

Recruitment patterns and growth of high-elevation pines in response to climatic variability (1883–2013), in the western Great Basin, USA

Constance I. Millar, Robert D. Westfall, Diane L. Delany, Alan L. Flint, and Lorraine E. Flint

Abstract: Over the period 1883–2013, recruitment of subalpine limber pine (*Pinus flexilis* E. James) and Great Basin bristlecone pine (*Pinus longaeva* D.K. Bailey) above the upper tree line, below the lower tree line, and across middle-elevation forest borders occurred at localized sites across four mountain ranges in the western Great Basin. A synchronous pulse at all ecotones occurred between 1963 and 2000 (limber pine) and between 1955 and 1978 (bristlecone pine) when pines expanded 225 m beyond forest borders. Little recruitment occurred before this interval or in the 21st century. No obvious environmental factors distinguished recruitment locations from nonrecruitment locations. Where their ranges overlap, limber pine has leapfrogged above bristlecone pine by 300 m. Limber pine tree-ring chronologies, developed to compare radial-growth responses with recruitment, showed dominant pulses of increased growth during the same interval as recruitment. Significant climate correlations of growth and recruitment indicated lead and lag effects as much as 6 years and complex relationships with climate variables, corroborating the importance of cumulative climate effects relative to any single year. Water relations were the most important drivers of growth and recruitment and interacted with growing-season minimum and maximum temperatures. These results underscore the importance of studying ecotones at all margins when evaluating conifer response to climate change.

Key words: recruitment, radial growth, dendrochronology, tree line, climate change.

Résumé : Au cours de la période 1883–2013, le recrutement de pin flexible (*Pinus flexilis* E. James) et de pin à longue vie (*Pinus longaeva* D.K. Bailey) en haut de la limite supérieure et en bas de la limite inférieure des arbres ainsi qu'en bordure des forêts situées à une altitude intermédiaire est survenu dans des stations localisées parmi quatre chaînes de montagnes dans l'ouest du grand Bassin des États-Unis. Une poussée synchrone dans tous les écotones est survenue entre 1963 et 2000 (pin flexible) et entre 1955 et 1978 (pin à longue vie) alors que les pins se sont étendus jusqu'à 225 m au-delà de la lisière de la forêt. Peu de recrutement est survenu avant cet intervalle ou au cours du 21^e siècle. Aucun facteur environnemental évident permettait de distinguer les endroits où il y avait eu du recrutement de ceux où il n'y en avait pas eu. Lorsqu'il y a eu chevauchement de l'aire de répartition des deux espèces, le pin flexible a dépassé de 300 m le pin à longue vie. Selon les séries dendrochronologiques du pin flexible, développées pour comparer les réactions de la croissance radiale au recrutement, cette espèce a connu des poussées dominantes d'augmentation de croissance durant le même intervalle que le recrutement. Des corrélations significatives du climat avec la croissance et le recrutement indiquent qu'il y a eu des effets d'avance et de retard pouvant aller jusqu'à 6 ans ainsi que des relations complexes avec les variables climatiques qui corroborent l'importance des effets cumulatifs du climat relativement à une seule année quelle qu'elle soit. Les relations hydriques étaient le plus important moteur de croissance et de recrutement et interagissaient avec les températures minimum et maximum durant la saison de croissance. Ces résultats soulignent l'importance d'étudier toutes les bordures des écotones lorsqu'on évalue la réaction des conifères au changement climatique. [Traduit par la Rédaction]

Mots-clés : recrutement, croissance radiale, dendrochronologie, limite des arbres, changement climatique.

Introduction

Mountain ecosystems are widely assumed to have characteristic vulnerabilities to changing global climates (Beniston et al. 1997; Beniston 2003). Isotherms are expected to shift upward as global temperatures rise, with a concomitant upward migration of mountain species as they seek preferred climates. These expectations are generally confirmed both empirically (Beckage et al. 2008; Lenoir et al. 2008; Felde et al. 2012; Bell et al. 2014) and in model projections (Hayhoe et al. 2004; Van de Ven et al. 2007; Loarie et al. 2008). In some contexts, however, species do not conform to the expectation of upward movement. Instead, downward migrations and other responses that do not involve change at the upper tree line have been

reported (Lenoir et al. 2008, 2010; Crimmins et al. 2011; Felde et al. 2012; Rapacciuolo et al. 2014).

For forest trees, the upper tree line elevation has long been recognized as being influenced dominantly by temperature (Körner and Paulsen 2004) and is used as an indicator of climate change. Projections based on regional warming widely indicate future upslope movement of tree line elevation, with estimates ranging from 140 m to 700 m (Moen et al. 2004; Hayhoe et al. 2004; Kullman and Öberg 2009). Observational studies show inconsistent interactions between tree line elevation and climate. Holocene responses generally record upslope movement during warming periods (LaMarche 1973; Graumlich and Lloyd 1996) and downslope movement during cooling periods (Kullman 1995), whereas responses

Received 16 January 2015. Accepted 15 April 2015.

C.I. Millar, R.D. Westfall, and D.L. Delany. Pacific Southwest Research Station, USDA Forest Service, 800 Buchanan St., Albany, CA 94710, USA.
A.L. Flint and L.E. Flint. California Water Science Center, U.S. Geological Survey, Placer Hall, 6000 J Street, Sacramento, CA 95819, USA.

Corresponding author: Constance I. Millar (e-mail: cmillar@fs.fed.us).

during the past 200 years have been more variable (Rocheffort et al. 1994; Kullman and Öberg 2009; Dolanc et al. 2013a, 2014). Although advances in systems-level understanding have been made to define the nature of temperature control on the upper tree line (Körner 2012), critical questions remain regarding seedling recruitment above the tree line, persistence of young trees into mature age stages, and the relationship between recruitment and climate.

Furthermore, the upper tree line is only one of several boundaries at which subalpine forests contract or expand in response to climate. The lower tree line in Great Basin forests is constrained by limitations of precipitation and soil moisture more than temperature (Hughes and Funkhouser 1998), although the nature of specific thresholds is poorly resolved. Internal boundaries between forests and nonforests at middle elevations are subject to different constraints than the upper and lower tree lines and more likely to be controlled by interactions of substrate, soil moisture, cold-air pooling, and competition with meadow-adapted plants (Taylor 1990; Rocheffort et al. 1994; Millar et al. 2004). The collective behavior of these forest ecotones determines net expansion or contraction of the subalpine forest zone and better represents its response to climate than any single border.

Responsiveness to climate change is complicated by tree form, height, and age. Seedlings are sensitive to daily, seasonal, and annual weather variability from germination to establishment phases (Germino et al. 2002; Bansal and Germino 2010) and, due to their low stature as seedlings and young trees, encounter different thermal environments than trees at mature crown heights (Rocheffort et al. 1994; Körner 2012). Once they reach ~3 m in height, trees become subject to canopy–soil feedbacks, and thermal conditions of the crown become coupled with the atmosphere, furthering its influence on survival and growth (Bader et al. 2014). Once established, mature trees become highly resistant to climate variability and extremes and can survive long periods of climate change that would be unfavorable to seedling survival (Bansal and Germino 2010). Climatic conditions promoting stem growth of mature trees often differ from those favorable to seedling survival and establishment (Barbeito et al. 2012; Dolanc et al. 2013a). Patterns of stem growth across elevational gradients, especially near the tree line, are complex and difficult to interpret (Salzer et al. 2009, 2014; Matias and Jump 2015). How these and other factors are expressed at diverse forest ecotones is poorly known.

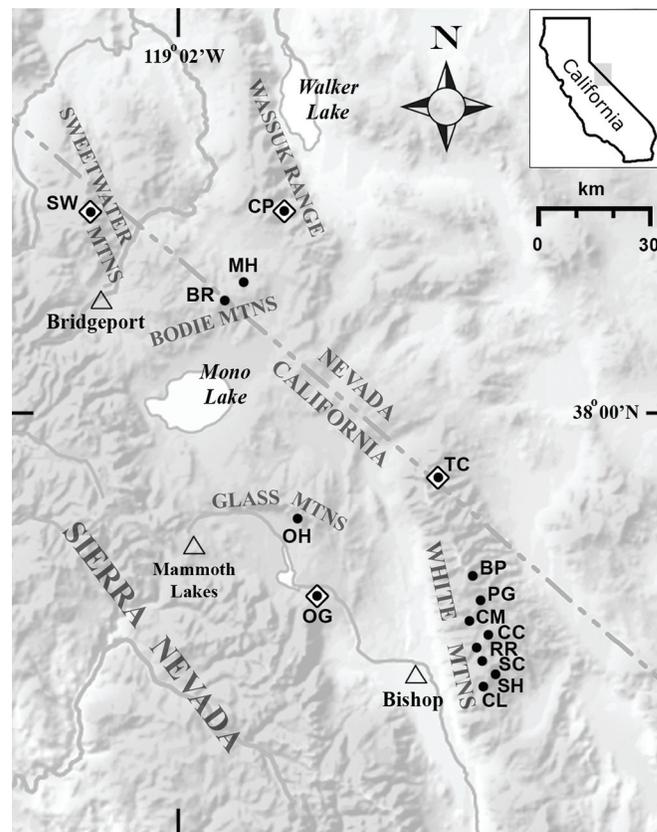
Taken together, limited understanding of the regeneration niche across subalpine forest ecotones, persistence or transience of seedlings in new environments, and the transition from seedlings to a mature forest constrains our ability to interpret and project cumulative climate-change effects on forests at high elevations (Wieser and Tausz 2007). In the present study, we investigated responses in regeneration of limber pine (*Pinus flexilis* E. James) and bristlecone pine (*P. longaeva* D.K. Bailey) subalpine forests in Great Basin ranges of eastern California and western Nevada, USA. We assessed age, abundance, and density of live trees that were ≤130 years old along ecotones at high, middle, and low elevations and evaluated environmental and climatic associations. We further analyzed climatic correlations of mature-tree radial growth, comparing these with conditions favored for seedling and young tree recruitment.

Materials and methods

Species, study sites, and field methods

Limber pine and bristlecone pine are the common subalpine conifers that form the upper tree line of the Great Basin mountains, excluding the Sierra Nevada where limber pine is a minor species and bristlecone pine is absent. At the latitude of our study, mature limber pine forests extend from ~2900 m to 3350 m on a variety of substrates but often avoid carbonate soils (e.g., dolomite and limestone). Of the ranges we surveyed, bristlecone pine grows only in the White Mountains, where it occurs in monotypic

Fig. 1. Map of study region showing distribution of pine recruitment and tree-ring sites in eastern California and western Nevada. Recruitment sites (solid circles): high elevation — BP, Bighorn Peak; CM, Campito Mountain; CP, Corey Peak; PG, Patriarch Grove; TC, Trail Canyon; middle elevation — CC, Crooked Creek; CP, Corey Peak; RR, Relay Ridge; TC, Trail Canyon; SG, Schulman Grove; low elevation — BR, Brawley Peaks; CL, Cell Ravine; CP, Corey Peak; MH, Mount Hicks; OG, Owens Gorge; OH, O'Harrell Canyon; SC, Silver Canyon; TR, Trail Canyon. Tree-ring sites (open diamonds): TC, Trail Canyon; CP, Corey Peak; SW, Sweetwater Mountains; OG, Owens Gorge.



stands, as well as in mixed stands with limber pine, and mature trees extend to higher elevations than limber pine (~3500 m). Bristlecone pine dominates on carbonate substrates, where it reaches its highest elevations (Wright and Mooney 1965). The lower elevation limits of bristlecone pine are similar to the elevation limits of limber pine.

