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Forest Ecology and Management 199 (2004) 191–217

 Forest Ecology
and
Management

www.elsevier.com/locate/foreco

Stand structure in eastside old-growth ponderosa pine forests of Oregon and northern California

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Received 2 March 2004; received in revised form 7 May 2004; accepted 7 May 2004

Abstract

Quantitative metrics of horizontal and vertical structural attributes in eastside old-growth ponderosa pine (*Pinus ponderosa* P. and *C. Lawson* var. *ponderosa*) forests were measured to guide the design of restoration prescriptions. The age, size structure, and the spatial patterns were investigated in old-growth ponderosa pine forests at three protected study areas east of the crest of the Cascade Range: Metolius Research Natural Area and Pringle Butte Research Natural Area in central Oregon and Blacks Mountain Experimental Forest in northern California. The three study areas represented sites characterized by deep accumulations of pumice from Cascade volcanism. All stems ≥ 15 cm in height (minimum height of an established seedling) were mapped and measured on a total of 27 1-ha plots. The distribution of trees within each individual plot was investigated by second-order spatial analysis with Ripley's $K(d)$ function, and then evaluated across each study area with functional data analysis. Coarse woody debris was sampled by using the strip-plot method to determine log density, mean log size, volume, and cover. The oldest trees were 618 years at Metolius, 613 years at Pringle Butte, and 330 years at Blacks Mountain. Stands were multi-aged, with as many as 16 cohorts at Metolius and 22 cohorts at Pringle Butte. Density of live old-growth ponderosa pine in the upper canopy ranged from 34 to 94 trees ha⁻¹ at Metolius, 35 to 79 trees ha⁻¹ at Pringle Butte, and 15 to 73 trees ha⁻¹ at Blacks Mountain; the differences between study areas were not significant, resulting in an overall mean density of 50 ± 3.5 live old-growth trees ha⁻¹. Mean diameters of these old-growth trees did not differ among the three study areas; the overall mean was 60.0 ± 1.55 cm dbh. Large dead ponderosa pines (overall mean diameter 61.7 ± 4.33 cm) were a common feature at all three study areas; the overall mean density was 9.0 ± 0.97 trees ha⁻¹. Ripley's $K(d)$ analysis of spatial point patterns using upper canopy trees revealed significant departure from randomness in 24 of the 27 plots. Functional data analysis of the spatial relationship of all sample plots by study area revealed two strong patterns. At scales of $1.2 \leq d \leq 2.6$ m at Metolius and $1.6 \leq d \leq 8.4$ m at Blacks Mountain, the deviation from random was not significant, suggesting the distribution of old-growth trees was random. More important, significant positive deviation from complete spatial randomness at larger scales at Metolius and Blacks Mountain suggested a clumped distribution. Maximum radii of the clumps were about 22.5 m in diameter at Metolius and about 24 m in diameter at Blacks Mountain. In contrast, old-growth trees at Pringle Butte were randomly distributed. Density of logs at Metolius and Pringle Butte was 47.0 ± 5.28 logs ha⁻¹, their mean large-end diameter was 37.6 ± 2.41 cm, the mean length of each log was 4.2 ± 0.09 m, the cumulative length of all logs averaged 512.9 ± 78.12 m, the total volume averaged 62.3 ± 6.30 m³ ha⁻¹, and the cover averaged $1.7 \pm 0.08\%$. A majority of the logs were in an advanced stage of decomposition, suggesting that they were in place for considerable time. These results are discussed in

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the context of reference conditions for restoration of ecosystem health and ecological integrity in eastside ponderosa pine forests.

Published by Elsevier B.V.

Keywords: Stand structure; Old-growth forests; Ponderosa pine; Spatial point patterns; Reference conditions; Ripley's $K(d)$ function; Functional data analysis

1. Introduction

Coniferous forests east of the crest of the Cascade Range in the Pacific Northwest have undergone dramatic physiognomic changes in the last 100 years. Early settlers and surveyors at the beginning of the 20th century passed through open forests of ponderosa pine (*Pinus ponderosa* P. and C. Lawson var. *ponderosa*, in contrast to *P. ponderosa* var. P. and C. Lawson var. *scopulorum* Engelm. found throughout the Rocky Mountains and the southwest) with widely spaced trees, few if any down logs, and little litter and woody undergrowth (Languille et al., 1903; Wickman, 1992; Bonnicksen, 2000). Witness trees marked by land surveyors during the late 1800s in central Oregon were predominantly ponderosa pine with diameters that exceeded 50 cm (Perry et al., 1995). The stem pattern of these eastside forests was a seemingly uniform park-land of widely spaced medium to large and old trees and continuous herbaceous undergrowth (Agee, 1994). This pattern best fits the “old forest single strata” stand structure class (O'Hara et al., 1996) and was largely the result of repeated surface fire. Historical fire regimes in these forests consisted of very frequent (<25 year mean fire-free interval) to frequent (26–75-year mean fire-free interval), low intensity fires that burned some or most forest floor plants, consumed litter, and killed primarily small trees (Kilgore, 1981; Agee, 1993). Estimated fire return interval was 4–11 years in central Oregon (Bork, 1984; Morrow, 1986), 10–11 years in north-eastern Oregon (Hall, 1980; Heyerdahl, 1997; Olson, 2000), and 7 years in eastern Washington (Everett et al., 2000).

Current amounts of eastside old-growth ponderosa pine forest are estimated to range from as low as 3–15% of pre-Euro-American settlement levels (Bolsinger and Waddell, 1993; Everett et al., 1994; Perry et al., 1995; Hann et al., 1997; Beardsley et al., 1999). Decline in the overall extent of eastside old-growth

ponderosa pine forest can be attributed to changes in natural disturbance regimes resulting from active management programs for fire suppression, livestock grazing, selective logging of old fire-resistant trees for timber and insect control, and extensive road building (Bergoffen, 1976; Johnson et al., 1994; Oliver et al., 1994). With effective fire exclusion, understory tree density in the remaining ponderosa pine stands has increased, stand composition now includes more fire-intolerant species, and stands are at greater risk of replacement (Agee, 1993, 1996; Covington and Moore, 1994). These stands now fit the “old forest multi-strata” stand structure class (O'Hara et al., 1996).

There is widespread recognition of the need to restore health and resiliency to eastside forest ecosystems (Quigley et al., 2001). Land managers are more aware of the many disturbance agents affecting forests, yet often lack the knowledge of how disturbance agents interact with each other and how they interact across multiple scales to cause changes that may affect ecosystem integrity. Increasingly, managers are attempting to restore the frequency and intensity of disturbances and thus the resulting periods of stability through thinning, underburning, and fuel reduction treatments that prevent stand-replacement fires (Arno and Ottmar, 1994; Fiedler, 1996; Weatherspoon, 2000; Conard et al., 2001; Oliver, 2001). Protection of remnant old-growth ponderosa pine stands and individual trees (Perry et al., 1995) as well as variability in thinning density to mimic the spatial distribution of stems in old-growth stands (Harrod et al., 1999) have been suggested as a key component of restoration efforts. Other efforts to accelerate the development of old-growth characteristics include retention of snags, and planning for future snags and down woody material.

While considerable attention has been given to describing old-growth characteristics of Douglas-fir (*Pseudotsuga menziesii* (Mirbel) Franco) forests west

of the crest of the Cascade Range (Franklin and Spies, 1991; Ansley and Battles, 1998; Acker et al., 1998; Van Pelt and Franklin, 2000), little attention has been directed at developing a detailed description of structural attributes in eastside old-growth ponderosa pine stands that could serve as a model in restoration efforts. Spatial point pattern as a component of old-growth structure is of particular interest because it reveals information on stand history, population dynamics, and competition (Haase, 1995). An interim definition¹ of eastside old-growth ponderosa pine forest attributes was prepared by the USDA Forest Service in 1993 and was based on structural features such as the number of large trees, number of snags, amount of down woody material, number of tree canopy layers, the native shrub or herb component, and the amount and size of tree or canopy gaps. While the interim definition was derived from a database used for plant association classification, little data was available to support the definition, and professional judgement was relied upon for much of the description. Harrod et al. (1999) postulated historical conditions after first measuring and mapping stumps, logs, snags, and live trees within mixed ponderosa pine—Douglas-fir stands in a relatively small area of eastern Washington, yet this work involved a narrow range of tree ages, and was conducted on a site that was extensively logged for timber during the late 1920s and early 1930s. In addition, Harrod et al. (1998) developed a model for determining historical snag densities in dry forests east of the Cascade Range. There remains a need for quantified descriptions of old-growth ponderosa pine forest structure that include the spatial point pattern if managers are to use the remaining old-growth stands as a guide for restoration efforts.

The purpose of this study was to develop quantitative measures of horizontal and vertical structural attributes in eastside old-growth ponderosa pine forests to guide the design of restoration prescriptions. In this context, horizontal and vertical structure is limited to live and dead trees and logs; we fully recognize the importance of understory vegetation, especially shrubs and graminoids as structural components that may be affected by ecological processes and may have

importance equal to that of tree strata when restoration activities are considered. Sampling was confined to the pumice-dominated portion of the range of eastside ponderosa pine, a broad band extending from about 47°N latitude in Washington south through Oregon to about 40°N latitude in California. Forests within this band develop in the orographic rainshadow of volcanic peaks of the Cascade Range. The following questions were addressed. (1) What diameter distributions were historically (pre-1900) present within old-growth ponderosa pine stands? (2) What were the historical ranges of densities of trees within old-growth ponderosa pine stands? (3) Were there common spatial patterns of trees in old-growth ponderosa pine stands? (4) How can this information be applied to support management of eastside ponderosa pine stands?

2. Methods

2.1. Study areas

Sampling for this study was conducted in three separate areas: Metolius, 23 km northwest of Sisters in north-central Oregon, Pringle Butte, 46 km southwest of Bend in south-central Oregon, and Blacks Mountain, 64 km northwest of Susanville in north-eastern California (Fig. 1). Each study area was dominated by ponderosa pine, with minor amounts of other conifers present. Each study area was unique with respect to the surrounding landscapes in that the study area was situated within a larger area designated and protected from all Euro-American logging. Consequently the legacy of historic stand structure was present. The Metolius study area is about 300 ha within the 581-ha Metolius Research Natural Area (RNA), established as a designated reserve for non-manipulative research in 1931 in recognition of the old-growth ponderosa pine stands present (Hall, 1972a). The Metolius study area (lat. 44°30'N, long. 121°37'30"W) lies on a nearly flat bench (elevation 900 m). Associated species include antelope bitterbrush (*Purshia tridentata* (Pursh) DC.) and western needlegrass (*Achnatherum occidentale* (Thurb. ex S. Wats.) Barkworth). Soils are well drained, developing in basalt and andesite residuum overlain with 2–5 cm of dacite pumice from the explosion of ancient Mount Mazama (now Crater Lake) some 6600 years ago and

¹ Unpublished report on file, USDA Forest Service, Pacific Northwest Research Station, LaGrande, OR.

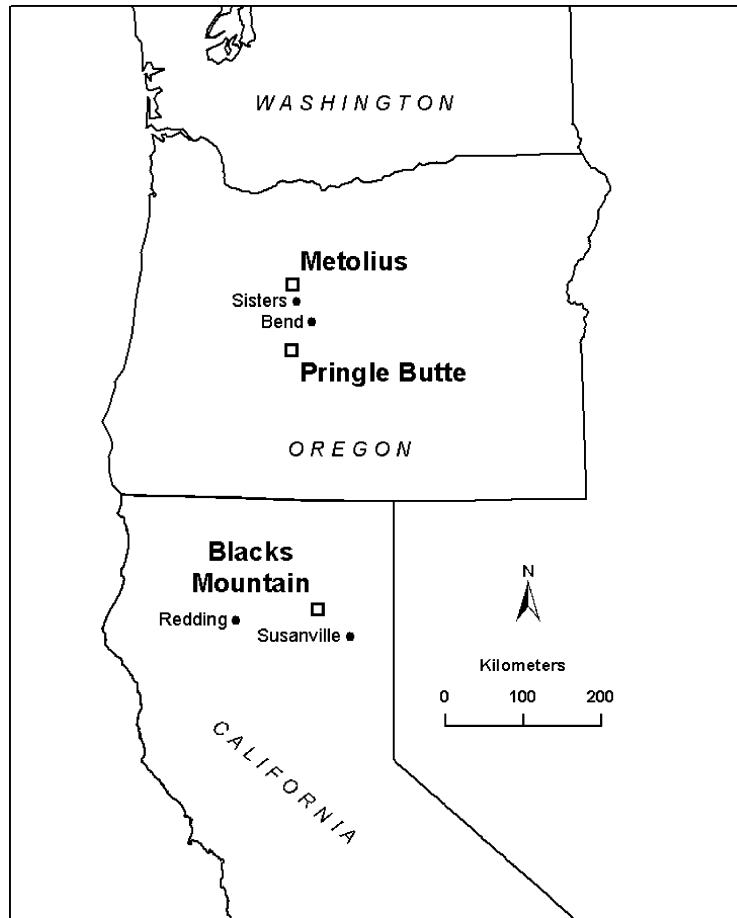


Fig. 1. Map of western USA, showing locations of old-growth ponderosa pine study areas sampled in this study.

<7 cm of basaltic ash from cinder cones to the east. The closest weather station is about 23 km southeast at Sisters, OR (lat. 44°17'N, long. 121°33'W) (Fig. 2) with continuous records since 1958; this station is at the margin of continuous forest, and probably receives less precipitation than the Metolius area. Mean annual temperature at the Sisters station is 7.5 °C and mean annual precipitation totals 357 mm, mostly as snow.

The Pringle Butte study area is about 200 ha in size, and lies within the 470-ha Pringle Falls RNA, established as a designated reserve for non-manipulative research in 1936 in recognition of its old-growth ponderosa pine stands (Hall, 1972b). Pringle Butte study area (lat. 43°42'N, long. 121°37'W) lies on a south slope (elevation 1460 m). Slope angle was <5%.

Associated vegetation includes lodgepole pine (*Pinus contorta* Dougl. ex Loud.) as a subordinate and antelope bitterbrush, snowbrush (*Ceanothus velutinus* Dougl. ex Hook.) and greenleaf manzanita (*Arctostaphylos patula* Greene). Soils are well drained, relatively undeveloped loamy coarse sands and ash 80–130 cm in depth, derived from aerial deposits after the explosion of ancient Mount Mazama. Three basaltic cinder cones form part of the RNA perimeter. The closest weather station is 130 m lower in elevation at Wickiup Dam, OR (lat. 4°41'N, long. 121°41'W) (Fig. 2), about 6 km to the southwest, with continuous records since 1941. The mean annual temperature at Wickiup Dam is 6.3 °C, and the mean annual precipitation totals 534 mm, mostly as snow during winter or rain during early summer convection storms.

