Influence of canopy structure on the understory environment in tall, old-growth, conifer forests

Robert Van Pelt and Jerry F. Franklin

Abstract: The effect of the spatial distribution of trees and foliage on understory conditions was examined in six tall old-growth forests along the Pacific Coast: two sites each in Washington, Oregon, and California. Detailed field measurements of crown parameters were collected on over 9000 trees encompassing over 14.5 ha in the stands. Crown parameters were used to construct a spatially explicit model useful in analyzing the variability of crown distributions in both vertical and horizontal dimensions. Sapwood measurements of over 400 trees in combination with published equations and 240 hemispherical photos were used to assess leaf area and understory light levels, respectively. Shrub and herb cover was used as a biological indicator of growing conditions in the understory. Although leaf area is often assumed to be correlated with the amount of light penetrating the canopy, this is not the case in tall, old-growth forests. The semivariance of the horizontal distribution of canopy volume was strongly correlated with shrub cover and understory light levels and was an overall predictor of canopy structure. This variability gives rise to potentially higher understory light levels and shrub cover values when compared with a forest lacking this vertical heterogeneity and may allow the stand to support a higher volume of foliage.

Résumé : Les auteurs ont examiné l'effet de la répartition spatiale des arbres et du feuillage sur les conditions du sous-étage, dans six vieilles forêts de forte dimension situées le long de la côte du Pacifique. Deux sites en ont été examinés dans chacun des États de Washington, de l'Oregon et de la Californie. Des mesures détaillées des paramètres de la cime ont été prises sur plus de 9000 arbres couvrant plus de 14,5 ha de peuplements. Les paramètres de la cime ont été utilisés pour construire un modèle spatialement explicite, utile dans l'analyse de la variabilité de la répartition de la cime selon les deux dimensions, soit verticale et horizontale. Des mesures d'aubier sur plus de 400 arbres, combinées à des équations publiées et à 240 photos hémisphériques, ont été utilisées pour estimer, respectivement, la surface foliaire et le niveau de luminosité en sous-étage. Le recouvrement des arbustes et des herbacées a servi d'indicateur biologique des conditions de croissance en sous-étage. Bien qu'on assume souvent que la surface foliaire soit corrélée avec la quantité de lumière qui traverse la canopée, ce n'est pas le cas dans les vieilles forêts de forte dimension. La semi-variance de la répartition horizontale du volume de la canopée est fortement corrélée avec le recouvrement des arbustes et avec le niveau de luminosité en sous-étage et sert, globalement, à la prédiction de la structure de la canopée. Cette variabilité donne lieu à des niveaux potentiellement plus élevés de luminosité en sous-étage et à des valeurs plus grandes de recouvrement des arbustes, comparativement à une forêt qui n'a pas cette hétérogénéité verticale. Cela permet au peuplement de supporter un plus grand volume de feuillage.

[Traduit par la Rédaction]

Introduction

During the last two decades there have been huge advances in the study of forest canopies (Lowman and Nadkarni 1995). What started with a few crudely equipped pioneers has blossomed into major a scientific field involving hundreds of researchers throughout the international scientific community. In western North America, canopy researchers have focused on the structure in old-growth coniferous forests, notably the old-growth research sites at the Wind River Experimental Forest (Parker 1996; Song et al. 1997; Lyons 1998; Van Pelt and North 1999) and the H.J. Andrews Experimental Forest (Pike et al. 1977; Massman 1982; Cohen and Spies 1992; McCune et al. 1997). The influence of canopy structure on the understory light environment and the distribution of understory plants is of particular interest (Van Pelt 1995; Song 1998).

A traditional approach to quantifying the canopy environment is to calculate leaf area index (LAI). LAI is the one-sided surface area of all leaves over a unit of ground. The old-growth forests along the Pacific coast of North America have some of the highest LAI values in the world; some stands have values over 12 (Franklin and Waring 1980). Although LAI values give some indication of potential light levels in an understory, they can be misleading (Parker et al. 1989; Smith et al. 1992). An even-aged forest composed of similar-sized trees with the foliage of the entire stand concentrated in one layer will have dramatically different understory light conditions than a tall, multilayered forest with the same amount of leaf area. This is particularly important at high latitudes where extreme sun angles are common. In these environments, the organization of the foliage in three-dimensional space may be much more important than the total amount of foliage (Van Pelt 1995).

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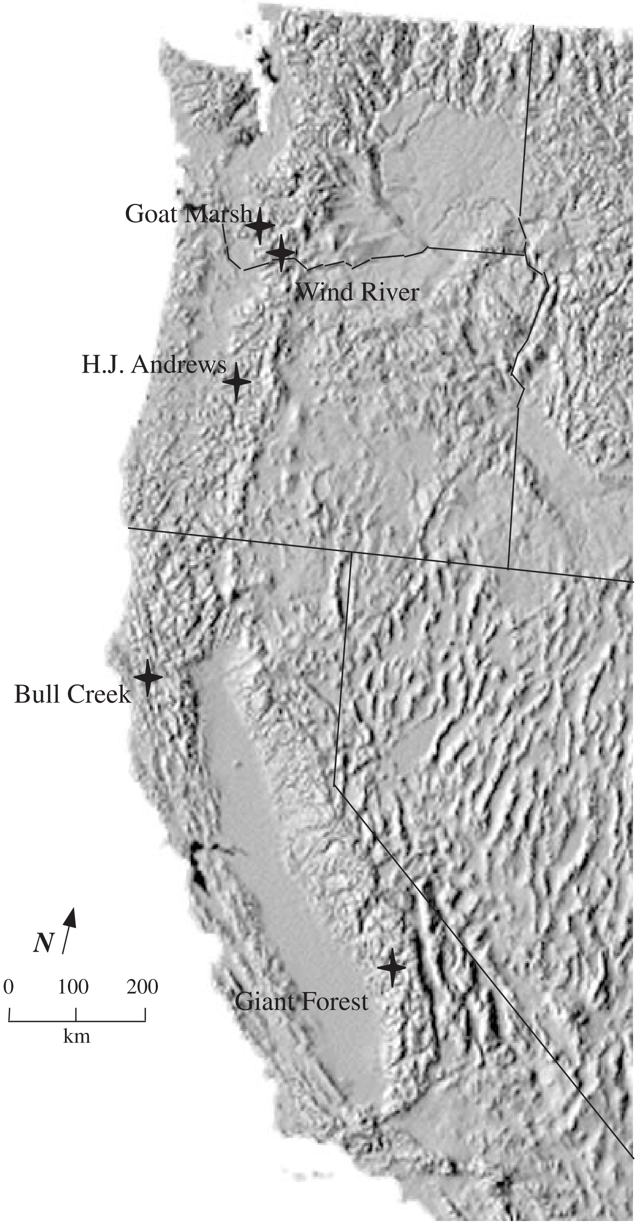
Fig. 1. Study site locations. Two sites were located in each of Washington, Oregon, and California. The two Oregon sites are both at H.J. Andrews Experimental Forest.



Gap-phase replacement has been cited as the primary driver of succession between major disturbances (Bray 1956) and often is used as the basis for models of stand dynamics (Botkin et al. 1972). While this has been shown to be useful in tropical (Brokaw 1985; Uhl et al. 1988) and temperate broadleaf (Runkle 1981, 1990; Hibbs 1982) forests, in the tall forests along the Pacific coast its use is limited (Van Pelt 1995; Van Pelt and North 1996). The primary problem with the gap-phase replacement concept when applied to Pacific coast forests is that it is a two-dimensional model. Pacific coast forests are much taller than other forest types while also tending to be at higher latitudes. Moreover, their gaps tend to be as small as or smaller than those in broadleaf forests because of the narrow-crowned nature of the coniferous trees (Spies et al. 1990*a*; Canham et al. 1990). Further, problems arise when a temporal framework is considered; trees in Pacific coast old-growth forests can survive for centuries in the forest understory without appreciable growth (Henderson et al. 1989), resulting in understory spatial patterns asynchronous with the gaps above.