We selected four mountain ranges for study, with differing geologies, soils, and topographies (Fig. 1; Table 1). All four are semi-arid ranges, lying in the rain shadow of the Sierra Nevada.

Pacific-origin storms nonetheless provide the dominant source of precipitation, which occurs as snow in the winter; limited monsoon rains fall in summer. We searched for sites at which abundant young pines were growing above or below the current forest border or were growing at middle-elevation forest borders. Forest ecotones were chosen where they appeared to be climatic boundaries and not where the tree limit appeared to be influenced by a local disturbance or lithologic transition. Stratifying in this manner, we selected 18 sites representing high (mean, 3373 m), middle (mean, 3125 m), and low (mean, 2699 m) elevation zones (Fig. 1; Table 1). The small Owens Gorge stand is at an exceptionally low elevation and is disjunct from typical limber pine forests by >10 km in distance and >700 m in elevation. At the study sites, young pines

Table 1. Study sites, context, number of transects, and number of trees for limber pine and bristlecone pine recruitment surveys.

Elevation zone	Site code	Site	Elevation range (m)	No. of transects	No. of trees ≤ 130 years		Conifer species in transect	Slope aspect(s)	Substrate
					Limber pine	Bristlecone pine			
White Mountains									
High	BP	Bighorn Peak	3463–3574	4	334	56	PiLo, PiFl	NE, E, S, W	Calcareous
	PG	Patriarch Grove	3474–3555	1	311	95	PiLo, PiFl	SE	Calcareous
	CM	Campito Mountain	3341–3427	1	57	8	PiLo, PiFl	NE, E, S, W	Sandstone
	TC	Trail Canyon	3133–3393	3	185		PiFl	N, E, NW	Granitic
Middle	CC	Crooked Creek	3104–3174	3	128	4	PiLo, PiFl	N, E, W	Granitic
	TC	Trail Canyon	3044–3140	2	170		PiFl	N, NW	Granitic
	RR	Relay Ridge	3184–3316	2	25	29	PiLo, PiFl	N, NE	Sandstone
	SH	Schulman Grove	3065–3110	1	3	6	PiLo, PiFl	W	Sandstone
Low	CL	Cell Ravine	2891–3050	3	59	6	PiLo, PiFl, PiMo	SW, W, NW	Sandstone
	TC	Trail Canyon	2757–3053	4	188		PiFl, PiMo	N, NE	Granitic
	SC	Silver Canyon	3028–3114	2	31	6	PiLo, PiFl	NW	Sandstone
Wassuk Range									
High	CP	Corey Peak	3168–3204	4	74		PiFl	N, NE, E, SE	Granitic
Middle	CP	Corey Peak	3054–3068	3	127		PiFl	N, NE, E	Granitic
Low	CP	Corey Peak	2100–2983	11	207		PiFl, PiMo	N, NE, E, S, SW	Granitic
Glass Mountains									
Low	OH	O'Harrell Canyon	2442–2534	1	25		PiFl, PiMo, PiJe, JuOc	SW	Volcanic tephra
Low	OG	Owens Gorge	2014–2161	4	123		PiFl, PiMo	N	Volcanic tuff
Bodie Mountains									
Low	BR	Brawley Peaks	2667–2863	14	545		PiFl, PiMo	N, NE, E, S, SW, W, NW	Volcanic flow
	MH	Mt Hicks	2685–2843	2	80		PiFl, PiMo	SE, NW	Volcanic

Note: PiFl, *Pinus flexilis*; PiLo, *Pinus longaeva*; PiMo, *Pinus monophylla*; PiJe, *Pinus jeffreyi*; JuOc, *Juniperus occidentalis*. Where more than one slope aspect is given, these are for different transects at the site. Totals: number of transects, 65; number of limber pine, 2672; number of bristlecone pine, 210.

(stem diameters, ≤ 10 cm) extended ≥ 20 m beyond the mature forest border.

We surveyed pine recruitment in 30 m wide belt transects laid perpendicular to the slope contour. Two exceptional locations had unusually dense recruitment, and in those, we used 20 m wide belt transects. Transects were divided into 30 m lengths, yielding 900 m² plots for all but the exceptional belts, which were 600 m². The number of plots and length of transects varied with the extent of local regeneration and ranged from 1 to 16 plots per transect. The number of transects at each site depended on the extent of regeneration and ranged from 1 to 14 transects per site.

Within the plots, all live limber and bristlecone pine trees ≤ 10 cm in stem diameter at a height of 0.5 m were tallied and assessed for age as of 2013. For trees with diameters of 5–10 cm at 0.5 m stem height from the ground, ages were determined by ring counts. For those trees, we extracted one increment core at a height of 0.5 m using a standard borer. For trees with diameters of < 5 cm at 0.5 m stem height, we counted the total number of stem internodes as a measure of tree age (Millar et al. 2004). To determine age to coring height, at ten sites, we estimated the age of 25 small trees each of limber and bristlecone pines by counting internodes to a height of 0.5 m and adding the mean of that number to the number of rings to the pith from the cores. To estimate basal area, all other live trees in the plot, including trees of any species with diameters greater than 10 cm or small-diameter trees other than limber or bristlecone pines, were tallied by species and diameter at a height of 18 cm. Dead trees in plots were recorded by stem diameter.

To assess radial growth in mature trees, we measured annually dated ring widths from highly correlated local tree-ring chronologies. These included four multimillennial chronologies that we have developed for limber pine stands in the vicinity of the recruitment sites (Fig. 1). For the purposes of this study, we focused on the past 130 years. More than 15 trees were included in each chronology for all time intervals.

Laboratory and analyses

Core preparation and recruitment analyses

Air-dried increment cores were prepared for ring-width measurement, dating, and analysis using standard tree-ring techniques (Holmes et al. 1986; Cook and Kairukstis 1990). Standard chronologies were developed for each site from mature trees using COFECHA (Holmes et al. 1986; CofechaOSX_pjk2012, Krusic 2012). Cross-dating was done with reference to local trees, to chronologies we have developed, and to standard chronologies extracted from the International Tree-Ring Database (available from the NOAA National Climate Data Center at www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets/tree-ring, accessed March 2014). We included only trees that were ≤ 130 years old in 2013 in the dataset. Separately, we estimated the densities of mature trees (> 130 years or > 10 cm stem diameter) and dead stems within transects and calculated the basal area of mature live trees for each transect. In developing standard ring-width chronologies to assess growth of mature trees, we used only series that had correlations to the master chronology greater than 0.4.

To compare recruit ages and densities among sites, we converted counts of trees by age classes (recruit, mature live, and dead) per plot into densities per hectare. Datasets were grouped by species, mountain range, and ecotone elevation zone (hereafter low, middle, and high). We fit smoothing splines with smoothing parameters (λ ; if equal to zero, then it fits every point) equal to 1 (to reveal high-frequency variation) and equal to 100 (to reveal low-frequency variation) for density over time. As λ diverges to infinity, the estimate becomes stiffer and converges to a straight line, estimated by least squares. Chronologies were developed in ARSTAN v.44h2 (Cook and Krusic 2013), with the RCS option and using a 200-year spline. With a number of relatively short series (~ 100 years), we stabilized variance at 90% n (where n is the series length (years)) with 50% cutoff.

Splines and regression statistics were calculated in JMP (SAS Institute Inc. 2010). A repeated measures MANOVA was used to test for significance in overall density differences among ranges

and elevations and density differences over time (birth years of recruits) among ranges and elevations. The fixed-effect model was as follows: range, elevation, and transect (range and elevation), with plot as the error term (SAS Institute Inc. 2010).

Episodes of recruitment and synchrony among sites were assessed by modeling abrupt changes in variance of recruitment density over time. To determine this, we modeled the heterogeneity of variance (PROC AUTOREG; SAS Institute Inc. 2010) based on combined datasets for each of the three elevation zones. We first fit an ARCH (autoregressive conditional heteroscedasticity) model to the data, which assesses short-memory variances dependent on squared deviations in prior years. When ARCH tests were significantly high order ($p < 0.01$), a generalized ARCH (GARCH) model is indicated, which provided better fit for situations in which variances were long memory or dependent on prior variances (Chatfield 2004).

Climatic analyses

To characterize the 1883–2013 climatic variability, we reviewed records from National Oceanic and Atmospheric Administration – National Weather Service (NOAA–NWS) COOP weather stations in the region of our study sites and selected stations that had long records, the most complete datasets, and were part of the revised and updated Historical Climate Network (HCN) group (NCDC 2014) that were corrected for inhomogeneities and missing data. Following the approach of Millar et al. (2004), we statistically combined the data from the individual stations into composite records (1883–2013) for mean monthly minimum and maximum temperatures and annual precipitation. Annual precipitation was transformed to water year precipitation (1 October – 30 September). We subjected climatic data from these stations to principal components analysis and created a composite climate record based on four weather stations that had the longest complete records (~120 years) and highest synchrony among each other (Table 2). Indices for the composite record were derived from the scores of the first principal component. Preliminary analysis indicated that the recruitment data were more highly correlated with these composite records than they were with data from individual COOP stations or with data extracted from the 800 m grid PRISM climate model (Daly et al. 1994).

To further explore water relationships of importance to plants, we modeled climatic water deficit (CWD) and snow depth for each of our sites using a regional water-balance model, the Basin Characterization Model (BCM; Flint et al. 2013). These data were modeled using PRISM regional climate projections downscaled to 270 m for the coordinates of each of our sites. CWD is a measure of moisture availability to plants as indicated by evaporative demand that exceeds available water. It is computed as potential evapotranspiration (PET) minus actual evapotranspiration (AET). CWD ranges from zero, when soils are fully saturated (i.e., at field capacity), to positive values with no upper limit. Higher values indicate soils that are depleted of water, i.e., water is increasingly unavailable to meet the transpirational demand. CWD has been shown to be a better indicator of climate effects on pine growth in the California mountains than direct climate variables (Millar et al. 2012).

Lead and lag year cross correlations were assessed in the time series analysis platform in JMP (SAS Institute Inc. 2010). Except where noted in the results, correlations of the annual measures were equal to or greater than those for the monthly data. Where there were significant lead or lag correlations, we summed the data over 1–6 lead or lag years. To test relationships of climate and recruitment responses, we analyzed a simple linear correlation, as well as nonlinear relationships (SAS Institute Inc. 2010). For the latter, we conducted a second-order least squares response-surface model (i.e., JMP, SAS Institute Inc. 2010), with maximum and minimum temperatures and water year (WY) precipitation, using annual and monthly (lag or lead, where appropriate) measures from the

Table 2. Weather stations providing long-term data used to assess climatic relationships and density of recruitment.

