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Abstract

Four independent studies of conifer growth between 1880 and 2002 in upper elevation forests of the central Sierra Nevada, California, U.S.A., showed correlated multidecadal and century-long responses associated with climate. Using tree-ring and ecological plot analysis, we studied annual branch growth of krummholz *Pinus albicaulis*; invasion by *P. albicaulis* and *Pinus monticola* into formerly persistent snowfields; dates of vertical branch emergence in krummholz *P. albicaulis*; and invasion by *Pinus contorta* into subalpine meadows. Mean annual branch growth at six treeline sites increased significantly over the 20th century (range 130–400%), with significant accelerations in rate from 1920 to 1945 and after 1980. Growth stabilized from 1945 to 1980. Similarly, invasion of six snowfield slopes began in the early 1900s and continued into snowfield centers throughout the 20th century, with significantly accelerated mean invasion from 1925 to 1940 and after 1980. Rate of snowfield invasion decreased between 1950 and 1975. Meadow invasion and vertical leader emergence showed synchronous, episodic responses. *Pinus contorta* invaded each of ten subalpine meadows in a distinct multidecadal pulse between 1945 and 1976 (87% of all trees) and vertical release in five krummholz *P. albicaulis* sites also occurred in one pulse between 1945 and 1976 (86% of all branches). These synchronies and lack of effect of local environments implicate regional climate control. Composite weather records indicated significant century-long increases in minimum monthly temperature and multidecadal variability in minimum temperature and precipitation. All ecological responses were significantly correlated with minimum temperature. Significant interactions among temperature, precipitation, Pacific Decadal Oscillation (PDO) indices, and multiyear variability in moisture availability further explained episodic ecological responses. Four multidecadal periods of the 20th century that are defined by ecological response (<1925; 1925–1944; 1945–1976; >1976) correlate with positive and negative PDO phases, as well as with steps in the rate of temperature increase. These diverse factors in spatially distributed upper-montane and treeline ecosystems respond directionally to century-long climate trends, and also exhibit abrupt and reversible effects as a consequence of interdecadal climate variability and complex interactions of temperature and moisture.

Introduction

Increasing evidence has led to widespread consensus that average global surface temperatures during the 20th century have increased 0.6°C with two periods of accelerated warming, from 1920 to 1945 and after 1976 (IPCC, 2001). This long-term trend represents a significant anomaly from conditions of the last millennium (Mann et al., 1999; Esper et al., 2002) and poses considerable challenges to assessing resource and social consequences in the 21st century. Significant interdecadal variability during the 20th century has also been observed at regional to global scales (Jones et al., 1999; IPCC, 2001), and is anticipated to affect future climates as well. In western North American, for instance, the Pacific Decadal Oscillation (PDO), a long-lived El Niño/Southern Oscillation (ENSO)-like mode of climate variability defined by North Pacific Ocean temperatures, affects regional climate at scales of several decades (Mantua et al., 1997; Zhang et al., 1997).

Ecological responses to 20th century climate changes have been reported from diverse ecosystems worldwide (Walther, et al., 2002; Parmesan and Yohe, 2003; Root et al., 2003). Partitioning climate from other natural and anthropogenic influences, however, remains difficult,

making climate-sensitive alpine and high-latitude environments critical for study (Parmesan and Yohe, 2003). Many studies of terrestrial ecological response have focused on average 20th century-long patterns or on specific periods within the 20th century (Easterling et al., 2000). In alpine and arctic locations, generalized warming trends have been linked to forest expansion (Payette and Delwaide, 1994; Taylor, 1995; Klasner and Fagre, 2002) and changes in tree-ring width (D'Arrigo et al., 2000; Barber et al., 2000; Linderholm, 2002). Century-long effects of interdecadal variability on subalpine forest dynamics, however, have not been investigated. Further, biogeographic models that predict ecological consequences of future global change often assume species will make directional shifts (Lenihan and Neilson, 1995; Sykes, et al., 1996) with little consideration for abrupt or reversible changes resulting from complex interactions of species with climate.

Upper-elevation forest ecosystems offer unique opportunities to assess century- and decadal-scale climate effects directly. Gradients in seasonal precipitation, temperature, wind, and snow regulate species composition, density, distribution, tree growth, crown architecture, age-class structure, and reproductive capacity (Tranquillini, 1979; Stevens and Fox, 1991; Körner, 1998, 1999). In the Sierra Nevada,

California, U.S.A., trees in subalpine communities are known to be sensitive indicators of climate change, have persisted for many centuries, and are reasonably isolated from typical disturbance events and inter- and intraspecific competition common in lower elevation Sierra Nevada forests (Graumlich, 1993; Lloyd, 1997; Anderson and Smith, 1997; Lloyd and Graumlich, 1997). Well-documented late Holocene climate variability of the Sierra Nevada provides the context in which 20th century changes are nested (Stine, 1996; Millar and Woolfenden, 1999a). In the Sierra Nevada, the Little Ice Age was the largest glacial advance and most extensive cold period since the late Pleistocene, and lasted from 1450 CE to 1850 CE (Clark and Gillespie, 1997; Konrad and Clark, 1998). Paleoecological changes in the Sierra Nevada, such as lowered treeline (Lloyd and Graumlich, 1997), decreased forest productivity (Graumlich, 1993), and changes in species distributions and fire regimes (Swetnam, 1993; Anderson and Smith, 1997; Davis, 1999), mark a transition from the previous warm and dry medieval centuries (900–1250 CE; Graumlich, 1993; Stine, 1996) into the generally cold and dry Little Ice Age. Subsequent warming of the late 19th and early 20th centuries was accompanied by changes in precipitation as well as temperature, with the result that relative to the previous millennium, the 20th century was anomalously wet and warm in the Sierra Nevada (Graumlich, 1993).

The central Sierra Nevada is also situated in a sensitive area for detecting interdecadal-scale climate effects. This region lies within or just south of a zonal transition in western North America where expression of both the El Niño/Southern Oscillation and the Pacific Decadal Oscillation switches (Redmond and Koch, 1991; Cayan et al., 1998). South of this transition, positive phase ENSO and PDO bring generally warmer and wetter conditions relative to negative phase ENSO and PDO, which bring drier and cooler weather. In the Sierra Nevada, winter storms are warmer and wetter during positive PDOs and drier and cooler during negative PDOs (Dettinger and Cayan, 2000). Positive departures of PDO indices in the 20th century characterize the periods from 1920 to 1945 and 1976 to 1998, while a strong negative departure occurred from 1946 to 1975, and a weak negative phase occurred prior to 1920 (Wolter, 2000).

Whereas the development and climatic expression of ENSO are relatively well understood (Diaz and Markgraf, 2000), the causes and effects of PDO remain unclear (Chao et al., 2000), and even the existence of PDO as a distinct phenomenon has been questioned (Pierce, 2001). Effects of PDO on tree growth have been recorded from tree-ring studies in temperate lowlands (Biondi et al., 2001) and montane forests in western North America (Peterson and Peterson, 2001; Peterson et al., 2002), but the role of PDO on forest spatial dynamics or crown architecture has been little studied. Given the proximity of the central Sierra Nevada to the zonal climate transition, a detectable signal there would help to clarify the existence, geographic extent and expression of the PDO mode.

As part of ongoing studies of vegetation response to climate of the late Holocene, we have been investigating ecological changes in diverse high-elevation Sierra Nevada forest ecosystems (King and Graumlich, 1998; Millar and Woolfenden, 1999b; Rogers et al., 1999). From this work emerged preliminary evidence of synchronous changes during the 20th century in independent traits of four pine species from disparate environmental locations widely scattered in this area. The existence of potential synchronies across broad elevational and spatial ranges led us to examine these changes more closely. We thus undertook specific investigations of these traits, and conducted a coordinated set of four studies of upper montane and subalpine tree growth and forest dynamics along the central Sierra Nevada crest in California. Our overall objective was to evaluate temporal patterns in tree growth and stand dynamics of high-elevation pine forests during the past 120 yr, and to assess resulting synchronous changes in relation to 20th century-long and interdecadal climate variability.

Study Objectives and Site Descriptions

The four studies we undertook, and their objectives, were as follows. *Annual branch growth*: Measure annual branch elongation in krummholz whitebark pine (*Pinus albicaulis*) growing at the upper forest border (treeline) and evaluate pattern, timing, and synchrony of significant variability. *Vertical branch release*: Estimate dates of whitebark pine krummholz "flags" at treeline and evaluate timing and synchrony of release of vertical branches emergent above krummholz crowns. *Invasion of subalpine meadows* and *Invasion of snowfield openings*: Estimate dates of lodgepole pine (*Pinus contorta*) invading meadows, and whitebark pine and western white pine (*P. monticola*) invading snowfield openings, respectively, and evaluate timing and synchrony of establishment and expansion in each situation. Analyses for all four studies focused on the period from 1880 to 2000. We assessed local effects of elevation, substrate, and land-use history on ecological responses and, where these were nonsignificant, interpreted synchronous responses across sites within studies and correlated responses among studies to reflect potential influence of regional climate (climate "diagnostic fingerprint," Root et al., 2003).

Study sites were located in the high Sierra Nevada of Tuolumne and Mono Counties, California, in the vicinity of northeastern Yosemite National Park (west of the crest) and adjoining national forest lands east of the Sierran crest (Fig. 1). With the exception of one location, each of the four studies included a unique set of sites, making a total of 26 locations and 27 study sites (Table 1, Fig. 1). Whitebark pine is the dominant high-elevation conifer in this area. At lower elevations (2400 to 3000 m) it forms a 300–600 m elevation zone of upright forest. This grades into a 100–500 m elevation zone of stunted krummholz that extends to treeline (approx. 3500 m in this area). The krummholz habit is enforced by severe climate conditions. Exposed vertical branches and stems are readily killed by the mechanical and physiological effects of wind, ice, and temperature on cuticle development, foliage desiccation, and stem breakage, effectively pruning the crowns into compact form (Baig and Tranquillini, 1980; Sowell et al., 1982; Hadley and Smith, 1983, 1986, 1989).

Expansion of krummholz crowns is by horizontal growth of branches, vegetative layering, which allows individual trees to persist over 1700 yr (King and Graumlich, 1998), and by intermingling of tightly packed independent genets (Rogers et al., 1999; unpubl. data). Winter snowpacks protect needles, buds, and stems from effects of wind, temperature, and radiation, and reduce soil freezing (Billings and Bliss, 1959; Sowell et al., 1982; Daly, 1984; Walsh et al., 1994). Growing-season temperature and duration are considered primary controls on crown expansion in the krummholz zone for whitebark and related treeline pine species (Weaver, 1994, 2001). Under extended favorable conditions, vertically oriented branches of krummholz whitebark pine undergo release growth and emerge above the dense, flat crowns, and, if favorable conditions persist, endure many years (Weisberg and Baker, 1995; Cairns and Malanson, 1997). Relative to more typical treeline environments, conditions promoting vertical branch growth include reduction in wind speed, favorable water balance, lower ice-abrasion of the foliage, warmer summers, and longer growing seasons (Butler et al., 1994; Payette and Delwaide, 1994; Weaver, 1994, 2001).

