretation of ecological changes in the last 3500 yrs.

As a result of pre- and postmortem decay, inner and outer ring dates established for each tree by crossdating are not exact establishment and mortality dates. The innermost wood in many dead trees was too decayed to sample with an increment corer, so the inner ring date obtained in our sampling is an unknown number of years from the true pith date of the sample. Because we were generally unable to estimate the distance from the innermost sampled ring to the pith of the tree, we did not correct inner ring dates to estimate the true establishment date, and therefore use caution in interpreting the precise timing of tree establishment. Because of postmortem decay of outer-surface wood, and pre-mortem decay if the tree suffered from cambial die-back (strip-barking) while alive, the outer ring date of our sample is in most cases not the true mortality date. Based on the observed condition of each tree, we applied two corrections to the outer ring date to obtain a closer estimate of the true mortality date. First, the outer ring date of all samples lacking sapwood, identifiable by a color change in the wood of both live and dead trees, was adjusted for loss of sapwood. A site-specific sapwood adjustment factor was estimated as the mean number of sapwood rings in an all-aged sample of live trees at current treeline at each site. The

adjustment ranged from  $68 \pm 0.1$  to  $70 \pm 0.2$  yr (mean  $\pm 1$  SE). Second, we adjusted the samples for rings not sampled on the outer wood surface. We scored each tree as having a surface that was furrowed (surface primarily covered by deep furrows), feathered (long, thin strips of wood peeling off the surface), or smooth. Because increment cores were always removed from within a furrow ( $\approx 3$  cm deep), outer dates on furrowed logs were adjusted for rings not sampled. Feathered samples were corrected for the loss of rings in the outer 1 cm that crumbled during sampling. No rings were lost during the sampling of trees with smooth surfaces. We calculated years lost due to surface condition by multiplying the estimated wood lost from its surface (0, 1, or 3 cm) by average growth rate (number of rings per centimeter) of each tree. Sapwood corrections and corrections for surface condition are additive. The total correction to outer ring date applied to dead trees ranged from 0 yr (for trees with sapwood) to  $\approx 220$  yr (for furrowed trees with no sapwood). The average correction applied to each tree ranged from a low of  $109 \pm 5$  yr for trees at Upper Treeline 1 to a high of  $129 \pm 3$  yr (mean  $\pm$  SE) for trees at Upper Treeline 2. These corrections were added to the crossdated outer ring date to obtain an estimated mortality date for each tree.

To account for the error involved in estimating death dates, we analyzed our data using 100-yr time steps, assuming that a tree's true death date falls within the 100-yr interval to which it is assigned. In order to evaluate the sensitivity of our results to errors in estimating death date, we repeated our analyses using time intervals of 50 and 200 yr (data not shown). These analyses, which assumed we had twice (50-yr intervals) or half (200-yr intervals) the precision we report in this paper (100-yr intervals), led to inferences identical to those presented here, indicating that our results are robust to relatively large errors in death date estimates. The reconstruction with 200-yr time intervals, for example, had the effect of smoothing the time series but did not alter our inference about the timing or climatic correlates of episodes of changing forest structure. The use of a 100-yr time step implies that we can confidently resolve only those changes occurring on 100-yr or greater time scales. We concentrate, therefore, on identifying long-term trends in forest structure and distribution. In addition, because error is likely to be greatest for the oldest samples, we have restricted our comparisons of paleoecological and paleoclimatic data to the last 2,000 yr.

Time is expressed in this paper as calendar years before present (yr BP), with AD 1950 as the zero year. Dates refer to the beginning of a 100-yr time interval (e.g., 50 yr BP is the period from AD 1900 to 1993, 150 yr BP is the period from AD 1800 to AD 1900).

We estimated abundance by calculating the number of trees that were alive during each 100-yr time interval from 3500 yr ago to present. Abundance estimates are subject to two specific errors. First, our sample is biased

toward larger trees. Saplings and small adults are likely to decompose more rapidly than large adults, resulting in their systematic exclusion from our sample. Second, the record fades over time because of the decomposition of all wood. Our sample therefore includes an increasing proportion of the original forest through time and would be expected, as a result of decomposition alone, to indicate a trend of increasing tree abundance through time. Although we have dated trees as far back as 4282 yr BP (Table 2), we truncated our analysis at 3450 yr BP in order to minimize the influence of the fading record.

We estimated treeline position at 100-yr intervals from the mapped position of live trees during each interval. In order to account for fine-scale variation in the elevation of treeline, we divided the map of each plot into four equal-sized sectors, each extending from the current forest edge up the slope to the upper edge of the plot. Treeline elevation is estimated for each time interval as the mean of the elevation of the highest live tree in each of the four sectors. At the East Slope site, sectors extended laterally to the easternmost edge of the plot. The standard deviation of the mean quantifies the variance in treeline elevation among sectors within each plot. This method serves the dual purpose of accounting for the irregular shape of treeline and minimizing the influence of isolated individuals beyond the actual forest limit. We did not reconstruct spatial changes at the flat, isolated Meadow site.

#### *Statistical analyses*

The goal of the statistical analyses in this study was to objectively define periods when changes in forest structure and position were similar among sites. Autocorrelation functions indicated significant first- and second-order autocorrelation in the time series of changing abundance and treeline elevation, so we were unable to use parametric tests. We transformed the time series of position and abundance to first differences, coded them as either positive, negative, or no change, and used a modified sign test (Sokal and Rohlf 1981) to compare sites. This approach is useful in allowing us to distinguish periods in which the changes among sites are likely to be noise, i.e., due to chance, from those that are unlikely to be due to chance alone. We compare our observed data to a null model in which sites are independent and each outcome (positive, negative, or no change) is equally probable in any time interval. To identify periods in which sites were more similar than would be expected by chance alone, we estimated the probability that 1, 2, 3, 4, or 5 sites would have the same value (positive, negative, or no change) for a given time period. The probability, for example, of any one site having a positive sign in time period  $t$  is 0.333. The probability of having three sites with a positive sign during the same time period is therefore  $0.333^3$ , or 0.037. Using a probability threshold of  $P < 0.05$ , we established the criterion that synchronous pe-

riods were those in which three or more sites had the same value (positive, negative, or no change). We will use "synchronous" to describe those periods in which three or more sites exhibit the same behavior.