While canopy structure may still be poorly defined (Van Pelt and North 1996), the controlling influence of canopy structure on many ecosystem functions has been recognized (Harr 1982; Campbell and Norman 1989; Lowman and Nadkarni 1995). At the stand scale, there is interest in how crowns occupy the three-dimensional space of the canopy and how the understory light environment is influenced by different canopy structures. The quantity of light that reaches the forest floor is affected by the quantity and spatial distribution of foliage in a stand (Reifsnyder et al. 1971; Oker-Blom and Kellomaki 1982; Massman 1982). The age of the stand, the spacing and sizes of canopy gaps, the species present, and the multilayering of foliage within the stand all influence the three-dimensional distribution of foliage (Stewart 1986; Spies and Franklin 1989; Van Pelt 1995; Van Pelt and North 1999).

In this paper we analyze the horizontal and vertical distribution of foliage in six tall, Pacific coast forests and assess how this distribution affects the amount of light reaching the forest understory and the spatial distribution of understory plants. Understory light levels and canopy leaf area were measured and then compared with understory tree locations as well as herb and shrub cover. Measures of canopy density, canopy gaps, and tree heights also were compared with these understory measures. Finally, we propose a measure of canopy structure superior to either LAI or the gap-phase replacement concept that incorporates the three-dimensional complexity and spatial heterogeneity of forest canopies.

Materials and methods

Study site descriptions

Six forest stands were used for this research, two each in Washington, Oregon, and California (Fig. 1). These six stands represented typical old-growth forest types found in this region. Two of the stands were located in intact sites near ongoing research into the effects of artificial gaps placed in old-growth forests (see Spies et al. 1990*b*; Gray and Spies 1996). These were located at the Wind River Experimental Forest and H.J. Andrews Experimental Forest. Three of the stands were placed in permanent sample plots. These plots are part of ongoing research into the population dynamics of old-growth forests (see Franklin and Van Pelt 1990; Acker et al. 2000). One of these was also at the H.J. Andrews Experimental Forest, one was near Goat Marsh in Mount St. Helens National Volcanic Monument, and the third was at Giant Forest in Sequoia National Park. An additional site was recently mapped along Bull Creek in Humboldt Redwoods State Park by researchers at Humboldt State University and the University of Washington (Table 1).

H.J. Andrews stands

The H.J. Andrews Experimental Forest occupies the 6400-ha Lookout Creek watershed which is located about 80 km east of Eugene, Oreg., in the McKenzie River Valley (Table 1). This old-growth stand is dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), and in some areas western redcedar (*Thuja plicata* Donn ex D. Don) is prominent. Dominant understory trees are western hemlock, western redcedar, and Pacific yew (*Taxus brevifolia* Nutt.). The oldest trees established after fires which burned in the late 1400s and early 1500s (Teensma 1987). This stand will be referred to as the HJA unburned stand. Nearby, an additional stand was used that had the same early history as that just mentioned, but between 1836 and 1857, four separate fires burned through the understory of this stand (Teensma 1987). The fires were severe enough to create large openings, although about half of the dominant Douglas-firs survived. A dense cohort of western redcedar and western hemlock developed in the openings. Survivors of this cohort now dominate the midcanopy section of the stand and outnumber the older trees. This 150-year-old midcanopy cohort has provided dense shade and limited understory in some areas. This stand will be reffered to as the HJA underburned stand. Plots were initially established in 1990 with additional plots added in 1992.

Wind River stand

The 4380-ha Wind River Experimental Forest lies within the Gifford Pinchot National Forest near Carson, Wash. The old-growth forests at this site are dominated by Douglas-fir and western hemlock. The study site is within the western hemlock zone (Franklin and Dyrness 1973) but is at the cooler end, as indicated by the dominance of Pacific silver fir (*Abies amabilis* (Dougl.) Forbes) in the understory (Table 1). Pacific yew is common as a small understory tree. There is no evidence of major fire episodes at the site in at least 300 years, and ring counts on stumps in nearby areas indicate that some trees were more than 500 years old when cut in the 1970s (Franklin and Waring 1980). The dominant disturbance now is one of small-scale gap formation from windthrow, insects, and pathogens (Franklin and DeBell 1988). Plots were initially established in 1990 with additional plots added in 1992 and 1993.

Goat Marsh stand

Goat Marsh Research Natural Area is a federally designated research natural area within the Mount St. Helens National Volcanic Monument in Washington. The study stand is about 350 years old and is dominated by noble fir (*Abies procera* Rehd.), a common, seral, montane species (Table 1). Smaller amounts of Douglas-fir are also present in the canopy. The main midcanopy and understory species are western hemlock and Pacific silver fir. The 4-ha plot was initially established in 1977 and remeasured in 1989, 1994, and 1996.

Giant Forest stand

The fifth stand is located at midelevation in the mixed conifer forest zone of the southern Sierra Nevada Mountains. A 2-ha permanent plot straddles Crescent Creek, a small stream flowing through Giant Forest at 2200 m in elevation (Table 1). While the giant sequoia (*Sequoiadendron giganteum* (Lindl.) Buchholz)is the dominant species in terms of volume or basal area, white fir has a much greater stem density. California red fir (*Abies magnifica* A. Murray), another shade-tolerant fir, is also abundant. Other species present include sugar pine (*Pinus lambertiana* Dougl.) and Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.). The plot was established in 1979 with remeasurements in 1987 and 1994.

Bull Creek stand

Bull Creek flows through the heart of Rockefeller Forest in Humboldt Redwoods State Park, California. The alluvial flats along Bull Creek have the highest recorded biomass of any forest known (Westman and Whittaker 1975; Fujimori 1977). This region also contains many of the world's tallest trees, several of which are over 110 m tall. The forests in this stand contains many trees between 1000 and 2000 years old, and it is overwhelmingly dominated by a single species, the coast redwood (*Sequoia sempervirens* D. Don,

Table 1. Summary of site characteristics.

Site	Elevation (m)	Slope (%) and aspect	Plots		Plant association	Precipitation (cm)			Mean annual temperature and range (°C)
			No.	Area (ha)		Annual	July–Sept.	Snowfall	
H.J. Andrews (underburned)	880	5–15, W	4	1.57	*Tsuga heterophylla/Berberis nervosa*	258	13	295	8.5 (0.6–17.8)
H.J. Andrews (unburned)	780	0–5, SW	3	1.71	*Tsuga heterophylla/Berberis nervosa*	258	13	295	8.5 (0.6–17.8)
Wind River	610	0–12, S	4	2.26	*Tsuga heterophylla/Achlys triphylla*	253	12	233	8.0 (0–17.5)
Goat Marsh	945	5, SW	1	4	*Abies amabilis/Tiarella unifoliata*	337*	17	767	4.7 (–0.4 to 10.7)
Giant Forest	2219	10, SW–SE	1	2	*Abies concolor/Pteridium aquilinum*	110	2	482	8.1 (0.2–17.9)
Bull Creek	31	0	1	3	*Sequoia sempervirens/Oxalis oregana*	146*	3	1	14 (6.8–21.9)

Note: Giant Forest is the driest site, but its deep, slow-melting snowpack and porous soils allow productivity throughout the summer. The Bull Creek stand is on an alluvial flat, thus reducing the need for summer precipitation.