Station	Agency-code	Latitude (N)	Longitude (W)	Elevation (m)
Tahoe City	WRCC-048758	39°10′	120°09′	1898
Mina	WRCC-265911	38°23′	118°06′	1387
Yosemite Valley	WRCC-049855	37°45′	119°35′	1250
Independence	WRCC-044232	36°48′	118°12′	1205

Note: All stations are in California, except Mina, which is in Nevada. Data provided by the Historical Climate Network (HCN), with periods of record for all stations 1895–2013, National Climate Data Center (www.ncdc.noaa.gov/oa/climate/research/ushcn/).

composites of regional weather stations, CWD, as well as standard indices of PDO (Pacific Decadal Oscillation), AMO (Atlantic Multidecadal Oscillator), NAO (North Atlantic Oscillation), and the AO (Arctic Oscillator). We evaluated the behavior of these variables in second-order response models of the form $(x + y + \dots) + (x + y + \dots)^2$ in which redundant interactions were omitted. Using stepwise regression, we filtered the model to select only the significant independent variables for further development of a best-fit model for the recruitment data and evaluated the behavior of these variables in second-order response surfaces. Models were fit by not only minimizing AIC_c (corrected Akaike's information criterion), but also noting the SBC scores (Schwarz Bayesian criterion) (SAS Institute Inc. 2010).

Results

In general, recruitment beyond forest borders at all elevations was uncommon in the mountain ranges that we surveyed and abundant only at a few locations (Fig. 2). At these sites, recruitment occurred on all major slope aspects, although northward slope aspects dominated. Recruits were distributed on substrates representative of the lithic diversity in the region (Table 1; Fig. 2). In the White Mountains, bristlecone pine and limber pine grew on the same diversity of soils in transects, including an unexpected abundance and dominance of limber pine recruitment over bristlecone pine recruitment on dolomite substrates (Fig. 2A).

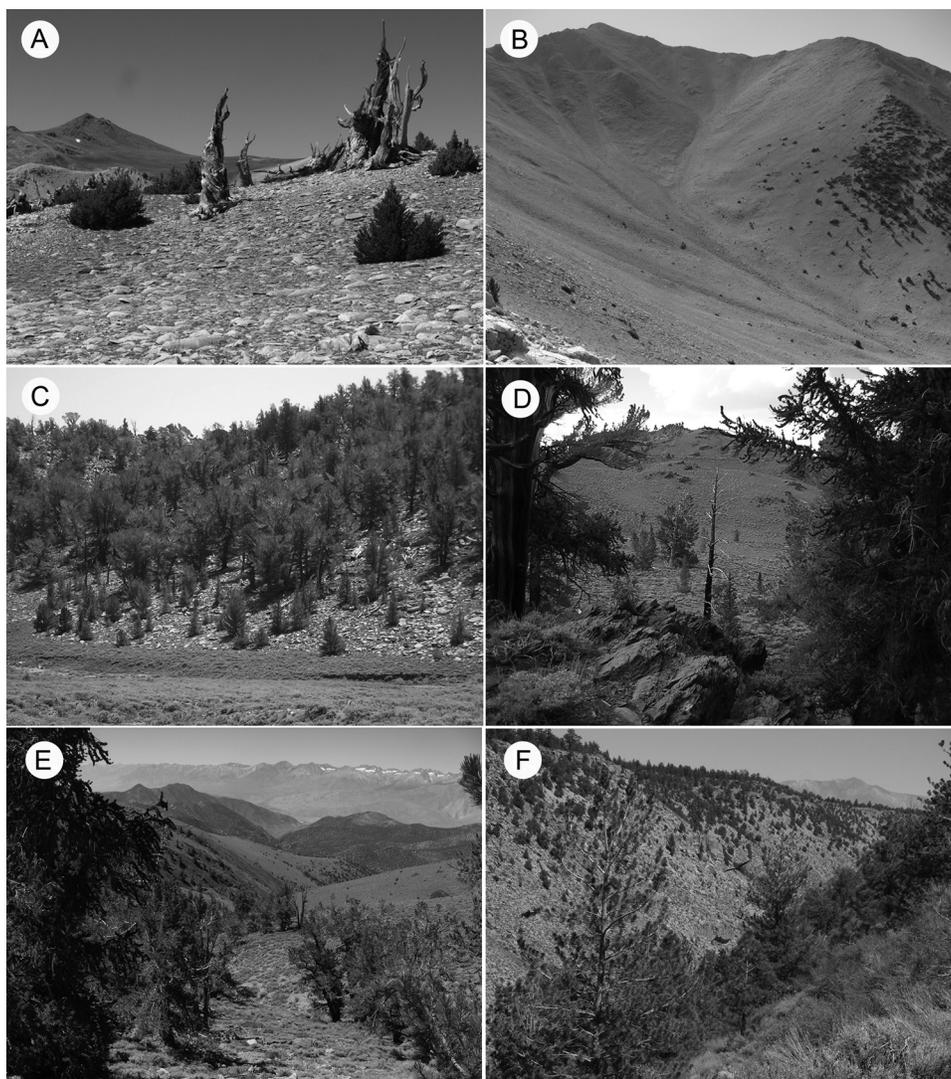
Density and age structure of recruitment

Over all sites, we counted a total of 2672 limber pines and 210 bristlecone pines whose ages were ≤ 130 years in 2013 (Table 1). In the MANOVA, differences in overall densities of pine recruits differed significantly among ranges ($p = 0.0015$) and among elevations ($p = 0.0009$). Pine recruits were most abundant in the high-elevation zone and least abundant in the low-elevation zone (Table 3A). Transects varied in the density of live and dead mature stems (Tables 3B and 3C, respectively). Mature limber pines were abundant in all middle- and low-elevation transects. Basal areas repeated these patterns (Table 3D). Recruits extended farthest beyond the mature forest border in upper elevation ecotones, in which limber pine recruits extended 40–225 m and bristlecone pine recruits extended 50–75 m.

At the lower forest border, canyons and ravines provided microsites that supported disjunct patches of mature forest considerably below the primary lower tree line. Recruitment below these lower forest patches and lower tree line occurred at lower densities than at upper tree lines and extended <75 m into adjacent sagebrush shrubland or pinyon pine (*Pinus monophylla* Torr. & Frém.) woodland. At middle elevations, pine recruits occurred with low densities 20–140 m beyond the mature forest border.

In the White Mountains, where both species occurred, the mean density of limber pine recruits was nearly six times that of bristlecone pine, with bristlecone pine composing 15% of high-elevation recruits, 11% of middle-elevation recruits, and 4% of low-elevation recruits (Tables 1 and 3). Dominance of limber pine in the recruit classes occurred even where upper tree line currently

Fig. 2. Recruitment of pines at high, middle, and low ecotones in western Great Basin ranges. Limber pine extending above current mature upper tree line: (A) southern White Mountains (Bighorn Peak), limited to sites of ancient bristlecone pine relict stems; (B) northern White Mountains (Trail Canyon), recruitment on treeless slopes. Limber pine recruiting into sagebrush meadows at middle elevations: (C) White Mountains, Crooked Creek; (D) White Mountains, Relay Ridge. Limber pine extending below the current lower mature tree line: (E) White Mountain ravines; (F) Owens Gorge. Photos: C.I. Millar.



comprises mature bristlecone pine forests. This created a leapfrog effect of young limber pines above the former bristlecone pine tree line.

Birth years of limber pine recruits were strongly episodic, with all sites showing a similar trend ($p < 0.0001$), although with different peak ages and distributions among elevation zones ($p = 0.0004$) and species (Tables 4 and 5; Figs. 3 and 4). The duration of the limber pine recruitment pulse was from 1960–1965 to 1990–2000, with the shorter intervals at middle and low elevations and the longer interval at high elevations (Figs. 3 and 4). The mean ages of limber pine recruits were 31 years old for high-elevation transects, 47 years old for middle-elevation transects, and 40 years old for low-elevation transects (Table 4). For bristlecone pine, mean ages were 40 (high-elevation transects), 56 (middle-elevation transects), and 28 (low-elevation transects) years old (Table 4). The episodic nature was strongest in high- and low-elevation transects, with the middle-elevation transects having recruits scattered throughout the 130-year interval (Fig. 5).

The episodic pattern in limber pine recruitment was corroborated through ARCH (high elevation, lag of 5 years) and GARCH

(middle and low elevation, long memory) analyses, conducted for combined limber pine data by elevation zone. ARCH and GARCH analyses showed the strongest variance episodes in density of recruits by birth year in the high-elevation transects, which had low but constant densities of recruits with birth years before 1965, a strong shift in variance peaking in 1982 with smaller peaks thereafter, and recruitment declining after 2000 (Table 5; Fig. 3A). The low-elevation transects also showed a strong pattern of episodic recruitment in ARCH and GARCH analyses, with similar changes in variance starting about 1965 and spiking in 1982 (Table 5; Fig. 3C). The major pulse at low elevations, however, was followed by a later, shorter, and smaller pulse in ~2003–2009, with GARCH variance peaking at 2005. GARCH analyses for middle-elevation transects corroborated the weaker trends in episodes, although both late-20th century pulses were indicated: the major episode peaked at 1980 and the minor peak occurred at 2005. In the middle-elevation zone, variances were noisier throughout the 130 years, and episodes of minor recruitment centered on 1915, 1930, and 1950 (Table 5; Fig. 3B). Differences in mean densities of recruit birth years among 43-year intervals of 1883–2013 were all

Table 3. Mean ages and densities of limber pine and bristlecone pine trees in 2013 by site and elevation zone.

Mountain range	Site	Lumber pine density (stems·ha ⁻¹)						Bristlecone pine density (stems·ha ⁻¹)						
		High elevation		Middle elevation		Low elevation		High elevation		Middle elevation		Low elevation		
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	
A. Mean densities of live trees (≤130 years old)														
White Mountains	Bighorn Peak	144	147					44	57					
	Patriarch Grove	242	216					78	46					
	Campito Mountain	67	55					13	11					
	Trail Canyon	62	81	114	83	50	54							
	Crooked Creek			73	69					7	10			
	Relay Ridge			20	15					27	25			
	Schulman Grove			33						67				
	Cell Ravine					22	33						2.0	4.1
	Silver Canyon					9	15						0.8	3.0
Wassuk Range	Corey Peak	69	43	141	61	53	50							
Glass Mountains	O'Harrell Canyon					15	20							
	Owens Gorge					132	108							
Bodie Mountains	Brawley Peaks					109	133							
	Mount Hicks					59	31							
Mean		113	138	82	75	70	92	52	52	24	25	1.4	3.4	
B. Mean densities of live trees (>130 years old)														
White Mountains	Bighorn Peak	22.2	—					25.9	12.8					
	Patriarch Grove							54.2	38.7					
	Campito Mountain							39.7	20.1					
	Trail Canyon			61.8	59.3	26.8	20.6							
	Crooked Creek			49.2	34.5					11.1	0.0			
	Relay Ridge			38.9	23.8					62.2	38.2			
	Schulman Grove													
	Cell Ravine					28.2	15.5					20.0	14.5	
	Silver Canyon					52.4	26.2					22.2	—	
Wassuk Range	Corey Peak	55.6	47.4	75.9	31.0	50.6	34.6							
Glass Mountains	O'Harrell Canyon					31.9	24.1							
	Owens Gorge					157.4	122.4							
Bodie Mountains	Brawley Peaks					32.2	22.2							
	Mount Hicks					40.5	28.8							
Mean		52.8	46.2	55.4	40.5	37.8	26.9	43.8	29.9	50.4	40.0	20.4	14.5	
C. Mean densities of dead trees														
White Mountains	Bighorn Peak							61.5	35.1					
	Patriarch Grove							63.3	44.8					
	Campito Mountain							66.7	23.3					
	Trail Canyon	11.1	—	42.0	24.2	27.8	21.3							
	Crooked Creek			42.2	26.5									
	Relay Ridge									52.5	35.5			
	Schulman Grove													
	Cell Ravine					29.6	17.6					11.1	—	
	Silver Canyon					38.9	23.1					22.0	—	
Wassuk Range	Corey Peak													
Glass Mountains	O'Harrell Canyon													
	Owens Gorge													
Bodie Mountains	Brawley Peaks													
	Mount Hicks					27.8	17.8							
Mean		11.1	—	42.1	24.0	30.2	18.3	63.1	35.6	52.5	35.5	14.8	—	
D. Mean basal area of live trees (>130 years old)														
White Mountains	Bighorn Peak	0.1	0.4					13.7	61.0					
	Patriarch Grove							34.9	50.1					
	Campito Mtn							47.6	36.6					
	Trail Canyon			29.0	48.5	17.6	29.2							
	Crooked Creek			24.8	42.7					0.6	1.3			
	Relay Ridge			24.5	50.9					39.7	62.4			
	Schulman Grove									tr				
	Cell Ravine					18.7	22.8					5.1	14.3	
	Silver Canyon					28.63	32.9					1.5	5.0	
Wassuk Range	Range Means	0.0	0.2	25.9	46.6	20.0	27.7	26.7	54.5	21.3	49.0	3.9	12.0	
Wassuk Range	Corey Peak	53.7	53.6	33.4	37.8	26.3	45.4							

Table 3. (concluded).