## RESULTS

### *Changes in tree abundance*

Live trees grew beyond the current treeline at all sites for most of the last 3500 yr (Fig. 2). Synchronous increases in tree abundance above current treeline, each affecting at least three sites, occurred from 2050 to 1850 yr BP, from 1750 to 1650 yr BP, and from 1450 to 1050 yr BP (Fig. 2). Within each site, episodes of increasing abundance persisting for >200 yr occurred at various times between 2350 and 1450 yr BP at the three northern sites (Upper Treeline 3, East Slope, and Meadow) and between 1450 and 1050 yr BP at all sites except Upper Treeline 3 (Tables 3).

Synchronous declines in tree abundance occurred from 3150 to 3050 yr BP, from 950 to 550 yr BP, and from 450 yr BP to present (Fig. 2). Long-term declines in tree abundance occurred between 2050 and 1750 yr BP at the two southern sites (Upper Treeline 1 and 2) and at various times since 950 yr BP at all sites (Table 3).

Patterns of changing tree abundance at each site were most similar to those of neighboring sites, regardless of the type of treeline involved (Fig. 2). For example, patterns of changing abundance at Upper Treeline 3, East Slope, and Meadow sites are very similar, although each is a different type of treeline (i.e., elevational vs. aspect-related vs. locally inverted).

An early peak of abundance at the two southernmost sites (Upper Treeline 1 and 2) indicates that forests existed above current treeline for at least several centuries before 2050 yr BP (Fig. 2). Approximately the same number of trees were alive at the Upper Treeline 3 site during the early part of this episode (e.g., prior to 3050 yr BP), suggesting that forests may have existed at all three upper treeline sites during the early part of the record. The disappearance of these forests was somewhat, although not always, synchronous among sites. Abundance declined from 2550 to 2250 yr BP at Upper Treeline 2 and from 2050 to 1750 yr BP at both Upper Treeline 1 and 2 (Table 3). Minimum abundances were reached at both sites during the interval AD 200 to AD 300 (Fig. 2).

At all five sites, a second period of high tree abundance beyond current treeline occurred between 1250 yr BP and 750 yr BP (Fig. 2). The demise of these forests occurred over several hundred years after 950 yr BP. At the Meadow site, abundance began to decline after 950 yr BP and all trees at the site had died by 550 yr BP (Fig. 2). At two sites, Upper Treeline 3 and East Slope, abundance declined continuously from 850 to <100 yr BP (Table 3). At Upper Treeline 2, abundance declined from 1050 to 650 yr BP, and sporadic

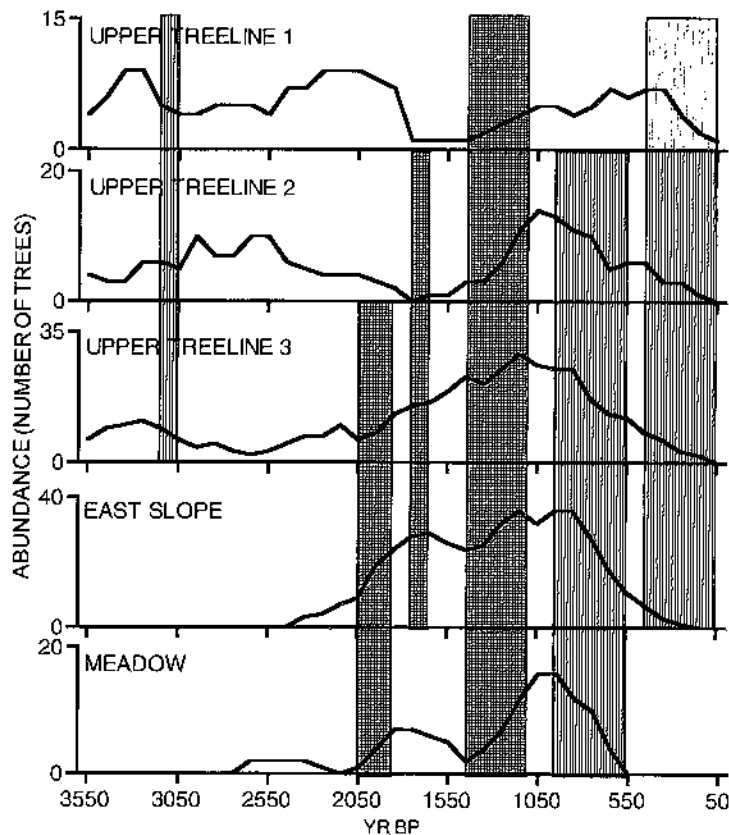


FIG. 2. Abundance of live trees in study plots in currently unforested areas. Abundance is the minimum number of trees that were alive during any part of each 100-yr time interval. Dates on the x axis are the first year, in units of years BP, of each 100-yr time interval; A.D. 1950 is the zero year. Thus 50 yr BP is the interval from AD 1900 to present. Note that the scale of the y axis differs among sites. Periods of synchrony among sites, as determined by a modified sign test, are indicated by the shaded rectangles. Rectangles shaded by vertical lines indicate synchronous declines, and rectangles with cross-hatching indicate synchronous increases.

periods of declining abundance occurred thereafter. Synchronous declines began again after 450 yr BP, and all trees had died at all sites by 50 yr BP (Fig. 2).

