Forest reproduction along a climatic gradient in the Sierra Nevada, California

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Abstract

To elucidate broad-scale environmental controls of coniferous forest reproduction in the Sierra Nevada, California, we monitored reproduction for 5 years in 47 plots arrayed across a steep elevational (climatic) gradient. We found that both absolute seedling densities (stems < 1.37 m) and seedling densities relative to overstory parent tree basal area declined sharply with elevation. Rates of seedling turnover (the average of birth and death rates) also declined with elevation. In contrast, seed production was not predicted by elevation and was highly variable from year to year. During a mast year of seed production, the intensity of masting was uneven among plots. Seedling densities were elevated only during the single year immediately following the mast year, suggesting reproduction in our forests may be primarily limited by abiotic factors such as the availability of suitable sites and weather. Disturbance also clearly affected reproduction; plots that had recently burned had significantly higher seedling to parent tree ratios for *Abies* species, suggesting that even though established *Abies concolor* may be relatively susceptible to fire, the species can recover rapidly through prolific reproduction. Since reproductive failures may be our earliest signal of changing forest conditions, seedling dynamics could provide a sensitive, if variable, indicator of environmental changes.
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1. Introduction

The distribution and dynamics of overstory forest trees are strongly influenced by climate. Recent work has demonstrated that forest tree recruitment and death rates in the overstory are correlated with site productivity (hence climate) (Stephenson and van Mantgem, 2005), with implications for understanding and predicting the effects of climatic changes on forest structure, composition, and dynamics. Yet given the great longevity of many forest trees, considerable time may pass between climatic changes and substantial vegetation change, with species persisting after conditions suitable for their establishment have disappeared (Idso, 1989). In contrast, reproduction is perhaps more sensitive to climate (Fowells and Stark, 1965; Kern, 1996; Stohlgren et al., 1998; Collins and Carson, 2004), responding to climatic change by varying patterns of cone initiation, seed production, and seedling recruitment and growth (Olszyk et al., 1998; LaDeau and Clark, 2001; Castro et al., 2004).

However, the limited spatial and temporal scale of past studies restricts our understanding of how current climatic conditions control reproduction. We present data from a series of 47 long-term monitoring plots arrayed across a steep elevational (climatic) gradient in the Sierra Nevada of California, where forest physiognomy and precipitation are relatively uniform but temperature differences are conspicuous. Using these data we ask: (1) Are there differences in reproduction among species or species groups regardless of elevation? (2) How does the structure of stems <1.37 m tall (hereafter referred to as seedlings) relate to elevation? (3) Do seedling turnover rates vary with elevation? (4) How might seed and seedling densities change over a short 5-year interval? Most studies of forest reproduction have not adequately tied seedling populations to the potential parent populations. Our seedling monitoring plots are nested within larger, long-term forest monitoring plots (van Mantgem and Stephenson, 2005), allowing us to associate understory structure and demography to potential parent trees. We also briefly consider the effects of

disturbance, in this case prescribed fire. If the Sierra Nevada continue to warm, with an associated earlier spring snowmelt (Dettinger and Cayan, 1995; Hayhoe et al., 2004; Stewart et al., 2005), the results of this study will supply valuable baseline information to assess future changes in forest reproduction.

2. Methods

2.1. Study design

This study takes advantage of 22 pre-existing long-term forest monitoring plots in Sequoia and Yosemite National Parks in the Sierra Nevada of California (36–38°N, 118–120°W), established in 1982–1994 and ranging in size from 0.9 to 2.5 ha (Table 1). Within the southern Sierra Nevada elevation rises from near sea level to 4418 m in less than 100 km horizontal distance, one of the most extreme elevational gradients in temperate North America. The approximate horizontal distance from the lowest to the highest plots in Sequoia and Yosemite National Parks is 11.3 and 27.3 km, respectively. All plots are on shallow slopes and are located on relatively young soils (mostly inceptisols) derived from granitic parent materials. Mean annual precipitation varies little with elevation (from ~1100 mm at 1500 m, peaking at ~1400 mm at about 2000 m elevation, but declining slightly with elevation >2000 m; Stephenson, 1988). In contrast, mean annual temperature declines sharply with elevation (~5.2 °C for every 1 km increase in elevation; Stephenson, 1988).

The plots are arranged along an elevational gradient from near lower to near upper treeline and encompass several different forest types, ranging from ponderosa pine-mixed conifer forests at 1500–1637 m, to white fir-mixed conifer forests at 2033–2210 m, red fir forests at 2484–2576 m, and subalpine forests at 2838–3097 m (Table 1). Our plot network also includes two mid-elevation xeric conifer forests at 2106 and 2405 m, where Jeffrey pines (*Pinus jeffreyi*) characterize the stands. Two mid-elevation plots (Lower and Upper Tharp) were burned in a single prescribed fire in 1990 and therefore analyzed separately (see Section 2.5). All trees ≥1.37 m in height were tagged, mapped, and identified to species within each plot. New trees reaching 1.37 m were recorded annually as recruitment. We took measurements of live tree stem diameter at breast height (DBH, 1.37 m), typically at 5-year intervals, with breast height marked with a nail for precise relocation. We assessed tree mortality (stems ≥ 1.37 m) annually starting at the time the plots were established.

