Spatial distribution of regeneration patches in an old-growth *Pinus jeffreyi*-mixed conifer forest in northwestern Mexico

Stephens, S.L.* & Fry, D.L.

*Division of Ecosystem Science, Department of Environmental Science, Policy, and Management, 137 Mulford Hall,
University of California, Berkeley, CA 94720-3114, USA;*
*Corresponding author; E-mail stephens@nature.berkeley.edu; Fax +1 510 643 5438

Abstract

Question: What are the shape, abundance, size, and structural characteristics of sapling patches in an old-growth *Pinus jeffreyi*-mixed conifer forest with a relatively intact disturbance regime?

Location: Sierra San Pedro Martir, Baja California, Mexico.

Methods: Regeneration was quantified by sampling sapling patches on seven 1200 m permanently marked line transects. For all patches intersected, tree size, species, age, and patch canopy cover were recorded. Patch structural characteristics were statistically compared to data from unbiased forest inventory plots. The minimum regeneration patch was defined as three saplings in a 49-m² area.

Results: We sampled 54 sapling regeneration patches. Patch size varied from 6.6 to 674.8 m². A small portion of the forest was in patches (patch fraction = 3.8%, patch abundance = 8.5 per ha). The majority of the patches were small; 64.8% were less than the mean patch area of 100.1 m². Patches were shaped as a rhombus. For all forest characteristics, mean values inside patches were significantly different than those from the unbiased forest inventory plots.

Conclusions: These forests have a fine-grained pattern of regeneration patches. Our largest patch size of 674.8 m² is the smallest reported in *Pinus jeffreyi, P. ponderosa*, and mixed conifer forests; other studies have probably had more difficulty delineating regeneration patches because of forest ingrowth from fire exclusion. Frequent fire, irregular seed crops, and seed dispersal by small mammals and birds could create this regeneration patch regime. High variation in nutrient availability after fire could also contribute to increased stand patchiness.

Keywords: Disturbance; Fire; Forest restoration; *Pinus ponderosa*; Reference condition.

Nomenclature: Hickman (1993) for vascular plants; Kays & Wilson (2002) for mammals.

Abbreviation: *Pj*-mc = *Pinus jeffreyi*-mixed conifer; SSPM = Sierra San Pedro Martir.

Introduction

Watt (1947) viewed an apparently stable forest community as the mosaic of patches differentiated by floristic composition and age of the dominant trees. This 'patch' model has repeatedly been applied to *Pinus ponderosa* and mixed conifer forests in the western United States (US) (Cooper 1960, 1961; Biswell 1961; West 1969; Bonnicksen & Stone 1981; White 1985; Moore et al. 1993; Fulé et al. 2002). This model (Watt 1947) suggests that even-aged patches of shade-intolerant seedlings originate in small forest openings after a surface fire has prepared a suitable seed bed. Wind dispersal of seeds from adjacent mature trees may be sufficient to regenerate the patches but other dispersal mechanisms such as seed caching by small mammals (Vander Wall 1992) and birds (Burns & Honkala 1990) may also be important.

Periodicity of *P. ponderosa* seed crops is a major limitation to successful regeneration in the southwestern US (Pearson 1950; Schubert 1974). In general, sufficient seed is available for a new generation of *P. ponderosa* in the southwestern US only once or perhaps twice a decade (Savage & Swetnam 1990; Allen et al. 2002; Bailey & Covington 2002). After establishment, seedlings contribute little flammable organic matter to the forest floor for several years, and surface fires that pass through surrounding stands ordinarily do not spread into the young seedling clumps (Biswell 1989). Separation of the seedling clumps from the litter fall of mature trees also reduces local fuel loads within the seedling patches.

Information on the size, shape, frequency, and structural characteristics of regeneration patches in *P. ponderosa* and mixed conifer forests is limited (Agee 1998). Most patch characteristic investigations have occurred in *P. ponderosa* forests in north-central Arizona (Cooper 1960, 1961; White 1985; Moore et al. 1993; Biondi 1998) and east-central Oregon (West 1969; Morrow 1985) (Table 1). All of these studies on patch size were done in remnant, old-growth forests that had

been subjected to decades of fire exclusion with the exception of one of the stands studied by Cooper (1960). No information on patch characteristics of *Pinus jeffreyi* has been reported. The rarity of information has occurred because there are few large, coniferous forests in western North America that have not been affected by fire exclusion, particularly those that once experienced frequent, low-moderate severity fire regimes.

One large forested ecosystem exists in northwestern Mexico where harvesting has never occurred and a policy of large-scale fire suppression was never initiated, the Sierra San Pedro Martir (SSPM), Baja California, Mexico (Minnich et al. 1997; Stephens et al. 2003). The forests in the SSPM are unique within the California floristic province in that they were influenced by lightning ignited fires until the late 1960s (Stephens et al. 2003). Median fire return intervals in *Pinus jeffreyi*-mixed conifer (*Pj*-mc) forests in the SSPM are shorter than 15 years (Stephens et al. 2003), and this is comparable to past fire frequency in similar forests in California (Skinner & Chang 1996; Stephens 2001; Taylor 2004). Though there are no *P. ponderosa* in the SSPM, the relationship of *P. jeffreyi* to fire is considered similar to ponderosa pine (Habeck 1992); however, there is more variability in *P. jeffreyi* fire regimes in regions where the two species overlap (Skinner & Chang 1996).

The seasonality of past fires in the SSPM differs from that in California with the majority of fires recorded in the early-wood portion of the annual ring, while most fires in Californian forests are recorded in the late-wood or dormant periods (Stephens et al. 2003; Stephens & Collins 2004). The SSPM has experienced livestock grazing at varying intensities over the last 200 years (Minnich et al. 1997; Minnich & Franco 1998).