#### *Levels of recruitment and mortality*

Time periods in which synchronous increases in tree abundance occurred were also characterized by periods of high recruitment and low (<25%) or no mortality (Fig. 3). Time periods in which synchronous declines in tree abundance occurred were associated with two distinct modes of population-level response. First, as exemplified by the decline from 950 to 550 yr BP, recruitment remained high, but mortality increased from low or none to >50%. Second, as exemplified by the decline after 450 yr BP, recruitment dropped to low levels and eventually to zero and mortality increased to moderate and then high rates (Fig. 3).

#### *Changes in treeline position*

Patterns of change in treeline position during the last 3500 yr were characterized by a few distinct periods of synchronous change interspersed with multi-century periods of stasis (Fig. 4). Changes in elevation occurred simultaneously with changes in abundance, but were typically of shorter duration (Table 3). Synchronous increases in treeline elevation occurred from 2250 to 2150 yr BP and from 1150 to 1050 yr BP (Fig. 4). These events were generally of small magnitude (e.g.,

<5 m change). Synchronous decreases in the elevation of treeline occurred from 850 to 750 yr BP, from 1500 to 1400 yr BP, and from 250 to 50 yr BP (Fig. 4).

## DISCUSSION

### *Patterns of change at treeline*

Synchrony among the different topographical expressions of treeline studied here (upper treeline, aspect-related treeline, lake basin treeline) indicates that past changes in ecotone position involved the expansion of subalpine forests across a complex topography rather than simple upward movements of the forest border. Relatively small changes in the elevational limit of subalpine forests may have therefore corresponded to large changes in total forested area at high elevations, as forests spread onto east-facing slopes and into valley bottoms as well as upslope.

The local and regional synchrony of changes in treeline forests in the Sierra Nevada during the last 3500 yr implies a common control, most likely climatic, over treeline movements. Errors in determining the timing of climate events and estimating tree death dates prevent us from correlating ecological changes with short-duration climate events (e.g., extreme single-year events; Minnich 1984), and we therefore restrict comparison of our data to climate events persisting for decades or longer. Such a comparison yields hypoth-

TABLE 3. Long-term trends in tree abundance and treeline elevation.

Site	Abundance		Elevation	
	Positive trend	Negative trend	Positive trend	Negative trend
Upper Treeline 1	1450-1050	2050-1750 350-50	...	350-50
Upper Treeline 2	1350-1050	2550-2250 2050-1750 1050-650	...	2450-2150 2050-1750
Upper Treeline 3	3550-3250 2650-1550 2050-1450	3250-2950 850-50	2550-2250 1350-1050	350-50
East Slope	2350-1650 1450-1150	850-150	2450-1950	650-150
Meadow	2150-1850 1450-1050	1750-1450 950-550	N/A	N/A

Note: Long-term trends are periods in which direction of change (positive or negative) is constant for 300 yr or more. Time periods are expressed as calendar-years before present (yr BP; see *Methods: Data analysis*).

eses about general climatic controls over treeline dynamics, but does not permit us to identify the specific climate events that lead to change at treeline. The potential for circularity exists in comparisons of our record of foxtail pine forest history with a climatic history derived in part from foxtail pine ring-widths (Graumlich 1993, Scuderi 1993). We have attempted to avoid such circular inferences by using a climate history from multiple proxy data sources, including tree ring records of multiple species (foxtail pine, bristlecone pine, giant sequoia [*Sequoiadendron giganteum*], western juniper [*Juniperus occidentalis*]) and geomorphic records (glacial history, lake sediments; Curry 1969, Graumlich and Lloyd 1996).

Previous retrospective studies have concluded that increases in treeline elevations are associated with extended warm periods (LaMarche and Mooney 1967, Denton and Karlen 1977, Kullman 1986a, 1995b, Scuderi 1987b, Payette et al. 1989, Shiyatov 1993). Evidence linking treeline forest expansion to warm temperatures is ambiguous in this study due to a lack of consensus in the paleoclimatic reconstructions. The increase in tree abundance and treeline elevation that we have identified between 2050 and 1850 yr BP corresponds to a period of relatively warm temperatures inferred from bristlecone pine ring-widths in the adjacent White Mountain range (LaMarche 1974). The episode of increasing tree abundance between 1450 and 1050 yr BP, however, corresponds to a period in which conflicting inferences have been made from paleoclimatic proxies. A reconstruction of summer temperatures from treeline foxtail pine ring widths indicates that the period from 1550 to 1150 yr BP is dominated by positive temperature anomalies relative to the 20th century (Scuderi 1993). In contrast, inference from bristlecone pine ring-widths suggests that the period from 1650 to 1050 yr BP was cooler than present (LaMarche 1974). If Scuderi's (1993) reconstruction describes climate at our sites during that time, then the hypothesis that the expansion of subalpine forests is always associated

with warm temperatures is supported by this study. If LaMarche's (1974) reconstruction describes climate at our sites during that time, then our data fail to support the hypothesis.

Synchronous declines in tree abundance from 950 to 550 yr BP and in treeline elevation from 850 to 750 yr BP are associated with warm, dry conditions. Warmth in this period is inferred from climatic reconstructions from foxtail pine, western juniper, and bristlecone pine ring-widths (LaMarche 1974, Graumlich 1993, Scuderi 1993). The warm temperatures were accompanied by severe, multi-decadal droughts, the magnitude and duration of which exceeded any experienced during the 20th century. Dry conditions at this time are indicated by lake-level records from nearby Mono Lake (Stine 1990, 1994), low-elevation bristlecone-pine ring-widths (LaMarche 1974), and precipitation reconstructions from tree-rings of western juniper, foxtail pine, bristlecone pine, and giant sequoia from the Sierra Nevada and adjacent White Mountains (Hughes and Brown 1992, Graumlich 1993, Hughes and Graumlich 1996).

