

The multivariate underpinnings of recruitment for three *Pinus* species in montane forests of the Sierra Nevada, USA

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Abstract Recruitment success can have significant consequences on forest community dynamics. Seedlings and saplings were studied for 3 five-needled white pine species: sugar pine (*Pinus lambertiana*), western white pine (*P. monticola*), and whitebark pine (*P. albicaulis*) across an elevational gradient, representing three distinct forest types, in the Sierra Nevada. This study was designed to determine the importance of local environmental and biological conditions versus broad regional climate patterns influencing conifer recruitment. No relationships were found between recruitment and precipitation, but increasing nighttime temperature was positively correlated with sugar pine and western white pine recruitment and negatively correlated with whitebark pine recruitment. Recruitment pulses were found for sugar pine and western white pine from 1995 to 2006. Whitebark pine recruitment is low and relatively steady from 1970 to 2000 with no observed new recruits after 2001. Source strength was the most consistent predictor of white pine recruitment along with soil properties, climate, light, and the presence of non-conspecifics. Source,

light, and soil explained 71 % of the variation in sugar pine recruitment. The presence of non-conspecifics, source, and climate explained 71 % of the variation in western white pine recruitment, and the presence of non-conspecifics and source explained 36 % of the variation for whitebark pine. Recruitment present in forest communities of the Sierra Nevada have successfully transitioned through critical stages (i.e., seed and germinant) and appear to be influenced by multiple factors at both local and regional scales.

Keywords Climate · Cone production · Environmental heterogeneity · Forest dynamics · Recruitment · Source strength · Five-needled white pines

Introduction

Fecundity and recruitment success are critical to forest community structure, dynamics, and evolutionary processes (e.g., selection and migration). These fundamental stages (e.g., germinant, seedling, and sapling) are challenged by biotic and abiotic pressures such as cone and seed predation, unsuitable site conditions (dense stands, poor soil and litter development, and light levels) climatic variability, variable cone (female and male) crops, heat stress, and competition. In temperate conifer forests, local environmental and biological factors can have a central role in recruitment success and dynamics (Gray and Spies 1997; Zald et al. 2008; Larson and Kipfmüller

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2010; Welch 2012). At local spatial scales factors such as microenvironmental conditions (e.g., substrate type, woody debris, and light), source strength (e.g., seed rain and seed trees), forest structures (e.g., canopy openings), and composition (e.g., diversity and nonconspecific abundance) can be important predictors of conifer regeneration (Gray and Spies 1997; Zald et al. 2008; Larson and Kipfmüller 2010; Welch 2012).

A basic question is whether broad regional patterns in climate and precipitation drive recruitment success versus local (e.g., stand-level) environmental and biological conditions. Studies report episodic recruitment for a number of conifer species in the Sierra Nevada with recruitment pulses correlated with regional climate and landscape features (Millar et al. 2004; Bunn et al. 2005). Yet, seed and cone production can also be variable and episodic and may not necessarily be influenced solely by climate. Species have adapted different strategies for seed production, and some species have mast seed production and others do not. For species that mast, the environmental and biological conditions determining mast years are complex, and masting patterns are not always related to climatic parameters (Koenig and Knops 2000; Kelly and Sork 2002; Crone et al. 2011). Whitebark pine is considered to have mast cone production, but the factors influencing these mast years are variable, ranging from differential site productivity, satiation by seed consumers versus attracting a specialist seed disperser, and infection by a non-native pathogen (Crone et al. 2011). There is also considerable seed and cone predation by insects and vertebrates, which can significantly affect seed crops (D. Welty, USDA Forest Service, pers. comm.) and subsequent regeneration opportunities, in some years, that is often overlooked.

Five-needled white pines, *Strobus*, represent an important and diverse group of conifers in forest ecosystems of western North America. These *Pinus* species span diverse habitats from low elevation to subalpine forests and from coastal to interior mountains. Sugar pine (*Pinus lambertiana*), western white pine (*Pinus monticola*), and whitebark pine (*Pinus albicaulis*) have vital roles in ecosystem function and services which comprise multiple consideration: forest cover, food resource, watershed protection, protracting snowmelt, soil and snow stabilization, biodiversity, wildlife habitat, greenhouse gas sequestration, as

well as recreational, economic, and aesthetic values (Hutchins and Lanner 1982; Tomback and Achuff 2010). Recruitment success of these species can have significant consequences on forest community dynamics. Thus, if seed from these species are able to successfully transition from seed → germinant → seedling, then what are the key biological and environmental influences? In the present study, the following specific questions were addressed: (1) Are white pine recruitment pulses correlated with regional patterns in precipitation and temperature? and (2) Are local stand conditions more influential than broad scale environmental conditions to white pine recruitment in the Sierra Nevada?

