Spatial variability in stand structure and density-dependent mortality in newly established post-fire stands of a California closed-cone pine forest

Brian J. Harvey *, Barbara A. Holzman, Jerry D. Davis

Department of Geography and Human Environmental Studies, San Francisco State University, San Francisco, CA 94132, USA

A B S T R A C T

Fire is an important process in California closed-cone pine forests; however spatial variability in post-fire stand dynamics of these forests is poorly understood. The 1995 Vision Fire in Point Reyes National Seashore burned over 5000 ha, initiating vigorous *Pinus muricata* (bishop pine) regeneration in areas that were forested prior to the fire but also serving as a catalyst for forest expansion into other locales. We examined the post-fire stand structure of *P. muricata* forest 14 years after fire in newly established stands where the forest has expanded across the burn landscape to determine the important factors driving variability in density, basal area, tree size, and mortality. Additionally, we estimated the self-thinning line at this point in stand development and compared the size–density relationship in this forest to the theorized (-1.605) log–log slope of Reineke's Rule, which relates maximum stand density to average tree size. Following the fire, post-fire *P. muricata* density in the expanded forest ranged from 500 to 8900 live stems ha^{-1} (median density = 1800 ha^{-1}). Post-fire tree density and basal area declined with increasing distance to individual pre-fire trees, but showed little variation with other environmental covariates. Self-thinning (density-dependent mortality) was observed in nearly all stands with post-fire density >1800 stems ha^{-1}, and post-fire *P. muricata* stands conformed to the size–density relationship predicted by Reineke's Rule. This study demonstrates broad spatial variability in forest development following stand-replacing fires in California closed-cone pine forests, and highlights the importance of isolated pre-fire trees as drivers of stand establishment and development in serotinous conifers.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

Ecological studies following severe disturbances such as stand-replacing fires have historically focused on temporal dynamics of stand development (Oliver, 1980). However, growing emphasis is being placed on how post-disturbance spatial heterogeneity changes through time as successional patterns and ecosystem function can vary greatly across landscapes (Turner et al., 1997, 2004; Franklin et al., 2002). For example, post-fire tree establishment and stand density can be spatially variable in serotinous conifers (Kashian et al., 2004, 2005; Pausas et al., 2004), which can drive variability in primary productivity (Turner et al., 2004), carbon storage (Kashian et al., 2006), and soil chemistry (Zinke, 1962). Development of new stands where pines expand into previously unforested areas following disturbance can have lasting impacts to an ecosystem (Johnstone and Chapin, 2003), and understanding modes of forest expansion is ecologically important (Harper, 1977; Nathan et al., 2002).

The California closed-cone pine species are adapted to high-severity, stand-replacing fires (Stuart and Stephens, 2006), yet little is known about their post-fire stand dynamics (Borchert et al., 2003; Barbour, 2007). Serotinous pines are considered fire obligate seeders because they hold seeds tightly bound in cones sealed with resin and release seeds en masse following fire (Keeley and Zedler, 1998). Fire initiates *in situ* tree regeneration for these species and can facilitate population expansion to new areas (Keeley, 1995; Johnstone and Chapin, 2003). In this study, we examined the spatial variability in stand structure and stand development patterns in newly established post-fire stands of *Pinus muricata* D. Don (bishop pine); a serotinous coastal pine endemic to the California Floristic Province (Millar, 1986b).

Spatial variability in forest stand structure can allow for different processes, typically assigned to a single temporal stage in stand development, to occur simultaneously across a landscape (Franklin et al., 2002). One important stage in forest stand development is the stem exclusion (Oliver, 1980), or biomass accumulation/competitive exclusion stage (Franklin et al., 2002) when self-thinning occurs (Peet and Christensen, 1987). As the average size of living trees and stand-level tree biomass increase, density (number of living individual trees per area) decreases because available resources can support fewer larger trees (Peet and Christensen,

* Corresponding author. Present address: Ecosystem and Landscape Ecology Lab, Department of Zoology, Birge Hall, University of Wisconsin, Madison, WI 53706, USA. Tel.: +1 650 521 1988.
E-mail address: bjharvey@wisc.edu (B.J. Harvey).

1987). Self-thinning can be spatially variable – beginning almost immediately following fire in patches of dense regeneration or much later (or potentially not at all) in areas of low density (Peet and Christensen, 1987; Kenkel et al., 1997; Franklin et al., 2002) or poor site conditions when stagnation can delay thinning even in dense stands (Oliver and Larson, 1996).

Much research has been devoted to quantitative size–density relationships in attempts to develop ecological laws regarding self-thinning (Reineke, 1933; Yoda et al., 1963). The −3/2 power law of self-thinning (Yoda et al., 1963) compares the biomass of plants to density (number of plants per unit area) in even-aged single-species stands with complete crown closure. Analogously, Reineke's Rule (*sensu* Pretzsch and Biber, 2005) instead utilizes the quadratic mean diameter (QMD) at breast height as the measure of tree size, and states:

$$\ln(\text{trees hectare}^{-1}) = -1.605 * \ln(\text{QMD}) + \ln(k)$$

where k is a constant that varies with species (Reineke, 1933). Although Reineke's Rule does not account for the third dimension in volume (height) that was initially used to establish ecological laws such as the −3/2 power law of self-thinning (Turnblom and Burk, 2000), mean diameter is closely correlated with crown width and can be a better measure of response to changes in stand density than average tree biomass (Zeide, 1987). Debate exists regarding the constancy of Reineke's (1933) self thinning slope of −1.605, as well as the slope in the −3/2 power law of self-thinning (Weller, 1987, 1991; Lonsdale, 1990). Nonetheless, quantitative size–density relationships are useful both for direct applications in forest management, as well as theoretical inquiries of natural selection in plants through self-thinning (Zeide, 2010).

The 1995 Vision Fire burned over 5000 ha in Point Reyes National Seashore (PRNS) (Folger, 1998; Pribor, 2002) including 423 ha of mature *P. muricata* stands that had not burned since 1927 (Sugnet, 1981). Nearly all trees within the fire perimeter were killed. However, by triggering the release of seeds from serotinous cones, the fire initiated dense regeneration of *P. muricata* in previously forested areas (Folger, 1998) and catalyzed forest expansion. The area forested by *P. muricata* increased by 360 ha (85%) following the fire, most notably down slope from Inverness Ridge and into pre-fire coastal scrub, grassland, and *Pseudotsuga menziesii*/mixed-evergreen forest communities (Forrestel et al., 2011) (Fig. 1).

The overall goal of this study was to examine, 14 years after fire, stand development of a California closed-cone pine species where the forest footprint expanded as a result of the Vision Fire. Specifically, we address three primary research questions: (1) How variable is the stand structure (density, tree size, and basal area, density-dependent mortality) in the post-fire cohort and what biotic (e.g. seed source) and abiotic (e.g. topography) factors best explain this variability? (2) What is the density where self-thinning initiates in newly established stands 14 years after fire in this forest? (3) Does the self-thinning relationship between density and average tree size for *P. muricata* conform to the log–log regression slope of −1.605 predicted by Reineke (1933)? We expected to find high spatial variability in stand structure, represented by high among-stand coefficients of variation (CV) for density, tree size, basal area, and mortality. We expected density and basal area to be negatively correlated with distance from pre-fire stands. Density was expected to be negatively correlated with mean tree size and positively correlated with mortality caused by density-dependent thinning. No *a priori* hypothesis was conjectured for the threshold density of self-thinning in newly established stands or our test of the conformity of *P. muricata* to the Reineke's (1933) Rule.

