Immaturity risk in a fire-dependent pine

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Abstract

Fire-dependent obligate-seeding species face two potential threats, a senescence risk associated with infrequent fires and an immaturity risk associated with high fire frequency. An opportunity to examine the latter risk arose in 1994, when a wildfire in central California, USA, burned extensive stands of 8 year old *Pinus attenuata*, a non-sprouting serotinous pine. This study examined the characteristics of the parent population (1986-cohort) at the time of fire and the resulting seedling recruitment (1995-cohort). The parent population averaged about 2000 trees per ha and density was negatively related to both slope inclination and calculated solar insolation. Growth and cone production was negatively related to tree density. The majority of trees initiated cones at the age of 2 and matured their first cone crop at 4 years. Many trees produced more than a single whorl of cones per year, calling into question the common practice of aging serotinous pines by counting whorls of cones. Estimated postfire seed rain varied from 40 - 200 seeds m^{-2}, but postfire seedling recruitment was not significantly higher than prefire tree density at three of the five sites. Seedling recruitment was very patchy and within the knobcone pine stands, 20% of the landscape lacked seedling recruitment. At all sites, seedling recruitment averaged less than 1 per m^2. Based on survivorship patterns published for a similar serotinous pine from the Mediterranean Basin, there is reason to believe this current cohort of *P. attenuata* will not restock at the same density as the parent population.

Introduction

Pinus attenuata, or knobcone pine, is a medium-size tree restricted to the mediterranean-climate region from southern Oregon to Baja California, USA (Griffin & Critchfield, 1972). It is distributed in widely disjunct patches of more or less pure knobcone forest, ranging in size from less than 1 to more than 100 ha. It often occurs juxtaposed with the highly flammable chaparral vegetation and thus fires spread readily into knobcone forests. Trees are densely spaced and do not self-prune, making them susceptible to stand-replacing fires that kill all aboveground biomass (Keeley & Zedler, 1998). Knobcones not only are resilient to fires, they are fire-dependent, because cones retain seeds until heat triggers cone opening and dispersal of seeds within days following wildfires. In the absence of fire, few cones open and seldom do seedlings successfully establish (Vogl et al., 1977).

Fire dependent species such as knobcone pine face two risks in their lifecycle (Lamont et al.,

1991); fire-free periods that exceed the longevity of the seed bank and fire-free periods that are too short to accumulate a seed bank – termed 'senescence risk' and 'immaturity risk', respectively (Zedler, 1995). The latter risk would seem to be small because although *Pinus attenuata* is not long-lived (75-100 years), only a very small portion of the mediterranean-climate wildlands are free of fire for this length of time (Keeley et al., In prep.).

In contrast, immaturity risk is potentially a greater threat because, unlike the higher montane environments, where fire-suppression has greatly reduced burning frequency (Swetnam, 1993), anthropogenic disruption of natural fire regimes has likely increased frequency of burning at lower elevations (Keeley, 1995). Previous studies have demonstrated the ability of frequent fires to cause localized extinction of obligate-seeding chaparral shrubs (Zedler et al., 1983, Keeley, 1999) and other obligate-seeding serotinous pines (Tsitsoni, 1997).

An opportunity for examining the potential effect of 'immaturity risk' was provided by a wild-

Fig. 1. Charred skeletons of 8 year old knobcone pine trees after the 'Hwy. 41 Fire' in San Luis Obispo County, California, USA.

fire in August 1994, which burned many hectares of knobcone forest in central California. USA. This forest was relatively immature at the time, as much of it had burned nine years earlier (J. Keeley, personal observations). The purpose of this study was to investigate the pattern of recovery of this eight year old knobcone forest following the recent fire and, using skeletons of burned trees (Fig. 1), compare pre- and postfire demographic patterns. Recovery of this forest is of particular concern to

resource managers because it is one of only three knobcone forests in the southern half of California.

