Canopy openness and leaf area in chronosequences of coastal temperate rainforests

Gordon W. Frazer, J.A. Trofymow, and Kenneth P. Lertzman

Abstract: We examined spatial and temporal differences in canopy openness and effective leaf area (L_e) in a series of eight forest chronosequences located on southern Vancouver Island, British Columbia. Structural attributes were measured on the west and east side of the island in immature, mature, and old-growth stands using hemispherical photography and the LAI-2000 plant canopy analyzer (PCA). Old-growth forest canopies were distinct from those of younger stands: they were more open, more heterogeneous in their openness, and maintained a lower stand L_e. Although the overall developmental trajectories of forests were similar across the study sites, site-to-site differences in the rate and magnitude of these temporal changes indicated that site-specific factors also play a significant role in determining the character of forest canopies and their development. The most significant changes in canopy structure did not emerge until the later stages of stand development (150–200 years). Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) dominated east-side forests were, on average, more open, more heterogeneous, and had a lower stand L_e than the stands dominated by western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) and western redcedar (*Thuja plicata* Donn.) forming the west-side chronosequences. Shoot clumping, along with other evidence, suggested that species-related differences in leaf display and the geometry of branching structure might have contributed significantly to these regional patterns.

Résumé : Les auteurs ont examiné les différences spatiales et temporelles dans l'ouverture de la canopée, ainsi que la surface foliaire effective (L_e) dans une série de huit chronoséquences forestières situées dans le sud de l'île de Vancouver, en Colombie-Britannique. Les attributs structuraux ont été mesurés sur les côtés ouest et est de l'île dans des peuplements immatures, matures et vieux, en utilisant la photographie hémisphérique et le LAI-2000 PCA (plant canopy analyzer). Les canopées des vieilles forêts sont différentes de celles des jeunes peuplements. Elles sont plus ouvertes, plus hétérogènes quant à leur ouverture et ont conservé une valeur de L_e plus faible. Bien que le sens général du développement des forêts soit similaire à travers les sites étudiés, les différences entre les sites situés côte-à-côte, dans le taux et l'amplitude de ces changements temporels, indiquent que des facteurs spécifiques au site jouent également un rôle important dans la détermination du caractère des canopées forestières et de leur développement. Les changements les plus importants dans la structure de la canopée ne sont pas apparus avant les derniers stades de développement du peuplement (150–200 ans). Les forêts dominées par le Douglas vert (*Pseudotsuga menziesii* (Mirb.) Franco) sur la côte est de l'île sont, en moyenne, plus ouvertes, plus hétérogènes et ont un L_e du peuplement plus faible que les peuplements dominés par la pruche de l'Ouest (*Tsuga heterophylla* (Raf.) Sarg.) et le thuya géant (*Thuja plicata* Donn.) qui forment les chronoséquences sur la côte ouest de l'île. Les bouquets de rejets, ensemble avec d'autres indices, suggèrent que les différences liées aux espèces dans la disposition des feuilles et la géométrie de la structure de la ramification contribuent, de façon importante, à la formation de ces patrons régionaux.

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Introduction

Population, community, and ecosystem characteristics all undergo a sequence of characteristic kinds of change as a forest establishes and develops after a disturbance (e.g., Oliver 1981; West et al. 1981; Huff 1995). Collectively, these features are reflected in the structural attributes of a forest stand. Structural attributes, such as the amount and distribution of coarse woody debris; leaf area; or the density, mass, and size distribution of live trees, tend to follow patterns through stand development that are general among forest types and culminate in the stage known as "old growth" (Franklin and Spies 1991*a*; Tyrrell and Crow 1994; Wells 1996; Wells et al. 1998). These patterns, however, are best documented for young to mature stands, and variability in structural attributes tends to increase with forest age (Arsenault and Bradfield 1995). Furthermore, comprehensive data sets exist for only a few forest types. In the forests of northwestern North America, forest structure has become a key focus for research because of its significance for biodiversity and ecosystem function (e.g., Harmon et al. 1986; Franklin 1988; Hansen et al. 1991; Franklin and Spies 1991*a*). Forest structure can be more directly addressed by silvicultural prescriptions and regulatory policies than other aspects of stand ecology, and thus has become a management focus as well (e.g., Forest Ecosystem Management Assessment Team 1993; McComb et al. 1993; B.C. Ministry of

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Forests 1995; Scientific Panel for Sustainable Forest Practices in Clayoquot Sound 1995; Franklin et al. 1997).

The temporal dynamics of forest canopies are one of the least understood components of forest ecosystems. The structure and function of forest canopies is relatively well known in younger managed stands (e.g., Waring and Running 1998), but the ecologically diverse and spatially heterogeneous canopies of older forests remain mostly unstudied (Schowalter et al. 1981; Brown and Parker 1994; Lowman and Nadkarni 1995). The developmental trajectories through which young forest canopies become old forest canopies are even less well known. We expect, however, that the processes implicit in models of stand development based on other attributes of forest structure will apply to forest canopies as well. The key process distinguishing old growth from earlier stages of stand development is the mortality of canopy dominants. The structural consequences of this mortality are the characteristics used to define, classify, and identify old-growth stands (Franklin and Spies 1991a, 1991b; Hansen et al. 1991; Wells et al. 1998). We thus expect that the spatial heterogeneity associated with developmental canopy gaps (Lertzman et al. 1996) will be one of the key features distinguishing old-growth canopies from younger canopies.

Heterogeneity of forest canopies is a major source of variation in the character of understory light environments. Heterogeneity thus plays a critical role in determining the patterns of tree regeneration and the composition and productivity of understory plant communities (Canham et al. 1990, 1994). Interest in documenting relationships between forest structure and the understory light regime has converged on a few methodological approaches from two distinct lines of research. On the one hand, community and population ecologists studying successional processes associated with canopy gaps formed by patchy tree mortality needed to quantify the environmental conditions associated with those gaps (Rich et al. 1993; Canham et al. 1994; Easter and Spies 1994). On the other, microclimatologists and production ecologists required easily replicated and nondestructive methods for quantifying the leaf area borne by forest stands (Runyon et al. 1994; Mencuccini and Grace 1996; Chen et al. 1997; Fassnacht and Gower 1997). In both cases, the challenges and constraints of direct measurement of the variables of interest (for instance, multiple light sensors running over several seasons or direct destructive sampling of tree crowns) led to the development of faster, less direct methods that lend themselves more easily to spatial and temporal replication (Norman and Campbell 1989; Welles and Cohen 1996).

In 1991, a large, integrative project established a series of 10 forest chronosequences on southern Vancouver Island, British Columbia, Canada (Trofymow et al. 1997). A forest chronosequence is a series of stands increasing in age but with similar histories and growing conditions (Oliver 1981). These chronosequences provided us with the opportunity to study structural differences in early- to late-successional coastal western hemlock (*Tsuga heterophylla* ((Raf.) Sarg.) and Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests. We utilized two different optical methods, hemispherical photography and the LAI-2000 plant canopy analyzer (PCA), to estimate canopy openness and leaf area within 8

of the 10 individual chronosequences each representing immature, mature, and old-growth stands. In this paper we will (*i*) present canopy openness and leaf area for the 24 individual stands, (*ii*) examine trends in these attributes across seral stages and regionally, and (*iii*) compare the results obtained from each of the two optical methods.

We expect that the spatial heterogeneity associated with developmental canopy gaps (Lertzman et al. 1996; Nicotra et al. 1999) will be one of the key features distinguishing old-growth canopies from younger canopies. This suggests both greater mean openness, or lower leaf area, and greater variability in openness. We also expected, a priori, much less change in the magnitude and variance of canopy openness before stands reached maturity than after, because gap-forming mortality becomes increasingly important during the transition from maturity to old growth. Finally, we anticipate that each optical method will produce somewhat different quantitative measures of openness and leaf area because of the distinct way in which they estimate gap fractions. We do, however, expect qualitative agreement between the techniques in their assessment of changes in canopy structure over time and space.

Materials and methods

Study area description

All study sites lie between 48°33′N and 49°03′N and from 123°38′W to 124°50′W within the Coastal Western Hemlock (CWH) biogeoclimatic zone of southern Vancouver Island, British Columbia, Canada. The CWH biogeoclimatic zone is characterized by relatively cool summers and mild winters (mean annual temperature is 8.8°C), and experiences the greatest amount of rainfall of all biogeoclimatic zones in British Columbia (mean annual precipitation is 2228 mm; Pojar et al. 1991, Green and Klinka 1994). Four of the eight individual chronosequences (Fig. 1; Renfrew (REN), Red/Granite Creek (RGC), Nitinat (NIT), and Klanawa (KLA)) are situated on the cooler and wetter west side of southern Vancouver Island within the Very Wet Maritime (CWHvm) subzone, while the remaining sites (Victoria Watershed South (VWS), Victoria Watershed North (VWN), Koksilah (KOK), and Nanaimo River (NAN)) are found on the opposing east side of the island in the Very Dry Maritime (CWHxm) subzone.

Potential chronosequence sites were located through interviews with area foresters, computer searches of digital forest cover information, and visual inspection of 1 : 20 000 forest cover maps. Final site selection came after field inspection of 31 possible sites (Trofymow et al. 1997). Each chronosequence was contained within a 5 km × 5 km or smaller area and composed of stands representing three distinct seral stages: immature (32–43 years), mature (66–92 years), and old growth (176–435 years). One permanently marked plot measuring 80 m in diameter was established in each of the different-aged stands. The plot centres were located at least 100 m (in most cases 200 m) from the stand edge. All plots were uniformly distributed with respect to aspect, and their slopes and elevations averaged 15.8 ± 8.7° and 305 ± 178 m asl, respectively (Table 1). The majority of immature and mature stands originated after harvesting followed by burning. Two mature stands (i.e., KOK, KLA) were in areas that established after wildfire. In both cases, to be comparable to the other sites, plots were sited in stands devoid of veterans (canopy trees surviving the fire). Stand ages were determined using increment cores from five or six dominant trees or ring counts on stumps in adjacent clearcuts (Trofymow et al. 1997).