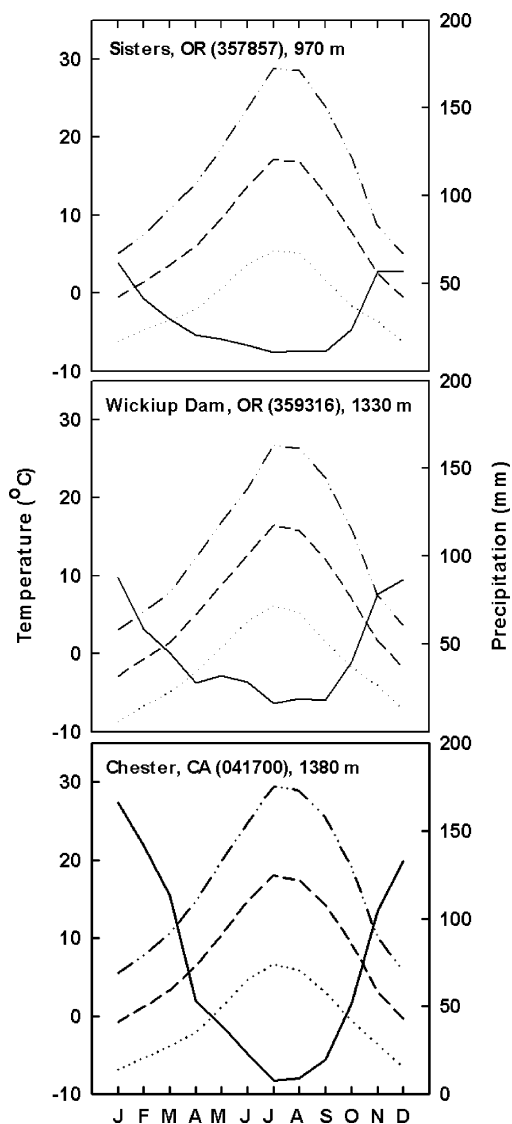


Fig. 2. Climatic features for weather stations in close proximity to study areas. Pattern of mean monthly maximum temperature, mean monthly temperature, and mean monthly minimum temperature (left axis and broken lines), with the pattern of mean monthly precipitation superimposed (right axis and solid lines) for Sisters near Metolius, Wickiup Dam near Pringle Butte, and Chesters near Blacks Mountain.

The Blacks Mountain study area lies within the 3715-ha Blacks Mountain Experimental Forest, established in 1934 as a principal site for management studies in eastside ponderosa pine forests. The Blacks Mountain study area (lat. $40^{\circ}40'N$, long.

$121^{\circ}10'W$) lies within a gently rolling basin with southern and western aspects (elevation 1700–2000 m). In addition to ponderosa pine, Jeffrey pine (*Pinus jeffreyi* Grev. and Balf.) occurs in limited amounts along the perimeter of frost pockets and at higher elevations. Incense-cedar (*Calocedrus decurrens* (Torr.) Florin) occurs as scattered individuals. White fir (*Abies concolor* (Gord. and Glend.) Lindl. ex Hildebr.) occurs occasionally at higher elevations. Other associated species include antelope bitterbrush, greenleaf manzanita, mountain big sage (*Artemisia tridentata* Nutt. spp. *vaseyana* (Rydb.) Beetle), Idaho fescue (*Festuca idahoensis* Elmer), and western needle grass. Soils are mostly moderately deep loams and sandy loams over fractured basaltic bedrock. The closest weather station is at Chesters, CA (lat. $40^{\circ}18'N$, long. $121^{\circ}14'W$) (Fig. 2) with continuous records since 1948; this station is about 40 km south of Blacks Mountain and probably receives less precipitation than the Blacks Mountain study area. Mean annual temperature at the Chester station is $8.1^{\circ}C$ and mean annual precipitation totals 860 mm, mostly as snow.

2.2. Sampling methods

Stand structure and spatial point patterns at Metolius were characterized between 1995 and 1997 within twelve $100\text{ m} \times 100\text{ m}$ plots, with the perimeter oriented in cardinal directions. Comparable data from five 1-ha plots were obtained during 1999 at Pringle Butte. Each plot was systematically established within a larger unit roughly 20-ha in size; plots were a fixed distance and direction from common benchmark points without regard for structural characteristics. All trees $\geq 15\text{ cm}$ tall were tagged, and species, diameter at breast height (dbh), and crown class (classified as dominant, codominant, intermediate, overtopped, or seedling) noted. Dominant trees had crowns that rose through or above the general canopy and received full sunlight from above and partial light from the side. Codominant trees had crowns in the upper canopy that were blocked from receiving light from the side by neighboring crowns. Intermediate trees had crowns that received little light from above and none from the side. Overtopped trees had crowns completely overtopped by one or more neighboring trees. Dominant and codominant trees are hereafter

referred to as “upper canopy” and intermediate and overtopped trees are referred to as “lower canopy.” Seedlings were defined as any stem between 15 cm and 1.37 m in height. Total tree height was measured with a clinometer or survey laser for randomly selected trees representing each of the four strata. A single increment core was taken at breast height from the same trees measured for height. Because some of the plots occurred in larger units in which low intensity underburning was applied within the previous five years, all stems were carefully assessed for bole char and crown scorch as indicators that the tree was either alive or dead before the fire.

Each stem was mapped by using a survey laser mounted on a tripod and a small reflector to measure bearing (nearest 0.1°) and horizontal distance (nearest 0.1 m) to the middle of each tree from reference points in $16.25\text{ m} \times 25\text{ m}$ cells. For small trees, the bole was bent to the side and the reflector was held directly over the root collar. For larger trees, the distance was measured to the side of the bole on the arc that passed through the pith. Reference points were established at the corners of cells that gave clear, unobstructed views to mapped trees and to the southwest corner of the plot. The number of reference points varied from 7 to 25, but most of the plots could be completely mapped by using 14 reference points. The maximum distance between any tree and a reference point was confined to $<35.4\text{ m}$. Finally, in each plot, the angle and horizontal distance from the southwest corner to each reference point was measured.

Coarse woody debris (CWD) sampling techniques followed the strip-plot method evaluated by Bate et al. (2002) and used by Torgersen (2002) for determining log density, large-end diameter, mean length, total length, volume, and percent cover of logs. The middle of a $4\text{ m} \times 40\text{ m}$ strip plot was centered over each of the nine interior cell corners, with the strip oriented at a bearing determined randomly. Only logs or parts of logs that were $\geq 1\text{ m}$ in length with large-end diameter $\geq 15\text{ cm}$ and small-end diameter $\geq 7.6\text{ cm}$ and the large end inside the strip plot qualified as contributing to log density. Large end, small end, and length of qualifying logs were measured. Only that portion of non-qualifying logs (those with large end falling outside the strip plot) that fell within the strip plot were measured for total length, volume, and cover, with diameter of the piece measured at the line of intercept

with the strip plot boundary. Volume of each log was calculated using Smalian’s formula:

$$\text{Vol}_i = \frac{1}{2}(\text{LEA}_i + \text{SEA}_i) \times L_i$$

where LEA_i and SEA_i are the cross-sectional areas of the large and small ends, and L_i is the length of the i th log. Percent cover was the vertical projection of logs as a percentage of the total area and assumed no overlap of pieces. In addition, the decomposition class of each log was recorded, following the protocol of Maser et al. (1979).

Data from Blacks Mountain were originally obtained as part of the long-term “methods of cutting” study (Dolph et al., 1995a) established in 1938. A complete control (no cutting treatment) was applied to an 8-ha experimental unit and replicated in 10 blocks uniformly distributed across the entire experimental forest. Within each control treatment unit, a $200\text{ m} \times 400\text{ m}$ plot was established with a transit and stadia with the long dimension roughly perpendicular to the contour lines. The plots were reinventoried in 1990 by using a staff compass and metal tape to map all live trees $>29.2\text{ cm}$ dbh in two hundred $20\text{ m} \times 20\text{ m}$ cells. Dead stems apparently were not noted at the time of plot establishment but were felled for fire-hazard reduction in 1947; all inventoried dead represent those stems that had died since this date. Hand-drawn maps of stem locations for the 10 control plots at Blacks Mountain were subsequently digitized by the staff at the Redding Silviculture Laboratory, Redding, CA, with locations converted to x, y coordinates (nearest 0.1 m). Because the original plots were larger than 1 ha, data from a $100\text{ m} \times 100\text{ m}$ subset were systematically extracted to provide conformity with the plot size used at Metolius and Pringle Butte. Increment cores were not collected and tree heights were not measured at Blacks Mountain. CWD data were not available from Blacks Mountain.

2.3. Analysis of age classes

Increment cores collected at Metolius and Pringle Butte were sanded to clarify the rings, and annual rings counted under a binocular microscope. For accuracy, counts were made independently by two people. The number of rings to the pith on cores where pith was not present was estimated using templates of concentric circles. Cores were discarded from further considera-

tion if the pith was not within an additional 10 rings. Total tree age was computed as the total number of annual rings in the core plus 10; based on local observation, 10 years was the average number of years required for a ponderosa pine seedling to reach 1.37 m in height.²

2.4. Analysis of structural components

Stem density, diameter class distribution, stand density index, basal area, mean tree height, and age distribution were computed to describe the population structure of standing trees in each plot and study area. Absolute density of stems was computed as the sum of all stems, including seedlings, within the plot. Because seedlings were defined as <1.37 m in height, they lack diameter and were not considered in subsequent summaries of class, stand density index, basal area, and mean tree height. Because sampling occurred on a full hectare, basal area of trees was computed as a summation of the cross-sectional areas of all trees ≥ 1.37 m in height. Trees were grouped into 10 cm dbh size classes to give size-frequency distributions for each plot. Stand density index (SDI) is a relative density measure based on the relationship between mean tree size and number of trees per unit area in a stand (Reineke, 1933), and has proved useful for quantifying relative density across a wide variety of stand conditions because it is independent of site quality and stand age (Long and Daniel, 1990). Because the diameter distribution was unknown or was not normal, SDI was calculated as a summation of individual tree values:

$$SDI = \sum \left(\frac{1}{25} dbh_i \right)^a$$

where SDI is stand density index, dbh_i is diameter in cm at breast height (1.37 m) of the i th tree in the plot, and the exponent a is a species-specific value (Shaw, 2000). Cochran (1992) defined a as 1.7653 based on a regional analysis of ponderosa pine density in Oregon rather than the more generally applied exponent 1.6 used for Blacks Mountain; 1.74 was used for lodgepole pine and 1.73 was used for all other species. SDI was calculated for each plot at Metolius, Pringle Butte, and Blacks Mountain. While dead trees (snags) are not normally summed for a determination of SDI, we

calculated a separate value of SDI for dead trees because the space they occupy is space not readily available for live trees.

A total of 251 trees were measured for total height at Metolius, ranging from 6 to 116 cm in diameter. An additional 211 trees were measured for total height at Pringle Butte; these sample trees ranged from 1.5 to 121.9 cm in diameter. Because it was not possible to measure heights of all trees at each study area, these two subsets were used to verify applicability of a general height–diameter equation especially developed for large tree sizes (Moore et al., 1996). This equation has the following form for ponderosa pine:

$$HT_i = 4.5 + 1769.17 \times e^{(-5.7742 \times dbh_i)^{-0.2197}}$$

where HT_i is the total height in feet of the i th tree and dbh_i is the corresponding diameter at breast height in inches. Regression of observed tree height against calculated height with a linear model resulted in an R^2 value of 0.94 for Metolius and 0.92 for Pringle Butte. Based on this fit, the equation was judged sufficient for estimating tree heights at Metolius and Pringle Butte. Height–diameter equations developed specifically for Blacks Mountain stands by Dolph et al. (1995b) were used for all pine, white fir, and incense-cedar at Blacks Mountain.

Log density (number ha^{-1}), mean large-end diameter, mean length of each log, cumulative length, volume of each log, total volume, percent cover, and frequency by decomposition class were summarized by species and plot for Metolius and Pringle Butte.

Analysis of variance (ANOVA) with least significant difference multiple comparison method was used to compare mean tree density, diameter, SDI, basal area, and height among the three study areas. Assumptions of normality and equal variances were tested graphically (Quinn and Keough, 2002). The t -tests were used to compare structural features between Metolius and Pringle Butte when comparable data were not available from Blacks Mountain. P -values from ANOVAs and t -tests are reported for all variables when significant ($P \leq 0.05$).

2.5. Analysis of spatial patterns

Angle and distance measurements for each tree within each cell were converted to a Cartesian coordinate system based on the respective reference point

² Unpublished data on file, USDA Forest Service, Pacific Northwest Research Station, LaGrande, OR.

using sine and cosine relations, then each entire plot was transformed to make the coordinate system correspond to an origin in the southwest corner. The distribution of trees within each plot was investigated by second-order spatial analysis with Ripley's $K(d)$ function, a cumulative density function which uses the second moment, i.e., the variance of all point-to-point distances in a closed plane (a fixed-area rectangular plot) to evaluate two-dimensional distribution patterns (Ripley, 1976; Diggle, 1983; Upton and Fingleton, 1985; Moeur, 1993; Haase, 1995). Ripley's $K(d)$ analysis compares the distribution of point-to-point (tree-to-tree) distances to a distribution for a hypothesized point pattern to test whether the observed pattern is random, aggregated, or regularly spaced. In this analysis, a circle of radius d is centered on each point and the number of individual points distributed within the circle is counted. For n individual points distributed in an area A , the density ($\lambda = n/A$) is the intensity or mean number of points per unit area. The function $\lambda K(n)$ is the expected number of additional points within radius d of any one arbitrary point. If the points are randomly (Poisson) distributed, the expected value of $K(d)$ is πd^2 . The cumulative distribution function of the distance from all trees on a plot to all other trees is estimated by $\hat{K}(d)$ as:

$$\hat{K}(d) = A \sum_{i=1}^n \sum_{j=1}^n \frac{w_{ij}(d)}{n^2}, \quad \text{for } i \neq j$$

where n is the number of trees, A is the area of the plot, d is the distance between tree i and tree j , and w_{ij} is an isotropic weighting parameter that corrects for boundary effects when the second tree is outside the plot (Ripley, 1977; Moeur, 1993). The $\hat{K}(d)$ distribution was computed for values of d from 0 to a maximum of 15 m at 0.2 m intervals for all trees and separately for upper and lower canopy trees. Selection of d is somewhat arbitrary but is influenced by plot size. After exploration with larger values we used a d of 15 m because this distance appeared to capture the distribution of all trees that might realistically influence any given tree. Conventionally, $\hat{L}(d)$ is reported rather than $\hat{K}(d)$. $\hat{L}(d)$ is a square root transformation that linearizes $\hat{K}(d)$, stabilizes its variance, and has expected value approximately zero under the Poisson assumption:

$$\hat{L}(d) = \sqrt{\frac{\hat{K}(d)}{\pi}} - d$$

Under this approach, we obtain an estimation of patch radius because the greatest positive deviation from zero within the bounds of d is an approximate indicator of patch radius (Martens et al., 1997).