The objectives of this study are to determine the shape, abundance, size, and structural characteristics of sapling patches in an old-growth *Pj*-mc forest with a relatively intact disturbance regime to (1) increase our understanding of old-growth forests, and (2) assist in the development of restoration objectives for similar forests in the western US. The absence of systematic fire suppression and harvesting suggests these forests may provide information useful for developing descriptions of reference conditions (Franklin et al. 2002; Lindenmayer & Franklin 2002; Bennett & Adams 2004; Stephens & Fule 2005) for similar forests in the western US.

Study area

The study was conducted in the SSPM National Park (31°37' N, 115°59' W) located ca. 120 km SE of Ensenada, Mexico. The SSPM is the southern terminus of the Peninsular Mountain Range that begins at the boundary between the San Jacinto and San Bernardino Mountains in California; ca. 350 km separates the SSPM from the San Bernardino Mountains.

Forests in the SSPM are composed of *Pinus jeffreyi*, *Abies concolor*, *P. lambertiana*, *P. contorta* var. *murrayana* and limited amounts of *Calocedrus decurrens* and *Populus tremuloides*. The most common forest types are *Pinus jeffreyi*, *Pinus jeffreyi*-mixed conifer, and mixed *Abies concolor* forests (Minnich & Franco 1998). Floristically, forests in the SSPM are very similar to portions of the eastern Sierra Nevada and southern California mountains (Minnich et al. 1995; Stephens 2001; Taylor 2004).

The soils of the SSPM are unclassified but those in the study area are Entisols (Stephens & Gill 2005). Soils are shallow, well to excessively drained, and relatively acidic. The most common soil texture is loamy sand. Parent material is diorite. Soil chemistry and texture from the study area are typical of granite-derived soils in similar forests in California (Potter 1998).

The SSPM is located in the southern margin of the North American Mediterranean climate zone (Pyke 1972; Markham 1972; Minnich et al. 2000); however, weather data from this area are limited. A group of temporary weather stations was installed in this range from 1989-1992 and mean annual precipitation in the upper plateau (Vallecitos Meadow) was 550 mm (Minnich et al. 2000). The Mediterranean climate in the SSPM possibly includes higher amounts of summer precipitation than most areas of California (Stephens et al. 2003).

Forest structure has been inventoried in *Pj*-mc forests in the SSPM using a systematic grid of plots from an area of ca. 144 ha (Stephens 2004; Stephens & Gill 2005). In this area, mean tree DBH was 32.6 cm (range 2.5 - 112 cm), mean tree density was 145.3 stems ha^{-1} (range 30 - 320 stems ha^{-1}), and mean basal area is 19.9 m^2 ha^{-1} (range 5.7 - 50.7 m^2 ha^{-1}). The forest is relatively open with an mean canopy cover of 25.3% (range 14 - 49.5%).

Topographic maps were used to select a sample area with uniform aspects (west, northwest), slopes (0-25%), soil parent material, and forest type (*Pj*-mc) to reduce variability in sapling patches that could be caused by these factors. Elevation in the sampled area varied between 2400 - 2500 m and it is ca. 1.2 km west of the northern portion of Vallecitos Meadow.

Methods

Regeneration patch definition and sampling

Regeneration patches were defined as areas within which regeneration is likely to persist; this is a subjective definition but one that helps define an ecologically significant and recognizable shift in forest structure (Agee 1998).

We focused on sapling sized trees because the repeated measurement of a completely inventoried 4 ha stem map in *Pj*-mc forests in the SSPM (S. Stephens, unpubl.) indicated that sapling mortality was low, and therefore, these trees should persist and affect forest structure. Analysis of the 4 ha stem map also indicated that the smallest sapling regeneration patch had a dimension of approximately 7 m × 7 m and contained three saplings. Cooper (1960) also defined a relatively small minimum patch size when measuring southwestern *P. ponderosa* forests that is equivalent to 6.3 m on a side (6.3 m × 6.3 m).

The smallest sapling regeneration patch was therefore defined as a group of three trees with diameters at breast height (DBH) between 2.5 - 15 cm within a 7 m × 7 m (49 m^2) area. A regeneration patch increased in size only when one of more of the areas adjacent (the four squares that share an edge with the original square) to a previously delineated 49-m^2 area contained at least three trees with a DBH between 2.5 - 15 cm in a new 49-m^2 area. This process was continued until no adjacent 49-m^2 areas met the minimum patch definition. White (1985) also identified a minimum sized group of trees to include three individuals and this corresponded to an area of approximately 0.02-ha for post-fire exclusion trees (defined as trees > 106 years old).

Patches were sampled by superimposing seven parallel line transects (Battles et al. 1996) on a systematic grid of plots (7 m × 7 m grid) used previously to survey trees, snags, fuels, and soils (Stephens 2004; Stephens & Gill 2005) (Fig. 1). The starting point of the grid was chosen randomly. Line transects were 200 m apart and each 1200 m in length.

For all sapling patches intersected, stem size (DBH), species, age, and patch canopy cover was recorded. Seedlings (DBH < 2.5 cm) occurring within patches were tallied by species. A random sample of trees within the patch were cored to determine age (cores taken ca. 10 cm above ground; ca. 10% of patch trees cored). Tree age was determined by cross-dating tree rings using standard dendrochronological techniques (Stokes & Smiley 1977; Swetnam et al. 1985). Most specimens were cross-dated by visually comparing them with a nearby chronology obtained from the International Tree-ring Data Bank (Grissino-Mayer & Fritts 1998).

Canopy cover was estimated using a systematic sampling grid placed in each sapling patch; the distance between grid points depended on patch size with most patches containing 15 grid points. A canopy sight tube was used to determine if a tree crown was directly overhead on each grid point; the species of the tree was recorded if the grid point was under canopy. Patch canopy cover was estimated by the total number of points under canopy divided by the total number of grid points in each patch.

