Developmental Trends of Canopy Structure in Coastal Forests of British Columbia

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Forest structure changes substantially as stands develop over successional time. These structural changes are expressed in various characteristics of living trees, dead trees (coarse woody debris), and spatial and vertical heterogeneity (e.g. Spies et al. 1988, Hansen et al. 1991). While some broadly consistent developmental patterns have emerged, there is substantial variability among stands due to differences in disturbance history, site conditions, and chance factors influencing early successional species mix (e.g. Huff 1995, Lertzman et al. 1996). Because of methodological challenges and great spatial variability, canopy structure is one of the least well understood aspects of these developmental trends. Structural characteristics of forest canopies have manifold effects on ecosystem composition and function, including their role as habitat and their influence on the microclimate and the distribution of resources on the forest floor (e.g. Schowalter et al. 1981, Canham et al. 1990, Canham et al. 1994). In this study we investigate changes in canopy structure over successional time in chronosequences of coastal temperate rainforest on the east and west coasts of Vancouver Island.

All stands in both groups of chronosequences we studied are in the Coastal Western Hemlock (CWH) zone of British Columbia's biogeoclimatic classification system (Pojar et al. 1987). The four chronosequences on the east side of Vancouver Island are in very dry variants of the CWH (CWHxm) and are dominated by Douglas-fir (*Pseudotsuga menziesii*). The four on the west side of the island are in very wet variants of the CWH (CWHvm) and are dominated by western hemlock (*Tsuga heterophylla*) and western redcedar (*Thuja plicata*).

For each chronosequence, we examined stands of three seral stages: immature (32-43 years old), mature (66-99 years old), and old (>200 years old). We used hemispheric canopy photography and the LAI-2000 Plant Canopy Analyzer (PCA) to estimate canopy openness and effective Leaf Area Index or L_e (Chen and Black 1991, Welles and Norman 1991, ter Steege 1993, Frazer et al. 1997). Our analyses were based on 168 canopy photographs and 1008 LAI-2000 measurements from 24 plots (one plot in each of three seral stages in each of the four chronosequences on each side of Vancouver Island). The Leaf Area Index is defined as one half the leaf area per unit ground surface area, and L_e is an estimate of leaf area based on optical methods, such as those we used, rather than direct, physical measurements. L_e often varies somewhat from true Leaf Area Index; optical methods generally underestimate leaf area in conifer stands because of the clumped distribution of needles.

Analyses based on the hemispheric canopy photographs and the LAI-2000 identified similar overall developmental and regional trends in canopy openness and stand L_e despite significant quantitative differences in their estimates. As forests age from immature to old stands, canopy openness increases and stand L_e declines. The old stands are not only more open, but are more heterogeneous in their openness and their distribution of leaf area than corresponding immature stnds. However, the pattern of change in time for these two attributes differed: while leaf area declined fairly consistently over the three seral stages, canopy openness increased more in the transition from mature to old stands than from immature to mature stands. The most significant changes in canopy openness did not occur until after the first 150 years of growth. This is consistent with models of the stand dynamics leading to the development of old-growth stands (see review by Wells et al.

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in press). In these models, the mature/old-growth transition is characterized by mortality of canopy dominants leading to a vertical reorganization of stand leaf area as understory development is reinitiated in the resulting canopy gaps. This pattern of an extended period of development prior to canopy openness attaining old-growth-like character is corroborated by other analyses of developmental processes in Vancouver Island forests which show very long-term developmental trajectories in the transition from mature to old-growth forests (Wells 1996).

While there was substantial variation among the chronosequences on each side of Vancouver Island, some broad patterns distinguished the east- and west-side forests. In general, the forests on the east side are more open, more heterogeneous, and have a lower stand L_e than the forests of the west side of the island. We expect that much of this pattern can be explained by the differences in the geometry of branching structure and leaf display of the species involved. This geographic variation in forest structure leads to a broad overlap in the attributes of immature and mature stands when samples from both sides of the island are compared. The least open and least variable stands were young and mature stands on the west side of Vancouver Island. The most open stands, and those which displayed the greatest variability in canopy openness, were all old stands on the east side of Vancouver Island.

Processes of stand development substantially reorganize and redistribute biomass in ways that directly influence light environments and ecosystems within and below forest canopies. Our results are consistent with the idea that the overstories of immature stands can be described as dense "monolayers" supported by numerous, relatively short, and uniformly distributed stems, whereas older forests have tall upper canopy layers, are multi-layered, and have a much more clumped distribution of stems (e.g. Parker 1995). The structure of mature stands falls somewhere between immature and old growth, but whereas they are roughly halfway between young and old stands in leaf area, they are much more similar to young stands in canopy openness. Furthermore, heterogeneity also increases with age: old forests provide environments that are not merely distinct from younger seral stages, but are more variable over a range of spatial scales. Despite these clear qualitative patterns, however, the significant variation in canopy structure displayed over regional gradients suggests caution in generalizing quantitative results from one type of forest to another.

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