Fig. 1. Location of the 10 coastal forest chronosequences on southern Vancouver Island, British Columbia (from Trofymow et al. 1997).
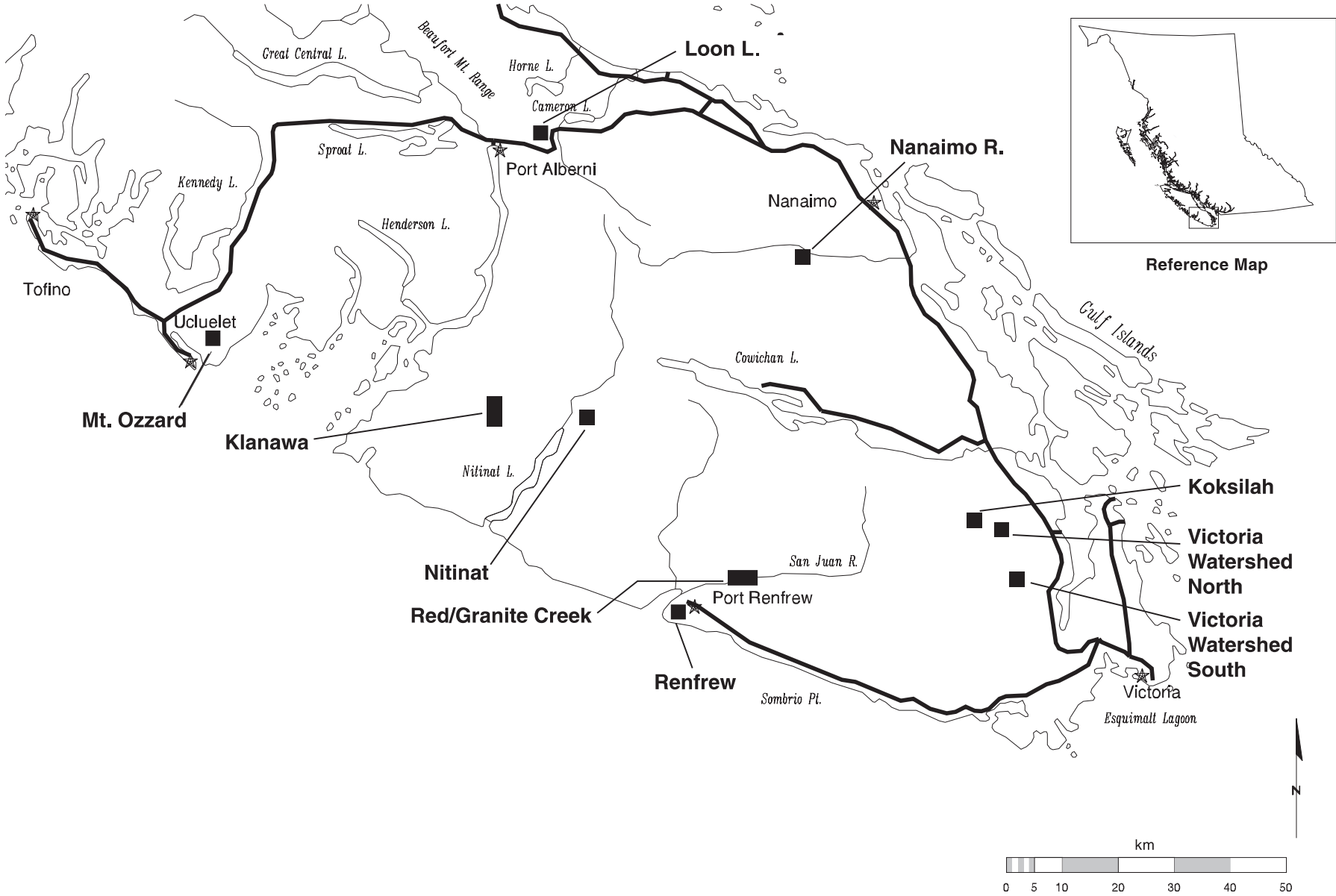
Table 1. Chronosequence locations, ages, and topographical characteristics.

Biogeoclimatic subzone	Chronosequence site	Plot No.	Latitude (N)	Longitude (W)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Seral class[a]	Age (years)
CWHxm	Victoria Watershed South (VWS)	2	48°33′51″	123°38′55″	305	22	20	I	32
		5	48°33′47″	123°39′45″	240	6	315	M	99
		6	48°33′44″	123°38′53″	390	22	30	O	245
	Victoria Watershed North (VWN)	12	48°38′08″	123°42′40″	355	3	360	I	42
		13	48°38′19″	123°44′09″	260	9	55	M	99
		15	48°36′59″	123°43′17″	465	22	250	O	316
	Koksilah (KOK)	22	48°39′30″	123°46′10″	710	9	170	I	43
		23	48°39′20″	123°44′50″	590	19	210	M	77
		24	48°39′30″	123°45′50″	630	9	180	O	288
	Nanaimo River (NAN)	33	49°03′10″	124°09′45″	430	11	180	M	66
		34	49°02′50″	124°10′40″	430	14	220	O	330
		35	49°02′55″	124°10′20″	440	11	138	I	39
CWHvm	Renfrew (REN)	52	48°33′28″	124°22′22″	135	24	350	I	42
		53	48°33′21″	124°23′26″	130	14	340	M	66
		54	48°32′50″	124°23′21″	320	19	270	O	255
	Red/Granite Creek (RGC)	62	48°34′14″	124°17′43″	130	19	360	I	43
		63	48°36′75″	124°17′20″	80	6	85	M	76
		64	48°34′35″	124°13′07″	180	45	360	O	176
	Nitinat (NIT)	72	48°50′42″	124°38′10″	185	24	225	I	39
		73	48°50′16″	124°38′39″	85	17	280	M	75
		74	48°50′03″	124°38′22″	325	12	245	O	270
	Klanawa (KLA)	82	48°51′45″	124°50′09″	230	19	135	I	32
		83	48°49′22″	124°50′27″	120	9	330	M	69
		84	48°49′22″	124°50′27″	150	15	340	O	435

The west-side chronosequences (CWHvm) are dominated by western hemlock with secondary components of *Abies amabilis* ((Dougl.) Forbes (amabilis fir), *Thuja plicata* Donn. (western redcedar), and Douglas-fir (Trofymow et al. 1997). In contrast, Douglas-fir is the dominant canopy species at the east-side sites (CWHxm) with a smaller component of western hemlock and western redcedar. *Alnus rubra* Bong. (red alder) and *Acer macrophyllum* Pursh (bigleaf maple) are of minor importance in the immature and mature stands of both west- and east-side sites. Patterns of species dominance in the forest canopy, however, varies markedly with stand age and location. Overall, mean stem densities decline significantly from a maximum of 2111 stems/ha in the immature stands to 603 stems/ha in old-growth plots. Immature and mature east-side sites maintain higher mean stand densities (2323 stems/ha) than west-side forests of similar age (1294 stems/ha). The decrease in stem densities between the mature and old-growth stages is significantly more abrupt within east-side chronosequences. East- and west-side, old-growth plots have equivalent stem densities (603 stems/ha).

Sampling design

We sampled a total of 24 permanent plots (i.e., one in each of three seral stages in eight chronosequences) between August 8 and September 12, 1995, for canopy openness and leaf area using hemispherical photography and the LAI-2000 PCA. Both optical techniques were used concurrently to sample each plot, so that understory light and sky conditions would be the same for each method at the time of sampling. In each plot, we placed seven subplot markers: one was located at the plot centre, while the others were positioned 30 m away and separated by 60° of arc (Fig. 2). A sampling grid composed of five additional stations was located within each subplot (each station was separated by 7.5 m and the long axis of the grid was aligned east–west). We took hemispherical photographs and LAI-2000 PCA measurements at each of the subplot markers. An additional five LAI-2000 PCA readings, however, were made at each of the temporary stations within a subplot to help compensate for the instrument's limited field of view. We thus used seven hemispherical photographs and 42 LAI-2000 PCA measurements to characterize each plot. In total, we collected 167 photographs and 1002 light readings from the eight chronosequences.

Optical techniques

Hemispherical photography

Hemispherical (fisheye) photographic lenses, which have a 180° field of view, are commonly used to capture and record the structure of forest canopies (Rich 1990). Photographs are taken skyward from the forest floor, digitized, and then processed using specialized imaging software (e.g., Canham 1995; ter Steege 1996; Frazer et al. 1999). To obtain hemispherical photographs for analysis, we used a Nikon F 35-mm camera and Nikkor 8-mm f/2.8 180° fisheye (equiangular) lens shooting black and white Kodak Tri-X Pan 400-ASA film. The camera was mounted on a tripod with the film plane leveled normal to the local zenith. The tripod was positioned over the centre point of each subplot marker unless there was undue interference from the boles of large trees (>30 cm DBH). In such cases, we offset the tripod from the subplot marker by no more than 3 m. The camera height was set to 1.3 m above the ground, and any understory vegetation that might have obscured the lens was pushed aside before exposure. Four or five replicate photos were obtained at each subplot using a fixed aperture of f/8 and various shutter speeds between 1/1000 and 1/60 s. Each plot was photographed at a different time of the day and under a variety of sky conditions ranging from clear to overcast. On clear days, pictures were taken early or late in the day when the view of the solar disk was blocked by the surrounding topography. On

Fig. 2. Sampling layout for optical measurements. A total of 7 photographs and 42 LAI-2000 PCA measurements were used to characterize each plot.
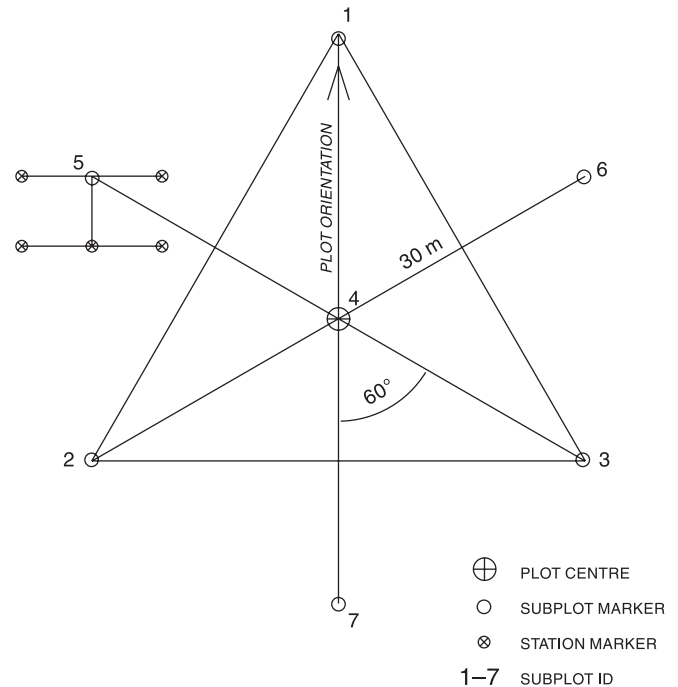
cloudy days with sunny breaks, pictures were taken while passing clouds eclipsed the sun.