In each patch the longest axis (A_{major}) and the maximum axis perpendicular to the longest axis (A_{minor}) were measured (m) (Battles et al. 1995). The end of each axis was located on the outside canopy drip line of patch perimeter trees. Patch metrics (i.e. area and perimeter) were estimated as a function of the major and minor axes. Since the patches were irregular in shape, we compared equations for area and perimeter for patches assuming they were shaped as an ellipse, a rhombus, and equations developed from linear regression. These equations were generated from a subsample of patches (detailed patches that included one-third of the total number of patches).

Detailed patches were measured by recording the distance (m) of multiple radii (every 45 degrees) from patch centre to patch edge (outside canopy drip line of perimeter trees) and then summing the areas of the resulting triangles (Spies et al. 1990; Lertzman & Krebs 1991; Runkle 1992). The equation for the area of an ellipse and rhombus include the product of the major and minor axes (App. 1). This product for the detailed patches was used as the independent variable in the linear regression model and the area of the detailed patches was included as the dependent variable. The regression coefficient was then used to estimate area of
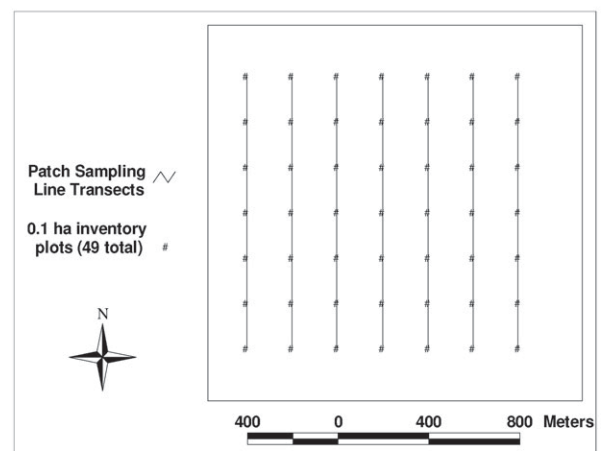

Fig. 1. Patch sampling design in an old-growth *Pinus jeffreyi*-mixed conifer forest in the Sierra San Pedro Martir, Mexico.

all the patches (regression coefficient∗[A_{major}∗A_{minor}]). The equation that gave the lowest error compared to the detailed patches was used to estimate patch dimensions. For patch perimeter, we used

$$\sqrt{\left(A_{major}^2 + A_{minor}^2\right)}$$

as the independent variable in the linear regression model since it appears in the formula for the perimeter of a rhombus and ellipse (App. 1). The equation that produced the lowest difference compared to the detailed patches was used to estimate patch perimeter.

Characterization of the spatial distribution of sapling patches

A number of attributes were used to quantify the spatial distribution of sapling patches. The equation used to calculate the fraction of the forest in a sapling patch (patch fraction) is:

$$\text{patch fraction} = \frac{1}{L}\sum_{j=1}^{n}\frac{A_j}{d_j}, \qquad (1)$$

(De Vries 1986; Battles et al. 1995) where L is the length of the transect, A_j is the area of the jth regeneration patch, and d_j is the effective diameter of the jth regeneration patch. The effective diameter is the mean breadth of an object when measured over every possible orientation. For a convex shaped object, a line transect will cross its perimeter at exactly two points. The probability of a line transect intersecting the object is half the probability of intersecting a line segment of the same length as its perimeter. The effective diameter (d) for a convex shape is

$$d = \left(\frac{1}{2}\right)\frac{2p}{\pi} \qquad (2)$$

where p is the object perimeter; the equation reduces to p/π for a convex shape. However, for a non-convex shape, the effective diameter cannot be calculated because there is the probability of a line transect intersecting the object perimeter in more than two places. Therefore, we calculated the perimeter for the smallest convex shape for each of the detailed sapling patches (Battles et al. 1995). The probability of a transect passing through a non-convex shape is the same as the probability of a line passing through the smallest convex cover of that shape. However, the perimeter of the smallest convex shape will be smaller than the perimeter of the actual non-convex shape (Battles et al. 1995).

The abundance of sapling patches was expressed as the number of patches per ha of forest and was calculated from

$$\text{sapling patch abundance} = \frac{1}{L}\sum_{j=1}^{n}\frac{1}{d_j}, \qquad (3)$$

(De Vries 1986; Battles et al. 1995) where L is the length of the transect and d_j is the effective diameter of the jth patch.

Inherent to both the patch fraction and abundance equations is a correction for the bias associated with using line transect sampling. The bias is produced because a line transect is more likely to intersect a large patch than a small one (De Vries 1986). This is corrected by using the effective diameter of the patch which gives the probability that the transect will intersect the patch. Therefore, in describing size frequency distributions of the patches, the bias needs to be corrected. For patch area and perimeter size distributions, each sapling patch was discounted based on its size using:

$$\frac{\dfrac{1}{d_j}}{\displaystyle\sum_{j=1}^{n}\dfrac{1}{d_j}} \qquad (4)$$

where d_j is the effective diameter of the jth patch.

Comparisons of mean forest characteristics (DBH, density of trees > 2.5 cm DBH, seedling density) between the sapling regeneration patches and the values obtained from the 49-plot systematic grid (Stephens & Gill 2005) were done by two-sample *t*-tests. Frequency distributions for all variables from the 49 plot grid were right-skewed, and therefore, were log transformed to meet assumptions of parametric statistical tests (Zar 1999). The relationship between sapling patch perimeter and area was determined using least squares nonlinear regression.

Table 1. Regeneration patch size characteristics of western North American forests with low-moderate severity fire regimes. - not available.

