AN ABSTRACT OF THE THESIS OF

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Abstract approved:

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Characterization of canopy structure, the horizontal and vertical distribution of the tree crowns in a forest, is important for the management of forests in the Pacific Northwest. The canopy is an important habitat element for many wildlife species, canopy structure affects understory development, and influences various natural processes, such as the intensity of propagation of wildfire. Thus, improving our understanding of canopy structures and trends can aid forest management.

The overall goal of this study was to characterize vertical and horizontal canopy structure for multiple forest groups in western Oregon. The specific objectives were to: 1) characterize vertical and horizontal canopy structure for dominant forest types in western Oregon, 2) evaluate methods for measuring canopy cover and structure, 3) compare methods to predict forest canopy cover and vertical diversity using standard inventory measurements, and 4) predict bird species occurrence with different canopy diversity measures.

I evaluated patterns of vertical and horizontal canopy structure and understory cover along a successional gradient using 934 forested plots in western Oregon. Observed data were from the USDA Forest Service Forest Inventory and Analysis (FIA) program from the 1995-97 survey on private and non-federal public lands. Patterns were examined for wet-conifer, wet-hardwood, and dry-hardwood forests. The upper tree canopy layer contributed the most to total cover except in

the dry-hardwood stands, where the vertical distribution of tree cover was more evenly distributed. However, mean canopy cover rarely exceeded 85%, even in productive young conifer forests. Shade-tolerant species rarely made up more than 20% of canopy cover, even in the lower canopy layers and in stands > 100 yrs old. Contrary to expectations, percent cover of understory shrubs and herbs was not substantially lower in young closed-canopy stands than in other stands.

Ground-based measures of canopy cover on inventory plots were compared to predictions with regression models that regressed canopy cover on standard forest measurements, with estimates from aerial photography, and predictions with the forest vegetation simulator (FVS) program. Model predictions from inventory measurements were within 15% of measured cover for > 82% of the observations. Standard inventory estimates of cover using 1:40,000 scale aerial photos were poorly correlated with ground-measured cover, especially in wet-hardwood (r=0.58) and dry-hardwood (r=0.61) stands. FVS tended to underestimate cover by up to 50% in wet-conifer and wet-hardwood stands. The aerial photos and FVS equations used in this study are not recommended as surrogates for ground-based measurements of cover. However, the level of accuracies of the predictive models developed in this study may be adequate for some purposes.

I compared fourteen measures of vertical structural diversity and layering using the inventory plots. I then attempted to predict selected vertical diversity indices from standard forest variables. Simpson's diversity index on tree heights best differentiated among the range of vertical structure classes of the inventory plots. I developed predictive equations for Simpson's height diversity index (SDI), Foliage Height Diversity (FHD), and Canopy Height Diversity Index (CHDI), which used basal area, standard deviation of dbh, and stem frequency of size classes as the best variables. Predicted SDI values were within 0.15 units of calculated SDI for ≥ 79% of the observations, predicted CHDI values were within 1.5 units for ≥ 91% of the observations, except in the dry-hardwood stands (only 69%), and predicted FHD measures were within 0.2 units for ≥ 85% of the observations among forest groups.

The equations for FHD and SDI were applied to a wildlife-habitat database for western Oregon to determine if classification efficiency of existing models using CHDI to predict presence of bird species could be improved. The classification efficiency of bird-habitat association models improved for 33% and 66% of models for the Oregon Coast Range with the FHD and SDI variables, respectively. Models with FHD and SDI had improved classification efficiency for 18% of Cascade Range models. Although improvements in classification efficiency were less than six percentage points, future use of these diversity indices is warranted in place of CHDI when estimates of FHD and/or SDI are available and CHDI estimates are not.

Four ground-based techniques for estimating forest overstory cover — line-intercept, spherical densiometer, moosehorn, and hemispherical photography — and estimates generated using FVS were compared across a range of stand structure types. Canopy cover estimates for the four ground-based methods were not correlated with structure type. Differences among estimates of cover using FVS and the other methods did depend on the forest structure type. Differences among ground-based methods were primarily related to differences in angle of view. Although the line-intercept had the narrowest angle of view, the moosehorn provided the most conservative estimates of overstory cover. Regression equations were derived to allow conversion among canopy cover estimates developed with the four ground-based methods. The FVS calculated cover should not be used as a substitute for ground-based measures in these forest types given that it was consistently much lower (up to 70%) than estimates from the ground-based methods within each forest-structure type.

Overall, this study provides researchers and forest managers with new information and tools that can be applied across the forested landscape of Oregon. Models to predict canopy cover and diversity, and bird habitat can be substituted for field studies, assuming the accuracies of predictions are adequate for desired purposes. In field studies where ground-based cover measures are needed, the moosehorn is recommended as the most conservative estimator of cover. For more detailed canopy data, the line-intercept method is warranted. Modifying the line-intercept method to use fixed height intervals may be preferable to the use of three relative layers. This adjustment will allow for more direct comparisons of canopy cover of layers among stands.

Forest Canopy Structure in Western Oregon: Characterization, Methods for Estimation, Prediction, and Importance to Avian Species.

by
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FOREST CANOPY STRUCTURE IN WESTERN OREGON: CHARACTERIZATION, METHODS FOR ESTIMATION, PREDICTION, AND IMPORTANCE TO AVIAN SPECIES

INTRODUCTION

Characterization of canopy structure, the horizontal and vertical spatial distribution of the tree crowns in a forest, is important for the management of public and private forests in the Pacific Northwest (PNW). Amount of cover and the vertical structure of forest canopies are associated with wildlife (e.g. MacArthur and MacArthur 1961, Carey et al. 1991, Hayes et al. 1997, Garman and Cole 1999, North et al. 1999, Johnson and O'Neill 2001, Shaw et al. 2002), insects (Humphrey et al. 1999), disease and insect susceptibility (e.g. Mathiasen 1996, Winchester and Ring 1996), fire hazard (e.g. Latham et al. 1998), atmospheric interactions (e.g. Rose 1996), microclimate (e.g. Yang et al. 1999), and habitat structure (e.g. Maguire and Bennett 1996). Species of wildlife associated with canopy structure are included in the Northwest Forest Plan Survey and Manage Program (USDA, USDI 1994). Current regulations for some wildlife species require the maintenance of certain levels of canopy cover (e.g., Weiss et al. 1991). Canopy cover data are also used for predicting tree volume, estimating potential forage production, and for evaluating forest pest damage (O'Brien 1989). Percent canopy cover is often used as a criterion when classifying stand structure (e.g., Azuma and Hanson 2002, Wisdom et al. 2000). Estimates of canopy cover are used as a surrogate for shade in monitoring stream temperatures (OWEB 1999) and to measure penetration of light to the understory (e.g., Canham et al. 1990, Lieffers et al. 1999, Englund et al. 2000). Thus, quantifying amounts and trends in canopy structure can guide management for economic and ecological objectives in the PNW.

When manipulating stand structure to achieve management objectives, managers may attempt to mimic natural forests based on perceptions of structural development stages (Franklin et al. 2002). However, knowledge of succession is vital for grasping changes in both managed and natural environments (McCook 1994). Therefore, forest management require a comprehensive understanding of natural stand development (Franklin et al. 2002), including changes in canopy structure associated with development. This study provides new information on patterns of canopy structure associated with stand development among forest types in western Oregon.