To test the statistical significance of departure from hypothesized complete spatial randomness of the test statistic $\hat{L}(d)$, we used a Monte Carlo simulation approach to construct a 95% confidence interval based on 100 iterations of a Poisson distribution, with n equal to the same number of trees in the plot (Moeur, 1993). When trees were relatively close to each other, $\hat{L}(d)$ became positive and extended beyond or outside the upper limit of the confidence region and the observed distribution was considered to have a clumped distribution. When trees were relative far from each other, $\hat{L}(d)$ became negative and extended below the confidence region and the interpretation was judged to be uniform or regular. When $\hat{L}(d)$ remained within bounds of the upper and lower confidence bounds for any given d , the null hypothesis of complete spatial randomness was not rejected.

Spatial analysis of an individual plot using Ripley's $K(d)$ function and the $\hat{L}(d)$ statistic is informative in identifying a single unique spatial point pattern for that plot, and revealing how that pattern changes with scale (levels of d). Because the function and the corresponding confidence interval are sensitive to the number of points, different plots cannot be directly pooled to test the hypothesis that various spatial point patterns from different plots are in agreement and represent model conditions. Interpretations of Ripley's $K(d)$ function and the $\hat{L}(d)$ statistic has thus been limited to those for the single plot. To overcome this limitation and thus evaluate historic old-growth spatial point patterns from a larger number of plots representing a larger set of conditions, we used functional data analysis (Ramsay and Silverman, 1997) to calculate a mean $\hat{L}(d)$ for each of the three study areas. Functional data analysis is the statistical analysis of data where the data are themselves functions, i.e., the relationship of y to x over some defined range and domain. Functional data analysis has proved beneficial in evaluating independent functional observations from various unrelated fields such as cyclic curves representing human bone outlines with specific landmarks, reaction time after a visual stimulus in children with attention deficit hyperactive disorder, and components of weather records such as phase and amplitude variation

in weather records of temperature and pressure (Ramsay and Silverman, 2002). Functional data analysis generally involves some level of smoothing to obtain continuous functions from the source data. While the amount of smoothing used is somewhat arbitrary, we explored various options and selected a general B-spline (basis spline) method with five basis functions to provide the most generic or smoothest overall function (Ramsay and Silverman, 1997).

Our nomenclature for the $\hat{L}(d)$ statistic was augmented as $\hat{L}_{kl}(d)$, for plots $k = 1, 2, \dots, m_l$, with $l =$ designating study areas 1, $\dots, 3$, and m designating the number of plots within each study area. From this, we summarized the estimated spatial pattern functions across replicate plots within study areas to obtain an estimate of the mean spatial pattern for each study area, $\hat{L}_l(d)$. Separately, we derived confidence bounds for $\hat{L}_l(d)$ to assess spatial randomness of the mean spatial pattern function for each study area. We computed estimates of the variance function $\hat{V}_{kl}(d)$ within each plot based on n_{ij} , the number of trees in each plot, 100 iterations of a Monte Carlo simulation, and a Poisson distribution of the n_{ij} points, assuming spatial randomness. Functional data analysis methods were again used to composite (average) estimates of the variance functions at the plot level to obtain a combined estimate of variance at the study area level, $\hat{V}_l(d)$. The average variance function was then used to compute a standard error function at the study area level. The standard error function represents the sampling error of the mean function $\hat{L}_l(d)$, based on the number of plots within a study area, and was computed as $S.E._l(d) = [\hat{V}_l(d)/n_l]^{1/2}$. Approximate 95% confidence bounds for assessing spatial randomness of the mean spatial pattern function at the study area level is then $\pm 2 S.E._l(d)$, since the expected mean is equal to 0 assuming spatial randomness. The resulting mean spatial pattern function, $\hat{L}_l(d)$, and $\pm 2 S.E._l(d)$ confidence bounds for the mean were plotted for each study area to assess when the mean function departed from spatial randomness. Thus $\hat{L}_l(d)$ and upper and lower confidence bounds were for determining spatial randomness were calculated using 12 unique distributions for Metolius, 5 distributions for Pringle Butte, and 10 distributions for Blacks Mountain. Lack of spatial randomness is indicated when the mean function occurs outside the confidence bounds $\pm 2 S.E._l(d)$.

3. Results

3.1. Age structure

Diameter and total age relations in ponderosa pine are usually obscure; young trees persist for decades with little diameter growth when suppressed, and old trees persist for centuries with little diameter growth when crowns deteriorate. Total ages of 215 trees were obtained at Metolius; these trees ranged from 37 to 618 year in age (Fig. 3). A total of 99 trees were from dominant or codominant trees in the upper canopy, with mean dbh of 63.9 cm and mean total age of 214 years (Fig. 4). There were two prominent peaks in the frequency of establishment of these aged trees; the first peak was 120–123 years and the second peak was 250–260 years before present. The remaining 116 aged trees were intermediate and overtopped trees in the lower canopy with mean dbh of 21.5 cm and mean total age of 78 years (Fig. 4). While no minimum dbh criterion was used for classifying live trees into the upper canopy classes, the upper canopy class trees that were aged were, with only one exception, >36 cm dbh and >100 years in total age. Conversely, lower canopy class trees that were aged were generally smaller in dbh and younger.

A total of 170 trees were sampled for total age at Pringle Butte. Trees ranged in age from 47 to 613 years in age (Fig. 3). A total of 118 ponderosa pine were from dominant or codominant positions in the upper canopy, with mean dbh of 56.5 cm and mean total age of 243 years (Fig. 4). While our random selection of trees for sampling to determine total age was not designed to identify discrete age classes, $>40\%$ of the dominant and codominant trees were between 150 and 190 years in age. Intermediate and overtopped trees in the lower canopy were represented by 40 ponderosa pine with mean dbh of 21.2 cm and mean total age of 105 years (Fig. 4). While upper canopy class trees were >36 cm dbh and >100 years in total age, similar to conditions at Metolius, lower canopy class trees often were <36 cm dbh yet >100 years in total age.

Additional size-age sampling at Pringle Butte included three upper canopy class lodgepole pine with mean dbh of 35.5 cm and mean total age of 123 years, and eight lower canopy class lodgepole pine with mean dbh of 17 cm and mean total age of 60 years.

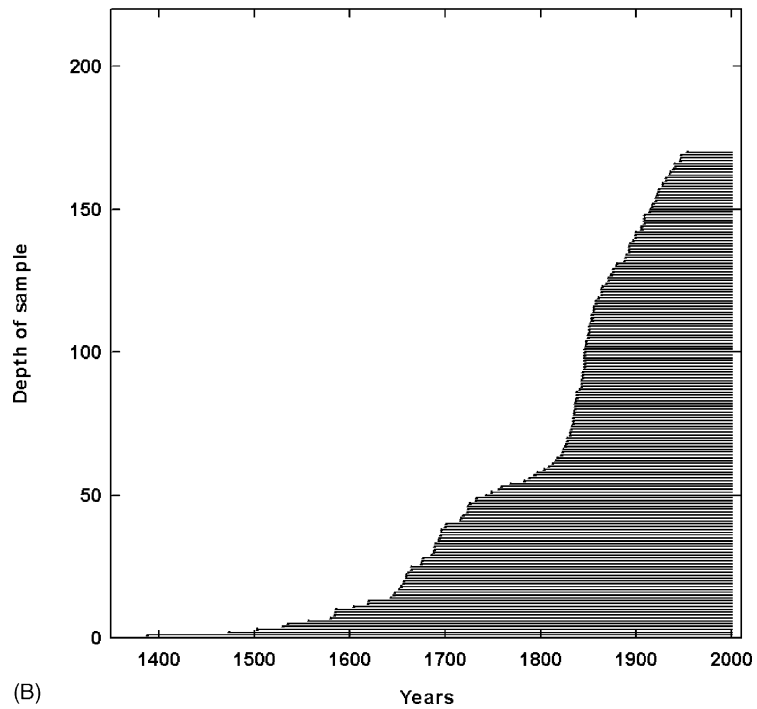
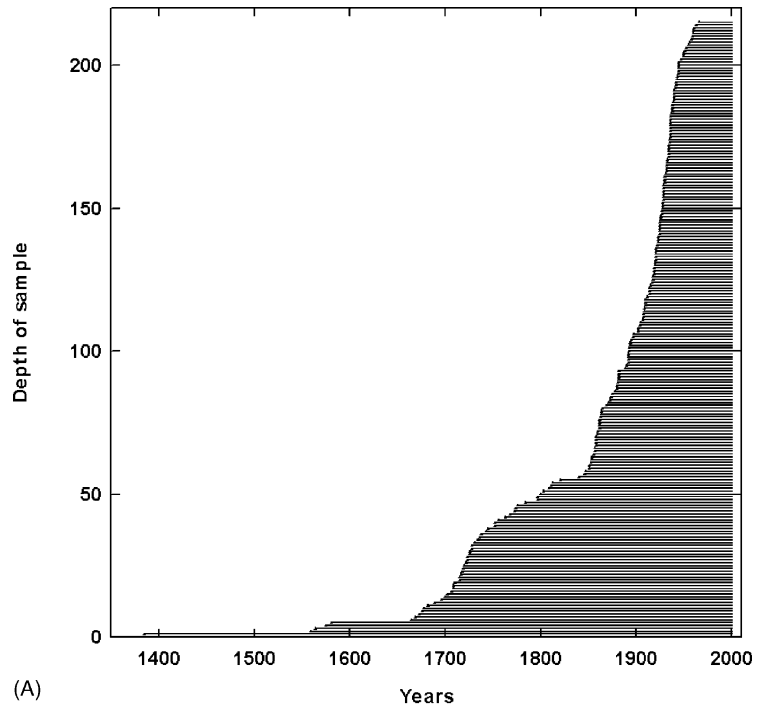


Fig. 3. Sample depth, the number of trees cored for total age at (A) Metolius and (B) Pringle Butte.

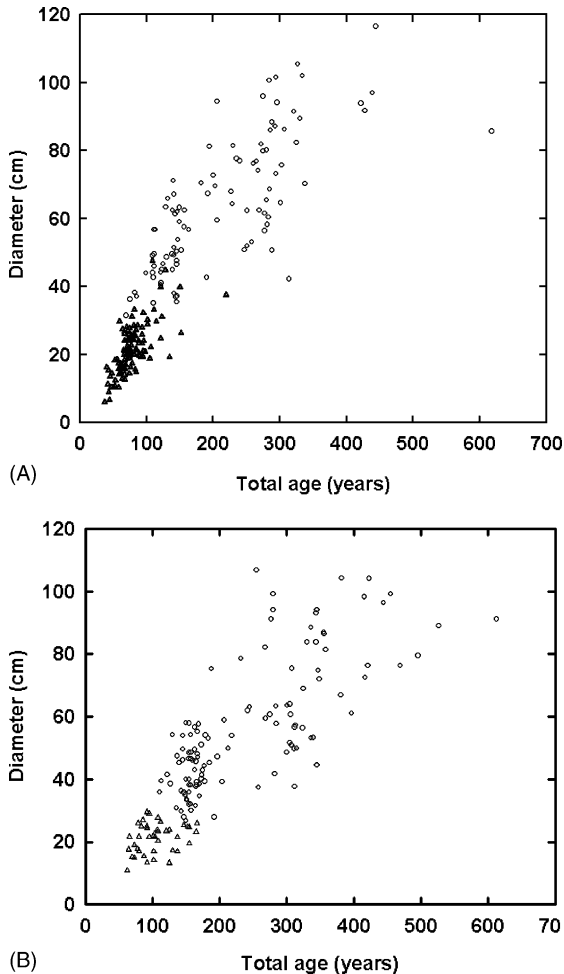


Fig. 4. Age–diameter distribution for two sets of sample trees at (A) Metolius and (B) Pringle Butte: dominant and codominant trees in the upper canopy (○) and intermediate and overtopped trees in the lower canopy (△).

We have no direct size–age data from Blacks Mountain; all of the stems were assumed to be in excess of 100 years in age because initial characterization was limited by minimum diameter. Recent work at Blacks Mountain supports this assumption; dominant and codominant trees occurred in three age classes with means of 330, 223 and 109 years, and intermediate and overtopped trees were <75 years in age (personal communication, Carl Skinner, Redding Silviculture Laboratory, Redding, CA).

The size–age distributions from each study area formed the basis of our generalization that trees that

were alive and in the upper canopy at each study area at the beginning of this study were present in 1900 and represent “old-growth” trees, and in contrast, the lower canopy trees and all seedlings noted in this study at Metolius and Pringle Butte were not present in 1900 and represent in growth that was added since 1900.

3.2. Size structure of standing trees

Structural features were characterized for 22,242 stems at Metolius, 11,307 stems at Pringle Butte, and 584 stems at Blacks Mountain. Density of all stems ranged from 510 to 3402 trees ha^{-1} at Metolius and 1474 to 3197 trees ha^{-1} at Pringle Butte. Density of all stems at Blacks Mountain was based only on those stems >29.5 cm in dbh and ranged from 28 to 105 trees ha^{-1} (Table 1).