Photographic negatives were digitized using a 35-mm film scanner at an image resolution of a 1000 dots per inch and 8-bit (256 gray-scale shades) colour depth. Of the four or five photographs taken at each subplot, only one was chosen for analysis. The selection process was entirely subjective and involved two steps. First, all film negatives from a single subplot were placed on a light table to identify the image with the best colour contrast between foliage elements and canopy gaps. Second, the selected image plus the two exposures taken at a speed above and below were digitized and compared once more. The best exposures were the ones that had a very high degree of colour contrast, yet still preserved the smaller gaps found closer to the horizon. A custom software application developed by Frazer et al. (1997) was utilized to analyze each of the hemispherical images for canopy openness and leaf area.

LAI-2000 plant canopy analyzer (PCA)

The LAI-2000 PCA is a commercial instrument (LI-COR, Inc., Lincoln, Neb.) that uses fisheye optics and five concentric silicon detector rings to measure the amount of diffuse solar radiation transmitted by a forest canopy at multiple view angles (0–74°). Each detector ring has an angular response of approximately 15° of zenith. A light filter (<490 nm) positioned between the optical lens and silicon detector helps to minimize the contribution of solar radiation transmitted and scattered by the foliage. A control box – data logger (LAI-2070 control unit) connected to the hand-held sensor is used to measure, record, and compute final results.

We used two intercalibrated LAI-2000 PCA sensors, both outfitted with 45° view caps, to measure the instantaneous diffuse solar radiation above and within each of the 24 stands. A remote reference instrument programmed to store above-canopy readings every 60 s was positioned in a clearing adjacent to each plot, while a second hand-held instrument was used to take below-canopy measurements at each of the predetermined subplots and stations. Our

primary reason for installing the view caps was to avoid the potential inaccuracies (underestimates) that occur when a single sensor ring attempts to average two very different skylight intensities, i.e., when the optical sensor is looking at a large gap in one direction and dense foliage in another (Welles and Norman 1991).

The sensors were calibrated prior to, and after, each plot was sampled using the methods proposed in the LI-COR, Inc. PCA Instruction Manual (LI-COR, Inc. 1992). During times of measurement, both instruments were leveled at height approximately 1.3 m above the ground, with the sensor heads directed towards geographic north. The instruments' field of view was therefore restricted to 22.5° on either side of geographic north. Slight adjustments in the horizontal (<3 m) and vertical (<1 m) position of the below-canopy instrument were required to avoid the shadowing produced by understory vegetation and tree boles of significant diameter (>30 cm DBH).

Canopy openness and leaf area index

Canopy openness refers to the relative amount of sky that is visible from a point beneath the forest canopy. We used the percent open sky derived from hemispherical photographs and diffuse noninterceptance (DIFN) produced by the LAI-2000 PCA as measures of canopy openness. These measures, however, are not exactly comparable, largely because the LAI-2000 PCA optical sensor has a more limited field of view and uses slightly different sine weightings.

Percent open sky was measured by (*i*) partitioning the hemispherical image into six concentric rings each corresponding to a 15° interval of zenith angle from 0° (zenith) to 90° (horizon), (*ii*) subjectively applying a single threshold value that separated the hemispherical image into sky (white) and nonsky (black) pixels, and (*iii*) calculating the fraction of sky (white) pixels to total number of pixels contained in each ring (gap fraction). Percent open sky was calculated using the following formula:

$$[1] \qquad \text{Sky}(\%) = \sum_{r=1}^{6} (\{[\cos(\theta_1) - \cos(\theta_2)]T_r\} \times 100)$$

where the subscript r represents the concentric ring number ranging from 1 to 6, θ_1 and θ_2 are, respectively, the smallest and largest angles of zenith that define the lower and upper bounds of each concentric ring (e.g., $\theta_1 = 0°$ and $\theta_2 = 15°$ for ring 1), and T_r is the estimated gap fraction for ring r.

DIFN was estimated using similar intervals ($\cong 15°$) of sky view; however, the geometry of the LAI-2000 PCA optical sensor was limited to only five rings (0–74°) and 45° of azimuth. DIFN was calculated with the LI-COR C2000 software using the formula:

$$[2] \qquad \text{DIFN} = \sum_{r=1}^{5} T_r W_r$$

where T_r is the gap fraction (measured as the ratio of diffuse skylight below to the diffuse skylight above the canopy) for ring r, and W_r is the normalized weighting value for ring r (i.e., ring 1 = 0.066, ring 2 = 0.189, ring 3 = 0.247, ring 4 = 0.249, and ring 5 = 0.249) (LI-COR, Inc. 1992).

Hemispherical photography and the LAI-2000 PCA are considered to measure only an "effective" leaf area index (LAI), because (*i*) neither technique is directly able to compensate for the clumping of foliage elements within the canopy, and (*ii*) gap fractions are a consequence of the shading effects produced by all plant elements (e.g., branches, boles, cones, etc.) and not just leaves (Chen et al. 1997). The definition of LAI used in this study is equivalent to the one proposed by Chen and Black (1992*a*), i.e., one half the total effective leaf area per unit ground surface area (L_e), or more precisely, per unit slope surface area, since the instrument was held

normal to the local zenith. We used the gap fractions obtained from each of the two optical techniques and the five-ring (zenith angles 0–75°) numerical integration presented by Welles and Norman (1991) to compute the stand L_e for each plot. Our measure of stand L_e, however, purposely omits the leaf area contributed by understory plants.

Within-shoot clumping factor

Shoots from branches collected as part of a foliar nutrient sampling study (Trofymow et al. 1997) in the autumn of 1995 were used to estimate within-shoot clumping factors following the methods of Gower and Norman (1991). Entire branches from the sixth to eighth whorl (counting from the top of the tree) were sampled from three trees of each species found in each of the 24 plots. In the laboratory, three shoots representing current growth were selected from each branch. The projected area of shoots, needles, and leaves was measured using a Delta-T area meter (Decagon Devices 1989). Shoots were oriented with their central axis parallel to the meter's scan axis, measured, the shoot turned over, remeasured, and the shoot area values averaged (SA). A subsample of 40 needles or four or five leaves were removed from each shoot, separated on a glass plate aligned perpendicular to the meter's scan axis and the area measured (LA40). The needle or leaf subsample was dried at 70°C overnight and weighed (LM40). The balance of the needles or leaves from each shoot were also removed, dried, and weighed (LMB). The shoot-level clumping factor (CF) was then calculated

$$[3] \qquad \text{CF} = \frac{(\text{LA40}/\text{LM40})(\text{LM40} + \text{LMB})}{\text{SA}}$$

Although most plots were dominated by one tree species, other tree species contributed to the total stand basal area. Basal area proportions for each species were calculated for each plot based on all live trees 3 m or greater in height in the three subplots for which mensurational data had been gathered (Trofymow et al. 1997). Proportional basal areas were used as a weighting term to calculate a weighted, shoot-clumping factor (WCF) for each plot.

Statistical analyses

Stand estimates (plot means and interquartile ranges) of percent open sky, DIFN, and L_e were stratified into distinct groups according to geographic location and age-class factors. Two-way analysis of variance (ANOVA) and Tukey post-hoc tests of pairwise differences (Tukey HSD) were used to test for statistically significant differences between these groupings. Two distinct ANOVA models were constructed to look at locational and stand-age differences in canopy structure across differing scales of the landscape: the first model looked at the main effects and interaction of biogeoclimatic subzone and seral stage on the canopy openness and L_e in all CWH forests, while the second model focused specifically on the main effects of site location and seral stage within each of the two biogeoclimatic subzones. Similarly, two-way ANOVA and Tukey HSD procedures were used to identify significant differences in shoot-level clumping factors between species, subzones, sites, and seral stages. Prior to running the ANOVA and Tukey HSD tests, all attribute data were tested for normality using a normal-probability plot and linear best-fit line. Non-normal data were transformed using either a logarithmic or square root transformation. Linear and nonlinear regressions were used to investigate the correlation between structural estimates produced by hemispherical photography and the LAI-2000 PCA. All statistical analyses were performed using SYSTAT for Windows, version 5.05 (Wilkinson et al. 1992).

Results

Overall patterns

Canopy openness (percent open sky and DIFN) and L_e varied considerably within and among individual plots and among chronosequences, indicating significant heterogeneity in canopy structure in both time and space (Fig. 3). The temporal change in canopy openness and L_e was significant, whereby openness increased and L_e decreased during forest succession. Changes in canopy structure, however, were less apparent during the earlier phases (immature to mature) of stand development as compared with the transition from mature to old growth. Old-growth canopies were noticeably more heterogeneous in their openness than younger aged forests. On the drier, east side of southern Vancouver Island, Douglas-fir dominated forests (CWHxm) had overstories that were more open and heterogeneous and had a lower L_e than the western hemlock forests (CWHvm) occupying the west side. Both optical methods identified trends that were similar despite quantitative differences. Finally, within-shoot clumping varied considerably amongst individual species, and species-specific clumping factors varied by age-class and site location.

Magnitude and range of canopy openness and L_e

Both optical techniques produced similar plot averages and ranges in canopy openness. DIFN estimates derived from the LAI-2000 PCA extended from a low of 0.01 (1%) at the Klanawa immature plot to a maximum of 0.152 (15.2%) within the Koksilah old-growth plot. These plots also represented the minimum and maximum limits in the range of percent open sky determined by hemispherical photographs (2.2–14.1%). The L_e estimates derived using the LAI-2000 PCA ranged from a maximum of 5.44 m^2/m^2 at the Klanawa immature plot to a low of 2.26 m^2/m^2 within the Nanaimo old-growth plot. The L_e data extracted from hemispherical photographs were somewhat more limited in range and magnitude; they ranged from a maximum of 4.25 m^2/m^2 at the Klanawa immature plot to a minimum of 2.04 m^2/m^2 in the Koksilah old-growth plot.

We used the interquartile range of within-plot canopy openness as an indicator of the degree of structural heterogeneity occurring within the finest spatial scales of this study. Both age- and site-related patterns of heterogeneity emerged. West-side, immature and mature stands were the least heterogeneous, whereas east-side, old-growth stands were the most heterogeneous (Fig. 4). Geographic variation however, leads to broad overlap in the openness and heterogeneity among seral stages when data were lumped across space.