Canopy attributes are often subject to multiple definitions, and it is important for researchers to clearly define the meaning of variables used in a study. In this study, forest canopy structure describes the horizontal and vertical spatial distribution of tree crowns in a forest stand. Vertical canopy structure refers to the division of canopy cover into three layers, which are relative to the height of individual stands. Stratification refers to a maximum of three canopy layers that are differentiated based on differing in their average heights by at least 5 m. I describe horizontal canopy structure using percent canopy cover as a single measure of the combined contributions from all vertical layers. For describing the measures of overstory tree crowns estimated using canopy measurement methods I follow Bunnel et al.'s (1985, p. 181) definition of crown completeness: "...the proportion of the sky obliterated by tree crowns within a defined angle (or determined with a described instrument) from a single point. It combines reduction in cover resulting from both the absence of tree crowns and from holes within tree crowns". Mean crown completeness (MCC) is the stand-level crown completeness. As the angle of MCC reduces to zero, only measuring the area directly overhead, MCC becomes equivalent to vertically-projected canopy cover.

There are a wide variety of ground-based techniques used to estimate overstory tree cover but there is no particular method mandated for quantification of cover in forest research and management activities. Yet there can be a large degree of variability among cover estimates depending on method used. The angle of measurement significantly impacts the accuracy of canopy cover or MCC estimates. Canopy gaps visually "close" as the angle of view is lowered from overhead toward the horizon. Thus devices with large viewing angles tend to over-measure canopy cover because they are less likely to count holes without canopy (Kirchoff and Schoen, 1987; Bunnell and Vales, 1990). Prior studies have suggested techniques with a narrow vertical projection have the least amount of bias (Bunnell and Vales, 1990). The line-intercept method, with theoretical zero width, has the most narrow vertical projection among methods. Previous studies have compared numerous canopy cover measurement methods (Bunnell and Vales 1990, Ganey and Block 1994, Comeau et al. 1998, Applegate 2000, Englund et al. 2000), but I am unaware of any previous studies that compare the line-intercept technique with other methods. Thus, further research is warranted to improve our understanding of the relationship among estimates of cover made by various techniques and the least-biased line-intercept method. In this study I compare the line-intercept method with five other methods for estimating canopy cover or MCC across a variety of forest structure types.

With the labor and cost involved in ground-based canopy sampling, alternative methods or surrogates for estimating canopy structure are often desirable. Aerial photography has been used to estimate canopy cover, although ground-based measurements with the line-intercept method are considered more accurate than ocular estimates of intercepts from photos (O'Brien 1989). Studies have evaluated the ability to estimate canopy cover from multiple stand- and tree-level biotic and abiotic variables, including basal area and stocking density (e.g. Lund et al. 1981, Moeur 1985, Bentley 1996, Cade 1997, Mitchell and Popovich 1997, Nelson et al. 1998, Crookston and Stage 1999). Alternate measures such as the standard deviation of dbh have been used to describe vertical forest structure (e.g. Buongiorno et al. 1994, Lahde et al. 1999, Edgar and Burk 2001, Neumann and Starlinger 2001).

Aside from prediction of cover using unpublished Forest Vegetation Simulator crown radii formulae, I am unaware of other equations that model canopy cover for the general forest groups of western Oregon. It is unclear how effective surrogate measures are at describing vertical diversity. New models for predicting canopy cover and vertical structural diversity using standard inventory measures may improve the ability of researchers to predict canopy attributes. Thus, further investigations of the use of surrogates to describe vertical canopy diversity and cover are warranted. In this study I examine the ability of standard forest measurements to predict canopy cover and vertical diversity among conifer and hardwood-dominated forests in western Oregon.

New predictive models may in turn improve classifications of wildlife habitat suitability, without the effort of ground-based cover measures. With cost often prohibiting or limiting field-based investigations of forest fauna (Thomas and Verner 1986), developing relationships to predict changes in abundance and fitness of wildlife over time, in response to various management alternatives, can reduce time spent in the field. Garman and Cole (1999) formulated logistic models to predict occupancy of habitat by bird species. It is of interest to see whether new measures of vertical canopy structure can improve upon existing bird habitat association models. In this study I will compare new bird habitat association models with existing models for canopy-associated bird species in the Oregon Coast and Cascade Ranges.

The inventory of western Oregon forests conducted by the USDA Forest Service Forest Inventory and Analysis (FIA) program from 1995-97 on private and non-federal public forested lands (Azuma et al. 2002) is of significant value because it provides a new, detailed look at canopy cover and structure across the landscape, and is expandable to similar stands in western Oregon. Line-intercept canopy data collected during the FIA inventory will be used to achieve four of the objectives of this study. The final objective will be achieved through a primarily field-based comparison of alternate methods for estimating cover.

The five main objectives of this study are:

1) Quantify the relationships of vertical canopy layering, percent canopy cover in three vertical cover layers, and total horizontal canopy coverage with broad descriptors of seral stage, forest type, land ownership, and thinning history;

2) Determine whether standard forest inventory measurements can be used to predict total percent canopy cover;

3) Compare the sensitivity of vertical diversity and stratification measures among gradients of vertical cover, structure, and stand development, and assess whether diversity measures can be predicted from standard forest mensuration variables;

4) Compare existing habitat models for bird species associated with the vertical forest structure, with new models using alternative vertical descriptors; and

5) Compare canopy cover estimates of the line-intercept method canopy estimates from four other techniques commonly used: a) hemispherical photography, b) the moosehorn, c) convex spherical densiometer, and d) cover generated with Forest Vegetation Simulator equations.

CHARACTERIZATION OF FOREST CANOPY STRUCTURE IN WESTERN OREGON

Abstract

Understanding trends in forest canopy structure can guide management for economic and ecological objectives in the Pacific Northwest. In this study, I evaluated patterns of vertical and horizontal canopy structure and understory cover along a successional gradient for western Oregon, including for three dominant forest types in western Oregon – wet-conifer, wet-hardwood, and dry-hardwood. I also examined the influences of ownership and management history on canopy structure patterns. Study data were from the USDA Forest Service western Oregon Forest Inventory and Analysis (FIA) program collected between 1995 and 1997 for private and non-federal public lands. Line-intercept measures of canopy cover were recorded on five sub-plots in each of 934 systematically located stands. Intercepts were measured for three vertical canopy layers, assigned relative to conditions within a stand. The upper tree canopy layer contributed the most to total cover except in the dry-hardwood stands, where the vertical distribution of tree cover was more evenly distributed. However, mean canopy cover rarely exceeded 85%, even in productive young conifer forests. Shade-tolerant species rarely made up more than 20% of canopy cover by age class, even in the lower canopy layers and in stands >100 yrs old. Contrary to expectations, diversity and cover of understory shrubs and herbs was not substantially lower in young closed-canopy stands than in other stands. Disturbance by thinning did not dramatically alter canopy structure. Canopy cover was higher for publicly-owned lands compared with the private landowners. The results provide forest managers and ecologists with information about canopy structure and its relationship with seral stage that can be applied across the forested landscape.

Introduction

Characterization of canopy structure is important in the management of public and private forests in the Pacific Northwest (PNW). Amount of cover and the vertical structure of forest canopies influence wildlife (MacArthur and MacArthur 1961; Thomas and Verner 1986; Hayes et al. 1997; North et al. 1999; Johnson and O'Neill 2001), disease and insect susceptibility (Mathiasen 1996; Winchester and Ring 1996), fire hazard (Latham et al. 1998), atmospheric interactions (Rose 1996), microclimate (Yang et al. 1999), and habitat structure (Maguire and Bennett 1996). Thus, management options in the PNW are impacted to varying degrees by concerns for the protection of native wildlife species, the reduction of fire hazard, control of insect susceptibility, as well as other issues.

It is vital to integrate understanding of canopy structure with knowledge of stand dynamics. When manipulating stand structure to achieve management objectives, managers may attempt to mimic natural forests based on perceptions of structural development stages (Franklin et al. 2002). However, a comprehensive understanding of succession is vital for grasping changes in both managed and natural environments (McCook 1994). Managing forests based on simple characterizations may not adequately replicate the stand structure of natural forests, including canopy structure. The challenge for forest managers and biologists is to describe canopy structure as a meaningful forest indicator that is also repeatable, efficient, and reliable across a wide-range of field-tested conditions. Characterizing canopy structure attributes across a stand development gradient can aid in achieving this.