Study Sites

Sites were off a dirt road east of Hwy 101 at Cuesta Pass, on the north and west face of Mt. Lowe, near the summit between 725 and 775 m. This is within the Black Butte Research Natural Area, above the town of San Luis Obispo, in San Luis Obispo County, California. Over a considerable area ($\sim10^2$ ha), *Pinus attenuata* is distributed in patches and forms a mosaic with chaparral and oak woodland. Here it is restricted to white weathering siliceous marine shale. It is interesting that throughout its range this pine is restricted to serpentine soils (Vogl et al., 1977). Yet vast expanses of serpentine are nearby, west of Cuesta Pass, where this pine has been displaced by the serotinous *Cupressus sargentii* (Ne'eman et al., submitted).

This knobcone forest burned most recently in the August 1994 'Highway 41' fire. The forest was relatively immature, comprising eight year old trees that were initiated following the 1985 'Las Palitas Fire' (J. Keeley, personal observations). Prior to that, the last recorded fire was in 1922 (M. Borchert, personal communication, based on US Forest Service fire history maps). Consistent with this assessment is the fact that the average diameter (Results Section) of the trees presumably arising after the 1922 fire (and burned in the 1985 fire and reburned in the 1994 fire) had diameters comparable to the 343 mm diameter Vogl (1973) reported for a 63 year old knobcone pine from southern California.

Five sites were located north and west of the F.A.A. Relay Station, each comprising an island of knobcone pine, separated by chaparral. Selection criteria were based on accessibility and biased towards including the apparent range of different prefire densities. Slope inclination and aspect were measured at each site, and total annual solar insolation was calculated from slope aspect, inclination and latitude (Frank & Lee 1966).

Sampling design

Sites were sampled in January 1996. At this time knobcone seedlings were approximately 6-9 months old and the 8 year old charred skeletons of the parent population were still standing (Fig. 1). In addition, stumps from the pre- 1985 population were still evident (it is unknown what portion of that cohort may have been destroyed after two fires). Since knobcone populations are even-aged from immediate postfire recruitment, these seedlings and skeletons are referred to as the 1923-cohort, 1986-cohort, and the 1995-cohort.

At each site a sample area of 20 x 50 m (0.1 ha) was permanently marked in the center, at each end of the long axes, with a steel reebar. The site was sub-divided into 10-100m² plots, in which all pine stumps of the 1923-cohort were counted and basal diameter measured. Also in these plots the number of pine skeletons from the 1986-cohort were counted and a subsample of five individuals nearest the upper interior corner were measured for basal diameter and height, and number of cones counted. Nested in the upper interior corner of each plot was a 5 x 5m subplot in which seedlings of the 1995-cohort were counted and five individuals nearest the upper interior corner were measured for height and basal diameter. In each plot a visual estimate of the total postfire cover (annuals dead at the time were also included) was made and the dominant species recorded (nomenclature according to Hickman, 1993).

Patterns of cone and seed production were analyzed for living trees of the 1986-cohort that grew in adjacent unburned stands. A sample of 17 trees were haphazardly selected and cut at ground-level (2 of the 17 trees lacked cones and were left standing). Cones were attached in whorls at widely spaced nodes along the main trunk. For each whorl, the number of cones were counted and a section of stem removed, polished and rings counted to determine age of cone initiation, which would be 2 years prior to seed maturation. Cones were dried to 105°C for 2 hours and later seeds were extracted by vigorously shaking the cones.

Using the SYSTAT 5.0 statistical package (Evanston, IL), differences in density between sites and between cohorts were tested with the non-parametric Kruskal-Wallis test. Dependence of diameter, height and seed production on site factors was determined with least squares regression.

Results

The five sites varied from steep west-facing slopes with high solar insolation to gentle mesic northeast-facing slopes (Table 1). The 1994 fire had killed all

Table 1. Knobcone pine study sites. Site aspect and inclination were measured, solar insolation was calculated and postfire cover (% of ground surface covered) was visually estimated. Pinus attenuata density of postfire seedlings (1995-cohort), prefire parent population represented by burned skeletons (1986-cohort) and remains of pre-1985-fire population (1923-cohort) (N=10).

