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Forest Expansion and Climate Change in the Mountain Hemlock (*Tsuga mertensiana*) Zone, Lassen Volcanic National Park, California, U.S.A.

Alan H. Taylor

Department of Geography, The Pennsylvania State University, University Park, Pennsylvania 16802-5011, U.S.A.

Abstract

The relationship between climate change and the dynamics of ecotonal populations of mountain hemlock (*Tsuga mertensiana* [Bong.] Carr.) was determined by comparing climate and the age structure of trees from 24 plots and seedlings from 13 plots in the subalpine zone of Lassen Volcanic National Park, California. Tree establishment was greatest during periods with above normal annual and summer temperatures, and normal or above normal precipitation. Seedling establishment was positively correlated with above normal annual and summer temperatures and negatively correlated with April snowpack depth. The different responses of trees and seedlings to precipitation variation is probably related to site soil moisture conditions. Mountain hemlock populations began to expand in 1842 and establishment increased dramatically after 1880 and peaked during a warm mesic period between 1895 and 1910. The onset of forest expansion coincides with warming that began at the end of the Little Ice Age (1850–1880). These data indicate that stability of the mountain hemlock ecotone is strongly influenced by climate. If warming induced by greenhouse gases does occur as climate models predict, then the structure and dynamics of near timberline forests in the Pacific Northwest will change.

Introduction

High-altitude treelines are dynamic tension zones between forest and tundra where climate, especially temperature, exerts strong control on tree growth and tree population dynamics. Tree population responses to climate may be nonlinear because inertia can cause lags in tree mortality or autogenic processes can facilitate recruitment so ecotone shifts may be out of phase with climate change (Franklin and Dyrness, 1973; Kullman, 1986, 1989, 1993; Steijilen and Zackrisson, 1987; Payette et al., 1989). Moreover, variation in other climatically related factors such as precipitation, snowpack, soil moisture, ground-cover characteristics, incidence of snow mold, or disturbances such as fire and grazing may trigger change in ecotonal forests (e.g., Fonda and Bliss, 1969; Kuramoto and Bliss, 1970; Franklin et al., 1971; Vale, 1981; Agee and Smith, 1984; Shankman, 1984; Daly and Shankman, 1985; Payette and Gagnon, 1985; Taylor, 1990a; Little et al., 1994). Despite the complex response of ecotone tree populations to climate change there is evidence that tree populations have expanded due to recent warming. Secular warming since the end of the Little Ice Age (1850–1880) and warm decades during the 20th century have caused treelines to advance or treeline sites to fill at several sites in the Northern Hemisphere (Payette and Filion, 1985; Kullman, 1986a, 1986b, 1987; Scott et al., 1987; Steijilen and Zackrisson, 1987). Few studies have determined if ecotone dynamics are driven by climate change or more local factors in the Pacific Northwest (Brink, 1959; Franklin et al., 1971; Lowrey, 1972; Heikkinen, 1984) and none have been conducted in the southern Cascades of California.

In Lassen Volcanic National Park in the southern high Cascades of California patches (>0.1 ha) of short (2–5 m tall) mountain hemlock (*Tsuga mertenisana* [Bong.] Carr.) stems are scattered amongst clumps of tall stems (>15 m tall) in the upper (>2400 m) subalpine zone. Tree clumps and regeneration patches occur on a variety of geologic substrates (andesite, dacite, volcanic ash; Williams, 1932), and on all slope aspects, and the short trees appear to be young populations invading sites not previously forested. There is no evidence (i.e., stumps, logs, rotten wood) of a previous forest stand in any of the patches of small trees that I saw in the park.

I hypothesized that the patches of short trees are a young, invading tree population and that climate change triggered the widespread regeneration of mountain hemlock that I observed in Lassen Park. I tested this hypothesis by comparing the age structure of trees and seedlings in regeneration patches to changes in climate, grazing, and fire regimes. Retrospective studies of ecotone dynamics like this one are essential for not only determining how treeline forest structures developed, but for determining how treelines may respond in the future to predicted greenhouse gas induced warming (Houghton et al., 1992).

Study Area

Lassen Volcanic National Park is located at the southern end of the Cascade Range in northern California (Fig. 1). Subalpine (>2400 m) forests on mesic sites in the park are dominated by mountain hemlock, while xeric sites on exposed ridges are occupied by whitebark pine (*Pinus albicaulis* Engelm.) (Pérez, 1990; Taylor, 1990b; Parker, 1992). The mountain hemlock zone in Lassen Park is most extensive on the southern flanks of Lassen Peak (3193 m) and other nearby mountains with summits >2600 m. Forests in the upper mountain hemlock zone are open, and clumps of trees usually occupy small ridges that are frequently oriented perpendicular to the slope or prevailing winds. Intervening depressions are areas of higher snow accumulation, and deeper snow in these basins retards forest development (Billings, 1969; Franklin and Dyrness, 1973). Patches of invading

