

Response of tree-line populations of foxtail pine (*Pinus balfouriana*) to climate variation over the last 1000 years

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Abstract: Stand density, recruitment rate, and mortality rate in tree-line forests of foxtail pine (*Pinus balfouriana* Grev. & Balf.) were reconstructed for the last 1000 years. Mortality and recruitment were uncorrelated over the 1000-year period of the reconstruction. At the majority of sites, variance in recruitment was not significantly greater than variance in mortality. Recruitment and stand density were significantly and inversely correlated with summer temperature during the last 1000 years. Mortality rates were uncorrelated with climate. The inverse correlation between recruitment and climate suggests that water balance may mediate the effects of temperature on tree-line forests, a hypothesis that is supported by a significant positive correlation between seedling establishment and winter snowpack during the last 50 years. Despite large changes in the elevation of tree line at these sites during the time period of the reconstruction, populations near tree line were largely unaffected by climate variation, suggesting that steep gradients in vulnerability to climate change may exist at tree line in the Sierra Nevada.

Résumé : La densité du peuplement ainsi que les taux de recrutement et de mortalité du pin de Balfour (*Pinus balfouriana* Grev. & Balf.) dans les forêts à la limite des arbres, au cours des 1000 dernières années, ont été reconstitués. La mortalité et le recrutement n'ont pas été corrélés durant cette période. Dans la majorité des sites, la variance du recrutement n'était pas significativement plus grande que la variance de mortalité. Le recrutement et la densité du peuplement ont présenté une corrélation, significative et inverse, avec la température estivale au cours des 1000 dernières années. Les taux de mortalité n'ont pas été corrélés avec le climat. La corrélation inverse entre le recrutement et le climat indique que le bilan hydrique peut modérer les effets de la température sur les forêts à la limite des arbres. Cette hypothèse est appuyée par une corrélation positive significative entre l'établissement des semis et la couverture de neige hivernale au cours des 50 dernières années. Malgré le fait que la limite des arbres a grandement oscillé dans ces sites durant la période reconstituée, les populations près de cette limite n'ont pas été fortement affectées par les variations climatiques. Ceci suggère que des gradients abrupts de vulnérabilité aux changements climatiques peuvent exister à la limite des arbres dans la Sierra Nevada.
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Introduction

The position of tree line varies over time in response to variation in climate (LaMarche and Mooney 1967; Denton and Karlén 1977; Scuderi 1987; Spear 1993; MacDonald et al. 1993; Kullman 1995; Lloyd and Graumlich 1997). A variety of physiological mechanisms underlying those large-scale correlations have been documented (Schulze et al. 1967; Daubenmire 1954; Baig and Tranquillini 1980; Black and Bliss 1980; Wardle 1981; Häsler 1982; Hadley and Smith 1986; Grace 1989). The apparent sensitivity of tree line to climate change observed at landscape and physiological scales, however, is at odds with the sensitivity that would be expected of organisms with life history traits characteristic of tree-line species. Tree-line forests are typically dominated by species that are moderately (200–500 years) or extremely (>500 years) long-lived and have long reproductive life-spans (hundreds of years). In addition,

tree-line species are often able to reproduce vegetatively (e.g., *Picea mariana* (Mill.) BSP, black spruce), and many have considerable architectural and morphological plasticity (e.g., *Pinus albicaulis* Engelm., whitebark pine). These traits have all been interpreted as lending inertia to established individuals during periods of unfavorable climate (Prentice 1986; Ritchie 1986). Populations of species exhibiting some or all of these traits should therefore be buffered to some extent against environmental variation.

Life history traits may buffer a population against environmental variation in two ways. First, certain life history traits, particularly the ability to reproduce vegetatively, may minimize variance in recruitment rates over time by allowing recruitment to occur during periods when establishment from seed would be impossible (Payette and Gagnon 1979; Piñero et al. 1984; Callaghan et al. 1992). Such species should maintain higher population growth rates during unfavorable periods than species that reproduce only sexually. Second, species with a resistant and long-lived pre-reproductive or reproductive life stage (e.g., dormant seeds, adults with low mortality) can endure unfavorable environmental conditions regardless of fluctuations in recruitment rates. Recruitment occurring during favorable periods is stored over subsequent unfavorable periods by the resistant life stage (Warner and Chesson 1985), maintaining the population in the absence of further recruitment.