A total of 1345 trees were classified as live ponderosa pine in the upper canopy across the three study areas. Density of live ponderosa pine in the upper canopy ranged from 34 to 94 trees ha^{-1} at Metolius, 35 to 79 trees ha^{-1} at Pringle Butte, and 15 to 73 trees ha^{-1} at Blacks Mountain. Despite the uneven sample sizes, Bartlett’s test did not indicate unequal variances. An *F*-test failed to suggest a significant difference in mean density of upper canopy ponderosa pine among the three study areas ($P = 0.181$); the overall mean density was 50 ± 3.5 trees ha^{-1} (mean \pm S.E.). Individual live upper canopy ponderosa pine ranged from 12.0 to 133.1 cm dbh and 10.9 to 49.3 m in height at Metolius, 16.0 to 121.9 cm dbh and 12.8 to 47.1 m in height at Pringle Butte, and 29.5 to 129.8 cm dbh and 15.6 to 42.2 m in height at Blacks Mountain. Frequency of large live ponderosa pine was somewhat evenly distributed between 20 and 100 cm dbh and tended to peak between 60 and 70 cm dbh at Metolius, was more narrowly distributed between 30 and 90 cm dbh and peaked between 40 and 50 cm dbh at Pringle Butte, and was right-skewed with a peak between 40 and 50 cm dbh at Blacks Mountain (Fig. 5). Mean diameter did not differ among the three study areas ($P = 0.832$); the overall mean was 60.0 ± 1.55 cm dbh. When the diameter distribution of the three study areas were pooled, the distribution was noticeably more modal (Fig. 6). In contrast, the mean maximum height (the single tallest tree in each plot) differed among study areas

Table 1

Structural attributes of density, diameter at breast height, stand density index, basal area and height (mean and standard error) in old-growth ponderosa pine stands at Metolius, Pringle Butte, and Blacks Mountain

	Species ^a	Density (stem ha ⁻¹)	dbh (cm)	SDI ^b	BA ^c (m ² ha ⁻¹)	Height (m)
Metolius						
All stems		1853 (262.6)	–	571 (31.9)	30.9 (1.40)	44.8 (0.74) ^d
Live upper canopy	Pp	54 (5.4)	60.5 (2.74)	267 (15.5)	16.7 (0.98)	30.9 (0.93)
Dead upper canopy	Pp	10 (1.4)	60.9 (6.06)	57 (9.3)	3.6 (0.60)	30.3 (2.85)
Live lower canopy	Pp	1619 (270.0)	7.9 (0.55)	245 (32.0)	10.6 (1.32)	6.7 (0.46)
Seedlings	Pp	156 (70.6)	–	–	–	–
Live lower canopy	Other	9 (2.1)	8.0 (1.79)	3 (0.7)	0.1 (0.03)	6.4 (1.51)
Seedlings	Other	6 (3.2)	–	–	–	–
Pringle Butte						
All stems		2261 (285.2)	–	552 (26.6)	30.7 (1.53)	44.8 (1.69) ^d
Live upper canopy	Pp	57 (7.7)	61.0 (2.08)	282 (31.2)	17.5 (1.87)	31.4 (0.61)
Dead upper canopy	Pp	11 (2.5)	59.4 (3.40)	58 (15.9)	3.6 (1.04)	30.7 (1.04)
Live lower canopy	Pp	1489 (179.0)	5.5 (0.58)	177 (25.5)	5.5 (0.58)	5.1 (0.45)
Seedlings	Pp	392 (85.3)	–	–	–	–
Dead upper canopy	Lpp	1 (1.1)	42.4 (1.94)	9 (7.0)	0.5 (0.40)	25.4 (0.40)
Live lower canopy	Lpp	195 (137.2)	8.9 (1.03)	31 (18.8)	1.3 (0.84)	7.4 (0.85)
Seedlings	Lpp	116 (108.4)	–	–	–	–
Blacks Mountain						
All stems ^e		58 (7.6)	59.8 (2.41)	261 (35.8)	18.9 (2.55)	38.1 (0.94) ^d
Live upper canopy	Pp	42 (5.2)	58.8 (2.31)	173 (21.0)	12.6 (1.56)	25.6 (0.69)
Dead upper canopy	Pp	7 (1.6)	63.8 (8.88)	35 (6.2)	2.7 (0.46)	25.8 (3.19)
Live upper canopy	Other	8 (2.1)	46.5 (11.11)	47 (13.5)	3.2 (0.94)	16.4 (3.62)
Dead upper canopy	Other	1 (0.6)	23.4 (9.80)	7 (3.2)	0.4 (0.21)	9.7 (4.01)

^a Species are: Pp: ponderosa pine, other: unspecified mixture of grand fir, Douglas-fir, western larch, white fir, and incense-cedar, Lpp: lodgepole pine.

^b Stand density index.

^c Basal area.

^d Height for all stems is maximum rather than mean.

^e Blacks Mountain data based on stems ≥ 29.5 cm dbh.

($P < 0.001$). The tallest tree in each unit were taller at Metolius and Pringle Butte compared to Blacks Mountain ($P < 0.001$); mean maximum height was 44.8 ± 0.69 m for Metolius and Pringle Butte, and 38.1 ± 0.94 m at Blacks Mountain. Similarly, the mean height of upper canopy ponderosa pine differed among the study areas ($P < 0.001$). Mean height of upper canopy ponderosa pine at Metolius and Pringle Butte was 31.1 ± 0.67 m, and the mean height of upper canopy ponderosa pine at Blacks Mountain was 25.6 ± 0.69 m (Table 1). Basal area of upper canopy ponderosa pine was marginally similar among the study areas ($P = 0.049$) with an overall mean basal area of 15.3 ± 0.80 m² ha⁻¹. Basal area of upper canopy ponderosa pine tended to be higher at Metolius and Pringle Butte than at Blacks Mountain. SDI is related to basal area through diameter, yet differences among study areas in

SDI were more pronounced than those for basal area. The SDI at Blacks Mountain was less than that for Metolius and Pringle Butte ($P < 0.002$). Mean SDI at Blacks Mountain for upper canopy ponderosa pine was 172.6 ± 19.37 compared to 271.2 ± 13.71 for Metolius and Pringle Butte.

Large dead ponderosa pine were a common feature at all three study areas; a total of 243 ponderosa pine snags were characterized. Variation in the density of dead ponderosa pine in the upper canopy was considerable; a few units were devoid of snags, while the maximum number observed was 21 snags ha⁻¹. Despite this variation in density, an *F*-test failed to suggest a significant difference in mean density of dead ponderosa pine in the upper canopy among the three study areas ($P = 0.271$); the overall mean density was 9.0 ± 0.97 trees ha⁻¹. Ponderosa pine snags

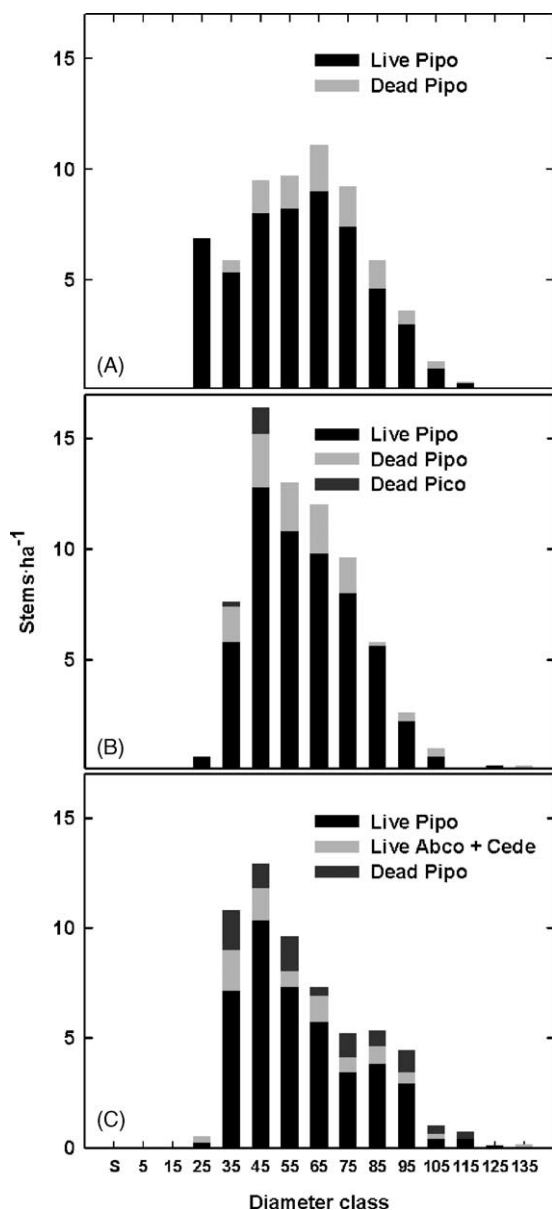


Fig. 5. Diameter distribution of large live and dead trees in the upper canopy of old-growth ponderosa pine stands at (A) Metolius; (B) Pringle Butte; and (C) Blacks Mountain. Species codes: Pipo, *Pinus ponderosa*; Pico, *P. contorta*; Abco, *Abies concolor*; Cede, *Calocedrus decurrens*.

in the upper canopy ranged from 36.4 to 110.8 cm dbh and 22.9 to 44.8 m in height at Metolius, 36.2 to 143.2 cm dbh and 22.9 to 51.2 m in height at Pringle Butte, and 30.2 to 118.6 cm dbh and 15.9 to 40.2 m in

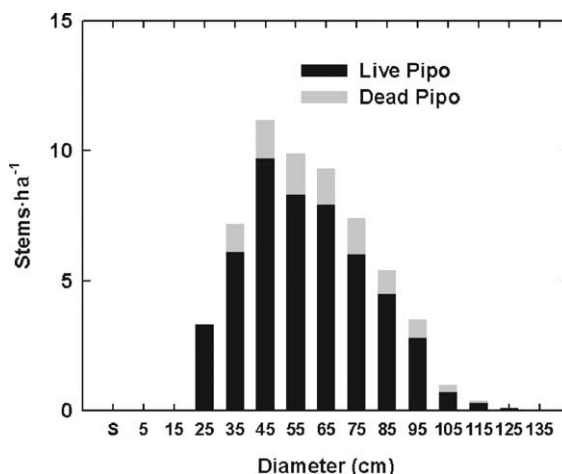


Fig. 6. Diameter distribution of large live and dead trees in the upper canopy of old-growth ponderosa pine stands, pooled from three study areas. Species code: Pipo, *Pinus ponderosa*.

height at Blacks Mountain. The frequency distribution of dead ponderosa pine followed the distribution of live ponderosa pine at each study area; the distribution of dead tree diameters tended to be relatively broad at Metolius, relatively narrow at Pringle Butte, and right skewed at Blacks Mountain (Fig. 5). When the diameter distribution of the three study areas were pooled, the distribution was broadly modal (Fig. 6). There were no differences among study areas in mean diameter ($P = 0.927$), height ($P = 0.261$), basal area ($P = 0.475$), and SDI ($P = 0.162$) for ponderosa pine snags; the overall mean diameter was 61.7 ± 4.33 cm, the overall mean height was 28.7 ± 1.76 m, the overall mean basal area was 3.3 ± 0.37 m² ha⁻¹, and the overall mean SDI was 49.0 ± 5.55 .

A large number of small ponderosa pine were characteristic of Metolius and Pringle Butte; a total of 26,873 stems in the lower canopy were mapped across the two study areas. Density ranged from 443 to 3313 trees ha⁻¹, and averaged 1619 trees ha⁻¹ at Metolius and 1489 trees ha⁻¹ at Pringle Butte (Table 1). Results of a *t*-test with unequal variances failed to indicate a significant difference in mean density of lower canopy trees between these two study areas ($P = 0.695$). The overall mean density was 1581 ± 194.8 trees ha⁻¹. Ponderosa pine in the lower canopy were larger in dbh ($P = 0.01$), and taller ($P < 0.024$), and accounted for more basal area ($P = 0.009$) at Metolius compared to Pringle Butte, yet there was no difference in the two

areas in SDI ($P = 0.117$). The overall mean SDI was 245 ± 24.6 .

Density of ponderosa pine seedlings ranged from 1 to 744 seedlings ha^{-1} , and averaged 156 at Metolius and 392 at Pringle Butte. Results of a t -test with unequal variances failed to indicate a significant difference in the mean density of ponderosa pine seedlings ($P = 0.06$); the overall density was 225 ± 60.6 seedling ha^{-1} .

3.3. Spatial distribution pattern

Ripley's $K(d)$ analysis of spatial point patterns using upper canopy trees revealed significant departure from randomness in 24 of the 27 plots. These departures are first illustrated with two examples of individual plots, and then presented as a general pattern for each of the three study areas.

The first example is plot 23 at Metolius, based on 99 upper canopy trees of which 83 were alive and 16 were dead trees (Fig. 7). The spatial point pattern is a direct representation of mapped tree coordinates, with the southwest corner of the plot corresponding to coordinates (0, 0). Large portions of the plot contained no upper canopy trees, especially gaps in the northeast and southeast corners. Trees generally were aggregated into clumps. The mean distance between each tree and its closest neighbor was 4.2 ± 3.1 m. The mean density within a maximum distance d (15 m) was 9.4 trees. Examination of the plot of $\hat{L}(d)$ as a function of d (Fig. 7) revealed several contrasting features. First, the distribution of upper canopy trees was not significantly different from random at scales of ≤ 1.8 m. Second, the distribution was significantly different from random at scales of ≥ 2.0 m. The significant positive deviation of the sample statistic from random suggests a general clumped distribution of the trees at these scales.

The second example is plot 281 at Pringle Butte, based on 92 upper canopy trees of which 80 were alive and 12 were dead trees (Fig. 8). Again, large portions of the plot contained no upper canopy trees, especially gaps in the western half. In contrast to plot 23, trees in plot 281 generally were not aggregated into recognizable clumps. The mean distance between each tree and its closest neighbor was 4.9 ± 3.3 m. The mean density within a maximum distance d (15 m) was 6.5 trees. Examination of the plot of $\hat{L}(d)$ as a function

of d (Fig. 8) revealed a single point pattern: the distribution of upper canopy trees tended to deviate from random at scales between 2.2 and 9.2 m but was not significantly different from random at all scales < 15 m except at 3.2 and 4.6 m. The significant positive deviation of the sample statistic from random at only these two distances suggests a general random distribution of the trees across all scales.

While not tested statistically, there was no apparent relationship between the number of age classes found on a sample plot and the type of spatial pattern, either a clumped or a random distribution of upper canopy trees.

The features portrayed in these two examples were found repeatedly at all three study areas. Across all three study areas, the mean distance between each tree and its closest neighbor was 6.5 ± 0.3 m and did not differ among the tree study areas. Similarly, the mean density within a maximum distance d (15 m) was 5.3 ± 0.4 trees and did not differ among study areas. The plots of $\hat{L}(d)$ as a function of d were highly similar to Fig. 7 for 6 of the 12 sample plots at Metolius, one sample plot at Pringle Butte, and 4 of the 10 sample plots at Blacks Mountain, with positive deviations that were significantly different from random at scales of ≥ 2.0 m, indicating a general clumped distribution of trees. In contrast, the plots of $\hat{L}(d)$ as a function of d for the remaining six study plots at Metolius, three sample plots at Pringle Butte, and six sample plots at Blacks Mountain were highly similar to Fig. 8, with little or no significant deviation from random across all scales of d . This indicated a general random distribution of trees in these sample plots. Occurring as an apparent anomaly, the plot of $\hat{L}(d)$ as a function of d for a single sample plot at Pringle Butte, containing 43 live and dead trees, contained negative deviations that were significantly different from random at scales of ≥ 6.2 m, indicating a general uniform distribution of trees.

