Forest Stand Structure and Pattern of Old-Growth Western Hemlock/Douglas-Fir and Mixed-Conifer Forests

Malcolm North, Jiquan Chen, Brian Oakley, Bo Song, Mark Rudnicki, Andrew Gray, and Jim Innes

ABSTRACT. With fire suppression, many western forests are expected to have fewer gaps and higher stem density of shade-tolerant species as light competition becomes a more significant influence on stand pattern and composition. We compared species composition, structure, spatial pattern, and environmental factors such as light and soil moisture between two old-growth forests: Pacific Northwest western hemlock/Douglas-fir at the Wind River Canopy Crane Research Facility exhibiting gap-phase replacement and southern Sierra Nevada mixed conifer at the Teakettle Experimental Forest after 135 years without a fire. We hypothesized that fire suppression at Teakettle would create a current tree composition and distribution more like Wind River where light is an important influence on stand dynamics. Wind River has nearly continuous canopy cover and a high foliage volume that severely reduces understory light and stratifies the canopy composition by shade tolerance. Large trees are regularly spaced from 0 to 15 m and shade-tolerant and intolerant species are "repelled." In contrast, Teakettle's canopy cover is discontinuous, foliage volume is one-fifth that of Wind River, and understory light is 15 times higher. Trees at Teakettle are significantly clustered in groups containing a mix of shade-tolerant and -intolerant species, separated by large gaps. Although Teakettle's gaps have higher moisture and a thinner litter layer than tree groups, regeneration in gaps is scarce. Fire suppression has increased stem density at Teakettle but it has not filled in gaps, stratified the canopy by shade tolerance, or produced a composition consistent with patterns at Wind River. Teakettle's distinctly clustered stem distribution may result from a minimum canopy cover threshold needed for tree establishment. If high temperatures produced by direct sunlight inhibit stem patterns, traditional stand management that reduces canopy cover to release regeneration should be applied with caution in the southern Sierra Nevada. FOR. SCI. 50(3):299–311.

Key Words: Spatial pattern, shade tolerance, stand dynamics, Wind River Canopy Crane Research Facility, Teakettle Experimental Forest, Ripley's K analysis, forest gaps, canopy cover.

Malcolm North, Sierra Nevada Research Center, Department of Environmental Horticulture, University of California, Davis, CA 95616—Phone: (530) 754-7398; Fax: (530) 752-1819, mnorth@ucdavis.edu. Jiquan Chen, Landscape Ecology and Ecosystem Science, Bowman-Oddy Lab, MS 604, University of Toledo, Toledo, OH 43606—Phone: (419) 530-2664; jiquan.chen@utoledo.edu. Brian Oakley, College of Forest Resources, Box 352100, University of Washington, Seattle, WA 98195—Phone: (206) 543-7940; boakley@u.washington.edu. Bo Song, Belle W. Baruch Institute of Coastal Ecology and Forest Science, Clemson University, P.O. Box 596, Georgetown, SC 29442—Phone: (843) 545-5673; bosong@clemson.edu. Mark Rudnicki, Department of Renewable Resources, University of Alberta, Edmonton, Alberta, T6G 2E3 Canada—Phone: (780) 492-6827; mrudnick@ualberta.ca. Andrew Gray, Forest Inventory and Monitoring, PNW Research Station, P.O. Box 3890, Portland, OR 97208—Phone: (541) 750-7252; agray01@fs.fed.us. Jim Innes, Sierra Nevada Research Center, 2121 2nd Avenue, Suite A-101, Davis, CA 95616—Phone: (530) 759-1711; jinnes@fs.fed.us.

A FOREST'S CURRENT STRUCTURE, composition, and pattern are influenced by many factors over its developmental history including competitive interactions between trees, disturbance, and microsite differences in resources. In several silvicultural models, competition for light is a significant driver in young stand development between major disturbance events (Shugart and West 1980, Oliver 1981, Shugart 1984, Smith 1986, Oliver and Larson 1996) and continues to influence seral development in old-growth forests where localized disturbance creates gap-phase replacement (Runkle 1985, Canham 1988, Stewart 1989, Lertzmann 1992). In many western conifer forests, however, historic frequent, low-intensity fire produced open canopies (Parsons and DeBenedetti 1979, Covington and Moore 1994) where light competition may have been a less significant influence on stem pattern and forest composition. Following a century of fire suppression, these forests often have increased stem density and fewer gaps, as shade-tolerant species fill in stand understory and canopy openings (Minnich et al. 1995, Bouldin 1999, Stephenson 1999). In the absence of fire, has stand structure and composition shifted toward patterns found in forests with more infrequent disturbance regimes? What do current stem patterns suggest about tree competition and resource distribution in the absence of frequent low-intensity fire?

While many factors influence forest structure, analysis of stem locations can help infer processes influencing stand dynamics (Watt 1947, Cooper 1961, Kenkel 1988). Szwagrzyk and Czerwczak (1993) hypothesized that competition and resource distribution should create two general patterns in stem distribution. Large trees should be regularly spaced at small distances due to growing space competition, and all stems should be clustered at larger scales reflecting localized differences in growing conditions. Departures from either of these trends and the scale over which it occurs can help identify other factors driving stem pattern. In some forests, the dynamic between competitive repulsion and microsite attraction may be relatively balanced, producing a highly dispersed stem pattern and continuous canopy cover (Armesto et al. 1986). If light, water, or nutrients, however, are highly variable due to microsite differences or disturbance history, resource distribution may override competitive repulsion, creating a spatial pattern and species composition driven by patch dynamics (Pickett and White 1985, Taylor and Halpern 1991). This pattern would be particularly evident if large trees, with their high resource requirements, are not regularly distributed at small scales.

After a century of fire suppression, many forests in California's Sierra Nevada may have a stem density and canopy cover outside their range of historic variability (Minnich et al. 1995, Stephenson 1999). What stem pattern have these conditions produced and what does the pattern suggest about tree competition for light and water? We compared stand structure, composition, and pattern between two old-growth western conifer forests: a *Pseudotsuga menziesii/Tsuga heterophylla* stand in the Pacific Northwest and a mixed-conifer stand in the southern Sierra Nevada. We also compared a set of light and soil moisture measurements made over the same period at each site. Both stands have a mix of long-lived, shade-tolerant and -intolerant conifers and have not burned in over 135 years. Our objectives were: (1) to compare stand composition, structure, and spatial distribution between the two forest types; (2) to examine differences in the vertical and horizontal pattern of shade-tolerant and -intolerant species; and (3) to compare tree spatial patterns to soil moisture and light conditions to assess how our measures of these resources correlate with forest structure and composition. In drier mixed-conifer forests, soil moisture and light could constrain the distribution of shade-tolerant infilling even in the absence of fire. We hypothesized that stem pattern could become highly clustered if spatial variation in water or light crossed tree tolerance thresholds.