Without standardized terminology, describing canopy structure can be challenging, as it is subject to multiple interpretations (Kirchoff and Schoen 1987). Confusion exists surrounding use of canopy cover, crown closure, and crown completeness. Canopy cover and closure are used interchangeably, even though they are distinct canopy features (Jennings et al. 1999). Parker and Brown (2000) compared definitions of canopy stratification in multiple studies and found ten separate definitions for canopy stratification among them. These definitions included using it as a synonym for height, as a descriptor of vertical distribution of foliage, and as an index of vertical structure. Thus, attempts to standardize definitions used to quantify canopy structure have been attempted (Moffett 2000).

In this study, forest canopy structure describes the horizontal and vertical spatial distribution of tree crowns in a forest stand. Vertical canopy structure refers to the division of canopy cover into height layers. I describe horizontal canopy structure using percent canopy cover as a single measure of the contributions from all vertical layers. Additional attributes used to describe canopy structure include the number of vertical canopy layers, heights of the vertical layers, and the percent and proportion of shade-tolerant cover for the vertical layers and total combined cover.

Forest canopy structure changes as forest stands develop (Oliver 1981; Van Pelt and North 1996; Bond and Franklin 2002; Franklin et al. 2002). Canopy structure is generally horizontally homogenous in young stands. For example, the canopy of young conifer forests may be a fairly uniform band of cone-shaped crowns. With time, the canopy may continue developing into a multi-layered array of polymorphous crown shapes. Eventually the stand may reach old-growth stage where increased canopy heterogeneity results from gap formation, with increased penetration of sunlight to the forest floor and freeing up of below-ground resources.

Multiple stand development models exist that describe forest succession patterns and processes (e.g. Oliver 1981; Carey and Curtis 1996; Spies and Franklin 1996; Franklin et al. 2002). The most commonly cited stand development model is Oliver's (1981) four-stage model. During the stand-initiation phase, seedlings become established on a disturbed site and begin developing crowns and roots. As the crowns expand horizontally and vertically, tree growth becomes limited by competition among tree crowns and tree roots. The stem-exclusion phase is characterized by very high levels of canopy cover and self-thinning, and a lack of understory vegetation associated with reduced light transmitted by the canopy. As trees die from competition and small-scale disturbances, gaps are formed in the canopy when canopy trees are unable to rapidly occupy holes through lateral branch development. During the stem reinitiation phase, increased light penetration through these gaps allows for growth of trees and shrubs in the understory. Eventually the old-growth stage is reached. This stage is often characterized by a multi-layered canopy, large-diameter live trees, a mix of dominant trees with shade-tolerant associates, large-diameter snags, large-diameter down wood, and canopy gaps (Franklin et al. 1986; Spies and Franklin 1991).

Franklin et al. (2002) proposed a newer stand development model for natural stands. This model highlights eight commonly encountered development stages and includes canopy attributes for these stages. In the disturbance and legacy creation stage, the starting point for stand development varies by the intensity of the disturbance that initiated the stand. Canopy cover is provided by remnant trees in partial-stand disturbances (e.g. wildfire) or may be totally absent (e.g. clearcut). In the cohort-establishment phase a new generation of trees is established. Stands with below "normal" stocking levels undergo gradual canopy closure, while stands with normal to high stocking undergo intense self-thinning in short time periods. In the canopy-closure phase overlap among tree crowns leads to reduced light levels in the understory. The rate of canopy closure is dependent on tree regeneration density and site productivity. Low productivity sites may never achieve canopy closure. The biomass accumulation/competitive exclusion stage is where growth in both tree diameter and height, natural pruning of lower tree branches, and crown-class differentiation occur. In the maturation phase the original cohort of trees attains maximum height and crown diameter. During this phase the understory reestablishes as the mortality of overstory stems allows increased light penetration and frees up water and nutrients in the soil. High light levels promote establishment of previously suppressed shade-tolerant tree species. In the vertical diversification stage continuity of the canopy from the ground to the taller trees is established. This vertical diversity results from the growth of shade-tolerant trees into the middle and upper canopy layers and the development of epicormic branches along exposed boles for species with this trait. The horizontal diversification stage is characterized by mortality of individual or small clusters of stems (gap formation, etc.), and low variability in the upper and lower canopy levels, but high variability at the mid-canopy level. The final stage is pioneer-cohort loss, where dominant shade-intolerant tree species in the overstory begin to die off and are replaced by a shade-tolerant overstory.

Various factors can influence the progression of forest canopy structure among the stages of these two development models. These factors include forest type, species composition, disturbance, and management practices of owners. It is important to further examine these factors to better understand how they might impact canopy structure development during succession. These factors are expanded upon in the following paragraphs.

The patterns and processes affecting forest development vary across forest types. In the coniferous forests of the Pacific Northwest succession progresses much more slowly, due to the longevity of some tree species, than in forest types with more rapid seral replacement of species (Ishii et al. 2000). Therefore, it is important to compare canopy structure along forest succession gradients separately for multiple forest types, including both conifer- and hardwood-dominated forests.

It is generally held that understory community development is related to changes in the overstory (Henderson 1981, Oliver 1981, Zamora 1981, Stewart 1988, Franklin et al. 2002, Naesset and Okland 2002). According to the "tolerance" model of succession (Connell and Slatyer 1977), shade-tolerant species are generally present in all stages of succession, but invade the understory and increase in abundance across the gradient of development stages. It is crucial to understand how variance of foliage and its patterns of distribution in the forest canopy impact understory conditions (Van Pelt and Franklin 2000). Therefore, it is important to examine patterns in overstory and understory cover across a successional gradient, including the quantities and proportions of shade-tolerant cover vertically distributed in the canopy. If the expected reduction in understory cover does not occur during canopy closure, this may reflect shifts in species composition rather than total understory die-back.

When managing forests for both ecological and economic goals, silviculturists require a comprehensive understanding of natural stand development (Franklin et al. 2002), including changes in canopy structure associated with development. In western Oregon, clearcut logging, monoculture restocking, and short stand rotation lengths have greatly reduced the structural variability of forests (Hansen et al. 1991; Garman et al. 1992; Smith et al. 1996). With increasing awareness of the value of structural heterogeneity for multiple wildlife species, there has been a recent push to implement silvicultural techniques that retain heterogeneity in stand structure throughout the rotation interval (Berg et al. 1996). Retention of canopy trees is meant to better represent patterns of disturbance and structural complexity of natural forests, with the objective of maintaining canopy complexity over the entire rotation cycle (Hansen et al. 1995). The vertical distribution of foliage can be altered by multiple silvicultural treatments, including pruning, fertilization, and thinning (Berg et al. 1996; Maguire and Bennett 1996), although studies also have found no effects of fertilizer and thinning on vertical foliage distribution (Gillespie 1994). Thus, it is of value to compare canopy structure attributes between undisturbed stands and stands that have been managed with varying levels of harvest.

Different landowner groups often have different management objectives for their lands (Campbell et al. 2002). Private-industrial forest owners are mainly focused on maximizing timber production and profit, while private non-industrial forest owners receive both investment and aesthetic value from their land. Public landowners tend to value a combination of timber, recreation, watershed protection, and aesthetic values. With the differing management objectives of the various owners, it is of interest to describe how canopy attributes differ among these general landowner groups.