Functional data analysis of the spatial relationship of all sample plots by study area revealed two strong patterns (Fig. 9). There was a significant negative deviation of the cumulative distribution of $\hat{L}_i(d)$ at scales ≤ 1 m and a significant positive deviation of $\hat{L}_i(d)$ scales > 2.8 m Metolius. Similarly, there was a significant negative deviation of the cumulative distribution of $\hat{L}_i(d)$ at scales ≤ 1.4 m and a significant positive deviation of $\hat{L}_i(d)$ scales ≥ 8.6 m at Blacks

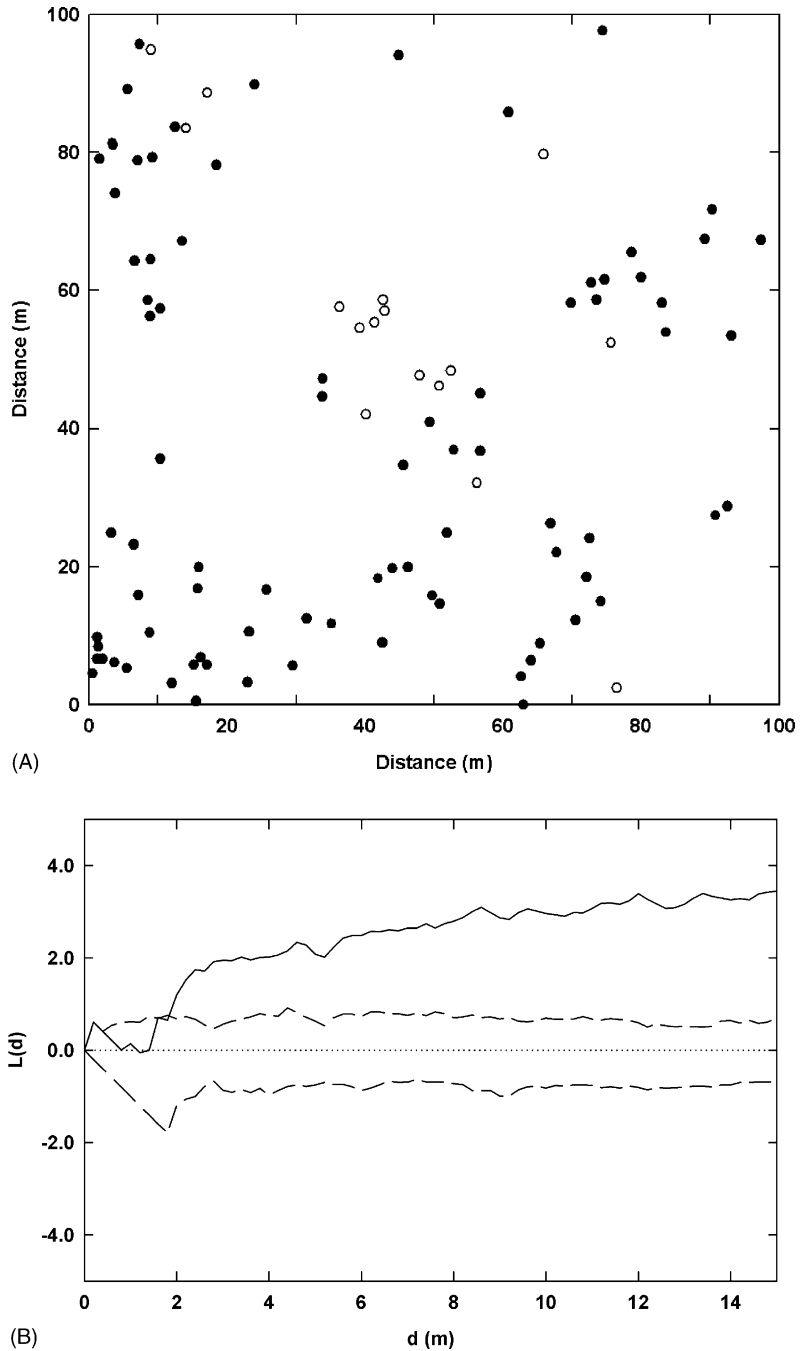


Fig. 7. (A) Spatial point pattern of large live (●) and dead (○) trees in the upper canopy of old-growth plot 23 at Metolius study area and (B) the results of Ripley's $K(d)$ analysis on these 99 trees, with the empirical cumulative distribution of $\hat{L}(d)$ shown as a solid line, the expected random distribution as a dotted line with mean equal to zero, and the point-wise 95% confidence envelope around the expected distribution of complete spatial randomness shown by dashed lines.

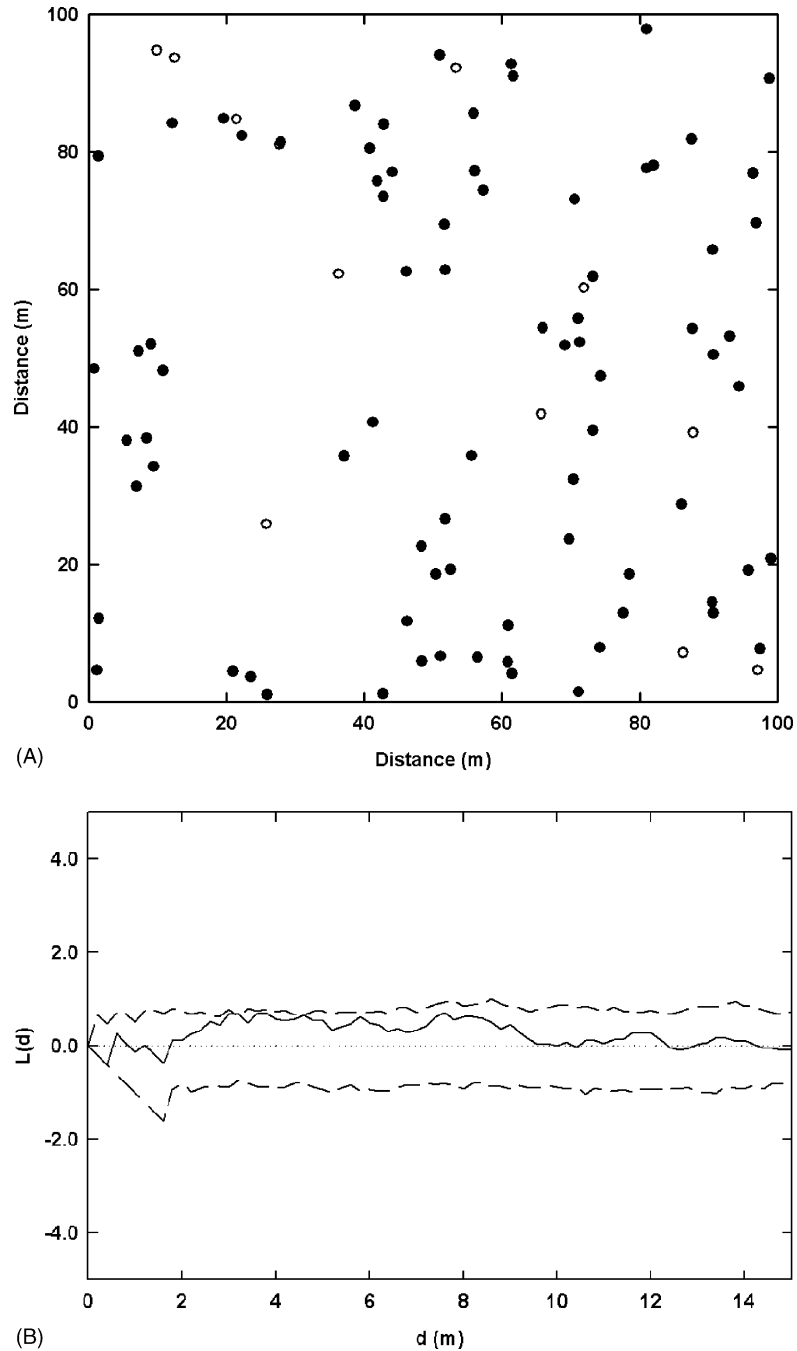


Fig. 8. (A) Spatial point pattern of large live (●) and dead (○) trees in the upper canopy of old-growth plot 281 at Pringle Butte study area and (B) the results of Ripley's $K(d)$ analysis on these 92 trees, with the empirical cumulative distribution of $\hat{L}(d)$ shown as a solid line, the expected random distribution as a dotted line with mean equal to zero, and the point-wise 95% confidence envelope around the expected distribution of complete spatial randomness shown by dashed lines.

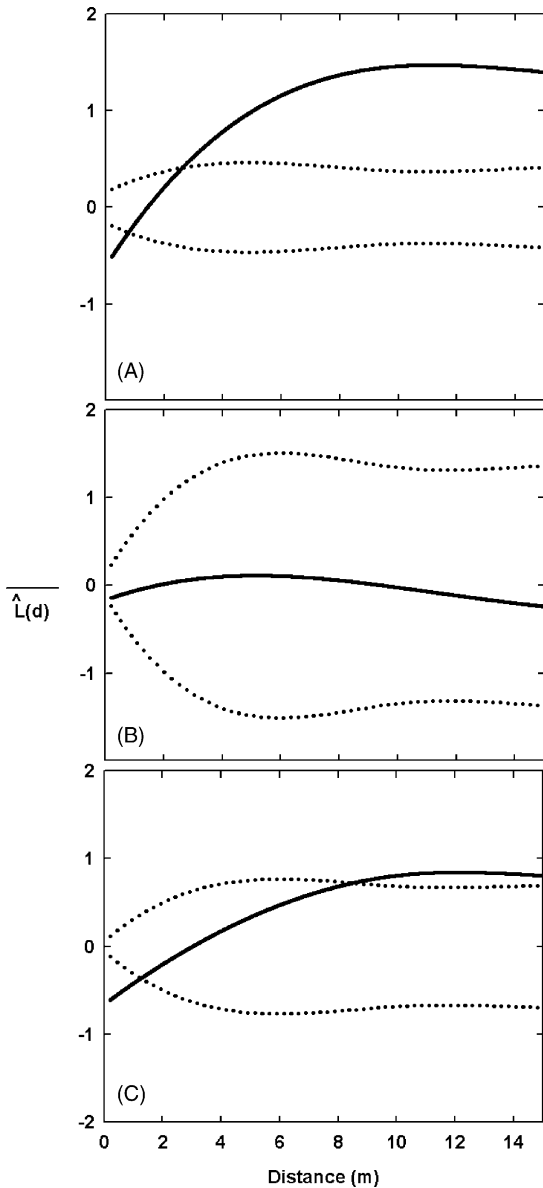


Fig. 9. Summary spatial distribution patterns resulting from functional data analysis for large live and dead trees in the upper canopy of old-growth stands at (A) Metolius; (B) Pringle Butte; and (C) Blacks Mountain study areas, with the empirical cumulative distribution of $\hat{L}_L(d)$ shown as a solid line, and the point-wise 95% confidence envelope around the expected distribution of complete spatial randomness shown by dashed lines.

Mountain. The significant negative deviation at scales ≤ 1.0 m at Metolius and ≤ 1.4 m Blacks Mountain suggest a uniform distribution, which likely

implies the minimum distance between individuals. At scales of $1.2 \leq d \leq 2.6$ m at Metolius and $1.6 \leq d \leq 8.4$ m at Blacks Mountain, the deviation from random was not significant, suggesting the distribution of trees was random. More importantly, significant positive deviation from complete spatial randomness at larger scales at Metolius and Blacks Mountain suggests a clumped distribution. Maximum radius of the clumps is suggested by the distance at which $\hat{L}_L(d)$ culminates. Thus, large live and dead upper canopy trees at Metolius were clumped and these clumps were about 22.5 m in diameter. Large live and dead upper canopy trees at Blacks Mountain also were clumped and these clumps were about 24 m in diameter.

In contrast, there was no significant deviation from complete spatial randomness across all scales ≤ 15 m at Pringle Butte. Thus, large live and dead upper canopy trees in old-growth plots at Pringle Butte were randomly distributed.

3.4. Size structure of CWD

Logs were a common feature of ponderosa pine plots at Metolius and Pringle Butte. A total of 170 logs at Metolius and 115 logs at Pringle Butte were measured; descriptive statistics for the two areas are presented as Table 2. Density ranged from 13.9 to 90.3 logs ha^{-1} across the two areas. Results of a *t*-test

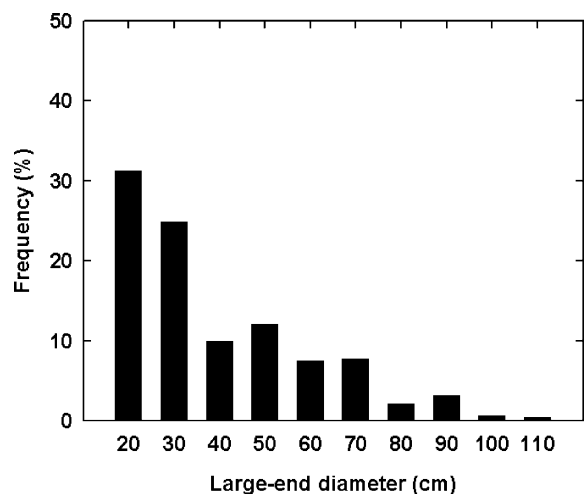


Fig. 10. Diameter distribution of the large end of logs in old-growth ponderosa pine stands at Metolius and Pringle Butte.

Table 2
Down wood characteristics (mean and standard error) for Metolius and Pringle Butte

	Density (stem ha ⁻¹)	LED ^a (cm)	Length (m)	Total length (m ha ⁻¹)	Volume (m ³ ha ⁻¹)	Piece volume (m ³)	Log cover (m ² ha ⁻¹)
Metolius	40.5 (5.5)	38.9 (3.2)	4.0 (0.2)	394.2 (39.9)	60.4 (7.4)	4.2 (0.4)	1.5 (0.2)
Pringle Butte	62.5 (9.8)	34.3 (3.0)	4.8 (0.4)	797.9 (209.1)	67.0 (13.1)	2.9 (0.4)	2.2 (0.4)

^a Large-end diameter.

with unequal variances failed to indicate a significant difference in mean density of logs between these two study areas. The overall mean density was 47.0 ± 5.28 logs ha⁻¹. Similarly, there was no difference between Metolius and Pringle Butte with respect to mean large-end diameter (mean \pm S.E. = 37.6 ± 2.41 cm), mean length of each log (4.2 ± 0.09 m), the cumulative length of all logs (512.9 ± 78.12 m), the total volume of all logs (62.3 ± 6.30 m³ ha⁻¹), and the cover of all logs ($1.7 \pm 0.08\%$). In contrast, individual logs were smaller in volume at Pringle Butte ($P = 0.036$); logs averaged 4.2 ± 0.36 m³ at Metolius and 2.9 ± 0.42 m³ at Pringle Butte. Because mean large-end diameter was similar at the two study areas, values for large-end diameter were pooled, and their frequency distribution revealed a strong negative exponential relation with

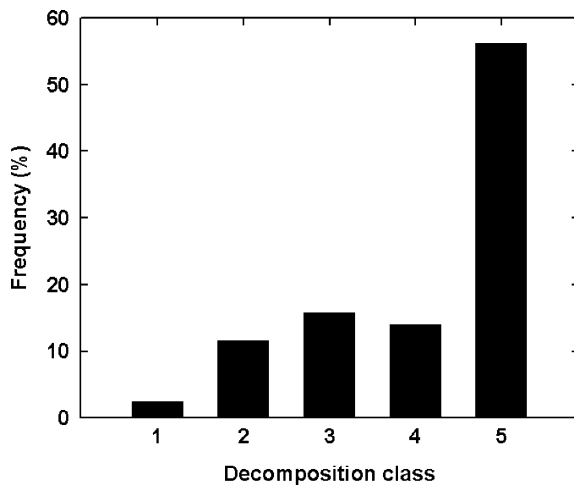


Fig. 11. Frequency distribution of logs by decomposition class in old-growth ponderosa pine stands at Metolius and Pringle Butte. Decomposition classes based on Maser et al. (1979); logs in decomposition class 1 had intact bark, were round with relatively intact, sound wood, and were elevated on support points, while logs in decomposition class 5 had missing bark, were soft and oval, and rested fully on the ground.

diameter (Fig. 10). More than 85% of the logs were between 15 and 65 cm in large-end diameter.