Methods

We focused on two sites with known disturbance histories, comparable light and soil moisture measurements, and extensive stem maps; the Teakettle Experimental Forest and the Wind River Canopy Crane Facility. Although 1,000 km apart, a 1,600-m difference in elevation creates similar seasonal precipitation patterns and mean temperature (Shaw et al. 2004, North et al. 2002). We selected Teakettle and Wind River because both sites have large stem maps allowing more in-depth analysis of differences between the two conifer forests. Although we lacked multiple sites to infer how representative each location is of its forest type, other studies have found Teakettle (North et al. 2002) and Wind River (Franklin et al. 1972; Van Pelt and Franklin 2000, Shaw et al. 2004) are fairly typical of old-growth mixed conifer and cool western hemlock/Douglas-fir forests, respectively.

Study Sites

The Teakettle Experimental Forest is a 1,300-ha old-growth watershed on Patterson Mountain located 80 km East of Fresno, California, on the Sierra National Forest. Teakettle's most common soil is a well-drained, mixed, frigid Dystric Xeropsamment, formed from decomposed

granite, typical of many southern Sierra forests (Anonymous 1993). The annual precipitation of 125 cm falls mostly as snow between Nov. and Apr. (North et al. 2002) (Figure 1). A nearby snow survey station (4 km NE of Teakettle at 1,920 m) with a 30-year record indicates average annual snowfall of 220 cm and a mean maximum depth of 114 cm (range 24–241 cm).

Our research in this study focused on an 8.4-ha contiguous block of mixed-conifer forest at 2,000 m in elevation within the Teakettle Experimental Forest. The mixed-conifer forest contains white fir (*Abies concolor* (Gord. & Glen.) Lindl.), sugar pine (*Pinus lambertiana* Dougl.), incense-cedar (*Calocedrus decurrens (*Torrey) Florin), Jeffrey pine (*Pinus jeffreyi* Grev. & Balf.), and red fir (*Abies magnifica* var. *magnifica* Andr. Murray). Understory species include black oak (*Quercus kellogii* Newb.), canyon live oak (*Q. chrysolepis* Liebm.), and bitter cherry (*Prunus emarginata* (Hook.) Walp.). Sugar and Jeffrey pine are the largest diameter and tallest trees. Mean dominant tree height is 50–60 m. Characteristic of the mixed-conifer forest type, white fir dominates stem density and basal area (Rundel et al. 1988), and this dominance has increased with fire suppression. On average, before 1865, Teakettle's mixed conifer burned every 12–17 years (Fiegener 2002). The last fire in our 8.4-ha block was in 1865.

The Wind River Canopy Crane Research Facility is located within the T.T. Munger Research Natural Area of the Gifford Pinchot National Forest in southern Washington at an elevation of 355 m. It has a temperate wet winter, dry summer climate with 253 cm of annual precipitation, with less than 10% occurring between June and Sept. Average annual snowfall is 233 cm (Franklin et al. 1972).

The Wind River site is a 450-year-old forest dominated by western hemlock (*Tsuga heterophylla* Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with the tallest trees averaging 50–55 m. Other tree species include red alder (*Alnus rubra* Bong.), western redcedar (*Thuja plicata* Donn), western white pine (*Pinus monticola* Dougl. ex D. Don), Pacific silver fir (*Abies amabilis* (Dougl.) Forbes), grand fir (*Abies grandis* (Dougl.) Lindl.), and noble fir (*Abies procera* Rehd.). Understory trees include Pacific yew (*Taxus brevifolia* Nutt.) and Pacific dogwood (*Cornus nuttallii* Aud. ex T. & G.). The Douglas-firs are believed to be 375–500 years old originating after an initial stand replacement fire, while the hemlocks are 300 years old or less. There is no evidence of subsequent fires since stand initiation (Shaw et al. 2004). Mortality is driven by wind, pests, and pathogens, creating small canopy gaps and a gradual shift in composition from Douglas-fir to western hemlock (Franklin and DeBell 1988).

Field Data Collection

An 8.4-ha (300 × 280 m) and a 12-ha (400 × 300 m) plot was established at Teakettle and Wind River (Chen et al. 2004), respectively. At both sites all trees ≥5 cm diameter at breast height (dbh) were measured and identified to species. Their cardinal stem position coordinates (x, y) and the elevation (z) were also measured using a surveyor's total station (WILD TC600 and Topcon 300).

At Wind River, soil moisture in the top 15 cm of soil was measured using time domain reflectometry (TDR) (Gray and Spies 1995). TDR measurements were made in Oct. 1998, before the onset of fall rains, every 5 m along two 400-m parallel east-west transects (Song et al. 2004). At each TDR location, canopy cover was estimated with a moosehorn—a funnel with a bubble level, a 30° angle of view off vertical, and a transparent grid with 100 intersections affixed over the top of the funnel (Garrison 1949). We used measurements of leaf area index (LAI) and diffuse light previously calculated from hemispherical photos (Van Pelt and Franklin 2000) taken along transects within the stem-mapped plot. Photosynthetically active radiation (PAR) was recorded with four sensors (Li-Cor model LI-190) at 2 m above ground level. Basal area and canopy cover were measured in 70 0.1-ha plots (7.0 ha in all) collected along a transect that bisected the crane site (Chen and Franklin 1997). Vertical foliage distribution by species was calculated at Wind River using measurements of the height to the base of the live crown, total tree height, two crown diameters, and crown shape for all trees ≥5 cm dbh in a 50 × 50-m plot (Van Pelt and North 1996). Total foliage volume and volume by 5-m height interval were calculated for all trees by species and standardized to per hectare values.

At Teakettle, soil moisture has been measured every snow-free month from 1998 to 2002 with TDR probes 0–15 cm in depth placed on a regular 25 × 25-m grid and probes 0–45 cm on a 50 × 50-m grid within the study area. We selected a set of measurements from May and Oct. 1998 that are typical of soil moisture content trends measured over the last 5 years. At each TDR probe, a hemispherical photograph of canopy cover was taken, canopy cover was visually estimated with a moosehorn, and shrub and herb cover was visually estimated in a 1/500-ha circular plot. At Teakettle, PAR was measured 2 m above ground at 18 locations within the mixed-conifer area. To facilitate site comparison, we selected four sensors at Teakettle with canopy cover similar to the mean cover level at Wind River and evaluated the data for the same cloudless day (Aug. 20, 1998) at Teakettle and Wind River. Teakettle basal area and canopy cover were measured in 150 0.05-ha plots (7.5 ha in all) systematically located on a 33.3-m grid in and around the stem map area.