Evidence suggests that the influence of temperature on treeline dynamics may be moderated by other climatic factors such as wind, moisture, and snowpack distribution (Minnich 1984, Spear 1989, Earle 1993). To our knowledge, however, no previous study has identified drought as a correlate of treeline decline. The coincidence of drought with declining tree abundance and contraction of high-elevation forests at our sites is, however, consistent with the finding that both low temperature and low precipitation limit radial growth of high elevation trees in the southern Sierra Nevada (Graumlich 1993, Scuderi et al. 1993).

Two explanations exist to explain the coincidence of drought and treeline decline identified in our study. First, although drought severity is unlikely to increase with elevation, some studies have shown that transpiration rates may increase with elevation, leaving trees at the alpine treeline more vulnerable to droughts



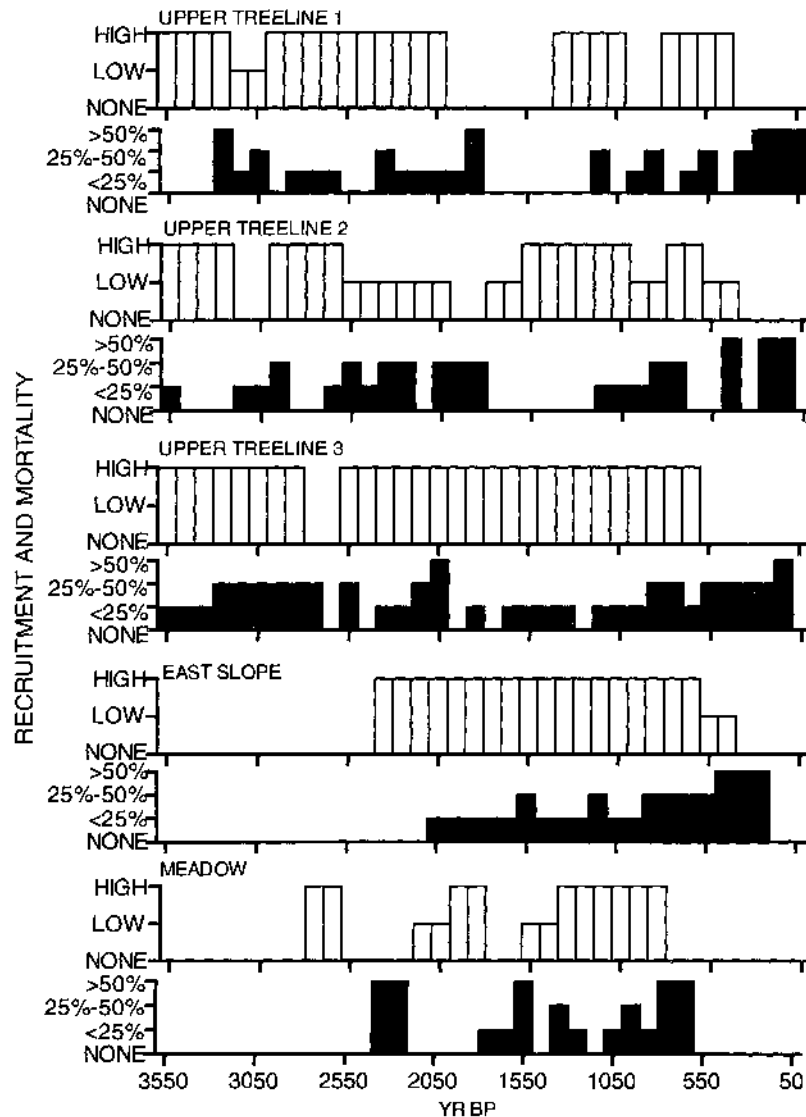


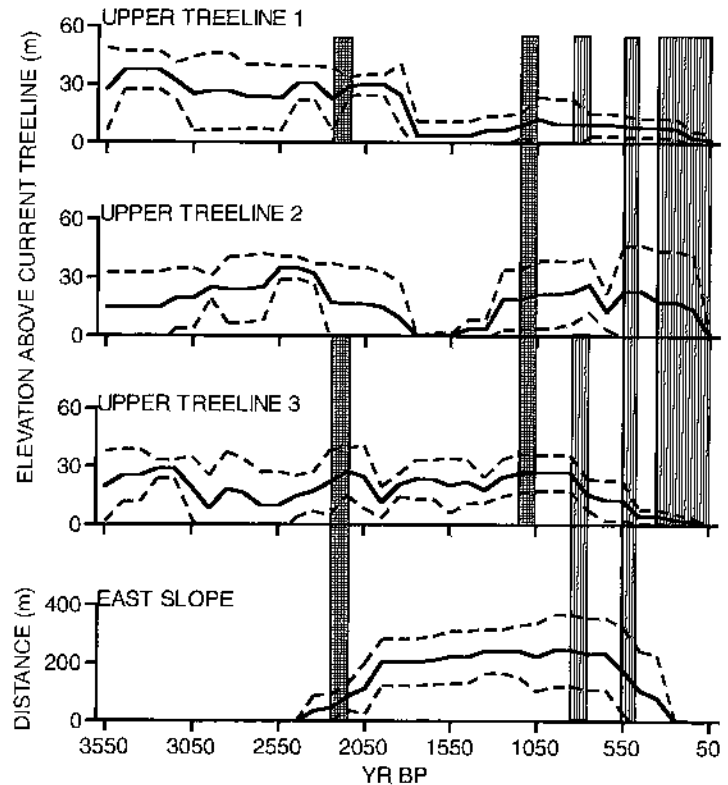
FIG. 3. Levels of recruitment and mortality. Recruitment is indicated by the white bars and is coded as none, low (1 tree per 200-yr interval), or high (>1 tree per 200-yr interval). Mortality is indicated by the solid bars and is categorized by the percentage of the total population that died during each 100-yr interval. Time intervals are the same as those described in Fig. 2.