Site	Aspect	Incline	Insolation (KC/cm2)	Postfire cover %	Density (# m^{-2}) 1923-cohort	1986-cohort	1995-cohort
1	NW	30	225	33±6	0.003±0.002	0.13±0.02	0.87±0.02
2	NE	12	235	29±6	0.007±0.003	0.12±0.03	0.56±0.04
3	NE	15	217	62±7	0.007±0.003	0.62±0.07	0.46±0.01
4	W	28	257	20±3	0.003±0.002	0.08±0.02	0.63±0.04
5	W	30	303	11±1	0.002±0,001	0.03±0.01	0.04±0.01
P=	-	-	-	0.000	0.369	0.000	0.001

aboveground biomass. Postfire cover varied significantly between sites, being highest on the north-facing slopes. Cover was contributed largely by annual species of *Lotus*, *Lupinus* and *Phacelia*. Shrub seedlings of *Dendromecon rigida* were abundant and widespread and resprouts of *Quercus wizlizenii* were important on north-facing exposures and of *Adenostoma fasciculatum* on western exposures.

Density patterns

Between sites there was no significant difference in density of the 1923- cohort but a highly significant difference for both the 1986 and 1995 cohorts (Table 1). Within all sites, there was a highly significant difference (P<0.01) in density of the three cohorts, reflecting the fact that the 1923-cohort had thinned considerably, relative to the two more recent postfire cohorts (or much of the remains of that cohort had been obliterated by two fires over the last 10 years).

Comparison of the 1986-cohort (burned parents) and the 1995-cohort (seedlings) revealed that at three sites (2,3&5) there was no significant (P>0.05) difference in density. In general, seedling density was relatively low at all sites, averaging just a single seedling per 1-2 m^2 at four of the sites and substantially lower at Site 5. This laffer site also had substantial seedling mortality (44%) relative to the other sites, which ranged from 2-8 % mortality. Total seedling recruitment at Site 5 (live + dead = 0.07 m^{-2}) was still nearly an order of magnitude less than at the other sites and the other two cohorts likewise were low, suggesting a long standing pattern at this site.

Seedling recruitment was quite patchy; Site 2 exhibited the greatest variance in seedling density,

with one plot having the highest density (4/m^2) observed in the study but over half of the 25-m^2 plots lacked seedlings. This highly clumped pattern for seedlings was observed at most sites, as illustrated by the high variance mean ratio from 6 - 67 for all but Site 5, where a ratio close to 1 indicated a random distribution. At all sites the variance/mean ratio declined from the 1995-cohort > 1986-cohort > 1923-cohort; the oldest cohort ranged from 0.8-1.0. Across all sites, 10 of the 50 subplots lacked seedlings, indicating that 20% of the area within the forest boundary lacked seedling recruitment.

Regression analysis showed that density of the 1986-cohort was negatively correlated with incline (r^2 =0.22, P<0.001 , N=50) and solar insolation (r^2 =0.32, P<0.00I). Seedling density was not significantly correlated with any site factor, although solar insolation was weakly related (P<0.08, N=50). Seedling density was also not significantly correlated with density, size or cone production of the parent population (1986-cohort). Seedling to parent ratio was significantly different between sites (P<0.01, N=48) and varied by an order of magnitude from 0.7-7.9.