To assess the effect of fire suppression on species composition and size, we aged 500 stumps from a recent thinning treatment in the 8.4-ha block and surrounding forest. We attempted to collect a representative sample by including all species and a diameter range of 5–170 cm. Ground-level stump cross sections or "cookies" were cut, sanded, and independently aged by two trained technicians with hand lens or under a dissecting microscope.

At Teakettle, vertical foliage distribution by species was calculated using allometric equations based on tree diameter. Equations to predict height to the base of the live crown and total height were calculated using 750 trees in and

Wind River Canopy Crane Facility

Teakettle Experimental Forest

Figure 1. Picture of the stand structure and location for the Wind River Canopy Crane Research Facility in southern Washington and the Teakettle Experimental Forest in the southern Sierra Nevada.

around the 8.4-ha plot from all five major species. Crown shapes for different species by size classes were calculated using direct crown diameter measurements taken every 5 m in trees accessed by climbing ropes (Tom Rambo, unpublished data). Crown radii were calculated from tree dbh using equations from Gill et al. (2000). Species- and size-specific equations were applied to all trees in the 8.4-ha plot at Teakettle. Total foliage volume and volume by 5-m height interval were calculated for all trees by species and standardized to per hectare values.

Analysis

For each site, data were standardized to per hectare values. Of the species sampled, white fir, red fir, and incense cedar were classified as shade-tolerant at Teakettle (Rundel et al. 1988), and Pacific silver fir, grand fir, Pacific dogwood, Pacific yew, western redcedar, and western hemlock (Minore 1979) were classified as shade-tolerant at Wind River.

Hemispherical photographs taken from regular gridpoint locations at each site were analyzed for LAI and indirect site factor (a measure of diffuse light in the understory) with SCANOPY software (Regents Instruments 2000). Canopy cover and soil moisture were evaluated for normality with the Lilliefors test and then compared using Pearson's correlation analysis (Sokal and Rohlf 1995). Tree stem maps of each site were generated in S-Plus (S-Plus 2000). Tests of spatial distribution were made using Spatial Point Pattern Analysis software (Haase 1995). Both univariate and bivariate Ripley's K analyses were performed. Ripley's K compares distances between all location points in the same plane (Ripley 1979, Diggle 1983) using the reduced second moment measure or K function to examine spatial associations over a greater range of scales than nearest neighbor analysis. We used a square root transformation, L(t) (Moeur 1993), and 95% confidence intervals calculated from 100 Monte Carlo simulations.

Results

Wind River had almost 37% more basal area than Teakettle and about 3% lower stem density (Table 1). The lower density was not apparent in the stem map comparison of the two sites because of the more regular stem distribution at Wind River (Figure 2). Teakettle's higher density was concentrated in tree clusters separated by gaps (Figure 2). Average dbh at Wind River was 19% higher than at Teakettle, a difference driven by the large mean diameter of Douglas-fir. The distribution of stems by 25-cm diameter class indicated Teakettle's higher stem density is mostly in the small size classes (Figure 3). Teakettle had more trees >150 cm and most of these were large sugar pine or white fir.

Differences in species composition between the two sites were compared by proportion and size distribution of shade-tolerant and -intolerant species. The high mean dbh and low standard deviation of Douglas-fir, noble fir, and white pine compared to sugar and Jeffrey pine indicated a more uniform large size for shade-intolerants at Wind River than at

Table 1. Average stem density, basal area, diameter at breast height (dbh), and standard deviation (SD) of dbh by species for the Wind River Canopy Crane Research Facility and Teakettle Experimental Forest. Values are calculated from all mapped stems ≥5 cm dbh within a 12-ha (*n* = 6,238) and 8.4-ha (*n* = 4,580) plot at Wind River and Teakettle, respectively.

Species	Density (stems/ha)	ba (m²/ha)	dbh (cm)	dbh (SD)
Wind River Canopy Crane				
Tsuga heterophylla	256.0	33.47	30.9	26.6
Taxus brevifolia	112.9	2.15	13.5	7.6
Pseudotsuga menziesii	62.7	45.65	91.7	29.3
Abies amabilis	54.8	1.69	14.0	14.1
Thuja plicata	15.7	6.97	59.5	45.9
Abies grandis	7.2	1.33	44.5	19.9
Cornus nuttallii	5.5	0.04	9.0	3.8
Pinus monticola	4.1	2.08	77.9	20.4
Abies procera	0.7	0.36	72.9	31.4
Alnus rubra	0.2	0.01	12.8	12.8
Total	519.8	93.75	33.9	33.8
Teakettle Experimental Forest				
Abies concolor	402.2	42.93	26.8	25.1
Calocedrus decurrens	95.0	13.00	30.1	28.2
Pinus lambertiana	26.6	9.93	46.7	48.9
Pinus jeffreyi	9.3	2.40	43.7	39.3
Quercus kelliggii	2.2	0.05	17.4	12.9
Quercus chrysolepis	0.7	0.01	8.7	3.4
Abies magnifica	0.6	3.13	53.0	9.8
Total	536.6	68.45	28.4	27.9

Teakettle (Table 1). At Wind River, 13% of the stems and 51% of the basal area were from shade-intolerant species. At Teakettle, 7% of the stems and 18% of the basal area were from shade-intolerants. In our age analysis at Teakettle, pre- and postsuppression composition (18.0% and 7.1% shade-intolerant, respectively) and size (64.5 cm [SD = 38.8]; 36.0 cm [SD = 16.7], respectively) were significantly different (Student's *t*-test, *P* < 0.05). Fire suppression has increased Teakettle's stem density, shifting the species composition toward shade-tolerants, particularly white fir, and reduced mean diameter. Even with an increased density of white fir from fire suppression, Teakettle had a much higher percentage of shade-intolerant species in the 0–25 cm diameter range (Figure 3). However, for trees between 25 and 175 cm, the relationship changed with Wind River having a higher percentage of shade-intolerants in larger diameter size classes.