Factors influencing the variation in canopy openness and L_e

Biogeoclimatic subzone and stand age effects within CWH forests

Significant mean differences ($p < 0.01$) in the magnitude of canopy openness and L_e (derived using either optical technique) were present among age-classes as well as between east- (CWHxm) and west-side (CWHvm) sites (see ANOVA results for ungrouped data, Table 2). Irrespective of biogeoclimatic subzone, mean canopy openness increased

and L_e declined as forests matured. Mean DIFN increased from 0.03 (3%) in immature to 0.044 (4.4%) in mature ($p = 0.12$) and to 0.077 (7.7%) at old growth ($p = 0.04$). Similarly, mean percent open sky increased from a low of 5.69% in immature to 6.98% in mature ($p = 0.402$) and finally to a maximum of 9.99% at old growth ($p = 0.016$). On average, there was approximately twice the fraction of sky visible beneath old-growth overstories compared with young forests. Mean interquartile ranges of canopy openness also increased significantly throughout forest succession. No significant ($p > 0.62$) mean differences occurred between immature and mature seral stages; however, significant ($p < 0.01$) increases in mean interquartile ranges of openness were evident as stands shifted in age-class from mature to old growth. LAI-2000 PCA estimates of mean stand L_e showed a significant ($p = 0.001$) decline of 25.1% between immature (4.42 m^2/m^2) and old-growth (3.31 m^2/m^2) stages, while photographic estimates indicated a somewhat smaller relative decline ($p = 0.01$) in mean stand L_e of 21.2% between immature (3.39 m^2/m^2) and old growth (2.67 m^2/m^2).

Both optical methods also identified similar regional differences in mean canopy openness and stand L_e. Mean canopy openness in CWHxm forests was approximately 1.9 times ($p = 0.001$, LAI-2000 PCA), and 1.5 times ($p = 0.001$, PHOTO) higher than CWHvm stands. Mean interquartile ranges of canopy openness were also significantly ($p < 0.01$) larger in CWHxm forests. CWHvm stands, however, exhibited a significantly higher ($p < 0.01$) mean L_e (4.31 m^2/m^2, LAI-2000 and 3.28 m^2/m^2, PHOTO) compared with CWHxm forests (3.48 m^2/m^2, LAI-2000 and 2.82 m^2/m^2, PHOTO) despite the fact that younger CWHxm forests maintained higher mean stand densities overall.
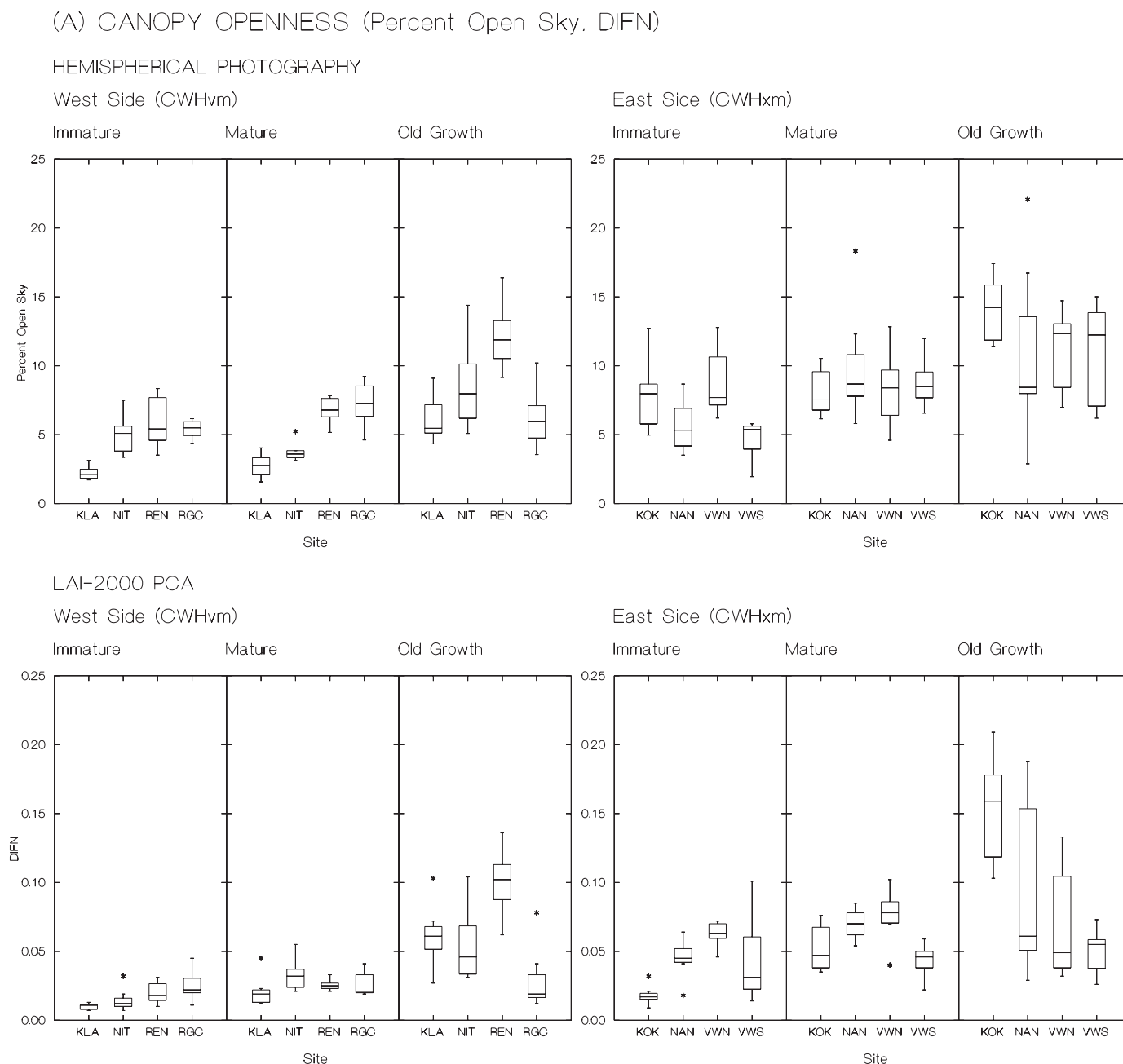
Site location and stand age effects within CWHvm forests

Contrary to the gap fraction estimates produced by the LAI-2000 PCA, photographic results indicated that there was some significant site-to-site variation in the magnitude of mean canopy openness and L_e within CWHvm forests (see CWHvm grouped data; Table 2, Fig. 5). Significant mean differences in percent open sky ($p = 0.05$) and L_e ($p = 0.02$) derived from photographs only occurred between the Klanawa and Renfrew chronosequences. Mean percent open sky and L_e were approximately 2.2 times higher and 1.4 times lower, respectively, at the Renfrew site compared with the Klanawa chronosequence site.

Both optical methods identified similar trends in the temporal development of canopy openness and L_e in CWHvm forests (Fig. 6). Mean percent open sky increased by 1.8 times ($p = 0.03$), and DIFN increased by 3.4 times ($p = 0.01$) as CWHvm forests developed from immature to old growth. Adjacent age-classes were not statistically different, although the p value for the difference between mature and old-growth stands was much smaller than for the difference between immature and mature stands (immature vs. mature: $p > 0.3$; mature vs. old growth: $p < 0.09$). Mean within-plot variability (i.e., interquartile ranges) of DIFN and percent open sky also increased as forests matured (Fig. 4).

Mean L_e declined significantly during forest succession (Fig. 6). The overall decrease in mean L_e from immature through to old growth was, respectively, 17.3 and 27.5% according to each of the optical methods. The mean difference

Fig. 3. Box-and-whisker plots summarizing the distribution of (A) canopy openness and (B) effective leaf area index (L_e) obtained from each plot using both optical techniques. The horizontal line contained with the box is the median, the box endpoints (hinges) signify the 25th and 75th percentiles (interquartile range), the whiskers define the largest and smallest observed values within 1.5 box lengths, and the asterisks and circles are measurements (outliers) falling outside and far outside the whiskers, respectively (Wilkinson et al. 1992).


in L_e between mature and old growth was only moderately significant (i.e., $p = 0.12$, PHOTO; $p = 0.06$, LAI-2000 PCA), while no significant ($p > 0.44$) difference existed between immature- and mature-aged stands.

Site location and stand age effects within CWHxm forests

We found no significant differences ($p > 0.44$) in mean DIFN, percent open sky, or L_e among the four CWHxm chronosequences (Table 2, Fig. 5). Photographic estimates of mean canopy openness and L_e showed significant differ-

ences ($p < 0.01$) among seral stages of stand development, while no significant ($p > 0.15$) stand-age differences were evident within the LAI-2000 PCA data set. Both optical methods, however, exhibited similar temporal trends in canopy openness and L_e despite the lack of statistical significance within the LAI-2000 PCA data. Both data sets indicated that canopy openness increased and L_e decreased during forest succession (Fig. 6).

Mean percent open sky was 1.7 times ($p = 0.01$) greater in old-growth than in immature-aged stands, and mature

Fig. 3 (*concluded*).