Mountain range	Site	Lumber pine density (stems·ha ⁻¹)						Bristlecone pine density (stems·ha ⁻¹)					
		High elevation		Middle elevation		Low elevation		High elevation		Middle elevation		Low elevation	
		Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Glass Mountains	O'Harrell Canyon					7.4	14.0						
	Owens Gorge					30.1	36.3						
	Range means					21.9	31.9						
Bodie Mountains	Brawley Peaks					9.4	15.0						
	Mount Hicks					35.5	23.4						
	Range means					15.4	20.4						
Mean		8.0	27.6	27.2	45.0	20.2	30.9	26.7	54.5	21.3	49.0	3.9	12.0

Note: Plot means are averaged over all transects for given site and elevation zone. SD, standard deviation.

Table 4. Mean ages of limber pine and bristlecone pine recruits (≤130 years old) in 2013 by site and elevation zone.

Site	Limber pine (age, years)						Bristlecone pine (age, years)					
	High elevation		Middle elevation		Low elevation		High elevation		Middle elevation		Low elevation	
	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD	Mean	SD
White Mountains range												
Bighorn Peak	31.1	14.7					40.1	14.9				
Patriarch Grove	30.2	16.1					39.7	11.9				
Campito Mountain	47.6	29.3					49.9	26.8				
Trail Canyon	19.2	15.1	49.7	39.3	43.1	20.4						
Crooked Creek			46.8	21.2					51.5	30.6		
Relay Ridge			37.1	20.3					61.7	29.4		
Schulman Grove			21.0	14.9					34.2	16.0		
Cell Ravine					36.9	17.6					22.5	25.9
Silver Canyon					27.6	31.6					34.2	16.0
Wassuk range												
Corey Peak	53.3	29.5	47.6	30.0	49.0	33.7						
Glass Mountains range												
O'Harrell Canyon					63.0	37.8						
Owens Gorge					54.0	29.3						
Bodie Mountains range												
Brawley Peaks					32.1	20.6						
Mount Hicks					39.8	24.0						
Overall mean	31.2	20.0	47.4	31.4	39.9	26.3	40.3	14.1	56.4	29.1	28.3	21.4

Note: SD, standard deviation.

Table 5. Mean densities in 2013 of limber pine and bristlecone pine recruitment (southern White Mountain sites only) by birth year dates for 43-year time intervals and entire 130-year period (1883–2013).

Elevation	Mean densities (stems·ha ⁻¹)			
	<1927	1927–1969	≥1970	1883–2013
A. Limber pine				
Low	7.1	18.9	43.6	70
Middle	11.0	26.5	44.8	82
High	3.4	14.4	95.4	113
Overall	6.8	20.6	55.8	82
B. Bristlecone pine				
Low	0.0	0.6	0.8	1
Middle	1.9	13.6	8.1	24
High	0.3	14.5	37.2	52
Overall	0.6	10.1	19.1	30

Note: Densities are for trees that are ≤130 years old.

significant ($p < 0.0004$; Table 5). The age structure was similar among the ranges, although the low-elevation Glass Mountain transects had a significantly shorter interval in the late-20th century and an earlier peak (1970) than the other ranges ($p = 0.0004$).

Bristlecone pines in the southern White Mountains also showed episodic age structure but only at high elevations (Tables 4 and 5; Fig. 4A). The pulse of recruitment was shorter and earlier than limber pine, with birth years from 1955 to 1973 and a smaller pulse from 1978 to 1988. In the middle-elevation transects, bristlecone pine densities were very low for all ages and showed nonsignificant differences over time. At both elevations, bristlecone pine recruits dated almost entirely after 1930 (Fig. 4B).

Spectral analyses of the limber pine recruitment birth year densities over 130 years resolved strong primary peaks at a period of 5 years, with weaker peaks at periods of 10 and 15 years, as well as a peak at a period of 2.5 years.

Mature tree radial growth

The four limber pine ring-width chronologies had high inter-series correlations among trees within each chronology (r values: Owens Gorge, 0.74; Corey Peak, 0.67; Sweetwater Mountains, 0.64; Trail Canyon, 0.54). No evidence for missing or false rings was apparent in any of the chronologies for the 130 years before 2013. Chronologies were relatively consistent among sites with the exception of Owens Gorge (Fig. 6). Owens Gorge was the most variable interannually ($s = 0.36$), with Trail Canyon and Sweetwater Mountains being the least variable ($s = 0.23$ and 0.20 , respectively). The data were highly persistent, with first-order autocorrelations

Fig. 3. Density of pine recruitment by birth year and elevation zone and composite climate records. A–C, limber pine, all sites: (A) high elevation; (B) middle elevation; (C) low elevation. Bold-line spline is fit at $\lambda = 100$; light-line spline is $\lambda = 1$. D–F, 120-year climate records from composite of four NOAA–NWS COOP stations: (D) annual minimum temperature; (E) annual maximum temperature; (F) water year precipitation; (G) climatic water deficit modeled from the Basin Characterization Model (Flint et al. 2013). Shaded panels highlight the recruitment episode. Y axes for D–F are principal component scores. Splines (solid lines) for D and E, $\lambda = 1000$; spline for F, $\lambda = 10$; spline for G, $\lambda = 1000$.

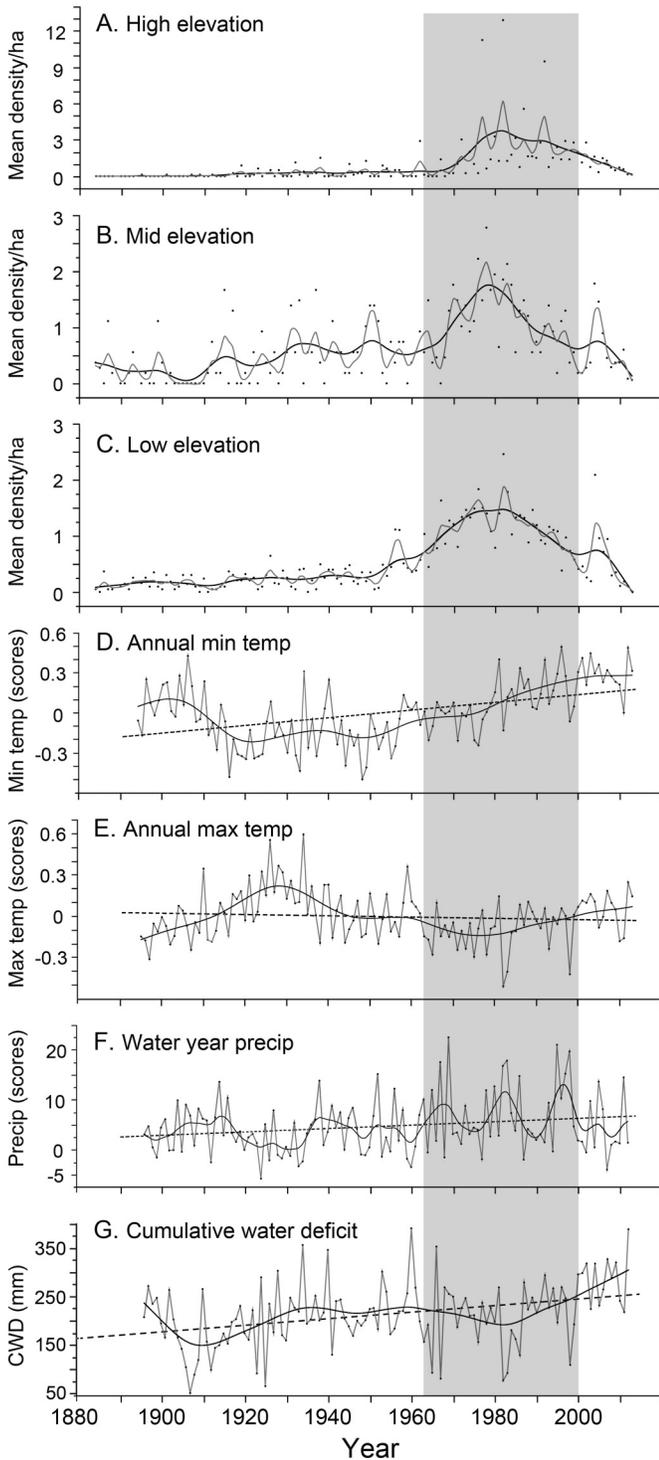
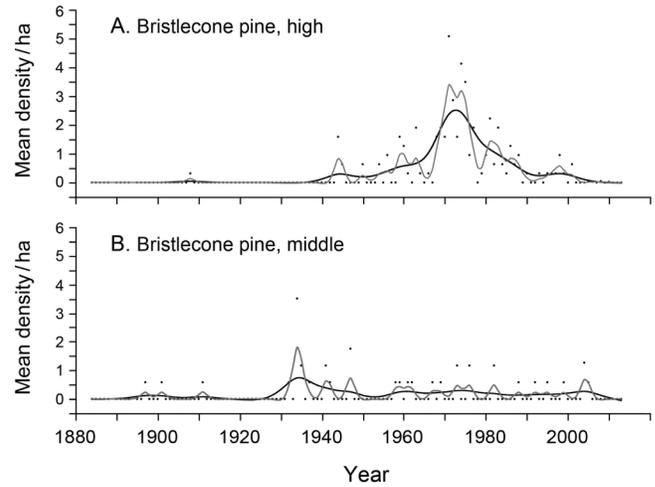


Fig. 4. Density of pine recruitment by birth year and elevation zone for bristlecone pine, southern White Mountains: (A) high elevation and (B) middle elevation. Splines are as in Fig. 3.



greater than 0.6 and significant autocorrelations persistent for 3–5 years. The two most persistent time series, Corey Peak and Sweetwater Mountains, were autoregressive, moving average (ARMA(2,1)) processes (Bunn et al. 2013). Ring widths for all sites showed a pulse of high growth coinciding with the late-20th century recruitment episode. In each of the chronologies, ring widths in that interval were greater than any other time during the last 130 years, as well as during the 260 years analyzed here, although Owens Gorge was more variable than the others. Ring widths began to increase above the average in 1965, peaked in 1980, and began to strongly decrease thereafter, culminating in very low ring widths (mostly below the 260-year average) during the period 2000–2013. These last 13 years of ring widths were often the lowest in the past 130 years. Other periods of low ring widths were 1880–1900 (Corey Peak, Sweetwater Mountains, and Trail Canyon) and 1920–1940 (Corey Peak, Sweetwater Mountains, and Owens Gorge); minor periods of higher ring widths occurred in 1900–1920 (Corey Peak, Sweetwater Mountains, and Owens Gorge).