Foliage volume and distribution was significantly different between the two sites. Wind River had almost five times as much crown foliage volume as Teakettle (Figure 4). Shade-intolerant Douglas-fir foliage dominated the canopy above 35 m; however, the majority of the stand's canopy was shade-tolerant western hemlock foliage in the 10- to 35-m strata. Stratification by shade tolerance was less pronounced at Teakettle. Sugar pine dominated the canopy above 40 m. Much of its foliage volume, however, as well as the other shade-intolerant species, Jeffrey pine, was present in all canopy strata.
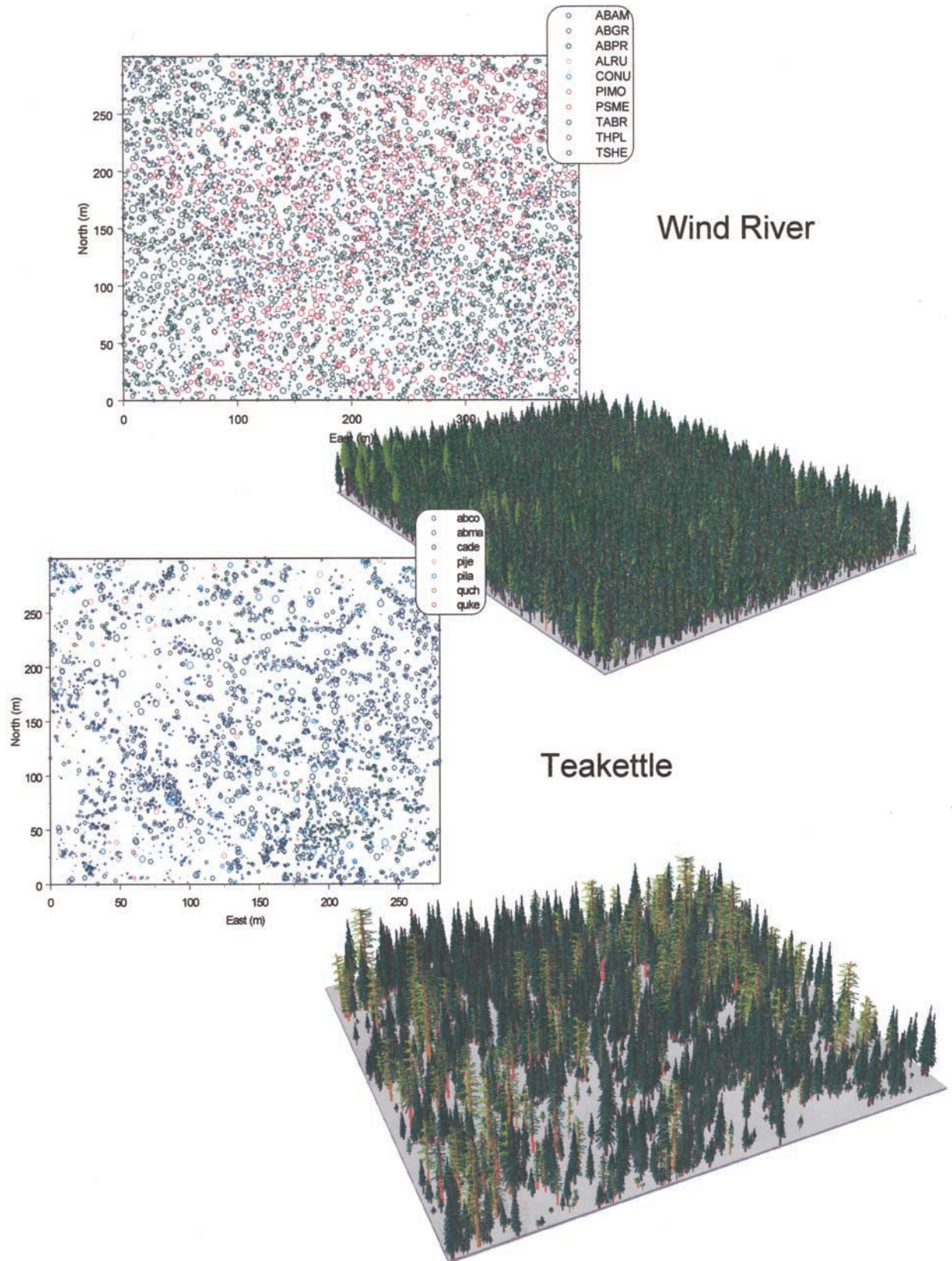
Figure 2. Map and stand visualization simulations (SVS) of all live stems ≥5 cm dbh at Wind River and Teakettle. Circles are proportional to diameter and color coded by species. To facilitate comparison, plots and diameter circle sizes have been scaled to the same dimension. Species codes at Wind River are *Abies amabilis* (ABAM), *A. grandis* (ABGR), *A. procera* (ABPR), *Alnus rubra* (ALRU), *Cornus nuttallii* (CONU), *Pinus monticola* (PIMO), PSME (*Pseudotsuga menziesii*), *Taxus brevifolia* (TABR), *Thuja plicata* (THPL), and *Tsuga heterophylla* (TSHE). Species codes at Teakettle are *Abies concolor* (ABCO), *A. magnifica* (ABMA), *Calocedrus decurrens* (CADE), *Pinus lambertiana* (PILA), *P. jeffreyi* (PIJE), *Quercus chryso-lepis* (QUCH), and *Q. kelloggii* (QUKE). Crowns representations of each tree by species were developed from shapes in SVS and drawn over the location of each stem.
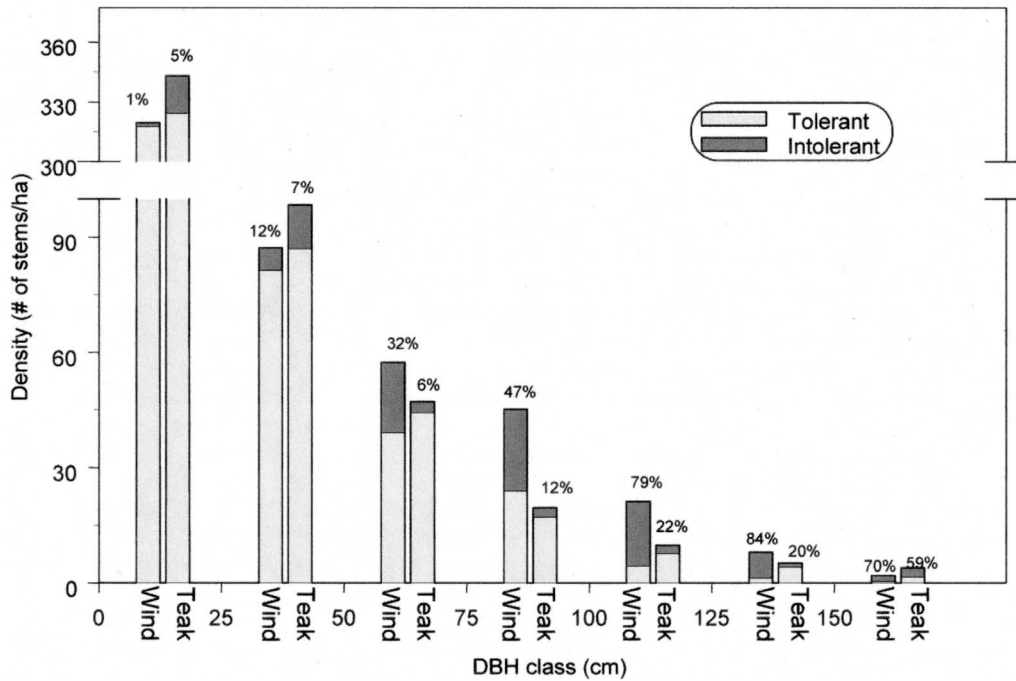
Figure 3. Distribution of shade-tolerant and -intolerant stems by 25-cm diameter class at the Wind River Canopy Crane Facility and the Teakettle Experimental Forest. Values at the top of each bar are the percentage of total stems for that size class that are shade-intolerant species.
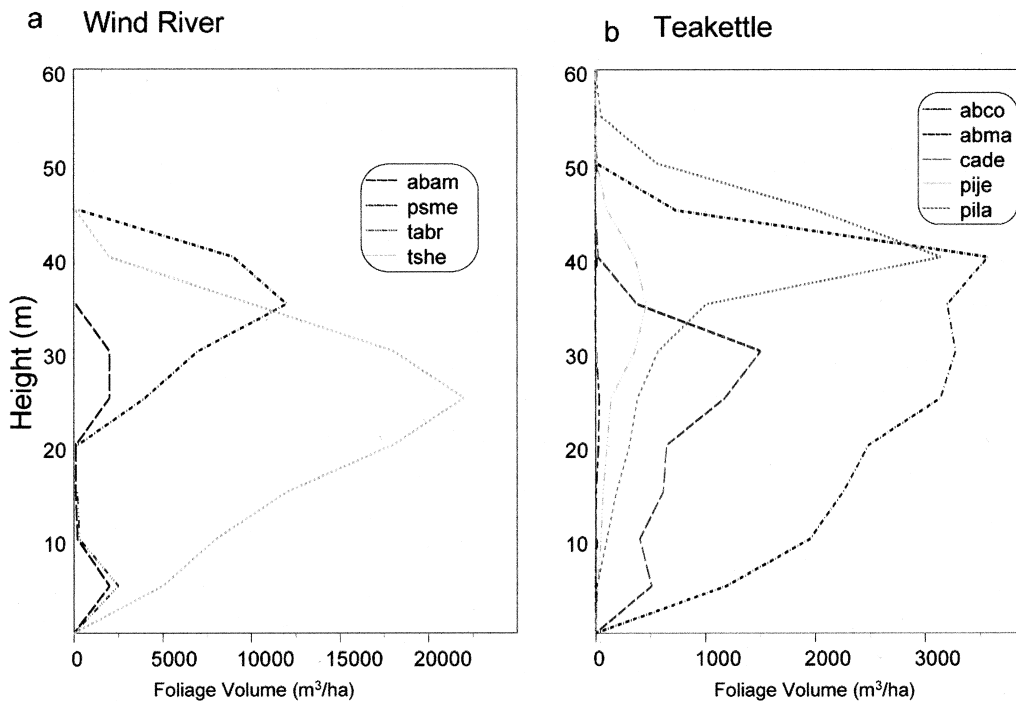