At each plot in 1999 we overlaid at least two 25 m^2 seedling subplots, for a total of 47 subplots (2.9 ha total; Table 1). The subplots were arrayed so that they were positioned 20–25 m from an edge of the forest plots and with non-adjacent perimeters. We identified seedlings by species and conducted annual counts using the following procedures: we counted

Table 1
Characteristics of permanent forest plots and their associated seedling subplots

Plot	Establishment year	Elevation (m)	Plot size (ha)	Seedling subplots	Basal area (m^2 ha^{-1})[a]	Overstory species composition[b]
YOHOPIPO	1991	1500	1.0	2	76.4	ABCO 35%; CADE 32%; PILA 26%; PIPO 5%; PSME 1%; QUKE 1%
BBBPIPO	1992	1609	1.0	2	66.5	CADE 55%; QUKE 24%; ABCO 12%; PILA 5%; PIPO 4%; QUCH 1%
CCRPIPO	1991	1637	1.1	2	68.3	ABCO 46%; CADE 30%; QUKE 15%; PILA 5%; PIPO 4%
Crane Creek	1993	1637	1.0	2	77.8	ABCO 44%; CADE 29%; PILA 19%; PIPO 6%; QUKE 2%
SuwCreek	1983	2033	1.4	2	56.0	ABCO 55%; CADE 20%; PILA 20%; ABMA 4%; QUKE 1%
SuwABCO	1983	2035	0.9	2	77.6	ABCO 59%; CADE 28%; PILA 9%; ABMA 4%
SuwPILA	1983	2059	1.1	2	64.1	ABCO 68%; PILA 21%; CADE 9%; QUKE 1%
FrPIJE	1983	2106	1.0	2	16.8	PIJE 79%; QUKE 9%; ABCO 7%; PILA 2%; CADE 2%; PIMO 1%
LMCC	1982	2128	2.0	3	160.0	ABCO 71%; ABMA 20%; SEGI 7%; PILA 2%
LogSEGI	1983	2170	2.5	4	150.8	ABCO 76%; ABMA 15%; PILA 5%; SEGI 3%
LogABCO	1987	2207	1.1	2	64.0	ABCO 75%; ABMA 22%; PILA 2%; SEGI 1%
LogPILA	1987	2210	1.0	2	52.2	ABCO 90%; PILA 6%; CADE 2%; PIJE 1%; QUKE 1%
LogPIJE	1985	2405	1.0	2	17.6	ABCO 59%; PIJE 39%; ABMA 2%; PILA 1%
SftrABMA	1992	2484	1.0	2	106.9	ABMA 100%
WtABMA	1993	2521	1.0	2	57.1	ABMA 99%; PIMO 1%
PoflABMA	1994	2542	1.0	2	109.2	ABMA 94%; PICO 4%
PgABMA	1992	2576	1.0	2	94.4	ABMA 100%
Emsalix	1983	2838	1.0	2	2.7	PIMO 76%; PICO 24%
Emslope	1983	2950	1.0	2	22.9	PIMO 78%; PICO 10%; PIJE 10%; ABMA 2%
Emridge	1984	3097	1.1	2	12.3	PIMO 98%; PICO 2%
LowTharp[c]	1984	2167	1.1	2	53.3	ABCO 80%; PILA 18%; PIJE 1%
UpTharp[c]	1984	2202	1.0	2	47.4	ABCO 96%; PIJE 2%; PILA 2%

[a] Basal area of trees defined as individuals ≥1.37 m tall at time of plot establishment. The high basal areas in plots LMCC and LogSEGI are due to the presence of the anomalously large giant sequoia, *Sequoiadendron giganteum*.

[b] Species composition of all overstory stems at time of plot establishment. Percentages may not add to 100 due to rounding. ABCO: *Abies concolor* (Gordon & Glend.) Lindley; ABMA: *A. magnifica* Andr. Murray; CADE: *Calocedrus decurrens* (Torrey) Florin; PICO: *Pinus contorta* Loudon spp. *murrayana* (Grev. & Balf.) Critchf.; PIJE: *P. jeffreyi* Grev. & Balf.; PILA: *P. lambertiana* Douglas; PIMO: *P. monticola* Douglas; PIPO: *P. ponderosa* Laws.; PSME: *Pseudotsuga menziesii* (Mirbel) Franco var. *menziesii*; QUCH: *Quercus chrysolepis* Liebm.; QUKE: *Q. kelloggii* Newb.; SEGI: *Sequoiadendron giganteum* (Lindley) Buchholz.