Ecology seeks to describe similarities and differences in patterns and processes associated with succession (McCook 1994). I am unaware of any previous study that examines canopy structure attributes along a successional gradient across a large landscape. Also, much of the current research in the PNW is focused on productive conifer forests, with less emphasis on hardwood forests. This study will provide forest managers with an improved understanding of how changes in canopy structure with stand development compare among forest types in western Oregon.

I hypothesize that as forest stands develop, canopy structure follows an ordered pattern of increasing vertical-height layering and horizontal canopy coverage. The contributions of the multiple vertical canopy layers to this ordered pattern of canopy development may be correlated with forest type, management intensity, and ownership group. I expect the lower cover layers will have higher proportions of shade-tolerant canopy, compared with the upper layers, due to light-limited conditions below the upper canopy layer. I also anticipate shade-tolerant levels in all layers will increase as stands develop, as shade-tolerant species replace earlier successional less-shade-tolerant species, including *Pseudotsuga menziesii* (Mirb.) Franco (Douglas-fir). I expect a decrease in understory richness and diversity associated with canopy closure.

This study sought to enhance understanding of canopy structure development using forest inventory data of western Oregon. The main objective of this paper was to quantify the relationships of vertical canopy layering, percent canopy cover in three vertical cover layers, and total horizontal canopy coverage with broad descriptors of seral stage, forest type, land ownership, and thinning history.

Methods

Study Area and Population of Interest

This study used the inventory of western Oregon forests conducted by the USDA Forest Service Forest Inventory and Analysis (FIA) program from 1995-97 (Azuma et al. 2002). Study sites were a permanent grid of plots located throughout western Oregon (Fig. 2.1). Western Oregon was defined as the area west of the crest of the Cascade Mountain Range, delimited by county boundary lines. The study sites included all private and public forested lands, excluding Bureau of Land Management (BLM) and USDA Forest Service National Forests.

The study sites encompassed five physiographic provinces: The Oregon Coast Range, The Willamette Valley, Oregon Western Cascades, Klamath Mountains, and High Cascades (Franklin and Dyrness 1973). The forest zones included in the FIA inventory included the *Picea sitchensis*, *Tsuga heterophylla*, *Abies amabilis*, *Tsuga mertensiana*, *Quercus* woodland, Interior Valley, Mixed-Evergreen, Mixed-Conifer, *Abies concolor*, and *Abies magnifica shastensis* (Franklin and Dyrness, 1973).

Sample Design

The FIA inventory design was based on a double sample for stratification (Cochran 1977). An exception was that permanently established primary photo-interpreted plots and secondary field plots were used for the design. In the first phase of sampling, conducted in 1994, 1:40000 scale aerial photos at photo-points systematically distributed on a 1.36-km grid were used to estimate land use type, successional stage, and canopy cover. The second phase completed from 1995-97 involved a ground plot sampling of approximately every 16th photo-point, with a grid density of 5.4-km. The systematic-grid design of this inventory allows for statistical inferences to the population from which the grid points were sampled. Information compiled and distributed from the FIA inventory is comprehensive, has minimal bias, is scientifically sound, and has known precision (Azuma and Hanson 2002). Therefore, results of analyses of the forested plots are representative of the entire population of non-federal forest lands in western Oregon.

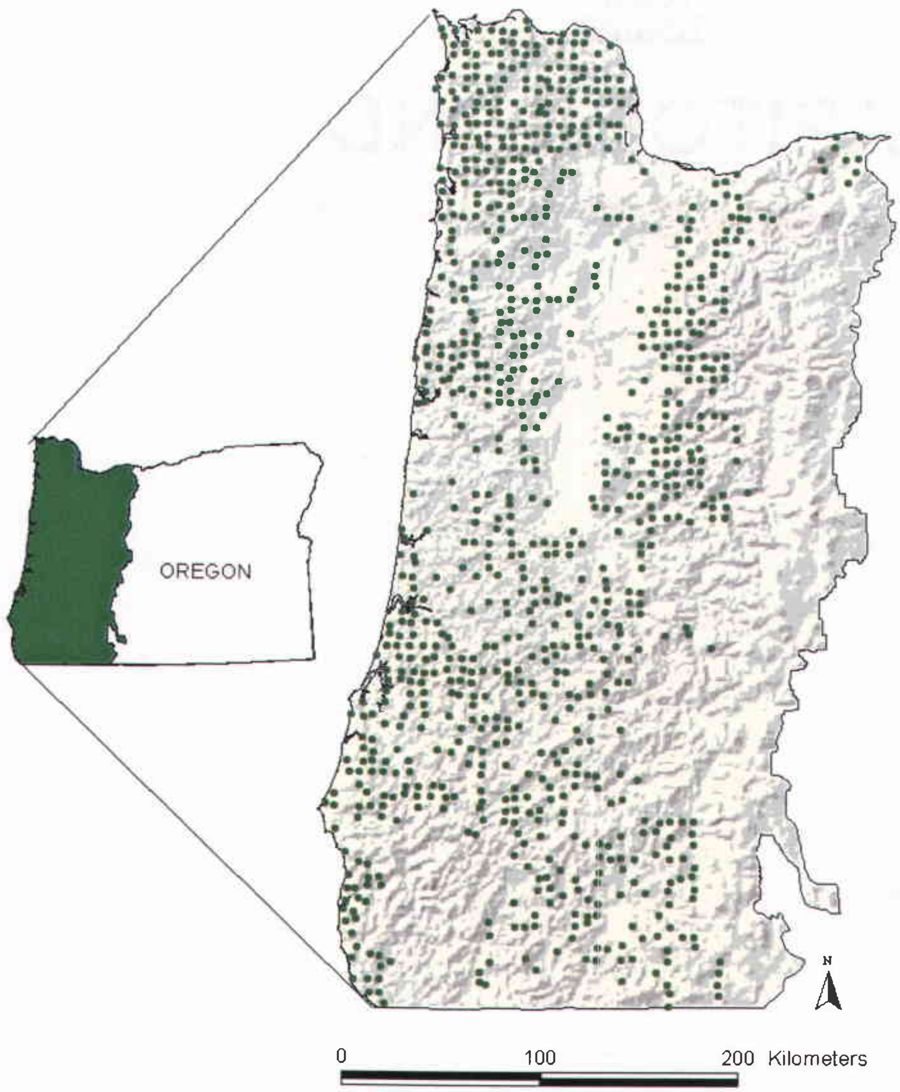

Fig. 2.1. Locations of the 934 forested FIA 1995-97 inventory plots analyzed in this study.

All 1127 forested plots consisted of a systematically-arranged cluster of 5 0.09-ha subplots encompassed in a 2.5-ha area, regardless of stand boundaries or forest types (Fig. 2.2). Subplots were delineated into multiple site-attribute classes to identify subplots that contained more than one forest type, stand-size class, management intensity category, or overlapped with non-forest land.