*Does not include interception from fog, which can add 20–30% (Harr 1982).

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Table 1). In openings or near streams tanoak (*Lithocarpus densiflorus* Hook. & Arn.), California laurel (*Umbellularia californica* Hook. & Arn.), and Douglas-fir are present in small numbers. A 3-ha plot was established in the summer of 1997 along the lower section of alluvial flat near the Eel River.

Field procedures

At each site, both plots and transects were used. Plots were needed for the point pattern analysis and transects for the semivariance and correlations. All sampling occurred in large, low-gradient blocks of forest located well away from openings such as roads or clearcuts. All data was pooled for the stand-level analyses. Plot areas ranged from 0.7 to 4 ha, depending on circumstances. In the three Douglas-fir forest types, plots were established as part of a larger study examining the effects of experimental gaps on understory processes (Spies et al. 1990*b*; Gray and Spies 1996, 1997; Van Pelt and Franklin 1999). The other three plots are part of the permanent plot network maintained by Oregon State University.

On both plots and transects, all trees taller than 50 cm in height were mapped and measured for species, vertical stratification (see below), and canopy class (dominant, codominant, intermediate, or suppressed). Breast height diameters were measured on all trees taller than 1.37 m; otherwise, basal diameters were measured. Height, crown height, and four cardinal crown radii were measured on as many trees as possible (85% overall), and nonlinear regression was used to estimate the remaining tree heights and crown radii (Van Pelt 1995; R. Van Pelt unpublished data). Tree heights and crown heights were measured with tape and clinometer. The clinometer was also used to find the edge of the crown for the crown radii measurements.

Two 200-m north–south transects were placed in each stand with the additional objective of measuring and correlating understory cover and potential light levels. Cover values for shrub and herbaceous species were subsampled in continuous 1 m diameter circular plots centered along transect lines. Hemispherical photos were taken along the transects and in the plots at a height of 1.5 m in each forest type for estimating light levels in the understory. Depending on the circumstances, up to 184 photos were taken at a site, although no less than 36 were taken at a given site. Additonal images were developed from computer-generated hemispherical images based on modeled trees (see Van Pelt and North 1996) so that a contour map of the understory light environment of each stand was generated. This allowed the understory light environment to be compared with understory measurements of growth and abundance.

Vertical stratification

The forest canopy was stratified into four levels to indicate the relative dominance of a given tree relative to its neighbors (Richards 1952). Each tree was classified as being part of the emergent layer, main canopy, intermediate canopy, or understory. Although this idea was developed in tropical forests, it has been adapted for use in temperate coniferous forests (Stewart 1986). As with tropical forests, this is a somewhat subjective procedure, because it is not based on absolute height but on relative height (i.e., relative to the trees immediately surrounding the subject tree). Therefore, the tree heights may overlap slightly between vertical layers.

Leaf area

Leaf area was estimated in each stand to compare with other estimates of species dominance. Sapwood area is significantly correlated with foliage biomass and leaf area (Waring et al. 1982; Maguire and Hann 1988). Several nearby trees were cut at the H.J. Andrews and Wind River sites in the winter of 1990 as part of another study (Spies et al. 1990*b*). Sapwood measurements were collected on 437 trees as they were removed. The trees represented the full array of species and sizes found on the plots. Four radii were measured on each stump from the center (pith) to the bark. The width of sapwood along each radius was measured. The four sapwood measurements on each tree were used to determine the sapwood area at stump height. Regressions were then developed for each species at each site that predicted sapwood area from DBH (diameter at breast height). Additional data relating DBH to sapwood area was obtained through published and unpublished reports (Parks 1952; Westman 1987; Means et al. 1994).

Analysis

To analyze the horizontal and vertical distribution of tree crowns, the location of each crown must be known. The crown parameters that were measured in the field were used to model each tree crown as a simple conic shape (Van Pelt and North 1996). Conics are simplistic models that provide an outer boundary for crown modeling and are easily analyzed in three-dimensional space, making them suitable for stand-scale analyses (Terborgh and Petren 1991; Van Pelt and North 1996). While this method ignores the fact that tree crowns are not solid foliage, it does keep the spatial arrangement of the crowns in three-dimensions intact (Van Pelt and North 1999).

Stand-scale calculations were made at each site for vertical and horizontal distribution of tree crowns. The three-dimensional models allowed for precise coordinates of crown parameters to be summed and tallied. The three-dimensional space of each plot was separated into 1-m cubes. Each cube was then tallied as to whether it contained all or part of a tree crown. These were used to examine the variability of tree crown distribution in both horizontal and vertical planes. Vertical projections of foliage density for three of the forest types were used to analyze the variability of canopy density.

Gaps – expanded gaps – closed canopy

Once the trees were mapped, all crown radii were then used to generate elliptical crown projections for use in a geographic information system (ARC-INFO 1997). A stem map and crown projection map was then generated to delineate areas and locations of gaps, expanded gaps, and closed canopy according to traditional gap sampling protocol (Runkle 1992). Using this terminology, a gap is an area that is not covered by the projection of a tree-crown. An expanded gap is an irregular polygon formed by connecting the trunks of the trees whose crowns define the gap. Cosed canopy is then all of the remaining space. This was then used in conjunction with the stem map of understory trees to determine their locations relative to gaps.

Hemispherical photographs

Each photo was analyzed and the amount of open sky in each photo was used to calculate the indirect site factor (ISF), which is an estimate of the amount of diffuse radiation that is annually received by that point (Anderson 1964). CANOPY image analysis software was used for calculations of ISF from black and white negatives (Rich 1989).

Semivariance analysis

The spatial distribution of tree crowns influences many understory variables, including light distribution and shrub cover. The variability of foliage distribution is key to this structure and to the comparisons between the six sites. Semivariogram analysis was used to test the variability of the foliage distribution between the six sites. Semivariograms for foliage distribution were based on the two 200-m transects in each stand. The data were extracted from the transect data to form two-dimensional series data, with one dimension being the distance along the transect and the other being the canopy volume in a 9 m^2 cylinder above that point. Semivariance analysis not only detects the dominant scale of pattern present in the data (the lag) but also measures the amount of variability within the data (the sill) (see Cohen et al. 1990).

Table 2. Summary of canopy volume distribution and stand dimensions.

Research site	Species	Canopy volume (m^3/ha)	Basal area (m^2/ha)	Stem volume (m^3/ha)	Height (m)
H.J. Andrews (underburned plot)	*Taxus brevifolia*	600	0.6	0.6	11
	Thuja plicata	19 700	38.3	408.5	57
	Tsuda heterophylla	56 900	24.1	458.5	57
	Pseudotsuga menziesii	20 400	41.9	1431.9	75
	Total	144 400	129.7	2397.0	
H.J. Andrews (unburned plot)	*Taxus brevifolia*	2 100	1.1	8.7	18
	Thuja plicata	13 700	17.5	243.7	51
	Tsuga heterophylla	75 100	24.7	391.7	70
	Tsuga heterophylla	75 100	24.7	391.7	70
	Pseudotsuga menziesii	53 500	86.1	1750.3	77
	Total	144 400	129.7	2397.0	
Wind River	*Taxus brevifolia*	1 500	0.6	5.8	12
	Abies amabilis	6 400	5.3	64.4	45
	Tsuga heterophylla	90 000	40.3	399.9	54
	Pseudotsuga menziesii	38 300	53.3	968.2	57
	Total	136 200	99.5	1447.7	
Goat Marsh	*Abies amabilis*	17 400	9.8	121.9	45
	Tsuga heterophylla	58 700	13.5	229.7	59
	Pseudotsuga menziesii	29 500	31.2	780.6	84
	Abies procera	48 100	67.5	1987.3	90
	Total	153 700	122.2	3119.5	
Giant Forest	*Abies magnifica*	4 700	3.8	68.8	77
	Abies concolor	39 000	37.4	653.1	72
	Pinus spp.	1 900	0.9	11.1	52
	Sequoiadendron giganteum	35 200	121.9	2597.7	87
	Total	80 800	164.0	3330.7	
Bull Creek	*Sequoia sempervirens*	229 300	265.2	8070.5	112
	Umbellularia californica	800	0.2	1.1	22
	Total	230 100	265.4	8071.6	