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Recruitment failures sustained over several years are likely to have little long-term impact on the fate (extinction versus persistence) of such populations, provided they do not exceed the life-span or viability of the resistant life stage.

Consideration of the life history traits common to tree-line species leads to two predictions about population-level responses to environmental change. First, populations may exhibit some inertia with respect to climate change, particularly to change that occurs on relatively short (multi-decadal or shorter) time scales. Empirical studies of population history in tree-line forests have provided some evidence to support this hypothesis (Payette and Gagnon 1979; Kullman 1987). Second, recruitment should be more sensitive to climate than adult mortality, because adult trees may constitute a resistant life stage in the sense described above. There is some evidence to suggest that recruitment rates vary with climate in many tree-line forests (Wardle 1963; Kullman 1986, 1987), but patterns of tree mortality over long time periods are poorly known.

In this study, I reconstructed a 1000-year record of recruitment rate, mortality rate, and forest stand density in tree-line populations of foxtail pine (*Pinus balfouriana* Grev. & Balf.) in the Sierra Nevada. I compared this ecological history to paleoclimate data (Graumlich 1993) to test the following hypotheses: (1) recruitment is positively correlated with temperature, (2) recruitment rates are more variable than mortality rates over time, (3) recruitment rates are more sensitive than mortality rates to climate variation.

Materials and methods

Field methods

I studied populations of foxtail pine at three study sites within Sequoia National Park in the eastern Sierra Nevada, California, U.S.A. (36°30'N, 108°15'W). The populations sampled in this study were all located at altitudinal tree line, at elevations ranging from approximately 3300 to 3400 m. At each study site, I established and permanently marked a single 2-ha study plot, within which I conducted a complete sample of live trees, standing dead trees, and fallen dead trees. I mapped the location of all live and dead stems in each plot and removed an increment core from the base of each stem (live and dead) with a basal diameter greater than 4 cm. For each tree I recorded the height at which the core was taken and the diameter of the tree at core height. For dead trees, I also recorded surface texture, degree of burial, and presence or absence of sapwood. For live trees that were too small to core, I estimated age by counting internodes on the main stem. Internode counts were calibrated against basal pith dates from nine harvested seedlings. The calibration indicated that ages estimated by basal pith dates and by internode counts were within 2 to 3 years of one another (Lloyd 1996).

Tree-ring methods

Reconstruction of past population dynamics required that I determine germination date and, when applicable, death date for each tree. All cores were mounted, sanded, measured, and cross-dated using standard dendrochronological procedures. Cross dating allowed assignment of a calendar year to each annual ring and was accomplished by visually comparing dated and undated samples (e.g., Stokes and Smiley 1968) and using the computer program COFECHA (Holmes 1995). For all trees, cross-dated inner ring dates were corrected for (i) years to core height and (ii) years to center when pith was missed. The number of years to core height was estimated from age–height regressions established from all seedlings and saplings in each study plot ($n > 30$ at each site). A separate regression was calculated for each of the three sites. Age and height were significantly related with either linear or logarithmic relationships at all sites ($R^2 > 0.8$, $P < 0.0001$). In trees for

which the pith was not obtained, the distance to the center of the tree was estimated either by fitting a circle template to the ring curvature or, if no ring curvature was present, by subtracting the core length from the measured radius at core height. The number of years to the center of the tree was estimated from age–diameter regressions established from seedlings and saplings at each site. Age and diameter were linearly related in trees with diameter < 90 cm at all sites ($R^2 > 0.85$, $P < 0.0001$).