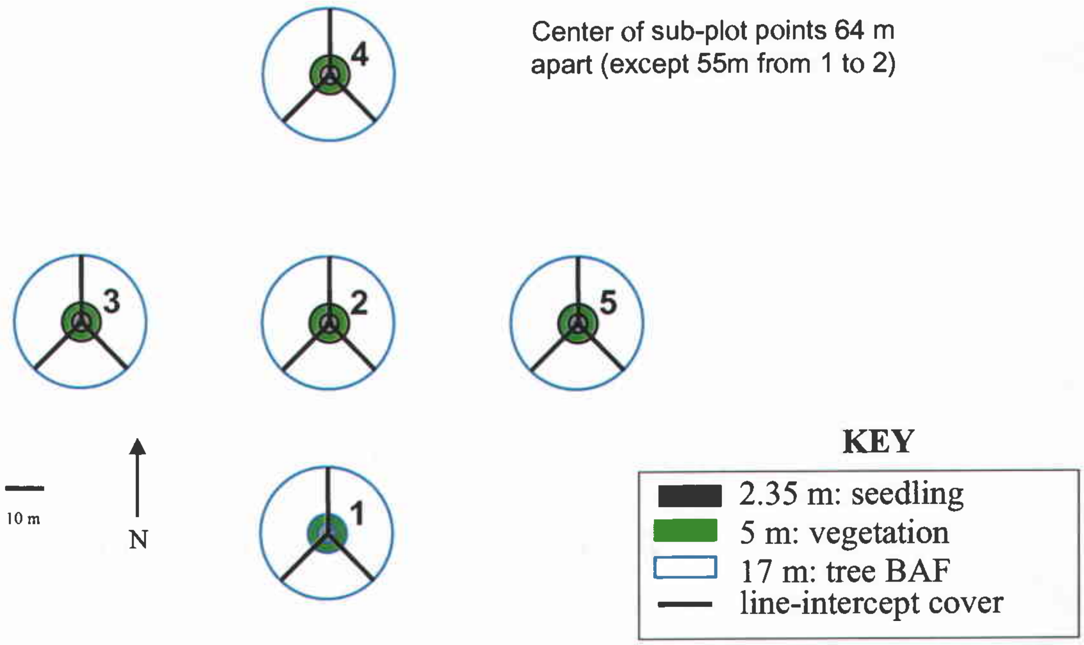

Fig. 2.2. Design of the 1995-97 FIA inventory ground plot lay-out for western Oregon.

I only used plot information for the single forested site-attribute class that comprised a minimum area of 0.27 ha (three subplots). A high degree of variability in canopy cover within a site-attribute class was expected. I excluded cover data from the other site-attribute classes in a plot because I felt areas < 0.27 ha could not adequately capture this variability. Out of the 1127 plots, there were 934 plots that met this criterion. Therefore, for each of these 934 plots the size of the experimental unit was the area of the plot contained in the single largest site-attribute class. I will use the term stand throughout this paper to refer to the experimental unit.

Data Collection

For each stand, multiple measurements were obtained. Composition, cover, and height of all shrubs, and forbs and grasses with $\geq$ 3% cover were measured on 5-m fixed-radius plots around each subplot center (see Fig.2.2). Trees were measured to a fixed-distance of 17 m from subplot centers in fixed-radius and variable-radius plots, using a 7-m^2/ha basal area factor (BAF) prism. Age, dbh, and height of all trees > 1.4 m tall were measured.

FIA field crews classified each stand into one of seven stand-condition classes (Table 2.1). Stand condition is defined as "the size, density, and species composition of a plant community following disturbance and at various time intervals after disturbance" (Brown 1985). Several of the FIA stand condition class definitions included canopy cover criteria (see Table 2.1). Open sapling-poletimber (OSP) and open sawtimber (OSAW) were defined as 'open' if percent cover was <60%. Closed sapling, poletimber, sawtimber (CSP) were classified as 'closed' if mean percent cover was >60%. These stand conditions were classified by the field surveyors based on visual estimates.

For each site-attribute class, ground-based canopy cover estimates were collected. Trees were assigned to one of three canopy layers, with discrete layers differing by a minimum of 5 meters in mean height. However, actual heights varied between stands, as canopy layers were relative to conditions within a stand. The line-intercept method was used to calculate percent canopy cover in each layer

Table 2.1. Description of stand-condition classes defined in the 1995-97 western Oregon FIA field manual (Azuma and Hanson 2002) and the sample sizes for stands used in this study.

Code	Stand condition	Description	Sample size by forest type: all forest types	wet conifer	wet hardwood	dry hardwood
GR	grass-forb	Shrubs <40% cover and < 1.5 m tall; plot can range from mainly devoid of vegetation to herbaceous species dominance; tree regeneration generally < 1.5 m tall and 40% cover.	52	38	6	2
SHR	shrub	Shrubs >40% cover and < 1.5 m tall; trees < 40% crown canopy and < 2.5 cm d.b.h., plot is "open sapling" or "closed sapling".	56	43	6	4
OSP	open sapling-poletimber	Average stand diameter 2.5-22.9 cm d.b.h. and tree crown canopy < 60%.	108	65	15	20
CSP	closed sapling, pole, sawtimber	Average stand diameter 2.5-53.3 cm d.b.h. and crown cover is ≥ 60%.	569	401	87	67
OSAW	open sawtimber	Average stand diameter 23-53.3 cm d.b.h. and cover is < 60%.	85	44	16	8
LSAW	large sawtimber	Average stand diameter >53.3 cm d.b.h.; cover may be < 100%; decay and decadence required for old-growth is generally lacking, successional trees needed for old-growth may be lacking, and dead and down material required by old-growth is lacking.	61	51	7	1
OG	old-growth	Average stand diameter >53.3 cm d.b.h. Stand over 200 years old with ≥ 2 layers, decay in living trees, snags, and down woody material. Some of overstory may be composed of long-lived successional species.	3	3	0	0
Total			934	645	137	102

(O'Brien 1989). Canopy layers were classified as upper, middle, and lower based on relative stature. For every tree species within a canopy layer, crown boundaries were vertically projected onto transects using a clinometer. The distance along a transect line that the crown intercepted was recorded. Canopy cover was sampled on three 17-m long horizontal transects originating at subplot center and radiating out at 0, 135, and 225 degrees. The proportion of transects that were intercepted by the crowns was the ground-estimated canopy cover.

Calculated FIA Variables

Multiple canopy cover values were calculated from the line-intercept data. Canopy transects that crossed condition classes were excluded because of errors assigning condition classes. Cover for individual tree species was calculated for each of the vertical layers. Then cover for the three layers were combined into a total cover by species. Combining of layers did not double-count cover from multiple layers that intercepted the same horizontal areas along each transect. Thus cover could not exceed 100%. Tree species were grouped as either shade-tolerant or shade-intolerant (Table 2.2), and percent canopy cover also was separated into shade-tolerant and shade-intolerant cover. Measures were calculated for both individual layers and total combined cover. All species were combined to calculate cover by layer and total cover, again accounting for overlap within and among layers.

Stand age, stand-size class, and forest type were calculated for each stand (Azuma and Hanson 2002). Stands were grouped into 10-year age classes up to age 200, lumped into a 100-year age class for ages 200-300, and stands >300 years were all combined into a single age class (age 400). Stand age calculations distinguished between evenaged and unevenaged stands. Stand size was grouped into five classes based on the average diameter of live trees (Table 2.3). The stand-size class was assigned by calculating relative stocking proportions of "mainstand" (i.e., not residual or 'understory') trees within each of the tree size classes and selecting the

Table 2.2. List of shade-tolerant tree species included in the 1995-97 FIA inventory plots found in stands used in this study (Vimmerstedt 1965; Minore 1979).

Species	Scientific name
Pacific silver fir	*Abies amabilis* (Doug) ex. Loud
White fir	*Abies concolor* (Gord. & Glend.) Lindl. ex Hildebr.
Grand fir	*Abies grandis* (Dougl.) Lindl.
Pacific dogwood	*Cornus nuttalii* Audubon
Western redcedar	*Thuja plicata* Donn ex D. Don
Pacific yew	*Taxus brevifolia* Nutt.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Holly spp.	*Ilex* spp.
Mountain hemlock	*Tsuga mertensiana* (Bong.) Carriere
Sitka spruce	*Picea sitchensis* (Bongard) Carriere

Table 2.3. Description of stand-size classes defined in the 1995-97 western Oregon FIA field manual (Azuma and Hanson 2002) and the sample sizes for stands used in this study.