Point pattern analysis

Ripley's *K*(*d*) statistic is a second-order analysis used to detect the type and scale of pattern, particularly concerning interactions between groups of trees (Ripley 1981). Because it uses all tree-pair combinations, Ripley's *K*(*d*) analysis provides opportunities for more detailed analysis of point interactions (univariate), as well as providing for both within-class and among-class analysis of points (multivariate). To detect patterns of aggregation, randomness, or regularity among the six stands, the univariate measure was used on both the canopy-dominant trees in each stand, as well as the understory trees.

A bivariate form of this analysis is also possible, allowing one to see attraction or repulsion between differing groups of data (Moeur 1993). In this analysis, the bivariate form of Ripley's *K*(*d*) was performed by comparing the observed *K*(*d*) to Monte Carlo simulations, using the shifting torus method described by Lotwick and Silverman (1982). Several bivariate comparisons were made using either understory trees or snags to see if patterns of mortality followed the gap-phase replacement idea of forest dynamics.

Results

The Results section is broken up into two main sections: Canopy structure and Canopy gaps and understory response. For the Canopy structure section, we examine the distribution of tree crowns among the six stands, both horizontally and vertically; the variability of this distribution; and the spatial pattern of canopy trees. For the Canopy gaps and understory response section, we examine understory light levels and shrub–herb cover values of the six stands and compare these with overstory variables. The spatial patterns of understory tree and shrub distribution are examined and related to overstory variables.

Canopy structure

Tree crown distribution

The peak in crown density on the H.J. Andrews underburned plots was between 15 and 20 m (Fig. 2*a*). This was due to the abundance of 150-year-old hemlock–redcedar canopy that developed following the fire. The trees were very uniform in size and form a dense canopy at 15–25 m. The Douglas-firs that survived the fire form an emergent canopy extending well above this, with heights of 60–70 m and crown volumes peaking at 40–45 m.

The unburned site at H.J. Andrews (Fig. 2*b*) not only has a greater canopy volume of Douglas-fir than the underburned site but also of hemlock. About half of the Douglas-fir population in the underburned site was lost in the fire (Tables 2 and 3). While hemlock is growing rapidly,

Table 3. Numbers of individuals for each species within each canopy layer.

Research site	Species	Emergent	Main canopy	Intermediate	Understory
H.J. Andrews (underburned plot)	*Taxus brevifolia*	—	—	1	86
	Thuja plicata	—	26	55	513
	Tsuga heterophylla	—	43	158	454
	Pseudotsuga menziesii	19	2	—	—
	Total	19	71	214	1053
H.J. Andrews (unburned plot)	*Taxus brevifolia*	—	—	2	95
	Thuja plicata	—	21	12	424
	Tsuga heterophylla	1	50	33	782
	Pseudotsuga menziesii	33	33	—	—
	Total	34	104	47	1301
Wind River	*Taxus brevifolia*	—	—	3	41
	Abies amabilis	—	11	16	1355
	Tsuga heterophylla	—	61	72	438
	Pseudotsuga menziesii	1	51	—	—
	Total	1	123	91	1834
Goat Marsh	*Abies amabilis*	—	18	35	81
	Tsuga heterophylla	—	20	18	293
	Pseudotsuga menziesii	2	14	—	—
	Abies procera	5	40	1	3
	Total	7	92	54	377
Giant Forest	*Abies magnifica*	1	3	8	97
	Abies concolor	1	34	57	240
	Pinus spp.	—	1	4	9
	Sequoiadendron giganteum	12	5	4	5
	Total	14	43	73	351
Bull Creek	*Sequoia sempervirens*	2	46	111	1794
	Umbellularia californica	—	—	3	27
	Lithocarpus densiflorus	—	—	1	11
	Total	2	46	115	1832

Note: Values are given on a per-hectare basis.

it has yet to attain the canopy volume of the unburned site, comprising only 75% of the volume of the unburned plots. While the density peak for hemlock is at about 20 m at both sites, it was achieved by far fewer stems of both larger and smaller size classes in the unburned plot (Figs. 2*a* and 2*b*).

While the canopy volume of the underburned site has almost returned to pre-burn levels (at least for hemlock; see Table 2), a much greater number of stems was required to achieve this. The number of trees in the main canopy layer is only slightly lower, but there are nearly five times as many stems in the intermediate layer as in nearby unburned portions of the forest (Table 2).

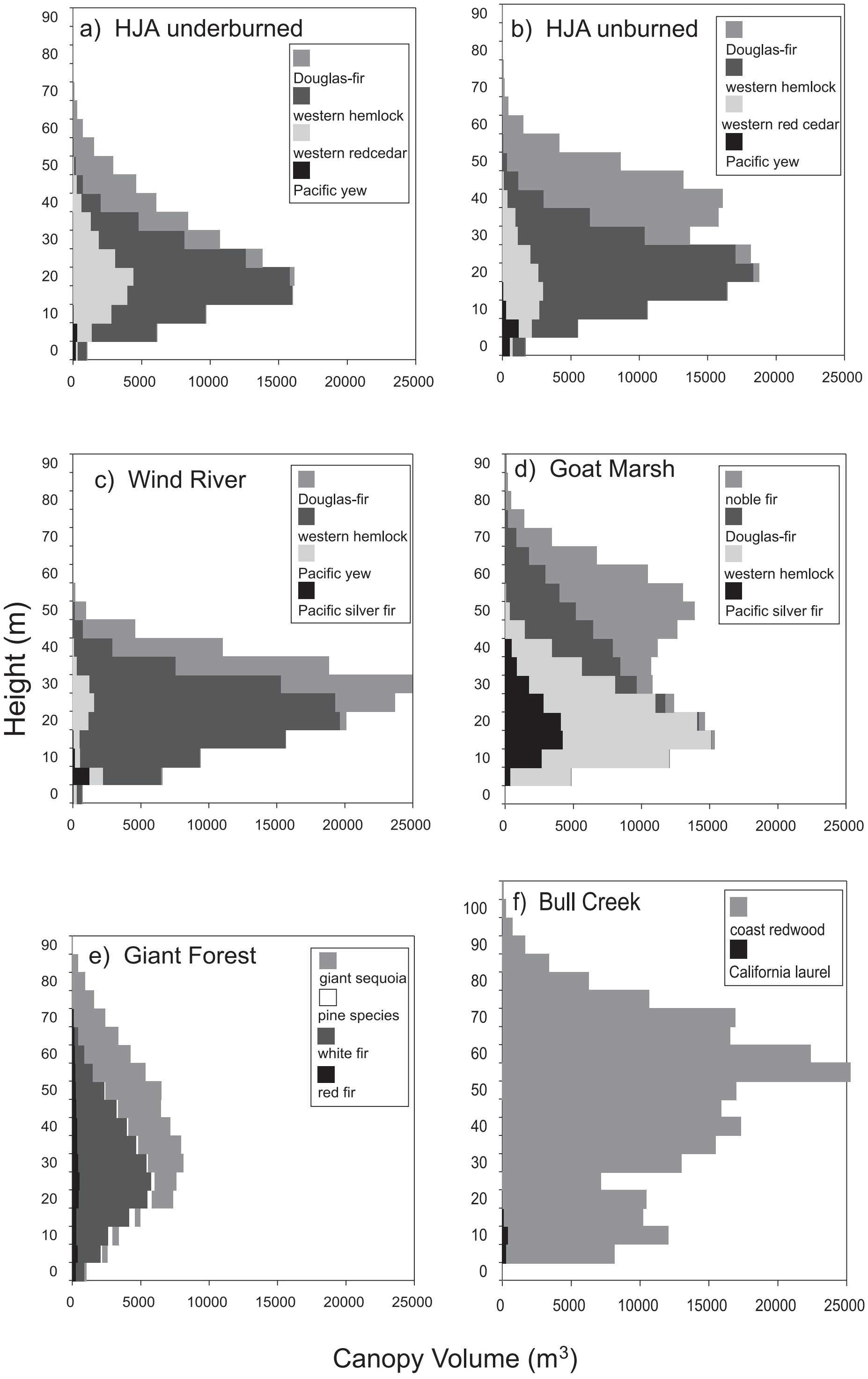
Based on plant associations and tree heights, the site productivity at Wind River is much lower than that of either of the H.J. Andrews sites (Wind River has no trees over 60 m tall versus 11/ha at the Andrews unburned site, even though both are the same age). In addition, the hemlocks at Wind River are nearly as tall as the Douglas-firs. An overwhelming canopy dominance of western hemlock is evident (Fig. 2*c*). Although the uppermost canopy is dominated by Douglas-fir, the entire middle and lower canopy is dominated by western hemlock.