Figure 4. Profiles of total crown volume (m³/ha) by species for Wind River (a) and Teakettle (b). The Wind River profile is from Van Pelt and North (1996) and the Teakettle profile is from a model of each crown for all trees in the 8.4-ha plot using measurements and allometric equations from a subsample of trees. Note the scale difference in foliage volume along the x axis between the two sites.

Canopy cover and PAR showed a significant difference in the distribution and intensity of light resources between Wind River and Teakettle. The forest was much more open at Teakettle with a lower mean LAI and much larger average gap size (Table 2). At both Wind River and Teakettle

there was a clustering of plots with ≥70% canopy cover and ≥65 m²/ha basal area, but Teakettle also had a second grouping of plots around 25% canopy cover and 20 m²/ha basal area (Figure 5). At Teakettle, few plots had values between these two extremes. Plots were either in open-gap

Table 2. Mean (and SD) of LAI, diffuse light, soil moisture (Oct. 1998), litter depth, and understory cover at the Wind River Canopy Crane Research Facility and Teakettle Experimental Forest. LAI and diffuse light (indirect site factor) are calculated from hemispherical photographs. Soil moisture was measured with TDR for the top 15 cm of soil.

	Wind River	Teakettle
LAI (modified Li-Cor) (m^2/m^2)	11.6*	2.7
Diffuse light levels (ISF) (fraction)	0.127 (0.07)*	0.296 (0.17)
Soil moisture in Oct. (%)	22.8 (7.2)	7.8 (1.2)
Litter depth (cm)	6.1 (2.1)	4.4 (4.5)
Total shrub and herb (% cover)	25.4 (26.3)*	17.7 (34.6)
Correlation of canopy cover and soil moisture	0.28†	−0.46†

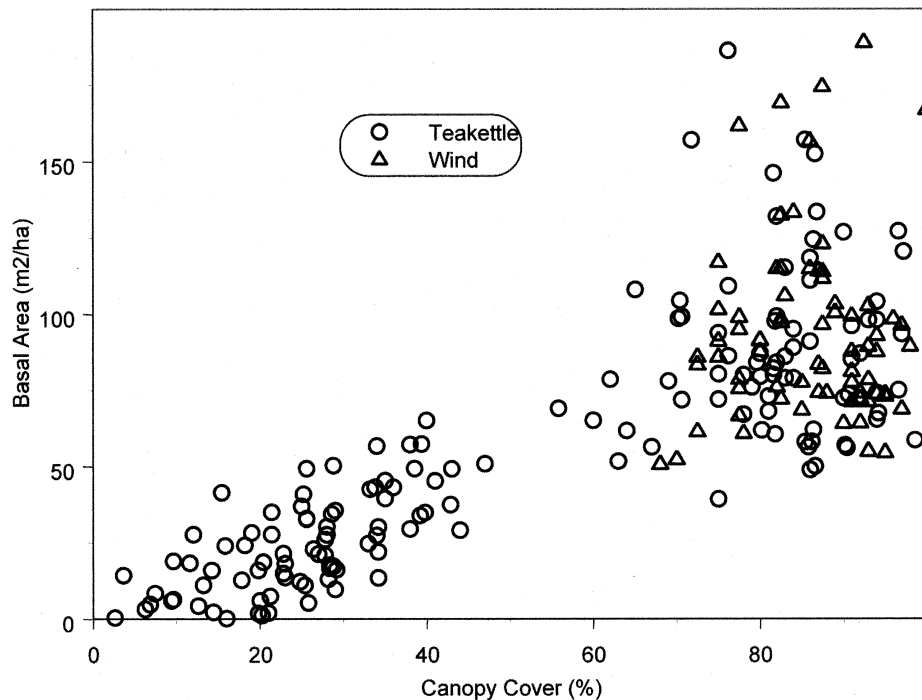* From Van Pelt and Franklin (2000) Table 4.
† $P < 0.05$.