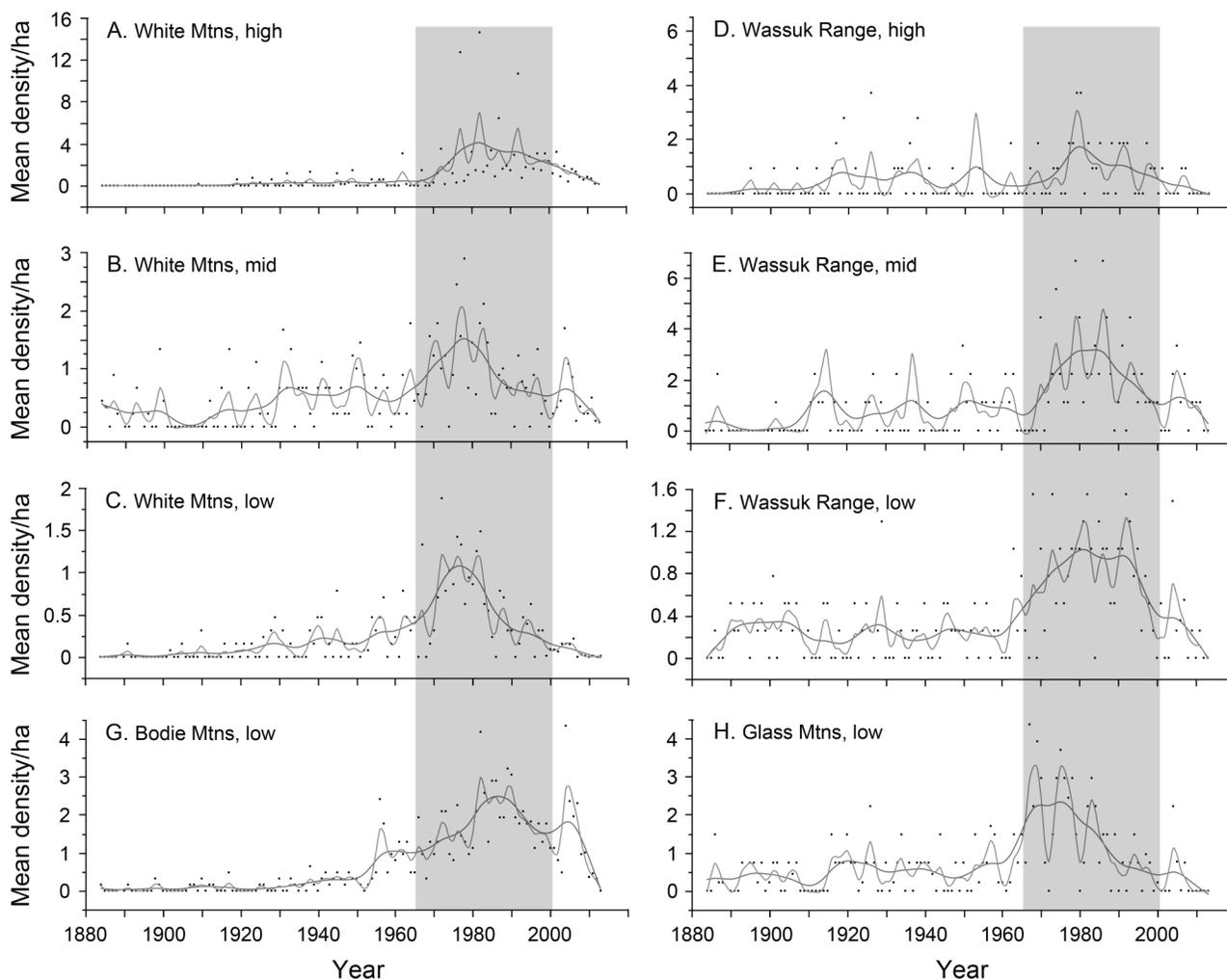
Climate trends and climatic relationships with recruitment and radial growth

Climate trends

The composite regional weather record of four stations showed significant increases in the minimum temperature ($p < 0.001$) but not in the maximum temperature ($p = 0.23$, which decreased slightly) over the past ~120 years, with an average warming of 1 °C from 1910 to 2013 (Figs. 3D and 3E). Century-long trends did not occur in maximum temperatures, although strong multiyear variability existed throughout the record. Similarly, WY precipitation was characterized by high interannual variability with a slight and significant ($p = 0.03$) increase in the mean over 120 years (Fig. 3F). Multiyear droughts persisted for 6–8 years. A GARCH estimate of interannual variation had increasing interannual variability in precipitation since the 1940s, with decreases in variability in the droughts of the mid-1970s, 1990, and the early-21st century.

CWD increased notably during the 20th century, implying increasing soil-moisture stress. With the smoothing spline, a prolonged interval of low CWD values (lower relative plant water stress) coincided with the period of pine recruitment from 1965 to 2000 (Fig. 3G). A period of similar conditions occurred from 1900 to 1920, for which CWD and maximum temperatures were low and minimum temperatures and precipitation were elevated, but no recruitment pulse was observed. However, from 1915, minimum temperatures and precipitation decreased and maximum

Fig. 5. Density of limber pine recruitment at four Great Basin mountain ranges by germination year and elevation zone (low, middle, or high): (A) White Mountains, high; (B) White Mountains, middle; (C) White Mountains, low; (D) Wassuk Range, high; (E) Wassuk Range, middle; (F) Wassuk Range, low; (G) Bodie Mountains, low; (H) Glass Mountains, low. Splines are as in Fig. 3. Shaded panels highlight the recruitment episode.



temperatures increased into the 1930s drought. Snowpack depths modeled for the analysis period showed very high interannual variance, increasing after 1965, with no obvious long-term trends.

Climatic correlations with recruitment

Recruitment data were analyzed by elevation zone. We assessed best-fit models by stepwise regressions, with overall model $R^2 \geq 0.5$ ($p < 0.00001$; Table 6). Climate variables with significant lead, current, or lagged correlations that were included in the models were as follows: positive climatic correlations with the year of recruitment included annual minimum temperature (T_{min}), water year precipitation (WY precip), and September precipitation (Sept precip); negative climatic correlations for the recruitment year were annual maximum temperature (T_{max}) and July maximum temperature (Jul T_{max}); lead (years before germination) and lag (years after germination) effects were important in the best-fit models, in which significant correlations of recruitment resulted ($p < 0.00001$). Variables with positive lead and lag correlations included were T_{min} (low, middle, and high; 1 to 6 years lag), WY precip (low, middle, and high; 1 to 3 years lag), Jul precip (low, middle, and high; 1 to 3 years lag and 2 years lead), and Sept precip (high; 1 and 2 year lead). Those with negative lag correlations included were T_{max} (low, middle, and high; 1 to 6 years lag) and Jul T_{max} (low, middle, and high; 1 to 6 years lag). Snowpack also had

positive lag correlations with recruitment at high (1 year lag) and middle (5 years lag) elevations. At all elevations, low-frequency indices (PDO and AMO) improved the model fits (Table 6). Although CWD had low individual correlations, the model fit improved considerably with its addition and resulted in interaction terms with WY precip and Sept precip, whereby when CWD was high, increases in WY precip and Sept precip increased recruitment. In addition, Jul precip, Sept precip, and WY precip tended to show compensatory relationships, whereby when one factor was low, increases in the other factors increased recruit. Although PDO and AMO increased fit in the models, the increases were not substantial.

We also explored recruitment data with the National Centers for Environmental Prediction and National Center for Atmospheric Research (NCEP/NCAR) geopotential heights (gravity-adjusted atmospheric pressures) at the 700 mb height (<http://www.esrl.noaa.gov/psd/cgi-bin/data/composites/printpage.pl>, accessed 12 November 2014). At high elevations, recruitment was correlated with high pressures over the northern Rockies. This is often associated with early snowmelt (Greg Pederson, U.S. Geological Survey (USGS), personal communication). At middle and low elevations, however, recruitment was correlated with zonal low pressures propagating from the Pacific and moving eastward, suggesting El Niño storm patterns. At

Fig. 6. Standardized ring widths for four limber pine tree-ring chronologies (1750–2013). The period assessed for recruitment extended to 1883 (marked by the solid vertical line). Shaded panels highlight the recruitment episode.

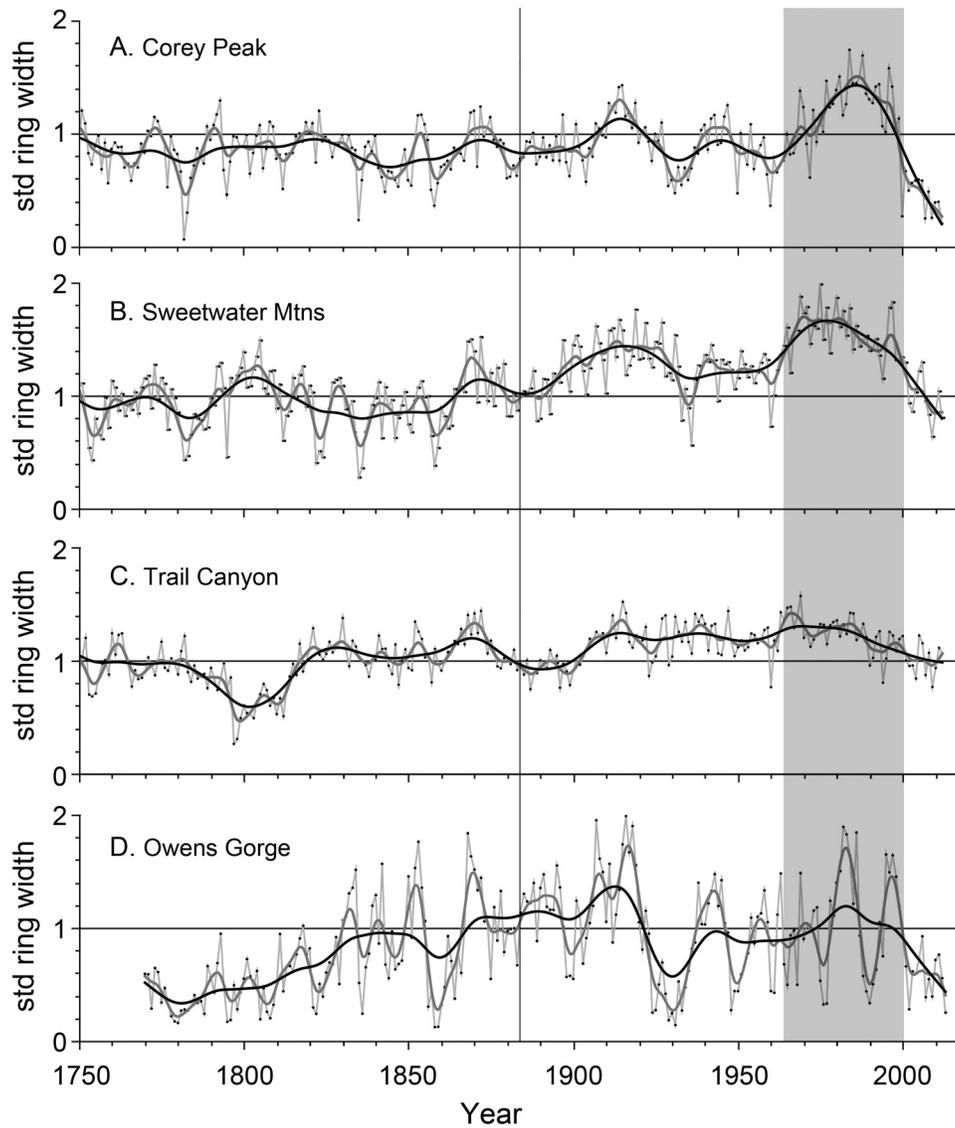


Table 6. Model correlations and climate variables included in best-fit stepwise regression analyses.