Tree crowns on the Wind River site are distributed similarly to the crowns on the unburned plot at H.J. Andrews. Although the Wind River site has much shorter trees and lower basal areas than the other five sites, crown volumes are comparable. This is primarily due to the greater dominance of western hemlock, resulting in a greater canopy volume.

The canopy at Goat Marsh is very tall. The main canopy trees average over 65 m, and several trees are over 85 m tall. While it is an old-growth stand (~350 years), the forest is still developing some of its old-growth structure. There is a distinct upper canopy layer composed of noble fir and Douglas-fir and an intermediate–understory layer composed of western hemlock and Pacific silver fir. The separation of these two canopy layers is evident in Fig. 2*d*. In addition, the shade-tolerant component of this canopy makes up a much lower percentage than in the three previously mentioned Douglas-fir stands (<50% as opposed to 79, 63, and 75% for HJA unburned, HJA underburned, and Wind River, respectively) (Tables 2 and 3).

The canopy at Giant Forest is much more open than the others in this study, as will be discussed later. Even though the basal area and wood volume are very high in this stand (Table 2), the canopy volume and stem density are much lower than the stands previously mentioned (Tables 2 and 3, Fig. 2*e*). The foliage is found at all levels as in the other old-growth forests, but the total number of tree crowns is much lower than the other five sites. Even though the forest

Fig. 2. Vertical canopy volume profiles for the six stands. Summary information is given in Table 2.



is more open, it still has a tall, multilayered canopy. Individual trees on the plot range up to 6 m in diameter (basal area of 28.3 m^2). The stem volume of the largest tree on the plot is nearly 1000 m^3, equal to more than half a hectare of trees in the Wind River stand.

The forest at Bull Creek is almost entirely composed of coast redwood, which is found in all size classes (Tables 2 and 3, Fig. 2*f*). This forest type comprises the world's tallest canopy; the 3-ha plot averages 15 trees/ha over 94 m in height. The volume of canopy is much higher than for the other plots, and the peak in density is also higher. The maximum occurs at a height of about 50 m, whereas the other plots peaked at 15–35 m.

Semivariance analysis

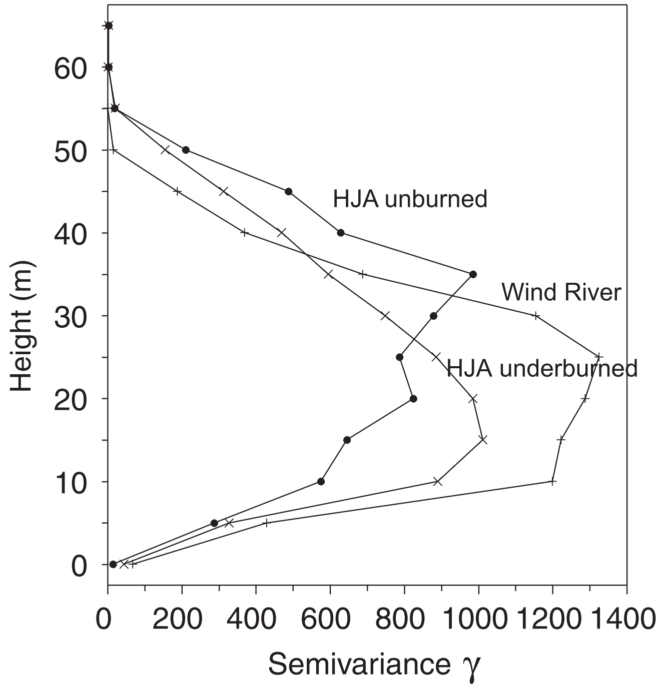
Underburned sections at the H.J. Andrews show a much lower semivariance than the five other forest types (Table 4). The concentration of foliage in one fairly uniform layer

Table 4. Semivariance results: gap size, understory light levels, shrub–herb cover, and leaf area index (LAI) for the six stands.

	H.J. Andrews					
	Underburned	Unburned	Wind River	Goat Marsh	Giant Forest	Bull Creek
Semivariance sill (γ)	2121	6043	3930	3482	3318	4434
Semivariance lag (m)	9.8	9.6	8.9	7.2	12.2	9.7
Gap area (m^2)	51.5 (13.2)	81.7 (83.3)	25.5 (16.6)	75.4 (172)	366 (373)	145 (119)
Light levels (ISF)	0.0827 (0.036)	0.1465 (0.085)	0.1267 (0.074)	0.0873 (0.027)	0.1917 (0.102)	0.0958 (0.037)
Shrub–herb cover (%)	7.64 (17.95)	23.38 (29.07)	25.42 (26.34)	19.67 (12.64)	37.63 (30.98)	45.92 (25.17)
LAI	11.07 (0.92)	13.75 (2.75)	11.58 (2.79)	11.63 (1.16)	8.17 (1.11)	11.71 (2.03)

Note: Values for gap area, light levels, shrub–herb cover, and LAI are means with SD given in parentheses. The lag value is a measure of the scale of the dominant pattern. ISF, indirect site factor (a measure of percent open sky).

Fig. 3. Semivariogram summaries for the vertical layers for the three Douglas-fir forest types. Each data point shows a sill value from semivariograms calculated separately for each 5-m layer. Note the overall low semivariance above 40 m at Wind River, yet this site has the highest below 30 m.



within the regenerated cohort contributes to this pattern. Since the main canopy is composed of smaller, more numerous trees, the gaps are smaller, and the densest areas based on vertical projections of crown volume are less dense than those in the unburned old-growth forest.