Figure 5. A graph of 70 Wind River and 150 Teakettle plots by canopy cover (%) and basal area (m^2/ha). Wind River plots were 0.1 ha and Teakettle plots were 0.05 ha in size.

or closed-canopy conditions, suggesting a binary distribution pattern rather than a gradient of stand conditions. Wind River had a much higher LAI and consequently diffuse light in the understory was much lower than at Teakettle. Daily mean PAR was 14.5 $\mu mol/m^2/s$ at Wind River compared with 222.2 $\mu mol/m^2/s$ at Teakettle (Figure 6). The peak in PAR value at Teakettle was four times the peak at Wind River, and the duration of high PAR levels was much longer.

Soil moisture was a much more limited resource at Teakettle than Wind River. In Oct., soil moisture in the top 15 cm was three times greater at Wind River (before fall rains) than at Teakettle (Table 2). Teakettle's Oct. soil moisture at greater depth (0–45 cm) averaged 10.3% (SD = 4.7%). In May, immediately after snowmelt, soil moisture at Teakettle averaged only 16.5% (SD = 5.3%) for 0–15 cm and 24.7% (SD = 9.3%) for 0–45 cm. The correlation between canopy cover and soil moisture was weakly posi-

tive at Wind River but was significantly negative at Teakettle.

The spatial distribution of trees stems was markedly different between the two sites. At Wind River, trees were clustered at all distances (Figure 7a), while at Teakettle trees were clustered between 0 and 20 m, random from 30 to 50 m, and again clustered at distances greater than 70 m (Figure 7b). Large trees (≥76 cm dbh) were regularly spaced from 0 to 15 m at Wind River and then clustered at distances >20 m (Figure 7c). At Teakettle, large trees were randomly distributed between 0 and 80 m and clustered at distances >90 m (Figure 7d). At Wind River, the bivariate analysis indicated shade-tolerant and -intolerant trees were "repulsed" from each other between 20 and 110 m (Figure 7e). The same analysis at Teakettle indicated shade-tolerant and -intolerant trees were "attracted" at scales greater than 20 m (Figure 7f).
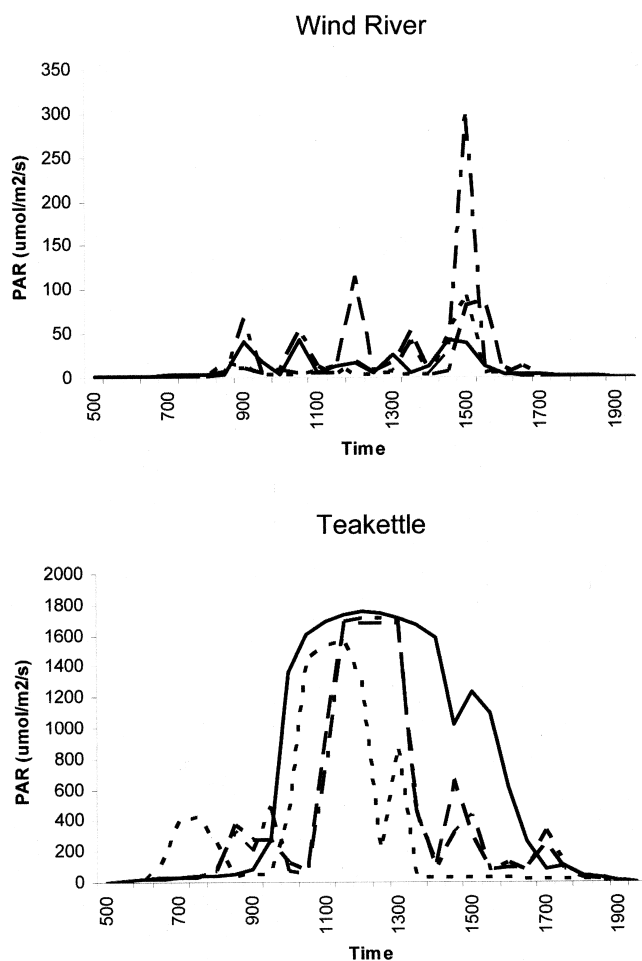
Figure 6. Photosynthetically active radiation (PAR) measured at Wind River and Teakettle on the same cloudless day (Aug. 20, 1998). Each line is the reading from one of four sensors under similar (75–82%) canopy cover. Plotted values are 30-min averages calculated from readings taken every 10 s between 5:00 am and 7:00 pm Pacific Standard Time. Note different scale of the y axes.

Discussion

In the absence of fire, Teakettle's composition and structure has not shifted toward the pattern found at Wind River. Gaps are a pronounced feature of Teakettle's mixed conifer forest even after 135 years of fire suppression. Following disturbance, canopy gaps on productive sites are usually ephemeral as adjacent crowns expand and understory trees are released (Runkle 1985, Lertzmann et al. 1996; Van Pelt and Nadkarni 2004). Tree crown competition for light is a principal driver in many models of gap dynamics, and species are considered shade-tolerant or -intolerant based on their ability to tolerate low light conditions typical of closed-canopy forests. In forests that do not have a closed canopy, biomass and basal area are often low, and either frequent disturbance or below-ground competition for moisture and nutrients are believed to structure tree spacing and species composition (West 1984, Payandeh 1974, Skarpe 1991). Teakettle's forest, however, is relatively productive with a basal area in tree groups comparable to Wind River. Many of the aged stumps, using tree measurements collected before cutting, indicate postsuppression trees often reach 80 cm dbh and 50 m in height within 100 years.

Our ability to infer influences on current forest composition and pattern is limited given the long time frame of stand development and the short duration of our environmental measurements. Over the 400-year period of both stand's oldest trees, disturbance history and changes in disturbance regimes have been significant influences on tree spatial patterns even though both stands have been fire-free for over 135 years. While fire may not have burned within the Wind River site for several centuries, wind disturbance, insect damage, and pathogens are all affecting gap pattern, stem distribution, and species composition (Shaw et al. 2004). Disturbance, both frequent fires and fire exclusion, has had a significant effect on Teakettle's stand structure. With 84% of aged trees becoming established and growing since fire exclusion, much of the current forest's pattern and composition has developed in a fire-free interval.