Methods

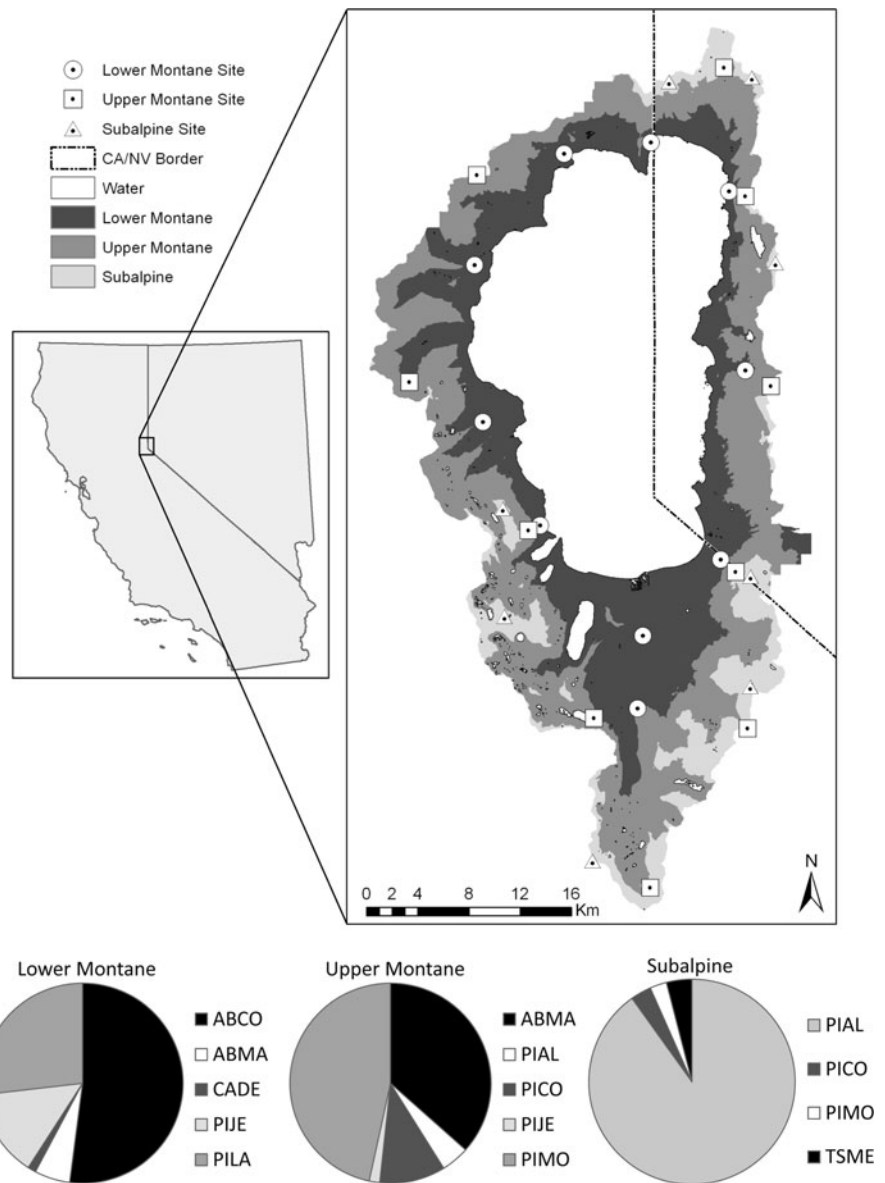
Study area

The Lake Tahoe Basin is located in the north-central Sierra Nevada at 120°W and 39°N within California and Nevada (Fig. 1). The Basin is flanked to the west by the Sierra Nevada crest and to the east by the Carson Range. The climate is Mediterranean and characterized by warm, dry summers, and cool, wet winters. Most of the precipitation falls as snow between the months of November and April, with a strong gradient from west to east. Research took place within the three dominant forest types: (1) low elevation mixed-conifer, (2) upper montane, and (3) subalpine. The geology of the region is dominated by igneous intrusive rocks, typically granodiorite; and igneous extrusive rocks, typically andesitic lahar, with small amounts of metamorphic rock (Table 1; United States Department of Agriculture 2007).

Study species

Five-needled white pine species (Subgenus *Strobus*) are important components in montane forests throughout the Sierra Nevada. Sugar pine is a key component in mixed-conifer forests of the North American Mediterranean-climate zone and can represent 5–25 % of the trees in stands and grows at elevations between 1,200 and 2,500 m (Kinloch and Scheuner 1990). Lower montane mixed-conifer forests in the Lake Tahoe Basin are a mix of white fir (*Abies concolor*), Jeffrey pine (*P. jeffreyi*), sugar pine

Fig. 1 Location of 28 study sites in the lower montane, upper montane, and subalpine vegetation zones in the Lake Tahoe Basin of California and Nevada. Pie charts depict forest tree species composition by vegetation zone. Species abbreviations are as follows: *ABCO* *Abies concolor*, *ABMA* *Abies magnifica*, *CADE* *Calocedrus decurrens*, *PIAL* *Pinus albicaulis*, *PICO* *Pinus contorta*, *PIJE* *Pinus jeffreyi*, *PILA* *Pinus lambertiana*, *PIMO* *Pinus monticola*, *TSME* *Tsuga mertensiana*. Vegetation zone boundaries adapted from Manley et al. 2000, Fig. 1–5



(*P. lambertiana*), ponderosa pine (*P. ponderosa*), incense cedar (*Calocedrus decurrens*), and occasionally lodgepole pine (*Pinus contorta* ssp. *murrayana*), and covers ~8,000 ha (Manley et al. 2000).

Western white pine (*P. monticola*) grows in mixed-species stands and is an important associate in upper montane forests growing at elevations ranging from 1,200 to 2,500 m, but can sometimes be found up to 3,300 m (Kinloch and Scheuner 1990). The upper montane zone is generally dominated by the red fir forest type and is a mix of red fir (*A. magnifica*),

western white pine, lodgepole pine, and occasionally Jeffrey pine and covers ~5,000 ha (Manley et al. 2000).

Mixed subalpine woodland is the most common high-elevation forest type in the Lake Tahoe Basin and covers ~10,000 ha (Manley et al. 2000) between the elevations of 2,600 and 3,200 m. Subalpine forests are a mix of whitebark pine, mountain hemlock (*Tsuga mertensiana*), lodgepole pine, western white pine, red fir, and occasionally Jeffrey pine. In some locations, there are pure stands of whitebark pine.

Table 1 Environmental (topography, climate, soil) characteristics of low elevation mixed-conifer (*Pinus lambertiana*—sugar pine), upper montane (*P. monticola*—western white pine), and subalpine (*P. albicaulis*—whitebark pine) forests in the Lake Tahoe Basin

	Forest type		
	Mixed conifer Sugar pine	Upper montane Western white pine	Subalpine whitebark pine
<i>n</i>	30	30	24
Elevation (m)	2,025 (9.89)	2,449 (28.46)	2,805 (13.73)
Slope (°)	15 (1.26)	17 (1.17)	14 (1.41)
% max. rad. input	76.41 (1.80)	71.18 (1.65)	81.18 (1.87)
Ann. ppt. (mm)	802 (30.62)	1,123 (49.26)	1,209 (61.39)
T_{min} (°C)	-7.01 (0.07)	-7.42 (0.13)	-7.50 (0.15)
T_{max} (°C)	23.67 (0.14)	22.73 (0.17)	22.23 (0.17)
May GDD	13 (1.75)	4 (0.78)	2 (0.71)
WC 3rd bar	9.95 (0.43)	9.75 (0.79)	9.59 (0.66)
AWC 0–50	5.18 (0.23)	4.22 (0.41)	2.84 (0.19)
% sand	75.08 (2.63)	68.33 (2.24)	77.85 (2.24)
CEC	10.01 (1.23)	9.12 (1.73)	2.13 (0.89)
Parent material	Granite (0.600), andesite (0.166), volcanic (0.133), mixed sources (0.100)	Granite (0.600), tuff/tuff breccia/lahar (0.136), andesite (0.100), metamorphic (0.100), alluvium and volcanic (0.033)	Granite (0.625), volcanic (0.250), andesite/tuff breccia (0.125)