[c] Plots prescribed burned in 1990.

seedlings ≤10 cm tall, distinguishing among first year seedlings, second year seedlings, and older seedlings ≤10 cm tall using field characteristics. Seedlings >10 cm tall were individually tagged and recorded by height class (11–25, 26–50, 51–75, 76–100, and 101–137 cm). Each year following seedling plot establishment we noted if tagged seedlings were alive, dead or had grown to a new size class, and we tagged new seedlings reaching >10 cm tall. We made an exception to this tagging scheme when we encountered dense seedling "thickets", defined as >20 individual seedlings of a species/size class combination within a permanently marked 5 m^2 quadrat within a seedling subplot. For these thickets we counted all individuals but only tagged an arbitrarily selected subsample of 20 seedlings.

At the time of the seedling subplot establishment we placed 0.5 m^2 seed traps at the corners and mid-points on all sides just outside each seedling subplot, plus an additional seed trap in the middle of the subplot, giving a total of nine seed traps per subplot. Traps consisted of wood frames lying on the ground covered with fine mesh screen on the bottom and 0.5 in. × 1 in. hardware cloth on the top. Seeds were collected from the traps annually soon after spring snow melt and sorted by species and counted in the laboratory.

We measured seed and seedling production using absolute densities and densities relative to the basal area of potential parent trees. Parents were defined as live trees ≥1.37 cm tall during the most recent plot measurement and found no further than 25 m distant in any direction from the edge of the seedling subplot. This relatively crude definition acknowledges that seed production scales with tree size (Niklas, 1993; Ribbens et al., 1994; Wright et al., 2003; Clark et al., 2004), although the exact relationships for our species may be more complex (Fowells and Schubert, 1956). We considered other distances for potential parent trees ranging from 0 to 15 m from the seedling subplot, but these distances provided results comparable to those of 25 m.

2.2. Variation among species

To test for differences among seed and seedling production we considered the ratio of seeds (ha^{-1}) or seedlings (ha^{-1}) to parent tree basal areas (m^2 ha^{-1}) (hereafter seeds/BA and seedlings/BA). The distributions of seeds/BA and seedlings/BA among subplots were highly skewed. We therefore used non-parametric randomization tests to determine differences. For species or species groups (e.g., *Abies* and *Pinus* groups) our randomization tests consisted of 10,000 random permutations of the average paired differences of ratios between groups found within the same seedling subplot using the two-tailed test statistic

$$\theta_{ij} = \left| \sum_{k=1}^{n} G_{ik} - G_{jk} \right|$$

where G_i and G_j signify paired values for species or groups i and j within subplots 1–n. Each random permutation was achieved by assigning values to different species or groups, regardless of their actual species identity. The frequency of randomized

values of $\theta \geq \theta_{obs}$ (the observed value of θ) provides a P value (Manly, 1997).

2.3. Variation in elevation

The elevations of seedling subplots nested within an overstory plot were identical, so we combined seedling subplot data within each overstory plot for elevational analyses. We modeled elevational effects on average seed and seedling densities and seeds/BA and seedlings/BA for the years 1999–2003 using a simple exponential decay function ($N(m) = B\,e^{-Am}$), where $N(m)$ is the number of seeds or seedlings at a given elevation and m is the elevation (meters). For all models the two estimated parameters were highly correlated (asymptotic correlation ≥ 0.98), therefore we fixed parameter B in order to better compare the exponential rate of decline A. Fixing B did not significantly reduce model fit. We included a term for canopy cover in these models by estimating crown area for all trees up to 25 m distant from the edge of the seedling subplots using published allometric equations (Means et al., 1994; Uzoh and Ritchie, 1996; Gill et al., 2000). We used a number of different starting values for each model and assessed model fit by calculating parameter confidence intervals using 5000 bootstrapped estimates (Manly, 1997). To explore differences in seedling size class distributions with elevation we grouped the seedling subplots into three elevation classes (low elevation < 2000 m; mid elevation = 2000–2500 m; high elevation > 2500 m) and compared proportions of seedlings in different size classes using χ^2 tests. We calculated seedling growth as the proportion of seedlings graduating to the next larger size class and examined elevational effects using linear regression.

We used linear regression to model changes in tagged seedling turnover rates over elevation. We used turnover rates, the average of mortality of seedlings >10 cm tall and recruitment (seedlings growing to >10 cm tall) to better compare demographic rates with previously published studies of overstory trees (Phillips, 1996; Phillips et al., 2004; Stephenson and van Mantgem, 2005). One plot, Emsalix (Table 1), had no seedlings >10 cm tall and was excluded from this analysis, giving a sample size of 19 plots.

2.4. Variation in time

We looked for anomalous years of seed densities, seedling densities, seeds/BA, and seedlings/BA. Our sample size was sufficiently large to find significant differences ($P < 0.05$) among most consecutive years using paired randomization tests, although the magnitude of these interannual differences were often small and biologically trivial. Instead, we looked for interannual variation by searching for large differences among confidence intervals of the yearly mean values. For each year, we created 95% confidence intervals using 10,000 bias corrected bootstrapped samples (Manly, 1997). We also compared annual forest reproduction and total water year precipitation (October 1–September 30) as measured by the nearby Grant Grove weather station (38°N, 119°W).