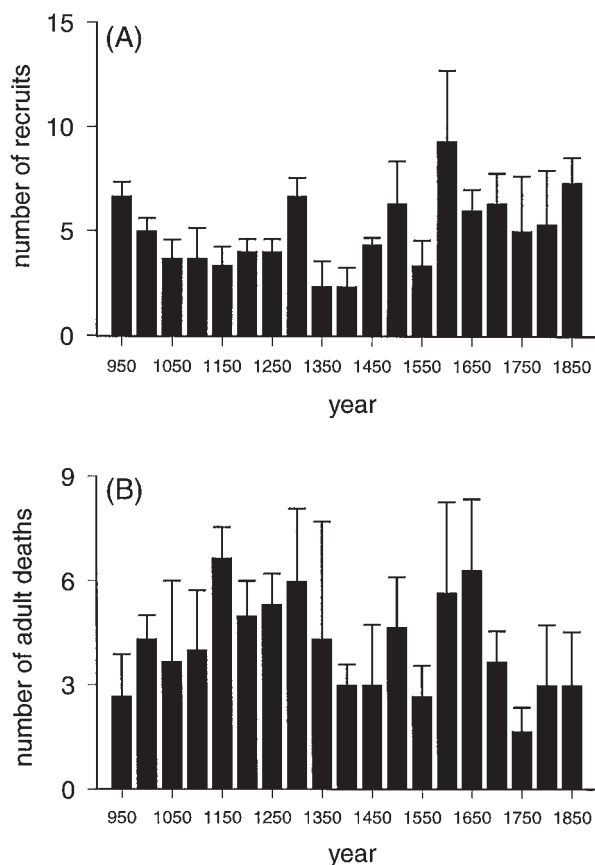
The corrections for core height and missed pith are the major sources of error in estimating a tree's germination date and set limits on the temporal resolution of the reconstruction. The temporal resolution on the estimates of germination dates was estimated from the 95% confidence intervals of age height (± 7.5 years) and age–diameter (± 8.5 years) regressions. Based on the combined error, I chose a relatively conservative time interval of 50 years as the finest resolution that could be interpreted robustly from these data. All recruitment data are therefore presented in 50-year time classes.

Cross-dated outer-ring dates of dead trees were corrected for the loss of rings from the outer surface due to pre- and post-mortem decay. A minimum estimate of years lost to decay was made by multiplying the mean lifetime growth rate of each dead tree by the estimated wood loss due to erosion of sapwood or furrowing of surface. Trees dead for 1000 years commonly retain medium branches (diameter > 2 cm), suggesting that loss of surface wood from decay is minimal on the time scale of this study. Corrections ranged from 0 to approximately 150 years. Death dates were also analyzed in 50-year time classes.

From the estimated germination and death dates, I calculated recruitment, mortality, and adult tree density for each 50-year time period in the last 1000 years. The record of tree deaths preserved in deadwood is biased strongly against small (young) trees. Preservation of the extremely resinous wood of foxtail pine is excellent in these cold, dry sites, so medium to large trees (greater than 10 cm diameter) are likely to be preserved for hundreds to thousands of years after death (Lloyd and Graumlich 1997). Smaller trees, as a result of small size and low proportion of resinous heartwood, are unlikely to be preserved for more than a few decades after death. The reconstruction presented here therefore pertains specifically to the adult segment of the population (i.e., those trees large enough to be preserved after death). I use "recruitment" to refer to the number of trees that germinated during a time interval and subsequently survived to a size large enough to be preserved (approximately 150 years old) and "mortality" to refer to the death of adult trees. To estimate a regional history of change in recruitment and mortality rates, I averaged the individual population histories. For each time period, therefore, data are presented as the mean \pm standard error of the three sites.

The length of time over which population history can be reconstructed and interpreted is limited by the fact that the record of tree death fades over time because of decomposition. Previous authors have defined the time period of a reconstruction of population history by the decomposition limit, or length of time that a dead tree takes to decompose, which was found to be related to stand age (Johnson and Fryer 1989; Johnson et al. 1994). Foxtail pine at tree line decay very slowly, and scattered individuals have persisted for thousands of years after death. Although decomposition of large trees may take in excess of 3500 years, the record of population structure probably fades more quickly. I set a conservative time limit on this reconstruction by examining the time series of reconstructed stand density for the last 3500 years and identifying the point at which stand density began to decline as time since present increased. Trends in stand density prior to that period are uninterpretable because ecologically meaningful trends can not be distinguished from those that would be produced by the fading record of tree death. The analysis is therefore limited to the last 1000 years, a period in which a relatively complete record of adult tree death is preserved. The reconstructions do not include the last 100 years, as estimates of recruitment rates in the last 100 years include seedlings and saplings, and are therefore not comparable to the adult recruitment rates estimated for previous intervals.

Fig. 1. (A) Number of recruits and (B) number of deaths for 50-year time intervals from A.D. 950 through A.D. 1900. Values are mean \pm 1 SE ($n = 3$ populations).