Values are means with standard errors in parentheses. Climate averages for each forest type based on PRISM data for 30-year averages (Daly et al. 1994)

Elevation elevation a.s.l. (m), *Slope* slope in degrees, *% max. rad. input* percentage maximum solar radiation input for 40° latitude (Buffo et al. 1972), *Ann. ppt.* total annual precipitation in millimeters (mm), T_{min} (°C) minimum January temperature, T_{max} (°C) maximum July temperature in degrees celcius, *May GDD* growing-degree days in May above 5 °C, *WC 1/3rd bar* soil water capacity at 1/3rd bar, *AWC 0–50* available water capacity in top 0–50 cm depth, *% sand* percentage sand content (as a percentage of sand:silt:clay), *CEC* cation exchange capacity, *parent material* common parent material (frequency in parentheses) found in each forest type. Soil data source: United States Department of Agriculture (2007)

Sugar pine and western white pine have cones that dehisce, and seeds of both species are winged and dispersed by wind, birds, and small mammals. Notable to whitebark pine is its wingless seed and its almost exclusive reliance on Clark's nutcracker, *Nucifraga columbiana*, family Corvidae, for dispersal (Hutchins and Lanner 1982; Lanner 1982; Tomback 1982; Hutchins 1990).

Field sampling

During the summers of 2008 and 2009, 28 study locations (10 lower montane–sugar pine, 10 upper montane–western white pine, and 8 subalpine–whitebark pine) were selected, with three permanent plots per site (sampling area within a location ≥ 4 ha), for a total of 84 plots (Fig. 1). This plot network was established on National Forest and State Park lands surrounding the Lake Tahoe Basin. Each of the 28

locations was located in a distinct watershed, and all were distributed around the Basin to capture variation in the physical environment (e.g., climate, geology, and topography). Within a location, each of the three replicate plots per location, was $40 \times 100 \text{ m}^2$ ($4,000 \text{ m}^2$) in which data were recorded on forest structure, composition, cone production (number of cones per tree—current and previous year), topography, and land-use history (for detailed field methods see Maloney et al. 2011, 2012).

Seedlings and saplings $< 1.37 \text{ m}$ tall (including first-year germinants but these were rare), were evaluated within each plot by establishing three nested recruitment subplots that were $15 \times 15 \text{ m}^2$ in size (totaling 225 m^2), for a total of nine regeneration plots/location. In each recruitment subplot, data were recorded for slope, aspect, rock cover (%), litter depth, shrub cover (%), and light conditions: open/exposed (no canopy intercepting light); partially closed (partial

light interception from an overstory tree or shrub); and closed (full light interception from overstory trees or shrubs). All seedlings and saplings were counted and identified to species. For all white pine species, data were collected on basal diameter (cm), height (cm), status (live or dead), and whorls counted for aging.

A limited number of white pine seedlings for each of the three species were sampled, throughout each species distribution in the Lake Tahoe Basin, to obtain size-age relationships by counting growth rings, measuring height, diameter, and whorl count. Multiple linear regression analysis was used to estimate age for recruitment. Independent variables loaded into the regression models were height, whorl count, and diameter of field-sampled white pines. Whorl count explained 84, 51, and 89 % of the variation in the models for sugar pine, western white pine, and whitebark pine, respectively. Each species yielded parameter estimates and the following regression equations: $Y_{\text{sugar pine}} = 0.058 + 1.16X_1$ ($r^2 = 0.843$; $F_{1,53} = 280.01$, $P < 0.0001$); $Y_{\text{western white}} = 5.312 + 0.567X_1$ ($r^2 = 0.505$; $F_{1,32} = 2.18$, $P = 0.0118$); $Y_{\text{whitebark}} = 6.89 + 0.853X_1$ ($r^2 = 0.895$; $F_{1,15} = 119.67$, $P < 0.0001$). These equations were used to estimate age and year that a seedling/sapling recruited into study plots.

The following data were recorded for each demographic plot: GPS location (UTM: NAD27 coordinates), slope (in degrees), aspect, and elevation

(meters a.s.l.). Climatic parameters of annual precipitation (mm), January minimum (T_{min} °C) and July maximum (T_{max} °C) monthly and annual temperatures, and May and August growing degree days (above 5 °C) for the period of 1971 to 2000 using the PRISM climatic model (Daly et al. 1994). Average annual precipitation and nighttime temperature data for the years 1978 to 2008 were used from Ward and Marlette SNOTELs (USDA NRCS National Water and Climate Center, <http://www.wcc.nrcs.usda.gov/snow/>). Parent material and soil survey data of available water capacity at 25 (AWC 25) and 50 (AWC 50) centimeters depth, percent sand, silt and clay contents, cation exchange capacity (CEC = total amount of exchangeable cations), and water capacity at $-1/3$ rd bar (WC $-1/3$ bar = matric potential at $-1/3$ bar) and -15 bar (WC -15 bar = matric potential at -15 bar) were provided by the South Lake Tahoe office of the USDA Natural Resources Conservation Service (United States Department of Agriculture 2007). Percentage maximum solar radiation input for 40° latitude was calculated using the slope and aspect (Buffo et al. 1972).