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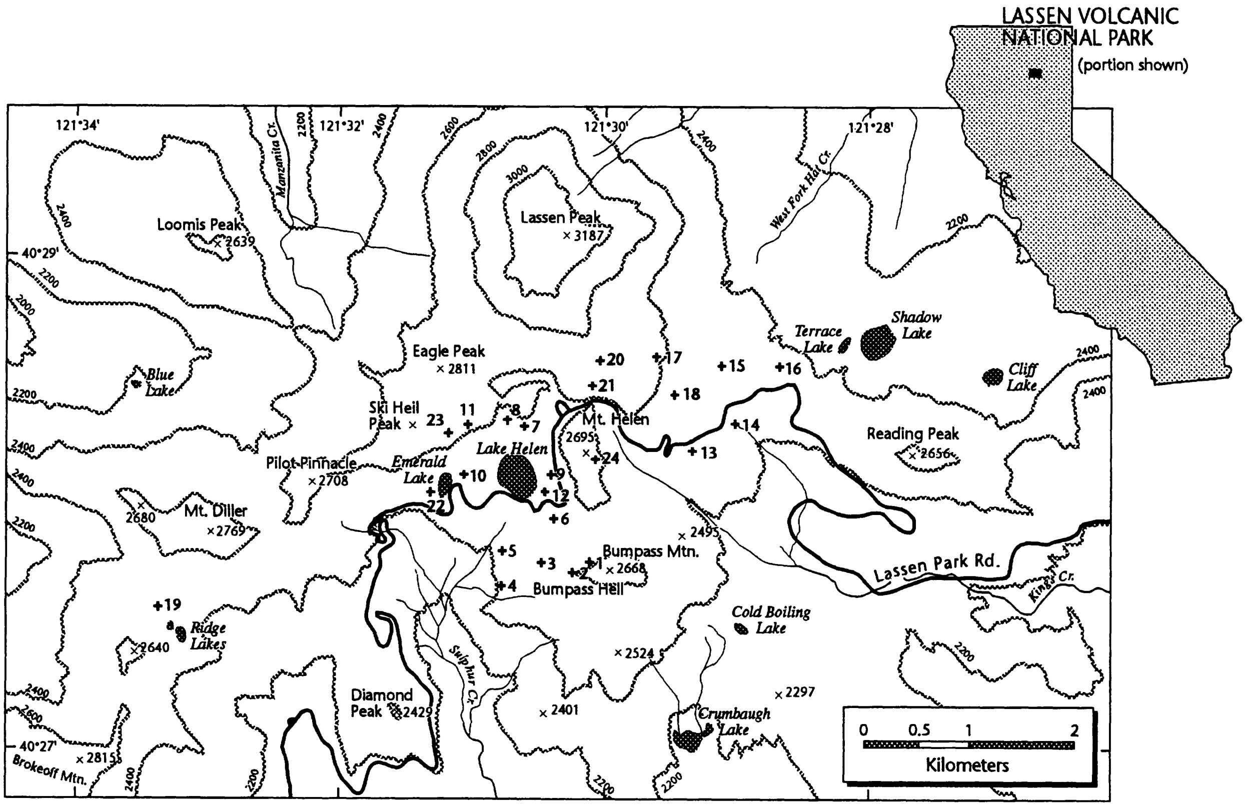

*FIGURE 1. Location of study area and sample plots in the mountain hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California.*

mountain hemlock occur on the flanks of small ridges and in snow accumulation basins (Fig. 2).

The climate in Lassen Volcanic National Park is characterized by cool snowy winters and warm dry summers (Mediterranean Type). Mean annual temperature near the southwest park boundary (Mineral, California, 1477 m) is 7.4°C. Most winter precipitation in the mountain hemlock zone falls as snow and snowpacks are deep. April snowpack depths in the park at 2500 m average 4.8 m (1934–1990) and snowpack depths in June may exceed 6.6 m (data on file Lassen Volcanic National Park, Mineral, California). Even in August, minimum daily temperatures can drop below 0°C in the mountain hemlock zone (Pérez, 1988).

Soils in the areas that were sampled are Lithic and Typic Cryorthents with high gravel (~60%) and sand content (77–93%) in the soil fraction; silt and clay content are low (Pérez, 1989; Parker, 1992). Frost weathering is the primary soil formation process in the study area (Pérez, 1990) and frost heaving occurs frequently even in summer on many sites in the mountain hemlock zone.

Methods

POPULATION STRUCTURE OF INVADING TREES

Stands of invading trees were sampled in plots of various sizes (50–1200 m^2) throughout the mountain hemlock zone. Different sized plots were used because stem density and stem size varied among the regeneration patches that were sampled. Areas recently disturbed by mudflows triggered by the eruptions of Lassen Peak (1914–1917) were not sampled in this study. Each plot included at least 40 trees (>2.0 cm diameter at breast height) and the altitude, slope aspect, and slope pitch of each plot was recorded. All trees were measured (dbh), and seedlings (0.2–0.5 m tall) and saplings (0.5 m tall-2.0 cm dbh) were counted in each plot. The date of establishment of at least 20 trees in each plot was determined by extracting a core 30 cm above the stem base and counting the stems annual growth rings. Twenty-nine years were added to ring counts to account for the number of years seedlings take to reach 30 cm in height. The number of years needed for seedlings to grow to 30 cm in height was estimated by counting basal growth rings on 33 30 cm tall seedlings that were cut-off at ground level (28.9 ± 5.6 yr, range 17–39 yr). Seedling and saplings were not aged in the tree plots because microclimatic influences from tree patches may promote establishment in years with poor climatic conditions (e.g., Brink 1959). All tree ring samples were sanded and ring counts were made beneath a binocular microscope.

POPULATION STRUCTURE OF INVADING SEEDLINGS

Dates of recent mountain hemlock seedling establishment were determined by ageing all seedlings (<50 cm tall; n = 150) in thirteen 5 × 5 m plots in an open flat with a surrounding fringe of invading trees in the upper mountain hemlock zone. There were no saplings in these plots. Seedlings ages were determined by cutting-off seedlings at ground level and counting basal growth rings beneath a binocular microscope or counting annual leaf scars on young (≤4 yr) stems. Seedling ages are probably accurate to within 2 to 3 yr. Errors in aging seedlings result from uncertainty in identifying a seedling's actual stem base and the possible occurrence of false or missing annual growth rings.