The *annual branch growth* study had six krummholz treeline sites, five west of the Sierran crest and one east of the crest (Table 1, Fig. 1). Sites were selected to include granitic and metamorphic substrates, near local treeline but not slope-controlled, distributed across the landscape, and in the proximity of existing whitebark pine tree-ring chronologies to enable accurate cross-dating. The selected sites ranged from 3430 to 3565 m elevation, and were primarily south facing with slopes averaging 17° to 27°. The *vertical branch release* study had five krummholz treeline sites, four west of the Sierran crest
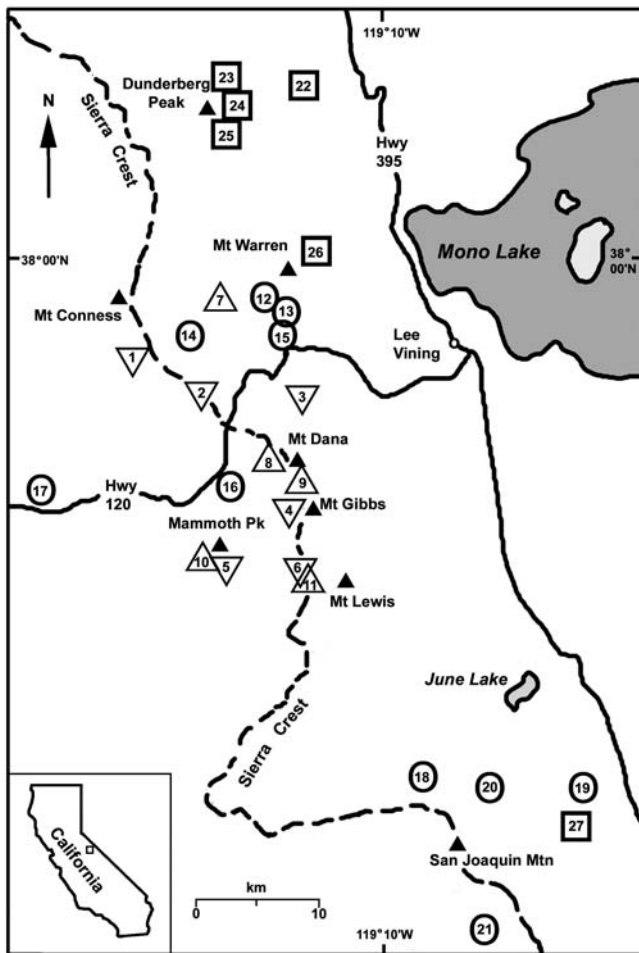
FIGURE 1. Locations of 27 study sites in the central Sierra Nevada, California, U.S.A., for annual branch growth (1–6; inverted triangle), vertical branch release (sites 7–11; open triangles), meadow invasion (sites 12–21; circles), and snowfield invasion (sites 22–27; squares) studies. Solid triangles are mountain peaks. Sites: 1. Young Lakes; 2. Granite Lakes; 3. Dana Plateau; 4. Mt. Gibbs; 5. Mammoth Peak; 6. Mt Lewis; 7. Saddlebag; 8. Mt. Dana; 9. Mt. Gibbs II; 10. Mammoth Peak II; 11. Mt. Lewis; 12. Rockbound; 13. Upper Warren; 14. Hall RNA; 15. Warren Fork; 16. Dana; 17 Tuolomne; 18. Spooky; 19. Glass Cr; 20. Yost; 21. Devils Postpile; 22. Fourth of July; 23. Dunderberg SN; 24. Dunderberg TP; 25. Dunderberg SB; 26. Warren Bench; 27. Whitewing.

Invasion of montane meadows by conifers has been observed in many parts of the Sierra Nevada (Boche, 1974; Wood, 1975; Vankat and Major, 1978; Vale, 1981a; Helms, 1987) as well as in other mountain ranges of California (Taylor, 1990, 1995) and western North America (Franklin et al., 1971; Dunwiddie, 1977; Vale, 1981b; Jakubos and Romme, 1993; Rochefort and Peterson, 1996). Composition and structure of invading trees varied among those studies, with considerable diversity in age of first invasion, and nature of invasion (gradual or episodic; transient or stable). Explanations for forest-meadow instability have included fire suppression (Vale, 1981b; deBenedetti and Parsons, 1984; Taylor, 1990, 2000), over-grazing by domestic livestock (Dunwiddie, 1977; Vankat and Major, 1978; Vale, 1981a; Taylor, 1990), changes in seedcrop and competitive interactions (Jakubos and Romme, 1993), and climate (Franklin et al., 1971; Wood, 1975; Helms, 1987; Jakubos and Romme, 1993; Rochefort and Peterson, 1996).

Our *meadow invasion* study included ten meadow sites, seven east of the Sierran crest and three west of the crest (Table 1, Fig. 1). We selected flat to slightly sloping, upper montane meadows that had evidence of invading conifers, ranging from sparse to abundant. To avoid flood influences, we chose meadows that were situated away from major rivers; thus the sites were mostly in upper watersheds. We selected sites to represent diverse substrates, including volcanic, metamorphic, and granitic soils, and a range of domestic livestock-grazing histories, from 95 yr of nonuse to currently active allotments (Table 1). All invading species were lodgepole pine. Sites ranged from 2315 to 3050 m.

Another type of tree invasion typical of the eastern slope of the Sierra Nevada occurs on slopes that formerly supported snowfields into the growing seasons. Most commonly these are moderate to steep north-facing slopes, below treeline, at elevations of 2700 to 3150 m. Forest openings have rocky, undeveloped soils, are generally elliptical in shape, with concave slopes and steep headwalls, and are surrounded by closed forest on lesser slopes. Apart from colonizing pines, the sites are mostly barren of vegetation. Similar to the commonly observed glacial retreat over the last 100 years in the Sierra Nevada and other western North American mountain ranges (Krimmel, 2002), these formerly persistent snowfields appear to be melting earlier in summer over the 20th century. Air photos from 1940, 1950, 1964, and 1972 (unpublished USDA Forest Service, Inyo National Forest archives, Bishop and Lee Vining, California), combined with recent observations, document the general trend toward earlier seasonal snowmelt of these sites, which creates new habitat for pine colonization. During the growing season, snowbanks melt inward from the forest border toward the center of the opening, where snow lingers longest. Increases in forest density have been observed in subalpine forests of western North America, where fire suppression, domestic livestock grazing and climate change have been considered causal factors (Peterson et al., 1990; Rochefort et al., 1994; Szeicz and MacDonald, 1995; Taylor, 1995, 2000; Murray et al., 2000; Klasner and Fagre 2002). These changes, however, have been described for forest stand conditions, whereas colonization into snowfield openings has not been investigated previously.

The *snowfield invasion* study had six sites, all east of the Sierran crest (Table 1, Fig. 1). We selected sites that had invading trees, from sparse to abundant, evidence from air photos for being historically persistent snowfields, and snowbanks that persisted into summer in recent years. The sites ranged from 2730 to 3105 m, had northern exposures with 16 to 21° slopes, and with volcanic or metamorphic substrates. Invading species included lodgepole pine, western white pine and whitebark pine (lower elevation sites) and whitebark pine (high-elevation sites). The snowfield openings were surrounded by tall, closed forests of the same species composition and mix as invading species.

and one east of the crest. The distribution of vertical branches on krummholz is irregular on the landscape; study locations were chosen to be near the annual branch growth study sites where possible. Sites ranged from 3300 to 3445 m and had southern and western exposures. Slopes averaged 15° to 27° and were underlain by granitic or meta-morphic soils. The Mt. Lewis site was the same for both annual branch and vertical branch release studies, although different krummholz individuals were sampled. No evidence of recent fire or insect/pathogen damage was present at any site.

Intermingled within and below the lower whitebark pine zone in this region are closed- and open-forest types, including those dominated variably by lodgepole pine, mountain hemlock (*Tsuga mertensiana*), white pine, red and white fir (*Abies magnifica* and *A. concolor*, respectively), and rarely limber pine (*Pinus flexilis*). Subalpine meadows are scattered in this landscape from 2600 to 3050 m. Meadows tend to be small on the eastern Sierran escarpment, due to its steep, arid, and rocky nature, whereas west of the Sierran crest, more gentle topography and wetter conditions support large as well as small meadows.

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TABLE 1

Study site locations, elevations, environmental conditions, and sample sizes for 27 study sites, central Sierra Nevada, CA, U.S.A.: A. Whitebark pine annual branch growth study, B. Vertical branch release study, C. Meadow invasion study, and D. Snowfield invasion study. Soil substrates: Meta = metamorphic; Gran = granitic; Volc = volcanic substrates

A. Annual Branch Growth

Site Name	Elev (m)	Lat°N, Long°W	Aspect, Slope	Soils	# Branches Dated	No. 25-cm Intervals
Young Lakes	3535	37°57′, 119°19′	SSE, 27°	Gran	28	122
Granite Lakes	3505	37°56′, 119°18′	S, 22°	Gran	30	150
Dana Plateau	3430	37°55′, 119°14′	S, 17°	Meta	14	28
Mt. Gibbs	3500	37°52′, 119°13′	SW, 24°	Meta	51	306
Mammoth Peak	3565	37°51′, 119°16′	WSW, 23°	Gran	14	77
Mt. Lewis	3445	37°50′, 119°12′	SW, 19°	Meta	21	116
Total					**158**	**799**

B. Vertical Branch Release

Site Name	Elev (m)	Lat°N, Long°W	Aspect, Slope	Soils	No. Vertical Branches Dated
Saddlebag	3430	37°59′, 119°16′	SW, 18°	Meta	35
Mt. Dana	3300	37°55′, 119°14′	WNW, 25°	Gran/Meta	24
Mt. Gibbs II	3325	37°51′, 119°13′	SSW, 15°	Meta	26
Mammoth Peak II	3415	37°51′, 119°16′	WSW, 27°	Gran	36
Mt. Lewis	3445	37°50′, 119°12′	SW, 19°	Meta	5
Total					**126**

C. Meadow Invasion

Site Name	Elev (m)	Size (ha)	Lat°N, Long°W	Grazing Status, Yr. Last Grazed	Soils	No. Trees	No. Seedlings
Rockbound	3025	0.6	37°58′, 119°15′	Terminated, 1950	Meta	68	2
Upper Warren	3050	2	37°57′, 119°16′	Terminated, 1950	Meta	101	0
Hall RNA	2950	4	37°56′, 119°14′	Terminated, 1933	Gran	55	0
Warren Fork	2805	1	37°55′, 119°17′	Terminated, 1950	Meta	36	10
Dana	2950	25	37°53′, 119°15′	Terminated, 1905	Meta	71	1
Tuolomne	2645	35	37°52′, 119°22′	Terminated, 1905	Gran	78	0
Spooky	2900	2	37°44′, 119°08′	Active, 2001	Gran	51	0
Glass Cr	2705	8	37°43′, 119°03′	Irregular, 1999	Volc	346	0
Yost	2865	2	37°42′, 119°06′	Active, 2001	Volc	20	0
Devils Postpile	2315	0.4	37°38′, 119°05′	Terminated, 1911	Volc	45	13
Total						**871**	**26**

D. Snowfield Invasion

Site Name	Elev (m)	Size (ha)	Lat°N, Long°W	Aspect, Slope	Soils	No. Trees	No. Seedlings
Fourth of July	2730	5	38°05′, 119°10′	NE, 18°	Meta	104	21
Dunderberg SN	3100	14	38°03′, 119°16′	NE, 16°	Meta	76	36
Dunderberg TP	3100	10	38°03′, 119°16′	NE, 16°	Meta	123	15
Dunderberg SB	3105	8	38°03′, 119°16′	NE, 16°	Meta	59	3
Warren Bench	3005	15	38°00′, 119°09′	NE, 18°	Meta	70	8
Whitewing	2765	12	37°42′, 119°03′	N, 21°	Volc	54	39
Total						**486**	**122**

Methods

FIELD SAMPLING METHODS AND DATING PROCEDURES

For the annual branch growth study, we cut branches approximately 2 m long and 5 cm basal diameter from 175 horizontally spreading krummholz branches around the perimeter of krummholz patches. We identified the terminus of secondary growth near the apical tip and used it as a reference point for cutting thin branch cross sections at 25-cm intervals along the stem. On each stem sample, we calculated the pith date using standard cross-dating techniques (Holmes et al., 1986; Cook and Kairiukstis, 1990) and locally available chronologies (King, 1998), augmented by reference to regionally synchronous frost-ring and marker-year events developed from a local small-stem whitebark pine

chronology (King, 1998; King and Graumlich, 1998). We estimated annual growth increments in each dated 25-cm interval by assuming an average growth rate between the pith dates of consecutive stem samples. In total, for the period 1895–1996, we estimated growth in 799 stem intervals from 158 branches at the five sites (Table 1).

For the vertical branch release study, we sampled 152 vertical stems by cutting stems at the plane defined by the current upper level of the krummholz crown. We estimated branch release dates on 126 of these stems (Table 1) using standard cross-dating techniques, local chronologies, and referencing the same frost-ring and marker-year whitebark pine chronology used in the annual branch growth study.