(B) EFFECTIVE LEAF AREA INDEX

HEMISPHERICAL PHOTOGRAPHY
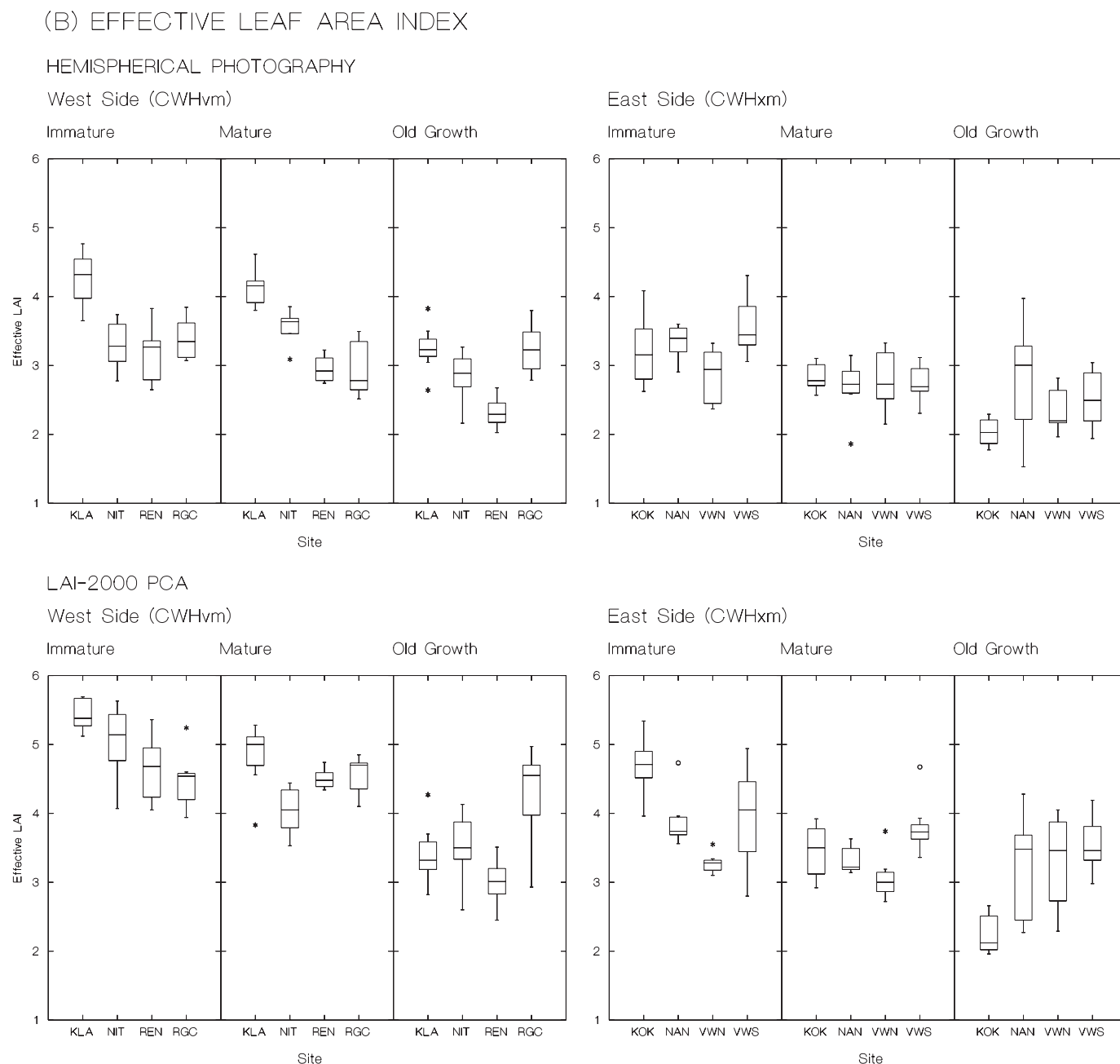
LAI-2000 PCA

forests, on average, were 1.3 times (p = 0.24) more open than immature stands. The average overall decline in L_e from immature (3.95 m^2/m^2) to old growth (3.07 m^2/m^2) was 22.3% (p = 0.134) according to data produced by the LAI-2000 PCA. These differences were slightly more substantial for photographic data, where L_e declined (p = 0.01) by approximately 25% from a maximum of 3.25 m^2/m^2 in immature forests to a low of 2.43 m^2/m^2 in old-growth stands. Similar to the patterns shown in CWHvm forests, the mean interquartile ranges of DIFN and percent open sky increased

($p < 0.08$) as CWHxm forests advanced from immature to old growth. Mean interquartile ranges of percent open sky and DIFN within old growth were, respectively, 2 and 3.5 times greater than immature stands ($p < 0.084$).

Within-shoot clumping factors

Shoot-level clumping factors varied significantly among species within both west- ($F = 41.74$, $p < 0.0001$) and east-side forests ($F = 103.83$, $p < 0.0001$). By rank, western white pine (*Pinus monticola* Dougl.) had, on average, the

Fig. 4. Scatterplots showing the relationship between the mean and interquartile range of canopy openness in immature (I), mature (M), and old-growth (O) stands. Data point symbols identify the biogeoclimatic subzone of the plot.
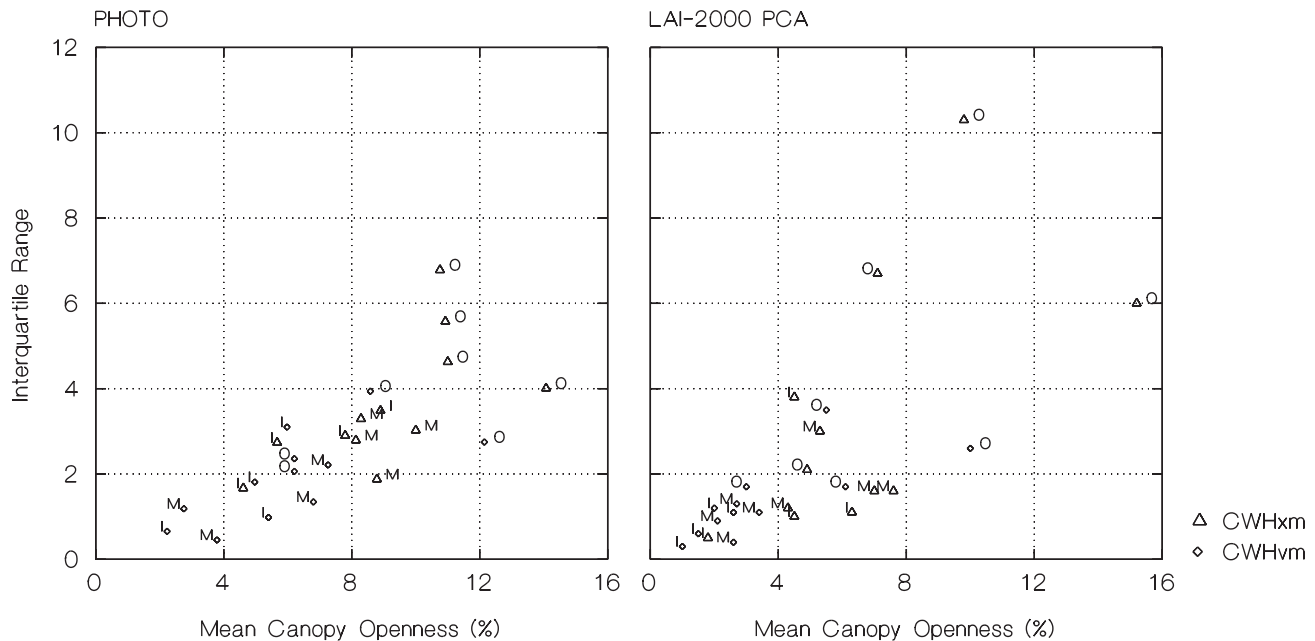
largest projected needle-to-shoot area ratio (3.40) followed by amabilis fir (2.35), Douglas-fir (2.16), western hemlock (1.38), and western redcedar (1.01). Significant and moderately significant mean differences in shoot clumping were found among age-classes for Douglas-fir and western redcedar, respectively; however, the magnitude of these differences also varied with biogeoclimatic subzone. Mean within-shoot clumping increased ($F = 9.85$, $p < 0.0001$) with age-class for Douglas-fir in CHWxm chronosequences (e.g., 1.87 in immature, 2.24 in mature, and 2.47 by old growth), while no such trend was found in CWHvm plots because of the absence of this species in mature and old-growth stands. Clumping factors for western redcedar also increased ($F = 3.45$, $p = 0.069$) with seral stage in the CWHvm chronosequences but varied little ($F = 0.18$, $p = 0.682$) within CWHxm chronosequences. Significant ($F = 3.01$, $p < 0.0001$) site-to-site differences in Douglas-fir clumping factors were noted in CWHxm chronosequences, with the largest within-shoot clumping occurring at the Koksilah site (2.34), followed by Victoria Watershed North (2.109), Victoria Watershed South (2.06), and Nanaimo River (1.96).

We used the weighted within-shoot clumping factors multiplied by a shape factor for flat needles (1.18) to correct the LAI-2000 PCA L_e estimates for each plot (Table 3). Mean corrected L_e was significantly higher in the Douglas-fir-dominated east-side chronosequences (8.60 m^2/m^2) than on the west-side of the island where western redcedar and western hemlock were the dominant canopy species (7.27 m^2/m^2). Only a moderately significant ($F = 2.51$, $p = 0.11$) mean difference in corrected L_e occurred between each of the age-classes: mean corrected L_e was lowest in old growth (6.90 m^2/m^2) and highest in the immature (8.56 m^2/m^2), and mature (8.34 m^2/m^2) age-classes. Within the east-side chronosequences, mean corrected L_e was stable across all age-classes (ranging from 8.53 to 8.69 m^2/m^2), while on the

island's west side a significant decline ($F = 6.68$, $p = 0.02$) in mean corrected L_e occurred as stand age increased.

Comparison of results obtained from hemispherical photography and LAI-2000 PCA

Surprisingly, there was only a moderate, positive relationship between the measurements produced by the two optical methods we used: for canopy openness, $R^2 = 0.49$, $p < 0.0001$, and for L_e, $R^2 = 0.47$, $p < 0.0001$ (Fig. 7). Hemispherical photography produced canopy openness estimates that exceeded LAI-2000 PCA measures of DIFN in 140 of 167 subplots. On average, photographic measures of canopy openness were 52% larger than estimates derived using the LAI-2000 PCA. In 154 of 167 subplots, the LAI-2000 PCA generated L_e estimates that, on average, exceeded photographic measures by 22%.

Mean gap fractions measured using either technique showed a steady decline with increasing zenith angle, while weighted-openness distributions were generally bell shaped and at their maxima between zenith angles 25 and 35°. The gap fractions extracted from hemispherical photographs averaged 2.3 times those estimated using the LAI-2000 PCA. This disparity, however, decreased with increasing zenith angle and the distribution curves often converged at zenith angles greater than 60°. The LAI-2000 PCA produced gap fraction distributions that were occasionally flat or rising between zenith angles 53° (ring 4) and 68° (ring 5), while all gap fractions extracted from photographs were monotonic in their decline towards the horizon.