Growth comparisons

Comparing diameter growth for the three cohorts indicates growth is relatively rapid early on and levels off after several decades (Fig. 2). Even plotting on a log-log scale failed to change the shape of this curve. During this first decade there was a highly significant negative relationship between local (plot) density and stem diameter (Fig. 3). Examination of the residuals showed that at high density (i.e., small diameters), the regression equation is a good predictor of diameter but as density
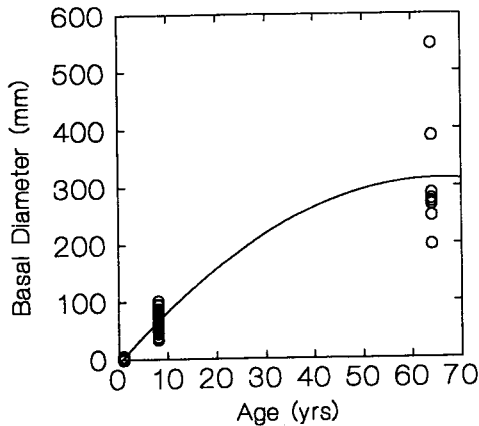
Fig. 2. Diameter growth exhibited by the 1923, 1986, and 1995-cohorts of knobcone pine in the Black Butte Research Natural Area. Curve was fitted with distance weighted least squares (DWLS).
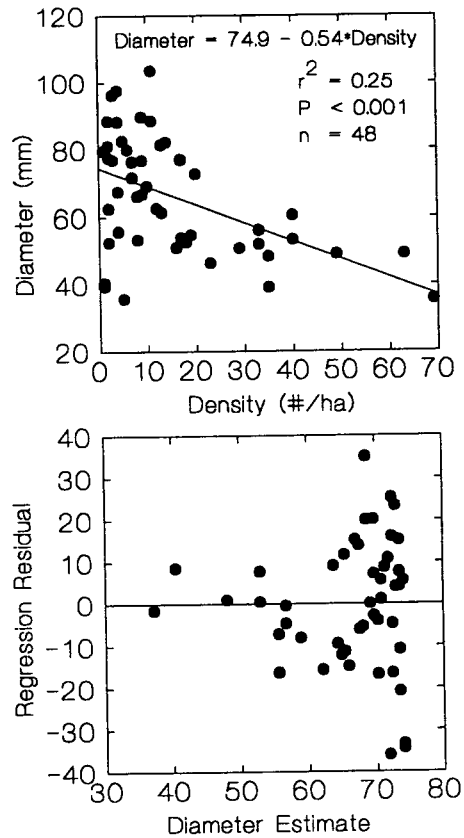

Fig. 3. Regression of basal diameter and density for the charred skeletons of the 1986-cohort.

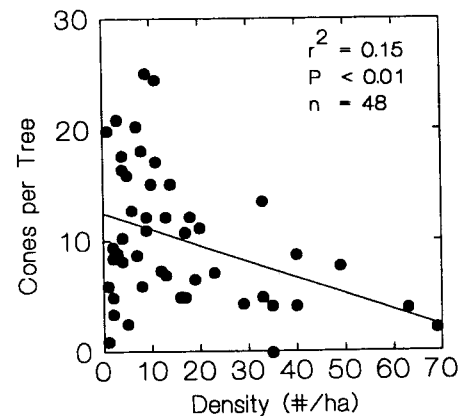
Fig. 4. Regression of cone crop size on individual trees and density for the charred skeletons of the 1986-cohort.

declines there is substantial scatter, suggesting that factors other than density are more important in determining growth.

Diameter growth of the parental (1986) -cohort was not significantly correlated with any site factor, but height was negatively correlated with both slope inclination (r^2 =0.14, P<0.01, N=48) and solar insolation (r^2 =0.37, P<0.001). Height of the seedling (1995) -cohort was also negatively correlated with insolation (r^2 =0.17, P<0.01, N=40). Height of the 1986-cohort was significantly different between sites (P<0.001), and varied from 2.3 m at Site 5 to 3.8 m at Site 2. Seedling height was also different between sites (P<0.05), ranging from 8-12 cm.

Cone production by the parent (1986) - cohod

The relationship between diameter and density in the parental cohort (Fig. 3) is important because larger diameter trees tended to produce larger cone crops, thus cone production per tree declined with increasing density (Fig. 4).

Cone production ranged from 0 - 65 cones per tree and varied significantly between sites (P< 0.01), with site averages ranging from 4.8 - 13.4 cones per tree. At the scale of 100 m², the estimated seed/seedling ratio (calculated as tree density * cones/tree * 125 seeds/cone [see below] per seedling) varied between approximately 250-1000 but was not significantly different between sites (P =0.54).

Annual pattern of cone production was analyzed on a sample of 17 living trees from the 1986-cohort. Cones occurred in whorls of 1-7 cones (x =