2.5. Effects of fire

The 14 ha Tharp Creek watershed containing two forest monitoring plots and four seedling monitoring subplots was prescribed burned by a combination of strip headfires and backing fires in October 1990. Total pre-fire fuel loads were relatively high (210 Mg ha^{-1}), primarily composed of large diameter woody fuels (58%) and litter and duff (35%). Backing fire flame lengths ranged from 0.05 to 0.15 m, while strip headfire flame lengths were from 0.6 to 2.4 m. Following the burn the total fuel load was reduced to 31 Mg ha^{-1}. For more details of this fire, see Mutch and Parsons (1998). We compared the seedling subplots established 9 years post-fire in the post-burn Tharp Creek (LowTharp and UpTharp; Table 1) watershed to the seedling subplots in the adjacent unburned Log Creek watershed (LogABCO, LogPILA; Table 1). Specifically, we looked for differences in the burned and unburned areas with respect to seed and seedling densities, seeds/BA and seedlings/BA using non-parametric Mann–Whitney U-tests, and seedling size distributions using χ^2 tests. Note that we are subsampling within a single fire and our fire effects data are therefore pseudoreplicated (Hurlbert, 1984). While this is common to many fire effects studies (van Mantgem et al., 2001), we present these findings only as a demonstration of one possible way the relationship between climate and forest reproduction could be disrupted.

3. Results

3.1. Variation among species

In unburned stands from 1999 to 2003 *Abies* species accounted for on average 68% of all seedling observations, while *Pinus* species were found at 6%, typically at the mid- and high-elevation plots. Other common species, particularly at low elevations, were *Calocedrus decurrens* (21%) and *Quercus kelloggii* (4%). Conifers had a higher reproductive output compared to non-coniferous *Quercus* spp. relative to their potential parent tree basal areas, although this difference was not significant (average conifer seedlings/BA = 994.4, average *Quercus* seedlings/BA = 425.4, $P = 0.115$, $n = 8$ seedling subplots). Reproductive output was significantly higher for *Abies* versus *Pinus* (average *Abies* seeds/BA and seedlings/BA = 428.0, 381.5, average *Pinus* seeds/BA and seedlings/BA = 56.9, 42.9, $P < 0.001$, $n = 30$ seedling subplots). *C. decurrens* did not have a high rate of seed production (seeds/BA = 180.8), but had the highest relative seedling densities of any individual species in the seedling subplots in which it was found (average *C. decurrens* seedlings/BA = 5244.0, range of other species seedlings/BA = 45.5–603.5, $P \leq 0.01$, $n \geq 8$ seedling subplots). In the subplots where adult ponderosa pines were found, the average seedlings/BA for *Pinus ponderosa* was 44.5, compared to average seedlings/BA of 436.5 for all other *Pinus* species at these same subplots ($P < 0.01$, $n = 8$ seedling subplots). Conversely, *Pinus lambertiana* appeared to produce more seedlings than other *Pinus* species at the subplots in which *P. lambertiana* was found,

although the difference was not significant (average *P. lambertiana* seedlings/BA = 234.5, average seedlings/BA for all other *Pinus* species = 94.9, $P = 0.10$, $n = 11$ seedling subplots). *P. lambertiana* showed a much more even seedling size class distribution compared to *P. ponderosa* in the plots where they were found together (Pearson $\chi^2 = 241$, d.f. = 5, $P < 0.0001$), with the number of individuals found in the smallest size class representing 38 and 89% of the seedlings, respectively.

3.2. Variation in elevation

Elevation appeared to be a good predictor of the average total number of seedlings found at each plot (Fig. 1). The 95% confidence intervals were tight around the regression line, but widened with decreasing elevation, reflecting high variance of seedling densities at lower elevations. *Abies* and *Pinus* seedling distributions considered separately also followed a negative exponential function. There was a greater amount of variance in the *Abies* species, reducing the fit of the model. *Pinus* species followed a steeper exponential decay pattern with elevation compared to *Abies*. When we included canopy cover the 95% confidence interval for this term overlapped 0 for all models, indicating canopy cover was not useful for predicting seedling densities.

Average values of seedlings/BA for all species decreased with elevation, indicating that reproduction was lower in our high-elevation plots (Fig. 1). The LogABCO plot (Table 1) total seedlings/BA value was an outlier, due to its dominance by fast reproducing *Abies* species. Seedlings/BA of *Abies* observed in the LogABCO plot was not, however, highly unusual compared to seedlings/BA of *Abies* at similar elevations (Fig. 1). The overall seedlings/BA values for *Abies* and *Pinus* species groups declined with elevation, although seedlings/BA for *Abies* was an order of magnitude larger than *Pinus*. The 95% confidence interval for the canopy cover term also overlapped 0 for these models.