Discussion

We found that canopy openness and L_e are highly variable within and among plots, sites, subzones, and seral stages. Forest canopies are strongly heterogeneous at a variety of

Table 2. Two-way ANOVA results.

| Grouped by	Descriptive statistic	Source (effect)	df	PHOTO (%sky)			LAI-2000 (DIFN)			PHOTO (L_e)			LAI-2000(L_e)		
				MS	F	P^a	MS	F	P^a	MS	F	P^a	MS	F	P^a
None	Mean	Zone	1	55.825	14.796	0.001	0.534	16.176	0.001	1.291	8.171	0.010	4.096	18.702	0.000
		Sere	2	38.866	10.301	0.001	0.380	11.512	0.001	1.034	6.543	0.007	2.487	11.355	0.001
		Zone × sere	2	1.392	0.369	0.697	0.022	0.656	0.531	0.064	0.404	0.673	0.188	0.857	0.441
		Error	18	3.773			0.033			0.158			0.219		
		Transformation			None			Logarithmic			None			None	
	Interquartile	Zone	1	1.651	19.386	0.000	0.577	8.613	0.009	0.080	2.061	0.168	0.000	0.000	0.992
		Sere	2	0.858	10.076	0.001	0.757	11.299	0.001	0.063	1.628	0.224	0.140	2.957	0.078
		Zone × sere	2	0.026	0.304	0.741	0.010	0.155	0.858	0.039	0.996	0.389	0.068	1.438	0.263
		Error	18	0.085			0.067			0.039			0.047		
		Transformation			Square root			Logarithmic			None			Logarithmic	
CWHvm	Mean	Sere	2	0.617	6.783	0.029	0.287	8.920	0.016	0.417	5.082	0.051	1.837	9.246	0.015
		Site	3	0.479	5.266	0.041	0.022	0.678	0.597	0.582	7.092	0.021	0.152	0.766	0.553
		Error	6	0.091			0.032			0.082			0.199		
		Transformation			Square root			Logarithmic			None			None	
	Interquartile	Sere	2	0.335	2.584	0.155	0.300	5.231	0.048	0.038	2.010	0.215	0.040	1.421	0.312
		Site	3	0.086	0.666	0.603	0.038	0.659	0.607	0.029	1.542	0.298	0.012	0.438	0.734
		Error	6	0.129			0.057			0.019			0.028		
		Transformation			Square root			Logarithmic			None			None	
CWHxm	Mean	Sere	2	24.700	9.833	0.013	0.115	2.620	0.152	0.676	10.394	0.011	0.787	2.658	0.149
		Site	3	2.050	0.816	0.530	0.024	0.540	0.672	0.068	1.039	0.440	0.157	0.532	0.677
		Error	6	2.512			0.044			0.065			0.296		
		Transformation			None			Logarithmic			None			None	
	Interquartile	Sere	2	0.549	7.871	0.021	0.466	3.818	0.085	0.064	0.848	0.474	0.168	1.603	0.277
		Site	3	0.026	0.371	0.777	0.005	0.038	0.989	0.015	0.204	0.890	0.012	0.112	0.950
		Error	6	0.070			0.122			0.075			0.105		
		Transformation			Square root			Logarithmic			None			Logarithmic	

[a]Significance level is 0.05.
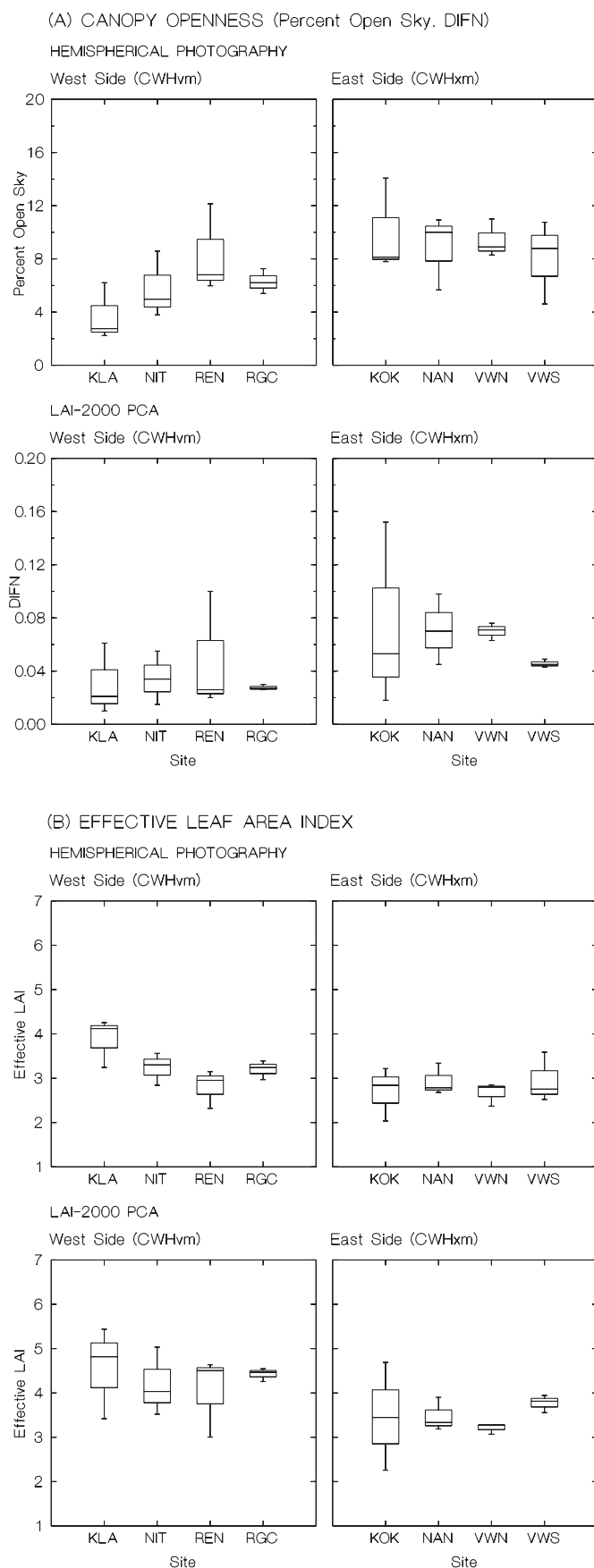
Fig. 5. Box-and-whisker plots summarizing the distribution of (A) canopy openness and (B) effective leaf area index (L_e) measured using each of the optical techniques. Data have been grouped by chronosequence site and biogeoclimatic subzone.

scales over the landscape and through time. A significant portion of this structural variability is influenced by stand age and site location. Stand means and interquartile ranges of canopy openness increase dramatically as forests mature. The most significant developmental changes in canopy structure, however, do not occur until the later stages of stand development. The increase in canopy openness with forest age is associated with a decline in L_e as gap-forming processes become more prevalent. Site-to-site and east–west regional differences in the temporal rates of change and structure of forest canopies suggest that site-specific environmental factors may exert a significant influence on the developmental trajectories of forests. The use of chronosequences to document changes during succession, however, can be complicated by variation among sites in soil, slope, aspect, vegetation, and disturbance history. Although careful site selection can minimize these variations, they cannot be eliminated. Hence, the differences noted between younger and older stands may not be entirely the result of changes with succession, but may also represent differences in stand history.

Successional changes in canopy structure

Gap fraction data provide limited information about the size, shape, and distribution of canopy gaps. However, the sample distributions derived from multiple measurements from within a single plot do offer insight into both the character and spatial arrangement of openings in the canopy. Immature stands are characterized by small, relatively evenly spaced canopy openings and exhibit little spatial variation in these characteristics. Old stands, on the other hand, are characterized by larger, relatively unevenly spaced canopy openings and exhibit substantial spatial variation in these characteristics. This is consistent with the notion that the overstories of immature stands can be described as dense "monolayers" supported by numerous, relatively short and uniformly distributed stems, whereas old-growth forests are tall, multistoried, and have a more clumped distribution of stems (e.g., Parker 1995). In our data, mature forest canopies are in between immature and old growth stands in character but more similar to younger stands than older ones.

Spies et al. (1990) also observed significant differences in the gap-size distributions of mature (100–150 years) and old-growth (>200 years) western hemlock and Douglas-fir forests of Washington and Oregon. The median area of canopy gaps was approximately 4.5 times larger in old-growth compared with mature stands, and this difference was due to the irregular height of canopy trees and the larger number and size of gapmakers present in old growth stands. In contrast, Lertzman et al. (1996) found that mature (100–250 years) CWHvm stands on the southwestern side of Vancouver Island had more area in gaps than old growth (>250 years) even though the old growth had a higher density of gapmakers. Lertzman et al. (1996), however, suggested that the different aged stands they had sampled may not have
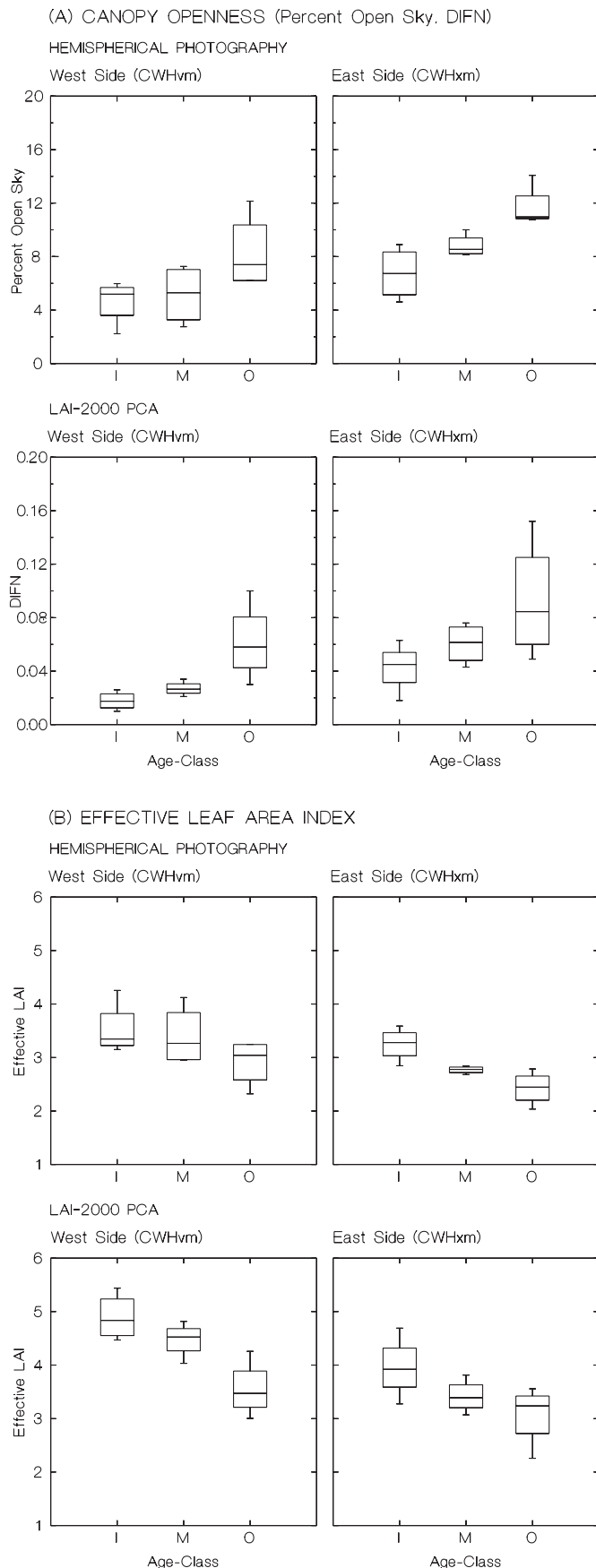
(A) CANOPY OPENNESS (Percent Open Sky, DIFN)

HEMISPHERICAL PHOTOGRAPHY

LAI-2000 PCA

(B) EFFECTIVE LEAF AREA INDEX

HEMISPHERICAL PHOTOGRAPHY

LAI-2000 PCA

Fig. 6. Box-and-whisker plots summarizing the distribution of (A) canopy openness and (B) effective leaf area index (L_e) measured using each of the optical techniques. Data have been grouped by age-class and biogeoclimatic subzone.

been on the same developmental trajectory and, therefore, may not have represented a chronosequence.