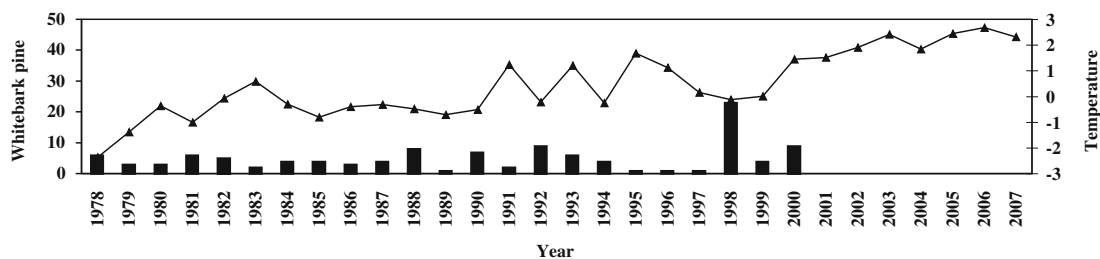
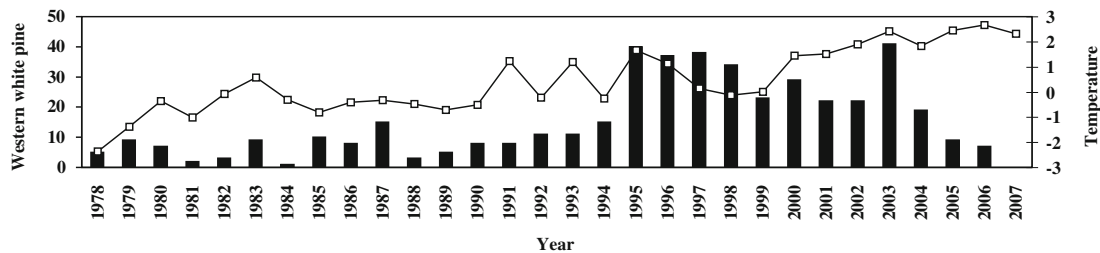
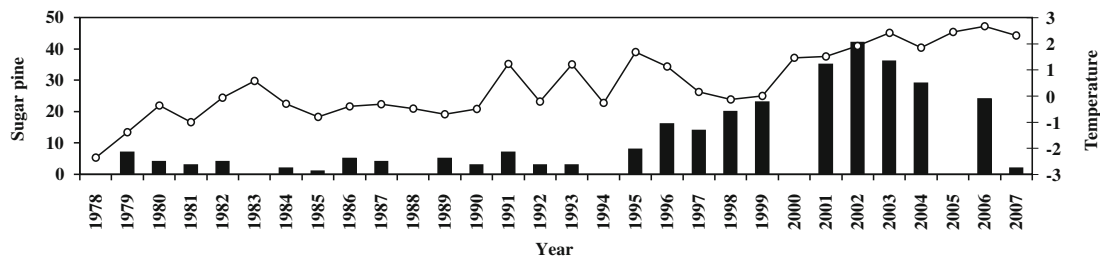
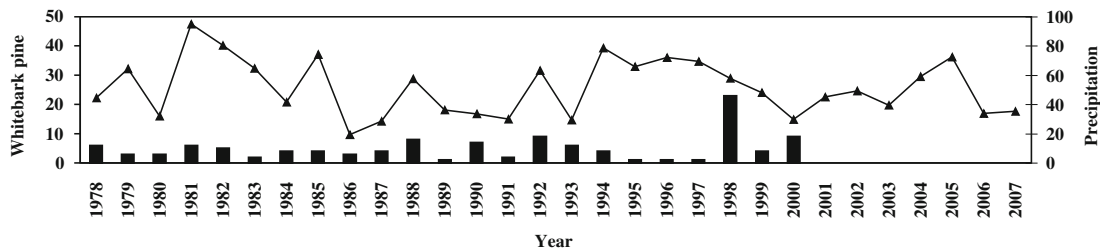
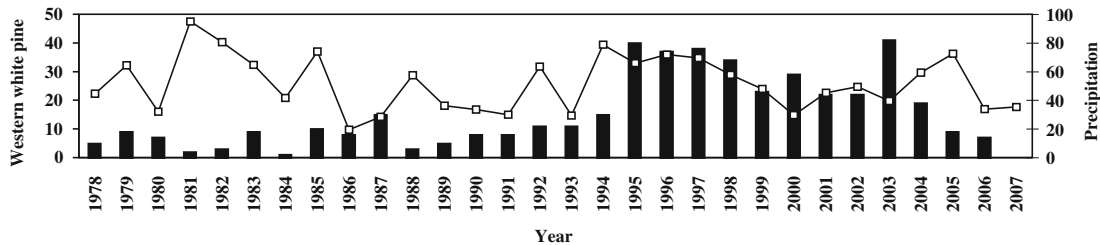
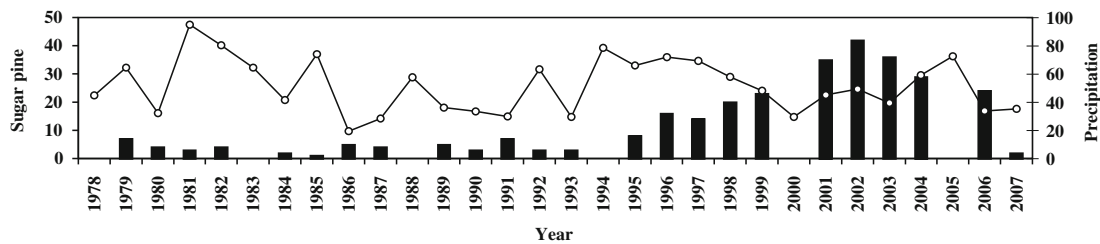
Data analysis

Correlations and simple linear regression analyses were used to relate climate variables (annual precipitation and nighttime temperature) with white pine

Table 2 Biological characteristics of low elevation mixed-conifer, upper montane, and subalpine forests in the Lake Tahoe Basin

	Forest type		
	Mixed conifer Sugar pine	Upper montane Western white pine	Subalpine Whitebark pine
White pines			
Density (inds./0.40 ha)	26.27 (4.18)	30.83 (2.41)	234.35 (20.77)
Relative density	0.18 (0.03)	0.38 (0.04)	0.91 (0.03)
Basal area (m ² /0.40 ha)	4.27 (0.32)	5.07 (0.50)	8.97 (0.68)
Relative basal area	0.38 (0.04)	0.43 (0.05)	0.86 (0.04)
No. cones (no./0.40 ha)	272.13 (37.67)	887.13 (89.28)	2,130.04 (278.16)
No. reproductive inds. (no./0.40 ha)	9.97 (1.17)	15.03 (1.69)	189.65 (18.37)
No. recruitment (inds./0.07 ha)	10.20 (3.89)	16.43 (5.07)	9.22 (2.44)
Non-conspecifics			
Density (inds./0.40 ha)	168.67 (20.21)	85.67 (16.04)	21.74 (5.90)
Basal area (m ² /0.40 ha)	8.84 (1.08)	9.44 (1.35)	1.77 (0.55)
No. recruitment (inds./0.07 ha)	33.13 (6.09)	54.07 (14.90)	4.63 (1.65)