The semivariance values for horizontal foliage distribution on the Wind River transects lie intermediate between the two transect types at H.J. Andrews (Table 4). Even though the unburned portions of the H.J. Andrews and Wind River transects have similar histories and multilayering, the larger stature of the H.J. Andrews forests are reflected in the higher variability of the tree crowns there. The forest at Bull Creek, while having the greatest stature of the forest types examined, has the bulk of its crowns up high in the stand, thus having less total variability than the unburned Douglas-fir – western hemlock stand at H.J. Andrews. The relatively low values for the Goat Marsh and Giant Forest are due to large areas of homogeneity in the two stands. The Goat Marsh stand has a dominance of trees taller than 60 m (48/ha; more than any of the other stands), which creates a realatively flat, homogeneous canopy when viewed from above. The Giant Forest stand has a dominance (>50%) of gap, which lowers the overall variability.

The semivariance lag values (in metres) for the six stands represent the dominant scale detected in the transects (Table 4). The Giant Forest stand has the highest lag, primarily because of the large size of the gaps in that stand. Goat Marsh had the lowest lag, which is a reflection of the uniformly tall canopy rather than of gap size. The lag detects the dominant scale in the tree crown distribution data. At Giant Forest this is caused by the gaps; at Goat Marsh and Bull Creek, this is due to the tree crowns; and with the others, it is probably a combination of both.

Semivariance patterns for the vertical distribution of foliage were calculated for the three Douglas-fir dominated plots only. This was done independently for each 5-m horizontal layer. The sill value for each layer was then used as a point, and all the points were then plotted to compare the three forest types. The vertical semivariance structures for all three forest types were then plotted together (Fig. 3). Overall, the Wind River transects have the highest semivariance of the three plots for values below 30 m but the lowest above 40 m. The Wind River's short stature relative to the H.J. Andrews forests accounts for this quick decline. The underburned transects at H.J. Andrews have higher semivariance values than the unburned transects for the canopy below 25 m. This lower section is where the bulk of the foliage in the underburned transects is located. The unburned section at H.J. Andrews, however, has much higher variability between 35 and 65 m, accounting for its overall high variance in the horizontally projected semivariograms.

Canopy tree spatial patterns

The spatial patterns of individual species were random or aggregated at each of the six sites. When only main canopy trees of all species were considered, however, inhibition (regular spacing) occurred at five of the six sites at scales of 4 m (Fig. 4). At three of the sites the regular spacing was pronounced over a greater range. The Goat Marsh and Bull Creek sites had main canopy trees regularly spaced at scales from 4 to 14 m.

Canopy gaps and understory response

The amount of light reaching the understory varied greatly among the six stands. Light levels were lower in the

Fig. 4. Results of the univariate Ripley's *K*(*d*) analysis for the main canopy trees. Each graph represents a single analysis. The solid lines with plus signs show *L*(*d*) (the square root transformation of *K*(*d*)), the broken lines are the confidence interval generated through 100 Monte Carlo simulations. The shaded areas indicate significant departures from a Poisson distribution; those above the zero line show significant aggregation and those below show dispersion to a uniform (regular) distribution. Note the regular distribution (inhibition) of trees at small scales for four of the six sites. The two exceptions are the HJA underburned site, which lost some of the main canopy trees in a fire, and the sequoia site, which has a partly open canopy.

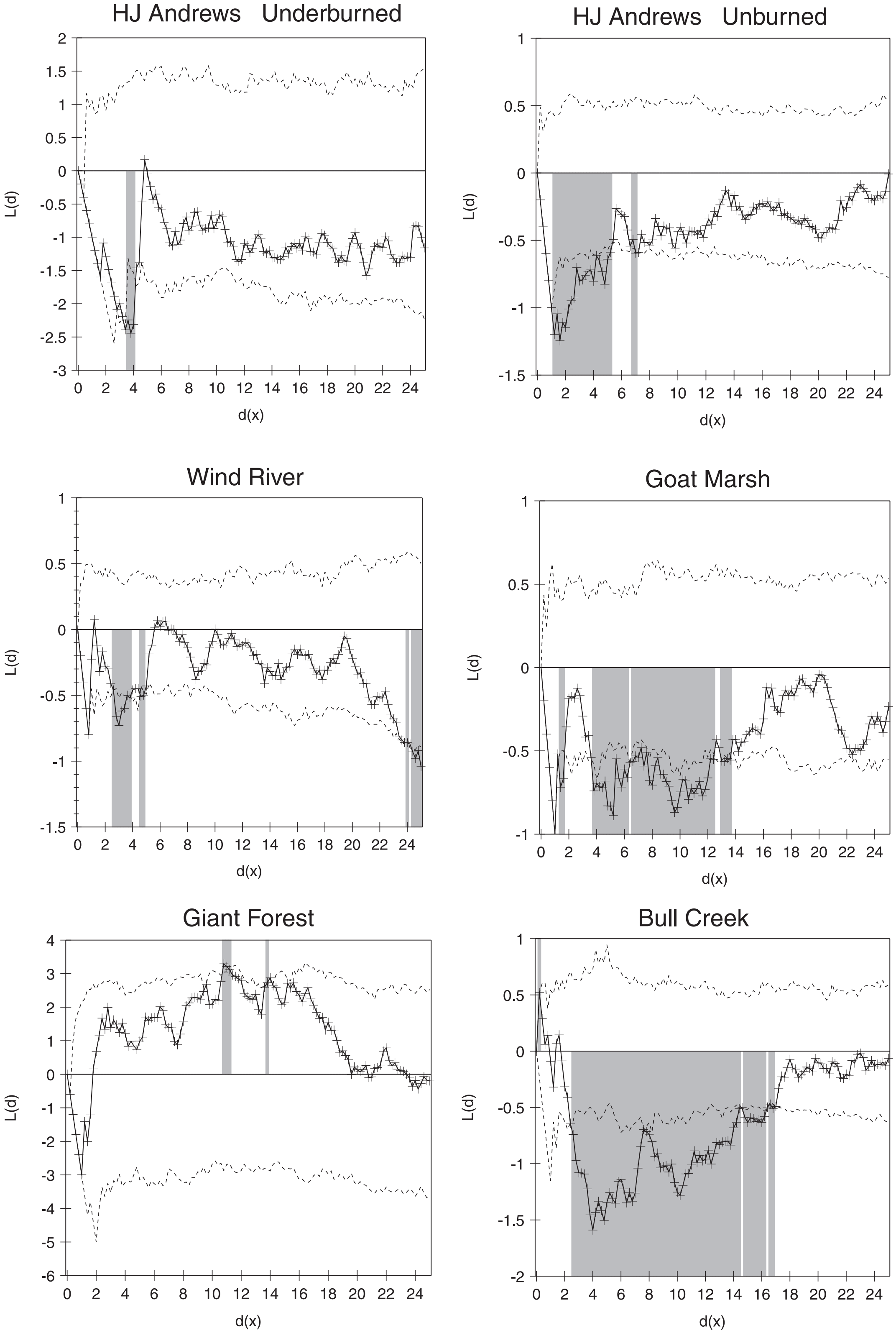


Table 5. Number of understory trees (>50 cm in height) per hectare in each canopy category.