For the meadow invasion and snowfield invasion studies, we first evaluated methods for determining ages of invading trees. Pine species

Estimates of mean tree age (and standard deviations) at coring height (0.5 m) based on counts of number of branch whorls from the ground to 0.5 m in 30 trees less than 1.5 m total height for meadow sites and 30 trees per species for snowfield sites. Not all species are present at each site. The mean values were added to ring counts at coring height to estimate total tree age

Meadows:	Glass Cr	Yost	Dana	Spooky	Tuolomne	Hall RNA	Warren Fork	Upper Warren	Rockbound	Postpile Devils
Pinus contorta										
Mean	10.4	10.2	10.8	9.7	12.6	14.4	10.3	9.5	12.0	5.1
SD	2.6	2.1	2.0	2.2	2.2	2.2	2.2	1.9	1.4	1.4

Snowfields:	Whitewing	Warren Bench	Dunderberg SN	Dunderberg TP	Dunderberg SB	Fourth of July
Pinus albicaulis						
Mean	15.1	13.9	24.5	24.7	25.3	–
SD	2.4	5.9	7.3	3.2	2.5	–
P. contorta						
Mean	10.0	–	–	–	–	9.6
SD	2.6	–	–	–	–	1.2
P. monticola						
Mean	15.0	–	–	–	–	16.7
SD	3.7	–	–	–	–	3.5

in the upper montane Sierra Nevada region are regularly uninodal, and branch whorl nodes can be detected with high accuracy on trees less than about 1.5 m height, making whorl count a reliable estimator of total age in small trees. We confirmed this assumption by counting rings at different internode levels in a set of small trees at each site. Ring counts are necessary in larger trees. Because we found basal cores to give unreliable age estimates, we cored at 0.5 m height for trees that were >5 cm basal diameter, and counted rings. To estimate average age at 0.5 m height, we counted branch whorls from the ground to 0.5 m height in a sample of 30 randomly selected trees of each species from each snowfield and each meadow site and obtained average values (Table 2). We added these site- and species-specific values to ring counts from 0.5-m cores to estimate total age for each cored tree.

For each meadow and snowfield site, we established line transects extending from the surrounding forest into meadow and snowfield centers, respectively. The number of transects per site varied with the size of the opening, and the distribution and abundance of invading trees. We established 3-m radius circular plots at 15-m intervals along the transects, starting with a forest plot. At each plot, we cored a maximum of 10 trees greater than 0.5 m height per plot. When more than 10 trees of this size were in the plot, we sampled the 10 trees closest to the plot center. When trees less than 0.5 m height were present in a plot, we randomly selected an additional 10 individuals per plot from this size class, and estimated tree age by counting total whorl numbers. In all, we dated 897 trees in the meadow invasion study and 608 trees in the snowfield invasion study (Table 1).

STATISTICAL METHODS

Ecological Response within and among Studies

Because we intentionally selected study sites to represent diverse environmental conditions, we expected heterogeneity in ecological response among sites within each study. We reasoned that synchronous directional or multiyear trends that might occur among sites could indicate response to common regional rather than local influences. Thus although we tested heterogeneity of means among sites within studies, we focused on comparisons of relative pattern, direction, and timing of responses over multiple years within and among studies.

For the annual branch growth study, we evaluated significant differences in mean growth among sites for the overall period (1880–1996) by a nested analysis of variance (ANOVA of plots within transects within sites) (all statistical analyses, except as noted otherwise, were conducted by *JMP* procedures from SAS Institute, 2000). We assessed differences in multiyear patterns and trends among sites by simple correlations analysis of individual site means with the pooled dataset from all sites, and by principal components analyses

Weather and water-gauging stations providing long-term data used in assessing climatic relationships of ecological response. All stations are in California, except Mina, which is in Nevada. Data provided by Western Regional Climate Center (WRCC: http://www.wrcc.dri.edu), National Climate Data Center (Yosemite Valley weather data prior to 1948, http://www.ncdc.noaa.gov/) and U.S. Geological Survey, Water Resources (USGS: http://www.ca.water.usgs.gov/)

| Station	Agency-Code	Lat°N Long°W	Elev (m)	Period-of-Record
A. Monthly precipitation, average monthly minimum temperature				
Scramento	WRCC-047633	38°31′ 121°30′	6	1890–2002
Mina (NV)	WRCC-265911	38°23′ 118°06′	1387	1897–2002
Yosemite Valley	WRCC-049855	37°45′ 119°35′	1250	1907–2002
B. Monthly streamflow				
Cole Creek	USGS-11315000	38°31′ 120°12′	1804	1927–2002
E Walker	USGS-10293000	38°19′ 119°12′	1951	1921–2002
Merced	USGS-11264500	37°44′ 119°33′	1224	1915–2002
N Fork Stanislaus	USGS-11294500	38°15′ 120°17′	1033	1914–2002

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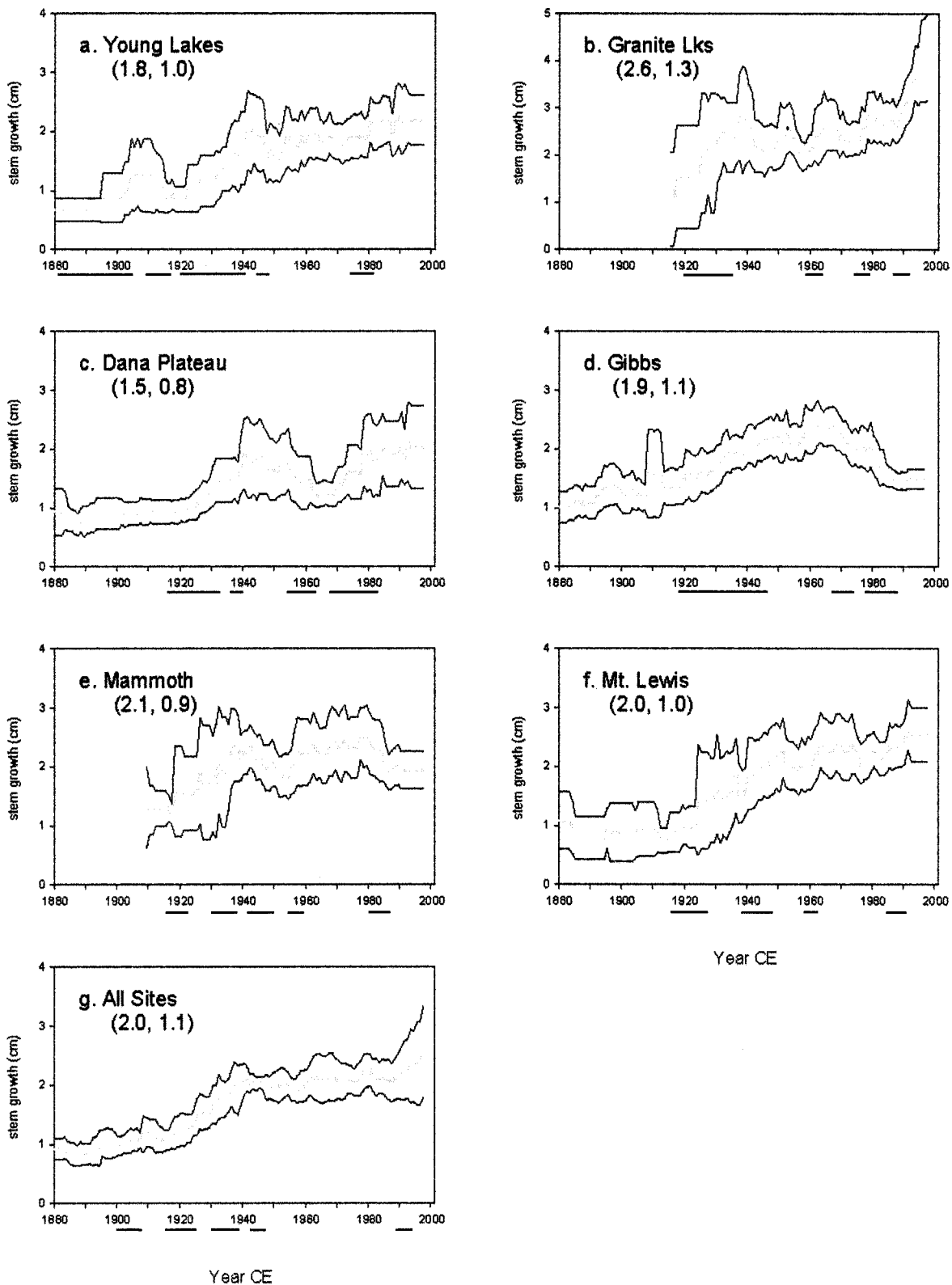
FIGURE 2. *Annual growth of horizontal branches in krummholz* Pinus albicaulis *at six Sierra Nevada treeline sites (a–f) and pooled (g) for the period 1880–2002. Site mean growth (cm) and standard deviations (cm) are given, respectively, below site labels. Horizontal lines indicate time periods of significant (P < 0.05) change in response from t-tests of Webster analyses on 6-yr moving windows.*

(PCA). We also fit the growth data using a mixed-model ANOVA of sites with third- and fourth-order polynomial regressions of year and site-by-year interactions. The results were plotted as site-by-regression interaction curves showing heterogeneity of response among sites. We analyzed synchrony as common trends in timing of significant multiyear growth shifts by assessing the difference in mean growth of 6-yr moving windows using the Webster method (Legendre and Legendre, 1998). This analysis begins with a window of 1880–1885 and compares to the period 1885–1890, then shifts one year (e.g., 1881–1886 vs 1886–1891) sequentially through the century. Resulting
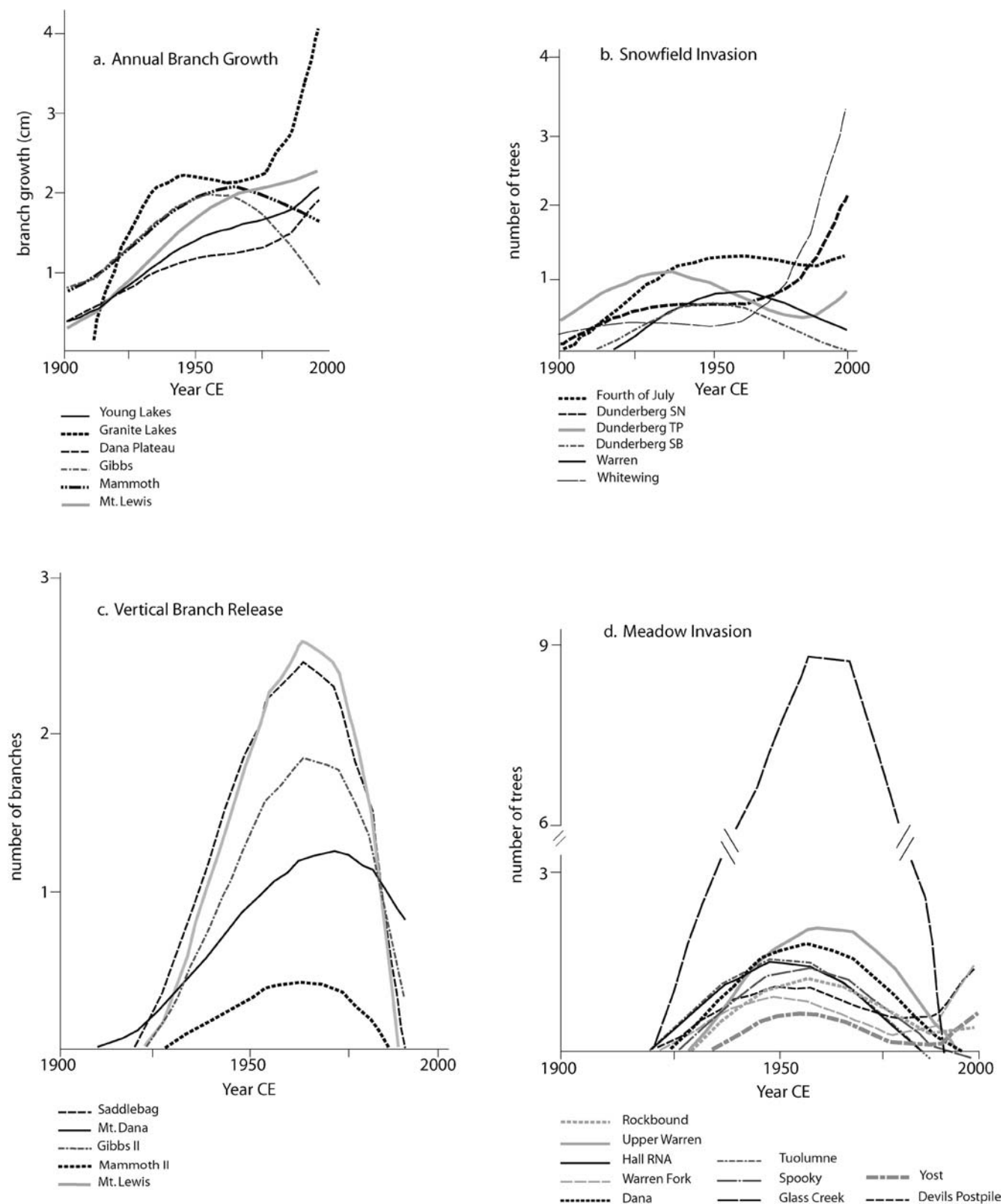
FIGURE 3. *Third- and fourth-order polynomial curves derived from fitting ecological data by mixed-model ANOVA to calculate differences among sites, and regressing year against growth. The results are plotted as site × regression interaction curves showing modeled heterogeneity of response among sites. a. Annual branch growth (cm yr^{-1}), b. Snowfield invasion (number of trees per year), c. Vertical branch release (number of branches per year), D. Meadow invasion (number of trees per year).*