2. Methods

2.1. Study area

Point Reyes National Seashore is a 28,761 ha unit of the US National Park Service (NPS) located along the Pacific Coast of California (USA) approximately 40 km northwest of San Francisco (Fig. 1) (National Park Service, 2006). The climate is Mediterranean, with cool rainy winters and warm dry summers; although heavy summer fog mitigates the impact of dry summers. Temperature (measured at the Bear Valley Visitor Center) ranges from a mean of 8.4 °C in January to 14.5 °C in September, and mean annual precipitation is 91 cm (National Park Service, 2010). Elevation in the study area ranges from 25 to 380 m above mean sea level. Forest stands are characterized by pure *P. muricata* canopies. Understory composition ranges from sparse vegetative cover where *P. muricata* density is high to a mixture of *Rhamnus californica*, *Rubus ursinus*, *Baccharis pilularis*, *Toxicodendron diversilobum*, and several graminoids in more open stands. *Pinus muricata* trees in the study area
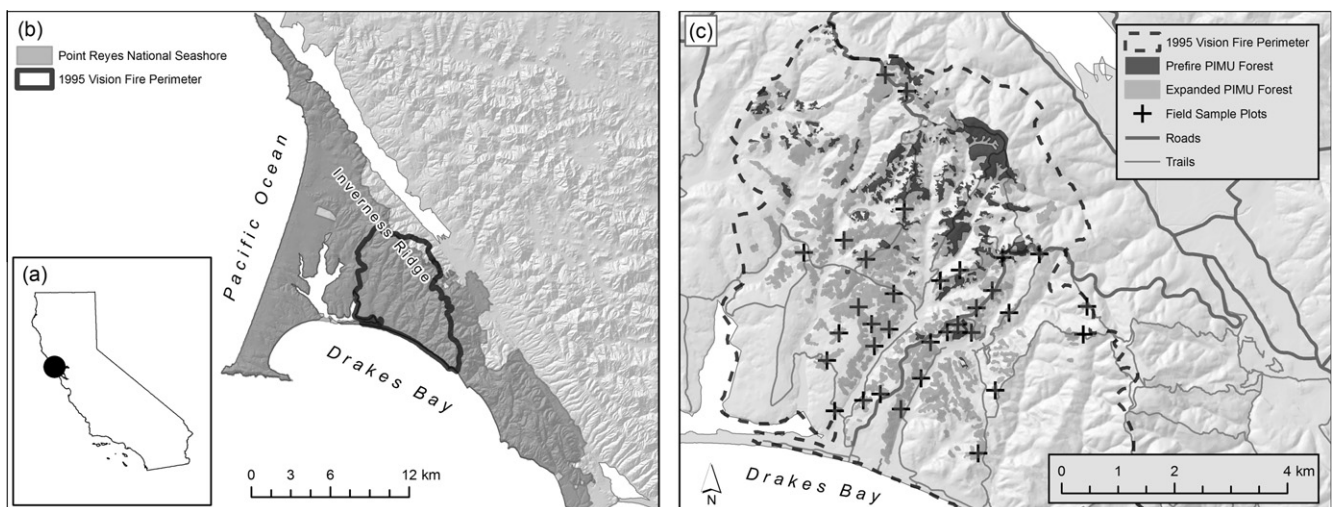

Fig. 1. (a) Point Reyes National Seashore, located along the Pacific Coast in Northern California. (b) The park extent is shaded and the perimeter of the 5000 ha Vision Fire is outlined. (c) Map of the *P. muricata* forested area within the perimeter of the Vision fire. Pre-fire (1994) stands are shown in black, while expanded forest, post-fire (2007) stands are shaded gray. Plot locations are shown within the expanded forest stands (+).

established after the 1995 Vision Fire and comprise a single cohort of trees ⩽14-years-old at the time of this study. Because other studies have examined *in situ* post-fire regeneration of *P. muricata* stands (Holzman and Folger, 2005; Harvey, 2010) and due to the significant expansion of *P. muricata* following the Vision Fire (Forrestel et al., 2011), we focused on stands that were non-forest prior to the fire (Fig. 1).

2.2. Forest stand selection

Sample plots were randomly located within mapped *P. muricata* forest patches identified on a map of post-fire vegetation digitized from 1-m resolution natural color aerial digital-orthophoto-quarter-quadrangles (DOQQs) taken in March 2004 (Forrestel et al., 2011). Stands were defined by a minimum of 5 trees per 100 m^2 (0.01 ha) and were not forested by *P. muricata* prior to the 1995 Vision fire. Plot locations were determined using the Random Point Generation function in the Hawth's Analysis Tools (Beyer, 2004) extension for ArcGIS with a minimum distance of 300 m enforced between points to minimize spatial autocorrelation among samples. To minimize effects of edges and vegetation management near thoroughfares, all plots were located a minimum of 15 m from the nearest road or trail.

2.3. Field data collection

Stand structure data were collected in 0.01-ha (10 × 10 m) plots between November 2009 and January 2010 (n = 33). Plot center-point coordinates were located in the field using a hand-held Trimble Juno GPS unit. In each plot, all live and dead trees that had established post-fire, were at least 1.4 m in height, and rooted within the plot boundary were measured for diameter at breast height (1.4 m; dbh) to the nearest 0.5 cm. No live trees below 1.4 m in height or surviving pre-fire trees were observed, as the stand-replacing fire regime of *P. muricata* produces narrow pulses of post-fire recruitment. The presence or absence of any solitary burned *P. muricata* snag, fallen logs, or cones was recorded. Stands were single-species, single-cohort stands, with very little or no observed spatial clumping of seedlings that can typically occur after *in situ* regeneration in previously forested areas of serotinous species (Kenkel, 1988). Therefore, stand structure was characterized by the number of live and dead trees, tree density, average tree size (dbh of live and dead post-fire trees), and basal area recorded and all summed to the whole plot. Slope (degrees), aspect (compass azimuth), elevation (in meters above mean sea level), and topographic curvature (either convex, concave, flat, or undulating in the planform and profile directions), and GPS coordinates were also recorded for each plot.

2.4. Additional GIS data collection

A 1994 NPS GIS vegetation map (Shirokauer, 2004) depicting plant community polygons was used to determine the size and location of pre-fire *P. muricata* stands within the Vision Fire perimeter and the pre-fire vegetation community in current post-fire expanded *P. muricata* stands. A United States Geological Survey National Elevation Dataset digital elevation model (DEM) was obtained for the study site at 1/3 arc second (10 m) resolution. Soils data were extracted from the Soil Survey Geographic (SSURGO) database (United States Department of Agriculture – Natural Resources Conservation Service, 2000), geologic parent material data were extracted from a NPS geologic resources map (National Park Service Geologic Resource Evaluation Program, 2008), and fire severity data were from the Burn Area

Emergency Rehabilitation Plan map (United States Department and of the Interior, 1995).

Using the 1994 NPS GIS vegetation map, Euclidean distance and direction from each sample plot to pre-fire *P. muricata* stands were calculated. Because pre-fire stands were delineated using a minimum polygon threshold of 0.1 ha for canopy cover, occasional evidence of solitary pre-fire trees situated outside of continuous stands was found within plots. To record the location of solitary pre-fire *P. muricata* trees outside of continuous stands, individual trees surrounding each plot were digitized into a GIS from 1-m resolution 1993 DOQQ black and white aerial photos. Euclidean distance and direction from solitary pre-fire trees to each plot were calculated in the GIS. Isolated *P. muricata* trees identified in the photos were verified in the field by the presence of a standing snag, fallen logs, or other evidence of burned *P. muricata* branches and/or cones.

The GIS layers were used to compute values for several additional potential explanatory variables. The DEM was utilized to generate the following elevation-derived raster layers: elevation, slope, Beers' transformed aspect (Beers et al., 1966), topographic curvature, topographic position (fine, moderate, coarse), and annual incident solar radiation.

2.5. Data analysis

To assess variability in stand structure among stands, descriptive statistics and distribution histograms were calculated for field measures of *P. muricata* density, mortality, average tree size, and basal area for each plot. To quantitate the within-stand variability in tree size, we calculated the CV for the dbh of all live trees in each stand. Independent-groups *t*-tests were used to compare mean stand structure values between stands with any evidence of solitary pre-fire *P. muricata* trees to those without.