Location	Forest type	Patch size (ha)		Source
		Average	Range	
White Mts, Arizona	*Pinus ponderosa*	0.08	0.06-0.13	Cooper (1960) Cooper (1961)
Flagstaff, Arizona	*Pinus ponderosa*	0.07	-	Biondi (1998)
Flagstaff, Arizona	*Pinus ponderosa*	0.10	0.02-0.29	White (1985)
Flagstaff, Arizona	*Pinus ponderosa*	0.16	0.08-0.64	Moore et al. (1993)
Warm Springs Reservation, Oregon	*Pinus ponderosa*	0.26	-	West (1969)
Pringle Falls, Oregon	*Pinus ponderosa*	-	0.025-0.35	Morrow (1985)
Sequoia Nat. Park, California	Mixed conifer	-	0.03-0.16	Bonnicksen & Stone (1981)
SSPM, Baja California, Mexico	*Pinus jeffreyi*-mixed conifer	0.01	0.001-0.07	This work

Results

In total 8.4 km were surveyed in line transects for sapling regeneration patches (Fig. 1); 54 such patches were intersected and measured; patch size varied from 6.6 - 674.8 m^2 (Table 2). A small part of the forest was in patches as indicated by the estimates of patch fraction (3.8%) and patch abundance (8.5 stems ha^{-1}) (Table 2). Mean canopy cover inside regeneration patches was 6.2% (SE 1.8, range 2-37.1%). The 18 patches measured in detail were irregular in shape and 14 were non-convex. Mean axis ratio (A_{major}/A_{minor}) for detailed patches was 2.15 against 2.23 for the other 36 patches.

Assuming sapling patches were shaped as ellipses overestimated patch area by a mean of 34.1% compared to the area calculated from the detailed patches. Assuming the patches were shaped as a rhombus gave a lower error. The equation for the area of a rhombus underestimated patch area by 1.1% on average. Our regression equation showed a significant relationship ($R^2 = 0.942, p < 0.0001$), while the intercept was significantly different from zero. Furthermore, the few large patches that were measured in detail strongly influenced the regression relationship and the regression residuals showed a non-random pattern. Using the regression coefficient underestimated patch area by an average of 41.5%. Based on these comparisons, the sapling regeneration patches in this forest were most accurately estimated assuming patches were shaped like a rhombus.

Most sapling patches were small (Fig. 2); 64.8% were less than the estimated mean patch area of 100.1 m^2 (Table 2). The perimeter of the smallest detailed patch was 6.4 m and the largest was 158.7 m (Fig. 3). The mean perimeter of the smallest convex cover for the detailed patches was 37.1 m, 0.8% less than the esti-
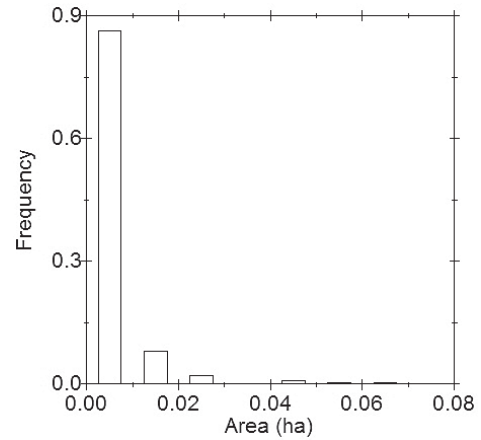

Fig. 2. Frequency distribution of sapling patch size (ha) in *Pinus jeffreyi*-mixed conifer forests in the Sierra San Pedro Martir, Mexico. Values were corrected for the patch size bias associated with line intersect sampling (Eq. 4).

mated actual mean perimeter.

The regression coefficient generated by the linear regression model for patch perimeter was similar to the coefficient in the perimeter equation for a rhombus (2.04 and 2, respectively). The regression coefficient generated from the linear regression model using the smallest convex perimeter as the dependent variable was also 2.0. Therefore, perimeters of the patches were assumed to be shaped like a rhombus. This agrees with the comparisons for the equation for patch area. Using the regression coefficient to estimate patch perimeter overestimated the perimeter by 10% compared to the perimeter estimated from the detailed patches.

The majority of the sapling patches (66.7%) had less than the estimated mean perimeter of 37.6 m (Fig. 3). The average of the perimeter to area ratio for the sapling patches was 1.21. The relationship between patch perimeter and area exhibited a curvilinear relationship (Fig. 5). Using non-linear regression ($p < 0.0001$) the equation describing the relationship was:

$$Perimeter = 11\sqrt{area} + 2.5 \tag{5}$$

where perimeter is in m and area in m^2.

For all forest characteristics compared, mean values inside the sapling patches were significantly different from the 49-plot grid ($p < 0.01$ for all tests, Table 3).

Table 2. Sapling regeneration patch characteristics of an old-growth *Pinus jeffreyi*-mixed conifer forest in the Sierra San Pedro Martir, Mexico. Values in parentheses represent one standard error of the mean.

Patch fraction (%)	3.8 (0.3)
Patch abundance (#/ha)	8.5 (4.6)
Mean area (m^2) [range]	100.1 (19.3) [6.6 – 674.8]
Mean perimeter (m) [range]	36.9 (3.8) [6.3 – 153]
Mean number of trees [range]	16.9 (2.7) [3 – 111]
Mean number of seedlings [range]	9.5 (1.8) [0 – 71]

Table 3. Comparison of forest characteristics inside sapling regeneration patches and from a systematic inventory (Stephens & Gill 2005) in an old-growth *Pinus jeffreyi*-mixed conifer forest in the Sierra San Pedro Martir, Mexico. * indicates significant difference ($p < 0.05$) using a 2-sample *t*-test.