			Sample size by forest type			
Code	Stand-size class	Description	all forest types	wet conifer	wet hardwood	dry hardwood
Nstock	nonstocked	1) Average diameter or live trees is <12.5 cm d.b.h. and <100 free-to-grow seedlings and saplings per average acre are broadly distributed. Or: 2) Average diameter of live trees is >12.5 cm d.b.h. and canopy cover is <10%. Or: 3) Recently clear-cut and has not been replanted.	17	0	0	0
Seed	seedlings and saplings	Average diameter of live trees is < 12.5 cm d.b.h. and ≥ 100 free-to-grow- seedlings and saplings per average acre are broadly distributed.	271	188	31	40
Pole	poletimber	Average diameter of live trees is 12.5 – 22.4 cm d.b.h. and tree canopy cover is ≥ 10%.	143	70	33	37
Small	small sawtimber	Average diameter of live trees is 22.5 – 52.4 cm d.b.h. and tree canopy cover is ≥ 10%.	457	348	68	25
Large	large sawtimber	Average diameter of live trees is ≥ 52.5 cm d.b.h. and tree canopy cover is ≥ 10%.	46	39	5	0
Total			934	645	137	102

size class with the highest level of stocking in each stand. Forest type was calculated in a two-step process. The first criteria determined whether hardwood or softwood trees dominated the stand. Then the forest type was assigned based on the stocking density of the predominant species of "mainstand" trees within the hardwood or softwood group.

Stocking density, basal area, mean annual increment, density, and quadratic mean diameter were also calculated from the tree data collected in the FIA inventory.

Analysis of Data

Mean annual precipitation was estimated with the PRISM climate model (Daly et al. 1994). The mean annual precipitation by stand age was calculated in each of four general forest groups that will be described further below (Fig. 2.3). I compared structural attributes of horizontal and vertical canopies along gradients of stand-age, stand-condition, and stand-size classes. Although age is not a predictor of successional stage, it provides a proxy for stand development pattern (Spies and Cohen 1992). Stand-condition and stand-size classes also are good surrogate measures for forest development or successional stage. Evenaged and unevenaged stands were combined for analysis, as only 11% of the samples were unevenaged (Table 2.4). The FIA stand-size class distribution is fairly coarse (see Table 2.3). I felt stand-size classes would not be sufficiently discrete to discriminate patterns in the smaller maximum dbh hardwood forest types. Therefore, canopy patterns by stand-size class were only examined for the wet-conifer forests, as they tend to have larger potential dbh. I excluded stands with <10% stocking of trees when looking at stand age and stand-size class gradients.

I evaluated canopy structure patterns for all forest types combined and by three general forest groups: wet conifer, wet hardwood, and dry hardwood (Table 2.5; Fig. 2.4). The fourth possible forest group, dry conifer, had limited samples and was not analyzed. The forest groups were first clustered based on hardwood

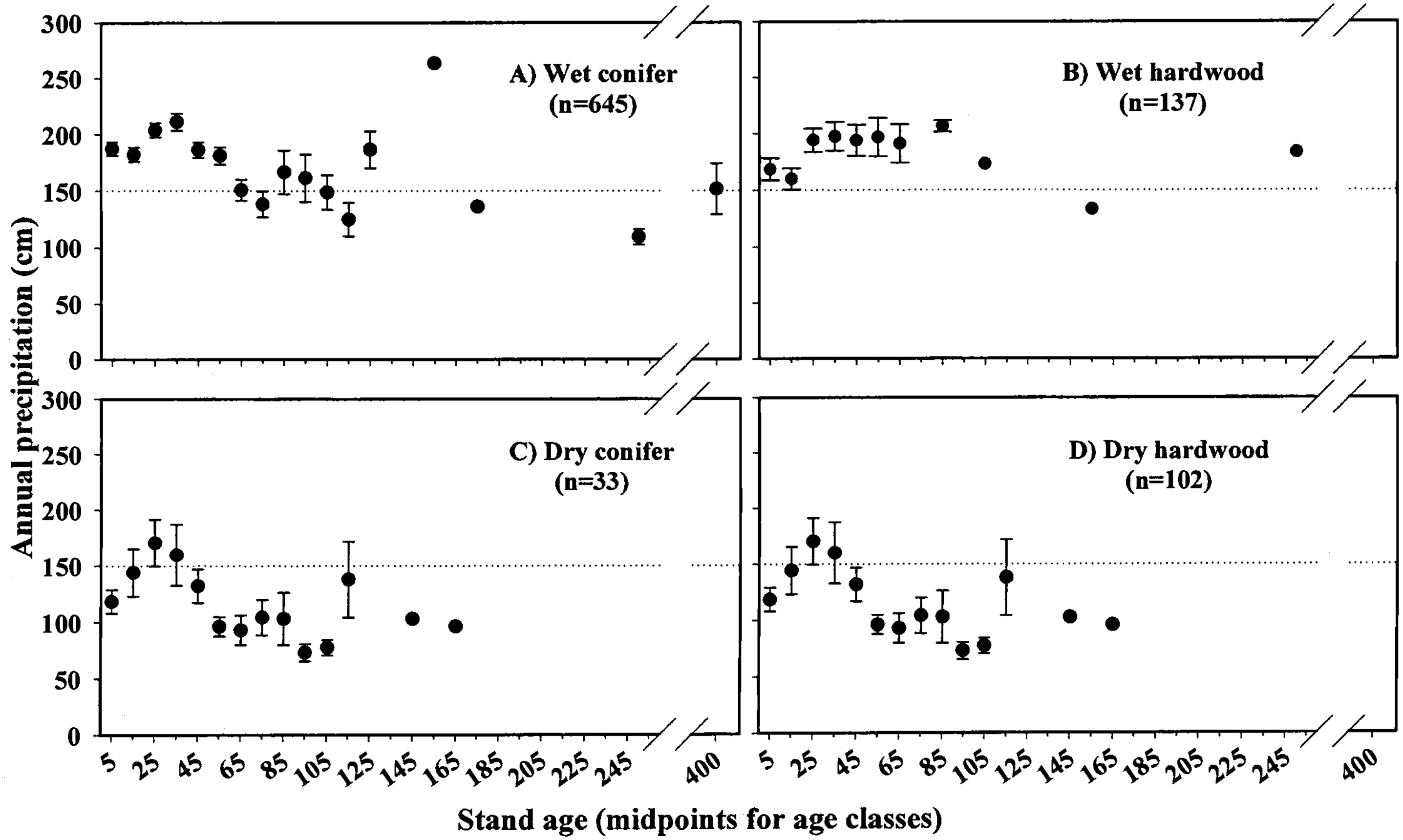

Fig. 2.3. Mean annual precipitation (± 1 SE) estimated using the PRISM model (Daly et al. 1994) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4). Dashed line at 150 cm represents the division between wet and dry mean precipitation levels.

Table 2.4. Sample sizes for each forest group and stand-age class combination in the 1995-97 FIA inventory stands used in this study.

	Sample size by forest type			
Stand-age class	all forest types	wet conifer	wet hardwood	dry hardwood
5	92	67	13	12
15	122	90	14	12
25	161	118	23	14
35	131	89	31	8
45	154	107	27	16
55	96	66	16	11
65	54	36	8	7
75	29	22	0	5
85	16	9	2	3
95	16	9	0	4
105	19	13	1	4
115	13	9	0	4
125	2	2	0	0
145	1	0	0	1
155	2	1	1	0
165	1	0	0	1
175	1	1	0	0
250	5	4	1	0
400[1]	2	2	0	0
Total	917	645	137	102

[1]All stands aged > 300 years were combined in the 400-year stand-age class.

Table 2.5. The four general forest groups included in the 1995-97 FIA inventory of western Oregon that met the criteria for inclusion in this study. Stands were grouped by hardwood and conifer type, and mean precipitation levels.