Stepwise linear regression was used to examine relationships between *P. muricata* stand structure (density, mortality, average tree size, and basal area) and potential explanatory biotic and abiotic variables (Table 1). Candidate variables (above critical$_{0.05}$ Spearman rank correlation with the response variable) were added into the model using forward stepwise regression. The Bayesian information criterion was used to conservatively select the best model with the fewest explanatory terms and variables with $P > 0.05$ were removed before the final model was selected. After removing stands from the analysis where no density-dependent thinning (characterized by dead *P. muricata* trees that established post-fire with no evidence of mechanical wounds, disease, insect infestation, or other tree death obviously not related to competition) was observed, ordinary least squares regression was used to

Table 1
Candidate predictor variables used in regression models for stand structure and for stand characterization.

Variable (units)	Units	Type
Elevation	m – msl	Continuous
Slope	Degrees	Continuous
Aspect (Beers' transformed)	Degrees	Continuous
Topographic curvature	1/100 – z units	Continuous
Topographic position index	n/a (index)	Continuous
Annual incident solar radiation	MWH m^{-2}	Continuous
Distance to prefire stand	m	Continuous
Distance to prefire tree	m	Continuous
Direction to prefire stand	Degrees	Continuous
Direction to prefire tree	Degrees	Continuous
Prefire vegetation cover	Community	Categorical
Soil type	Various	Categorical
Geologic parent material	Various	Categorical
Fire severity	Low, moderate, high	Categorical
Evidence of burned *P. muricata* tree	Yes/no	Binary

test Reineke's (1933) log–log model and a *t*-test was used to compare the size–density slope found in this study to Reineke's size–density slope of −1.605.

All variables used in parametric tests or regression models were transformed as necessary to satisfy normality assumptions. Live tree density, total tree density (live and dead trees), and basal area (m^2 ha^{-1}) were log_{10} transformed. Percent mortality did not meet assumptions for normality, so non-parametric correlations were performed to assess relationships between mortality and explanatory factors. After excluding plots where no mortality was observed, percent mortality was log_{10} transformed to achieve normality. Live tree density and QMD were natural-log-transformed to test Reineke's (1933) log–log relationship. Within-stand mean dbh, QMD, and CV of dbh values for all stands did not require transformations to meet normality assumptions.

Regression models were assessed for heterogeneity of residuals, normality of errors, multicolinearity among explanatory variables, and overly influential data points (Cook's Distance value >0.5). All *t*-tests were performed conservatively using the Welch's *t*-test assuming unequal variances. Sample plots were tested for spatial autocorrelation using the number of live stems $plot^{-1}$ and were not significantly correlated ($P > 0.10$, Moran's $I = 0.13$). Statistical analyses were performed using R (R Development Core Team, 2009).

3. Results

3.1. Spatial variability in stand structure in newly established stands

Stand structure in areas where *P. muricata* expanded following the Vision fire varied widely. Density of live *P. muricata* trees ranged from 500 to 8900 trees ha^{-1} (Table 2). Because sampling was restricted to stands containing a minimum of 5 trees 100 m^{-2}, the actual minimum and mean number of trees ha^{-1} in mapped *P. muricata* forest is lower than that recorded in our data. The density of dead *P. muricata* trees (established post-fire) among the 33 stands ranged from 0 to 15,900 trees ha^{-1}. When live and dead trees were pooled together in each plot (a measure of total trees that established post-fire), the number of trees ranged from 500 to 23,400 total trees ha^{-1}. All three measures of tree density were characterized by extreme positively skewed distributions (Table 2; Fig. 2), indicating that lower densities are more common than higher densities among the expanded *P. muricata* forest stands. Median tree density was 2100 total trees ha^{-1} and 1800 live trees ha^{-1}. The CV of among-stand tree density ranged from 84% for live trees to 228% for dead trees, further indicating a great deal of variability in density in this forested landscape.

The density of live trees was best explained by distance to the nearest pre-fire *P. muricata* tree and annual incident solar radiation (adj. $r^2 = 0.59$, $p < 0.001$), as was total tree density (live and dead) (adj. $r^2 = 0.63$, $p < 0.001$) (Table 3). Using distance to nearest pre-fire tree as the lone predictor variable, both live ($r^2 = 0.50$, $p < 0.001$) and total ($r^2 = 0.57$, $p < 0.001$) tree density fit a negative log–log relationship resembling a dispersal kernel function with slopes of −0.37 and −0.51, respectively (Fig. 3). *Pinus muricata* density in plots that contained evidence of a solitary burned *P. muricata* tree ($n = 6$) was significantly higher than plots containing no

Table 2
Tree density in the expanded forest of newly established *P. muricata* stands following the 1995 Vision Fire.

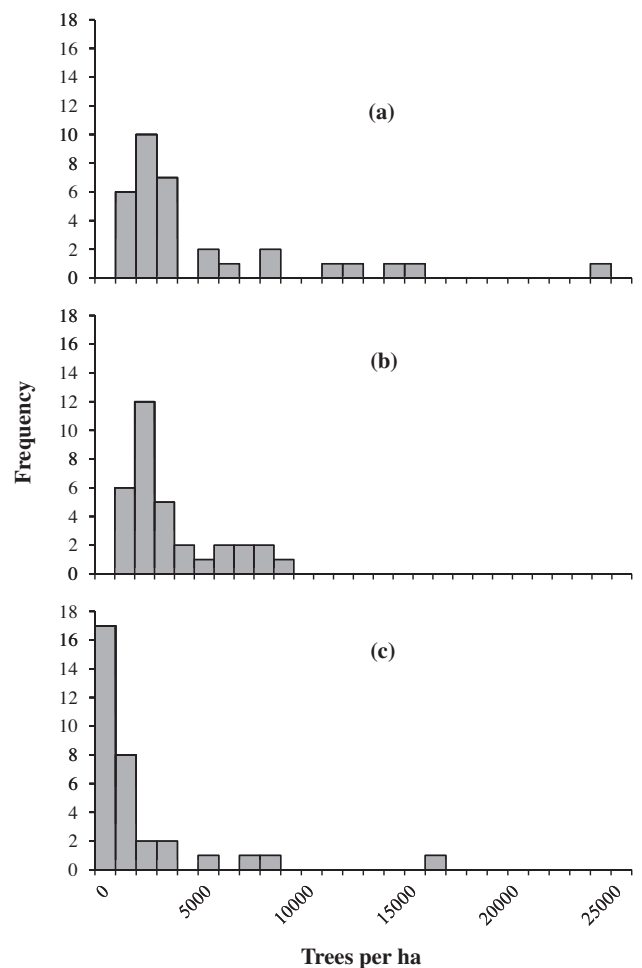|	Trees (ha^{-1})				Skew	CV (%)
	Mean	Min	Max	Range		
Live	2779	500	8900	8400	+1.16	84
Dead	1403	0	15,900	15,900	+3.12	228
Total	4182	500	23,400	22,900	+2.03	124

Fig. 2. (a) Histogram of sample stands illustrating *P. muricata* density (trees ha^{-1}) for total trees (live and dead), (b) live trees only, and (c) dead trees only.

evidence of a burned *P. muricata* tree ($n = 27$) (Fig. 4a). This difference was significant for both live trees ($t = 7.19$, $p < 0.001$) and total trees (live and dead) ($t = 3.51$, $p < 0.01$).

Basal area in *P. muricata* stands newly established following the fire ranged from 8.92 to 65.27 m^2 ha^{-1}, with a mean value of 31.26 m^2 ha^{-1} and a CV of 43%. Basal area was positively associated with live tree density and elevation, and negatively associated with slope (adj. $r^2 = 0.70$, $p \leqslant 0.001$) (Table 3).

Within-stand mean dbh ranged from 6.3 to 19.1 cm (average = 12.9 cm) among all plots. Mean dbh was negatively associated with live tree density and slope, but positively associated with elevation (adj. $r^2 = 0.81$, $p \leqslant 0.001$) (Table 3). The average tree dbh in plots with evidence of a burned *P. muricata* tree ($n = 6$) was significantly lower than in plots containing no evidence of a *P. muricata* tree prior to the Vision Fire ($n = 27$) (Fig. 4b). This difference was significant for both mean dbh ($t = -6.20$, $p \leqslant 0.001$) and QMD ($t = -5.94$, $p \leqslant 0.001$).