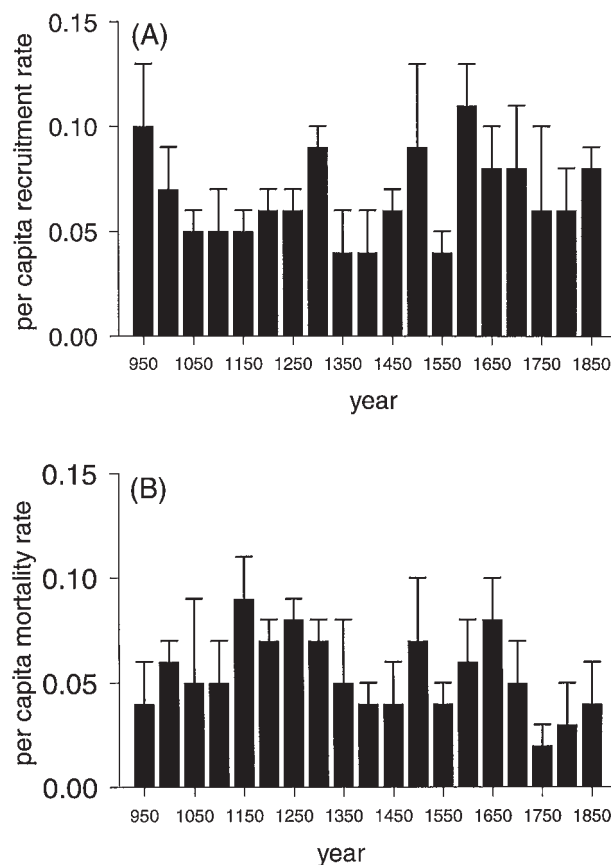


To examine 20th century stand dynamics, I estimated the age of young trees from node counts and constructed a static age structure of trees less than 45 years old (i.e., those that have established since 1950). The age structure of live seedlings provides some information on the recruitment dynamics of young age-classes that are not represented in the reconstruction of long-term population dynamics. Interpretation of static age structures of live seedlings is problematic, however, because both recruitment and mortality vary over time to produce a given age structure (Veblen 1992; Johnson et al. 1994). The interpretations of post-1950 recruitment patterns presented in this paper are predicated on the assumption that mortality has been constant for all cohorts.

Statistical analyses

The hypothesis that recruitment is more sensitive to climate than mortality leads to the prediction that recruitment rates will be significantly correlated with climate over time and that mortality rates will be less well correlated. To test this, I transformed population and paleoclimate data to ranks and compared them using Spearman's rank correlation coefficient (Sokal and Rohlf 1981). Paleoclimatic data used in this study are a reconstruction of summer temperature and winter precipitation from tree-ring widths of foxtail pine and western juniper in the Sierra Nevada (Graumlich 1993). Although there is the potential for circularity in comparing an ecological record from foxtail pine ring widths with a climate record reconstructed in part with foxtail pine ring widths, the reconstruction used here is verified by extensive cross-comparison with other physical and biological climate proxies (Graumlich and Lloyd 1996). For the period 1950 to present, I calculated Spearman's rank correlation coefficients between the number of pith dates per 5-year interval and meteorological data averaged over

Fig. 2. (A) Per capita recruitment rate and (B) per capita mortality rate for 50-year time intervals from A.D. 950 through A.D. 1900. Values are mean \pm 1 SE ($n = 3$ populations).



the same 5-year interval. Meteorological data were from the Grant Grove, California, meteorological station (National Climatic Data Center 1996), with snowpack data from the California Cooperative Snow Survey (State of California Department of Water Resources 1996).

I used one-way analysis of variance (ANOVA) to test for significant differences in mortality and recruitment between two time intervals: a warm, dry period from A.D. 1000 to A.D. 1350 and a cold, wet period from A.D. 1500 to A.D. 1850. I used mean values (of three sites) for recruitment and mortality as data in the ANOVA. There was no significant autocorrelation in the time series of recruitment and mortality, so values for the seven 50-year time intervals in each of the two periods (A.D. 1000–1350 and A.D. 1500–1850) were treated as independent replicates. I used an F -test to test the hypothesis that variance in recruitment was significantly greater than variance in mortality (Shaw and Wheeler 1985).