Webster graphs plot the difference between pairs of windows at the overlap year. Although longer windows (e.g., 20- or 30-yr) test multidecadal trends better because of increased degrees of freedom, the lag in timing of the resulting Webster plots makes them less useful than

shorter windows for pinpointing the timing of potential abrupt shifts. Shorter windows indicate timing more precisely but accentuate interannual differences rather than longer trends. Because we were interested in timing of abrupt decadal shifts, we settled on 6-yr

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*Correlations of individual annual-branch-growth sites with pooled growth data, and eigenvectors showing correlation of sites with first principal component. Principal component 1 (PC1) accounted for 66% of the variation. Correlations are simple parametric R^2. Significant correlations ***$P < 0.001$*

Site	Correlation	Eigenvector to PC1
Young Lakes	0.96***	0.96
Granite Lakes	0.87***	0.83
Dana Plateau	0.93***	0.83
Mt. Gibbs	0.76***	0.87
Mammoth Peak	0.76***	0.78
Mt. Lewis	0.97***	0.94

windows as a compromise. We tested the difference in 6-yr means within sites for each window with t-tests and estimated periods of significant differences. We used the Satterthwaite approximation for degrees of freedom in the t-tests to account for heterogeneous variances (Steele and Torrie, 1980). Because we were interested in multiyear trends, we ignored significant differences among sequential periods when they were less than 5-yr duration.

We used analogous approaches in each case for the other three studies. To accommodate frequency data in these cases, however, we used comparable nonparametric rank correlations (Spearmans rho) for comparing multiyear responses of individual sites to pooled datasets. Because no appropriate nonparametric test allows comparison of the Webster analyses, we used a parametric approximation of t-tests to estimate probability values. To accentuate multiyear trends and improve degrees of freedom in tests, for meadow invasion, snowfield invasion, and vertical branch release, we grouped data in 8-yr bins and compared nonoverlapping pairs of windows by Webster analysis, graphing the values at the eighth year of the first window in each pair. To compare means of meadow and snowfield trees with respective means of forest trees, we conducted 2-way nested ANOVAs (plot within transect within site [forest] × plot within transect within site [meadow or snowfield, respectively]) on each dataset. We also tested spatial relationships of tree age within meadows and snowfields, respectively, by assessing relationship of age with distance of invading trees to the adjacent forest border. For this analysis we used both nested ANOVAs (plot within transect within site), and a mixed model of distance as a covariate and sites, and assessed significance of slopes in each case.

Relationships with Local Environmental Conditions

Although the overall study was not designed to test relationships of specific environmental factors on growth or colonization, the variability of our sites allowed preliminary assessment of elevation, substrate, and livestock grazing effects. For meadow and snowfield invasion, the sites extended over a range of elevations (735 m and 375 m, respectively); in the meadow study, sites had a range of grazing histories (Table 1); and all studies had more than two sites each on contrasting substrates (Table 1), which allowed for a preliminary evaluation of these local factors. The sites in the annual branch growth and vertical branch release studies traversed less than 120 m and 145 m, respectively, and were excluded from the elevation analysis. To assess elevation effects, we conducted simple linear regressions for each dataset, standardizing counts by site to account for variability in sample size among sites. To assess effect of domestic livestock grazing on meadow invasion, we similarly standardized counts by site, converted the dates of most recent livestock use (Table 1) to a continuous score of 0 to 100, and ran simple linear regression analysis with frequency of trees invading meadows. We used models of both

continuous and ordinal scaling of the grazing scores. To assess substrate effects for the annual branch growth dataset, we used a nested ANOVA (substrates and site within substrates) where sites were treated as a random effect. We used analogous, nominal-logistic nonparametric tests for the two invasion studies. Unbalance in the vertical branch dataset was too great to allow for analysis of substrate on growth.

Climate Relationships

To characterize 20th century climate, we reviewed records from weather stations in the climatic region of our study sites (WRCC, 2003; NCDC, 2003), and from this set selected stations that had the longest records and most complete datasets. We also reviewed streamflow data from gauging stations in the Sierra Nevada (USGS, 2003; http://www.ca.water.usgs.gov/) and the general region of our study sites. We subjected both climate and streamflow datasets to PCA. From these datasets, we created a composite climate record with three weather stations (Sacramento, Calif.; Mina, Nevada; Yosemite Valley, Calif.; Table 3). These stations had the longest complete records and high synchrony among each other. Indices for the composite record were derived from the scores of the first principal component, which were standardized to standard deviations from the mean for each variable. A composite streamflow record was similarly compiled with four stations (Table 3) after assessing synchrony among the datasets from an initial larger set of stations. Preliminary analysis indicated that the ecological data were more highly correlated with the composite records than they were with data from individual stations. We used the composite weather and streamflow records in subsequent tests of ecological response to climate.

To test relationships of climate and ecological responses, we analyzed simple linear correlation as well as assessed nonlinear relationships. For the latter, we conducted a second-order least squares response-surface model, using minimum monthly temperature, monthly precipitation, and two measures of interannual variability in precipitation from the regional weather stations as well as standard indices of PDO (Mantua et al., 1997; indices from http://tao.atmos.washington.edu/pdo/), Palmer Drought Severity Indices (PDSI, Palmer, 1965; California Division 7, southeastern California; indices from http://www.drought.noaa.gov/) and average annual streamflow in the analysis. Using stepwise regression, we filtered the model to select only the significant independent variables for further development of a best-fit model for each of the four ecological datasets and evaluated the behavior of these variables in second-order response surfaces. We graphed predicted ecological responses using the response-surface model of variables screened, where contour intervals represent ecological response and axes are units of standard deviation from the mean for each climate variable (Wolfram Research, 2003).

Results

ECOLOGICAL RESPONSES WITHIN AND AMONG STUDIES

Annual Branch Growth

Overall mean growth for the period 1880–1996 was 2.0 cm yr^{-1} for all sites combined, with significant differences ($P < 0.001$) among means for individual site (range 1.5 cm yr^{-1}–2.6 cm yr^{-1}; Fig. 2). Despite statistically significant heterogeneity, multiyear trends in growth over time were similar and correlated among sites ($R^2 = 0.88$, $P < 0.05$). Mean branch growth at all sites more than doubled from the first to the last decade of the 20th century (range 130%–400%); the overall mean increased from 0.88 cm yr^{-1} to 2.4 cm yr^{-1}. The response was not constant throughout the century, as shown by mean growth at individual sites (Fig. 2a–f), pooled data (Fig. 2g), and
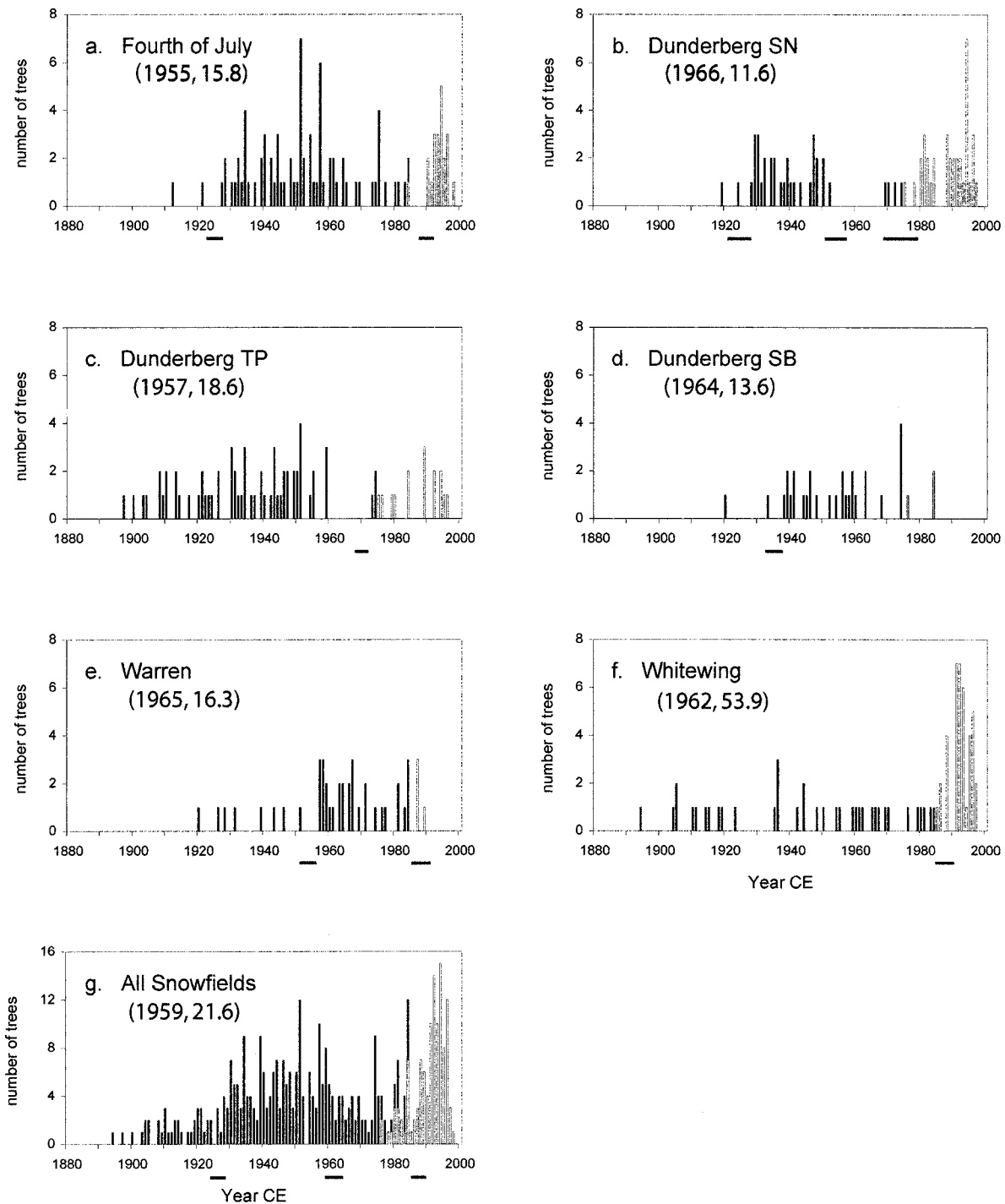
FIGURE 4.   Dates of invasion of Pinus albicaulis, P. monticola, *and* P. contorta *into six Sierran snowfield sites (a–f) and pooled (g) for the period 1880–2001. Solid bars are trees ≥0.5 m height; open bars are trees <0.5 m height (seedlings). Site mean date of invasion (year) and standard deviations (yr) are given, respectively, below site labels. Horizontal lines below x-axis indicate time periods of major change in response from Webster analyses on 8-yr moving windows.*

modeled response derived from regression of site by year (Fig. 3a). The latter model resolved good fit at all sites (R^2 range: 0.80–0.96, all $P <$ 0.001). Significantly accelerated growth occurred from 1920–1945 (all sites) and after 1980 (4 of 6 sites) as indicated by Webster analyses (Fig. 2). During the period from about 1945 to 1980, growth at all sites either stabilized or declined. The period after 1980 showed most variability among sites, with four sites continuing the increasing trend but two sites (Mammoth Peak and Mt. Gibbs) declining. Little significant directional change in mean annual growth occurred in the

four decades prior to 1920 in the sites that had data from this period. This overall synchrony in response among sites was further indicated by high and significant correlations (R^2 range: 0.76–0.96; $P < 0.001$) of individual site growth means to the average growth pooled over all sites, as well as high correlations of individual sites to the first principal component (range: 0.78–0.96), which accounted for 66% of the total variation (Table 4).