Values are means with standard errors in parentheses



◀ **Fig. 2** Estimates of white pine recruitment year in relation to annual precipitation (in inches) for sugar pine, western white pine, and whitebark pine in *first, second, and third panels*, respectively and nighttime temperature (°C) for sugar pine, western white pine, and whitebark pine in the *fourth, fifth, and sixth panels*, respectively, from 1978 to 2007 SNOTEL data. Y-axis numbers/species/year

recruitment. Regression and correlation analyses were conducted with the SAS, version 9.2 (SAS Institute 2011). The interactive effects of ecological and environmental variables on white pine recruitment were assessed employing principal component analysis (PCA), which is generally robust regarding issues associated with multicollinearity. PCA was used to reduce the dimensionality of ecological and environmental data. Environmental data and ecological data used for PCA were climate (4 variables), light (5 variables), microhabitat (5 variables), nonconspecifics (3 variables), soil (4 variables), and source (4 variables). Variable reductions for PCA were determined from 30 sample units of sugar pine and western white pine and 25 sample units for whitebark pine. Factor loading scores from PCA were evaluated, and scores >0.7 are strongly correlated with the corresponding PC; factor loading scores between 0.4 and 0.6 indicate a moderate correlation, and scores <0.4 represent a weak correlation (Quinn and Keough 2002). To model white pine recruitment, ecological and environmental principal components with eigenvalues >1 were regressed against sugar pine, western whitepine, and whitebark pine recruitment using multiple linear regressions. An additional check of collinearity in our regression model was done employing leverage plots and bivariate scatterplots. PCA and MLR analyses were conducted in SAS, version 9.2 (SAS Institute 2011). For all parametric analyses, assumptions of normality and homogeneity of variances were verified.

Results

Montane forest environments

Montane forests, across elevation zones, vary in climate, microclimate, topography, and geology (Table 1). Locations ranged in elevation from 1918 to 2946 meters. Slopes ranged from 2° to 30° , and aspect varied as well (Table 1). Microclimate as measured by percent maximum solar radiation input

($\text{Cal}/\text{cm}^2/\text{yr}$) was the highest in subalpine stands, mean = 81.18, followed by lower montane (76.41) and upper montane forests (71.18) (Table 1). Precipitation amounts range from 566 to 1686 mm, with the highest being received in subalpine forests (Table 1). January minimum and July maximum temperatures and growing-degree days differed across elevation zones with warmer temperatures and relatively longer growing seasons in lower montane forests, followed by upper montane, with colder temperatures and shorter growing seasons in the subalpine (Table 1). The geology of the Lake Tahoe Basin is diverse with sites spanning a range of geological substrates influencing soil properties (Table 1). Water capacity at $-1/3\text{rd}$ bar and available water capacity at 50 cm depth were the highest in lower montane forests, followed by upper montane forests and the lowest in the subalpine (Table 1). Percent sand content was the highest in subalpine stands, followed by lower montane and upper montane forests (Table 1). Cation exchange capacity was the highest in lower montane forests (10.01) followed closely by the upper montane (9.12), and very low in subalpine stands (2.13) (Table 1).

Lower montane forests were dominated by white fir with sugar pine and Jeffrey pine as important associates (Fig. 1). In upper montane forests, western white pine and red fir were co-dominant, and whitebark pine dominates in subalpine woodlands (Fig. 1). From lower montane to subalpine forests, focal species' density, basal area, cone production, and the number of reproductive individuals increase with elevation (Table 2). White pine recruitment was the highest in upper montane, followed by lower montane and subalpine (Table 2). The highest density of non-conspecifics is found in lower montane forests (mainly white fir), followed by upper montane forests, with the least in subalpine forests (Table 2; Fig. 1). The greatest non-conspecific basal area is found in the upper montane, mostly comprising red fir, followed by lower montane with the lowest in subalpine (Table 2). Similarly, non-conspecific recruitment was high in the upper montane, followed by lower montane, and the lowest in the subalpine (Table 2).

Recruitment growing conditions

Heterogeneous microenvironmental conditions exist across forest types. In lower and upper montane, white pine recruitment is found in a mix of canopy