CLIMATIC VARIABILITY

Climatic data for Mineral, California, on the western side of Lassen Park were used to identify changes in temperature and

*FIGURE 2. Patches of invading mountain hemlock (*Tsuga mertensiana*) next to mature tree clumps and in late-lying snow basins, Lassen Volcanic National Park (2520 m).*

precipitation that may have influenced tree and seedling establishment. I calculated the following climatic variables for the length of the instrumental record (1932–1990): mean annual, mean spring (March–May), and mean summer (June–August) precipitation; mean annual, mean spring, and mean summer temperatures; and mean minimum and maximum summer temperatures. Winter temperatures were not calculated because seedlings were beneath snow during this period. The influence of snowpack depth on seedling establishment was assessed by using April snowpack depths (1934–1990) from a snow survey site (2500 m) in the middle of the study area. There were 2 yr (1967, 1986) with missing April snowpack depths so I predicted snowpack depths in these years using a regression of April snowpack depth on March snowpack depth ($n = 47$, $r^2 = 0.68$, $P < 0.001$).

Climatic data for Mineral were extended beyond the instrumental record using least squares regression with data from Chico, Red Bluff, and Redding, California, all nearby stations with long instrumental records (Table 1). Both annual and seasonal climatic variables were predicted using the regression equations with the highest coefficients of determination. All regression equations were highly significant (Table 1). April snowpack depth and mean summer maximum and minimum temperatures were not predicted beyond the instrumental record.

The associations between recent seedling establishment and

TABLE 1

Regression equations for predicting annual and seasonal temperature and precipitation for Mineral, California in Lassen Volcanic National Park, from nearby climate stations[a]

Dependent variable	Independent variable[b]	n	r^2	Cnst	Slope
Annual temp.	Chico annual temp.	39	0.63	0.96	0.73
Annual temp.	Red Bluff annual temp.	48	0.35	8.44	0.59
Spring temp.	Red Bluff spring temp.	55	0.80	−14.40	0.93
Summer temp.	Chico summer temp.	55	0.80	−25.70	1.12
Summer temp.	Red Bluff summer temp.	53	0.46	−1.22	0.77
Annual precip.	Chico annual precip.	55	0.63	12.82	1.60
Spring precip.	Redding spring precip.	57	0.68	0.79	1.13
Summer precip.	Chico summer precip.	57	0.63	1.05	1.60

[a] All regressions are significant ($P < 0.001$); temperature is in °F and precipitation is in inches. Spring is March to May, Summer is June to August.
[b] Distances of California climate stations from Mineral: Chico, 89 km; Red Bluff, 74 km; Redding, 79 km.

TABLE 2

*Characteristics of invading mountain hemlock (*Tsuga mertensiana*) stands near timberline in Lassen Volcanic National Park, California*[a]

Plot	Altitude (m)	Aspect (°)	Slope (°)	Trees (ha^{-1})	Saplings (ha^{-1})	Seedlings (ha^{-1})	Age (yr) Mean	Age (yr) Min.	Age (yr) Max.	dbh (cm) Mean	dbh (cm) Min.	dbh (cm) Max.
1	2560	54	5	933	22	0	87	68	106	12.8	5.5	23.5
2	2570	198	6	1640	320	120	95	62	137	15.0	2.7	35.3
3	2500	216	6	2171	57	171	93	45	119	15.0	5.0	25.3
4	2500	285	11	3280	480	720	90	61	108	9.9	3.5	16.4
5	2440	360	14	1560	80	40	86	59	109	11.5	2.8	18.9
6	2490	20	3	6400	1067	133	80	60	101	6.6	2.0	13.5
7	2606	28	19	9000	4200	800	97	74	136	5.6	2.2	12.3
8	2600	136	7	3333	333	200	81	53	100	6.1	2.9	12.5
9	2480	70	8	480	350	290	88	61	112	7.7	2.1	20.7
10	2480	238	10	950	67	17	91	66	123	8.6	2.1	14.3
11	2610	165	11	1333	33	67	97	61	116	12.0	3.7	20.0
12	2424	354	5	1320	1480	1190	87	53	140	10.3	6.1	27.3
13	2460	56	24	3600	533	0	118	85	136	9.6	2.4	21.6
14	2425	10	13	1020	400	200	84	59	107	8.5	2.3	21.6
15	2400	38	23	1438	281	63	77	57	97	7.1	2.3	13.3
16	2640	112	14	367	42	25	91	53	111	9.9	4.3	19.5
17	2540	140	3	1839	442	185	93	53	117	10.7	2.6	21.0
18	2457	20	29	1520	920	70	95	71	127	12.9	6.5	30.0
19	2485	120	6	2440	0	0	107	69	135	11.3	3.6	20.8
20	2584	120	4	960	0	0	87	52	124	11.0	5.6	17.5
21	2540	132	6	610	0	40	96	74	126	13.3	5.8	20.6
22	2484	60	11	470	340	380	86	57	118	15.7	5.5	25.3
23	2624	153	6	410	40	50	69	50	95	7.7	5.0	12.7
24	2666	90	18	740	10	50	106	51	107	11.0	5.3	15.7

[a] Ages are ring counts of trees cored at 30 cm plus 29 yr. Trees are ≥2.0 dbh, saplings are >1.4 m tall and <2.0 cm dbh and seedlings are 0.5–1.5 m tall.

climate were determined as follows. First, 3-yr averages for each climatic variable were calculated for the length of record (1949–1990) for each variable (seedling ages, temperature, precipitation). Second, density of mountain hemlock seedlings in the seedling plots was averaged for stems initiated during these same 3-yr periods. Finally, correlation coefficients (r) were calculated between climate variables and average mountain hemlock seedling density for the 3-yr periods ($n = 14$).

The relationship between climate variation and tree establishment was examined using a different approach. First, 5-yr averages for each climatic variable (annual and seasonal temperature and precipitation) were calculated for the same 5-yr periods used to summarize the tree age data. For temperature this was 1876–1925 and for precipitation it was 1871–1925. Climate-tree establishment relationships were not determined for years after 1925 because younger age-classes (seedling and saplings) were not aged in the 24 tree plots. Second, normal deviates for each climatic variable for each 5-yr period were calculated using the mean and standard deviation for the length of the climatic record. Third, each 5-yr period was then grouped into an above normal, normal, or below normal category describing climatic conditions during that period. Five-year periods were distributed equally among categories using Z scores of ±0.43 as group limits. Plots of normal scores and the climate data indicated that the climate variables were normally distributed. Finally, the median density of trees for each climate category and each climate variable were compared using a Kruskal Wallis H test.