Elevation zone	Model R ² (1)	Model R ² (2)	T _{min}	T _{max}	July T _{max}	Water year precip	July precip	Sept precip	CWD	Snow pack
A. Recruitment										
Full period (1883–2013)										
High	0.62	0.56	+	-	-	+	+	+	-	+
Middle	0.63	0.52	+	-	-	+	+	+	-	+
Low	0.84	0.78	+	-	-	+	+	+	-	-
Recruitment episode (1965–2013)										
High	0.89	nd	+	-	-	+	+	+	-	-
Middle	0.73	nd	-	-	-	-	+	+	-	-
Low	0.89	nd	-	-	-	-	+	+	-	-
B. Radial ring width full period (1883–2013)										
Corey Peak	0.75	0.70		-	-	+	+	+	-	
Sweetwater Mountains	0.71	0.67		-	-	+	+	+	-	
Trail Canyon	0.50	0.38		-	-	+	+	+	-	
Owens Gorge	0.85	0.78	+	-	-	+	+	+	-	+

Note: Plus or minus signs refer to the sign of the simple correlation coefficient. Squared multiple correlation coefficients are given for models with (1) and without (2) low-frequency indices included. Precip, precipitation; CWD, climatic water deficit; nd, not done.

Can. J. For. Res. Downloaded from www.nrcresearchpress.com by USDA 2015 on 12/16/15 For personal use only.

all elevations, recruitment was correlated with low pressures in September, propagating northward from the Sea of Cortez, both in the current year and 1-year lead and lagged years. In all cases, correlations with atmospheric pressures were low (~ 0.3), suggesting a cumulative effect (Daniel Cayan, USGS, personal communication). We observed a similar pattern in the relation of our climate data to recruitment: individual correlations with climate were low (< 0.4), yet R^2 for model fits were rather high, indicating a cumulative impact of climate (Table 6).

Models run for the recruitment episode (1965–2000) had higher overall correlations and more consistency among elevations than models for the entire 130 years, with $R^2 = 0.7\text{--}0.9$ ($p < 0.00001$; Table 6). Variables included in the best-fit models for the recruitment period were mostly similar to the entire interval, with several important differences: as in the full interval model, T_{\min} at high elevations was correlated with lag years (4 years), whereas at middle and low elevations, T_{\min} was negatively correlated with the lead years (6 years). CWD was negatively correlated with the recruitment year and also the 1–6 years lag at all elevations. T_{\max} had lead, as well as lag, correlations at the high and low elevations. Positive correlations of Jul precip with lag years were important (1–6 years) for all elevations, as were positive correlations with Sept precip at all elevations but, in this case, for lead years rather than lag years (1–4 years).

Overall relationships are shown in Fig. 3, in which mean data for high-, middle-, and low-elevation recruitment are graphed against T_{\min} , T_{\max} , WY precip, and CWD. On average, during the 1965–2000 pine recruitment episode, snowpack levels were above average, although a very low snowpack characterized the 1970s and 1990s droughts as well.

Climatic correlations with radial growth

Best-fit models of ring width to climate with stepwise regressions yielded $R^2 \geq 0.4$ and most were ≥ 0.6 ($p < 0.00001$; Table 6). Positive correlations for growth included WY precip, Jul precip, and Sept precip; negative correlations included T_{\max} , Jul T_{\max} , and CWD. Lead effects were also important in the ring-width data, extending to a 2-year lead for WY precip, Jul precip, Sept precip and a 6-year lead for Jul T_{\max} .

Models run with ring-width data for the recruitment episode had higher overall correlations and more consistency among chronology sites, with the exception of Corey Peak, than models for the entire 130 years, with $R^2 = 0.5\text{--}0.9$ ($p < 0.00001$; Table 6). However, except for Owens Gorge, AIC_c and SBC values were higher in these models than for the entire period, probably due to the lower degrees of freedom in the models, so we chose to use only results from the full interval.

Discussion

The rarity of locations in which subalpine pines are establishing across high-, low-, or middle-elevation ecotones was a surprising result. No factors were obvious in our study as to why recruitment occurred where it did and not in other similar sites. A similar lack of environmental pattern among sites for recruitment above the tree line has been observed in a small number of studies (Butler et al. 1994; Klasner and Fagre 2002; Elliott and Kipfmüller 2010).

The dominance of limber pine recruitment and leapfrog nature above bristlecone pine, especially on carbonate soils, was unexpected from paleohistoric analysis (LaMarche 1973) and recent historic analysis (Wright and Mooney 1965) or from modeled future conditions (Van de Ven et al. 2007). Climate envelope models project bristlecone pine to shift rapidly upward with intensified warming, eventually becoming restricted to the highest elevations in the range at White Mountain Peak (Van de Ven et al. 2007). Limber pine recruitment might be advancing upslope more rapidly than bristlecone pine due to greater germinative capacity afforded by its large seeds, dispersal and planting by Clark's Nutcracker (*Nucifraga columbiana* (A. Wilson)), or masting tendency.

Whether the relative abundance of limber pine will persist or bristlecone pine will eventually recruit successfully and recover dominance across ecotones remains to be observed. Changing species dominance near and above the upper tree line in response to climate change was documented in the Swedish Scandes (Kullman and Öberg 2009) and in the Mealy Mountains of central Labrador, Canada (Trant and Hermanutz 2014).

Shifts downslope in response to paleohistoric climate change have not been widely reported, but several studies are reporting downward shifts of plant species in response to contemporary climate changes (Lenoir et al. 2008; Beckage et al. 2008; Crimmins et al. 2011). A proposed mechanism is that under relatively stable climates, competition dominantly influences the location of the lower tree line (Callaway and Walker 1997). In ecosystems that this occurs, especially those in which drought-induced stress is not prominent, species are likely to be characterized by realized climatic niches that are smaller than fundamental niches (Vetaas 2002). If changing climates alleviate competitive exclusion, species may be able to shift downslope and expand into fundamental niches (Lenoir et al. 2010). More relevant to the western Great Basin, in which moisture limitations influence the position of the lower tree line, niche tracking of regional changes in climatic water balance likely overrides temperature and competitive effects to catalyze downhill shifts, as documented in a suite of 64 plant species in California (Crimmins et al. 2011). In such cases, increases in water availability from precipitation outpace increased the evaporative demand from warming, allowing downward recruitment. Changes in cold-air drainage (CAD) might also create temperature gradients favorable for plants to move downslope (Pepin and Lundquist 2008). If changing synoptic atmospheric conditions create more CAD events in the future, the net effect in mountain regions could be for temperatures to decrease rather than increase in contexts in which CAD develops (Daly et al. 2008).

Episodic recruitment and climate

In subalpine forests in which disturbance is of minor influence, regeneration patterns historically have been found to be directional or episodic (Lloyd and Graumlich 1997). Barber (2013) reported a regeneration episode in bristlecone pine forests of the White Mountains for the same time as our study, suggesting similar processes within subalpine forests as at the upper tree line. Rapid nonlinear shifts in recruitment have also been reported for conifers advancing above the upper tree line in the southern Rocky Mountains (Elliott and Kipfmüller 2010), Spanish Pyrenees (Camarero and Gutierrez 2007), southern Cascades of California (Taylor 1995), and Rocky Mountains of Montana (Alftine et al. 2003). In these cases, the timing of episodes varied regionally, and climate was inferred as the driving force.

The correspondence in timing and pattern of recruitment across four Great Basin mountain ranges, combined with a lack of other nonclimatic factors that would enforce synchrony, implicates climate as a driver of pine recruitment in our study. Whereas Barber (2013) concluded that high summer precipitation was the primary driver for recruitment in White Mountains bristlecone pine, her best-fit model also included minimum and maximum summer temperatures. Climate relationships for limber pine in the same region appear to be even more complexly related to recruitment. A combination of factors including increased summer and autumn precipitation, increased snowpack, higher T_{\min} , and lower summer temperatures favored episodic recruitment within the last 130 years. Warming night (i.e., minimum) temperatures without increases in daytime T_{\max} in the latter half of the 20th century improved conditions for seedling requirements, especially at upper and lower forest border environments. In semi-arid mountain ranges such as the Great Basin ranges, precipitation — including soil moisture at the driest and warmest times of the year (late summer and autumn) — is a key limiting factor for regeneration,

and recruitment is benefited by previous-year snowpack and warm-season precipitation. The interval of the recruitment pulse had higher precipitation (mean, 495 mm) than the following 12 years (mean, 453 mm), as well as during the prior 20 years (mean, 405 mm; extracted from the 800 m grid PRISM climate model (Daly et al. 1994) for upper Crooked Creek, White Mountains), and WY precip was higher during this interval (Fig. 3F). Years with these conditions resulted in lower CWD values, favoring recruitment.

Importantly, our analyses highlighted the importance of relatively long lead and lag climate effects (extending 6 years before and after the germination year), which explained recruitment better than conditions in any single year. Pine sexual regeneration is a complex multiyear process, requiring 1 year for ovulate-cone primordia and bud initiation and 2 years for cone development before seeds are ripe (Krugman and Jenkinson 1974). Adding the year of germination and ~5 years subsequently during the vulnerable seedling stage, the time required for successful seedling establishment is 9 or more years (see also Barbeito et al. (2012)). The spectral analysis result of peaks of recruitment at 2.5, 5, and 10 years possibly reflect mast years that were followed by resource depletion. Physiologically distinct phases in this period (e.g., bud initiation, seed ripening, germination, and seedling survival and growth) also have distinct climatic requirements (Allen and Owens 1972). Thus the successful establishment of a juvenile tree depends on a sequence of years having the appropriate cumulative climatic conditions rather than any single optimum year. This complexity might partially explain why there were not more recruitment episodes within 130 years. Low interannual variability in key conditions also would favor successful cone development, germination, and establishment; GARCH analyses indicated low variability in WY precip from 1970 to 1980. Similar conditions were found for recruitment into Sierra Nevada subalpine meadows, in which a single 30-year recruitment pulse of pines into meadows within the last 120 years was related to low interannual variability, combined with a complex set of climate conditions (Millar et al. 2004).