In addition to the variability in forest structure among stands, there was variability within stands. The mean within-stand CV of live tree dbh was 37% and ranged from 22% to 62%. No statistically significant relationships were apparent between the mean within-stand CV of live tree dbh and measures of *P. muricata* density.

3.2. Density-dependent mortality and the self-thinning line in newly established stands

Mortality was highly variable throughout the expanded *P. muricata* forest, consistent with the high degree of variation in

Table 3
Final regression models for *P. muricata* stand structure in newly established stands: (a) live tree density, (b) total (live and dead) tree density, (c) basal area, (d) mean dbh in all ($n = 33$) post-fire stands; and (e) percent mortality from stands where mortality was observed ($n = 16$). Adj. r^2 and F-statistic is reported for the entire model; t-statistic is reported for each predictor variable.

Variable(s)	Adj. r^2	Coefficient	F/t	p
(a) Log_{10} (live trees ha^{-1})	0.59		23.96	<0.001
Log_{10} (distance [m] from prefire tree +1)		−0.35	−5.82	<0.001
Direct solar radiation (MWH/m^2)		2.67	3.04	0.005
(b) Log_{10} (total trees ha^{-1})	0.63		28.03	<0.001
Log_{10} (distance [m] from prefire tree +1)		−0.49	−6.62	<0.001
Direct solar radiation (MWH/m^2)		2.89	2.69	0.01
(c) Log_{10} (basal area [m^2 ha^{-1}])	0.70		26.1	<0.001
Log_{10} (live trees ha^{-1})		0.36	5.94	<0.001
Sqrt (elevation [m])		0.04	2.95	0.006
Slope (degrees)		−0.01	−2.43	0.02
(d) Mean dbh (cm)	0.81		34.1	<0.001
Log_{10} (live trees ha^{-1})		−3.19	−6.71	<0.001
Sqrt (elevation [m])		0.24	3.21	0.003
Sqrt (slope [degrees])		−0.68	−2.47	0.02
(e) Log_{10} (percent mortality)	0.55[a]			<0.001
Log_{10} (total trees ha^{-1})		−7.46	−5.19	<0.001

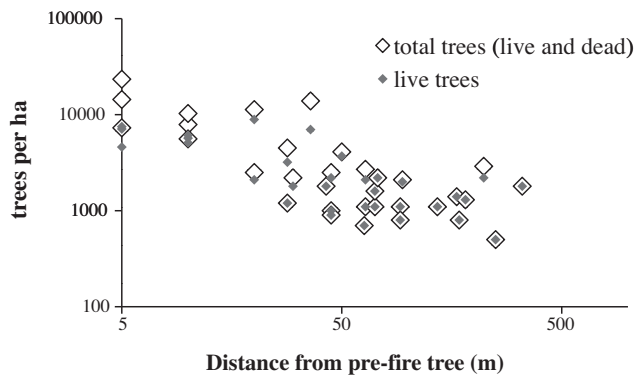[a] Model r^2 instead of adj. r^2 when only one variable included.

Fig. 3. Plot of the negative (log–log) relationship between *Pinus muricata* density (for both live and total trees) and distance from pre-fire tree for each of the ($n = 33$) plots.
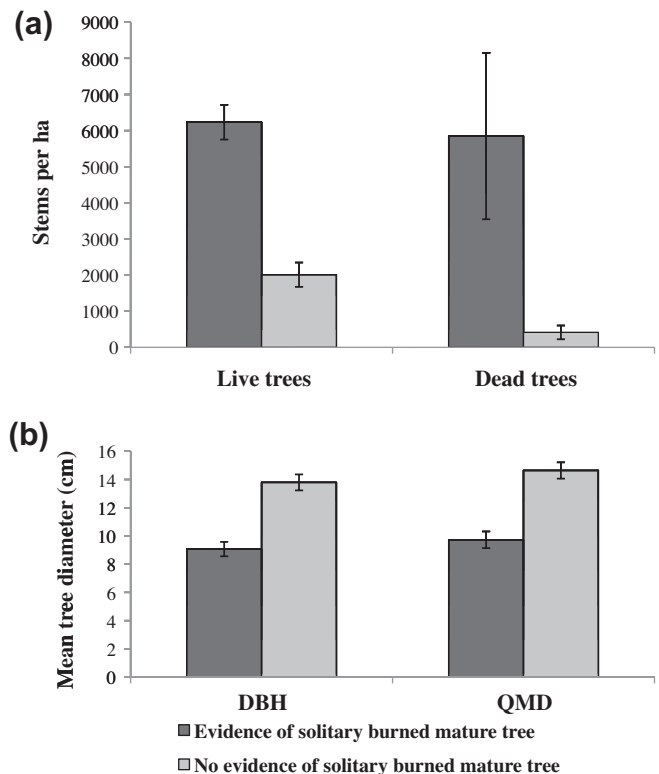

Fig. 4. (a) Density (trees ha^{-1}) and (b) mean tree size (cm diameter) in plots where there was evidence of pre-fire *P. muricata* trees, and plots where no evidence was observed. Error bars represent ±1 SE.

density among stands. Mortality ranged from 0% to 68% (CV = 139%) among stands, with a mean mortality of 13%. Seventeen of the 33 stands exhibited no mortality, and percent mortality was highly correlated with density (Spearman's *rho* (r_s) = 0.90, $P < 0.001$). No mortality was observed in any stand with a density less than 1800 total trees ha^{-1} ($n = 17$), indicating that this is the approximate density when self-thinning initiates in the expanded forest at this stage after fire (Fig. 5). Mortality was recorded in nearly all stands with a density greater than 1800 trees ha^{-1} (Fig. 5), and (log$_{10}$ transformed) percent mortality was best explained by total tree density ($r^2 = 0.55$, $p \leqslant 0.001$) (Table 3).

When all trees from all plots were pooled together, there was a significant difference between the average dbh of live trees (10.73 ± 0.18 cm, $n = 917$) and dead trees (2.63 ± 0.07 cm, $n = 463$) ($t = 8.38$, $p \leqslant 0.001$) (Fig. 6), with a greater range in live tree dbh than in dead tree dbh (Fig. 6).

3.3. Size–density relationships in self-thinning stands

When only stands exhibiting density-dependent mortality (>0% mortality) were included ($n = 16$) and fit to Reineke's (1933) log–log regression model ($r^2 = 0.75$, $p \leqslant 0.001$), the self-thinning relationship was:

$$\ln(\text{trees ha}^{-1}) = -1.743 * \ln(\text{QMD}) + 12.487$$

The slope of this self-thinning line was not significantly different from −1.605 ($t = 0.52$, $p > 0.05$) (Fig. 7).

4. Discussion

4.1. Spatial variability in stand structure in newly established stands

Contrary to our original hypothesis, the presence of and proximity to individual pre-fire trees was the most important driver
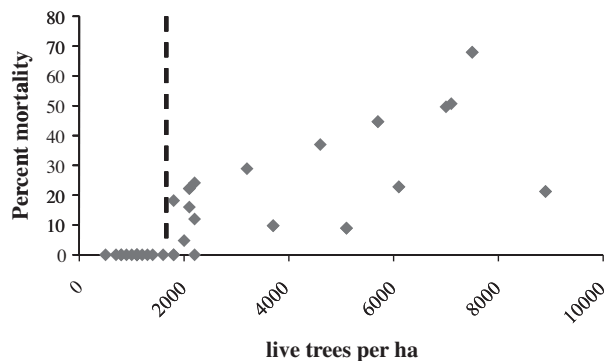
Fig. 5. Relationship between density and percent mortality, illustrating the density (1800 trees ha^{-1}) at which density-dependent mortality initiates newly established stands 14 years following fire.
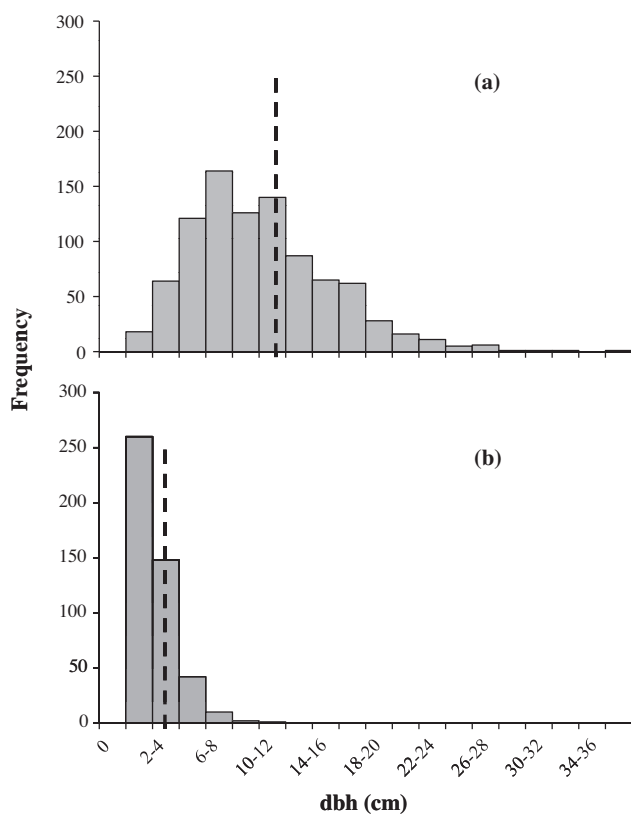