Results

Population history since A.D. 1000

Variation in the number of births and deaths (Fig. 1) and the rate of recruitment and mortality (Fig. 2) over the last 1000 years was relatively small. Recruitment and mortality rates were uncorrelated during the last 1000 years ($r_s = 0.105$, $P > 0.05$). The number of recruits was moderately lower during the period A.D. 1000 to A.D. 1350 than during the period A.D. 1500 to A.D. 1850 ($F = 3.95$, $P = 0.07$, error df = 12), but there were no significant differences in number of deaths between these time periods ($F = 1.91$, $P = 0.192$, error df = 12). There

Fig. 3. Absolute change in population size for 50-year time intervals from A.D. 950 through A.D. 1900. Change in population size is calculated as the number of recruits (births) minus the number of deaths. Values are mean \pm 1 SE (n = 3 populations).

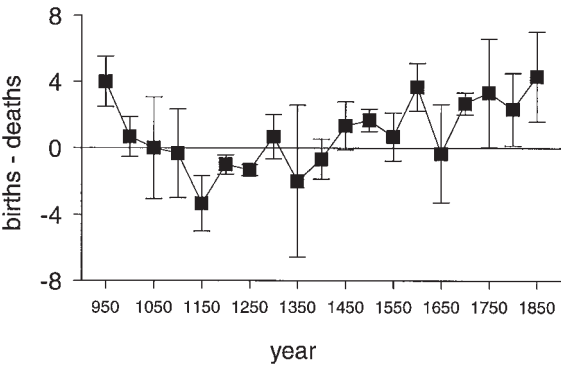


Table 1. Variance among 50-year time intervals in level of recruitment and mortality, and recruitment and mortality rates at each study site.

Site	Recruitment	Deaths	Recruitment rate	Mortality rate
1	5.53ns	6.15	0.0011ns	0.0010
2	13.32ns	8.94	0.0010ns	0.0007
3	9.18*	5.66	0.0014ns	0.0018

Note: ns, the difference between variance in recruitment and variance in mortality, as determined by the F -test for equal variance, was not significant at that site; *, the difference between variance in recruitment and variance in mortality was significant at P < 0.05.

was a small difference in mortality rate between the two time periods (F = 3.73, P = 0.077, error df = 12) but no significant difference in recruitment rate (F = 1.90, P = 0.194, error df = 12).

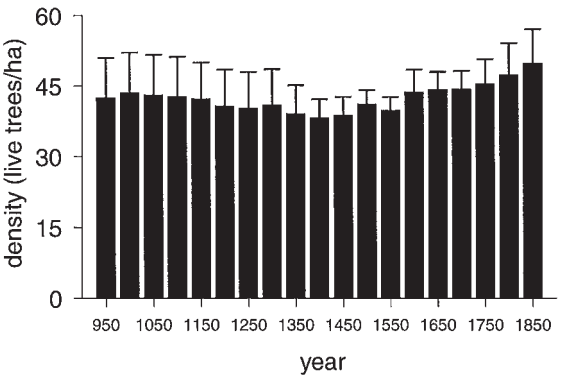
The number of deaths exceeded the number of births for most of the period A.D. 1100 to A.D. 1450, and births have exceeded deaths since A.D. 1450 (Fig. 3). The increase in population size (births – deaths) was significantly greater for the period A.D. 1500–1850 than for the period A.D. 1000–1350 (F = 12.33, P = 0.004, error df = 12). Stand density changed only slightly during the last 1000 years, rarely increasing or decreasing by more than 5% from one time interval to the next and never changing by more than 10% (Fig. 4). Variance among time intervals in number of recruits was significantly greater than the variance in number of deaths at only one of three sites, and variance in recruitment rate was never significantly greater than variance in mortality rate (Table 1).

Change in stand density (percent change from one time interval to the next) was significantly and inversely correlated with summer temperature during the last 1000 years, as was recruitment rate (Table 2). Mortality rate was uncorrelated with summer temperature. There were no significant correlations between winter precipitation and stand density, recruitment rate, or mortality rate (Table 2).

Recruitment since A.D. 1950

Most live seedlings at the sites germinated before 1970 (Fig. 5). Successful establishment was low at all sites after

Fig. 4. Density of adult trees for 50-year time intervals from A.D. 950 through A.D. 1900. Density is the number of trees that were alive during any part of a given time interval. Values are mean \pm 1 SE (n = 3 populations).