In nearby regions, Bunn et al. (2005) observed episodic foxtail pine (*Pinus balfouriana* Balf.) seedling survival and persistence in wet plots relative to dry plots in the high Sierra Nevada. Warming temperatures and increasing precipitation from 1934 to 2007 promoted an increase in seedling recruitment and establishment of several subalpine species at upper elevation zones within Sierra Nevada subalpine forests (Dolanc et al. 2013a). Whitebark pine (*Pinus albicaulis* Engelm.) recruitment over the period 1978–2008 in the Lake Tahoe Basin of the Sierra Nevada had low and steady recruitment from 1970 to 2000, negatively correlated with increasing T_{\min} (Maloney 2014). In the southern Cascades of California, seedling establishment of mountain hemlock (*Tsuga mertensiana* (Bong.) Carrière) across ecotones was greatest during years with warm annual and summer temperatures but negatively correlated with the April snow depth (Taylor 1995). In the Snowy Range of Wyoming, seedling mortality was greatest at the upper tree line when cold nights were followed by hot days with high levels of sunlight, corroborating our correlations with T_{\min} and T_{\max} (Germino et al. 2002). In temperate mountains elsewhere, the advancing tree line has also been correlated with climate, especially negative correlations with high T_{\min} in the growing season and negative correlations with T_{\max} in the spring and early summer (Camarero and Gutierrez 2007). Low multiyear interannual variability has been found important for regeneration episodes in Spain, the Ural Mountains (Russia), and northern Patagonia (Shiyatov 1993; Camarero and Gutierrez 2004; Daniels and Veblen 2004).

Fewer studies have investigated climatic correlates with regeneration across middle-elevation forest ecotones or downslope across lower elevation forest borders. At the lower tree line, increasing warmth would be expected to inhibit downward shifts of the tree line, whereas increased moisture in some environments

appears to drive downward shifts of the tree line, at least in the short term (Crimmins et al. 2011). Higher precipitation during the interval of recruitment in the western Great Basin, coupled with the relative cool of northern ravines, might override warming thermal constraints at lower elevations. The simpler climate model for our middle-elevation transects, wherein increased September precip and lower summer T_{\max} promoted recruitment, suggests that recruitment is not as constrained by climate in this zone. At shrubland–forest borders in middle elevations, warming conditions and adequate soil moisture may have released effects of CAD of prior decades in concavities in which forest and meadows and (or) shrublands commonly meet at middle elevations, enabling advance into nonforest communities in which competitive interactions become as important as climate.

Radial growth relationships with recruitment and climate

Correspondence of climatic correlations and episodes of limber pine radial growth with recruitment was unexpected. In contrast, climatic conditions that facilitate conifer recruitment at the upper tree line in other locations have been found to be distinct and opposite in direction to those that promote increased radial growth, following an expectation that distinct physiological processes respond to different environmental factors (Daniels and Veblen 2004; Camarero and Gutierrez 2007; Barbeito et al. 2012). These studies, however, were conducted in mountain regions that are generally cooler and wetter than those in the Great Basin, where water relations appear to be important overriding and limiting factors.

Furthermore, radial growth is typically assumed to respond to different climatic factors at the upper and lower tree line locations, with the upper forest border being temperature sensitive (LaMarche 1973) and the lower forest border being precipitation sensitive (Hughes and Funkhouser 1998). In Great Basin limber pine, radial growth at both the upper and lower tree line was facilitated by similar complex conditions involving temperature and water relations. In these arid mountain ranges, conditions are likely to be so strongly water limited that high and low elevations do not differ significantly in their driving factors. This is suggested by patterns of synchrony in radial growth, as well as correspondence in climate correlations, among six subalpine conifers from diverse elevation stands across the Mediterranean (dry) climate region of the Sierra Nevada for the period 1896–2006 (Dolanc et al. 2013b). Similarly, radial growth of Sierra Nevada foxtail pine populations on dry sites (as opposed to wet sites) correlated with precipitation regardless of stand elevation (Bunn et al. 2005).

Recent studies of bristlecone pine in the White Mountains document a remarkable sensitivity of radial growth limited to a very narrow band extending from the upper tree line to a threshold elevation that was 60–80 m below it (Salzer et al. 2009, 2014). Within this band, radial growth correlates with temperature, whereas below the threshold elevation, although still high in the upper subalpine zone, growth is precipitation dependent. Our high-elevation chronologies likely do not reflect this pattern, because cored trees were located at variable elevations in the upper subalpine zone, and one chronology location (Owens Gorge) was at a very low elevation for the species, which was highly sensitive to droughts and snowpack compared with the other sites. Thus, it seems likely that water relations exerted dominant but not exclusive control across the forests in which we measured radial growth. The significant correlations of radial growth with as many as 6 years lead underscore the role of persistence in stem growth and importance of cumulative climatic effects that lead to long-duration episodes of increased (or decreased) growth.

Conclusions

Recruitment of subalpine limber and bristlecone pines across forest borders at high-, low-, and middle-elevation ecotones is occurring on a limited number of sites across four mountain ranges of the western Great Basin. Where it occurs, recruitment is

most abundant at the upper tree line. Between 1883 and 2013, a single dominant pulse of recruitment occurred in limber pine at 1963–2000 and in bristlecone pine at 1955–1988; recruitment in the 21st century has been very low for both species. Where the two species co-occur, changes in species dominance above the upper tree line is a consequence of limber pine leapfrogging above bristlecone pine by as much as 300 m. Radial stem growth of high-elevation forests had a similar pattern to recruitment, with an episodic increase in growth from 1963 to 2000 and decreasing growth after 2000. Climate appears to be the primary driver of recruitment and radial growth, which correlate with similar combinations of climate variables. Complex factors of water relations (precipitation, snowpack, and CWD) and temperature during cumulative intervals of up to 9 years explain recruitment better than factors related to any single year or to elevation. Low inter-annual variance in climate variables facilitates both recruitment and radial growth. In these arid mountain ranges, water limitations appear to exert an overriding influence, complexly interacting with temperature on recruitment and radial growth in pines. Understanding future changes in the extent of subalpine species will be improved by further research on upper, lower, and interior ecotones rather than on any single tree line.

Acknowledgements

We thank Chris Fettig (USDA Forest Service, Davis, California), Kaitlin Lubetkin (University of California, Merced), and Brian Smithers (University of California, Davis) for useful discussions and review of the draft manuscript. We also benefited from discussions with Adelia Barber (University of California, Santa Cruz), Dan Cayan (USGS, LaJolla, California), Greg Pederson (USGS, Bozeman, Montana), and Stu Weiss (Creekside Center for Earth Observation, Menlo Park, California).

References

- Alftine, K.J., Malanson, G.P., and Fagre, D.B. 2003. Feedback-driven response to multidecadal climatic variability at an alpine treeline. *Phys. Geogr.* **24**: 520–535. doi:10.2747/0272-3646.24.6.520.
- Allen, G.S., and Owens, J.N. 1972. The life history of Douglas-fir. Information Canada, Ottawa, Ontario.
- Bader, M.Y., Loranger, H., and Zotz, G. 2014. A cool experimental approach to explain elevational treelines, but can it explain them? *Am. J. Bot.* **9**: 1403–1408. doi:10.3732/ajb.1400256.
- Bansal, S., and Germino, M.J. 2010. Variation in ecophysiological properties among conifers at an ecotonal boundary: comparison of establishing seedlings and established adults at timberline. *J. Veg. Sci.* **21**: 133–142. doi:10.1111/j.1654-1103.2009.01127.x.
- Barbeito, I., Dawes, M.A., Rixen, C., Senn, J., and Bebi, P. 2012. Factors driving mortality and growth at treeline: a 30-year experiment of 92,000 conifers. *Ecology*. **93**: 389–401. doi:10.1890/11-0384.1.
- Barber, A. 2013. Physiology and early life-history associated with extreme longevity: an investigation of *Pinus longaeva* (Great Basin bristlecone pine). Doctoral dissertation, Department of Ecology and Evolutionary Biology, University of California, Santa Cruz.
- Beckage, B., Osbourne, B., Gavin, D.G., Pucko, C., Siccama, T., and Perkins, T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. *Proc. Natl. Acad. Sci. U.S.A.* **105**: 4197–4202. doi:10.1073/pnas.0708921105.
- Bell, D.M., Bradford, J.B., and Lauenroth, W.K. 2014. Mountain landscapes offer few opportunities for high-elevation tree species migration. *Glob. Chang. Biol.* **20**: 1441–1451. doi:10.1111/gcb.12504.
- Beniston, M. 2003. Climatic change in mountain regions: a review of possible impacts. *Clim. Change*, **59**: 5–31. doi:10.1007/978-94-015-1252-7_2.
- Beniston, M., Diaz, H.F., and Bradley, R.S. 1997. Climatic change at high elevation sites. An overview. *Clim. Change*, **36**: 233–251. doi:10.1007/978-94-015-8905-5_1.
- Bunn, A.G., Waggoner, L.A., and Graumlich, L.J. 2005. Topographic mediation of growth in high elevation foxtail pine (*Pinus balfouriana* Grev. et Balf.) forests in the Sierra Nevada. *Glob. Ecol. Biogeogr.* **14**: 103–114. doi:10.1111/j.1466-822X.2005.00141.x.
- Bunn, A.G., Jansma, E., Korpela, M., Westfall, R.D., and Baldwin, J. 2013. Using simulations and data to evaluate mean sensitivity as a useful statistic in dendrochronology. *Dendrochronologia*, **31**: 250–254. doi:10.1016/j.dendro.2013.01.004.
- Butler, D.R., Malanson, G.P., and Cairns, D.M. 1994. Stability of alpine treeline in Glacier National Park. *Phytocoenologia*, **22**: 485–500. doi:10.1127/phyto/22/1994/485.
- Callaway, R.M., and Walker, L.R. 1997. Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology*, **78**: 1958–1965. doi:10.1890/0012-9658(1997)078[1958:CAFASA]2.0.CO;2.
- Camarero, J.J., and Gutierrez, E. 2004. Pace and pattern of recent treeline dynamics: response of ecotones to climate variability in the Spanish Pyrenees. *Clim. Change*, **63**: 181–200. doi:10.1023/B:CLIM.0000018507.71343.46.
- Camarero, J.J., and Gutierrez, E. 2007. Response of *Pinus uncinata* recruitment to climate warming and changes in grazing pressure in an isolated population of the Iberian System (NE Spain). *Arctic, Antarctic and Alpine Research*, **39**: 210–217. doi:10.1657/1523-0430(2007)39[210:ROPURT]2.0.CO;2.
- Chatfield, C. 2004. The analysis of time series: an introduction. 6th edition. Chapman and Hall, CRC Press, Boca Raton, Florida.
- Cook, E.R., and Kairukstis, L.A. (Editors). 1990. Methods of dendrochronology. Kluwer, Dordrecht, Netherlands.
- Cook, E.R., and Krusic, P.J. 2013. ARSTAN for Mac OS X, v44h. Available from <http://www.ldeo.columbia.edu/tree-ring-laboratory/resources/software>.
- Crimmins, S.M., Dobrowski, S.Z., Greenberg, J.A., Abatzoglou, J.T., and Mynsberge, A.R. 2011. Changes in climatic water balance drive downhill shifts in plant species' optimum elevations. *Science*, **331**: 324–327. doi:10.1126/science.1199040.
- Daly, C.R., Neilson, R.P., and Phillips, D.L. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *J. Appl. Meteorol.* **33**: 140–158. doi:10.1175/1520-0450(1994)033<0140:ASTMFM>2.0.CO;2.
- Daly, C., Conklin, D.R., and Unsworth, M.H. 2008. Local atmospheric decoupling in complex topography alters climate change impacts. *Int. J. Climatol.* **30**: 1857–1864. doi:10.1002/joc.2007.
- Daniels, L.D., and Veblen, T.T. 2004. Spatiotemporal influences of climate on altitudinal treeline in northern Patagonia. *Ecology*, **85**: 1284–1296. doi:10.1890/03-0092.
- Dolanc, C.R., Thorne, J.H., and Safford, H.D. 2013a. Widespread shifts in the demographic structure of subalpine forests in the Sierra Nevada, California, 1934 to 2007. *Glob. Environ. Change*, **22**: 264–276. doi:10.1111/j.1466-8238.2011.00748.x.
- Dolanc, C.R., Westfall, R.D., Safford, H.D., Thorne, J.H., and Schwartz, M.W. 2013b. Growth-climate relationships for six subalpine tree species in a Mediterranean climate. *Can. J. For. Res.* **43**(12): 1114–1126. doi:10.1139/cjfr-2013-0196.
- Dolanc, C.R., Safford, H.D., Dobrowski, S.Z., and Thorne, J.H. 2014. Twentieth century shifts in abundance and composition of vegetation types of the Sierra Nevada, CA, US. *Appl. Veg. Sci.* **17**: 442–455. doi:10.1111/avsc.12079.
- Elliott, G.P., and Kipffmueller, K.F. 2010. Multi-scale influences of slope aspect and spatial pattern on ecotonal dynamics at upper treeline in the southern Rocky Mountains, U.S.A. *Arct. Antarct. Alp. Res.* **42**: 45–56. doi:10.1657/1938-4246-42.1.45.
- Felde, V.A., Kapfer, J., and Grytnes, J.-A. 2012. Upward shift in elevational plant species ranges in Sikkildalen, central Norway. *Ecography*, **35**: 922–932. doi:10.1111/j.1600-0587.2011.07057.x.
- Flint, L.E., Flint, A.L., Thorne, J.H., and Boynton, R. 2013. Fine-scale hydrologic modeling for regional landscape applications: the California Basin Characterization Model development and performance. *Ecol. Process.* **2**: 25. doi:10.1186/2192-1709-2-25.
- Germino, M.J., Smith, W.K., and Resor, A.C. 2002. Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecol.* **162**: 157–168. doi:10.1023/A:1020385320738.
- Graumlich, L.J., and Lloyd, A.H. 1996. Dendroclimatic, ecological and geomorphological evidence for long-term climatic change in the Sierra Nevada. In *Tree rings, environment, and humanity*. Edited by J.S. Dean, D.M. Meko, and T.W. Swetnam. Radiocarbon 51–59.
- Hayhoe, K., Cayan, D., Field, C.B., Frumhoff, P.C., Maurer, E.P., Miller, N.L., Moser, S.C., Schneider, S.H., Cahill, K.N., Cleland, E.E., Dale, L., Drapek, R., Hanemann, R.M., Kalkstein, L.S., Lenihan, J., Lucht, C.K., Neilson, R.P., Sheridan, S., and Verville, J.H. 2004. Emissions pathways, climate change, and impacts on California. *Proc. Natl. Acad. Sci. U.S.A.* **101**: 12422–12427. doi:10.1073/pnas.0404500101.
- Holmes, R.L., Adams, R.K., and Fritts, H.C. 1986. Tree-ring chronologies of western North America: California, Eastern Oregon, and Northern Great Basin with procedures used in the chronology development work including user's manuals for computer programs COFECHA and ARSTAN. Lab. of Tree-Ring Research, University of Arizona, Chronology Series VI.
- Hughes, M.K., and Funkhouser, G. 1998. Extremes of moisture availability reconstructed from tree rings for recent millennia in the Great Basin of western North America. The impacts of climate variability on forests. *Lect. Notes Earth Sci.* **74**: 99–107. doi:10.1007/BFb0009768.
- Klasner, F.L., and Fagre, D.B. 2002. A half century of change in alpine treeline patterns at Glacier National Park, Montana, U.S.A. *Arct. Antarct. Alp. Res.* **34**: 49–56. doi:10.2307/1552508.
- Körner, C. 2012. Alpine treelines. Functional ecology of the global high elevation tree limits. Springer Basel.
- Körner, C., and Paulsen, J. 2004. A world-wide study of high altitude treeline temperatures. *J. Biogeogr.* **31**: 713–732. doi:10.1111/j.1365-2699.2003.01043.x.