More than half of the logs were classified as decomposition class 5 (Fig. 11), characterized by the absence of bark and twigs, soft, blocky pieces of wood that have faded to light yellow or gray, overall log shape round to oval, and the log resting fully on the ground. This suggested that most of the logs were in place for considerable time. In contrast, <3% were classified as decomposition class 1, characterized by fully intact bark, presence of twigs, the wood sound with no fading in color, the log round and usually elevated on support points. This suggested that only a few logs represented recent recruitment. The frequencies of logs classified in decomposition classes 2, 3, and 4 were relatively similar to each other. We made no attempt to distinguish between logs that showed the effects of recent burns, logs that showed the effects of fires that occurred presumably before the beginning of fire protection, and logs that showed no effect of fire. We did note at both Metolius and Pringle Butte the presence of logs with char in plots where fire has been excluded since establishment of the RNA.

4. Discussion

4.1. Disturbance regimes

Metolius, Pringle Butte, and Blacks Mountain are all study areas that belong to formally designated Research Natural Areas or Experimental Forests that were established in the early 1930s because of their predominance of old-growth ponderosa pine stands unaffected by human intervention or activity. Outside of these formally designated areas, the common management objective was to convert these multi-aged forests to even-aged stands under a strategy of reducing the risk of losses to insects, diseases, and wildfire

(Johnson et al., 1994). These three study areas are easily distinguishable as large islands of old-growth surrounded by vast landscapes of young ponderosa pine stands resulting from the extensive harvesting that occurred during the 1940s and 1950s. Much of the area encircling Pringle Butte, for example, is fragmented by clearcuts that were replanted with uniformly-spaced ponderosa pine seedlings.

Natural disturbance regimes in eastside ponderosa pine stands represented by our three study areas are characterized by the combined effects of insects, diseases, and fire. Major insects associated with old-growth ponderosa pine forests include the pandora moth (*Coloradia pandora* Blake), the western pine beetle (*Dendroctonus brevicomis* LeConte), and the turpentine beetle (*D. valens* LeConte). Old-growth ponderosa pine forests at each of our study areas are subject to defoliation from pandora moth whose larvae consume the needles produced during the previous year. Periods of reduction in radial growth at Metolius were consistent with growth reductions identified by Speer et al. (2001) at Pringle Butte in response to pandora moth outbreaks. While outbreaks rarely led to tree mortality, repeated overstory defoliation affects the amount of sunlight, water, and nutrients available for understory trees and associated vegetation. Mortality from western pine beetle in old-growth ponderosa pine stands occurs at low levels unless regional droughts affect tree vigor across entire watersheds, leading to greater than normal host availability. Low-level mortality from western pine beetle results in widely scattered snags. The turpentine beetle attacks wounded trees near their base or at shallow roots, often after the litter has been consumed by fire. While normally nonlethal, attacks by turpentine beetles place an additional stress on old-growth ponderosa pine subjected to competition and climatic stresses when boles are wounded by fire.

Comandra blister rust (*Cronartium comandrae* Pk.) is common at Metolius and Pringle Butte, but apparently is lacking at Blacks Mountain. This native disease invades the fine twigs and main branches in the crown and develops cankers high in the bole which slowly progress down the bole, eventually killing the top and producing excessive resin flows above the canker as the wood becomes case hardened (Childs, 1968). Top-killed trees survive many years, eventually developing a resin-soaked, case hardened snag that persists for decades.

Individual ponderosa pine at all three study areas were infected at low levels with dwarf mistletoe (*Arceuthobium campylopodum* (Engelm.) Gill) which parasitizes the tree and can reduce vigor and tree growth. Occasionally, dwarf mistletoe-caused brooms develop at heights that affect fire behavior.

The most comprehensive fire history study of ponderosa pine forests in this region was conducted by Bork (1984) in stands surrounding our Pringle Butte study area; using dendrochronology techniques she reconstructed a 619-year chronology for six disjunct plots totaling 100 ha and found a composite fire free interval of 7–20 years. Between the years 1700 and 1800, 48 fires occurred, with 41 fires occurring during the next century. With the advent of fire suppression activities, only 17 fires occurred during the next eight decades.

Lightning has long been known as the principal nonhuman ignition mechanism for fires in eastside ponderosa pine forests. Annual lightning patterns for broad regions containing our study areas apparently are higher than for surrounding regions as a result of storm tracks and a propensity for anticyclonic storms to develop in July and August (Agee, 1993). Frequent dry lightning days, during which cloud-to-ground lightning strikes develop without accompanying precipitation, occur throughout this region when both stability and moisture levels in the lower atmosphere are low (Rorig and Ferguson, 1999). Frequency of dry lightning in eastside ponderosa pine forests also coincides with the time of year when moisture content of fine fuels is lowest. Frequent low-intensity fires resulting from lightning thin stands from below by killing small-diameter stems through a combination of cambial and root damage and crown scorch, consume litter and down wood, open the stands to increased sunlight, and lead to vertical stratification of fuels by eliminating fuel ladders between the forest floor and the overstory canopy (Saveland and Bunting, 1988; Agee, 1993).

In contrast to other regions within the distribution of ponderosa pine (Agee, 1993), our three study areas probably are outside the range of influence of early burning by Native Americans. Our reconstruction of historic conditions for the past several hundred years suggests that intentional ignitions by hunters and gathers likely were unnecessary because stands were already open and allowed unrestricted travel, produced little desirable foods or medicinal plants, and

Table 3
Reference conditions for eastside old-growth ponderosa pine forests

Condition	Description
Stand age	Multi-aged, >3 age classes in the upper canopy, the youngest age class dating from before 1900
Live upper canopy trees	Density 50 ± 3.5 trees ha^{-1} (mean \pm S.E.); mean diameter 60.0 ± 1.55 cm dbh with a modal distribution ranging from 25 to 125 cm dbh
Snags	Density 9.0 ± 0.97 trees ha^{-1} , mean diameter 61.7 ± 4.33 cm with a modal distribution ranging from 25 to 125 cm
Coarse woody debris	Density 47.0 ± 5.28 logs ha^{-1} , large-end diameter 37.6 ± 2.41 cm, mean length 4.2 ± 0.09 m, cumulative length 512.9 ± 78.12 m, total volume 62.3 ± 6.30 m^3 ha^{-1} , cover $1.7 \pm 0.08\%$
Spatial pattern of upper canopy trees	Either aggregated, clumped distribution, with clumps >22 m in diameter, or random distribution

provided little grazing or browsing opportunities. Thus our three study areas represent old-growth condition where all natural processes except frequent low-intensity fires have continued unimpaired by Euro-American settlement.

4.2. Regeneration patterns

Selection of a base date for establishing reference conditions is somewhat arbitrary and site specific; in this work we base our reference conditions on the reconstruction of stand structure in 1900. This predates all known fire suppression, livestock grazing, and timber logging activities in central Oregon.³ The year 1900 also was used as a base date to describe stand dynamics before and after Euro-American presence in the Bitterroot River region of Montana (Arno, 1988). Others have used the date 1883 as the beginning of Euro-American influence in southwestern ponderosa pine because of the construction of the transcontinental railroad across northern Arizona coincident with the initiation of heavy commercial logging and widespread livestock grazing (Fulé et al., 1997), or 1851 as the date of the last major fire in the ponderosa pine-dominated Cheesman Lake landscape in the Front Range of Colorado (Kaufmann et al., 2000).

Our three study areas contain ponderosa pine stands that clearly are multi-aged (Fig. 3), our first common reference point (Table 3) for characterizing old-growth ponderosa pine forests. Ponderosa pine seed crops are not regularly periodic at our study areas, and good seed crops rarely occur more than every 4–5

years (Barrett, 1979). Successful recruitment of a new cohort depends on adequate seed production, adequate soil moisture, protection from frost, and lack of competition from shrubs and graminoids, and protection from fire until trees develop protection in the form of thickened bark. Recruitment at our study areas also is influenced by small mammals that cache seeds in open pumice soil. Sampling to determine total age of individual trees and presumably establishment date of cohorts was based on diameter distribution and canopy stratification, and was not designed to identify all discrete age classes. When all sampled trees were grouped into 10-year age classes, individual plots were highly heterogeneous with respect to age, and contained as many as 16 10-year age classes at Metolius and as many as 22 10-year age classes at Pringle Butte. As expected, young age classes (less than 100 years) were well represented; some ponderosa pine recruitment occurred every decade during the last 100 years, and almost every decade since 1850. This recruitment likely is related to the gradual climate warming after the Little Ice Age and above-normal precipitation between 1885 and 1910, the wettest period during the past 275 years (Garfin and Hughes, 1996), and reflects strongly the effectiveness of fire suppression beginning about 1910. In contrast, recruitment represented by sample trees in age classes >150 year old was increasingly infrequent, with a gap of essentially no cohort recruitment between 1800 and 1850. Recruitment during the period 1670–1700 was relatively common. Our sample depth becomes progressively shallow beyond the mid-1600s (Fig. 3), making interpretations tenuous. Establishment of cohorts at Blacks Mountain around the 1890s, the 1770s, and the 1670s was consistent with common cohorts at Metolius and Pringle Butte, and suggests

³ Unpublished data on file, USDA Forest Service, Deschutes National Forest, Bend, OR.

remarkably similar conditions across the entire east-side ponderosa pine region.

4.3. Historic forest structure

Our work to identify old-growth ponderosa pine structural components serves as a key element in developing descriptions of reference conditions for managing ponderosa pine. Despite great heterogeneity at the plot level within study areas, the lack of overall difference between mean density of live upper canopy trees suggests a threshold beyond which stands rarely develop, and a second common reference point (Table 3). Our density of live upper canopy trees is lower than the 65 ± 7 trees ha^{-1} reported for a site in north-central Arizona with soils derived from a mixture of volcanic, limestone, and sandstone formations (Fulé et al., 1997). It closely resembles reported densities of 57 trees ha^{-1} for old-growth stands on the Mogollon Rim Plateau on volcanic soils (Covington and Moore, 1994). Other studies in the southwest have reported densities of old-growth ponderosa pine ranging from 37 to 111 trees ha^{-1} (Covington et al., 1997). Harrod et al. (1999) reported historical conditions characterized by a mean of 61 trees ha^{-1} after reconstructing the structure from stumps, logs, snags, and live trees in plant associations comparable to those in our study areas on one site in eastern Washington.

The diameter distribution of trees in the upper canopy (Fig. 6) represents an additional component of reference conditions for the live overstory useful for comparing conditions in other stands with large ponderosa pine. The broad range of diameters found across the three study areas presumably represents differential growth rates because of tree-tree competition and the effects of numerous cohorts resulting from past disturbance events.

Similarly, the common number of large dead ponderosa pine in the upper canopy across the three study areas (9 ± 0.97 snags ha^{-1}) suggests a third common reference point (Table 3). We made no attempt to cross-date dead ponderosa pine with our master tree-ring chronology using dendrochronology techniques, thus we are unable to establish the date of death for these trees. We assume that processes contributing to mortality of large and old ponderosa pine remain essentially unaffected by recent fire exclusion, and thus the current population of snags provides the best

representation of conditions before 1900. This assumption may be problematic; clearly the exclusion of fire has led to establishment of new cohorts, and increased density of stems may negatively impact growth rates of large live trees and contribute eventually to accelerated snag creation (Boindi, 1996; Mast et al., 1999). In contrast, work in central Oregon suggests that repeated underburning may reduce growth rates of smaller diameter trees (Cochran and Hopkins, 1991) and prevent the establishment of understory vegetation that plays an important role in maintaining soil quality through N_2 fixation (Busse et al., 1996). In addition, stems in the lower canopy usually incur more competition-induced mortality than larger stems (Fiedler and Morgan, 2002). The number of snags has rarely been reported in other work to reconstruct historic stand structure, presumably because many of these studies have occurred after the historic structure has been compromised by some degree of harvest activity. Our three study areas contained a higher density of snags than that reported for uncut forests in western Montana (Harris, 1999). Many of the existing snags occurring at Metolius and Pringle Butte were created by Comandra blister rust; because of slow mortality rate and longevity of the resulting standing snag, Comandra blister rust plays an important role in the development of snags that differ in wood density compared to those that develop after lethal attacks by western pine beetle. Presumably some of the snags noted at Metolius result from an especially virulent period of infection by Comandra blister rust during the 1950s, with infection probably occurring during a period of cooler, more moist climate that favored spore production (Filip, 1977). The vascular plant, common comandra (*Comandra umbellata* Nutt.), is the alternate host for Comandra blister rust, yet is especially uncommon under the dense canopy created by post-1900 cohorts (Youngblood and Riegel, 2000). We speculate that under historic disturbance regimes that maintained more open conditions, common comandra was more prevalent, providing greater opportunity for Comandra blister rust infection.

Under pre-1900 disturbance regimes, snag creation presumably involved the combined effects of all disturbance processes: competition, insects, diseases, and fire, individually and in all possible combinations were responsible for tree mortality. Our understanding

of the interactions among these disturbance factors under historic and current climatic regimes at various spatial and temporal scales is limited. For example, reintroduction of fire into fire-dependent systems after decades of exclusion may result in immediate mortality of large old-growth trees through excessive heat to tree roots, cambium, or crown. Subsequent mortality of additional large old-growth trees for several years after the fire may occur because of the delayed effects of tree wounding and second-order effects of insects or disease. Initial results of prescribed burning in southwestern ponderosa pine indicated mortality extending years after the burn (Harrington and Sackett, 1992). Our presentation of snag density and size characterization is accompanied with the following caveat: our understanding of long-term demographics of eastside old-growth ponderosa pine snags under natural disturbance regimes is weak. Research focused on the creation of large diameter ponderosa pine snags in disturbance regimes of high frequency fire and the contribution of frequent fires to snag fall rates (Landram et al., 2002) will help fill this gap in our understanding.