According to current theory, stand LAI typically increases until canopy closure, after which, LAI stabilizes and then slowly declines as tree mortality (gap development) leads to a progressive opening of the canopy (Waring and Schlesinger 1985; Parker 1995). In this study, LAI-2000 PCA and photographic estimates of L_e declined steadily, on average, by 25 and 21%, respectively, as forests advanced in stand age from immature to old growth. Stand mensuration data reported by Trofymow et al. (1997) for these same sites indicate that there is, on average, a greater than threefold decrease in the density of live stems between immature and old growth. We expect, however, that this decline in leaf area will not continue ad infinitum but, instead, will reach some kind of steady state during the later stages of old growth when the regeneration in gaps begins to offset and balance processes of gap-creating mortality. Yoder et al. (1994) also reported an overall decline of 35% in stand LAI from a high of 5.1 m²/m² in immature (40 years) stands to a low of 3.3 m²/m² in old-growth (245 years) lodgepole pine stands. Similarly, Mencuccini and Grace (1996), working in Scots pine (*Pinus sylvestris* L.) forests aged 7 to 59 years, noted that stand LAI increased from 0.945 m²/m² at 7 years to a maximum of 5.4 m²/m² at 14 years and subsequently declined to 2.7 m²/m² (50%) and 4.05 m²/m² (25%) thereafter.

Less-significant differences in the structure of canopies between immature and mature as compared with mature to old growth can largely be explained by the nonlinear time scale between age-classes. For example, on average, there are approximately 40 years between immature- and mature-aged stands and 215 years from mature to old growth. We can, however, conclude that the most prevalent changes and diversity in canopy openness and L_e do not emerge until late in the developmental process. Thus, the types of structural characteristics that distinguish mature from old-growth stands may not appear until after the first 150–200 years of growth. We would expect, however, to see substantial differences between such young old-growth stands and older old growth (Wells et al. 1998).

Geographic variation in canopy structure

To some extent, the geographic variation in canopy structure noted within biogeoclimatic subzones is due to the absolute age difference between stands of a given age-class. For example, the mean age of the mature plot at Victoria Watershed South is 33 years older than the mature stand at Nanaimo River (i.e., the approximate age difference between most of the immature and mature stands), and 259 years separate the Red/Granite Creek (176 years) and Klanawa (435 years) old-growth stands. However, the fact that the younger Red/Granite Creek old growth is almost twice as open as the older Klanawa old-growth stand, suggests that site-specific factors, (e.g., site orientation, soil chemistry and moisture, disturbance history, etc.), also play a role in defining the

Table 3. Weighted shoot clumping factors and corrected L_e estimates.

| Subzone	Sere[a]	Site[b]	Plot	Basal area proportions by species[c]						Projected needle/shoot area ratio by species[c]						Plot WCF	LAI-2000 L_e	Corrected LAI-2000 L_e[d]
				BA	CW	DR	FD	HW	PW	BA	CW	DR	FD	HW	PW			
CWHxm	I	VWS	2	—e	—	—	0.748	0.252	—	—	—	—	1.873	1.312	—	1.732	3.94	8.05
		VWN	12	—	—	—	1.000	—	—	—	—	—	1.660	—	—	1.660	3.27	6.41
		KOK	22	—	0.068	—	0.882	0.050	—	—	1.009	—	2.101	1.526	—	1.998	4.69	11.06
		NAN	35	—	—	—	1.000	—	—	—	—	—	1.910	—	—	1.910	3.90	8.79
	M	VWS	5	—	0.054	0.016	0.923	0.006	0.001	—	1.009	1.000	2.196	1.312	3.401	2.109	3.81	9.48
		VWN	13	—	0.024	—	0.976	—	—	—	1.009	—	2.002	—	—	1.978	3.07	7.17
		KOK	23	—	—	—	1.000	—	—	—	—	—	2.637	—	—	2.637	3.45	10.74
		NAN	33	—	0.012	—	0.702	0.286	—	—	1.009	—	2.115	1.337	3.401	1.879	3.33	7.38
	O	VWS	6	—	0.035	0.011	0.885	0.069	—	—	1.009	1.000	2.240	1.312	—	2.119	3.56	8.90
		VWN	15	—	0.061	—	0.905	0.034	—	—	1.009	—	2.789	1.374	—	2.632	3.29	10.22
		KOK	24	—	—	—	0.994	0.006	—	—	—	—	2.714	1.526	—	2.707	2.26	7.22
		NAN	34	—	0.020	—	0.914	0.065	0.001	—	1.009	—	2.142	1.337	3.401	2.068	3.19	7.79
CWHvm	I	REN	52	0.089	0.066	—	—	0.845	—	2.352	0.972	—	—	1.388	—	1.446	4.64	7.92
		RGC	62	—	0.052	0.534	0.103	0.311	—	—	0.972	1.000	1.932	1.388	—	1.215	4.47	6.41
		NIT	72	—	0.069	0.008	0.647	0.276	—	—	0.972	1.000	1.932	1.388	—	1.708	5.03	10.14
		KLA	82	0.134	0.004	—	—	0.862	—	2.352	0.972	—	—	1.388	—	1.516	5.44	9.73
	M	REN	53	0.205	0.008	—	—	0.787	—	2.352	1.007	—	—	1.388	—	1.583	4.50	8.40
		RGC	63	—	—	—	—	1.000	—	—	—	—	—	1.388	—	1.388	4.55	7.45
		NIT	73	—	—	—	—	1.000	—	—	—	—	—	1.388	—	1.388	4.03	6.60
		KLA	83	0.297	—	—	—	0.703	—	2.352	—	—	—	1.388	—	1.674	4.82	9.52
	O	REN	54	0.009	0.749	—	—	0.242	—	2.352	1.068	—	—	1.388	—	1.157	3.00	4.10
		RGC	64	—	0.394	—	—	0.606	—	—	1.068	—	—	1.388	—	1.262	4.26	6.34
		NIT	74	0.085	0.233	—	—	0.682	—	2.352	1.068	—	—	1.388	—	1.395	3.52	5.80
		REN	84	0.035	0.705	—	—	0.260	—	2.352	1.068	—	—	1.388	—	1.196	3.42	4.83

[a]I, immature; M, mature; O, old growth.
[b]See Table 1 for site abbreviations.
[c]BA, amabilis fir; CW, western redcedar; DR, red alder; FD, Douglas-fir; HW, western hemlock.
[d]Corrected L_e = leaf shape factor × weighted clumping factor (WCF) × L_e.
[e]Species was not present on the sample plot.

Fig. 7. Scatterplots showing the coincidence between both optical measures of (A) canopy openness and (B) effective leaf area index (L_e).
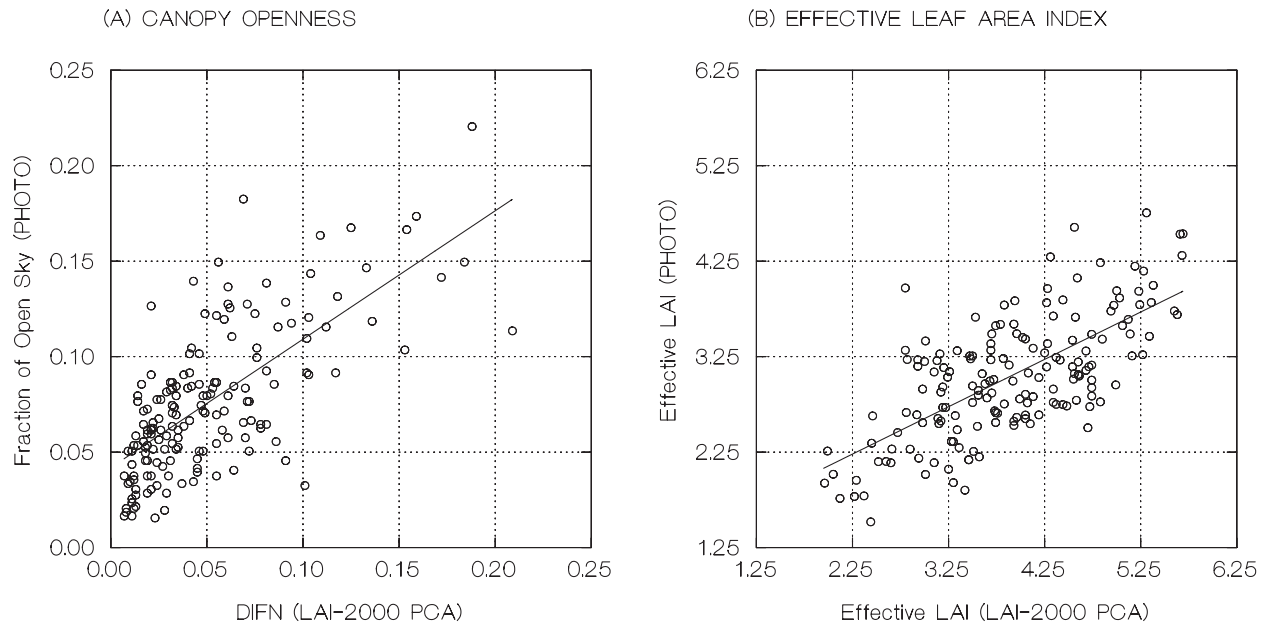
rates of change and character of aging forests even within relatively narrow landscape units.