GRAZING AND FIRE HISTORY

Livestock grazing and fire can influence patterns of tree establishment in subalpine forests. I evaluated the possible roles of grazing and fire on tree establishment by examining (1) fire and grazing records for Lassen Park and the surrounding Lassen National Forest; and (2) government reports, survey records, newspapers, and descriptions of early settlement for evidence of grazing or fires in the upper subalpine zone of the park.

Results

INVASIVE TREES

Trees in the sample plots occurred on moderate to steep slopes and on all slope aspects between 2400 and 2666 m (Table 2). Stand density varied widely (range 367–9000 trees ha^{-1} and the average diameter of an invading tree in the plots was 10.4 cm dbh (range 5.6–15.7 cm) (Table 2). All plots had trees that were sexually reproducing. Seedlings and saplings occurred in most plots, 83 and 88%, respectively, and their density also varied among plots (Table 2). An average of 75% (range 24–100%) of the trees in each plot were aged successfully.

The date of initial establishment of mountain hemlock varied among plots. Initial establishment in 21% of the plots occurred in the 1840–1860 period (plots 2, 7, 13, 14, 21) while trees in most plots (79%) first established between 1870 and 1890 (Fig. 3). Tree age was only correlated ($P < 0.05$) with diameter (dbh) in 25% of the plots suggesting strong local microenvironmental control on stem growth. The composite age structure for all plots indicates that establishment began to increase dramatically after 1880, and that initial recruitment peaked between 1895–1910 (Fig. 4). Tree establishment was also abundant between 1910 and 1930 but few trees established after 1931. The apparent decline in mountain hemlock establishment after 1931 is a sampling artifact. Seedlings and saplings in the

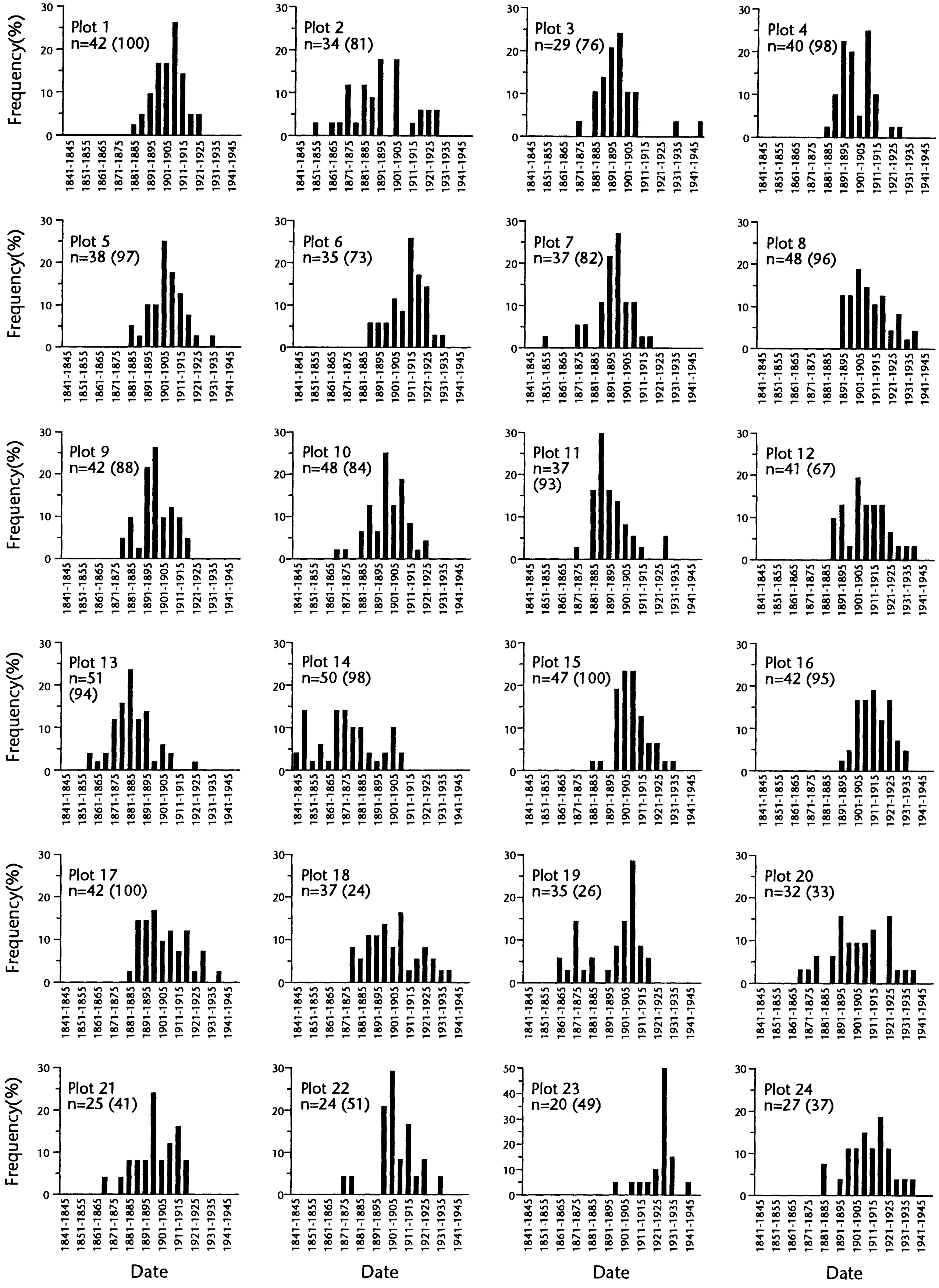

*FIGURE 3. Ages of invading mountain hemlock (*Tsuga mertensiana*) in five year age-classes in 24 plots sampled in Lassen Volcanic National Park, California.* n *is the number of trees (>2.0 cm dbh) aged and the value in parentheses is the percentage of trees aged in a plot. Plot locations are given in Figure 1.*