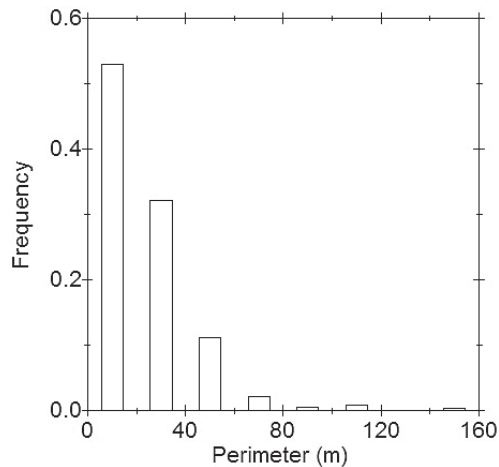| Location	Inside regeneration patches		General forest	
	Average (1 SE)	Range	Average (1 SE)	Range
DBH (cm)*	13.2 (0.3)	2.5 - 44.5	32.6 (0.9)	2.5 - 112.0
Tree (> 2.5 cm DBH) density ha^{-1}*	4843.4 (1091.0)	387.6 - 45454.5	145.3 (10.4)	30 - 320
Seedling density ha^{-1}*	1704.2 (329.1)	0 - 11724.1	124.7 (15.7)	0 - 470

Fig. 3. Frequency distribution of sapling patch perimeter (m) in *Pinus jeffreyi*-mixed conifer forests in the Sierra San Pedro Martir, Mexico. Values were corrected for the patch size bias associated with line intersect sampling (Eq. 4).
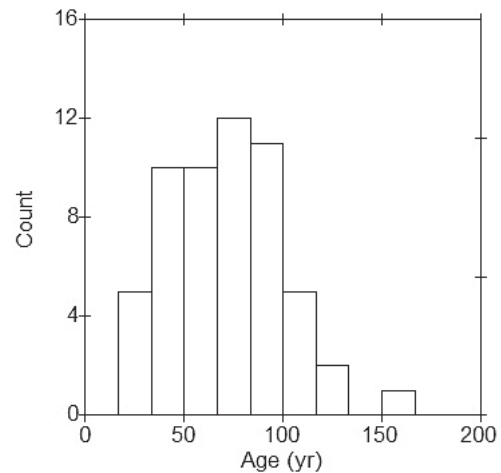

Fig. 4. Frequency distribution of tree ages inside sapling patches in *Pinus jeffreyi*-mixed conifer forests in the Sierra San Pedro Martir, Mexico.

Mean DBH was 60% smaller inside the sapling patches compared to the grid plots.

Pinus jeffreyi was the dominant species both inside the sapling regeneration patches and in the 49-plot grid (Table 4). The next most abundant species was *Abies concolor*; both *P. lambertiana* and *P. contorta* var. *murrayana* were relatively uncommon.

Fifty-six trees inside the sapling regeneration patches were cored (Fig. 4) and mean age was 72.1 years (SE = 3.7). Mean age for *P. jeffreyi* (n = 41) was slightly less than the overall mean (mean of 70.9 years, SE = 4.5 years) while *Abies concolor* was higher (mean of 77 years, SE = 7.7).

Discussion

The smallest sapling regeneration patch was defined in this work as at least three saplings with a DBH between 2.5 - 15 cm in a 7 m × 7 m area. Only one other patch study (Cooper 1960) has explicitly defined the lower patch size (6.3 m × 6.3 m). Our largest patch size of 674.8 m² is the smallest reported in similar forests (Table 1); Cooper (1960) and Bonnicksen & Stone (1981) reported a maximum patch size that is approximately two times larger than this work. Other maximum patch size estimates are four to nine times larger (Table 1) but it should be noted that patch definitions varied among studies. Larger regeneration patches were found in mixed conifer forests in the Southern Cascades of northeastern California where fire regimes were strongly

Table 4. Percent species composition by size inside sapling regeneration patches and from a systematic inventory (Stephens & Gill 2005) in an old-growth *Pinus jeffreyi*-mixed conifer forest in the Sierra San Pedro Martir, Mexico.

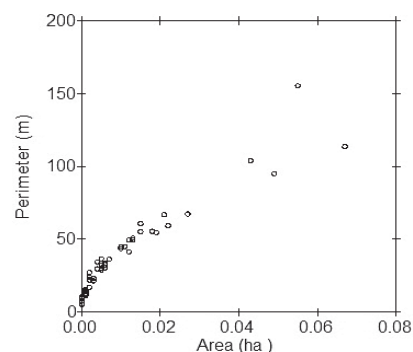| Species	Trees		Seedlings	
	Inside patches	General forest	Inside patches	General forest
Pinus jeffreyi	86.8	74.1	78.6	81.2
Abies concolor	10.6	17.7	11.7	10.8
Pinus lambertiana	1.4	5.9	9.2	7.7
Pinus contorta var. *murrayana*	1.2	2.3	0.6	0.3
N	910	730	513	611

Fig. 5. Perimeter-to-area ratio patterns inside sapling patches in *Pinus jeffreyi*-mixed conifer forests in the Sierra San Pedro Martir, Mexico.

affected by slope position and topography (Bekker & Taylor 2001; Beaty & Taylor 2001).

Age structure data from this study and White (1985) illustrate the variation of successful establishment in *Pj*-mc and *P. ponderosa* forests in northwestern Mexico and the southwestern US, respectively. Part of the variation is likely due to erratic seed production in pre-settlement years that was probably similar to the erratic seed production reported for this century (Larson & Schubert 1970). Some regeneration patches (24%) in the SSPM included moderate sized trees (DBH > 30 cm) and this was also found in southwestern *P. ponderosa* forests. Cooper (1961) found that 2 - 8.2% of the quadrats (6.3 m × 6.3 m) examined in largely intact, old-growth *P. ponderosa* forests contained young and mature trees in the same quadrat. Since only a subset of patch trees were cored in this work, the temporal dynamics of the SSPM sapling patches have not been fully characterized.

In contrast to the pattern observed by Cooper (1960, 1961) in the White Mountains of Arizona, within group age data in this study and those of White (1985) indicate a wider range of ages within each patch. A possible explanation is that rather than the whole patch of trees regenerating simultaneously, a few trees regenerate early followed by additional trees for the next few decades. This could also occur if a fire killed a group of trees resulting in a patch of seedlings, but as dead wood accumulated on the ground (from the snags), subsequent fires would kill some seedlings and open space for further recruitment.