(Smith and Geller 1979, Baig and Tranquillini 1980). In addition, lower snowpack in drought years may lead to increases in winter desiccation injury of trees in exposed sites at treeline (e.g., Hadley and Smith 1983, Minnich 1984, Grace 1989). Alternatively, declining temperatures with increasing altitude may set up a gradient of vulnerability in which trees at high-elevation sites, stressed by cold temperatures, are more vulnerable to other stress, including drought. In this scenario, the additional stress imposed by severe, sustained drought may be sufficient to kill trees in the most marginal sites, producing a landscape-level response that mimics the effects expected to be produced by temperature. Both hypotheses lead to the prediction that tree mortality at treeline should increase during

droughts, as the most marginal trees succumb to either direct or indirect effects of water stress. This is precisely what the paleoecological record shows: adult mortality increases during the period in which the severe droughts occurred, from 950 to 550 yr BP.

The most recent decline in tree abundance and tree-line elevation, after 450 yr BP, corresponds to a well-documented cold, wet period in the Sierra Nevada. Low temperatures are indicated in the Sierra Nevada by tree-ring reconstructions of temperature (LaMarche 1974, Graumlich 1993, Scuderi 1993) and evidence of glacial advances (Curry 1969, Scuderi 1987a). Intermittent wet periods between 450 yr BP and present are indicated by tree-ring reconstructions in the Sierra Nevada and adjacent White Mountains (Hughes and Brown

FIG. 4. Changes in the position of treeline. Elevation of treeline is estimated at four points in each plot, as described in *Methods*. The mean elevation per 100-yr time interval is indicated by the solid line. Dashed lines indicate  $\pm 1$  SD. Standard deviation is based on the variance in treeline elevation among sectors within each plot. Treeline elevation is expressed relative to the current elevation of treeline. At the East Slope site, changes in treeline position are measured as distance from the current forest edge. We did not reconstruct spatial changes at the Meadow site. Time intervals are identical to those in Fig. 2. Periods of synchrony among sites, as determined by a modified sign test, are indicated by the shaded rectangles. Rectangles cover only those sites at which the change occurred. Rectangles shaded by vertical lines indicate synchronous declines, and rectangles shaded by cross-hatching indicate synchronous increases.



1992, Graumlich 1993, Hughes and Graumlich 1996) and by the episodic appearance of ephemeral lakes in southern California (Enzel et al. 1989, 1992). This correspondence between treeline decline and extended periods of cold is consistent with the results of previous studies in the region (LaMarche 1973, Scuderi 1987b) and elsewhere (Denton and Karlen 1977, Kullman 1979, 1986a, Payette et al. 1989) and confirms the hypothesis that temperature is an important control over forest dynamics at treeline (e.g., Tranquillini 1979).

Changes in the position of treeline and the structure of treeline forests are therefore associated with multicentury temperature fluctuations and multidecadal precipitation fluctuations. Water supply can apparently reverse the expected response of treeline forests to temperature, indicating that these forests may be simultaneously limited by both water balance and warmth. Effects of temperature and precipitation on forest structure are likely interactive; warm temperatures 950 to 550 yr BP, for example, may have exacerbated drought effects.

#### *Dynamics of change at treeline*

Reconstructed estimates of recruitment and mortality rates allow us to identify the population-level processes that may drive changes in tree abundance. Since changes in either recruitment or mortality rates can affect population size, different pathways may lead to the same pattern of changing tree abundance. Our data

suggest two modes of population decline. In the first mode, exemplified by patterns of recruitment and mortality between 950 and 550 yr BP, a decline in tree abundance is caused by an increase in the adult mortality rate. In the second mode of response, illustrated by patterns of recruitment and mortality since 450 yr BP, both recruitment and mortality are affected. These results further suggest that low-temperature anomalies may have had fundamentally different effects on population dynamics than low-precipitation anomalies. Recruitment was low and mortality high during the low-temperature anomaly, while mortality was high and recruitment unaffected during the low-precipitation anomaly.

Although changes in recruitment rates are an important process driving treeline forest dynamics (Wardle 1963, Payette and Filion 1985, Payette and Gagnon 1985, Kullman 1986a, 1987, 1993, Payette et al. 1989), our study suggests that adult mortality of foxtail pine is at least as important as recruitment into adult age classes in driving changes in tree abundance at treeline. Recruitment failure can lead to the extinction of a population only if it persists for as long as the average remaining lifespan of the adult trees in the population (e.g., Kullman 1993). In a species like foxtail pine, where lifespan commonly exceeds 1000 yr, population decline is unlikely to occur without an increase in adult mortality. Populations of shorter lived trees may therefore be more sensitive to changes in recruitment rates.

Tree abundance changed nearly continuously through time, with synchronous increases and declines occurring during 75% of the 100-yr time intervals in the last 2000 yr. In contrast, treeline elevation exhibited long periods of stasis punctuated by brief periods of change. These patterns suggest that high-elevation tree abundance may be more sensitive to environmental variation than treeline position, a result consistent with Payette and Filion's (1985) observation that recent climate warming has led to increases in forest density below treeline rather than causing major change in ecotone position. At our sites, changes in tree abundance preceded changes in treeline position by up to 400 yr.