The stem distribution is much more continuous at Wind River, providing a consistent, high level of canopy cover with few, small gaps. Previous studies of foliage distribution at Wind River (Van Pelt and North 1996 and 1999, Van Pelt and Franklin 2000) have described a stand where the canopy is vertically stratified with shade-intolerant Douglas-fir dominating the upper layer (35–50 m), although most of the foliage volume is concentrated at lower (20–35 height) levels dominated by shade-tolerant western hemlock (Figure 4). Parker (Parker 1997, Parker et al. 2002) found that light levels followed this pattern in canopy layering with high PAR levels above 40 m, a transition zone between 20 and 40 m, and a low light level in the understory. Our measures of PAR show consistently low levels of understory light where peak values are small and short in duration.

At Wind River, shade tolerance and crown competition for light also appear to create horizontal segregation in the stem pattern. Large Douglas-fir stems are regularly spaced or repelled for distances up to 15 m, and there is significant separation between shade-tolerant and intolerant stems. Shade-intolerant saplings (>5 cm dbh) are largely absent. Unless a gap is large, Wind River's tall, layered canopy and low sun angle significantly reduce direct understory light in most or all of a gap's ground projected area (Van Pelt and Franklin 2000).

Teakettle does not have the direct canopy access afforded by the crane at Wind River; however, the foliage profiles developed from crown models imply a much different canopy structure. In the strata with the highest total volume, 35–40 m, foliage occupies only 12% of available space, compared to Wind River's foliage filling 70% of the 25- to 30-m strata. Most of Teakettle's foliage of shade-intolerant sugar and Jeffrey pine is distributed throughout the same strata as shade-tolerant white fir's foliage. Teakettle has a mean canopy cover of 60% and 68 m²/ha basal area, but the distribution is bimodal with most values grouped around either 80% cover and 85 m²/ha basal area, or 25% cover and 20 m²/ha basal area. This is indicative of the strong clustering of stem locations where tree groups are
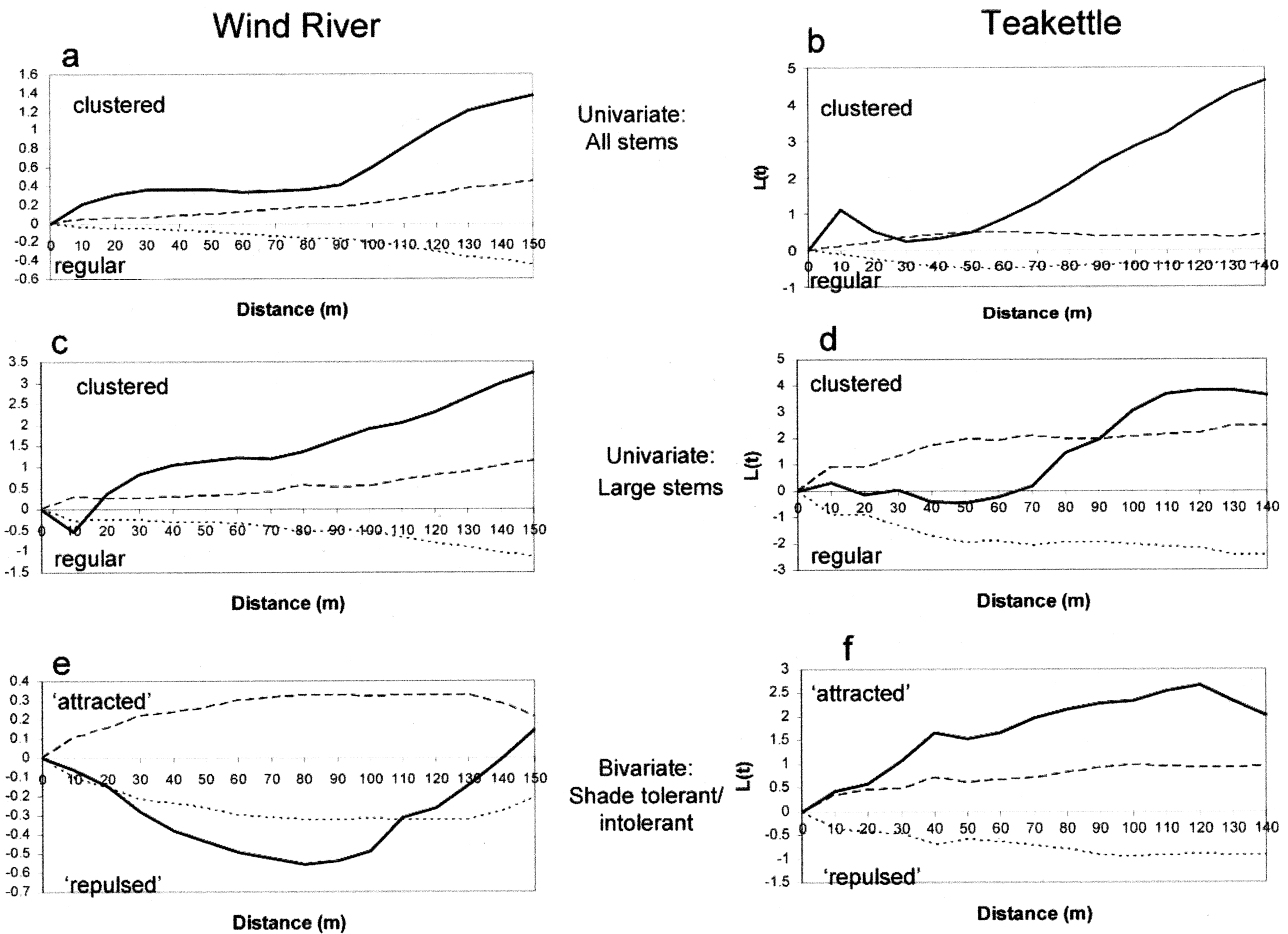
Wind River

Teakettle

Univariate: All stems

Univariate: Large stems

Bivariate: Shade tolerant/ intolerant

Figure 7. Ripley's K analysis of stem patterns. Figures (a) and (b) are univariate analyses of all stems ≥5 cm dbh at Wind River and Teakettle, respectively. Figures (c) and (d) are univariate analyses of large trees (dbh ≥ 76 cm). Figures (e) and (f) are bivariate analyses of shade-tolerant and -intolerant stems. Solid lines, L(t), are the stem distribution, and dashed lines are 95% confidence intervals (CI) calculated from 100 Monte Carlo simulations. For the univariate figures, portions of the stem distribution line above CI are significantly clustered and below CI are significantly repelled or regular for those distances along the x axis. For the bivariate figures, portions of the stem distribution line above the CI are significantly "attracted" and below CI are significantly "repulsed" for those distances along the x axis.