The concept of *P. ponderosa* and *Pj*-mc forests as a mosaic of groups (Schubert 1974) is upheld by the study of stem spatial distribution, but age data indicate that many groups are not even-aged. That only 25.3% of the SSPM study area was covered by trees (Stephens & Gill 2005) supports the idea that only limited 'safe sites' were available for regeneration (White 1985). This is reinforced by the lack of evidence that earlier groups of trees occupied much of the area between current groups in *P. ponderosa* forest in the southwestern US (White 1985) and *Pj*-mc forests in the SSPM (S. Stephens pers. obs.).

The majority of regeneration studies done in *P. ponderosa* and mixed conifer forests have quantified regeneration dynamics by sampling older trees (> 100 years) or stumps to remove the effects of US fire exclusion policies. Sampling these older materials does not allow for a direct reconstruction of sapling sized patches. This may be one reason why the patch characteristics in this work are different from those previously reported (Table 1).

Before Euro-American settlement in the US, fire enhanced stand patchiness by thinning trees that periodically became established. By letting only a few trees per group survive and reach maturity, fire perpetuated patchiness because isolated point source of seeds were left across the landscape (Cooper 1960; Biondi 1998; Taylor 2004). Spatial variation in fuel loads and resultant fire behaviour and effects could also contribute to stand patchiness. The SSPM currently has high variability in forest fuel loads and this is probably the result of the relatively intact frequent surface fire regime and because no harvesting has occurred in this forest (Stephens 2004). The high variability in surface fuel loads would produce equally diverse fire behaviour and effects, and this would maintain high spatial heterogeneity if the forest continued to burn under a low-moderate severity fire regime (Stephens 2004).

Many *Pj*-mc forests in the eastern Sierra Nevada are largely even-aged because they were almost completely harvested 120 years ago to support the gold and silver mining industries (Elliott-Fisk et al. 1997; Taylor 2004). Most of these forests lack the fine-grained pattern of regeneration patches that occur in the SSPM (Taylor 2004) and many have high fire hazards (Stephens 2005). In addition to the need to manage to reduce fire hazards and promote old trees, small patches of regeneration should also be encouraged. The use of prescribed fire alone or in combination with group selection silviculture could be used to create fine-grained patterns of regeneration. The size of the group selection openings would need to be small in comparison to common group selection practices in California that use openings of 0.1-1.0 ha (Stephens et al. 1999; York et al. 2004).

The creation of small sapling patches of *Pj*-mc regeneration in the SSPM could have been influenced by seed dispersal from small mammals and birds. In a study in *P. jeffreyi* forests in western Nevada, *Tamias amoenus* (yellow pine chipmunks) repeatedly moved *Pinus jeffreyi* seeds from primary to secondary caches (Vander Wall & Joyner 1998). Rodents ate some of the seeds that they took from the primary caches (7.1%), and some seeds disappeared (17.2%), but most of the seeds (74.7%) served as the source for 722 new caches made by the rodents (Vander Wall & Joyner 1998). The repeated caching of *P. jeffreyi* seeds resulted in seedlings that were spatially clumped.

Small mammal inventories of the SSPM are incomplete but include *Eutamias obscurus* (Merriam chipmuck), *Tamiasciurus mearnsii* (a SSPM chickaree), and three species of mice, *Peromyscus boylii*, *P. maniculatus*, *P. truie* (Minnich et al. 1997). Caching behaviours of small mammals in the SSPM are unknown but the senior author has observed multiple *Pinus jeffreyi* seedlings emerging from single points inferring that seeds have been cached by small mammals or birds.

Frequent fires can increase spatial variability in nutrient availability, depending on the distribution of organic matter and, ultimately, the spatial distribution of

net primary production (Adams et al. 2003). The high variation in SSPM litter and surface fuel loads (Stephens 2004) would produce high variability in nutrient availability when the forest burns. This high variation in nutrient availability after fire could also contribute to increased stand patchiness because of differential net primary production.

In this work, the density of *Abies concolor* seedlings inside the sapling patches was similar to that recorded from the systematic plot inventory representing the entire forest (Table 4). This indicates that the number of shade tolerant *Abies concolor* seedlings (Burns & Honkala 1990) becoming established is almost equal in areas with very different canopy covers (canopy cover of forest = 25.3%; canopy cover of sapling regeneration patches = 6.2%). Forest canopy cover in the SSPM is relatively low and this probably results in high amounts of solar radiation throughout this mountain range which may minimize differences in the location of *Abies concolor* establishment. Root competition for moisture is probably a more significant competition factor in these xeric forests (Cooper 1961).

Old-growth forests with relatively intact disturbance regimes are extremely rare in western North America because of the management practices of fire suppression, livestock grazing, and forest harvesting (Stephens & Fule 2005; Stephens & Ruth 2005). As a result, there are few forests that could serve as models or 'references' for forests functioning under the continuing influence of climate variation, insects, diseases, and frequent fires. Conservation of the forests in the SSPM is therefore critical because they can assist in the development of desired conditions in similar US forests and will allow scientists to understand how relatively intact forests will respond to future conditions.

References

Adams, M.A., Grierson, P.F. & Burrows, C. 2003. Fires, soils and plant nutrition in south-west Western Australia forests: a focus on spatial and temporal variability. In: Abbott, I. & Burrows, N. (eds.) *Fire in ecosystems of south-west Western Australia: Impacts and management*, pp. 189-203. Backhuys Publishers, Leiden, NL.

Agee, J.K. 1998. The landscape ecology of western forest fire regimes. *Northwest Sci*. 72: 24-34.

Allen, C.D., Savage, M.A., Falk, D.A., Suckling, K.F., Swetnam, T.W., Schulke, T., Stacey, P.B., Morgan, P., Hoffman, M. & Klingel, J.T. 2002. Ecological restoration of southwestern ponderosa pine ecosystems: A broad perspective. *Ecol. Appl*. 12: 1418-1433.

Bailey, J.D. & Covington, W.W. 2002. Evaluating ponderosa pine regeneration rates following ecological restoration treatments in northern Arizona, USA. *For. Ecol. Manage*. 155: 271-278.