Fig. 6. Histograms of all trees when data from all plots were pooled together illustrating differences in the average *P. muricata* tree size (dbh in cm) between live trees (a) and dead trees (b). Mean dbh (cm) for live and dead trees is denoted by the dotted lines.

P. muricata trees present an important alternative mode of localized forest expansion following disturbance, and are an important driver of heterogeneity among stands. While a contiguous stand of *P. muricata* forest undoubtedly provides a greater seed source for post-fire seedling establishment than a single tree, we provide evidence that isolated trees constitute a non-trivial seed source for high-density post-fire stands to establish across a burned landscape. The shallow log–log regression slopes between distance to the nearest pre-fire tree and post-fire density (live and total trees) we found were comparable to those of seed shadows of many wind-dispersed conifers (Willson, 1993). *Pinus muricata* seeds are small, winged, and light – characteristics that should allow for long-distance wind dispersal (Greene and Johnson, 1989). Wind speeds over 65 km h^{-1} during and around the time of the Vision Fire likely played a key role in long-distance dispersal, resulting in post-fire densities of 1800 trees ha^{-1} in stands over 300 m from the nearest pre-fire tree and over 1.5 km from the nearest pre-fire stand (Fig. 3).

Whether the expansion of *P. muricata* forest into previously unforested areas following fire described in our study and Forrestel et al. (2011) is typical or atypical is difficult to answer given the paucity of fire ecology research in these forests. *Pinus muricata* and the other California closed-cone pines were widespread in continuous forests along the California coast as recent as 12,000 years ago, but changes toward a regionally hotter and drier climate in recent millennia have restricted their distribution to a narrow band of disjoint populations where maritime conditions persist (Axelrod, 1967). At PRNS, vegetation associations have been fairly consistent since the late Holocene (Anderson, 2005), while logging and fire suppression after the onset of Euro-American settlement (ca. 1850) potentially have reduced forested area (Brown et al., 1999) and prevented widespread tree regeneration or forest expansion following fire. Because the 1995 Vision Fire was the first large fire to occur in PRNS since the park was established in 1962, it remains difficult to assess if the forest expansion we characterize is typical, or an anomaly.

This study demonstrates, however, modes by which *P. muricata* is capable of significant expansion into previously unforested areas given the appropriate fire conditions. High winds originating from the east were blowing downslope and toward the west and southwest during the Vision Fire, enabling dispersal of *P. muricata* seeds onto burned areas where other pre-fire vegetation communities had existed (Forrestel et al., 2011). After being largely restricted to the granitic soils of Inverness Ridge prior to the Vision Fire, *P. muricata* now is well-established in many other amenable substrates in closer proximity to the ocean. Since *P. muricata* is adapted to maritime conditions (Axelrod, 1967), it seems plausible that dispersal and establishment (thus forest expansion) toward the coast similar to what was observed following the Vision Fire could be expected under dry, warm, and windy conditions typical of extreme fire weather in coastal California.

While evidence of continual and directional forest expansion into non-forested areas in the absence of fire has been found in other serotinous forests (Jakubos and Romme, 1993), our findings illustrate the importance of episodic fire for local population expansion in *P. muricata*. Comparatively stable *P. contorta* var. *latifolia* forest/non-forest boundaries were observed following the 1988 Yellowstone fires (W. Romme, Colorado State University, personal communication), and in *Cupressus sargentii* forests following a 1994 fire in central California (Ne'eman et al., 1999). Our results suggest the capacity of *P. muricata* for potential rapid local population expansion following fire – similar to patterns of non-equilibrium succession found in boreal *P. contorta* var. *latifolia* forests (Johnstone and Chapin, 2003). Data presented in Forrestel et al. (2011) further suggest that forest/non-forest boundaries in *P. muricata* forest are considerably unstable following fire. However, future studies examining

of stand structure variability in newly established stands, while the proximity to contiguous pre-fire stands was not significant. Our results, coupled with those found in a study examining broad-scale vegetation change following the Vision Fire, present evidence of multiple modes of forest expansion in this California closed-cone pine forest. Using mapped GIS vegetation polygons, Forrestel et al. (2011) found the binary presence or absence of post-fire *P. muricata* vegetation community polygons to be best predicted by proximity to mapped pre-fire stands, which implies that *P. muricata* can expand in gross area and at broad scales following fire via an advancing front (*sensu* Harper, 1977). The stand-level scale of our analysis and results, however, suggest that isolated

multiple fires in *P. muricata* forests under a range of conditions are needed to further evaluate the uniqueness of the forest expansion observed in the present study.

The significant differences in density between plots with evidence of burned *P. muricata* trees and those without (Fig. 4) suggest that while seed dispersal may cover long distances, most post-fire *P. muricata* seedlings establish in close proximity to burned adult trees. While these results are not surprising, patterns of post-fire regeneration in newly established stands have never before been presented for *P. muricata* and they support findings in other serotinous conifers (Ne'eman et al., 1992, 1999; Pausas et al., 2004). Post-fire seedling and juvenile density of *Pinus coulteri*, a moderately serotinous pine sometimes included in the California closed-cone pine group, also is highest near burned mature trees (Borchert et al., 2003; Franklin and Bergman, 2011) – albeit with much lower densities than we found in *P. muricata*. Other studies have shown that fire severity and soil conditions were better predictors of initial (2.5 years) post-fire seedling density (Pausas et al., 2003), but seedling survival and growth may be higher in closer proximity to burned trees (Ne'eman, 1997). Fire severity was not significantly correlated to stand structure variables for *P. muricata*, although the variability in fire severity across the study area was comparatively low as there was no above-ground survival of pre-fire vegetation in any plots. The positive association found between density and annual incident solar radiation (modeled in the GIS) is noteworthy, as the areas of highest incoming solar radiation exist on south-facing convex ridges. This pattern is consistent with post-fire regeneration in areas that were forested by *P. muricata* prior to the Vision Fire where *P. muricata* dominates convex ridges and *Ceanothus thyrsiflorus* dominates concave drainages (Harvey, 2010), as well as *P. muricata* populations further inland found on dry, rocky exposed ridges (Millar, 1986a). In summary, our results support conclusions in other studies that solitary burned mature trees represent an important seed source for regenerating and establishing forest stands in serotinous species.