General forest group	n	Age range	Dominant tree species in the stand[a]
Wet conifer	645	5-400[1]	*Pseudotsuga menziesii* (n=558), *Tsuga heterophylla* (n=57), *Picea sitchensis* (n=15), *Thuja plicata* (n=7), *Abies procera* Rehd. (n=4), *Abies amabilis* (n=2), *Chamaecyparis lawsoniana* (A. Murr.) Parl. (n=2)
Dry conifer	33	15-105	*Abies grandis* (n=9), *Calocedrus decurrens* (Torrey) Florin (n=9), *Pinus contorta* var. murrayana (Grev. & Balf.) Engelm. (n=6), *Abies concolor* (n=6), *Pinus ponderosa* var. ponderosa Dougl. (n=3)
Wet hardwood	137	5-250[1]	*Alnus rubra* (n=99), *Acer macrophyllum* Pursh. (n=25), *Populus balsamifera* L. ssp. trichocarpa (Torr. & Gray) Brayshaw (Salicaceae) (n=5), *Salix* spp. (n=3), *Umbellularia californica* (Hook. & Arn.) Nutt. (n=3), *Fraxinus latifolia* Benth. Ore a. (n=2)
Dry hardwood	102	5-165[1]	*Quercus garryana* (n=42), *Arbutus menziesii* (n=32), *Lithocarpus densiflora* (Hook. & Arn.) Rehd. (n=18), *Quercus kelloggii* Newb. (n=6), *Quercus chrysolepis* Liebm. (n=3), *Castanopsis chrysophylla* (Dougl.) DC. (n=1)

[a]The number in brackets is the number of plots in which the given species was dominant in the stand.

[1] Refer to Table 2.4 for number of stands associated with each stand-age class.

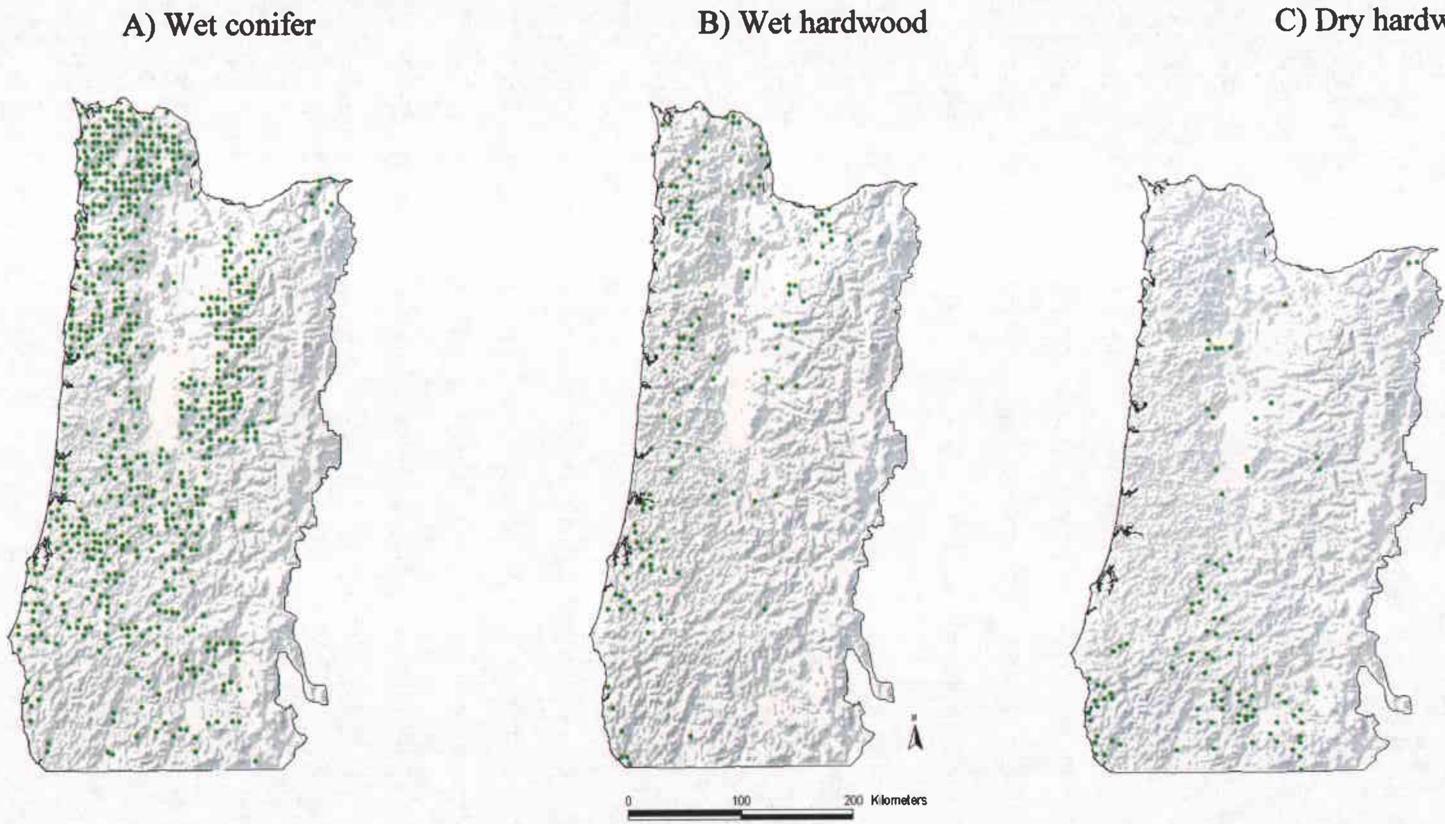

Fig. 2.4. 1995-97 FIA inventory plot locations for three general forest groups across western Oregon used in this study. General forest groups are described in Table 2.5.

or softwood dominance. They were further divided based on the moisture levels characteristic of sites occupied by the dominant tree species in each forest group. Douglas-fir was the predominant species in the wet-conifer group, *Alnus rubra* Bong. (red alder) was the dominant species in the majority of wet-hardwood stands, and *Quercus garryana* Dougl. ex Hook (Oregon white oak) and *Arbutus menziesii* Pursh (Pacific madrone) dominated most of the dry-hardwood stands. With 70% of the stands located in the wet-conifer group, canopy attribute patterns for all forest types combined were expected to parallel trends of the wet-conifer group. Therefore, beyond describing total canopy cover and canopy cover for the three vertical layers, canopy structure analyses were focused on the three general forest groups.

Comparison of management history was restricted to light and heavy thinning levels for Douglas-fir forests 15 – 45 years old (Table 2.6). The thinning levels were based on crew estimates of harvest activity in the previous ten years. This comparison was constrained by limited samples (see Table 2.6). Management history was expected to play the largest role for Douglas-fir forests as these comprise the highest proportion of private-industrial forest lands, and management is generally focused on younger forests to sustain maximum growth throughout the rotation interval. Canopy cover relationships with stand age and stand condition were evaluated for three ownership classes: public, private-industrial, and private-non-industrial (Table 2.7) in wet-conifer stands. I only examined ownership effects for wet-conifer forests because these are the forests most managed for timber production in western Oregon (Azuma et al. 2002). Comparable canopy data do not exist for federal lands. Federal forest land excluded from this study constitutes 52% of forested land in western Oregon. Therefore, this study's scope of public lands was limited.

I calculated the mean and standard errors of canopy structure attributes by stand-age, stand-condition and stand-size classes for the forest groups. Attributes included mean horizontal percent canopy cover for shade-tolerant, shade-intolerant, and all species combined, mean percent canopy cover in each of the three vertical

Table 2.6. Previous 10-year thinning history of Douglas-fir stands aged 15-45 in the 1995-97 FIA inventory stands used in this study.