Average seed densities and seeds/BA values did not follow a clear elevational trend, with mid-elevation plots showing the greatest seed production. There was a mast year for *Abies* in 2001 in the mid-elevation plots (see Section 3.3), which partially explained this observation. Taken individually seed production in 1999, 2000, and 2002 was also not related to elevation ($R^2 < 0.01$, d.f. = 19, $P \geq 0.79$). This result also held when the data were broken into *Abies* and *Pinus* species groups.

Seedling height class distributions were characterized by high frequencies of small seedlings. This pattern held across all elevation classes (Fig. 2), with small, but statistically significant differences among elevation classes ($\chi^2 = 2779$, d.f. = 10, $P < 0.0001$). The differences among the elevation classes were primarily driven by differences in the relative number of seedlings in the smallest two height classes (0–10 and 11–25 cm). The mid-elevation plots had the greatest proportion of seedlings in the smallest size class relative to the low- and high-elevation plots, which was due to a mast year of seed production centered mostly in the mid-elevation plots (see Section 3.3). This trend was driven by the *Abies* species group ($\chi^2 = 2448$,
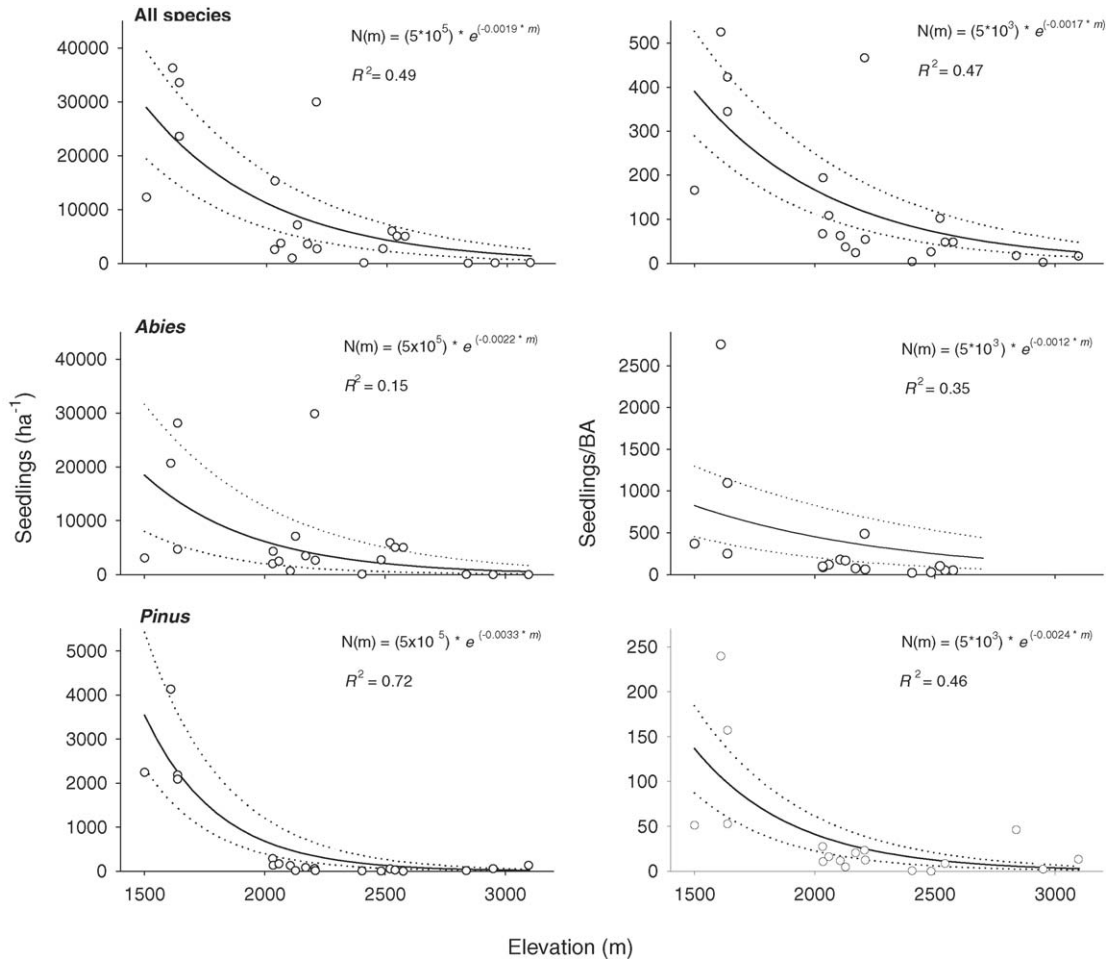
Fig. 1. Relationship between elevation and the average number of seedlings (ha^{-1}) from 1999 to 2003 for all species, *Abies* and *Pinus*. The relationships are also shown relative to the basal area (m^2 ha^{-1}) of potential parent trees (seedlings/BA). The solid line is the regression estimate, with the dashed lines showing the 95% confidence intervals calculated from 5000 bootstrapped estimates. $N(m)$ is the number of seeds or seedlings at a given elevation and m is the elevation (meters). Note the different scales for the vertical axes.