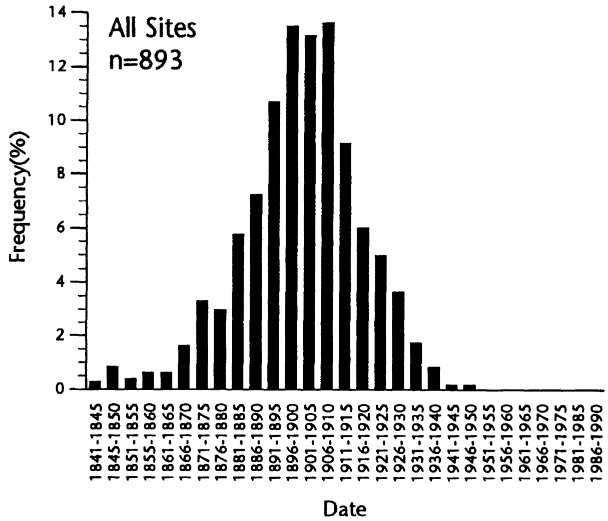

*FIGURE 4. Composite age structure (five year age-classes) of mountain hemlock (*Tsuga mertensiana*) of 24 plots in Lassen Volcanic National Park, California.* n *is the number of aged trees.*

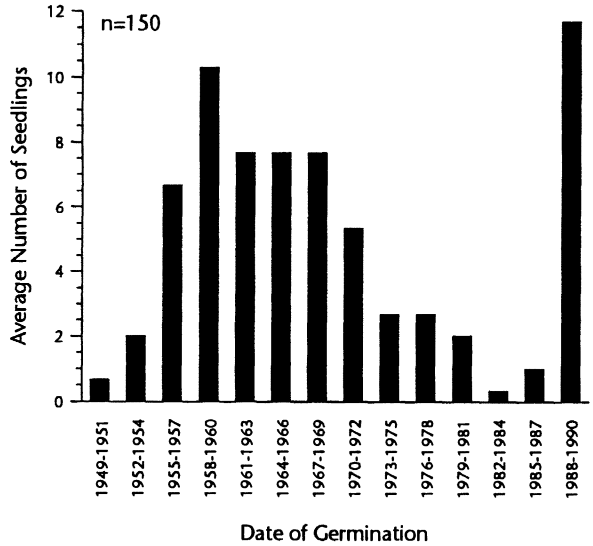

*FIGURE 5. Average number of mountain hemlock (*Tsuga mertensiana*) seedlings in 3-yr age-classes in 13 25-m² quadrats in Lassen Volcanic National Park, California.* n *is the number of aged seedlings.*

plots were not aged and these size-classes represent stems that are mostly <60 yr old. So establishment has continued since 1931 but temporal patterns of establishment for these sized stems are unknown.

POPULATION STRUCTURE OF SEEDLINGS

Mountain hemlock in the thirteen seedling plots established between 1949 and 1990. There was temporal variation in the pattern of establishment (1) few seedling established between 1949–1954 and 1973–1987; and (2) seedling establishment was high in 1955–1972 and 1988–1990 (Fig. 5).

GRAZING AND FIRE HISTORY

Livestock grazing began in what is now Lassen Park in about 1850 when Noble's Emigrant Trail was opened along the present north park boundary. Grazing by cattle, horses, and especially sheep, was heavy between 1860 and 1905. Livestock numbers declined in 1905 when the park became part of the federal forest reserve system (Strong, 1973; Taylor, 1990a). Sheep grazing was eliminated in Lassen Park in 1916 when it became part of the national park system but cattle and horses grazed until 1933 (Taylor, 1990a). The few historical descriptions and records of grazing in the park suggest that grazing was confined to (1) lush subalpine and montane meadows on the lower flanks of Lassen Peak; and (2) meadows and lodgepole pine flats in lower elevation forests in the eastern part of the park.

Fire records for Lassen Park for the period 1933–1977 (n = 393 fires) indicate that natural ignitions are rare in the subalpine zone. Only nine fires during this period occurred in the mountain hemlock zone. All of these fires burned only single trees. Fuels are sparse and discontinuous in mountain hemlock forests that were sampled, so fires are unlikely to spread even if ignitions occur. Moreover, no fire scars were observed on trees near sample plots and there was no charcoal on the soil surface in any of the plots.

CLIMATIC VARIABILITY

Variability in temperature and precipitation that could influence mountain hemlock seedling establishment occurred between 1949 and 1990. Average (3 yr) annual temperature, maximum annual temperature, and minimum annual temperatures were above normal between 1958–1969 and 1988–1990 (except minimum annual), and below average from 1970 to 1987 (Fig. 6a). Average (3 yr) summer temperature, minimum summer temperature, and maximum summer temperatures were above normal from 1952 to 1954, and 1973 to 1987 (Fig. 6b). Periods of above or below normal spring temperatures were short between 1949 and 1966 and they were below normal between 1967 and 1987 and above normal between 1988 and 1990 (Fig. 6b).

Temporal patterns of average (3 yr) seasonal and annual precipitation were also variable (Fig. 6c). Overall, annual and summer precipitation was above normal between 1966 and 1975; spring precipitation was below normal during this same period. Summer precipitation was below normal between 1955 and 1957 when other variables were near normal.