all sizes of both shade-tolerant and -intolerant species. Within these groups, canopy cover and basal area is comparable to Wind River. Between the tree groups, which average 30 m in diameter, are large gaps (10–30 m) evident in Teakettle's stem map (Figure 2) and in the Ripley's K analysis indicating a random distribution of all stems between 30 and 55 m. The pattern of tree groups and gaps is strong enough that large tree distribution is never regular and only clustered at distances greater than 90 m. Shade-tolerant and -intolerant species are not "repelled," rather all trees are grouped. At Teakettle, gaps have little or no litter layer, which can reduce germination (Gray and Spies 1997), yet they have very little shade-tolerant or -intolerant regeneration (Gray, unpublished data). Unlike Wind River, understory light in gaps can be intense because of gap size, low canopy foliage in adjacent tree groups, and Teakettle's lower latitude.

At Wind River, a high LAI, small average gap size, and low PAR values indicate how much light diminution results from the tall, complex canopy. Soil moisture is fairly high even in Oct. and positively but weakly correlated with canopy cover, suggesting gaps may be slightly drier due to

evaporation (Gray et al. 2002). At Teakettle, the open canopy produces long duration, high PAR levels. Soil surface temperatures in gaps have been found to exceed 50° C for several hours while temperature remained at 28° C in an adjacent tree group (Siyan Ma, University of Toledo, July 26, 2003). Even though the gaps have intense surface heat, there is a negative correlation between canopy cover and soil moisture both in May and Oct. measurements. Over the winter, gaps develop deeper snow packs providing more water in May. In Oct., soil water in tree groups is still more depleted than in gaps, possibly due to water competition by the densely spaced trees.

Teakettle's lack of regeneration in gaps may be due to heat and higher transpiration demands. In spring of 2000 and again in late fall, 180 3-year-old shade-tolerant white fir and shade-intolerant sugar pine "plugs" were planted in gaps or under greenleaf manzanita (*Arcostaphylus patula* E. Greene) or whitethorn ceanothus (*Ceanothus cordulatus* Kellogg). Despite frequent watering, after each planting more than 96% of the seedlings died. The few survivors were located under heavy shrub cover or in shade cast by

temperature sensor housings (Ruth Kern, unpublished data). Another Teakettle study of transpiration rates in 2-year-old planted white fir and sugar pine seedlings in gaps and closed-canopy found minimal transpiration in gap seedlings. After sustained watering, however, gap seedling transpiration rates exceeded forest seedling rates (Agneta Plamboeck, unpublished data).

At Wind River, light competition is a significant influence on growth, mortality, and canopy stratification. Diameter growth and tree survival are strongly correlated with a tree's height and relative canopy position (Rudnicki and Chen 2000; Ishi et al. 2000). A 36-year mortality study found little change in stem density or diameter distribution by size class, but a significant slow shift in composition from Douglas-fir to western hemlock. The major cause of mortality over the 36-year period was wind for overstory trees and suppression for understory stems. Unless disturbance produces large gaps, Franklin and DeBell (1988) predicted Douglas-fir would become locally extinct in 755 years.

Teakettle lacks a long-term demography study; however, mortality patterns suggest water limitation may be an important factor after more than a century of fire suppression. In an investigation of snags by size, location, and pest or pathogen evidence, dead trees were concentrated in patches that included both shade-tolerant and -intolerant species (D. Rizzo and T. Smith, unpublished data). The most prevalent cause of mortality was bark beetles. Using a series of aerial photographs take over the last 50 years, many dead tree patches appeared during or shortly after the last prolonged drought in the Sierra Nevada (1987–1993). High stem densities resulting from fire suppression can concentrate bark beetle mortality in moisture-stressed tree patches during droughts (Ferrell et al. 1994, Ferrell 1996). Our shallow TDR measurements may not be a good indication of water availability for larger trees. Studies suggest established trees in the southern Sierra use water deep in the soil or from fissures in the underlying bedrock (Arkley et al. 1981, Hubbert et al. 2001). Patches of dead trees and gaps at Teakettle might represent areas with less deep water due to shallow soils or limited bedrock fractures. Under this theory, increases in stem density from fire suppression might increase stand-level water stress, leaving trees clustered in areas with deep water and producing gaps where bedrock is closer to the soil surface.

Tree distribution and abiotic conditions suggest some fundamental differences in stand dynamics between Pacific Northwest and Sierra Nevada forests. At Wind River, closed canopy forests influence vertical stratification and horizontal separation of species by shade tolerance. Canopy cover is an important influence on succession and stand composition as gap size influences shade-intolerant establishment or release of suppressed shade-tolerant species. At Teakettle, after 135 years without a fire, large gaps remain a distinct feature of stand structure. In mixed-conifer forests of the southern Sierra Nevada, light may constrain seral development. Gaps inhibit tree regeneration and there is no horizontal and little vertical segregation by shade tolerance.

Increases in light do not favor shade-intolerant species, and there are few areas with trees in mixed conifer where canopy cover drops below 50%. Trees are concentrated in groups that have less surface moisture than adjacent gaps and yet the basal area, number and size of large trees in the groups is similar to productive Pacific Northwest old-growth. The clustering of shade-tolerant and -intolerant species, the distinct patchy stem distribution, and the lack of regeneration in gaps suggest tree establishment could have a canopy cover threshold. Below the threshold, temperature and transpiration rates may be high, limiting tree establishment in open gaps.

Teakettle's tree pattern has at least two implications for forest management based on traditional stand dynamics. In southern Sierra Nevada mixed-conifer forests, mechanical thinning may not release shade-intolerant species if canopy cover is significantly reduced. High regeneration failure rates in the Sierra (Laacke and Tomascheski 1986, Tappeiner and McDonald 1996) suggest stand dynamics are complex and that understory trees and planted seedlings may not always benefit from canopy reduction. Careful site-specific experimentation is needed to see if there is a canopy cover threshold that significantly affects tree regeneration. Another problem with mixed-conifer distribution is defining an appropriate management scale. The pattern and structure of Teakettle's mixed-conifer forest does not fit a traditional definition of a stand as "a spatially continuous group of trees and associated vegetation having similar structures" (Oliver and Larson 1996, p. 1). The forest is a combination of gaps and heterogeneous tree groups, and gaps as well as tree groups will need to be managed for silviculture to influence stand dynamics.

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