These results suggest that landscape-level patterns of response to climate variation may differ from population-level patterns of response. The inferred pattern of change in the position of treeline, a landscape-level response, is one of long periods of stasis punctuated by periods of relatively rapid change. This pattern is consistent with the model that treeline responds primarily to thresholds in climate, remaining static or moving gradually upward for long periods, and declining quickly in response to disturbance (Slatyer and Noble 1992, Noble 1993) or extreme climate (Kullman 1993). Treeline position therefore alternates between periods of stasis or gradual change when it is unresponsive to climate variation and periods of rapid change during times when critical climate parameters exceed some threshold value. In contrast, the reconstructed pattern of change in tree abundance, a population-level response, indicates slow, continual change. This pattern is consistent with the model that treeline is in a dynamic equilibrium with climate and that treeline forests therefore adjust continuously to variation in climate. The scale at which the ecological response occurs can, in this model, be modified by a species' life history traits (Prentice 1986, Stevens and Fox 1992, Kullman 1993) and by feedbacks between forest structure and microclimate (Minnich 1984, Wilson and Agnew 1992) that buffer treeline forests against short-duration climate variation. The dependence of the inferred treeline sensitivity on the hierarchical level of the analysis suggests that there may be a lag between the initiation of a demographic response (e.g., change in recruitment and mortality rate) and the landscape-scale expression of that response (e.g., a change in treeline position). Long-lived, persistent adults are a likely source of such a lag (Kullman 1993).

#### *Implications for future change at treeline*

Our results have three primary implications for the potential of anthropogenically induced warming to cause future changes at treeline. First, although large changes in forest structure and distribution occur on time scales of hundreds of years, the rate at which these forests respond to rapid future climate change is likely to be slow, and treeline position may lag climate change by decades to centuries. Monitoring efforts at treeline

might therefore emphasize change in density of existing stands as well as change in the position of treeline.

Second, the period from 950 to 550 yr BP illustrates the extent to which water balance can reverse treeline response to temperature. Whereas climate appears to have been warm when treeline forests expanded, warmth does not necessarily lead to subalpine forest expansion. The observational record of the relatively wet 20th century (e.g., Graumlich 1993) leads to the prediction that treeline will rise if temperatures rise. The paleoecological record, however, indicates that future warming is unlikely to cause an expansion of subalpine forests if it is accompanied by a reduction in water supply.

Third, responses to past climate variation have involved more than simple upward or downward movements of the treeline boundary: they have involved relatively complex changes in distribution, accompanied by changes in forest structure. The impacts of even minor changes in the elevation of treeline are therefore likely to be substantial. A warming-induced rise in treeline elevation is likely to involve landscape-scale increases in biomass, productivity, and carbon pools as a result of increases in both forested area and density of current forests.

#### ACKNOWLEDGMENTS

We are grateful for the continued support of the Research Office of Sequoia National Park, especially D. Parsons, N. Stephenson, and A. Esperanza. Assistance with fieldwork was provided by A. Arians, A. Dimitri, A. Esperanza, C. Fastie, J. King, E. Lloyd, J. Lloyd, P. Lloyd, J. Miller, K. Prettyman, C. Pranka, P. Sheppard, and N. Stephenson. We thank V. Begay, J. Curtis, and B. Green for assistance with lab work. The manuscript was greatly improved by comments from J. Bronstein, C. Fastie, S. Jackson, L. McDade, R. Robichaux, D. Venable, and one anonymous reviewer. Funding for this project was provided by a National Science Foundation Dissertation Improvement Grant to Lloyd and Graumlich, the National Biological Service Global Change Research Program, the Graduate College at The University of Arizona, and the Department of Ecology and Evolutionary Biology at The University of Arizona.

#### LITERATURE CITED

- Baig, M. N., and N. J. Tranquillini. 1980. The effects of wind and temperature on cuticular transpiration of *Picea abies* and *Pinus cembra* and their significance in desiccation at the alpine treeline. *Oecologia* 47:252-256.
- Black, R. A., and L. C. Bliss. 1980. Reproductive ecology of *Picea mariana* (Mill.)B.S.P. at tree line near Inuvik, Northwest Territories, Canada. *Ecological Monographs* 50:331-354.
- Bray, J. R. 1971. Vegetational distribution, tree growth and crop success in relation to recent climatic change. *Advances in Ecological Research* 7:177-233.
- Briffa, K. R., P. D. Jones, T. S. Bartholin, D. Eckstein, F. H. Schweingruber, W. Karlen, P. Zetterberg, and M. Eronen. 1992. Fennoscandian summers from AD 500: temperature changes on short and long time scales. *Climate Dynamics* 7:111-119.
- Briffa, K. R., P. D. Jones, F. H. Schweingruber, S. G. Shiyatov, and E. R. Cook. 1995. Unusual twentieth-century summer warmth in a 1000-year temperature record from Siberia. *Nature* 376:156-159.