	Gap	Expanded gap	Closed canopy	Percentage in gap
HJA, underburned	21.1%	44.0%	34.9%	27/19
Taxus	21 (21)	48 (32)	17 (19)	24
Thuja	87 (7)	304 (9)	122 (3)	17
Tsuga	172 (41)	216 (55)	66 (26)	38
HJA, unburned	32.3%	46.9%	20.8%	21/50
Taxus	20 (12)	49 (25)	27 (6)	21
Thuja	59 (8)	101 (30)	264 (127)	14
Tsuga	196 (99)	222 (76)	364 (219)	25
Wind River	12.0%	39.9%	48.1%	20/29
Abies	277 (188)	630 (447)	448 (202)	20
Taxus	7 (<1)	20 (1)	14 (<1)	17
Tsuga	87 (39)	281 (49)	70 (32)	20
Goat Marsh	24.2%	35.1%	40.7%	29/23
Abies	11 (2)	49 (11)	21 (7)	14
Tsuga	98 (22)	129 (19)	66 (28)	33
Giant Forest	56.0%	36.6%	7.4%	30/3
A concolor	69 (12)	162 (13)	9 (3)	29
A. magnifica	34 (11)	62 (14)	1 (<1)	35
Pinus spp.	2 (<1)	7 (2)	0 (0)	22
Bull Creek	19.3%	42.9%	37.8%	21/29
Sequoia	382 (111)	892 (189)	520 (227)	21
Umbellularia	4 (2)	17 (8)	6 (4)	15

Note: Values are means with SD given in parentheses. The first row at each site is the percentage of land area in each canopy category. In this analysis, gaps were defined as holes in the emergent, main canopy, and intermediate layers that were at least 10 m^2. The final column is the percentage of each understory tree species found in the gaps.

underburned H.J. Andrews stand than in the other stands (Table 4) because of the uniformly dense canopy of the post-fire cohort in the underburned stand. The other Douglas-fir dominated plots had light values (ISF) similar to each other, which are 153–177% of those on the underburned plots. Light levels were also low in the Goat Marsh and Bull Creek plots. These two plots have very high levels of standing biomass. The Goat Marsh stand had a very dense upper canopy in addition to over 20% of the potential light being intercepted by tree boles. The Bull Creek stand had over 30% of the potential light being intercepted by tree boles as well as the greatest amount of foliage of the six stands. The Giant Forest stand had the highest light levels. This stand had a much lower density of trees thus allowing more light to penetrate to the forest floor.

Shrub cover values were related to those of the light values with some significant differences (Table 4). For the three Douglas-fir stands, there was a strong correlation between the amount of light reaching the understory and the abundance of shrubs and (or) herbs present. The Goat Marsh stand had light levels only slightly higher than the underburned stand at H.J. Andrews yet had over twice as much understory vegetation. The two California stands had the highest cover values of understory vegetation, although most of the cover in the Bull Creek stand was represented by a single species of shade-tolerant ground cover, *Oxalis oregana* (Nutt.).

Leaf area was calculated for each tree and then summed by species to calculate LAI for each stand (Table 4). The unburned plot at H.J. Andrews had the highest LAI, while the underburned plot had among the lowest. The effect of the fire was to remove significant portions of leaf area from the stand. The subsequent regrowth has not yet brought the leaf area back up to pre-fire levels. The lowest LAI was the sequoia mixed conifer forest at Giant Forest, largely due to the openness of the stand. The remaining three stands (two very tall, complex forests and the Wind River site with its high proportion of western hemlock) had similar values.

Understory trees grew in gaps at all sites (Table 5). However, in all cases, more understory trees were found growing outside of gaps than in gaps. The percentage of trees found in gaps varied from 21.2 to 30.3% across the six sites (Table 5). In all cases, more trees were found growing in expanded gaps than in either closed canopy or canopy gap positions. In addition, most plots had more understory trees growing under closed canopy conditions than under canopy gaps.

Understory tree spatial patterns

Understory trees are very strongly aggregated at all six of the research sites (Fig. 5). The bivariate form of Ripley's *K*, in which understory tree locations are compared with canopy variables, provided the most interesting analyses. In five of the six sites, a significant repulsion was detected between the locations of understory trees and canopy trees (Table 6). The exception, Goat Marsh, was probably due to the dominance of western hemlock in the understory, which was very strongly associated with logs or stumps (98.4%), whether in gaps or not.

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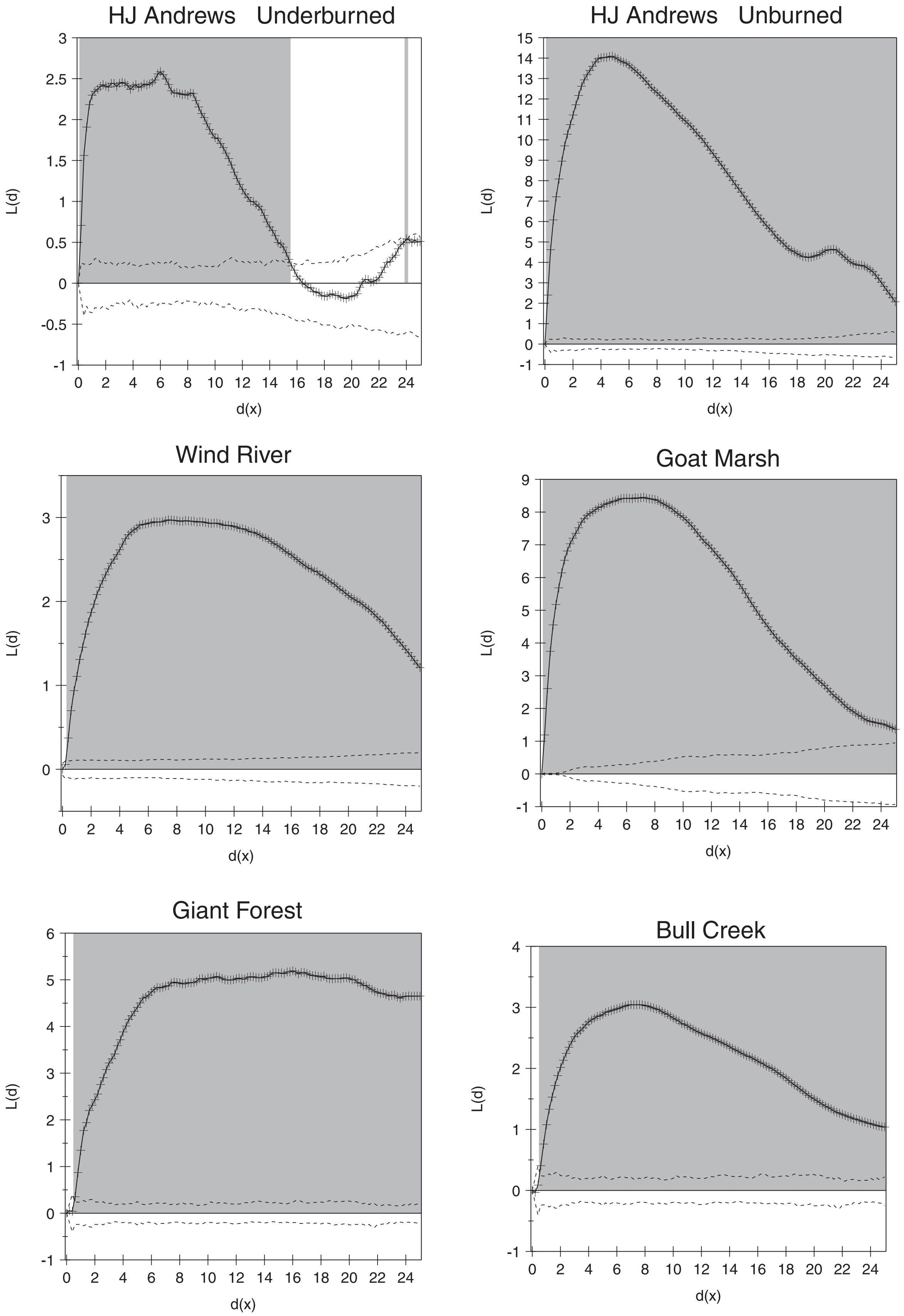

Fig. 5. Results of the univariate Ripley's *K*(*d*) analysis for understory trees. See description for Fig. 4. The strong aggregation of the understory trees is evident in all plots, as is common in most forest types.