1975, and at all but one site there was no successful establishment in the last 5 years. Because this is a static age structure, it is impossible to determine whether the low rates of successful establishment after 1975 resulted from low germination rates or high seedling mortality rates. At two sites, I observed no seed germination from 1993 through 1995, suggesting that the former explanation may at least partly explain the low number of seedlings in younger age-classes. The mean number of pith dates per time interval was uncorrelated with any climate variable (n = 3 sites, Table 3). The number of pith dates per time interval was significantly and positively correlated with average January snowpack, however, at the two sites that have had little or no successful establishment since 1985 (Table 3).

Discussion

Climatic control over tree line

The hypothesis that low temperature is a limit on tree population growth in tree-line forests (Wardle 1963, 1981; LaMarche and Mooney 1967; Tranquillini 1979; Kullman 1986; Grace 1989) is not supported by this investigation of tree-line forest population dynamics on either long (last 1000 years) or moderate (last 50 years) time scales. On long time scales, rates of recruitment into adult age-classes and changes in stand density are inversely correlated with summer temperature. The inverse correlation with summer temperature may point to an important role for water balance in regulating population growth in these cold, dry sites, a finding that is consistent with the paleoecological record of tree-line history at these same sites, in which tree-line elevation declined during a warm, dry interval at A.D. 1000 (Lloyd and Graumlich 1997). Although there is no evidence that low temperature limits population growth or the establishment of adult trees on long to moderate time scales, a role for low temperature in controlling rates of germination and early seedling survivorship cannot be ruled out.

The inverse correlation between recruitment and temperature on long time scales is unexpected in the context of the numerous studies that have identified low temperatures as a limit over growth and recruitment at tree line at a wide variety of sites (LaMarche and Mooney 1967; Tranquillini 1979; Black and Bliss 1980; Kullman 1987; Grace 1989). The inverse

Table 2. Spearman's rank-correlation coefficients for relationships between population parameters and climate for 50-year intervals from A.D. 950 to A.D. 1900.

	Summer temperature	Winter precipitation
% change in stand density	-0.713*	0.012
Recruitment rate	-0.679*	0.175
Mortality rate	0.254	-0.009

Note: *, correlations are significant at $P < 0.05$. Percent change in stand density is the percent change in time t relative to time $t - 1$. Recruitment and mortality rates are per capita (number of births or deaths/population size). Climate data are mean values for each 50-year interval, based on dendroclimatological reconstructions for the Sierra Nevada region (Graumlich 1993). Summer temperature is the mean for June through August, and winter precipitation is the sum of October through June precipitation.

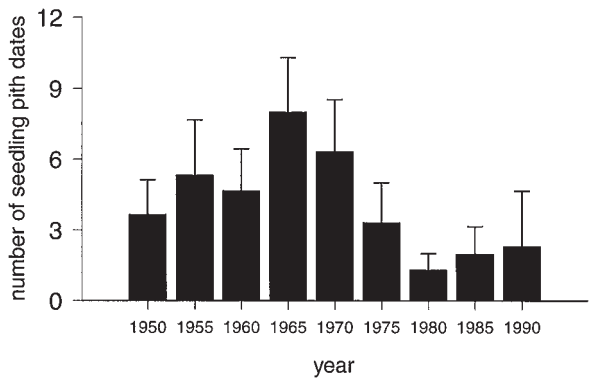
relationship between temperature and foxtail pine recruitment may be related to the inverse correlation between temperature and moisture in the region during the past 1000 years (Hughes and Brown 1992; Graumlich 1993; Stine 1994; Hughes and Graumlich 1996). Warm temperatures may exacerbate the effects of drought (i.e., by increasing rates of evapotranspiration), thus limiting recruitment. The beneficial effects of temperature at this particular tree line may therefore be contingent on the availability of adequate moisture. This hypothesis is supported by the positive correlations between winter precipitation and number of seedling pith dates during the last 50 years. My data do not show a positive relationship between recruitment and estimated winter precipitation during the last 1000 years. The absence of this relationship may be an artifact of the 50-year time intervals used in this study. Graumlich (1993) has shown that precipitation has varied at higher frequencies than temperature during the last 1000 years in the region, so a relationship between recruitment and precipitation may be obscured by the coarse temporal resolution of this study.