3.3, SE=0.2, N=67) and trees averaged 4.6 (SE=0.4, N=17) whorls. Sixty percent of the trees produced more than one whorl of cones in a single year and some trees did this repeatedly. Only 4% of the cones had opened prior to collecting. The number of seeds per cone was very different between years, but because of the tremendous variability between trees, there was no statistically significant difference between years. Averaged over all trees and years there were 125 (SE=9, N=200) seeds per cone. Over three-fourths of the trees initiated cones in their second year and matured cones in year 4. Approximately 10% of the trees failed to produce cones in any year but the remaining 90% matured a cone crop in years 5, 6, and 7 (Fig. 5).
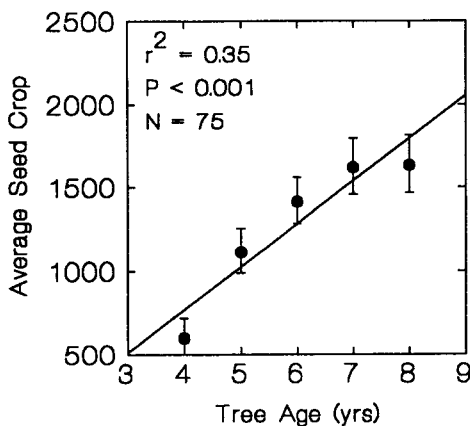

Fig. 5. Rate of seed bank accumulation in knobcone pine measured on living trees of the 1986-cohort (bars = SE).

Discussion

This study illustrates the well-known fire-adapted nature of *Pinus attenuata*. Characteristics of the 1986-cohort demonstrate that postfire growth is rapid and by the 5th year a seed bank is already accumulating for the next fire. Successful seedling recruitment in this forest burned twice in less than 10 years indicates some measure of resilience to frequent wildfire.

However, there are indications that fires at this frequency do pose an immaturity risk for this pine, since it is questionable whether or not seedling populations are of sufficient density to restock the site at the same density as the parent population. The 1986-cohort had densities that ranged from 300-6200 per ha, well within the range of 284-830 per ha

reported for knobcone stands in southern California (Vogl 1973). Following the 1994 fire, a majority of sites failed to recruit seedling populations significantly greater than the parent density. Whether or not this will result in a decline in population size is dependent upon the shape of the survivorship curve during the early stages of the population, information that is unavailable for knobcone pine.

The problem potentially facing the most recent cohort of knobcone pine is reflected in the apparent survivorship curve documented for the European counterpart of knobcone pine, *Pinus halepensis* Mill. This serotinous pine has a similar stature, habitat and lifespan as *P. attenuata*. Tree density in different postfire aged sites may reflect survivorship during the early stages of establishment (Fig. 6). Second year seedling density of *P. halepensis* (following burning of a 50 year stand) was an order of magnitude higher (Ne'eman and Izhaki, 1998) than observed in the present study for *P. attenuata*; other studies of *P. halepensis* report comparable densities to that shown in Figure 6 (Tsitsoni, 1997, but c.f. Herranz et al., 1997). If we assume a thinning curve for *P. attenuata* that is comparable to that of *P. halepensis* (Fig. 6), we would predict that when the 1995-cohort of *P. attenuata* is 8 years old, the density will be substantively lower than the previous generation.

In support of this is the rapid thinning that subsequent sampling at this site has demonstrated. Dr Scoff Stephens (California Polytechnic University, San Luis Obispo, personal communication) resampled these plots in the third postfire year and recorded sapling densities at all but one site that were at or below the density of the parent cohort.

This interpretation, however is dependent upon the source of mortality during the establishment of these pines. If the sharp drop in survivorship observed for *P. halepensis* (Fig. 6) is due to density-dependent effects, then the sparsely distributed *P. attenuata* population is not likely to experience the same degree of stand thinning. On the other hand if the survivorship curve (Fig. 6) is driven by density-independent effects, such as drought stress, predation, interspecific competition, then a steep drop in density would be expected in sparse as well as dense populations.

Studies of *P. halepensis* have shown both density-dependent and density independent mortality (Schiller, 1978; Ne'eman & Izhak, in press), and the same would appear to be the case for *P. attenuata*. Density-dependent effects on growth are certainly
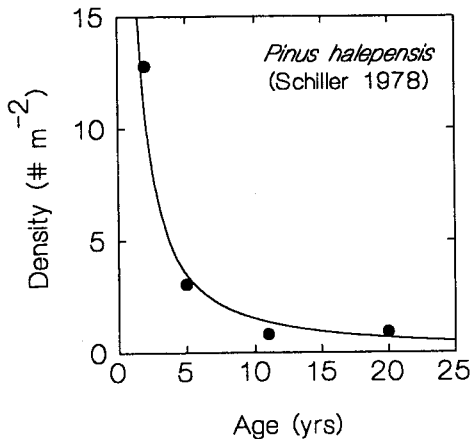
Fig. 6. Pinus halepensis density in 2, 5, 1 1 and 20 year stands in Israel (bars = SE) fitted with a power function (from Schiller 1978).