d.f. = 10, $P < 0.0001$), while the *Pinus* species group showed slightly greater proportions of smaller seedlings at low elevations ($\chi^2 = 61$, d.f. = 10, $P < 0.0001$). Variation in seedling growth was not explained by elevation for all species combined ($R^2 = 0.01$, d.f. = 18, $P = 0.73$) or for the *Abies* and *Pinus* groups ($P \geq 0.38$).

Average turnover rates for tagged seedlings >10 cm tall declined with elevation (Fig. 3). This trend was weak, indicating
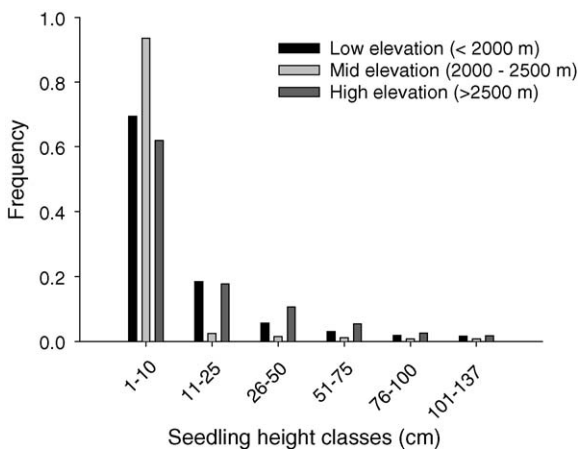

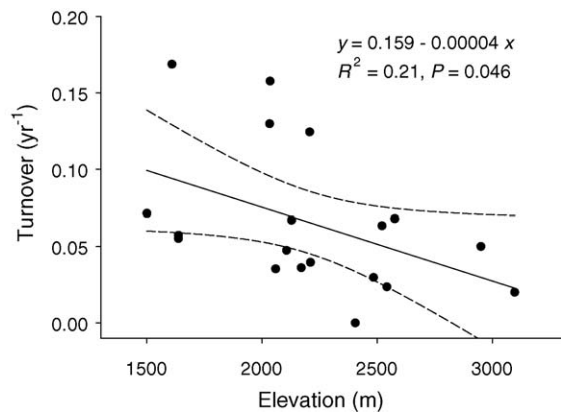Fig. 2. Height class distributions of seedlings by elevation classes.

Fig. 3. Relationship between elevation and turnover rates of tagged seedlings (>10 cm tall). The solid line is the regression estimate with the dashed lines showing the 95% confidence interval.
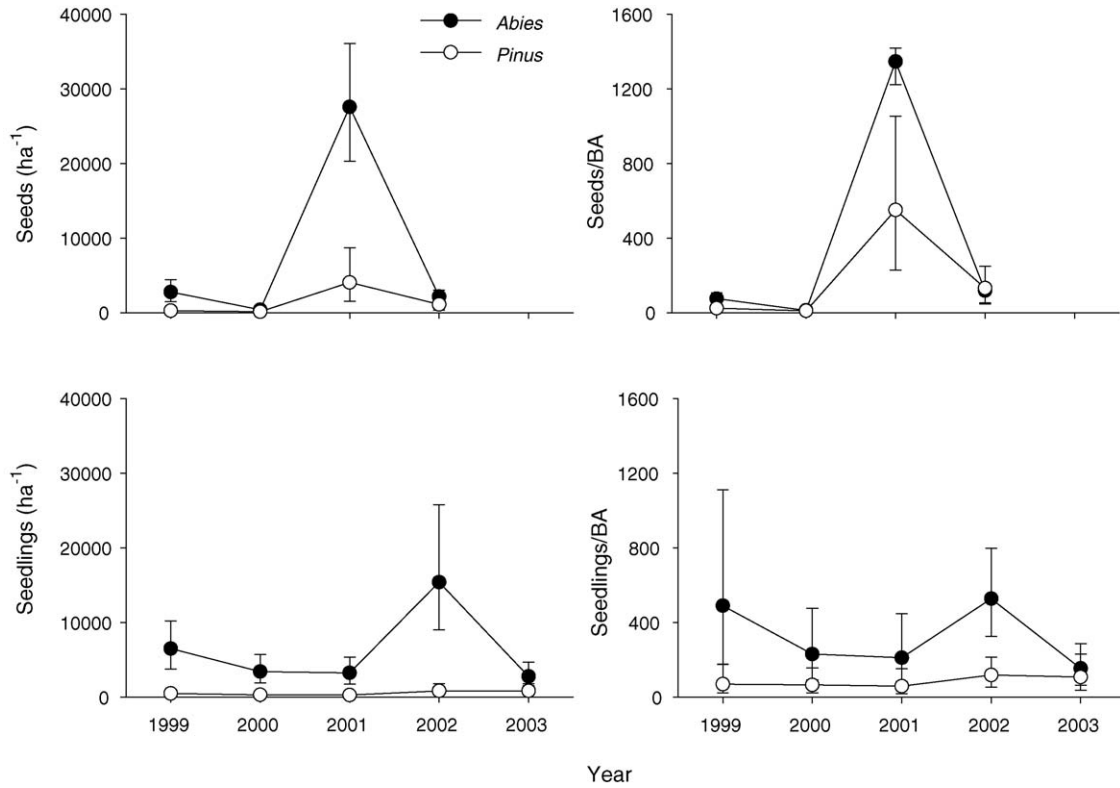
Fig. 4. Annual averages and 95% confidence intervals for *Abies* and *Pinus* seed densities, seed density relative to parent tree basal area, seedling densities, and seedling density relative to parent tree basal area. Note different scales for the vertical axes of the graphs.