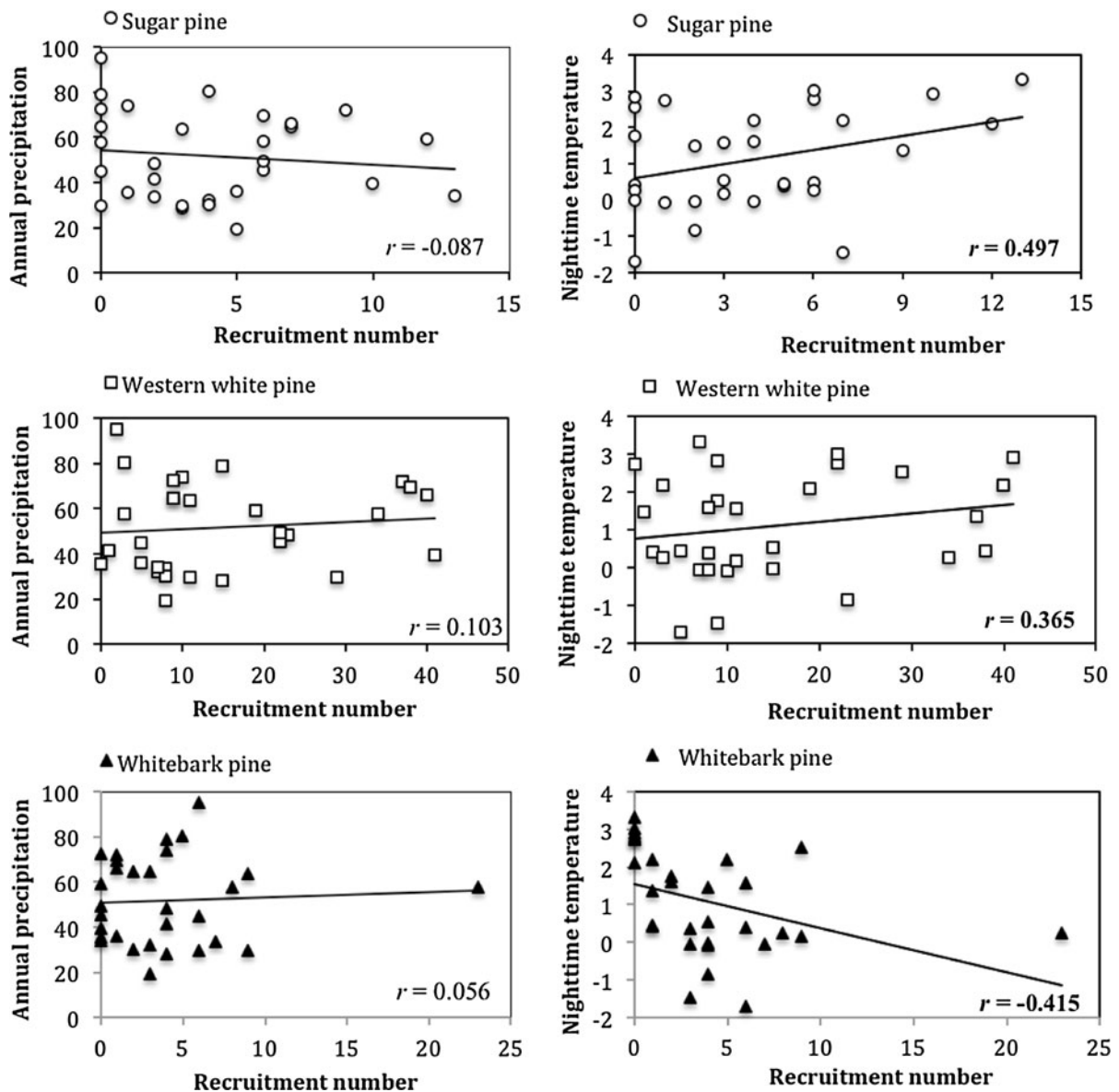


Fig. 3 Scatterplots and correlations between white pine recruitment and climatic variables. Average annual precipitation (in inches) and nighttime temperature ($^{\circ}$ C) from Ward

Canyon (west-side of Basin) and Marlette Lake (east-side of Basin) SNOTELs from 1978 to 2008. Correlations, r , are given and **bold values** are significant at $\alpha = 0.05$

conditions—more frequently in open and partially closed and less frequently growing in a closed canopy. Whitebark pine recruitment is commonly found in open canopy conditions (data not shown). Sugar pine recruitment was associated with high shrub cover and low shrub cover for western white and whitebark pines. Relatively high average litter depth was associated with sugar pine and western white pine, and lower litter depth for whitebark pine. High rock cover was

commonly associated with whitebark pine recruitment, followed by western white pine, with low rock cover for sugar pine in lower montane forests (data not shown).

Recruitment patterns

Recruitment patterns were correlated with local climate data from two SNOTEL locations. Pulses in recruitment for sugar pine and western white pine

Table 3 Multivariate measures of ecological and environmental factors for sugar pine, western white pine, and whitebark pine recruitment in the Lake Tahoe Basin

	Eigenvalue	PVE	Description
Sugar pine			
Source			
SOURCE PC1	2.29	57.30	No. repro. trees (0.59), sugar pine density (0.56), basal area (0.51)
SOURCE PC2	1.21	30.27	No. cones (0.79), sugar pine density (-0.43)
Climate			
CLIM PC1	2.20	55.14	T_{\max} (0.64), May GDD (0.57), ann ppt (-0.47)
CLIM PC2	1.18	29.67	T_{\min} (0.80), ann ppt (0.50)
Soil			
SOIL PC1	2.46	61.55	CEC (0.61), AWC50 (0.57), % sand (-0.52)
SOIL PC2	1.06	26.40	WC3rdbar (0.91)
Non-conspicifics			
NONCONSP PC1	1.80	60.23	Non-consp. density (0.70), non-consp. basal area (0.62)
NONCONSP PC2	0.96	32.01	No. non-consp.recruits (0.88), non-consp. basal area (-0.47)
Light			
LIGHT PC1	1.94	38.97	Partially closed canopy (0.69), closed canopy (-0.66)
LIGHT PC1	1.09	21.85	Closed canopy (0.72), shrub cover (-0.61)
Western white pine			
Source			
SOURCE PC1	2.43	60.90	No. repro. trees (0.56), western white density (0.52), no. cones (0.48)
SOURCE PC2	0.81	20.17	Basal area (0.64), western white density (-0.52), no. cones (0.43)
Climate			
CLIM PC1	2.43	60.83	T_{\max} (0.60), May GDD (0.56), T_{\min} (0.52)
CLIM PC2	1.15	28.72	Ann ppt (0.86), T_{\min} (0.43)
Soil			
SOIL PC1	2.45	61.30	AWC50 (0.60), CEC (0.50), WC3rdbar (0.54)
SOIL PC2	1.10	27.65	% sand (0.92)
Non-conspicifics			
NONCONSP PC1	1.45	48.57	Non-consp. density (0.74), non-consp. basal area (0.51)
NONCONSP PC2	1.11	37.01	No. non-consp. recruits (0.74), non-consp. basal area (-0.66)
Light			
LIGHT PC1	2.15	43.17	Open canopy (0.67), partially closed canopy (-0.56)
LIGHT PC1	1.25	25.02	% max. sol. rad. (0.66), closed canopy (0.50), shrub cover (0.50)
Whitebark pine			
Source			
SOURCE PC1	2.81	70.14	Whitebark density (0.55), no. repro. trees (0.54), no. cones (0.45)
SOURCE PC2	0.65	16.29	No. cones (0.55), basal area (0.54)

Table 3 continued

	Eigenvalue	PVE	Description
Climate			
CLIM PC1	2.23	55.86	Ann ppt (0.63) T_{\max} (0.57), May GDD (−0.40)
CLIM PC2	1.26	31.50	T_{\min} , May GDD
Soil			
SOIL PC1	2.54	63.65	AWC50 (0.62), WC3rdbar (0.57), % sand (−0.54)
SOIL PC2	1.20	30.05	CEC (0.89)
Non-conspecifics			
NONCONSP PC1	2.04	68.06	Non-consp. density (0.62), no. non-consp. recruits (0.57), non-consp. basal area (0.54)
NONCONSP PC2	0.60	20.23	Non-consp. basal area (0.76), no. non-consp. recruits (−0.64)
LIGHT			
LIGHT PC1	2.16	43.22	Open canopy (−0.66), partially closed canopy (0.63)
LIGHT PC1	1.29	25.92	Closed canopy (0.72), shrub cover (−0.61)

PC principal component, PVE percent variance explained, Description see description and definitions of factor loadings in notes of Tables 1, 2, 3 and in “Methods” section

Factor loading scores are in parentheses

occurred during the years from 1995 to 2006 (Fig. 2). For sugar pine, the highest amount recruiting was in the early 2000s (Fig. 2). Recruitment patterns for western white pine remain steady during this time period and decrease in 2004 (Fig. 2). Whitebark pine recruitment is low but steady from 1978 to 2000 with a relatively high pulse occurring in 1998 (Fig. 2). No significant relationships were found between recruitment patterns and precipitation for all three species from the period of 1978 to 2007 (Fig. 3). There were significant correlations between white pine recruitment and nighttime temperature (Fig. 3). A positive correlation was found between sugar pine and western white pine recruitment and nighttime temperature, and a negative correlation with whitebark pine (Fig. 3).