The high density of small diameter stems and seedlings in the lower canopy is a direct result of numerous cohorts becoming established since the late 1800s and the number of missed fire-return intervals due to essentially complete fire exclusion since the early 1900s. High density of small diameter stems and seedlings is a pervasive characteristic across much of the ponderosa pine ecosystems (Arno, 1988; Covington et al., 1997; Fulé et al., 1997; Kaufmann et al., 2000; Brown et al., 2001). The presence of several to many cohorts of small diameter stems represents the single most dramatic difference between historic and present-day conditions.

Characterization of coarse woody debris (CWD) resources in old-growth ponderosa pine forests has received less attention than has characterization of standing live and dead stems (Chambers, 2002). Perhaps this is because many may believe that historic fire in ponderosa pine forests eliminated CWD, leaving a forest floor devoid of all but scattered bunch grasses and small shrubs. Our results indicate a rich and diverse assemblage of CWD on the forest floor and provide a fourth common reference point (Table 3). Logs at Metolius and Pringle Falls were more abundant and were larger than those reported for old-growth ponderosa pine stands in

northeastern Oregon (Torgersen, 2002). We made no attempt to cross-date pieces of CWD so we can not say with certainty what portion of our CWD is representative of conditions pre-1900. Because Comandra blister rust caused resin impregnation which may prevent moisture infiltration necessary for decay, some of the logs may have persisted for decades. The preponderance of logs in an advanced stage of decomposition (Fig. 11) also suggests longevity of CWD but is likely biased upward because of fire exclusion over the past century. Similar to snag density, our presentation of CWD characterization is accompanied with the following caveat: our understanding of long-term demographics of CWD in eastside old-growth ponderosa pine forests under natural disturbance regimes is weak. Research focused on the decay rates of CWD and the fate of individual pieces under repeated fire will help fill this gap in our understanding.

Perhaps the most significant portion of our work is the characterization of spatial patterns in eastside old-growth ponderosa pine forests. The distribution pattern of plants across environments increasingly is of interest to plant ecologists because of the information on stand history, dynamics, and plant–plant interactions that can be revealed. Earlier work in the northern Rocky Mountains showed that in old-growth forests of western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn ex D. Don), cohorts of seedlings begin in clusters within canopy gaps that result from mortality of an overstory tree, the cohorts are thinned through density-dependent mortality, and eventually a regular or uniform spacing of individual dominant trees is achieved through tree-tree inhibition (Moeur, 1997). Density-dependent mortality also apparently leads to uniform spacing in some deciduous forest types that lack prominent disturbance factors (Ward et al., 1996). In contrast, Martens et al. (1997) found strong clumping or aggregation within semi-arid woodlands in New Mexico which they attribute to competition for both above-ground resources and below-ground resources. Work in Sierra Nevada mixed-conifers forests showed a strong clumped distribution for four species, with the distribution attributed to fine-scale disturbance patterns (Knight, 1997). While ponderosa pine stands have often been described as open and park-like, few quantitative studies that explore the spatial point

pattern of trees exist. White (1985) used nearest neighbor analysis to identify a wide range in the size of clumps or groups of old-growth ponderosa pine northwest of Flagstaff, Arizona; his work with 373 trees from a single stand identified clumps from 0.02 to 0.29 ha in size, compared to clumps 0.04 to 0.05 ha in size in work reported here. Perhaps the first to use Ripley's $K(d)$ analysis in ponderosa pine forests was Getis and Franklin (1987) who found clumping at scales of 6–42 m on the Klamath National Forest in extreme northern California. Given that clumping is a predominant spatial pattern in ponderosa pine, and that a complete random distributions also occurs, little effort has focused on the ecological functioning of either of these arrangements. It seems clear that frequent, low intensity disturbance serves to create these two spatial patterns, yet it is unclear how this pattern relates to below ground resources, wildlife attributes, and long-term site productivity.

While exploration of spatial patterns within single plots, the 1.44 ha sample plot used by Getis and Franklin (1987) or the 2.5 ha sample plot used by Knight (1997), provide insights into stand structure at one specific location, these results cannot be widely extrapolated to other similar stands. Our approach has been to analyze the spatial pattern within replicated plots across a study area to discern variation across similar stands, and then look for repeated patterns across the landscape by working at geographically disjunct locations. Previous efforts to summarize the results of multiple Ripley's $K(d)$ analysis from closely adjacent plots (Harrod et al., 1999) were hampered by the inability to combine various distributions or functional data. Our use of functional data analysis demonstrates the strength of this tool and suggests a mechanism for more robust spatial analyses that employ the results of Ripley's $K(d)$ analyses from multiple sample plots distributed across the landscape. Our work also demonstrates the existence of common spatial patterns in old-growth ponderosa pine forests that are repeated across the landscape (Fig. 9), thus providing a fifth common reference point (Table 3).

4.4. Implications for designing restoration treatments

What are the implications for future management of eastside ponderosa pine, given that the current

amount of old-growth is far less than before pre-Euro-American settlement? Our results have direct application within the context of forest management activities designed to renew ecosystem health and ecological integrity of eastside forest ecosystems through both structural and process restoration (Stephenson, 1999). The three study areas used in this work provided unique opportunities to examine the structure of eastside old-growth ponderosa pine stands and characterize reference conditions that could serve as a model in restoration efforts. Our concept of reference condition follows that of Moore et al. (1999) in providing the following: (1) the range of natural variability in composition and structure in eastside old-growth ponderosa pine ecosystems; (2) a point of reference against which to evaluate departures within the ecosystem; and (3) a criterion for measuring the success of restoration treatments designed to return sites to sustainable conditions. Our work provides managers an important description of natural variability that may aid in understanding historic conditions, a description of conditions in stands that are dramatically under represented across the landscape, and a set of conditions that may serve as a reference for setting regional management goals (Landres et al., 1999). Clearly, establishment of these reference conditions has inherent limitations; even our current understanding of eastside old-growth ponderosa pine may be of limited relevance today without considering the conditions within the context of climate changes (Millar and Woolfenden, 1999). Despite this limitation, our reference conditions represent the accumulated structure that has been influenced by past climatic events rather than a static condition at a single point in time (Zulé et al., 2002). Reference conditions, because they presumably represent conditions that existed pre-Euro-American settlement, provide a point against which to evaluate change since Euro-American settlement and a point against which to evaluate change under restoration treatment. As such, they may be a useful management goal, but more likely they will be one of several goals representing ecological, social, and political considerations; in this context, our reference conditions may guide the direction of a desired condition without specifically limiting the detail of a desired condition (Landres et al., 1999). Our results suggest that designing and implementing restoration treatments

specifically for eastside ponderosa pine ecosystems involves the following.

1. Identification of eastside old-growth ponderosa pine stands by using the reference conditions (Table 3). While our reference conditions focus on means as the central tendency, the means are not intended to be applied as strict rules across all situations. We also provide measures of variation that are equally important.
2. Retention and protection of existing upper canopy layers (live and dead) in eastside old-growth ponderosa pine stands.
3. Creation and retention of trees in clumps or a random distribution of stems. This probably represents the most significant departure from past thinning guides that emphasized uniform spacing to optimize the growing space and resources available for each residual tree.
4. Reintroduction of fire to reduce fuels, recycle nutrients, and change forest structure by eliminating high densities of stems in lower canopies. This involves active management to create conditions for regeneration of new seedling cohorts and associated vegetation, while at the same time managing for low densities in lower canopy layers.
5. Retention of coarse woody debris. This involves active management to ensure a continual presence of logs in spite of reintroduced fire.

Acknowledgements

The authors acknowledge the able assistance of the many individuals who have participated in field sampling, especially M. Banta, S. Greene, S. Love, B. McKinnen, K. Metlen, M. Metlen, and E. Sandoz. K. Hyer provided essential assistance in conducting the functional data analysis. Helpful reviews of an earlier draft of the manuscript were provided by R. Everett, M. Moeur, W. Shepperd, and P. Fulé.

References

Acker, S.A., Sabin, T.E., Ganio, L.M., McKee, W.A., 1998. Development of old-growth structure and timber volume

- growth trends in maturing Douglas-fir stands. *For. Ecol. Manage.* 104, 265–280.
- Agee, J.K., 1993. *Fire Ecology of Pacific Northwest Forests*. Island Press, Washington, DC, 493 pp.
- Agee, J.K., 1994. Fire and weather disturbances in terrestrial ecosystems of the eastern Cascades. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-320, Pac. Northwest Res. Stn., Portland, OR, 52 pp.
- Agee, J.K., 1996. Fire in the Blue Mountains: a history, ecology and research agenda. In: Jaindl, R.G., Quigley, T.M. (Eds.), *Search for a Solution: Sustaining the Land, People, and Economy of the Blue Mountains*. American Forest in cooperation with the Blue Mountains Natural Resources Institute, Washington, DC, pp. 119–145.
- Ansley, J.S., Battles, J.J., 1998. Forest composition, structure, and change in an old-growth mixed conifer forest in the northern Sierra Nevada. *J. Torrey Bot. Soc.* 125, 297–308.
- Arno, S.F., 1988. Fire ecology and its management—implications in ponderosa pine forests. In: Baumgartner, D.M., Lotan, J.E. (Eds.), *Proceedings of the Ponderosa Pine, the Species and its Management*, Spokane, Washington, 29 September–1 October 1987. Washington State University, Pullman, pp. 134–139.
- Arno, S.F., Ottmar, R.D., 1994. Reintroduction of fire into forests of eastern Oregon and Washington. In: Everett, R.L. (Comp.), *Restoration of Stressed Sites, and Processes*, vol. IV. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-330, Pac. Northwest Res. Stn., Portland, OR, pp. 65–67.
- Barrett, J.W., 1979. *Silviculture of ponderosa pine in the Pacific Northwest: the state of our knowledge*. USDA For. Serv. Gen. Tech. Rep. PNW-97, Pac. Northwest For. Range Exp. Stn., Portland, OR, 106 pp.
- Bate, L.J., Torgersen, T.R., Garton, E.O., Wisdom, M.J., 2002. Accuracy and efficiency of methods to sample logs for wildlife research and management. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coord.), *Proceedings of the Ecology and Management of Dead Wood in Western Forests*, Reno, NV, 2–4 November 1999. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southwest Res. Stn., Albany, CA, pp. 817–822.
- Bergoffen, W.W., 1976. 100 years of Federal forestry. *Agric. USDA For. Serv. Info. Bull.*, vol. 402, Washington, DC, 200 pp.
- Beardsley, D., Bolsinger, C., Warbington, R., 1999. Old-growth forests in the Sierra Nevada: by type in 1945 and 1993 and ownership in 1993. USDA For. Serv. Res. Pap. PNW-RP-516, Pac. Northwest Res. Stn., Portland, OR, 46 pp.
- Boindi, F., 1996. Decadal-scale dynamics at the Gus Pearson natural area: evidence for inverse (a)symmetric competition? *Can. J. For. Res.* 26, 1397–1406.
- Bolsinger, C.L., Waddell, K.L., 1993. Area of old-growth forests in California, Oregon, and Washington. USDA For. Serv. Res. Bull. PNW-RB-107, Pac. Northwest Res. Stn., Portland, OR, 26 pp.
- Bonnicksen, T.M., 2000. *America's Ancient Forests—From the Ice Age to the Age of Discovery*. Wiley, New York, 594 pp.
- Bork, J.L., 1984. Fire history in three vegetation types on the eastern side of the Oregon Cascades. Ph.D. thesis, Oregon State University, Corvallis, OR, 94 pp.