Nested ANOVA to test the effect of granitic versus metamorphic substrates on the growth rates showed no significant differences.

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TABLE 5

TABLE 6

Correlations of individual snowfield invasion sites with pooled snowfield data, and eigenvectors showing correlation of sites with first principal component. Principal component 1 (PC1) accounted for 30% of the variation. Correlations are nonparametric Spearman's rho. Significant correlations ***P < 0.001

Site	Correlation (rho)	Eigenvector to PC1
Fourth of July	0.66***	0.78
Dunderberg SN	0.56***	0.66
Dunderberg TP	0.57***	0.65
Dunderberg SB	0.43***	0.60
Warren	0.45***	0.32
Whitewing	0.37***	0.33

Average age in 2002 and variability (standard deviation, SD) of trees invading openings compared to adjacent forest plots in (A) snowfield and (B) meadow studies

Plot Type	Average Age	SD
A. Snowfields		
Snowfield	43.4	21.6
Forest	134.7	75.5
B. Meadows		
Meadow	42.1	10.6
Forest	126.9	76.6

Snowfield Invasion

The mean date of trees invading snowfields was 1959, with nonsignificant differences among sites (range 1955–1966). Multiyear trends of invasion over the century were relatively similar among sites

(Fig. 4). Invasion into snowfields began in the late 1800s and early 1900s and continued through the 20th century. The oldest tree in a snowfield plot dated to 1894. Considering all snowfields, 3% of trees established during the first 30-yr period (1880–1909), and 40% established during 1970–1999. The overall similarity in response among sites is illustrated by graphs of the site establishment frequency
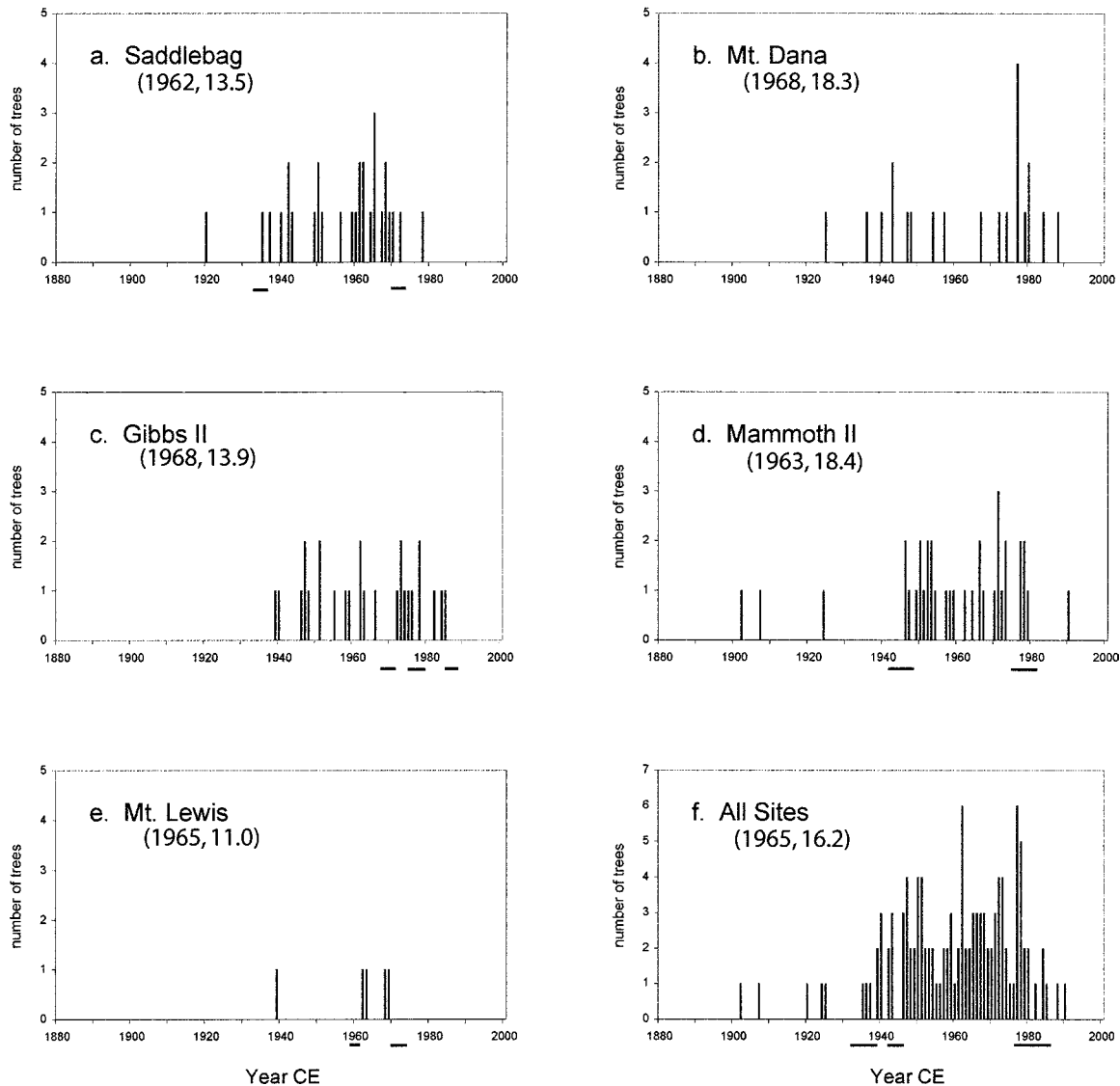

FIGURE 5. *Dates of release of vertical leaders in krummholz* Pinus albicaulis *at five Sierra Nevada treeline sites (a–e) and pooled (f) for the period 1880–1996. Site mean date of branch establishment (year) and standard deviations (yr) are given, respectively, below site labels. Horizontal lines below* x-axis *indicate time periods of major change in response from Webster analyses on 8-yr moving windows.*

data (Fig. 4 a–g) and modeled response derived from regression of site by year (Fig. 3b). Although the latter approach resolved low fit at all sites (R^2 range: 0.15–0.30), all R^2 values were significant ($P < 0.001$). Overall similarity of invasion trends was indicated by the significant rank correlations of sites to the pooled dataset (Table 5). The correlations were relatively high (0.43–0.66) with the exception of one site (Whitewing; 0.37), and all correlations were highly significant ($P < 0.001$). In PCA, high correlations of individual sites to the first principal component, which accounted for 30% of the total variation, indicated overall synchrony of response (Table 5). The primary heterogeneity among sites occurred after 1976, and was due to variability in the seedling class. Four sites had significant establishment after 1990, while two sites did not. Webster analyses highlighted intersite synchrony of increasing establishment from 1925 to 1945, decreasing from 1950 to 1980, and increasing again after 1990 (Fig. 4).

Trees in snowfields were a significantly distinct age class compared to trees in adjacent forests at each site ($P < 0.001$ for all plot, transect, and site levels). The mean age of invading trees in snowfields (all sites) was 43.4 yr versus 134.7 yr in the forest plots (Table 6). Variability in mean age of snowfield trees (SD = 21.6 yr, all sites) was much smaller than that for trees in forest border plots (SD = 75.5 yr). Seedlings made up about 31% of the snowfield populations; no seedlings occurred in forest plots.

The age of trees invading snowfields showed a significant relationship to distance from the forest border ($R^2 = 0.64$; $P < 0.001$), with younger trees at greater distance from the forest border and older trees nearer the forest. Nested ANOVA indicated significant differences among transects within sites, with about half of the transects having significant effects with distance. Transects that had plots containing only seedlings had higher correlations with distance from the forest border; these plots were located toward the center of the snowfields.

Differences in elevation of snowfield sites accounted for 10% of the total variation. Although the effect was significant, the curve was nearly flat, and the main effect of elevation occurred after 1975, where frequencies in the youngest age classes were greater at lower elevations (Whitewing, Fourth of July) than higher elevation sites. Tests of the effect of substrate showed all nonsignificant differences.

Vertical Branch Release

In contrast to annual branch growth and snowfield invasion, release dates of vertical branches above krummholz crowns were concentrated in a single distinct pulse in the mid- to late 20th century (Fig. 5). Mean date of establishment for the pooled dataset was 1965, with nonsignificant differences among sites (range 1962–1968) (Fig. 5). More than 85% of all branches dated between 1945 and 1976; the oldest branch dated to 1902 and the youngest dated to 1990. Seven leaders died between 1970 and 1985; all other leaders were alive at the time of measurement. Webster analyses of multiyear shifts in response showed a surge in establishment of vertical leaders starting around 1940, a second surge at several sites starting in 1965 and near-total termination of vertical branch release by 1980 (Fig. 5). Overall similarity among sites was further indicated by modeled response derived from regression of site by year (Fig. 3c), which resolved low to moderate, but significant, fit (R^2 range: 0.26–0.53, all $P < 0.001$). Significant correlations of site responses to total data set and high correlations to the first principal component, which accounted for 45% of the variation (Table 7), further highlighted synchrony among sites in multiyear responses.

Meadow Invasion

As in vertical branch release, dates of trees invading meadows were concentrated in a single distinct pulse within the mid- to late- 20th

century (Fig. 6). Mean date of establishment of the pooled dataset was 1965, with nonsignificant differences among nine sites (range 1956–1974). More than 87% of cored meadow trees dated between 1945 and 1976. The oldest tree established in 1928 and the youngest seedling dated to 2001. Webster analysis of multiyear shifts corroborated the episodic timing of invasion. For all meadows, except Yost and Warren Fork, the primary onset of invasion occurred between 1940 and 1945, with rate of establishment increasing until about 1960. In all meadows there was a plateau between 1960 and 1970 in number of trees establishing, after which the rate of establishment declined to very low or absent by 1980. Two meadows (Devils Postpile and Warren Fork) had a minor pulse of seedlings establishing after 1990. Yost Meadow and Warren Fork had the same episodic nature of invasion as the other meadows, but differed in that their establishment pulses peaked slightly later and slightly earlier, respectively, than the rest of the meadows. The overall similarity in response among sites was illustrated by curves derived from regression of site by year (Fig. 3d), which resolved low to moderate, significant fit (R^2 range: 0.19–0.46, $P < 0.001$). Overall similarity of invasion pattern was indicated by high and significant rank correlations (0.53–0.88) of sites to the pooled climate dataset (Table 8), with the exception of Yost (0.34). In PCA, high correlations of individual sites to the first principal component (0.42–0.80), which accounted for 40% of the total variation, indicated overall synchrony of response, with the exception of Yost (0.32).

The age classes of trees in meadow plots were significantly distinct from those in adjacent forest plots at each site ($p < 0.001$ for all plot, transect, and site levels). The mean age of invading trees in meadows (all sites) was 42.1 versus 126.9 yr in the forest plots (Table 6). Variability in age of meadow trees (SD = 10.6 yr, all sites) was much smaller than forest border trees (SD = 76.6 yr). In about half the transects, the age of trees invading meadows showed a significant relationship between mean age and distance from the forest border ($R^2 = 0.57$; $P < 0.001$). The effect of distance was primarily due to contrast of the first meadow plot from the forest and remaining meadow plots; other comparisons were mostly nonsignificant. Thus, unlike snowfields where the negative trend of age with distance extended from the forest border into snowfield centers, in the meadows, there was little relationship between age and distance except near the forest border.

Analyses of elevation, livestock grazing, and substrate with dates of meadow invasion indicated nonsignificant differences for all effects.