- Krusic, P.J. 2012. CofechaOSX_pjk2012, v6.02p. Available from www.ideo.columbia.edu/res/fac/tr/publicSoftware.html.
- Kullman, L. 1995. Holocene tree-limit and climate history from the Scandes Mountains. *Ecology*, **76**: 2490–2502. doi:10.2307/2265823.
- Kullman, L., and Öberg, L. 2009. Post-Little Ice Age tree line rise and climate warming in the Swedish Scandes: a landscape ecological perspective. *J. Ecol.* **97**: 415–429. doi:10.1111/j.1365-2745.2009.01488.x.
- Krugman, S.L., and Jenkinson, J.L. 1974. Pinaceae — pine family. In *Seeds of woody plants in the United States*. C.S. Schopmeyer, technical coordinator. USDA Forest Service, Washington, D.C., Agriculture Handbook 450. pp. 598–637.
- LaMarche, V.C., Jr. 1973. Holocene climate variations inferred from treeline fluctuations in the White Mountains, California. *Quat. Res.* **3**: 632–660. doi:10.1016/0033-5894(73)90035-5.
- Lenoir, J., Ge'gout, J.C., Marquet, P.A., Ruffray, P., and Brisse, H. 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science*, **320**: 1768–1771. doi:10.1126/science.1156831.
- Lenoir, J., Ge'gout, J.C., Guisan, A., Vittoz, P., Wohlgemuth, T., Zimmerman, N.E., Dullinger, S., Pauli, H., Willner, W., and Svenning, J.C. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**: 295–303. doi:10.1111/j.1600-0587.2010.06279.x.
- Lloyd, A.H., and Graumlich, L.J. 1997. Holocene dynamics of treeline forests in the Sierra Nevada. *Ecology*, **78**: 1199–1210. doi:10.1890/0012-9658(1997)078[1199:HDOTF]2.0.CO;2.
- Loarie, S.R., Carter, B.E., Hayhoe, K., McMahon, S., Moe, R., Knight, C.A., and Ackerly, D.D. 2008. Climate change and the future of California's endemic flora. *PLoS One*, **3**: e2502. doi:10.1371/journal.pone.0002502.
- Maloney, P. 2014. The multivariate underpinnings of recruitment for three *Pinus* species in montane forests of the Sierra Nevada, U.S.A. *Plant Ecol.* **215**: 261–274. doi:10.1007/s11258-013-0295-6.
- Matias, L., and Jump, A.S. 2015. Asymmetric changes of growth and reproductive investment herald altitudinal and latitudinal range shifts of two woody species. *Glob. Chang. Biol.* **21**(2): 882–896. doi:10.1111/gcb.12683.
- Millar, C.I., Graumlich, L.J., Delany, D.L., Westfall, R.D., and King, J.K. 2004. Response of subalpine conifers in the Sierra Nevada, U.S.A., to 20th-century warming and decadal climate variability. *Arct. Antarct. Alp. Res.* **36**: 181–200. doi:10.1657/1523-0430(2004)036[0181:ROSCIT]2.0.CO;2.
- Millar, C.I., Westfall, R.D., Delany, D., Bokach, M., Flint, L., and Flint, A. 2012. Forest mortality in high-elevation whitebark pine (*Pinus albicaulis*) forests of eastern California, U.S.A.; influence of environmental context, bark-beetles, climatic water deficit, and warming. *Can. J. For. Res.* **42**(4): 749–765. doi:10.1139/x2012-031.
- Moen, J., Aune, K., Edenius, L., and Angerjörn, A. 2004. Potential effects of climate change on treeline position in the Swedish mountains. *Ecol. Soc.* **9**: 1–11.
- NCDC (National Climate Data Center). 2014. HCN version 2.5. Instrumental weather data. Available from <http://www.ncdc.noaa.gov/oa/climate/research/ushcn/#access>.
- Pepin, N., and Lundquist, J.D. 2008. Temperature trends at high elevations: patterns across the globe. *Geophys. Res. Lett.* **35**: L14701. doi:10.1029/2008GL034026.
- Rapacciuolo, G., Maher, S.P., Schneider, A.D., Hammond, T.T., Jabis, M., Walsh, R.E., Iknayan, K.J., Walden, G.K., Oldfather, M.F., Ackerly, D.D., and Beissinger, S.R. 2014. Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. *Glob. Chang. Biol.* **20**(9): 2841–2855. doi:10.1111/gcb.12638.
- Rochefort, R.M., Little, R.L., Woodward, A., and Peterson, D.L. 1994. Changes in sub-alpine tree distribution in western North America: a review of climatic and other causal factors. *Holocene*, **4**: 89–100. doi:10.1177/095968369400400112.
- Salzer, M.W., Hughes, M.K., Bunn, A.G., and Kipfmüller, K.F. 2009. Recent unprecedented tree-ring growth in bristlecone pine at the highest elevations and possible causes. *Proc. Natl. Acad. Sci. U.S.A.* **106**: 20348–20353. doi:10.1073/pnas.0903029106.
- Salzer, M.W., Larson, E.R., Bunn, A.G., and Hughes, M.K. 2014. Changing climate response in near-treeline bristlecone pine with elevation and aspect. *Environ. Res. Lett.* **9**: 114007. doi:10.1088/1748-9326/9/11/114007.
- SAS Institute Inc. 2010. SAS Online Doc 9.03. JMP statistics and graphics guide. Cary, North Carolina.
- Shiyatov, S.G. 1993. The upper timberline dynamics during the last 1100 years in the polar Ural Mountains. *Palaeoclim. Res.* **9**: 195–203.
- Taylor, A.H. 1990. Tree invasion in meadows of Lassen Volcanic National Park, California. *Prof. Geogr.* **42**: 457–470. doi:10.1111/j.0033-0124.1990.00457.x.
- Taylor, A.H. 1995. Forest expansion and climate change in the mountain hemlock (*Tsuga mertensiana*) zone, Lassen Volcanic National Park, California, U.S.A. *Arct. Antarct. Alp. Res.* **27**: 207–216. doi:10.2307/1551951.
- Trant, A.J., and Hermanutz, L. 2014. Advancing towards novel tree lines? A multispecies approach to recent tree line dynamics in subarctic alpine Labrador, northern Canada. *J. Biogeogr.* **41**: 1115–1125. doi:10.1111/jbi.12287.
- Van de Ven, C., Weiss, S., and Ernst, G. 2007. Plant species distributions under present conditions and forecasted for warmer climates in an arid mountain range. *Earth Interact.* **11**(9): 1–33. doi:10.1175/EI205.1.
- Vetaas, O.R. 2002. Realized and potential climate niches: a comparison of four Rhododendron tree species. *J. Biogeogr.* **29**: 545–554. doi:10.1046/j.1365-2699.2002.00694.x.
- Wieser, G., and Tausz, M. (Editors). 2007. *Trees at their upper limit. Treeline limitation at the alpine timberline*. Springer, Dordrecht.
- Wright, R.D., and Mooney, H.A. 1965. Substrate-oriented distribution of bristlecone pine in the White Mountains of California. *Am. Midl. Nat.* **73**: 257–284. doi:10.2307/2423454.