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Table 6. Bivariate results from Ripley's *K*(*d*) analysis.

	Understory trees vs. main canopy		Understory snags vs. main canopy		Understory trees vs. recent canopy snags	
	Significance	Scale (m)	Significance	Scale (m)	Significance	Scale (m)
HJA, underburned	R	4–13	A	4 to >24	No	—
HJA, unburned	R	1–13	A	>20	R	>23
Wind River	R	1–19	A	>14	No	—
Goat Marsh	No	—		na	A	1–4
Giant Forest	R	14–22	A	18–22	No	—
Bull Creek	R	2–20		na		na

Note: When significance occurs in comparisons of the understory variables with either main canopy trees or snags, trees are categorized as either attracted (A) or repulsed (R). Scale gives the range in metres where the significant result was acting. na, not applicable (insufficient snags to do the analysis).

Table 7. Spearman rank correlation coefficients for transect data.

	Understory tree density	Shrub density
H.J. Andrews, underburned		
Heights	–0.069	–0.308*
Vertical density	–0.093	–0.251*
Gap – expanded gap – canopy	0.009	0.164*
H.J. Andrews, unburned		
Heights	–0.092	–0.271*
Vertical density	0.015	–0.198*
Gap – expanded gap – canopy	0.075	0.301*
Wind River		
Heights	–0.092	–0.271*
Vertical density	–0.041	–0.033
Gap – expanded gap – canopy	0.039	0.121
Goat Marsh		
Heights	–0.155	–0.016
Vertical density	–0.069	–0.126
Gap – expanded gap – canopy	0.032	0.064
Giant Forest		
Heights	–0.125	–0.373*
Vertical density	–0.054	–0.271*
Gap – expanded gap – canopy	0.154	0.412*
Bull Creek		
Heights	–0.059	0.184
Vertical density	–0.058	–0.248

Note: Significant correlations ($\alpha = 0.05$) are indicated by an asterisk. Note understory variables generally show negative (although weak) correlations with overstory canopy variables. Also, while understory tree density or shrub density is occasionally correlated with gaps, the correlation is weak and at times even negative.

A spatial attraction was shown (at various scales) when locations of recently dead understory trees were compared with the locations of canopy trees (Table 6). The Bull Creek stand had so few snags of any size that it was excluded from the analysis. A significant interaction of understory tree locations and canopy tree locations was indicated by the combination of understory trees being repulsed from canopy trees and dead understory trees being attracted to canopy tree locations.

In general there was no significant pattern between understory trees and recent canopy snags, which would indicate an attraction to canopy gaps (Table 6). While a repulsion of understory trees away from main canopy trees was indicated, this repulsion was random with regard to gaps.

Canopy–understory interactions were also tested using transect data. Three canopy variables (tree heights, canopy density, and canopy gaps) were compared with shrub–herb cover and understory tree locations to look for interactions. Each of the data sets were extracted from the transect data and represented a spatially continuous 200 m long data set. These were then compared with each other using a simple Spearman rank correlation. In all cases the occurrence of understory trees was not correlated with canopy conditions directly above them (Table 7). Shrub–herb cover often was correlated with canopy measures, which may indicate a closer temporal link than in the case of long-lived understory trees.

Discussion

A relationship between understory tree locations and canopy gaps was not detected in this study. This is in sharp contrast with gap studies from outside this region (Runkle 1981; Hibbs 1982; Brokaw 1987; Martinez-Ramos et al. 1989; Uhl et al. 1988). Tall, narrow-crowned trees at high latitudes combined with long-lived understory trees contribute to this lack of pattern. While shade-tolerant understory trees may need a gap to establish and perhaps also to eventually ascend to the canopy, a "snapshot" view of the forest at any given time does not reflect this. The ability of the understory trees to persist between disturbance events allows the canopy environment to change, while the understory tree locations remain the same. In addition, the changes in light due to canopy gaps often do not affect the same piece of ground where the belowground resources of the same gap appear. This decoupling of above- and below-ground resources after a disturbance is more pronounced in this region than in other temperate or tropical regions (Canham et al. 1990).

Other gap studies from within this region, however, show mixed results. The gap area and percent gap found in this study is comparable with other research from this region (Spies et al. 1990*a*; Lertzman and Krebs 1991). This is due simply to the nature of the stands and their structure. Conifer trees tend to have relatively narrow crowns, regardless of their size or age. Gaps, in this study and others, tend to be small and formed by one or a few trees. Seedling presence in gaps was shown to be not much different from the surrounding forest in young–mature stands of Douglas-fir in Oregon (Stewart 1988). However, underneath western hemlock there were fewer seedlings. Stewart’s sites were chosen to study the influence of fire on understory development and not for old-growth structure. Lertzman (1989) actually found that sapling density was lowest within gaps compared with the surrounding forest. Conversely, Spies et al. (1990*a*) found a higher density of western hemlock seedlings within gaps. The present study found that, while western hemlock seedlings were strongly associated with logs (84%), there was no greater abundance in gaps.

Overall understory conditions were influenced by canopy structure as indicated by the higher correlation between the herb–shrub layer and the canopy light environment. Even though Stewart (1988) found spatial patterns in the herb and shrub layer, he found no correlation between the light environment and what was directly above, illustrating the need to consider three dimensions. Knowledge of how the patterns of distribution and variance of foliage within a forest canopy affect understory conditions is essential. Further research may reveal how canopy structure influences not only understory plant dynamics but also many other ecosystem processes by creating greater habitat diversity.

Traditional measurements of the canopy environment have focused on LAI and visual approximations of foliage layers. These have provided needed, but rough, information on a complex three-dimensional ecosystem. However, LAI is a poor indicator of the understory light environment, which is unfortunate since many measures of LAI are based on optical measurements. These will necessarily be erroneous, since the same LAI can have wildly different optical conditions as determined by differing canopy structures. Structural analysis is necessary to examine patterns and variance of occupied space among forest canopies.

While the underburned H.J. Andrews stand had the lowest LAI of the three Douglas-fir forests, it also had the lowest understory light levels. This directly contravenes the common assumption that leaf area is related to the amount of light transmitted through the canopy. Without examining the vertical and horizontal heterogeneity of the canopy, one might incorrectly assume that the higher LAI indicated reduced understory light conditions.

The semivariance sill value of the horizontal distribution of tree crowns was the best single measure of canopy structure. It not only incorporates the vertical diversity of tree heights, but also the horizontal distribution of trees and their associated gaps. The cathedrallike Douglas-fir stand at the H.J. Andrews with its dense, multilayered western hemlock understory and the coast redwood stand were the most structurally diverse. The other stands, while sharing many features with these stands, all had one or more elements that simplified their structure enough to reduce the semivariance.

Dynamics in understory light and plant communities can be better understood as being driven by the heterogeneity of foliage distribution rather than simply the amount of canopy leaf area. The semivariance results indicate a much lower variability in the horizontal distribution of foliage for the burned sections at H.J. Andrews, leading to the lower light and shrub cover values found.

The strongly varied canopy, both vertically and horizontally, is highly correlated with understory light and shrub cover values. Although these forests have among the highest LAI values in the world, the understory light levels are relatively high when compared with smaller stature forests with high LAI values (Fujimori 1971). The relative amount of space occupied by foliage is not exceptional when compared with some other forest types because of the height of the forest. For any given vertical layer, there is usually more than 50% open space. When a LAI of 11 is spread out over a vertical dimension of 70 m or more, there is plenty of opportunity for light to penetrate. The high latitudes of western forests combined with the height of the canopy forces light to penetrate at relatively low angles, reducing the significance of a canopy gap on the point of ground directly beneath it.

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