- Brink, V. C. 1959. A directional change in the subalpine forest-heath ecotone in Garibaldi Park, British Columbia. *Ecology* **40**:10-16.
- Bryson, R. A., W. N. Irving, and J. A. Larsen. 1965. Radiocarbon and soil evidence of former forest in the southern Canadian tundra. *Science* **147**:46-48.
- Campbell, I. D., and J. H. McAndrews. 1993. Forest disequilibrium caused by rapid Little Ice Age cooling. *Nature* **366**:336-338.
- Curry, R. R. 1969. Holocene climatic and glacial history of the Central Sierra Nevada, California. Geological Society of America Special Paper **123**.
- Delcourt, P. A., and H. R. Delcourt. 1992. Ecotone dynamics in space and time. Pages 19-54 in A. J. Hansen and E. di Castri, editors. *Landscape boundaries: consequences for biotic diversity and ecological flows*. Springer-Verlag, New York, New York, USA.
- Denton, G. H., and W. Karlen. 1977. Holocene glacial and tree-line variations in the White River valley and Skolai Pass, Alaska and Yukon Territory. *Quaternary Research* **7**: 63-111.
- Earle, C. J. 1993. Forest dynamics in a forest-tundra ecotone, Medicine Bow Mountains, Wyoming. Dissertation. University of Washington, Seattle, Washington, USA.
- Elias, S. A., P. E. Carrara, L. J. Toolin, and A. J. T. Jull. 1991. Revised age of deglaciation of Lake Emma based on new radiocarbon and macrofossil analysis. *Quaternary Research* **36**:307-321.
- Enzel, Y., W. J. Brown, R. Y. Anderson, L. D. McFadden, and S. G. Wells. 1992. Short-duration Holocene lakes in the Mojave River drainage basin, southern California. *Quaternary Research* **38**:60-73.
- Enzel, Y., D. R. Cayan, R. Y. Anderson, and S. G. Wells. 1989. Atmospheric circulation during Holocene lake stands in the Mojave Desert: evidence of regional climate change. *Nature* **341**:44-47.
- Franklin, J. F., W. H. Moir, G. W. Douglas, and C. Wiberg. 1971. Invasion of subalpine meadows by trees in the Cascade Range, Washington and Oregon. *Arctic and Alpine Research* **3**:215-224.
- Gagnon, R., and S. Payette. 1981. Fluctuations Holocènes de la limite des forêts de mélèzes, Rivière aux Feuilles, Nouveau-Québec: une analyse macrofossile en milieu tourbeux. *Géographie Physique et Quaternaire* **35**:57-72.
- Gorchakovskiy, P. L., and S. G. Shiyatov. 1978. The upper forest limit in the mountains of the boreal zone of the USSR. *Arctic and Alpine Research* **10**:349-363.
- Grace, J. 1989. Tree lines. *Philosophical Transactions of the Royal Society of London* **B234**:233-245.
- Graumlich, L. J. 1993. A 1000-year record of temperature and precipitation in the Sierra Nevada. *Quaternary Research* **39**:249-255.
- Graumlich, L. J., and M. B. Davis. 1993. Holocene variation in spatial scales of vegetation pattern in the Upper Great Lakes. *Ecology* **74**:826-839.
- Graumlich, L. J., and A. H. Lloyd. 1996. Dendroclimatic, ecological and geomorphological evidence for long-term climatic change in the Sierra Nevada, U.S.A. Pages 51-59 in J. S. Dean, D. M. Meko, and T. W. Swetham, editors. *Tree rings, environment and humanity*. Radiocarbon, Tucson, Arizona, USA.
- Griggs, R. F. 1934. The edge of the forest in Alaska and the reasons for its position. *Ecology* **15**:80-96.
- Hadley, J. L., and W. K. Smith. 1983. Influence of wind exposure on needles desiccation and mortality for timberline conifers in Wyoming, U.S.A. *Arctic and Alpine Research* **15**:127-135.
- Hadley, J. L., and W. K. Smith. 1986. Wind effects on needles of timberline conifers: seasonal influence on mortality. *Ecology* **67**:12-19.
- Hasler, R. 1982. Net photosynthesis and transpiration of *Pinus montana* on east and north facing slopes at alpine timberline. *Oecologia (Berlin)* **54**:14-22.
- Holmes, R. L. 1995. Dendrochronological Program Library. Laboratory of Tree-Ring Research, The University of Arizona, Tucson, Arizona, USA.
- Hughes, M. K., and P. M. Brown. 1992. Drought frequency in central California since 101 B.C. recorded in giant sequoia tree rings. *Climate Dynamics* **6**:161-167.
- Hughes, M. K., and H. F. Diaz, editors. 1994. *The medieval warm period*. Kluwer Academic, Dordrecht, The Netherlands.
- Hughes, M. K., and L. J. Graumlich. 1996. Multimillennial dendroclimatic studies from the western United States. In R. S. Bradley, P. D. Jones, and J. Jouzel, editors. *Climatic variations and forcing mechanisms of the last 2000 Years*. NATO Advanced Studies Workshop Series.
- Jackson, S. T., R. P. Futyma, and D. A. Wilcox. 1988. A paleoecological test of a classic hydrosere in the Lake Michigan dunes. *Ecology* **69**:928-936.
- Klikoff, L. G. 1965. Microenvironmental influence on vegetational pattern near timberline in the central Sierra Nevada. *Ecological Monographs* **35**:187-211.
- Kullman, L. 1979. Change and stability in the altitude of tree-limit in the southern Swiss Scandes, 1915-1974. *Acta Phytogeographica Suecica* **65**:1-121.
- . 1986a. Late Holocene reproductional patterns of *Pinus sylvestris* and *Picea abies* at the forest limit in central Sweden. *Canadian Journal of Botany* **64**:1682-1690.
- . 1986b. Recent tree-limit history of *Picea abies* in the southern Swedish Scandes. *Canadian Journal of Forest Research* **16**:761-771.
- . 1987. Long-term dynamics of high-altitude populations of *Pinus sylvestris* in the Swedish Scandes. *Journal of Biogeography* **14**:1-8.
- . 1993. Pine (*Pinus sylvestris*) tree-limit surveillance during recent decades, central Sweden. *Arctic and Alpine Research* **25**:24-31.
- . 1995a. Holocene tree-limit and climate history from the Scandes Mountains, Sweden. *Ecology* **76**:2490-2502.
- . 1995b. New and firm evidence for Mid-Holocene appearance of *Picea abies* in the Scandes Mountains, Sweden. *Journal of Ecology* **83**:439-447.
- LaMarche, V. C. 1973. Holocene climatic variations inferred from treeline fluctuations in the White Mountains, California. *Quaternary Research* **3**:632-660.
- . 1974. Paleoclimatic inferences from long tree-ring records. *Science* **183**:1043-1048.
- LaMarche, V. C., and H. A. Mooney. 1967. Altithermal timberline advance in western United States. *Nature* **213**:980-982.
- Magee, T. K., and J. A. Antos. 1992. Tree invasion into a mountain-top meadow in the Oregon Coast Range, USA. *Journal of Vegetation Science* **3**:485-494.
- Marr, J. W. 1977. The development and movement of tree islands near the upper limit of tree growth in the southern Rocky Mountains. *Ecology* **58**:1159-1164.
- Minnich, R. A. 1984. Snow drifting and timberline dynamics on Mount San Geronio, California, U. S. A. *Arctic and Alpine Research* **16**:395-412.
- Moser, K. A., and G. M. MacDonald. 1990. Holocene vegetation change at treeline north of Yellowknife, Northwest Territories, Canada. *Quaternary Research* **34**:227-239.
- Noble, I. R. 1993. A model of the responses of ecotones to climate change. *Ecological Applications* **3**:396-403.
- Pake, C. E., and D. L. Venable. 1995. Is coexistence of Sonoran desert annuals mediated by temporal variability in reproductive success? *Ecology* **76**:246-261.
- Patten, D. T. 1963. Vegetational pattern in relation to en-