Mensurational data for all chronosequences show that there are significant differences in species composition and live stem density between east- and west-island forests but little variation in mean basal area (Trofymow et al. 1997). Within east-island chronosequences, Douglas-fir accounts for approximately 90% of the total stem basal area. In contrast, west-side sites are predominately western hemlock (63% of the total stem basal area) and western redcedar (24% of the total stem basal area). Immature and mature forests on the east side, maintain mean stem densities that are, respectively, 1.4 and 2.5 times greater than similar aged stands on the west side. No significant regional differences occur in mean basal area despite the variability in stem density. Thus, we suspect that regional differences in openness and L_e are largely due to species-related differences in canopy architecture. We cannot tell from these data, however, whether these regional patterns are a consequence of species-related differences in biomass and leaf area, differences in leaf display and orientation (light-interception efficiency), or some combination thereof.

Relationship between L_e and LAI in CWH forests

In general, the LAI-2000 PCA significantly underestimates direct measures of LAI in conifer forests, and the source of this error is largely due to foliage clumping within shoots (Chason et al. 1991; Smith et al. 1993; Fassnacht et al. 1994; Stenberg et al. 1994). In contrast, the shadowing effects produced by branches and boles tend to cause L_e to be higher relative to LAI (Deblonde et al. 1994; Chen et al. 1997). Since published L_e data are consistently lower than direct LAI estimates in conifer forests, we can assume that the negative effect of foliage clumping dramatically outweighs the shadowing errors of branches and boles. Nevertheless, we suspect that, as stands shift from immature to old

growth, there will be an increasing effect of bole area on L_e arising from the great heights and diameters of the larger trees in old-growth stands.

The nearest approximation of LAI for each of the plots was estimated by multiplying L_e (derived from the LAI-2000 PCA) by the weighted within-shoot clumping factors calculated for each plot (Table 3). To remain consistent with the definition of LAI proposed by Chen and Black (1992*a*), a shape factor for flat needles was also applied to convert from projected needle area to one-half the total needle area. Corrected L_e estimates for all plots averaged 7.93 ± 1.83 m^2/m^2 (mean ± SD) and ranged from a minimum of 4.10 to 11.06 m^2/m^2. However, the reliability of these corrected L_e data as an accurate estimate of LAI is strongly dependent on the following assumptions: (*i*) the interception of light by the woody fraction of the canopy is negligible, (*ii*) the shoots are the basic foliage elements seen by the LAI-2000 PCA optical sensor, (*iii*) shoots are randomly distributed within the canopy, and (*iv*) the correction factors determined in this study are an accurate measure of within-shoot clumping.

We know from stem densities and basal areas measured at each of the plots, and from other optical studies of leaf area by Chen and Black (1992*b*), Smith et al. (1993), Fassnacht et al. (1994), Stenburg et al. (1994), and Chen et al. (1997), that all four of the above assumptions have been violated to some extent in this study. Nevertheless, the magnitude and range of our corrected L_e measures, at least for immature and mature stands, appear to be in line with direct LAI estimates published by Brix (1981) and Smith et al. (1993) for similar-aged CWHxm forests on southern Vancouver Island, British Columbia. Other published studies by Marshall and Waring (1986), Easter and Spies (1994), and Runyon et al. (1994) report LAI values ranging from 3.93 to 12 m^2/m^2 in young to old coastal western hemlock and Douglas-fir forests of Washington and Oregon states.

Successional and regional patterns in corrected L_e

Both the successional and regional patterns exhibited by the corrected L_e data differ from those in the L_e data set in two ways. First, the mean corrected L_e of CWHxm forests (8.60 m²/m²) exceeds CWHvm forests (7.27 m²/m²) by 1.2 times ($F = 4.564$, $p = 0.047$) even though CWHxm forests are twice as open. Second, corrected L_e still declines ($F = 6.67$, $p = 0.02$) with increasing stand age in CWHvm forests, but in CWHxm forests it remains stable from immature (8.58 m²/m²) through to old growth (8.53 m²/m²).

We expect that the regional variation in species composition and canopy architecture will explain both the above differences. For example, in the CHWxm plots, the dominant canopy species, Douglas-fir, is characterized by foliage shoots, which are twice as clumped as those of western redcedar or western hemlock, and a horizontal branch structure that allows a significant amount of skylight to penetrate at large zenith angles (Black et al. 1991). Since optical methods are insensitive to the surface area of individual needles, and the theoretical value of L_e is heavily weighted (approximately 70%) upon the gap fractions from 45 to 74°, it is reasonable to assume that the higher canopy openness and lower L_e in CWHxm forests are in fact a response to differences in light-interception efficiency rather than to real differences in leaf area.

The stability of corrected L_e in young to old CWHxm forests is due to the age-related increases in shoot clumping that was found in the east-side Douglas-fir stands; however, we are still unsure whether other factors have contributed to this result. For example, it may be that the seral effect on foliage clumping was largely an artifact of our sampling technique, since specific leaf area is known to vary with crown height (Chen and Black 1992b). If this is not the case, then we might conclude that the LAI of aging Douglas-fir stands instead reaches some type of a steady state after canopy closure (Marshall and Waring 1986). We still would, however, expect to see an overall decline in LAI once the contribution of woody biomass was factored into the computations.

Differences between the LAI-2000 PCA and hemispherical photography

We believe three main factors have contributed to the significant unexplained variance between estimates produced by hemispherical photography and the LAI-2000 PCA. First, both instruments did not view identical portions of a strongly heterogeneous canopy because of the limited view of the LAI-2000 PCA optical sensor. Second, each technique used a different method to estimate gap fractions. Third, each technique was subject to unique measurement and analytical biases that were minimized under different canopy architectures and sky conditions.

Light transmission versus gap size

A comparison of the frequency distributions of openness data derived from both optical methods indicates that there are marked differences between gap fractions based on light transmission and those based on the size of canopy openings. Frequency distributions of DIFN estimates are noticeably more (positively) skewed and leptokurtic than photographic measures of percent open sky. This suggests that either the relationship between diffuse light transmis-

sion and gap size is nonlinear and (or) that there are inherent inaccuracies or biases associated with measuring gap fractions using either technique. It is well documented in the literature that the LAI-2000 PCA optical sensor is sensitive to the presence of scattered radiation (320–490 nm) at large zenith angles (45–74°) (Welles and Norman 1991). As well, canopy openings may be poorly defined and considerably overestimated by photographs at small zenith angles, because of the scattering and diffraction of light around the edges of individual shoots, branches, and large canopy gaps (Chen et al. 1991). Both problems were evident in the gap fractions collected in this study.

Measurement and analytical biases

Although the scattering of solar radiation negatively affects both optical methods, each technique will attain optimum performance under certain environmental settings. Because we have no independent baseline data for openness or LAI at these sites, we cannot tell under which conditions the performance of one instrument might exceed the other. We did, however, use regression to compare the LAI-2000 PCA and photographic results, grouped by stand age and sky conditions at the time of sampling, to identify the kinds of canopy characteristics and field conditions under which these techniques show the greatest or least agreement. Both the slopes and the coefficients of determination for these select data groupings fluctuate significantly from the regression parameters calculated for ungrouped data. In general, measures of canopy openness produced by the LAI-2000 PCA and hemispherical photography were most alike in CWHvm chronosequences ($R^2 = 0.52$, $\beta_1 = 0.77$, $p < 0.001$), old-growth stands ($R^2 = 0.51$, $\beta_1 = 0.6$, $p < 0.001$), and under clear-sky conditions ($R^2 = 0.72$, $\beta_1 = 0.81$, $p < 0.001$). The least agreement between the techniques was in east-side immature stands ($R^2 = 0.001$, $\beta_1 = 0.03$, $p = 0.9$) and under overcast skies ($R^2 = 0.39$, $\beta_1 = 0.75$, $p > 0.001$).

The differences in the regression parameters between east- and west-side stands may be related to the distinct way in which each of the optical techniques responds to the characteristic horizontal branching noted by Black et al. (1991) in Douglas-fir stands. In east-side stands, a rise in gap fraction between rings 4 and 5 in the LAI-2000 PCA was more common, indicating the presence of reflected light at large zenith angles. This problem is unique to the LAI-2000 PCA, and no evidence of similar problems were found in west-side stands. The decline in R^2 with decreasing stand age is likely related to the differences in the gap-size distributions representing each of the seral stands and the inability of photographs to sometimes accurately define or record exceedingly small gaps. A large part of this problem is that most image-analysis software uses a single threshold value to classify pixel spectra into sky and nonsky, when in fact a number of thresholds should be applied to compensate for the increased scattering and diffraction of light at small zenith angles. A single threshold value will cause gaps to be over- and under-estimated at large and small zenith angles, respectively. In immature stands, gaps are generally smaller, more frequent, and characterized by large perimeter-to-total area ratios as compared with mature or old-growth forests. Consequently, overestimation due to the scattering of light around small openings becomes cumulative and disproportionately large

relative to the total amount of open sky found in immature stands.

The fact that the LAI-2000 PCA and photographic results are most alike under clear-sky conditions is unusual, especially since data averaged for these conditions are significantly lower than the ungrouped means. Frequency counts indicate that all three sky conditions are somewhat evenly distributed across all subzones and age-classes; however, this still does not preclude the possibility of confounding sky-condition with stand-structure effects. Assuming that these differences are due to sky conditions only, then the only conclusion that can be made is that clear skies may have had an equally debilitating effect on both optical techniques, while overcast skies may have significantly reduced the amount of blue light scattered at large zenith angles, thus improving the LAI-2000 PCA results relative to the photographic ones.

Although both optical techniques have identified similar qualitative changes in canopy openness and L_e, quantitative differences in the leaf area at these sites are still not well understood. Other alternative methods (e.g., Chen et al. 1997) designed to measure the shadowing effects of branches and boles, and the foliage clumping occurring at all scales, must be used to properly characterize the spatial and successional changes in leaf area. Without these additional data, L_e results from either of these two techniques can be somewhat misleading, particularly in ecological applications that demand accurate estimates of leaf area.

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