CLIMATE CORRELATIONS

20th-Century Climate Trends

Principal components analysis indicated high synchrony among the six weather stations. Combining data among three of the stations (Table 3) into a composite record lowered the variability of individual stations, thus giving a more robust regional record than did individual
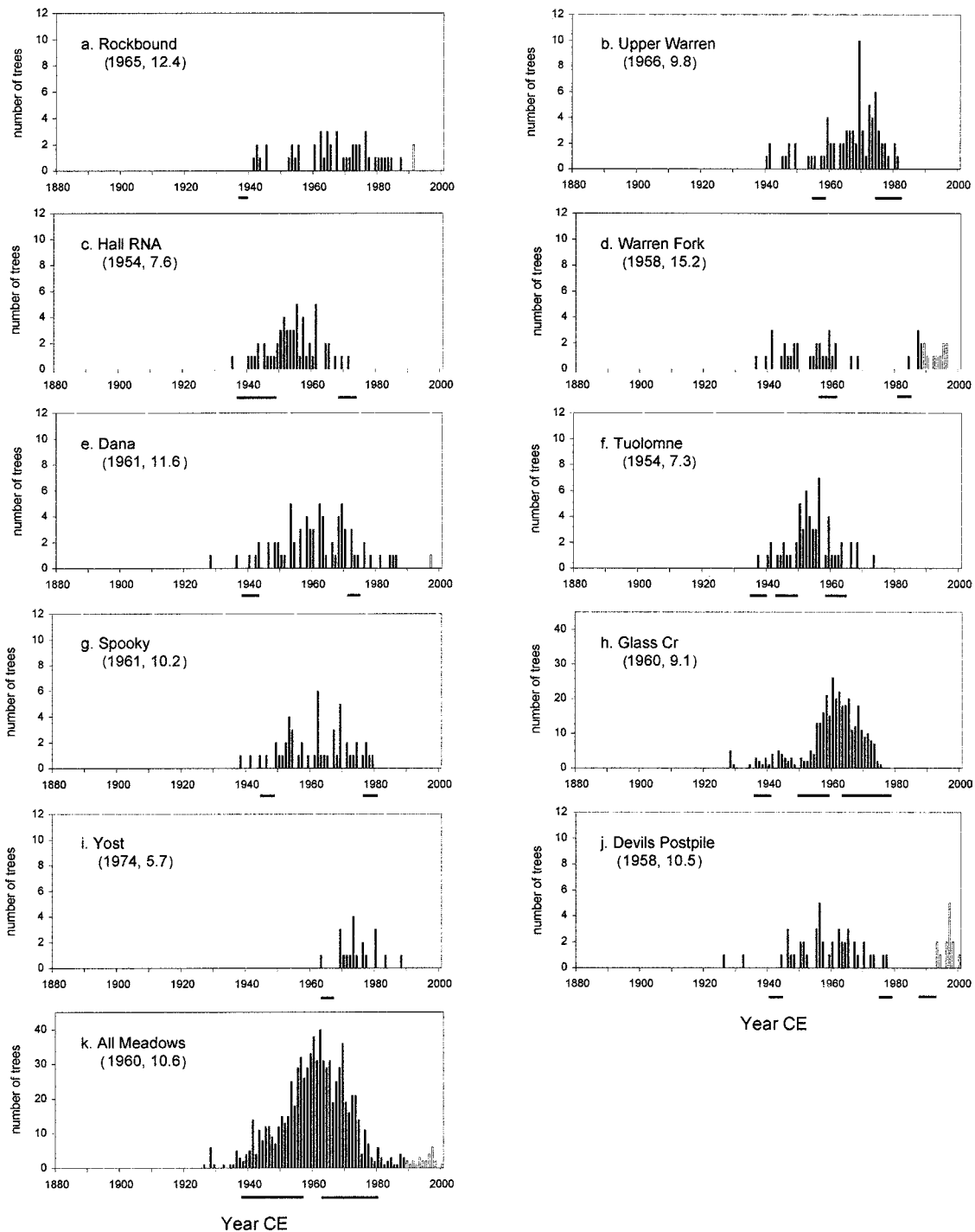
Site	Correlation (rho)	Eigenvector to PC1
Saddlebag	0.78***	0.73
Mt. Dana	0.63***	0.58
Mt. Gibbs II	0.81***	0.79
Mammoth Peak II	0.76***	0.72
Mt. Lewis	0.39***	0.59

FIGURE 6. Dates of invasion of Pinus contorta into ten Sierran meadows (a–j) and pooled (k) for the period 1880–2002. Solid bars are trees ≥0.5 m height; open bars are trees <0.5 m height (seedlings). Site mean date of invasion (year) and standard deviations (yr) are given, respectively, below site labels. Horizontal lines below x-axis indicate time periods of major change in response from Webster analyses on 8-year moving windows.

stations. The three stations each had greater than 90% correlation to the first principal component for temperature and precipitation variables.

The composite record, as well as the individual weather stations, showed significant century-long and multidecadal trends in minimum monthly temperature and total monthly precipitation (averaged annually, respectively, Fig. 7). Because they also had highest correlations to the ecological data, we used these climate variables in subsequent analyses (hereafter referred to as minimum temperature and precipitation). Average minimum temperature increased 3.7°C over the 20th century

in the composite record, from an average of 3.8°C for the decade of 1910–1920 to 7.5°C for 1990–2000 (Figure 7b). Warming accelerated primarily in two multidecadal periods, from 1920 to 1940 and from 1976 to 2000, during which times there were also high interannual variabilities. By contrast, the period from 1941 to 1975 was relatively stable, with no significant increase in temperature and even slight cooling in the early part of that period, and low interannual variability.

Compared to minimum temperature, precipitation was more variable, especially in the early and late decades of the 20th century (Fig. 7c). Precipitation increased 21.5 cm, from an average of 41.7 cm

for the decade 1910 to 1920 to an average of 63.2 cm for 1990 to 2000. Considering half-centuries, precipitation averaged higher during 1951–2000 (mean = 52.6 cm) than during 1900–1950 (mean = 45.2 cm); the increase in the latter half-century was due mostly to an increase in precipitation after 1975. Drier decades during the 20th century included the periods from 1910 to 1935 and from 1945 to 1970.

Similar to the weather data, water data from the four stations we selected were highly correlated among sites, as indicated by PCA, which gave correlations of annual streamflow to the first principal component over 90%. Annual streamflow was highly correlated with annual precipitation, although with some deviations (Fig. 7c). For instance greater reductions were recorded by streamflow than precipitation during the years 1976 to 2000.

Relationships of Climate and Ecological Response

In simple linear correlation analysis, annual branch growth was positively correlated with minimum temperature, while vertical branch release and meadow invasion were negatively correlated with PDO indices (Table 9). In the simple linear case, snowfield invasion was not significantly correlated with any of the climate variables. The least squares response-surface models had significant best-fits for all datasets, although fits were low for vertical branch release and snowfield invasion (Table 9). Despite the low fits in the latter cases, the models provided better heuristic analysis of potential complex climate relationships and interactions than linear correlation analysis alone. In the least-squares model, minimum temperature was a significant main effect for annual branch growth, snowfield invasion, and vertical branch release, and PDO was a significant main effect for annual branch growth, vertical branch release, and meadow invasion. Of special note were the second-order interaction effects (Table 9). The annual branch growth and meadow invasion datasets had significant interactions with streamflow, minimum temperature, and PDO. Variability in precipitation (measured as variance in ten-year windows) was also a term in several significant interactions for annual branch growth.

Effects of interaction among two and three climate variables and ecological responses are graphed as contour plots that illustrate the complex role of climate (Fig. 8). In the plots, ecological response (e.g., growth, invasion) increases as contour lines increase, and recorded 20th century climate combinations are shown as a scatter of points in each graph. Annual branch growth (Fig. 8a, b) increased with increasing minimum temperature, but reached a temperature optimum after which growth response depended on PDO condition and precipitation. Under low precipitation, growth declined at high minimum temperatures when PDO was negative, but stabilized when PDO was positive. Under high precipitation, growth stabilized at high minimum temperatures during negative PDO, but continued to increase with minimum temperature during positive PDO conditions.

Interactions were stronger in the case of meadow invasion (Fig. 8b–c), where different combinations of minimum temperature, precipitation, and PDO significantly altered the invasion response. During negative PDO, rate of establishment was modeled to increase when minimum temperature was low and precipitation was high (a situation not encountered in the recorded 20th century climate dataset) and when minimum temperature was high and precipitation was low. Conversely, during positive PDO, establishment was modeled as low or not occurring at all under many conditions of the 20th century, except at relatively moderate minimum temperature and precipitation, where invasion was also moderate. The conditions during positive PDO modeled to trigger high rates of establishment, that is, low minimum temperatures and high precipitation, did not occur in the 20th century record.

Vertical branch release also showed an interaction with PDO and temperature (Fig. 8e). Branch release was low to nil during positive PDO conditions for most minimum temperatures, and was more likely

Site	Correlation (rho)	Eigenvector to PC1
Rockbound	0.60***	0.64
Upper Warren	0.73***	0.64
Hall RNA	0.66***	0.64
Warren Fork	0.53***	0.42
Dana	0.70***	0.76
Tuolomne	0.64***	0.60
Spooky	0.69***	0.74
Glass Cr	0.88***	0.80
Yost	0.34***	0.32
Devils Postpiles	0.64***	0.68

to occur during negative PDO periods, especially at higher temperatures. Precipitation did not greatly alter the response surface.

In the snowfield invasion dataset, interactions among effects were nonsignificant. Minimum temperature as a simple main effect explained much of the response.

Discussion and Conclusions

CORRELATED 20TH-CENTURY ECOLOGICAL RESPONSES

An emergent result from our studies was the presence of multiple time-series synchronies in 20th century ecological responses across environmentally heterogeneous sites within each study and across independent ecological traits in three different species among the four studies. Each study recorded significant change over the duration of the 20th century. Changes from the beginning to the end of the century in rate of annual branch growth of treeline whitebark pine and white pine colonization into formerly persistent snowfields below treeline were directional and ongoing, from low to high branch growth, and from minimal to significant establishment, respectively. Similar directional changes over the 20th century have been observed in the Sierra Nevada and other treeline ecosystems in North America and Europe. Populations of lodgepole pine and whitebark pine in the southeastern Sierra Nevada had trends of increasing growth throughout the 20th century regardless of age or competitive relations of trees (Peterson et al., 1990). Repeat photo studies of subalpine fir (*Abies lasiocarpa*) populations below treeline of the northern Rocky Mountains showed trends of increased density between 1945 and 1991, and forest inventory studies of whitebark pine in the same region showed 85% increase in tree volume since the late 1870s (Murray et al., 2000).