Recruitment and multivariate relationships

Source strength (or propagule pressure), climate, soil, non-conspecific presence, and light conditions are important factors that influence white pine recruitment. PCA was used to reduce the dimensionality for these ecological and environmental variables. For all three species, SOURCE PC1 had eigenvalues >2 (Table 3). SOURCE PC1 explained 57, 60, and 70 %

of the variation in source variables for sugar pine, western white pine, and whitebark pine, respectively. CLIMATE PC1 also had eigenvalues >2 for all three species explaining 55, 60, and 55 % of the variation in climate parameters for sugar pine, western white pine, and whitebark pine, respectively (Table 3). SOIL PC1 had eigenvalues >2 explaining 61, 61, and 63 % of the variation in soil variables for sugar pine, western white pine, and whitebark pine, respectively (Table 3). NONCONSP PC1 and LIGHT PC1 had eigenvalues >1 (Table 3). NONCONSP PC1 explained 60, 48, and 68 % of the variation in nonconspecific variables and LIGHT PC1 explained 38, 43, and 43 % of the variation in light conditions for sugar pine, western white pine, and whitebark pine, respectively (Table 3).

Recruitment models

Multiple linear regression of sugar pine recruitment used three PCs explaining 71 % of the variation (Table 4). SOURCE PC1 contributed a significant amount of predictive power to the regression model followed by LIGHT PC1 and SOIL PC1 (Table 4). SOURCE PC1 had positive factor loading scores with

the number of reproductive trees, sugar pine density, and basal area. LIGHT PC1 had a positive factor loading with partially closed canopy and a negative factor loading with a closed canopy; and SOIL PC1 had positive factor loadings with CEC and AWC50 (Table 3).

The western white pine recruitment MLR employed four PCs explaining 71 % of the model variance (Table 4). NONCONSP PC2 explained 33 % of the variance followed by SOURCE PC1, CLIMATE PC1, and CLIMATE PC2 (Table 4). NONCONSP PC2 had a strong positive factor loading with the number of non-conspecific recruits and a negative factor loading with non-conspecific basal area (Table 3). SOURCE PC1 had positive factor loading scores with the number of reproductive western white pine trees, density, and the number of cones; CLIMATE PC1 had positive factor loadings with T_{\max} and May GDD; and CLIMATE PC 2 had a strong positive factor loading with annual precipitation (Table 3).

Multiple linear regression of whitebark pine recruitment employed two PCs and explained only 36 % of the variation (Table 4). The two predictors of whitebark pine recruitment were NONCONSP PC1 and SOURCE PC1 (Table 4). NONCONSP PC1 had positive factor loadings scores for non-conspecific density, recruitment, and basal area, and SOURCE PC1 had positive factor loadings for whitebark density, the number of reproductive trees, and the number of cones (Table 3).

Discussion

This study demonstrates that local biological and environmental conditions as well as regional climatic conditions influence white pine recruitment in the mountains of the Sierra Nevada, but the strength and importance varies by species across elevational forest types. This study identified recruitment pulses for sugar pine starting around 1996, and upper montane forests appear to have the most consistent pulses of western white recruitment and overall higher numbers of regeneration. Unlike the two lower elevation species, whitebark pine recruitment is low and steady from 1970 to 2000 with no observed new recruits beyond 2001.

There were no strong relationships between precipitation and recruitment for these species. However,

Table 4 Multiple regression analysis of white pine recruitment with ecological and environmental principal components (PC) with eigenvalues >1 for source, climate, soil, non-conspecifics, microhabitat, and light

Predicted parameter	Parameter estimates	Regression coefficient	P value
Sugar pine recruitment (model $R^2 = 0.71$, $F_{3,26} = 21.69$, $P < 0.0001$)			
	Intercept	10.20	<0.0001
	$X_1 = \text{SOURCE PC1}$	10.00	<0.0001
	$X_2 = \text{LIGHT PC1}$	-4.82	0.0719
	$X_3 = \text{SOIL PC1}$	-4.75	0.0463
	$Y_{\text{sugar pine}} = 10.20 + 10.00X_1 - 4.82X_2 - 4.75X_3$		
Western white pine recruitment (model $R^2 = 0.71$, $F_{4,25} = 15.51$, $P < 0.0001$)			
	Intercept	16.43	<0.0001
	$X_1 = \text{NONCONSP PC2}$	12.31	0.0010
	$X_2 = \text{SOURCE PC1}$	5.36	0.0232
	$X_3 = \text{CLIMATE PC1}$	7.93	0.0004
	$X_4 = \text{CLIMATE PC2}$	-8.19	0.0103
	$Y_{\text{western white pine}} = 16.43 + 12.31X_1 + 5.36X_2 + 7.93X_3 - 8.19X_4$		
Whitebark pine recruitment (model $R^2 = 0.36$, $F_{2,20} = 5.54$, $P = 0.0122$)			
	Intercept	9.08	0.0003
	$X_1 = \text{NONCONSP PC1}$	4.46	0.0064
	$X_2 = \text{SOURCE PC1}$	2.18	0.0994
	$Y_{\text{whitebark pine}} = 9.08 + 4.46X_1 + 2.18X_2$		