Pinus muricata density declined quickly after the first several post-fire years through self-thinning after profuse *in situ* post-fire seedling establishment (Holzman and Folger, 2005; Harvey, 2010), however we illustrate high spatial variability in density at any one point in time in newly established stands where the forest has expanded. Variability in live-tree density among newly established *P. muricata* stands fourteen years after the Vision Fire (CV = 84%) was almost as great as the temporal variability in density observed over fourteen years in a study site along Inverness Ridge (CV = 106%) (author, unpublished data) that was forested by *P. muricata* prior to the fire. The frequency distribution of live and total trees (Fig. 2), coupled with smaller mean patch size in the post-fire forest than the pre-fire forest (author, unpublished data) indicates that the expanded forest landscape is characterized by a background of fairly low density *P. muricata* stands with a mosaic of high-density patches in close proximity to solitary burned trees. Our results support the high variability found in other systems dominated by serotinous conifers. For example, following the extensive Yellowstone fires of 1988, *Pinus contorta* var. *latifolia* sapling density varied by six orders of magnitude over broad scales (Kashian et al., 2004) and correlated positively with serotiny level of burned mature trees (Tinker et al., 1994).

The question remains as to whether the variation in live-tree density that we found will decrease with time as the forest potentially shifts toward a more homogenous structure through self-thinning. Following self-thinning in dense stands and infilling of sparse stands, initial heterogeneity among stands generally (with some evidence of persistent sparse stands) converged toward a more uniform structure within centuries following fire in *P. contorta* var. *latifolia* forests in Yellowstone National Park (Kashian et al., 2005). Because *P. muricata* seedling establishment is rare in

the absence of fire, little infilling of open spaces in sparse stands is expected. While initially dense stands will continue to self-thin, sparse stands that have established as a result of the 1995 Vision Fire will likely remain sparse until subsequent fire provides conditions suitable for the next post-fire cohort. Future repeat surveys are needed to quantitatively compare temporal stand dynamics in *P. muricata* forests to other longer-lived serotinous species with a longer fire-return interval.

As hypothesized, basal area varied substantially in the expanded *P. muricata* forest stands (CV = 43%), but did not decline with distance from pre-fire stands. Rather, our results revealed strong evidence of the importance of individual isolated *P. muricata* trees on basal area, as basal area was a function of density. However, the positive association between basal area and elevation supports the findings of Forrestel et al. (2011) and suggests that proximity to pre-fire stands is important over longer distances, as the majority of stands prior to the fire were at higher elevations along Inverness Ridge. These findings further support dual modes of forest expansion – an advancing front along the edge of pre-fire stands, and localized expansion around isolated individual trees.

As expected, tree stem diameter was negatively correlated with live-stem density. Ne'eman et al. (1999) found greater basal diameter in trees beneath the canopy of burned *C. sargentii* trees than in trees growing outside of the projected burned canopy. While the results in Ne'eman et al. (1999) were hypothesized to be due to high nutrient input from decaying burned mature trees, our results indicate that tree size was more strongly a function of density, thus indirectly a function of distance from mature pre-fire trees. Not surprisingly, we found average tree size to be negatively correlated with slope; indicating that, on average, larger trees are found on gentler slopes where soils can be deeper and retain more moisture. Similar results correlating mean tree diameter and actual measurements of soil depth and moisture were found in *P. halepensis* following fire (Tsitsoni and Karagiannakidou, 2000).

4.2. Density-dependent mortality and the self thinning line in newly established stands

Our data support the prediction that mortality is highly variable across the burned landscape, as indicated by the 139% CV for percent mortality among all plots. While mortality could potentially arise from factors other than competition for resources in dense forests, the strong negative correlation between percent mortality and within-plot mean dbh ($r_s = -0.68$) further indicates that observed mortality is density dependent, as smaller trees are outcompeted by larger trees and eventually die. Additionally, in order to isolate density as the cause of mortality, sample stands were located in areas not impacted by pine pitch canker disease, a non-native pathogen currently spreading through the *P. muricata* forest at PRNS (Crowley et al., 2009).

While mortality was variable, the approximate density when self-thinning occurs 14 years following fire in newly established *P. muricata* stands was remarkably consistent at 1800 trees ha^{-1} (Fig. 5). Stands exhibiting density-dependent mortality approximately conform to the expected -1.605 slope of size–density relationships proposed by Reineke (1933), while more open stands where self-thinning has not commenced had much steeper (more negative) slope on the size–density line. The further the observed slope deviates from the theoretical thinning slope, the further the stand is from self-thinning processes, which is related to initial density (Peet and Christensen, 1987). Our observations in these *P. muricata* stands highlight the impact of spatial variability in density as some stands are undergoing intense self-thinning while others are not, which can affect successional processes and species composition (Peet and Christensen, 1987).
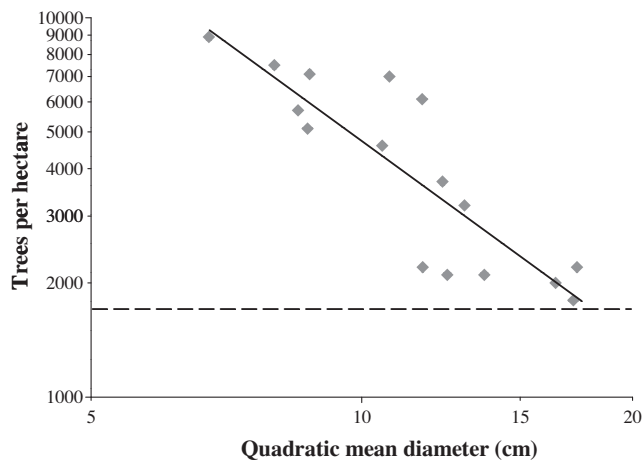
Fig. 7. Size–density, or self-thinning line using plots with observed mortality (>0% mortality) (*n* = 16). The horizontal dashed line represents the natural log of the density at which density-dependent mortality initiates in newly established stands 14 years following fire (1800 trees ha^{-1}).

4.3. Size–density relationships in self-thinning stands

We found a consistent relationship between density and average tree size with *P. muricata* when tree stem diameter was used as a proxy for biomass. Weller (1987) proposed that the −3/2 slope be treated as a variable used to measure ecological differences between and within species in different environments, as differences in site quality can significantly affect the rate of progression through stand development stages in single-species, single-cohort forests (Turnblom and Burk, 2000). Future studies could build on this and specifically test the impact of topography or soil type on the slope of the self-thinning line in newly established *P. muricata* stands, but our results show consistency with this relationship in an area of diverse topography, soils, and growing conditions. *Pinus muricata* could be considered a conformer to the theoretical self-thinning law, as the expanded *P. muricata* stands in PRNS are characterized by a size–density slope near the middle of the range of results found in other studies examining several tree species and Reineke's Rule (Table 4).

4.4. Ecosystem implications of forest expansion and stand structure variability

The expansion of *P. muricata* forest to previously non-forested areas and the spatial pattern in forest structure across the burned landscape will have potential implications for continued change in vegetation patterns. Within five years following the Vision Fire, saplings had developed cones (Pribor, 2002), and nearly all trees in the 14-year-old stands in this study were cone bearing. This now represents a substantial seed source for continued forest regeneration and potential further expansion when subsequent fire occurs. Expansion of *P. muricata* into areas previously covered by grassland and coastal scrub will have lasting implications for species composition and diversity in these newly established stands. Nutrient cycling from plant litter into the soil may also spatially vary with the heterogeneous stand density as *Pinus* species have some of the slowest litter decomposition rates and lowest leaf nitrogen content of all trees (Singh and Gupta, 1977). Karlsson and Orlander (2002) found an increase in needle concentrations of nitrogen, potassium, and phosphorous for *P. sylvestris* trees in stands where density was reduced through manipulative thinning. Further studies could measure foliar nutrient concentrations in

Table 4
Results of the regression slope in Reineke's (1933) log–log size–density equation found in other studies for single-species, single-cohort stands of various tree species.

Tree species	Regression slope	Source
Pinus sylvestris	−1.844	Hynynen (1993)
Pinus sylvestris	−1.836	Rojo and Montero (1996)
Pinus sylvestris	−1.829	del Río et al. (2001)
Chamaecyparis obtusa	−1.799	Inoue et al. (2004)
Fagus sylvatica	−1.789	Pretzsch and Biber (2005)
Pinus muricata	−1.743	This study
Pinus banksiana	−1.712	Zeide (2001)
Picea abies	−1.664	Pretzsch and Biber (2005)
Various	−1.605	Reineke (1933)
Pinus sylvestris	−1.593	Pretzsch and Biber (2005)
Quercus patraea	−1.424	Pretzsch and Biber (2005)
Pinus densiflora	−1.301	Inoue et al. (2004)

high and low density *P. muricata* stands to test if a similar relationship exists in *P. muricata*.