- vironments in the Madison Range, Montana. *Ecological Monographs* **33**:375–406.
- Payette, S., and L. Filion. 1985. White spruce expansion at the tree line and recent climatic change. *Canadian Journal of Forest Research* **15**:241–251.
- Payette, S., L. Filion, A. Delwaide, and C. Begin. 1989. Reconstruction of tree-line vegetation response to long-term climate change. *Nature* **341**:429–432.
- Payette, S., L. Filion, L. Gauthier, and Y. Boutin. 1985. Secular climate change in old-growth tree-line vegetation of northern Quebec. *Nature* **315**:135–138.
- Payette, S., and R. Gagnon. 1985. Late Holocene deforestation and tree regeneration in the forest-tundra of Quebec. *Nature* **313**:570–572.
- Payette, S., and C. Morneau. 1993. Holocene relict woodlands at the eastern Canadian treeline. *Quaternary Research* **39**:84–89.
- Prentice, I. C. 1986. Vegetation responses to past climatic variation. *Vegetatio* **67**:131–141.
- Risser, P. G. 1995. The status of the science examining ecotones. *BioScience* **45**:318–325.
- Schulze, E. D., H. A. Mooney, and E. L. Dunn. 1967. Wintertime photosynthesis of bristlecone pine (*Pinus aristata*) in the White Mountains of California. *Ecology* **48**:1044–1047.
- Scuderi, L. A. 1987a. Glacier variations in the Sierra Nevada, California, as related to a 1200-year tree-ring chronology. *Quaternary Research* **27**:220–231.
- . 1987b. Late-Holocene upper timberline variation in the southern Sierra Nevada. *Nature* **325**:242–244.
- . 1993. A 2000-year tree ring record of annual temperatures in the Sierra Nevada mountains. *Science* **259**:1433–1436.
- . 1994. Solar influences on Holocene treeline altitude variability in the Sierra Nevada. *Physical Geography* **15**:146–165.
- Scuderi, L. A., C. B. Schaaf, K. U. Orth, and L. E. Band. 1993. Alpine tree growth variability: simulation using an ecosystem process model. *Arctic and Alpine Research* **25**:175–182.
- Shiyatov, S. 1993. The upper timberline dynamics during the last 1100 years in the Polar Ural Mountains. *European Palaeoclimate and Man* **4**:195–203.
- Slatyer, R. O., and I. R. Noble. 1992. Dynamics of montane treelines. Pages 346–359 in A. J. Hansen and F. di Castri, editors. *Landscape boundaries: consequences for biotic diversity and ecological flows*. *Ecological Studies*, volume 92. Springer-Verlag, New York, New York, USA.
- Smith, W. K., and G. N. Geller. 1979. Plant transpiration at high elevation: theory, field measurements, and comparisons of desert plants. *Oecologia* **41**:109–122.
- Sokal, R. R., and F. J. Rohlf. 1981. *Biometry*. Second edition. Freeman, New York, New York, USA.
- Spear, R. W. 1989. Late Quaternary history of high-elevation vegetation in the White Mountains of New Hampshire. *Ecological Monographs* **59**:125–151.
- . 1993. The palynological record of Late-Quaternary arctic tree-line in northwest Canada. *Review of Palaeobotany and Palynology* **79**:99–111.
- Stevens, G. C., and J. E. Fox. 1991. The causes of treeline. *Annual Review of Ecology and Systematics* **22**:177–191.
- Stine, S. 1990. Late Holocene fluctuations of Mono Lake, eastern California. *Palaeogeography, Palaeoclimatology, Palaeoecology* **78**:333–381.
- . 1994. Extreme and persistent drought in California and Patagonia during mediaeval time. *Nature* **369**:546–549.
- Stokes, M. A., and T. L. Smiley. 1968. *An introduction to tree-ring dating*. University of Chicago Press, Chicago, Illinois, USA.
- Tranquillini, W. 1979. *Physiological ecology of the Alpine timberline*. Springer-Verlag, Berlin, Germany.
- Wardle, P. 1963. The regeneration gap of New Zealand gymnosperms. *New Zealand Journal of Botany* **1**:301–315.
- . 1968. Engelmann spruce (*Picea engelmannii* Engel.) at its upper limits on the Front Range, Colorado. *Ecology* **49**:483–495.
- Wilson, J. B., and A. D. Q. Agnew. 1992. Positive-feedback switches in plant communities. *Advances in Ecological Research* **23**:263–336.