Battles, J.J., Fahey, T.J & Harney, E.M.B. 1995. Spatial patterning in the canopy gap regime of a subalpine *Abies-Picea* forest in the northeastern United States. *J. Veg. Sci*. 6: 807-814.

Battles, J.J., Dushoff, J.G. & Fahey, T.J. 1996. Line intersect sampling of forest canopy gaps. *For. Sci*. 42: 131-138.

Beaty, R.M. & Taylor, A.H. 2001. Spatial and temporal variation of fire regimes in a mixed conifer forest landscape, Southern Cascades, California, USA. *J. Biogeogr*. 28: 955-966.

Bekker, M.F. & Taylor, A.H. 2001. Gradient analysis of fire regimes in montane forests of the Southern Cascade Range, Thousand Lakes Wilderness, California, USA. *Plant Ecol*. 155: 15-28.

Bennett, L.T. & Adams, M.A. 2004. Assessment of ecological effects due to forest harvesting: approaches and statistical issues. *J. Appl. Ecol*. 41, 585-598.

Biondi, F. 1998. Twentieth-century growth trends at the Gus Pearson Natural Area, Arizona, USA. In: Dallmeier, F. & Comiskey, J.A. (eds.) *Forest biodiversity in North, Central and South America, and the Caribbean: Research and monitoring*, pp. 107-147. Man and the biosphere series, vol. 21. Unesco and The Parthenon Publishing Group, Pearl River, New York, NY, US.

Biswell, H.H. 1961. The big trees and fire. *Nat. Parks Conserv. Magaz*. 35: 11-14.

Biswell, H.H. 1989. *Prescribed burning in California wildland vegetation management*. UC Press, Berkeley, CA, US.

Bonnicksen, T.M. & Stone, E.C. 1981. The giant sequoia-mixed conifer forest community characterized through pattern analysis as a mosaic of aggregations. *For. Ecol. Manage*. 3: 747-762.

Burns, R.M. & Honkala, B.H. (eds.) 1990. *Silvics of North America, Vol. 1, conifers*. USDA Forest Service, Agricultural Handbook 654. Washington, DC, US.

Cooper, C.F. 1960. Changes in vegetation, structure, and growth of southwestern pine forests since white settlement. *Ecol. Monogr*. 30: 129-164.

Cooper, C.F. 1961. Pattern in ponderosa pine forests. *Ecology* 42: 493-499.

De Vries, P.G. 1986. *Sampling theory for forest inventory*. Springer-Verlag, New York, NY, US.

Elliott-Fisk, D.L., Cahill, T.C., Davis, O.K., Duan, L., Goldman, C.R., Gruell, G.E., Harris, R., Kattelmann, R., Lacey, R., Leisz, D., Lindstrom, S., Machida, D., Rowntree, R.A., Rucks, P., Sharkey, D.A., Stephens, S.L. & Ziegler, D.S. 1997. *Lake Tahoe case study. Sierra Nevada Ecosystem Project. Addendum,* pp. 217-276. University of California, Centers for Water and Wildland Resources, Davis, CA, US.

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

Fulé, P.Z., Covington, W.W., Moore, M.M, Heinlein, T.A. & Waltz, A.E.M. 2002. Natural variability in forests of Grand Canyon, USA. *J. Biogeogr.* 29: 31-47.

Grissino-Mayer, H.D. & Fritts, H. (eds.) 1998. *International Tree-Ring Data Bank*. IGBP PAGES/World Data Center-A for Paleoclimatology. NOAA/NGDC Paleoclimatology Program, Boulder, CO. URL: http://www.ngdc.noaa.gov/paleo/treering.html]

Habeck, R.J. 1992. *Pinus jeffreyi*. Fire effects information system. In: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. http://www.fs.fed.us/database/feis/plants/tree/pinjef/introductory.html (September 21, 2005).

Hickman, J.C. (ed.) 1993. *The Jepson manual: higher plants of California*. University of California Press, Berkeley, CA, US.

Kays, R.W. & Wilson, D.E. 2002. *Mammals of North America*. Princeton University Press, Princeton, NJ, US.

Larson, M.M. & Schubert, G.H. 1970. *Cone crops of ponderosa pine in central Arizona, including the influence of Abert squirrels*. USDA Forest Service, RM-RP-58. Fort Collins, CO, US.

Lertzman, K.P. & Krebs, C.J. 1991. Gap-phase structure of a subalpine old-growth forest. *Can. J. For. Res.* 21: 1730-1741.

Lindenmayer, D.B. & Franklin, J.F. 2002. *Conserving forest biodiversity. A comprehensive multiscaled approach*. Island Press, Washington DC, US.

Markham, C.B. 1972. Baja California's climate. *Weatherwise* 25: 64-76.

Minnich, R.A., Barbour, M.G., Burk, J.H. & Fernau, R.F. 1995. Sixty years of change in California conifer forests of the San Bernardino Mountains. *Conserv. Biol.* 9: 902-914.

Minnich, R.A., Franco-Vizcaino, E.F., Sosa-Ramirez, J., Burk, J.H., Barry, W.J., Barbour, M.G. & de la Cueva Salcedo, H. 1997. A land above: protecting Baja California's Sierra San Pedro Martir within a Biosphere Reserve. *J. Southw.* 39: 613-695.

Minnich, R.A. & Franco, E. 1998. *Land of chamise and pines: historical accounts and current status of northern Baja California's vegetation*. University of California publications in Botany, vol. 80. Berkely, CA, US.

Minnich, R.A., Barbour, M.G., Burk, J.H. & Sosa-Ramirez, J. 2000. Californian mixed-conifer forests under unmanaged fire regimes in the Sierra San Pedro Martir, Baja, California, Mexico. *J. Biogeogr*. 27: 105-129.

Moore, M.M., Covington, W.W. & Fule, P.Z. 1993. Spatial changes in southwestern ponderosa pine since settlement. *Bull. Ecol. Soc. Amer.* 74: 365.