The variability in mortality in the expanded forest has important implications for carbon dynamics, due to associated variation in both aboveground net primary productivity (ANPP) and biomass decomposition. While ANPP can increase with sapling density, high mortality rates can potentially dampen this relationship (Turner et al., 2004). Decaying biomass from dead saplings can represent significant inputs of organic matter and influence soil conditions.

4.5. Management implications and future research

Studies of stand dynamics following major fire events are critical to the appropriate management of *P. muricata* and other California closed-cone pine species (Barbour, 2007). Native only to the California Floristic Province (Millar, 1986b), these species are threatened by habitat loss, altered fire regimes, and introduced diseases and pests (Barbour, 2007). With unprecedented global climate change predicted over the next century (IPCC, 2007) forecasted to increase fire frequency and severity in Northern California (Fried et al., 2004), studies such as this one are needed to gain a better understanding of the complex responses of closed-cone pine forests to fire. Non-native pine pitch canker disease has recently been discovered and has rapidly spread through the *P. muricata* forest at PRNS (Crowley et al., 2009), and the size–density relationships detailed in this study can be informative for examining relationships between pitch canker disease and stand density. Although the data in this study are from a random sample of plots, they could be utilized in further research to map *P. muricata* density and approximate self-thinning across the entire forested landscape using the plots as training set in conjunction with remotely-sensed imagery as has been done in similar studies in Yellowstone National Park (Kashian et al., 2004).

5. Conclusion

For *P. muricata*, a large high-severity fire presents a significant opportunity for population expansion into previously non-forested areas. Post-fire stand structure in areas where *P. muricata* expands following fire can be highly spatially variable, and post-fire tree density is largely driven by distance to the nearest individual pre-fire tree. Fourteen years following a severe stand-replacing fire, newly established stands where *P. muricata* expanded post-fire contained evidence of self-thinning at approximately 1800 trees ha^{-1}; which was also the median density of expanded forest stands. *Pinus muricata* conforms to the predicted size–density relationship suggested by Reineke's (1933) Rule. By characterizing the spatial dimension of stand dynamics and coupling these data with

information on the temporal dimension of post-fire succession we can gain a more thorough understanding of the complexity of vegetation response to disturbance in fire-adapted ecosystems. This information is critical to understanding the impacts of changing climate and disturbance regimes on these forests.

Acknowledgements

References

Anderson, R.S., 2005. Contrasting vegetation and fire histories on the Point Reyes Peninsula during the pre-settlement and settlement periods: 15, 000 years of change. Final Report. Northern Arizona University, Flagstaff, pp. 1–44.

Axelrod, D.I., 1967. Evolution of the California closed-cone pine forest. In: Philbrick, R.N. (Ed.), Proceedings of the Symposium of the Biology of the Islands. Santa Barbara Botanical Garden, Santa Barbara, pp. 93–149.

Barbour, M.G., 2007. Closed-cone pine and cypress forests. In: Barbour, M.G., Keeler-Wolf, T., Schoenherr, A.A. (Eds.), Terrestrial Vegetation of California, third ed. University of California Press, Berkeley, pp. 296–312.

Beers, T.W., Dress, P.E., Wensel, L.C., 1966. Aspect transformation in site productivity research. J. Forestry 65, 691–692.

Beyer, H.L., 2004. Hawth's analysis tools for ArcGIS. <http://www.spatialecology.com/htools> (accessed 06.05.11).

Borchert, M., Johnson, M., Schreiner, D.S., Vander Wall, S.B., 2003. Early postfire seed dispersal, seedling establishment, and seedling mortality of *Pinus coulteri* (D. Don) in central coastal California, USA. Plant Ecol. 168, 207–220.

Brown, P.M., Kaye, M.W., Buckley, D., 1999. Fire history in Douglas-fir and coast redwood forests at Point Reyes National Seashore, CA. Northwest Sci. 73 (3), 205–216.

Crowley, B.J., Harvey, B.J., Holzman, B.A., 2009. Dynamics of pitch canker disease in bishop pines (*Pinus muricata*) at Point Reyes National Seashore, CA. Annual Meeting. Association of American Geographers, Las Vegas, NV.

del Río, M., Montero, G., Bravo, F., 2001. Analysis of diameter–density relationships and self-thinning in non-thinned even-aged Scots pine stands. For. Ecol. Manag. 142 (1–3), 79–87.

Folger, K., 1998. Post-fire succession in the Inverness Ridge bishop pine forest, Point Reyes National Seashore. M.A. Thesis. San Francisco State University.

Forrestel, A.B., Moritz, M.A., Stephens, S.L., 2011. Landscape-scale vegetation change following fire in Point Reyes, California, USA. Fire Ecol. 7 (2), 114–128.

Franklin, J., Bergman, E., 2011. Patterns of pine regeneration following a large, severe wildfire in the mountains of southern California. Can. J. For. Res. 41, 810–821.

Franklin, J.F., Spies, T.A., Van Pelt, R., Carey, A.B., Thornburgh, D.A., Rae Berg, D., Lindenmayer, D.B., Harmon, M.E., Keeton, W.S., Shaw, D.C., Bible, K., Chen, J., 2002. Disturbances and structural development of natural forest ecosystems with silvicultural implications, using Douglas-fir forests as an example. For. Ecol. Manag. 155 (1–3), 399–423.

Fried, J., Torn, M., Mills, E., 2004. The impact of climate change on wildfire severity: a regional forecast for northern California. Clim. Change 64 (1), 169–191.

Greene, D.F., Johnson, E.A., 1989. A model of wind dispersal of winged or plumed seeds. Ecology 70, 339–347.

Harper, J.L., 1977. Population Biology of Plants. Academic Press, London.

Harvey, B.J., 2010. Post fire vegetation change and stand dynamics in a *Pinus muricata* forest. M.A. Thesis. San Francisco State University.

Holzman, B., Folger, K., 2005. Post-fire vegetation response in the bishop pine forest at Point Reyes National Seashore. In: Allen, S.G., Shook, W. (Eds.), Vision Fire, Lessons learned from the October 1995 Fire. United States Department of the Interior, Washington, D.C., pp. 49–57.

Hynynen, J., 1993. Self-thinning models for even-aged stands of *Pinus sylvestris*, *Picea abies* and *Betula pendula*. Scand. J. For. Res. 8 (1), 326–336.

Inoue, A., Miyake, M., Nishizono, T., 2004. Allometric model of the Reineke equation for Japanese cypress (*Chamaecyparis obtusa*) and red pine (*Pinus densiflora*) stands. J. For. Res. 9 (4), 319–324.

IPCC, 2007. Summary for policymakers. In: Solomon, S., Qin, D., Manning, M., Chen, Z., Marquis, M., Averyt, K.B., Tignor, M., Miller, H.L. (Eds.), Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Jakubos, B., Romme, W.R., 1993. Invasion of subalpine meadows by lodgepole pine in Yellowstone National Park, Wyoming, USA. Arctic Alpine Res. 25 (4), 382–390.

Johnstone, J., Chapin, F.S., 2003. Non-equilibrium succession dynamics indicate continued northern migration of lodgepole pine. Glob. Change Biol. 9, 1401–1409.

Karlsson, C., Orlander, G., 2002. Mineral nutrients in needles of *Pinus sylvestris* seed trees after release cutting and their correlations with cone production and seed weight. For. Ecol. Manag. 166, 183–191.

Kashian, D.M., Tinker, D.B., Turner, M.G., Scarpace, F.L., 2004. Spatial heterogeneity of lodgepole pine sapling densities following the 1988 fires in Yellowstone National Park, Wyoming, USA. Can. J. For. Res. 34 (11), 2263–2276.

Kashian, D.M., Turner, M.G., Romme, W.H., Lorimer, C.G., 2005. Variability and convergence in stand structural development on a fire-dominated subalpine landscape. Ecology 86 (3), 643–654.