evident (Figs. 2 and 3), but the negative relationship between density of the 1986-cohort and solar insolation suggests mortality is controlled by abiotic factors. Consistent with this latter interpretation is the very high seedling mortality observed on Site 5, which had the highest insolation. Thus, there is reason to believe that at those sites where seedling recruitment is equal to or less than the density of the parent trees, further attrition will follow resulting in lower density populations than present prior to the last fire. This study supports the contention that there is some risk to the burning of immature knobcone stands.

Acknowledgments

We thank Dr. Mark Borchert who provided much specific information on the knobcone forest under study and contributed valuable comments on an earlier version of the manuscript.

References

Frank, E.C. & Lee, R. 1966. Potential solar beam irradiation on slopes. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Research Report RM-18. 57 p.

Griffin, J.R. & Critchfield, W.B. 1972. The distribution of forest trees in California. USDA Forest Service, Research Paper PSW-82.

Herranz, J.M., Martínez-Sánchez, J.J., Marín, A. & Ferrandis, P. 1997. Postfire regeneration of *Pinus halepensis* Miller in a semi-arid area in Albacete Province (southeastern Spain). Ecoscience 4:86-90.

Hickman, J.C. (ed). 1993. The Jepson manual. Higher plants of California. University of California Press, Los Angeles, CA. USA

Keeley, J.E. 1995. Future of California floristics and systematics: wildfire threats to the California flora. Madrono 42:175-179.

Keeley, J.E.1999. Chaparral. pp. 201-251. In: Barbour, M.G. & Billings, W.D. (eds), North American terrestrial vegetation. Second edition. Cambridge University Press, Cambridge, U.K.

Keeley, J.E., Fotheringham, C.J., & Morais, M. In preparation. Impact of past, present, and future fire regimes on North American mediterranean-climate shrublands. In: Swetnam, T.W., Montenegro, G., & Veblen, T.T. (eds), Fire and climate change in the Americas.

Keeley, J.E. & Zedler, P.H. 1998. Evolution of life histories in *Pinus*. pp. 219-251. In: Richardson, D. (ed), Ecology and biogeography of pines. Cambridge University Press, Cambridge, U.K.

Lamont, B.B., Le Maitre, D.C., Cowling, R.M. & Enright, N.J. 1991. Canopy seed storage in woody plants. Botanical Review 57:277-317.

Ne'eman, G., Fotheringham, C.J. & Keeley, J.E. (submitted). Patch to landscape patterns of post-fire recruitment in a serotinous conifer. Journal of Vegetation Science.

Schiller, G. 1978. Factors involved in natural regeneration of Aleppo pine. Ph.D. dissertation, Tel Aviv University, Tel Aviv, Israel.

Swetnam, T.W. 1993. Fire history and climate change in giant sequoia groves. Science 262:885-889.

Tsitsoni, T. 1997. Conditions determining natural regeneration after wildfires in the *Pinus halepensis* (Miller, 1768) forests ·of Kassandra Peninsula (North Greece). Forest Ecology and Management 92:199-208.

Vogl, R.J. 1973. Ecology of knobcone pine in the Santa Ana Mountains, California. Ecological Monographs 43:125-143.

Vogl, R.J., Armstrong, W.P., White, K.L. & Cole, K.L. 1977. The closed-cone pines and cypress, pp. 295-358. In: Barbour, M.G. & Major, J. (eds), Terrestrial vegetation of California. John Wiley & Sons, New York.

Zedler, P.H. 1995. Fire frequency in southern California shrublands: biological effects and management options. pp. 101-1 12. In: Keeley, J.E. & Scott, T. (eds), Brushfires in California Wildlands: Ecology and Resource Management. International Association of Wildland Fire, Fairfield, WA.

Zedler, P.H., Gautier, C.R. & McMaster, G.S. 1983. Vegetation change in response to extreme events: the effect of a short interval between fires in California chaparral and coastal scrub. Ecology 64:809-818.