Century-long change also occurred in the other two studies. Krummholz whitebark pine thickets began the century with compact, flat-topped crowns at the upper treeline and ended the century with krummholz crowns having more abundant vertical branches, which gives a mixed krummholz-upright tree architecture to this zone. Subalpine meadows in the early 20th century had abrupt borders with surrounding forests, and were dominated by grasses, sedges, and forbs. By the end of the century, forest-meadow transitions were less distinct, and pine trees were scattered throughout many portions of the meadows. In contrast to the patterns of the annual branch growth and snowfield invasion, however, the latter two types of change resulted primarily from a single period of activity in mid-century. Naturally occurring episodic invasion has similarly been documented for pine invasion of subalpine meadows in the Sierra Nevada (Helms, 1987), the Pacific Northwest (Franklin et al., 1971), and the northern Rocky Mountains (Jakubos and
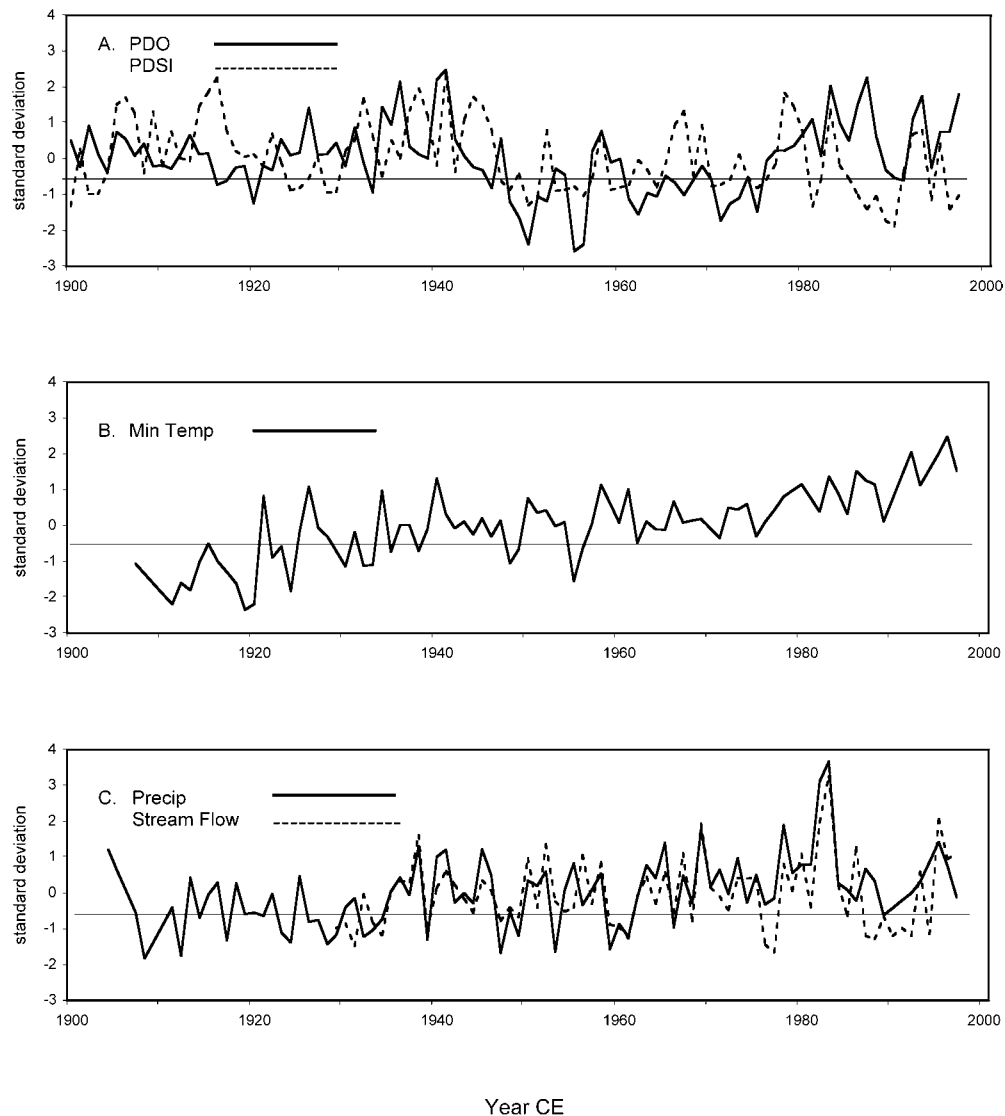
FIGURE 7. Composite 20th-century records of standardized climate and streamflow indices used in modeling relationships of ecological response. A. Annual indices of standardized Pacific Decadal Oscillation (PDO; Mantua et al. 1997; http://tao.atmos.washington. edu/pdo/; solid line) and standardized annual Palmer Drought Severity Indices (PDSI; Palmer, 1965, California Region 7; http:// www.drought.noaa.gov/; dashed line). B. Composite record of standardized monthly minimum temperature (averaged annually) derived from four regional weather stations (Table 8). C. Composite records of standardized monthly precipitation (averaged annually) derived from four regional weather stations (Table 8) (solid line) and standardized annual streamflow derived from four Sierran water-gauging stations (Table 8) (dashed line).

Romme, 1993). Changes in height of krummholz crowns in the northern Rocky Mountains, however, have been gradual over the 20th century (Weisberg and Baker, 1995), although in some cases, available methods such as repeat photo interpretation did not allow high resolution time series analysis, so an episodic response might have been overlooked (Klasner and Fagre, 2002).

Multidecadal variability occurred within each study, regardless of whether the response was gradual or episodic; these changes were correlated within studies and comparable across studies. When all four studies are considered together, four multidecadal periods were described by ecological responses during the 20th century, approximately defined as; <1920 (extending at least to 1880), 1920 to 1945; 1946 to 1976; and >1976 (Table 10). During the first period, no, or only minor, changes were observed in any of the traits examined; during the second period, positive response was initiated in two traits (snowfield invasion and increased branch growth); during the third period, response stabilized in the these traits and initiated in meadow invasion and vertical branch release; and during the final period,

response terminated in meadow invasion and vertical branch release, and accelerated again in snowfield invasion and branch growth. Multidecadal responses that correspond to at least some of the time periods we identified have been documented in other subalpine ecosystems for the 20th century. Radial growth of subalpine fir and mountain hemlock (*Tsuga mertensiana*) populations in the Olympic and Cascade Ranges during the 20th century exhibited growth patterns roughly paralleling the four periods we defined (Peterson and Peterson, 2001; Peterson et al., 2002). Episodic invasion by lodgepole pine of dry meadows in Yosemite National Park occurred between 1948 and 1973 (Helms, 1987), and between 1928 and 1937 in the Cascades Range (Franklin et al., 1971).

RELATIONSHIPS TO REGIONAL CLIMATE

Regional climate influence is implicated in the synchronies within and among four unrelated ecological traits across broad environmental

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TABLE 9

*Relationships of ecological response to climate. **A.** Simple linear correlations of annual branch growth, snowfield and meadow invasion, and vertical branch release with 20th century climate variables. **B.** Model fits with linear and second-order effects from least squares response-surface model. Only significant correlations and tests shown: *** P < 0.001; ** P < 0.01; * P < 0.05. Min temp is minimum monthly temperature, precip is monthly precipitation, PDO is Pacific Decadal Oscillation, PDSI is Plamer Drought Severity Index, V10 is variance in precipitation in 10-yr windows, shifted 1-yr increments*

Annual Branch Growth	Snowfield Invasion	Vertical Branch	Meadow Invasion
A. Simple Linear Correlations			
Min temp: 0.69***			
		PDO: −0.40***	PDO: −0.51**
B. Least Squares Response-Surface Model			
Model fit:			
0.86***	0.18*	0.38***	0.58***
Effects Tests:			
Min temp***	Min temp***	Min temp**	
PDO*		PDO***	PDO**
Streamflow × PDSI*			Streamflow × PDSI*
Streamflow × PDO***			
Streamflow × Precip**			
Streamflow × V10***			
PDO × Min Temp*		PDO × Min Temp*	
			Precip × Min Temp*
V10 × Min Temp**			
V10 × PDSI*			

gradients involving three pine species, together with the lack of significant effects of either elevation, substrate, or livestock grazing history, and the temporal "sign switching" related to climate variability. Significant positive linear and second-order correlations with climate variables corroborate this relationship. Monthly minimum temperatures, mirroring global trends but at a greater rate (Jones et al., 1999), increased significantly over the 20th century in the broad region of the study, as indicated by composite climate records from three long-term weather stations. Minimum temperature was a significant correlate with 20th century change in each of the four studies here, as it has been in other time-series studies of subalpine forest dynamics.

Minimum temperature was the main effect related to accelerating annual branch growth in krummholz whitebark pine and initiation of pine invasion into formerly persistent snowfield openings. In the case of treeline whitebark pines, length of the growing season and snow cover over krummholz crowns constrains growth (Sowell et al., 1982; Daly, 1984; Weisberg and Baker, 1995). Warmer minimum temperatures hasten spring snow- and soil-melt, lengthening growing season as well as directly stimulating growth in an environment where maximum temperatures for growth are unlikely to have been encountered in the current range of conditions (Weaver, 2001). Increased summer temperatures and longer growing season have been observed as drivers of ecotonal and landscape changes in other treeline environments in western North America and Europe (Butler et al., 1994; Rochefort et al., 1994; Linderholm, 2002) and of radial growth of high-elevation tree populations at millennial- (Hughes and Graumlich, 1996) and century-scales (Peterson and Peterson, 2001; Linderholm, 2002; Peterson et al., 2002). Accelerated branch growth in our krummholz stands coincided with periods of rapid warming between 1920 and 1945, and after 1975, and stabilized during the mid-century period when minimum temperatures similarly plateaued.

Colonization of persistent snowfields is limited mechanically by barriers of snow and frozen ground. Increases in minimum temperatures reduce the extent of night-time freezing and stimulate earlier snow- and soil-melting, creating environments conducive for pine colonization, and directly stimulating germination and growth in the growing season. Increases in subalpine forest density in the Rocky Mountains and European Alps were related to lower snowpack and longer growing season (Körner, 1998; Klasner and Fagre, 2002; Peterson et al., 2002), although the habitats studied were not snowfield openings. The presence of abundant seed from adjacent tall forests and lack of competition in these steep, rocky sites further favors pine invasion. Once the sites are free of snow in the growing season, temperature and length of remaining growing season are more limiting than soil moisture on these north-facing, well-drained, but mesic, aspects. Weaver (2001) indicates that throughout the range of whitebark pine, and even in summer-dry climates such as the Sierra Nevada, soil moisture is unlikely to limit whitebark pine establishment in its upper elevation zones, although wind-induced desiccation does. The concave topography and north-facing slopes of the Sierran snowfield sites afford protection from prevailing winds, and seedlings and saplings are relatively protected. Paralleling the annual branch growth pattern, the pattern of snowfield invasion had multidecadal steps as expected if colonization and establishment were primarily responding to temperature increase. Lack of significant main or second-order effects with other climate variables further corroborated the primary importance of temperature in triggering and maintaining colonization of such openings.

Increasing minimum temperature was also a main effect factor in stimulating vertical branch release above krummholz crowns. Persistent snowpacks that cover krummholz crowns and freezing winds that desiccate buds and emergent stems maintain krummholz architecture. In contrast, longer growing seasons as a result of earlier snowmelt, and warmer minimum temperatures that reduce number of freezing events and lower wind desiccation during the growing season, favor vertical branches emergence and elongation (Weaver, 2001). In the Rocky Mountains, change in krummholz height and leader growth in the 20th century was attributed to warmer weather that allowed upright shoots to persist (Weisberg and Baker, 1995).

The dominant main effect of the Pacific Decadal Oscillation on annual stem growth, meadow invasion, and vertical branch release, together with significant interactions of PDO and precipitation/streamflow with minimum temperature, pointed to complex relationships of water and temperature influencing episodic response at interdecadal scales. These interactions suggest that unique combinations of climate conditions can trigger pulsed events such as meadow invasion and vertical branch release, or accelerate directional change such as branch growth. The time periods of our studies corresponded to the four alternating phases of PDO in the 20th century. The PDO has been implicated in effecting changes in other temperate ecosystems (Biondi et al., 2001) including subalpine and montane forests (Peterson and Peterson, 2001; Peterson et al., 2002; Gray et al., 2003). The strength and persistence of the mid-century negative PDO, and its abrupt termination in 1976 as a significant synchronous step change, have been documented in over 40 physical and ecological variables of the Pacific Ocean and North America (Ebbesmeyer et al., 1991; Nigam, et al., 1999). While the specific implications of PDO are still unclear, this mode appears to bring distinct climate. Gershunov and Barnett (1998) found that annual weather conditions are influenced by interaction of PDO and ENSO, with positive PDO phases enhancing El Niño effects and weakening La Niña, and negative PDO phases having the opposite effect. In the Sierra Nevada, Dettinger and Cayan (2000) found PDO in the Sierra Nevada to have a measurable distinct effect even during years of minor ENSO strength.