Climate variability that may have influenced tree establishment occurred between 1871 and 1925 too. Average (5 yr) summer and annual temperatures were cool in the early 1880s and above normal between 1886 and 1915. Spring temperatures had an opposite pattern over the same period. Summer, spring, and annual temperatures were near or below normal between 1915 and 1925. Overall, precipitation was low between 1871 and 1890 and 1916 and 1925, and above or near normal between 1890 and 1915 (Fig. 7).

CLIMATIC VARIABILITY AND POPULATION AGE STRUCTURE

Establishment of mountain hemlock seedlings during 3-yr periods was associated with variation in temperature and precipitation. Seedling establishment was positively correlated with periods with warm: average annual (r = 0.70, P < 0.01), average maximum annual (r = 0.72, P < 0.01), average summer (r = 0.64, P < 0.05), average summer minimum (r = 0.56, P < 0.05), and average summer maximum (r = 0.61, P < 0.05) tempera-

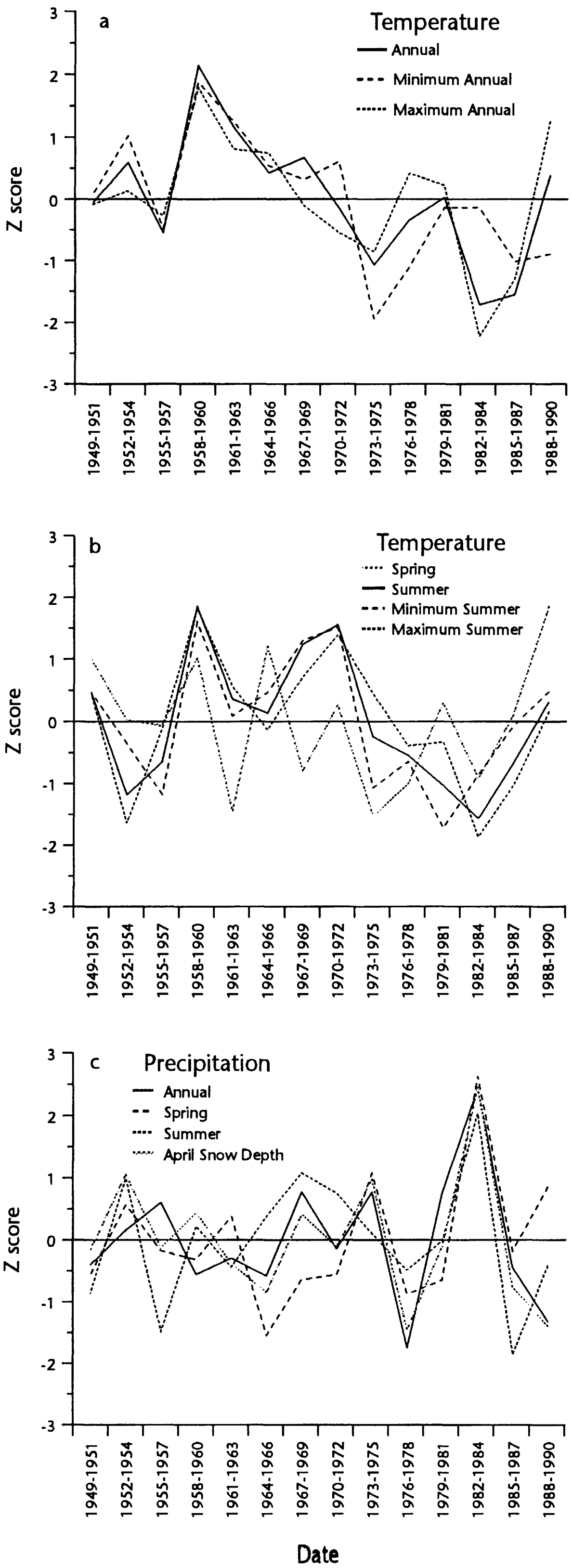

FIGURE 6. Variation (Z scores) in average (3-yr periods) (a) annual, (b) spring (March–May) and summer (June–August) temperature, and (c) annual, spring, and summer precipitation and April snowpack depth. Temperature and precipitation data are for Mineral, California (1477 m) and April snowpack depth from near Lake Helen, Lassen Volcanic National Park, California.

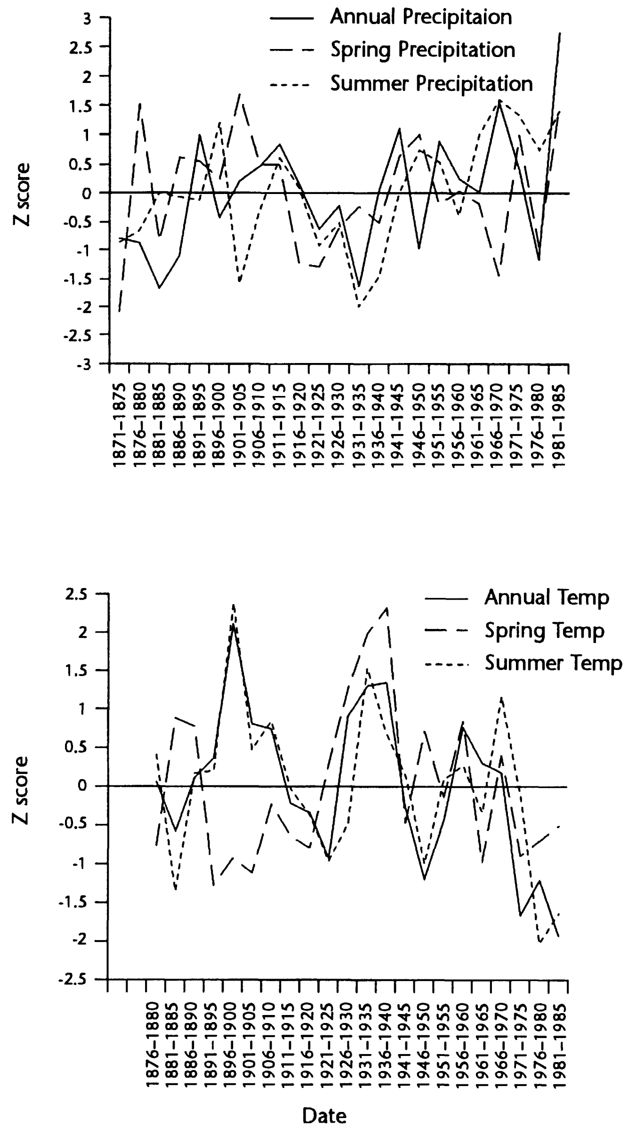

FIGURE 7. Variation (Z scores) in average (5-yr periods) annual, spring (March–May) and summer (June–August) temperaure and precipitation for Mineral California.