Morrow, R.J. 1985. *Age structure and spatial pattern of old-growth ponderosa pine in Pringle Falls Experimental Forest, central Oregon*. M.Sc. Thesis, Oregon State University, Corvallis, OR, US.

Pearson, G.A. 1950. *Management of ponderosa pine in the southwest*. USDA Agriculture Monograph No. 6. Washington DC, US.

Potter, D.A. 1998. *Forested communities of the upper montane in the central and southern Sierra Nevada*. USDA Forest Service PSW-GTR-169. Berkeley, CA, US.

Pyke, C.B. 1972. *Some meteorological aspects of the seasonal distribution of precipitation in the western United States and Baja California*. University of California Water Resources Center Contribution No. 139. Los Angeles, CA, US.

Runkle, J.R. 1992. *Guidelines and sampling protocol for sampling forest gaps*. USDA Forest Service PNW-GTR-293.

Savage, M. & Swetnam, T.W. 1990. Early 19th century fire decline following sheep pasturing in a Navajo ponderosa pine forest. *Ecology* 71: 2374-2378.

Schubert, G.H. 1974. *Silviculture of southwestern ponderosa pine: the status of our knowledge*. USDA Forest Service RM-RP-123. Fort Collins, CO, US

Skinner, C.N. & Chang, C. 1996. Fire regimes, past and present. In: *Sierra Nevada ecosystem project: final report to Congress. Vol. II Assessments and scientific basis for management options*, pp. 1041-1069. Wildland Resources Center Report No. 37, Centers for Water and Wildland Resources, University of California, Davis, CA, US.

Spies, T.A., Franklin, J.F. & Klopsch, M. 1990. Canopy gaps in Douglas-fir forests of the Cascade Mountains. *Can. J. For. Res.* 20: 649-658.

Stephens, S.L. 2001. Fire history of adjacent Jeffrey pine and upper montane forests in the Eastern Sierra Nevada. *Int. J. Wildl. Fire* 10: 161-167.

Stephens, S.L. 2004. Fuel loads, snag density, and snag recruitment in an unmanaged Jeffrey pine-mixed conifer forest in northwestern Mexico. *For. Ecol. Manage.* 199: 103-113.

Stephens, S.L. 2005. Forest fire causes and extent on United States Forest Service lands. *Int. J. Wildl. Fire* 14: 213-222.

Stephens, S.L. & Collins, B.M. 2004. Fire regimes of mixed conifer forests in the north-central Sierra Nevada at multiple spatial scales. *Northw. Sci.* 78: 12-23.

Stephens, S.L. & Fule, P.Z. 2005. Western pine forests with continuing frequent fire regimes: Possible reference sites for management. *J. For.* 103 (8) (in press).

Stephens, S.L. & Gill, S.J. 2005. Forest structure and mortality in an old-growth Jeffrey pine-mixed conifer forest in northwestern Mexico. *For. Ecol. Manage.* 205: 15-28.

Stephens, S.L. & Ruth, L.W. 2005. Federal forest fire policy in the United States. *Ecol. Appl.* 15: 532-542.

Stephens, S.L, Dulitz, D. & Martin, R.E. 1999. Giant sequoia regeneration in group selection openings in the Southern Sierra Nevada. *For. Ecol. Manage.* 120: 89-95.

Stephens, S.L., Skinner, C.N. & Gill, S.J. 2003. Dendrochronology-based fire history of Jeffrey pine-mixed conifer forests in the Sierra San Pedro Martir, Mexico. *Can. J. For. Res.* 33: 1090-1101.

Stokes, M.A. & Smiley, T.L. 1977. *An introduction to tree-ring dating.* University of Chicago Press. Chicago, IL, US.

Swetnam, T.W., Thompson, M.A. & Sutherland, E.K. 1985. *Spruce budworm handbook, using dendrochronology to measure radial growth of defoliated trees.* USDA Forest Service Agriculture Handbook 639. Washington, DC, US.

Taylor, A.H. 2004. Identifying forest reference conditions on early cut-over lands, Lake Tahoe Basin, USA. *Ecol. Appl.* 14: 1903-1920.

Vander Wall, S.B. 1992. Establishing of Jeffrey pine seedlings from animal caches. *Western. J. Appl. For.* 7: 14-20.

Vander Wall, S.B. & Joyner, J.W. 1998. Recaching of Jeffrey pine (*Pinus jeffreyi*) seeds by yellow pine chipmunks (*Tamias amoenus*): potential effects on plant reproductive success. *Can. J. Zool.* 76: 154-162.

Watt, A.S. 1947. Pattern and process in the plant community. *J. Ecol.* 35: 1-22.

West, N.E. 1969. Tree patterns in central Oregon ponderosa pine forests. *Amer. Midl. Nat.* 81: 584-590.

White, A.S. 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66: 589-594.

York, R.A., Heald, R.C., Battles, J.J. & York, J.D.. 2004. Group selection management in conifer forests: relationships between opening size and tree growth. *Can. J. For. Res.* 34: 630-641.

Zar, J.H. 1999. *Biostatistical Analysis,* 4th ed. Prentice Hall. Upper Saddle River, NJ, US.

App. 1. Area and perimeter equations.

Area of an ellipse

$$\text{Area} = \pi \frac{A_{major} * A_{minor}}{4} \tag{A1}$$

Area of a rhombus

$$\text{Area} = \frac{A_{major} * A_{minor}}{2} \tag{A2}$$

Perimeter of an ellipse

$$\text{Perimeter} = 2 * A_{major} * K(k) \tag{A3}$$

where

$$k = \frac{\sqrt{A_{major}^2 - A_{minor}^2}}{A_{major}} \tag{A4}$$

and

$$K(k) = \int_0^{\pi/2} \sqrt{1 - k^2 * \sin^2 w} \; dw \tag{A5}$$

Perimeter of a rhombus

$$\text{Perimeter} = 2 * \sqrt{A_{major}^2 + A_{minor}^2} \tag{A6}$$