My results suggest that the model of tree line as a boundary in which the effect of a single variable (temperature) predominates (e.g., Tranquillini 1979) is probably more applicable to mesic tree lines than to arid tree lines such as the one studied here. The eastern Sierra Nevada are both very cold, as a result of the high elevation, and very dry, as a result of the rain shadow of the western crest of the range. The position of tree line may therefore be controlled by interactions between temperature and water variability.

Sensitivity of tree-line forests to climate variation

My results support the hypothesis that recruitment is more sensitive to climate than mortality, but do not support the hypothesis that recruitment is more variable than mortality. The sensitivity of recruitment to climate was indicated by a significant inverse correlation between recruitment rate and summer temperature. Mortality rates were uncorrelated with precipitation or temperature, suggesting either that adult tree death occurred because of local or endogenous factors or that adult mortality rates responded only to extreme climatic events. Despite apparent differences in sensitivity to climate, recruitment was not more variable than mortality: variance in recruitment among time intervals was significantly different from variance in mortality at only one of three sites. This is unsurprising in

Fig. 5. Number of seedlings alive in 1995 that germinated during each 5-year interval from 1950 through 1995. Values are mean \pm 1 SE ($n = 3$ populations).



light of the fact that the paleoecological data provided no estimate for the variance in the earlier stages of the recruitment process (germination, seedling establishment), which would be expected to be most variable.

Changes in stand density over time were minor, despite the apparent sensitivity of recruitment to climate. This result is consistent with the expectation that populations of a long-lived species, particularly one in which adult mortality rates are unrelated to climate, should be little affected by climate variation on time scales that are short relative to the average life-span. This conclusion does not necessarily imply similar stasis in younger life stages for which no long-term data are available. Large fluctuations in seedling density, for example, may have occurred over the past 1000 years. If such changes in the abundance of younger individuals occurred, however, they had little or no lasting effect on the fate or structure of the populations studied here, as the number of adults of reproductive age remained relatively constant.

The lack of population sensitivity to climate observed in this study contrasts with the record of tree-line position at these same sites. During the last 1000 years, the elevation of tree line at these sites declined by up to 30 m, reaching its current elevation only within the last 100–200 years (Lloyd and Graumlich 1997). The comparative stasis of the forests at current tree line during the same time interval (this study) indicates that there are steep gradients of vulnerability to climate change at tree line in the Sierra Nevada. The results of this study suggest a mechanism for reconciling the apparent sensitivity of the tree-line ecotone with the insensitivity of tree populations near tree line. Past episodes of unfavorable climate led to the death of the most marginal individuals (those within approximately 100 m of tree line; Lloyd and Graumlich 1997), while leaving individuals short distances from the edge (100–200 m) unaffected (this study). This finding is consistent with the hypothesis that there may be positive-feedback switches operating at tree line, particularly in cases like the Sierra Nevada where tree line is a sharp boundary (Wilson and Agnew 1992). Intrinsic resistance to climate change resulting from life history characteristics may be reinforced in some populations by the protective influence of moderate densities of adult trees, which are able to moderate their microclimate enough to buffer themselves against substantial variation in external conditions. Trees in marginal locations do not experience the full protective

Table 3. Spearman's rank-correlation coefficients for relationships between recruitment and climate for 5-year intervals from 1950 to present.

Climate parameter	Mean	Site 1	Site 2	Site 3
Winter temperature (Nov.–Feb.)	–0.467	–0.445	–0.293	–0.457
Spring temperature (March–May)	–0.133	–0.227	–0.050	–0.123
Summer temperature (June–Aug.)	–0.134	–0.329	0.227	–0.137
Summer precipitation (June–Aug.)	–0.133	–0.345	0.092	–0.079
Snowpack depth (late Jan.)	0.441	0.772*	0.434	0.844*

Note: *, correlations are significant at $P < 0.05$.

influence of this buffering, so marginal populations are more vulnerable to extirpation during periods of environmental stress than non-marginal populations. Steep gradients of exposure to environmental stress at forest margins have been documented in other forested ecosystems: in subalpine balsam fir (*Abies balsamea* (L.) Mill.) forests in the northeastern United States, for example, waves of tree mortality have been attributed to differential wind exposure of edge versus nonedge individuals (Foster 1988; Marchand et al. 1986; Sprugel 1976). In the Sierra Nevada, tree line appears to be characterized by similarly abrupt thresholds of vulnerability, where immediately adjacent populations have differed markedly in their responsiveness to climate variation.

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