large variation in demographic rates independent of elevation. Splitting the data into species groups resulted in weaker relationships ($P \geq 0.05$), suggesting that larger or longer term samples might be required to see clear trends between elevation and turnover for these groups.

3.3. Variation in time

We found a significant spike in seed production in 2001, followed by an increase in seedling densities and seedlings/BA values in 2002. These results were driven primarily by increases in *Abies* seed production in 2001 and seedling production in 2002 (Fig. 4). Although 2001 was also a high year of *Pinus* seed production, this translated to only slightly higher seedling densities and seedlings/BA values for *Pinus* in the following years (Fig. 4). The degree of masting was not equivalent in all plots where *Abies* species were found, with 21% of the 2001 *Abies* seed production and 37% of subsequent 2002 *Abies* seedling production occurring in the two LogABCO subplots. This mast event appeared to have little effect on longer term patterns, as the high densities of first year seedlings produced in 2002 did not survive into 2003 (Fig. 4). Correlations among annual forest reproduction and total water year precipitation (October–September) as measured by the nearby Grant Grove weather station were not significant ($P > 0.15$) for 0, 1, and 2-year lags, which may reflect the relatively short duration of our observations.

3.4. Effects of fire

We found lower seed densities and higher seedling densities in the burned Tharp Creek seedling subplots compared to the unburned Log Creek subplots, although these differences only approached statistical significance (seed density, Mann–Whitney $U = 3$, $P = 0.15$, $n = 8$; seedling densities, Mann–Whitney $U = 14$, $P = 0.08$, $n = 8$). The higher seedling densities in the burned areas were mostly in the form of additional *Abies* establishment. The size class distribution of seedlings found in
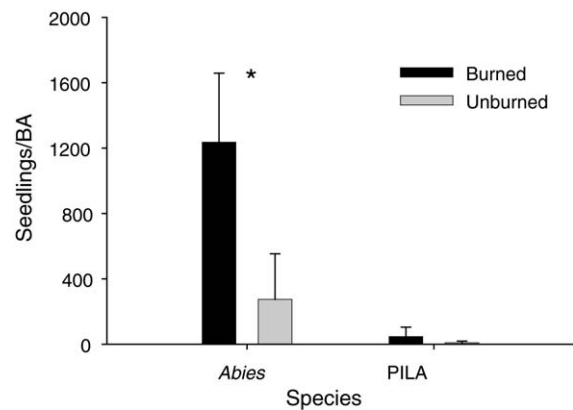

Fig. 5. Ratio of seedlings to parent tree basal area for two burned and two paired unburned plots. The asterisk denotes a difference at $P < 0.05$, the other comparison is non-significant. *Abies*: *Abies concolor* and *A. magnifica*; PILA: *P. lambertiana*.

the burned and unburned plots were different ($\chi^2 = 4110.8$, d.f. = 5, $P < 0.001$), with fewer of the burned subplot seedlings being found in the smallest size class (proportion of seedlings <10 cm tall, burned 41%, unburned 98%). Differences among the burned and unburned subplot seeds/BA were not significant for any species or species group ($P \geq 0.08$). In contrast, the seedlings/BA for *Abies* species appears to have increased in the burned plot (average seedlings/BA$_{burned}$ = 1235.6, average seedlings/BA$_{unburned}$ = 273.9, Mann–Whitney $U = 16$, $P = 0.02$, $n = 8$), though this pattern was not significant for *P. lambertiana*, the other dominant species in these plots (Fig. 5).