Kashian, D.M., Romme, W.H., Tinker, D.B., Turner, M.G., Ryan, M.G., 2006. Carbon storage on landscapes with stand-replacing fires. Bioscience 56, 598–606.

Keeley, J.E., 1995. Seed-germination patterns in fire-prone Mediterranean climate regions. In: Arroyo, M.T.K., Zedler, P.H., Fox, M.D. (Eds.), Ecology and Biogeography of Mediterranean Ecosystems in Chile, California and Australia. New York, Springer–Verlag, pp. 239–273.

Keeley, J.E., Zedler, P.H., 1998. Evolution of life histories in *Pinus*. In: Richardson, D.M. (Ed.), Ecology and Biogeography of *Pinus*. Cambridge University Press, Cambridge, UK, pp. 219–249.

Kenkel, N.C., 1988. Pattern of self-thinning in jack pine: testing the random mortality hypothesis. Ecology 69 (4), 1017–1024.

Kenkel, N.C., Hendrie, M.L., Bella, I.E., 1997. A long-term study of *Pinus banksiana* population dynamics. J. Veg. Sci. 8 (2), 241–254.

Lonsdale, W.M., 1990. The self-thinning rule: dead or alive? Ecology 71 (4), 1373–1388.

Millar, C.I., 1986a. Bishop pine (*Pinus muricata*) of inland Marin County, California. Madrono 33 (2), 123–129.

Millar, C.I., 1986b. The Californian closed cone pines (Subsection Oocarpae Little and Critchfield): a taxonomic history and review. Taxon 35 (4), 657–670.

Nathan, R., Katul, G.G., Horn, H.S., Thomas, S.M., Oren, R., Avissar, R., Pacala, S.W., Levin, S.A., 2002. Mechanisms of long-distance dispersal of seeds by wind. Nature 418, 409–413.

National Park Service, 2006. Point Reyes: Park statistics. <http://www.nps.gov/pore/parkmgmt/statistics.htm> (accessed 28.04.09).

National Park Service, 2010. Point Reyes: Weather. <http://www.nps.gov/pore/planyourvisit/weather.htm> (accessed 30.05.10).

National Park Service Geologic Resource Evaluation Program, 2008. Digital geologic map of Point Reyes National Seashore and vicinity, California. <http://science.nature.nps.gov/nrdata/quickoutput2.cfm?UnitSearch=&Action=Search&nps_quicksearch=%2B> (accessed 20.03.10).

Ne'eman, G., 1997. Regeneration of natural pine forest – review of work done after the 1989 fire in Mount Carmel, Israel. Int. J. Wildland Fire 7 (4), 295–306.

Ne'eman, G., Lahav, H., Izhaki, I., 1992. Spatial pattern of seedlings 1 year after fire in a Mediterranean pine forest. Oecologia 91 (3), 365–370.

Ne'eman, G., Fotheringham, C., Keeley, J., 1999. Patch to landscape patterns in post fire recruitment of a serotinous conifer. Plant Ecol. 145 (2), 235–242.

Oliver, C.D., 1980. Forest development in North America following major disturbances. For. Ecol. Manag. 3, 153–168.

Oliver, C.D., Larson, B.C., 1996. Forest Stand Dynamics. John Wiley and Sons, New York.

Pausas, J.G., Ouadah, N., Ferran, A., Gimeno, T., Vallejo, R., 2003. Fire severity and seedling establishment in *Pinus halepensis* woodlands, Eastern Iberian Peninsula. Plant Ecol. 169 (2), 205–213.

Pausas, J.G., Ribeiro, E., Vallejo, R., 2004. Post-fire regeneration variability of *Pinus halepensis* in the eastern Iberian Peninsula. For. Ecol. Manag. 203 (1–3), 251–259.

Peet, R.K., Christensen, N.L., 1987. Competition and tree death. Bioscience 37 (8), 586–595.

Pretzsch, H., Biber, P., 2005. A re-evaluation of Reineke's rule and stand density index. For. Sci. 51 (4), 304–320.

Pribor, P., 2002. Post-fire succession in bishop pine forest at Point Reyes National Seashore, California (1995–2001). M.A. Thesis. San Francisco State University.

R Development Core Team, 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. <http://www.R-project.org> (accessed 10.03.10).

Reineke, L.H., 1933. Perfecting a stand-density index for even-aged forests. J. Agr. Res. 46, 627–638.

Rojo, A., Montero, G., 1996. El pino silvestre en la Sierra de Guadarrama, Ministerio de Agricultura. Pesca y Alimentacion, Madrid.

Shirokauer, D., 2004. Vegetation Map: Point Reyes National Seashore and Golden Gate National Recreation Area (1994 aerial photos). Point Reyes National Seashore. Geospatial Dataset 1035593.

Singh, J.S., Gupta, S.R., 1977. Plant decomposition and soil respiration in terrestrial ecosystems. Bot. Rev. 43 (4), 449–528.

Stuart, J.D., Stephens, S.L., 2006. North coast bioregion. In: Sugihara, N.G., Van Wagtendonk, J.W., Shaffer, K.E., Fites-Kaufman, J., Thode, A.E. (Eds.), Fire in California's Ecosystems. University of California Press, Berkeley, CA, pp. 147–169.

Sugnet, P.W., 1981. Fire history and post-fire stand dynamics of Inverness bishop pine populations. M.S. Thesis. University of California, Berkeley.

Tinker, D.B., Romme, W.H., Hargrove, W.W., Gardner, R.H., Turner, M.G., 1994. Landscape-scale heterogeneity in lodgepole pine serotiny. Can. J. For. Res. 24, 897–903.

Tsitsoni, T., Karagiannakidou, V., 2000. Site quality and stand structure in *Pinus halapensis* forests of north Greece. Forestry 73 (1), 51–64.

Turnblom, E.C., Burk, T.E., 2000. Modeling self-thinning of unthinned lake states red pine stands using nonlinear simultaneous differential equations. Can. J. For. Res. 30 (9), 1410–1418.

Turner, M.G., Dale, V.H., Everham, E.H., 1997. Fires, hurricanes, and volcanoes: comparing large disturbances. Bioscience 47 (11), 758–768.

Turner, M.G., Tinker, D.B., Romme, W.H., Kashian, D.M., Litton, C.M., 2004. Landscape patterns of sapling density, leaf area, and aboveground net primary production in postfire lodgepole pine forests, Yellowstone National Park (USA). Ecosystems 7 (7), 751–775.

United States Department and of the Interior, 1995. Mt. Vision Fire incident: burned area emergency rehabilitation plan. National Park Service, Point Reyes National Seashore.

United States Department of Agriculture – Natural Resources Conservation Service, 2000. Soil Survey Geographic (SSURGO) database for Marin County, California. <http://science.nature.nps.gov/nrdata/ quickoutput2.cfm?UnitSearch=&Action=Search&nps_quicksearch=%2B> (accessed 20.03.10).

Weller, D.E., 1987. A reevaluation of the $-3/2$ power rule of plant self-thinning. Ecol. Mon. 57 (1), 23–43.

Weller, D.E., 1991. The self-thinning rule: dead or unsupported? – a reply to Lonsdale. Ecology 72 (2), 747–750.

Willson, M.F., 1993. Dispersal mode, seed shadows, and colonization patterns. Vegetatio 108, 261–280.

Yoda, K., Kira, T., Ogawa, H., Hozumi, K., 1963. Intraspecific competition among higher plants. XI. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol. Osaka City Univ. 14, 107–129.

Zeide, B., 1987. Analysis of the 3/2 power law of self-thinning. For. Sci. 33 (2), 517–537.

Zeide, B., 2001. Natural thinning and environmental change: an ecological process model. For. Ecol. Manag. 154 (1–2), 165–177.

Zeide, B., 2010. Comparison of self-thinning models: an exercise in reasoning. Trees 24, 1117–1126.

Zinke, P.J., 1962. The pattern of influence of individual forest trees on soil properties. Ecology 43 (1), 130–133.