A contributing climate factor to mid-century episodic response of meadow invasion and vertical branch growth appears to be the low
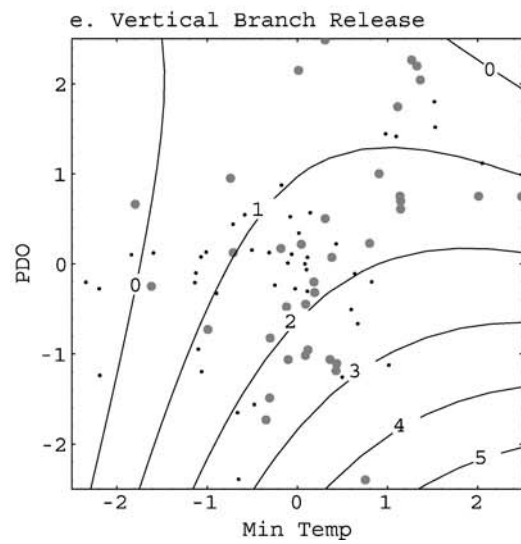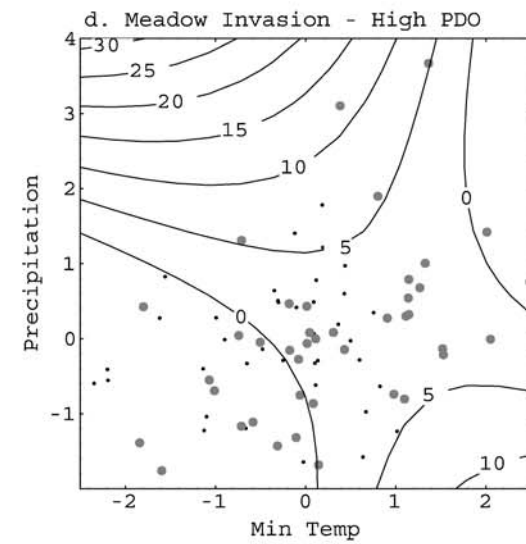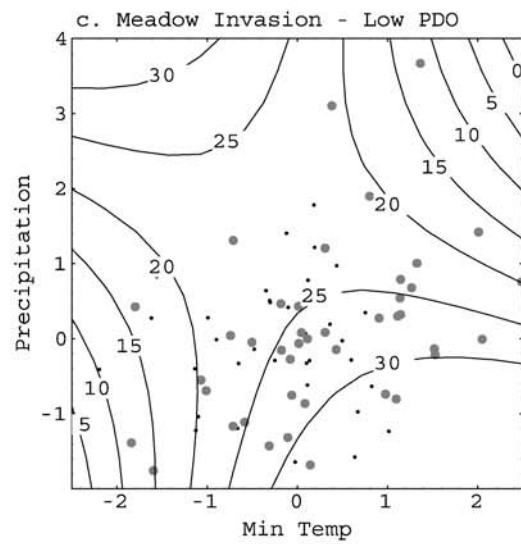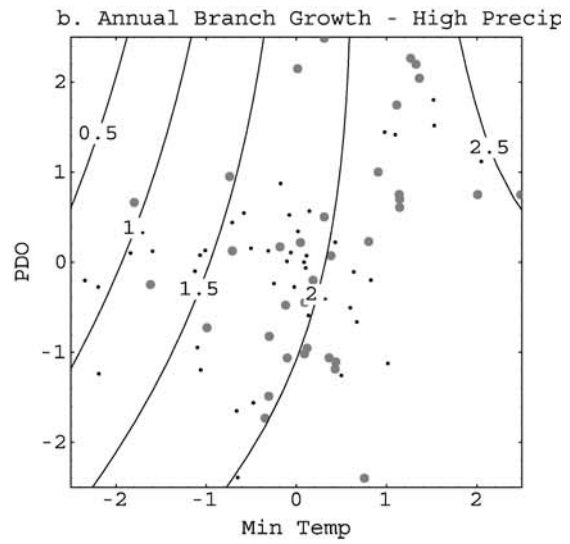
a. Annual Branch Growth - Low Precip

b. Annual Branch Growth - High Precip

c. Meadow Invasion - Low PDO

d. Meadow Invasion - High PDO
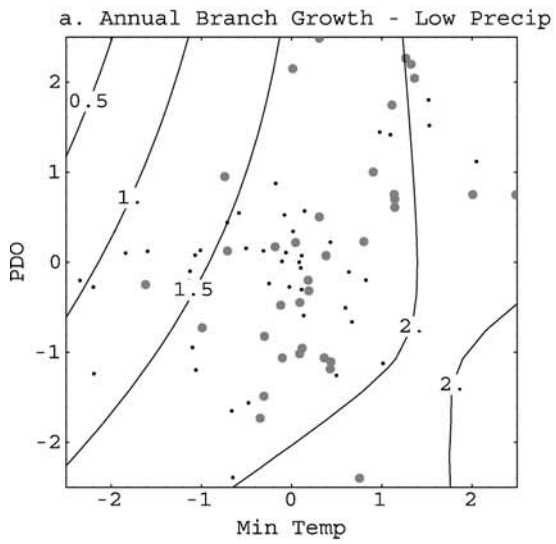
e. Vertical Branch Release

TABLE 10

Patterns of multidecadal climate phases and growth and invasion in subalpine Sierra Nevada conifers from 1880 to 2000, based on timing of significant periods of ecological response. Plus signs indicate accelerating minimum temperatures, wet phase of PDO, high PDSI variability (as defined in text and Table 11), increasing growth rate, accelerating invasion in snowfields and meadows, and increasing vertical branch release, respectively. Minus signs indicate stable or declining temperatures, dry phase of PDO, low PDSI variability, stable or declining annual branch growth rates, snowfield and meadow invasion, and vertical branch release respectively

Time Period	Minimum Temp	PDO Phase	PDSI Var	Annual Br Growth	Snowfield Invasion	Meadow Invasion	Vertical Br Release
1880–1920	−	−	+	−	−	−	−
1921–1945	+	+	+	+	+	−	−
1946–1979	−	−	−	−	−	+	+
>1980	+	+	+	+	+	−	−

TABLE 11

Summary of monthly Palmer Drought Severity Indices for four multidecadal periods of the 20th century. The periods are defined by timing of significant ecological responses and primary PDO phases: 1880-1919 (300 months); 1920-1945 (312 months); 1946-1975 (360 months); and 1976-2001 (302 months), and period of record (1274 months). A. Division 5, West-Central California, and B. Division 7, Southeast California. Study sites lie at northern end of Division 7, and are ecologically allied to Division 5. Deviation from mean indicates the direction (positive or negative) of the multidecadal divisional mean from the period-of-record divisional mean. Months with values of 4.0 and above are categorized as "extreme moist spells"; months with values of −4.0 and below are "extreme droughts" (Palmer, 1965). Percentage of extreme months is given for each period

Time Period	Mean PDSI	Dev from Mean	SD	% Extreme Months
A. Division 5				
1880–1919	0.70	+	2.32	10
1920–1945	0.30	+	1.93	2
1946–1975	−0.30	−	1.90	<1
1976–2001	−0.08	−	3.13	15
Period of Record	*0.13*		*2.38*	
B. Division 7				
1880–1919	0.60	+	2.87	17
1920–1945	0.87	+	2.56	13
1946–1975	−0.94	−	2.06	5
1976–2001	−0.93	−	3.06	25
Period of Record	*−0.14*		*2.77*	

interannual variability in available moisture that was unique during this period within the 20th century. The Palmer Drought Sensitivity Index is a complex indicator of effective soil moisture that integrates relative regional dryness or wetness significant to plant growth, and is calculated for state divisions. Precipitation was low and PDSI values were on average negative from 1945 to 1975, whereas precipitation increased significantly after 1975 (Fig. 7, Table 11). Significantly, the period from 1945 to 1975 had low interannual variability in both precipitation and especially PDSI, showing a marked contrast to high interannual variability after 1975 (Table 11).

Low interannual variability combined with favorable conditions of warm and low moisture between 1945 and 1976 appear to be primary factors stimulating the dramatic pulse of meadow invasion mid-century in the central Sierra Nevada. The ten meadows we selected were all relatively flat upper montane to subalpine locations, and although not dominated by river-flood events, were mostly wet during the early growing season. Saturated soils and low dissolved oxygen in Sierra Nevada meadows maintain forb and grass dominance (Wood, 1975), whereas persistent conditions of warm, dry periods, such as in the mid- 20th century, would allow pine seeds to germinate and establish roots that penetrate below zones of grass and forb root competition (Franklin et al., 1971; Rochefort and Peterson, 1996;

←

FIGURE 8. *Contour maps showing effects of significant second-order interactions between climate variables and ecological response. a and b. Interactions of minimum monthly temperature and Pacific Decadal Oscillation (PDO) indices with annual branch growth for contrasting situations of low precipitation (a) and high precipitation (b). c and d. Interactions of minimum monthly temperature and monthly precipitation with meadow invasion for contrasting situations of low (negative) PDO (c) and high (positive) PDO (d) e. Interactions of minimum temperature and PDO with vertical branch release. In each case, ecological response (branch growth, meadow invasion, or vertical branch initiation) increases as contours increase. Contour intervals are in units of ecological response: cm for annual branch growth, number of trees for meadow invasions, and number of branches for vertical branch release. Main axis units are standard deviations from the mean of each variable. Scatter of dots in each graph is the set of recorded points derived from 90 yr of composite weather records, with large dots indicating above average precipitation conditions (a, b, e) or positive PDO index values (c, d) and small dots indicating below average precipitation conditions (a, b, e) or negative PDO index values (c, d).*

Brady, 2001). Seed availability is unlikely to control invasion capacity in lodgepole pine, which reproduces prolifically every year in this region (Helms, 1987). Similarly the ability of pine seed to disperse fully throughout meadows in any one year is indicated by the lack of a relationship of tree age in meadows to distance to forest borders. Likely, seed is abundant throughout meadows annually, and weather and competitive conditions regulate germination and establishment success, as was found in another study of lodgepole pine invasion of Yosemite National Park meadows (Helms, 1987). With 30 yr of favorable conditions mid-century, root systems of invading trees could develop sufficiently that trees were able to persist even when conditions became unfavorable for new germination after 1975.

The interactions with PDO, precipitation, temperature, and interannual variability in our results suggest an explanation for why pine invasion and vertical branch release did not occur during the shorter and weaker negative PDO period of the early century. Relative to 20th-century climate space, these ecological responses occur only when specific combinations of climate occur. The model predicts that meadow invasion and vertical branch release would occur when negative PDO occurred together with warmer temperatures, low precipitation, and low variability of the mid-century, but not in combination with cool temperatures, low precipitation, and high variability of the early 20th-century negative PDO. A new pulse of seedling germination in two meadows after 1990 coincided with a weak negative PDO period, but whether these seedlings persist over time or not may depend partly on the persistence of negative PDO conditions, the level of interannual variability, and the effect of higher temperature and greater precipitation on seedling survival.

Similar episodic invasion of meadows by lodgepole pine in wet meadows of Yosemite National Park and the Olympic Mountains of Washington was linked to persistent low precipitation years (Helms, 1987; Woodward et al., 1995) and extended periods of low soil moisture (Franklin et al., 1971). In contrast, in historically dry meadow systems of Yellowstone National Park, Wyoming, ongoing invasion by lodgepole pine since the mid-1800s was interpreted as a response to warmer, wetter growing season conditions since the end of the Little Ice Age (Jakubos and Romme, 1993). Dominant climate interactions have not been identified in these invasion events.

Low interannual variability between 1945 and 1975, combined with longer, warmer summers, would also contribute to persistence of vertical branches above krummholz crowns. An extended period of favorable climate enabled multiple years of growth in vertical branches in other regions (Weisberg and Baker, 1995; Woodridge et al., 1996), although specific climatic relationships were not assessed. The resulting stem height growth allows branches to emerge vertically above the snowpack, and, combined with development of multiple years of needles and thickened bark, increases the likelihood of stem persistence even if conditions reverse (Hadley and Smith, 1989; Weisberg and Baker, 1995), as they apparently did in the Sierra Nevada. The lack of new vertical branches initiating after 1980 and the death of seven vertical branches around 1980 point to the termination of favorable combination of conditions in the Sierra Nevada in our study plots.

Our results corroborate other studies of subalpine ecosystems that found climate-related ecological changes often occur in unanticipated patterns. Although global warming at high elevations is commonly assumed to exert primary effect by causing altitudinal shifts in treeline, complex changes in spatial distribution, productivity, and type conversions below treeline may be more important, at least in the early decades of the 21st century, as found in other montane forests (Hättenschwiler and Körner, 1995; Klasner and Fagre, 2002). The existence of significant interactions between ecological traits and climate variables that result in abrupt changes and reversible responses cautions against general projections of global change that assume simple, linear ecological responses. Further, the specific linear and interaction effects of climate with the ecological traits we observed must be viewed only in the context of 20th-century climate space. As the models showed, for combinations of precipitation, temperature, and PDO that lie beyond this range, ecological responses could be quite different from observed in the 20th century. Such abrupt changes and ecological "surprises" are likely to be common as the conditions of the 21st century move outside the climate space of the last millennium (Bugmann and Pfister, 2000; Alley et al., 2003).

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