- Brown, P.M., D'Amico, D.R., Carpenter, A.T., Andrews, D., 2001. Restoration of montane ponderosa pine forests in the Colorado Front Range. *Ecol. Restoration* 19, 19–26.
- Busse, M.D., Cochran, P.H., Barrett, J.W., 1996. Changes in ponderosa pine site productivity following removal of understory vegetation. *Soil Sci. Soc. Am. J.* 60, 1614–1621.
- Chambers, C.L., 2002. Forest management and the dead wood resource in ponderosa pine forests: effects on small mammals. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coord.), Proceedings of the Ecology and Management of Dead Wood in Western Forests, Reno, NV, 2–4 November 1999. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southwest Res. Stn., Albany, CA, pp. 679–693.
- Childs, T.W., 1968. Comandra rust damage to ponderosa pine in Oregon and Washington. USDA For. Serv. Pac. Northwest For. Range Exp. Stn., Portland, OR, 8 pp.
- Cochran, P.H., 1992. Stocking levels and underlying assumptions for uneven-aged ponderosa pine stands. USDA For. Serv. Res. Note. PNW-RN-509, Pac. Northwest Res. Stn., Portland, OR, 10 pp.
- Cochran, P.H., Hopkins, W.E., 1991. Does fire exclusion increase productivity of ponderosa pine? In: Harvey, A.E., Neuenschwander, L.F. (Comp.), Proceedings of the Management and Productivity of Western-Montane Forest Soils, Boise, ID, 10–12 April 1990. USDA For. Serv. Gen. Tech. Rep. INT-280, Intern. Res. Stn., Ogden, UT, pp. 224–228.
- Conard, S.G., Hartzell, T., Hilbruner, M.W., Zimmerman, G.T., 2001. Changing fuel management strategies—the challenge of meeting new information and analysis needs. *Intern. J. Wildland Fire* 10, 267–275.
- Covington, W.W., Moore, M.M., 1994. Postsettlement changes in natural fire regimes and forest structure: ecological restoration of old-growth ponderosa pine forest. *J. Sustainable For.* 2, 153–181.
- Covington, W.W., Fulé, P.Z., Moore, M.M., Hart, S.C., Kolb, T.E., Mast, J.N., Sackett, S.S., Wagner, M.R., 1997. Restoring ecosystem health in ponderosa pine forests of the southwest. *J. For.* 95, 23–29.
- Diggle, P.J., 1983. *Statistical Analysis of Spatial Point Patterns*. Academic Press, New York, 148 pp.
- Dolph, K.L., Mori, S.R., Oliver, W.W., 1995a. Long-term response of old-growth stands to varying levels of partial cutting in the eastside pine type. *West. J. Appl. For.* 10, 101–108.
- Dolph, K.L., Mori, S.R., Oliver, W.W., 1995b. Height–diameter relationships for conifer species on the Blacks Mountain Experimental Forest. USDA For. Serv. Res. Note PSW-RN-418. Pacific Southwest Res. Stn., Berkeley, CA, 5 pp.
- Everett, R., Hessburg, P., Lehmkuhl, J., Jensen, M., Bourgeron, P., 1994. Old forests in dynamic landscapes. *J. For.* 92, 22–25.
- Everett, R.L., Schellhass, R., Keenum, D., Spurbeck, D., Ohlson, P., 2000. Fire history in the ponderosa pine/Douglas-fir forests on the east slope of the Washington Cascades. *For. Ecol. Manage.* 129, 207–225.
- Filip, G.M., 1977. Crown mortality of ponderosa pine caused by *Cronartium comandrae*. *Plant Disease Rep.* 61, 1083–1085.
- Franklin, J.F., Spies, T.A., 1991. Composition, function, and structure of old-growth Douglas-fir forests. In: Ruggiero, L. (Ed.), *Wildlife and Vegetation of Unmanaged Douglas-fir Forests*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-285, Pac. Northwest Res. Stn., Portland, OR, pp. 71–80.
- Fiedler, C.E., 1996. Silvicultural applications: Restoring ecological structure and process in ponderosa pine forests. In: Hardy, C.C., Arno, S.F. (Eds.), Proceedings of the Use of Fire in Forest Restoration, Annual Meeting of the Society for Ecological Restoration. USDA For. Serv. Gen. Tech. Rep. INT-GTR-341, Intermountain Res. Stn., Ogden, UT, pp. 39–40.
- Fiedler, C.E., Morgan, T.A., 2002. Mortality as a source of coarse woody debris in managed stands. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coord.), Proceedings of the Ecology and Management of Dead Wood in Western Forests, Reno, NV, 2–4 November 1999. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southwest Res. Stn., Albany, CA, pp. 637–648.
- Fulé, P.A., Covington, W.W., Moore, M.M., 1997. Determining reference conditions for ecosystem management of southwestern ponderosa pine forest. *Ecol. Appl.* 7, 895–908.
- Garfin, G.M., Hughes, M.K., 1996. Eastern Oregon divisional precipitation and Palmer drought severity index from tree-rings. Laboratory of Tree-Ring Research, University of Arizona, Tucson, AZ, 53 pp.
- Getis, A., Franklin, J., 1987. Second-order neighborhood analysis of mapped point patterns. *Ecology* 68, 473–477.
- Haase, P., 1995. Spatial pattern analysis in ecology based on Ripley's *K*-function: Introduction and methods of edge correction. *J. Veg. Sci.* 6, 575–582.
- Hall, F.C., 1972a. Metolius research natural area. In: Franklin, J.F., Hall, F.C., Dyrness, C.T., Maser, C. (Eds.), *Federal Research Natural Areas in Oregon and Washington—A Guidebook for Scientists and Educators*. USDA For. Serv., Pacific Northwest For. Range Exp. Stn., Portland, OR, pp. MI-1–MI-9.
- Hall, F.C., 1972b. Pringle Falls research natural area. In: Franklin, J.F., Hall, F.C., Dyrness, C.T., Maser, C. (Eds.), *Federal Research Natural Areas in Oregon and Washington—A Guidebook for Scientists and Educators*. USDA For. Serv., Pacific Northwest For. Range Exp. Stn., Portland, OR, pp. PR-1–PR-11.
- Hall, F.C., 1980. Fire history—Blue Mountains, Oregon. In: Proceedings of the Fire History Workshop, University of Arizona, Tucson, AZ, 20–24 October 1980. USDA For. Serv. Gen. Tech. Rep. GTR-RM-81, Rocky Mountain For. Range Exp. Stn., Fort Collins, CO, pp. 75–81.
- Hann, W.J., Jones, J.L., Karl, M.G., Hessburg, P.F., Keane, R.E., Long, D.G., Menakis, J.P., McNicoll, C.H., Leonard, S.G., Gravenmier, R.A., Smith, B.G., 1997. Landscape dynamics of the basin. In: Quigley, T.M., Arbelbide, S.J. (Eds.), *An Assessment of Ecosystem Components in the Interior Columbia Basin and Portions of the Klamath and Great Basins*. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-405, Pac. Northwest Res. Stn., Portland, OR, pp. 337–1055.
- Harrington, M.G., Sackett, S.S., 1992. Past and present fire influences on southwestern ponderosa pine old growth. In:

- Proceedings of the Old Growth Forest in the Southwest and Rocky Mountain Regions. USDA For. Serv. Gen. Tech. Rep. RM-GTR-213, Rocky Mt. For. Range Exp. Stn., Ft. Collins, CO, pp. 44–50.
- Harris, R.B., 1999. Abundance and characteristics of snags in western Montana forests. USDA For. Serv. Gen. Tech. Rep. RMRS-GTR-31, Rocky Mt. Res. Stn., Ft. Collins, CO, 19 pp.
- Harrod, R.J., Gaines, W.L., Hartl, W.E., Camp, A., 1998. Estimating historical snag density in dry forests east of the Cascade Range. USDA For. Serv., Gen. Tech. Rep. PNW-GTR-428, Pac. Northwest Res. Stn., Portland, OR, 16 pp.
- Harrod, R.J., McRae, B.H., Hartl, W.E., 1999. Historical stand reconstruction in ponderosa pine forests to guide silvicultural prescriptions. *For. Ecol. Manage.* 114, 433–446.
- Heyerdahl, E.K., 1997. Spatial and temporal variation in historical fire regimes on the Blue Mountains, Oregon and Washington: influence of climate. PhD. Dissertation, University of Washington, Seattle, WA, 224 pp.
- Johnson Jr., C.G., Clausitzer, R.R., Mehninger, P.J., Oliver, C.D., 1994. Biotic and abiotic processes of eastside ecosystems: the effects of management on plant and community ecology, and on stand and landscape vegetation dynamics. USDA For. Serv. Gen. Tech. Rep. PNW-GTR-322, Pac. Northwest Res. Stn., Portland, OR, 66 pp.
- Kaufmann, M.R., Regan, C.M., Brown, P.M., 2000. Heterogeneity in ponderosa pine/Douglas-fir forests: age and size structure in unlogged and logged landscapes of central Colorado. *Can. J. For. Res.* 30, 698–711.
- Kilgore, B.M., 1981. Fire in ecosystem distribution and structure: western forests and scrublands. In: Mooney, H.A., Bonnicksen, T.M., Christensen, N.L., Lotan, J.E., Reiners, W.A. (Eds.), *Proceedings of the Fire Regimes and Ecosystem Properties*, Honolulu, HI, 11–15 December 1987. USDA For. Serv. Gen. Tech. Rep. WO-GTR-26, Washington, DC, pp. 58–89.
- Knight, F.R., 1997. A spatial analysis of a Sierra Nevada old-growth mixed-conifer forest. M.S. thesis, University of Washington, Seattle, WA, 84 pp.
- Landram, F.M., Laudenslayer, W.F., Atzet, T., 2002. Demography of snags in eastside pine forests of California. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coord.), *Proceedings of the Ecology and Management of Dead Wood in Western Forests*, Reno, NV, 2–4 November 1999. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southwest Res. Stn., Albany, CA, pp. 605–620.
- Landres, P.B., Morgan, M., Swanson, F.J., 1999. Overview of the use of natural variability concepts in managing ecological systems. *Ecol. Appl.* 9, 1179–1188.
- Languille, H.D., Plummer, F.G., Dobwell, A., Rixon, T.F., Leiberg, J.B., 1903. Forest conditions in the Cascade Range forest reserve—Oregon. USDI, Geological Survey, Professional Paper 9, Series H., Forestry, vol. 6, Washington, DC, 298 pp.
- Long, J.N., Daniel, T.W., 1990. Assessment of growing stock in uneven-aged stands. *West. J. Appl. For.* 5, 93–96.
- Martens, S.N., Breshers, D.D., Meyer, C.W., Barnes, F.J., 1997. Scales of above-ground and below-ground competition in a semi-arid woodland detected from spatial pattern. *J. Veg. Sci.* 8, 655–664.
- Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), *Wildlife Habitats in Managed Forests, the Blue Mountains of Oregon and Washington*. USDA Agricultural Handbook, vol. 553, Washington, DC, pp. 78–95.
- Mast, J.N., Fulé, P.Z., Moore, M.M., Covington, W.W., Waltz, A.E.M., 1999. Restoration of presettlement age structure of an Arizona ponderosa pine forest. *Ecol. Appl.* 9, 228–239.
- Millar, C.I., Woolfenden, W.B., 1999. The role of climate change in interpreting historical variability. *Ecol. Appl.* 9, 1207–1216.
- Moer, M., 1993. Characterizing spatial patterns of trees using stem-mapped data. *For. Sci.* 39, 756–775.
- Moer, M., 1997. Spatial models of competition and gap dynamics in old-growth *Tsuga heterophylla/Thuja plicata* forests. *For. Ecol. Manage.* 94, 175–186.
- Moore, M.M., Covington, W.W., Fulé, P.E., 1999. Reference conditions and ecological restoration: a southwestern ponderosa pine perspective. *Ecol. Appl.* 9, 1266–1277.
- Moore, J.A., Zhang, L., Stuck, D., 1996. Height–diameter equations for ten tree species in the Inland Northwest. *West. J. Appl. For.* 11, 132–137.
- Morrow, R.J., 1986. Age structure and spatial pattern of old-growth ponderosa pine in Pringle Fall Experimental Forest, central Oregon. M.S. thesis, Oregon State University, Corvallis, OR, 80 pp.
- O'Hara, K.L., Latham, P.A., Hessburg, P., Smith, B.G., 1996. A structural classification for inland Northwest forest vegetation. *West. J. Appl. For.* 11, 97–102.
- Oliver, W.W., 2001. Can we create and sustain late successional attributes in interior ponderosa pine stands? Large-scale ecological research studies in northeastern California. In: Vance, R.K., Edminster, C.B., Covington, W.W., Blake, J.A. (Comps.), *Proceedings of the Ponderosa Pine Ecosystems Restoration and Conservation: Steps Toward Stewardship*, Flagstaff, AZ, 25–27 April 2000. USDA For. Serv., RMRS-P-22, Rocky Mountain Res. Stn., Ogden, UT, pp. 99–103.
- Oliver, C.D., Irwin, L.L., Knapp, W.H., 1994. Eastside forest management practices: historical overview, extent of their applications, and their effects on sustainability of ecosystems. USDA For. Serv., Gen. Tech. Rep. PNW-GTR-324, Pac. Northwest Res. Stn., Portland, OR, 73 pp.
- Olson, D.L., 2000. Fire in riparian zones: a comparison of historical fire occurrence in riparian and upslope forests in the Blue Mountains and southern Cascades of Oregon. M.S. thesis, University of Washington, Seattle, WA, p. 93.
- Perry, D.A., Henjum, M.G., Karr, J.R., Bottom, D.L., Bednarz, J.C., Wright, S.G., Beckwith, S.A., Beckwith, E., 1995. Interim protection for late-successional forests, fisheries, and watersheds: a summary of the report of the eastside forests scientific society panel. In: Everett, R.L., Baumgartner, D.M. (Comps.), *Proceedings of the Ecosystem Management in Western Interior Forests*, Spokane, WA, 3–5 May 1994. Department of Natural Resource Sciences, Washington State University, Pullman, WA, pp. 103–114.

- Quigley, T.M., Hayes, J.L., Starr, L., Datermann, G.E., 2001. Improving forest health and productivity in eastern Oregon and Washington. *Northwest Sci.* 75, 234–251 (special issue).
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge, 537 pp.
- Ramsay, J.O., Silverman, B.W., 1997. *Functional Data Analysis*. Springer-Verlag, New York, 310 pp.
- Ramsay, J.O., Silverman, B.W., 2002. *Applied Functional Data Analysis, Methods and Case Studies*. Springer-Verlag, New York, 190 pp.
- Reineke, L.H., 1933. Perfecting a stand-density index for even-aged stands. *J. Agric. Res.* 45, 627–638.
- Ripley, B.D., 1976. The second-order analysis of stationary processes. *J. Appl. Prob.* 13, 255–266.
- Ripley, B.D., 1977. Modeling spatial patterns. *J. R. Stat. Soc. B.* 39, 172–212.
- Rorig, M.L., Ferguson, S.A., 1999. Characteristics of lightning and wildland fire ignition in the Pacific Northwest. *J. Appl. Meteorol.* 38, 1565–1575.
- Saveland, J.M., Bunting, S.C., 1988. Fire effects in ponderosa pine forests. In: Baumgartner, D.M., Lotan, J.E. (Eds.), *Proceedings of the Ponderosa Pine, the Species and Its Management*, Spokane, Washington, 29 September–1 October 1987. Washington State University, Pullman, pp. 125–131.
- Shaw, J.D., 2000. Application of stand density index to irregularly structured stands. *West. J. Appl. For.* 15, 40–42.
- Speer, J.H., Swetnam, T.W., Wickman, B.E., Youngblood, A., 2001. Changes in pandora moth outbreak dynamics during the past 622 years. *Ecology* 82, 679–697.
- Stephenson, N.L., 1999. Reference conditions for giant sequoia forest restoration: structure, process, and precision. *Ecol. Appl.* 9, 1253–1265.
- Torgersen, T.R., 2002. Characteristics of log resources in northern Oregon: case studies of four management treatments. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, C.P., Lisle, T.E. (Tech. Coord.), *Proceedings of the Ecology and Management of Dead Wood in Western Forests*, Reno, NV, 2–4 November 1999. USDA For. Serv. Gen. Tech. Rep. PSW-GTR-181, Pac. Southwest Res. Stn., Albany, CA, pp. 795–810.
- Upton, G.J.G., Fingleton, B., 1985. *Spatial Data Analysis by Example*, vol. 1. Wiley, New York, 410 pp.
- Van Pelt, R., Franklin, J.F., 2000. Influence of canopy structure on the understory environment in tall, old-growth, conifer forests. *Can. J. For. Res.* 30, 1231–1245.
- Weatherspoon, C.P., 2000. A proposed long-term national study of the consequences of fire and fire surrogate treatments. In: Neuenschwander, L.F., Ryan, K.C., Gollberg, G.E. (Eds.), *Proceedings of the Joint Fire Science Conference and Workshop*, Boise, ID, 15–17 June 1999. University of Idaho, Moscow, ID, pp. 117–126.
- White, A.S., 1985. Presettlement regeneration patterns in a southwestern ponderosa pine stand. *Ecology* 66, 589–594.
- Wickman, B.E., 1992. Forest health in the Blue Mountains: the influence of insects and disease. USDA For. Serv., Gen. Tech. Rep. PNW-GTR-295, Pac. Northwest Res. Stn., Portland, OR, 15 pp.
- Youngblood, A., Riegel, G., 2000. Reintroducing fire in eastside ponderosa pine forests: a long-term test of fuel treatments. In: Neuenschwander, L.F., Ryan, K.C., Gollberg, G.E. (Eds.), *Proceedings of the Joint Fire Science Conference and Workshop*, Boise, ID, 15–17 June 1999. University of Idaho, Moscow, ID, pp. 142–150.
- Zulé, P.Z., Covington, W.W., Moore, M.M., Heinlein, T.A., Waltz, A.E., 2002. Natural variability in forests of the Grand Canyon, USA. *J. Biogeog.* 29, 31–47.