tures. There was a negative association ($r = -0.53$, $P < 0.05$) between seedling establishment and April snowpack depth.

Mountain hemlock tree establishment between 1871 and 1925 also varied with temperature and precipitation. Establishment was greater during periods with above normal summer and annual temperatures and normal or above normal annual, spring, and summer precipitation (Table 3).

Discussion

Climatic change strongly influenced patterns of mountain hemlock recruitment in the upper subalpine forests of Lassen Park. Seedling establishment was concentrated during two periods: 1955–1972 and 1988–1990. These were warm periods with low April snowpack depths compared to periods with little or no establishment. The correlations between seedling establishment, temperature, and snowpack depth suggest that snow free growing season length is a strong control on mountain hemlock seedling establishment and recruitment. Snow-free growing-season length is controlled by the duration of snow cover (Billings and Bliss, 1959; Kuramoto and Bliss, 1970; Heikkinen,

TABLE 3

Median tree density (ha^{-1}) in 5-yr age-classes by climate group for the period 1871–1925 in the 24 mountain hemlock tree plots, Lassen Volcanic Natural Park, California

	Temperature			Precipitation		
	Annual[a]	Spring	Summer[a]	Annual[a]	Spring[a]	Summer[a]
Above normal	70 (72)[b]	22 (48)	60 (96)	50 (72)	50 (144)	50 (48)
Normal	40 (120)	40 (48)	40 (96)	50 (48)	70 (24)	44 (120)
Below normal	20 (48)	40 (144)	20 (48)	20 (144)	20 (96)	20 (96)

[a] Significant at $P < 0.01$.

[b] Number of 5-yr age-classes in each group is in parentheses.

1984; Kullman, 1984, 1985; Evans and Fonda, 1990). Snowpacks melt earlier in warmer and/or drier years extending the snow free growing season.

The relationship between climate and mountain hemlock seedling establishment is undoubtedly more complex than the correlations suggest. Other climatically related factors such as the length of favorable climatic periods, germination temperatures, incidence of snow mold, soil moisture, frost heaving, and annual seed crop size probably explain why establishment and/or survivorship varied between periods with similar climate (Wardle, 1968; Tranquillini, 1979; Kearney, 1982; Kullman, 1984, 1985, 1993; Woodward et al., 1994). For example, temperature and snowpacks were near normal in 1955–1957 and 1979–1981, yet establishment was three-fold greater in 1955–1957. Higher establishment in 1955–1957 could be due to larger seed crops during that period, or smaller ones between 1979–1981. Alternatively, survivorship of seedlings that established in 1979–1981 may have been low. The 1979–1981 period was followed by 6-yr of below normal temperatures and above normal snowpacks that may have increased seedling mortality. In contrast, 1955–1957 was followed by a 14-yr period of above and near normal temperatures and below or near normal snowpacks, both conditions favorable for seedling growth and survival. Moreover, the length of warm periods increases the chance that seedlings will establish because there is a higher probability of a good seed crop year.

Climatic change also influenced mountain hemlock tree establishment between 1871 and 1925. During this period establishment was greatest when temperatures (annual, summer) were above normal; this is the same response to temperature that was observed for seedlings between 1949 and 1990. Tree establishment was also affected by precipitation. Establishment was greatest during normal or wet periods. The different responses of tree and seedling populations to precipitation are probably related to the different characteristics of the sites where these populations were sampled.

Tree samples in the park were collected on sloping, well-drained sites and compared to the seedlings samples taken in a flat basin. The positive association between precipitation and tree establishment, in warm periods suggests that low growing season soil moisture may limit mountain hemlock recruitment on more xeric sites. In mesic flats, however, deep snowpacks that are correlated with annual precipitation ($r = 0.78$, $P < 0.01$) can retard recruitment. Similar precipitation-site recruitment patterns have been identified for mountain hemlock in the Olympic Mountains (Agee and Smith, 1984) and for other treeline species (e.g. *Betula pubescens* Ehrh. spp. *tortuosa* [Ledeb] Nyman) (e.g., Kullman, 1985).

Associations between climate change and tree establishment during the 20th century have been identified in other Pacific Northwest forests. In late-lying snow basins and subalpine meadows in the coast range of British Columbia (Brink, 1959), the northern and central Cascades (Franklin et al., 1971; Lowrey, 1972; Heikkinen, 1984) and the Olympic Mountains (Fonda and Bliss, 1969; Agee and Smith, 1984) forests expanded rapidly during warmer periods between 1910 and 1960. Peak recruitment on the highest snow accumulation sites coincided with both the warmest and driest periods. Twentieth-century climate–mountain hemlock establishment patterns in Lassen Park, in general, are similar to those described for these other forests. But, initial forest expansion began earlier in Lassen Park and there is evidence that treeline forests on the Pacific slope are responding to regional climatic changes that began earlier in the 1800s.