4. Discussion

Elevation, and therefore climate, appeared to strongly affect forest tree reproduction. Although reproductive differences in our plots may also arise independently of climate (e.g., slight differences in soil characteristics among plots, differences in reproduction intrinsic to species and species groups), elevation was correlated with seedling density, seedling density relative to parental basal area, and seedling demographic rates. Canopy cover did not appear to affect these relationships, perhaps because our estimates of canopy cover were overly crude. The response of *Pinus* seedlings to changes in elevation was more pronounced compared to *Abies* seedlings, supporting the idea that taxa may respond individualistically to climate (Kern, 1996; Green, 2005), although more fine scale data are needed to fully explore this idea. The slope of the relationship between elevation and turnover of seedlings is similar to that of trees ≥ 1.37 m tall in the same plots (Stephenson and van Mantgem, 2005), although the strength of the seedling–elevation relationship is weaker. Unexplained variance likely reflects both differences among local site conditions (Fowells and Stark, 1965) and the relatively short 5-year interval of our observations. Since climatic data indicate that site potential for primary production may decrease with elevation in the forested zone of the Sierra Nevada (Stephenson, 1988), a negative relationship between seedling turnover and elevation is consistent with broader patterns of forest productivity (Stephenson and van Mantgem, 2005).

Seed production and seedling sizes did not, however, follow a consistent pattern with elevation. Additionally, seed production was highly variable over time, particularly for *Abies*. Large fluctuations in seed production have been reported elsewhere in the Sierra Nevada (Fowells and Schubert, 1956; McDonald and Abbott, 1994). Although a single year of high seed production, primarily at middle elevations, was not responsible for obscuring elevational trends for seed production, the subsequent high year of seedling establishment did alter the 5-year average frequency of seedling sizes. The weak association of seed production with elevation suggests that seed production could be driven by specific reproductive traits of species that are not strongly influenced by climate.

Seed production seems to be independent of elevation, yet seedling density (and seedling density relative to parental basal area) declines with elevation. This could be a result of some combination of the following: (1) seedlings grow faster at higher elevations, therefore graduating more quickly out of the seedling stage, (2) seedling mortality rates are higher at higher elevations, or (3) a greater proportion of seeds successfully become established at lower elevations. Currently, we can eliminate the first two possibilities; seedling growth was not strongly associated with elevation and mortality rates were lower at higher elevations. As a rough check of the final possibility we estimated the proportion of seeds "establishing" by dividing the number of first year seedlings by the seed output in the previous year for the 4 years where we had seed output data. The average annual proportion of seeds "establishing" declined sharply with elevation ($y = 150 \times e^{-0.003 \times m}$, $R^2 = 0.72$, $n = 20$). Measuring establishment rates directly will require following the fates of individual seeds, but this demonstration suggests that variation in early phases of recruitment (e.g., proportion of sound seeds, seed predation, germination, first year mortality) may warrant closer study.

Two points are relevant with respect to the temporal variation in seed production. Firstly, although a majority of plots containing *Abies* showed a spike in seed production during 2001, there was wide variation among plots, with a single plot (LogABCO) radically outproducing other plots in terms of absolute seed density. *Pinus* seed production also increased in the same year, so perhaps trees were responding to an external biotic or abiotic signal rather than internal cycles (Curran et al., 1999). Secondly, the mast year did not seem to affect seedling densities beyond the following year, indicating that reproduction in the Sierra Nevada may be chiefly limited by abiotic factors such as the presence of suitable sites for germination or weather patterns following seed inputs (Caspersen and Saprunoff, 2005; North et al., 2005).

Additional evidence of site limitation comes from our comparisons of burned and unburned plots found at similar elevations. Seed output was not radically different (although slightly higher in the unburned plots because of the highly productive LogABCO plot). In contrast, the burned plots contained higher seedling densities along with greater seedlings/BA values. We had only four plots within a single fire to detect differences, so it seems likely that these differences would become statistically significant with even a slightly larger sample. Even with our limited data it was evident that reducing canopy cover and removing the litter and duff layers by burning allowed for greater reproduction, presumably without drastically changing seed inputs for these non-serotinous species. In the mixed conifer forests of the Sierra Nevada *Abies* adults are more sensitive to fire than other co-occurring species (Stephens and Finney, 2002). Our results also demonstrate, however, that *Abies* species may recruit heavily into both burned and unburned sites, suggesting that *Abies* may be more fire tolerant in these forests than commonly thought. The reproductive outcome of a particular fire may depend on numerous factors including adult tree survival, the coincidental timing of fire and mast years of seed production, and post-fire weather conditions (Little et al., 1994; North et al., 2005; Peters et al., 2005).

Reproductive failures may be our earliest signal of changing forest conditions (van Mantgem et al., 2004). Compared to

overstory trees, seedlings lack extensive storage reserves, have less extensive canopies and root systems, and are therefore likely to be a sensitive, if variable, indicator of environmental changes. Climatic responses may be obscured by the individualistic response of species, the likelihood that some reproductive responses are relatively insensitive to climate (e.g., seed production), and short-term weather patterns that may not reflect overall climate. Extracting the response signal of forest reproduction from this variation will only be possible with long-term monitoring data. Our capacity to understand and predict forest responses to climatic shifts will therefore depend in part on maintaining and expanding these monitoring networks.

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