Variables entered into the sugar pine multiple linear regression (MLR) model were: NONCONSP PC1, SOURCE PC1 and PC2, CLIM PC1 and PC2, LIGHT PC1 and PC2, SOIL PC1 and PC2. Variables entered into the western white pine MLR model were: MICRO PC1 and PC2, LIGHT PC1 and PC2, NONCONSP PC1 and PC2, SOURCE PC1, CLIM PC1 and PC2, SOIL PC1 and PC2. Variables entered into the whitebark pine MLR model were: LIGHT PC1 and PC2, NONCONSP PC1, SOURCE PC1, CLIM PC1 and PC2, SOIL PC1 and PC2

regional patterns of increasing nighttime temperature show a positive correlation with sugar pine and western white pine. This positive response may be due to an increase in seed production as a result of increasing atmospheric CO_2 . Ladeau and Clark (2006) found that loblolly pine (*Pinus taeda* L.) grown in elevated CO_2 matured earlier and also produced more seeds and cones per unit basal area than ambient grown trees. In the case of the subalpine species, there was a negative correlation of increasing nighttime temperature and whitebark pine recruitment. The negative effect of warmer nighttime temperatures on

whitebark pine may be the result of (1) decreasing number of cold days (i.e., stratification) required for germination and/or (2) warmer temperatures may decrease seedling survival in some locations. A conflicting scenario with the abovementioned is that if warmer temperatures increase seed production, as a result of increasing CO₂, this could possibly correspond with an increase in seed predation and caching, given the abundance of an important food resource in subalpine forests. These above patterns with nighttime temperature are correlative only and thus causation is not implied, but the patterns and potential response of increases in reproductive output parallel those studies investigating elevated CO₂ on seed production (Ladeau and Clark 2006), and warrants mention. An important limitation, regarding the above statements on recruitment and temperature, is the estimates of age based on whorl counts are somewhat tenuous particularly for western white pine. The intent was to determine if there were relationships between white pine recruitment patterns (from field-based aging) and local climatic parameters, not to develop a predictive model but to report on existing patterns, be it weak or strong.

Many low-elevation mixed conifer forests of the Sierra Nevada are characterized by high stand densities and, in some locations, a disproportionate number of shade intolerant species such as white fir and incense cedar, given fire suppression policies (Barbour et al. 2002; North et al. 2007; Zald et al. 2008). Despite shifts in structure and composition in these historically pine-dominated communities, sugar pine is recruiting in a 1:3 ratio with non-conspecifics. Source strength, represented by number of reproductive sugar pine trees and sugar pine density, was the best predictor of sugar pine recruitment. Altered stand conditions in low elevation mixed-conifer forests with high tree densities and closed canopies do not favor species that are relatively shade intolerant, such as sugar pine. Hence light conditions are important to sugar pine recruitment. Soil type and soil properties are often common factors influencing conifer recruitment (Gray and Spies 1997; Zald et al. 2008). In this study, the soil properties of cation exchange capacity (a measure of soil fertility and nutrient retention) and available water capacity were also important variables explaining the variation in sugar pine recruitment. A feature of well-developed soils is higher nutrient concentrations and available water capacity. Low elevation mixed-conifer

forests generally have well developed soils and hence favorable soil properties compared to higher elevations with cooler temperatures that limit soil development.

Upper montane forests are dominated by red fir and western white pine and from a watershed perspective this forest type has the deepest and longest lasting snowpacks than any other forested zone in California (Barbour et al. 2007). Hence upper montane forests can be the most mesic forest type in the Sierra Nevada, characterized by moderate to high stand densities and high basal area. Non-conspecific recruitment and basal area were important variables explaining western white pine recruitment. This positive association may reflect favorable growing conditions at sites for recruitment opportunities of all species. In some forest communities, competition and negative interspecific interactions can limit recruitment success within and between species, but this often promotes species coexistence (Wright 2002; Paine et al. 2008; Svenning et al. 2008). Source strength, represented by number of reproductive western white pine trees, density, and number of cones, was an important co-predictor of western white pine recruitment along with two climate PCs.

In subalpine forests, recruitment dynamics differ from the patterns observed in the lower and upper montane forests of the Lake Tahoe Basin, which may be a result of the ecology of whitebark pine communities. NONCONSP PC1 and SOURCE PC1 explained only 36 % of the variation in whitebark pine recruitment, much lower than sugar pine and western white pine (both model $R^2 = 71$ %). Similar to western white pine, the presence of non-conspecifics was a predictor of whitebark pine recruitment. This may also be reflecting favorable growing conditions for all coexisting species, when opportunities for recruitment occur. Yet the common variable important to all three white pine species is source strength. For whitebark pine, this is represented by whitebark pine density, number of reproductive trees, and number of cones.

Whitebark pine seed is under significant vertebrate pressure (Hutchins and Lanner 1982) and if not considered, is a limitation for any model predicting whitebark pine recruitment and/or population dynamics. Predation of whitebark pine seed can be significant, and over a 2-month period Hutchins and Lanner (1982) estimated that Clark's nutcrackers and red

squirrels (*Tamiasciurus* spp.) spent 97 and 60 % of their time successfully foraging on whitebark pine seeds and harvesting 364,000 and 633,000 seeds, respectively. Clark's nutcrackers are one of the primary consumers of whitebark pine seed, and this tree species relies almost exclusively on the bird for dispersal (Hutchins and Lanner 1982; Lanner 1982; Tomback 1982; Hutchins 1990; McKinney and Fiedler 2010). This bird-pine interaction is a positive one, however, red squirrel seed consumption and caching behavior (e.g., deep in soil or midden debris) are not conducive to successful germination or seedling establishment (Hutchins and Lanner 1982; Lanner 1982), hence large quantities of seed are lost to predation and consumption. This is a limitation to our whitebark pine recruitment model as vertebrate abundance, and foraging behavior have a central role on whitebark pine dispersal and recruitment dynamics.

Conclusion

Seedlings and saplings present in forest communities in the Lake Tahoe Basin of the Sierra Nevada have successfully transitioned through critical stages (i.e., seed and germinant) and are influenced by multiple factors and complex interactions, at both local and regional scales. This study highlights the importance of elucidating some of the factors critical to recruitment dynamics, across elevation zones. Clark et al. (2011) stress the importance of considering demographic parameters such as fecundity when evaluating, and for some modeling, the vulnerability of species to climate change. The long-life span, high rates of gene flow (seed and pollen dispersal), differential mortality, and year-to-year variability in cone production and recruitment have important demographic and evolutionary consequences on forest tree populations. Gaining a better understanding of the multiple factors and complex interactions influencing recruitment success is fundamental, as this important stage in a plants life cycle can have significant consequences on forest community dynamics, genetic architecture, and adaptive potential (Ladeau and Clark 2006; Petit and Hampe 2006).

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