North of Lassen Park (1000 km) in the north Cascades and coastal range of British Columbia, mountain hemlock forests began to expand in the 1880s (Brink, 1959; Heikkinen, 1984). Near treeline in the White Mountains south (450 km) of Lassen Park, bristlecone pine (*Pinus longaeva* Bailey) increased after 1850 after a period of low recruitment from 1500–1850 (LaMarche, 1973). Foxtail pine (*Pinus balfouriana* Engelm.) regeneration also increased at treeline after 1850 in southern Sierra Nevada (Scuderi, 1987).

Mountain hemlock forest expansion in Lassen Park began as early as 1842 but establishment at most sites (96%) began in the mid to late 1800s. The onset of forest expansion in the park is coincident with the initial resurgence of tree regeneration that occurred in the north Cascades, the coastal range of British Columbia, the White Mountains, and the southern Sierra Nevada. Forest expansion at these other sites is correlated with secular warming which began at the end of the Little Ice Age in the mid to late 1800s (Fig. 8a-c) (LaMarche, 1974; LaMarche and Stockton, 1974; Heikkinen, 1984; Graumlich and Brubaker, 1986; Graumlich, 1993). Moreover, regeneration in boreal forests in the Northern Hemisphere also increased at this time (e.g., Payette and Filion, 1985; Kullman, 1986a, 1986b, 1987; Scott et al., 1987; Steijilen and Zackrisson, 1987). There are no long-term proxy temperature records for Lassen Park but treeline temperatures north and south of the park rose after 1850 and it is reasonable to assume that they did so in Lassen Park too. However, it is possible that local factors other than climate could have triggered the expansion of mountain hemlock forests in the 1800s.

Livestock grazing has been identified as a trigger causing trees to expand into subalpine meadows in the Sierra Nevada (Vankat and Major, 1978; Helms, 1987; Vale, 1987), Cascades (Vale, 1981) and in Lassen Park (Taylor, 1990a). Heavy grazing, especially by sheep, followed by light grazing or no grazing is associated with the onset or invasion in these studies. In Lassen Park, most trees began to invade meadows in the early 1900s after sheep grazing was reduced or eliminated (Taylor, 1990a).

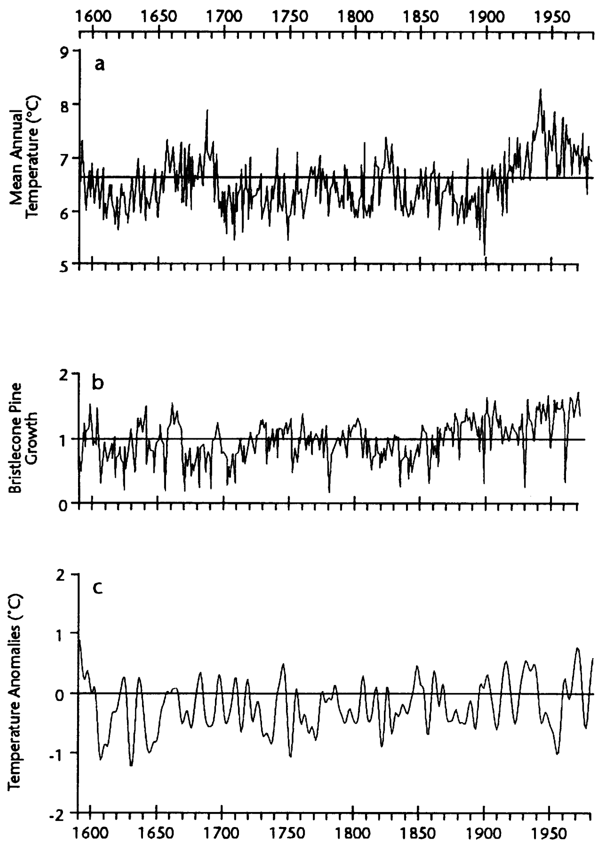

*FIGURE 8. Proxy timberline temperatures from tree rings: (a) north Cascades (Longmire, Washington) 700 km north of Lassen Volcanic National Park (Graumlich and Brubaker, 1986), (b) bristlecone pine (*Pinus longavea*) growth (correlated with spring and summer temperature) Campito Mountain (White Mountains, California) 450 km south of Lassen Volcanic National Park (LaMarche and Stockton, 1974), (c) filtered (Fritts, 1976) annual temperature anomalies in the southern Sierra Nevada (Sequoia National Park) 550 km south of Lassen Volcanic National Park (Graumlich, 1993).*

Expansion of mountain hemlock in the subalpine zone began earlier, in the 1850s, which coincides with the introduction of livestock into the region. But sheep grazing retards tree establishment (e.g., Ratliff, 1985) so forests would not have expanded between 1850 and 1900 if they were being grazed. Moreover, there are no historical records that document grazing in the upper subalpine forests I studied (Strong, 1973; Taylor, 1990a); it is unlikely, therefore, that grazing triggered forest expansion. Fires occur rarely in the mountain hemlock zone and forest expansion predates (1840–1880) the fire suppression era (1930s) in Lassen Park (Taylor, 1990a), so a change in fire regime did not cause forest expansion.

Conclusions

Near treeline mountain hemlock forests in Lassen Park have increased in density since the mid 1800s because of climate change. Warming since the end of the Little Ice Age (1850–1880) triggered population expansion and initial recruitment peaked during a warm mesic period between 1886 and 1915. Recruitment response is spatially variable, however, because high precipitation (i.e., high snowpack) retards recruitment on mesic flats with late lying snow and promotes it on xeric sites. Mountain hemlock populations have continued to expand despite cooling since the 1940s suggesting that inertia, in the form of microclimatic amelioration by developing tree patches, is causing further recruitment despite unfavorable climatic conditions. The temperature driven change in the mountain hemlock ecotone in the last 150 yr suggests that predicted greenhouse gas induced warming (Houghton et al., 1992) will have a significant effect on ecotonal forests in Lassen Park and elsewhere in the Pacific Northwest.

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