Code	Management	n	Criteria for management
ND	No disturbance	254	No evidence of tree harvest or wildfire.
LT	Partial harvest – light	21	Remaining trees comprise $\geq$ 25% crown cover and <20% of trees live and 12.5 cm dbh were harvested. The residual stand usually consists of commercially desirable trees. Not a firewood or local use harvest.
HT	Partial harvest - heavy	20	Remaining trees comprise $\geq$ 25% crown cover and $\geq$ 20% of the live trees 12.5 cm dbh or larger were harvested. The residual stand usually consists of commercially desirable trees. Not a firewood or local use harvest.

Table 2.7. Ownership groups and their sample sizes included in the 1995-97 FIA inventory used in this study.

Code	Ownership	Definition	Sample size by forest type	
			all forest types	wet conifer
Public	Public	Federal, state, county, and municipal public lands (excludes National Forest and BLM lands).	122	86
Forind	Private-industrial	Private land owned by companies that grow wood for industrial purposes	527	414
Nonind	Private-non-industrial	Private lands not qualifying as industrial forest, includes miscellaneous private lands.	285	145

canopy layers, mean heights of the three vertical layers, and the mean number of vertical canopy layers. For stands without cover present in one of the three layers, canopy height measures for that layer were omitted when calculating layer averages. For layers with cover present, the proportions of shade-tolerant and intolerant canopy cover were also derived. Mean percent shrub cover and forb cover were also calculated to compare understory and overstory vegetation cover along the development gradient. Species richness and Simpson's diversity index (Simpson 1949), to examine relative dominance of shrub species, were also calculated for shrub species. For shrub and herb species present in ≥ 20% and ≥ 10% of the stands respectively, mean species cover by stand age was calculated. I plotted individual shrub species cover as a function of the total overstory cover. Values of overstory and understory canopy attributes were plotted against stand-age, stand-condition, and stand-size classes to examine the trends in canopy cover among stand development surrogates.

Results

Stand Age

Cover by vertical layer

In general, total canopy cover and cover in the three vertical layers exhibited expected development trends for the multiple forest groups (Fig. 2.5). For all forest types total mean percent canopy cover increased with stand age up to age 35 and subsequently remained high (60-96%). Mean percent cover of the upper layer contributed the most to total cover and thus closely mirrored trends in total canopy cover, except in the stands ≥ 250 years. Mean percent cover of the middle layer increased with age. Mean percent cover of the lower layer was nominal (< 20%) except in the stands ≥ 250 years. Canopy cover values and trends for wet conifer and wet hardwood forests paralleled those for all forest types combined. The

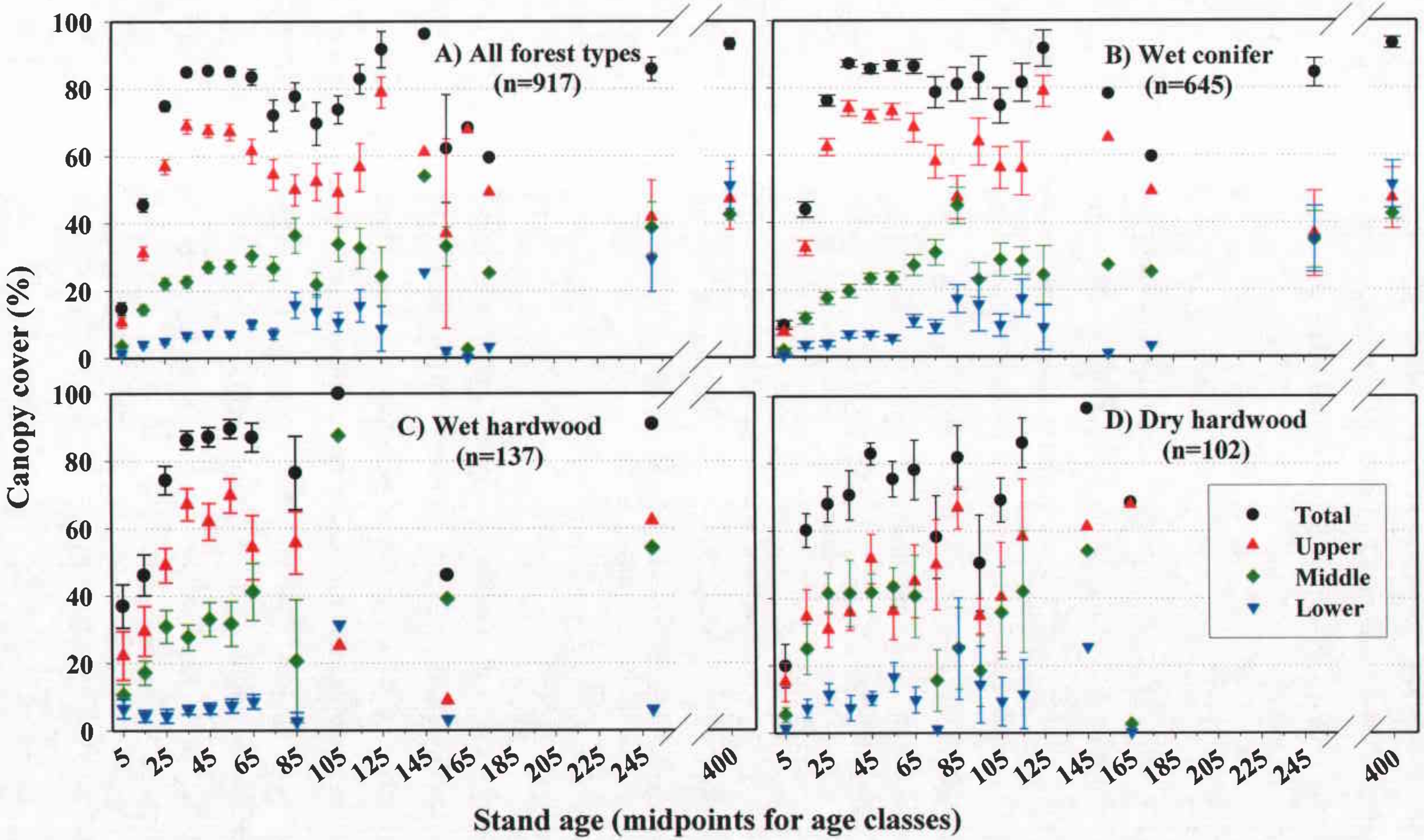

Fig. 2.5. Mean percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

dry-hardwood forest type deviated from the other forest groups in two ways. First, total canopy cover was lower than in the other forest groups. Second, both the upper and middle cover layers contributed similar cover amounts across stand ages.

Height by vertical layer

In general, heights of canopy layers for the forest groups increased with stand age, indicating differentiation of canopy layer structure (Fig. 2.6). The upper and middle cover layer heights for wet-conifer forests increased with stand age to 55 years, and then remained fairly constant. The wet-hardwood forest group followed a similar pattern, except that the height of the upper layer was similar for ages 5-25, and heights of the upper and middle layers only increased to age 35. The lower layer heights for both wet-conifer and wet-hardwood forests remained consistently short among stand ages. The dry-hardwood group differed in that mean heights of its three canopy layers increased minimally across the 165-yr chronosequence. Also, mean heights of the dry-hardwood upper and middle canopy layers were shorter than for the other two forest groups.

Number of vertical layers

Layering generally increased with stand age in all forest groups (Fig. 2.7). For the wet-conifer stands, the mean number of layers developed from one in 5-year stands to greater than two layers from age 15 to 55 and then leveled off at three layers. Layer development in the wet-hardwood stands paralleled trends in the wet-conifer stands, except that even the 5-15 year stands had greater than two layers of cover. Vertical layering in the dry-hardwood stands did not consistently increase with stand age, but fluctuated between two and three layers for stands older than 5 years.

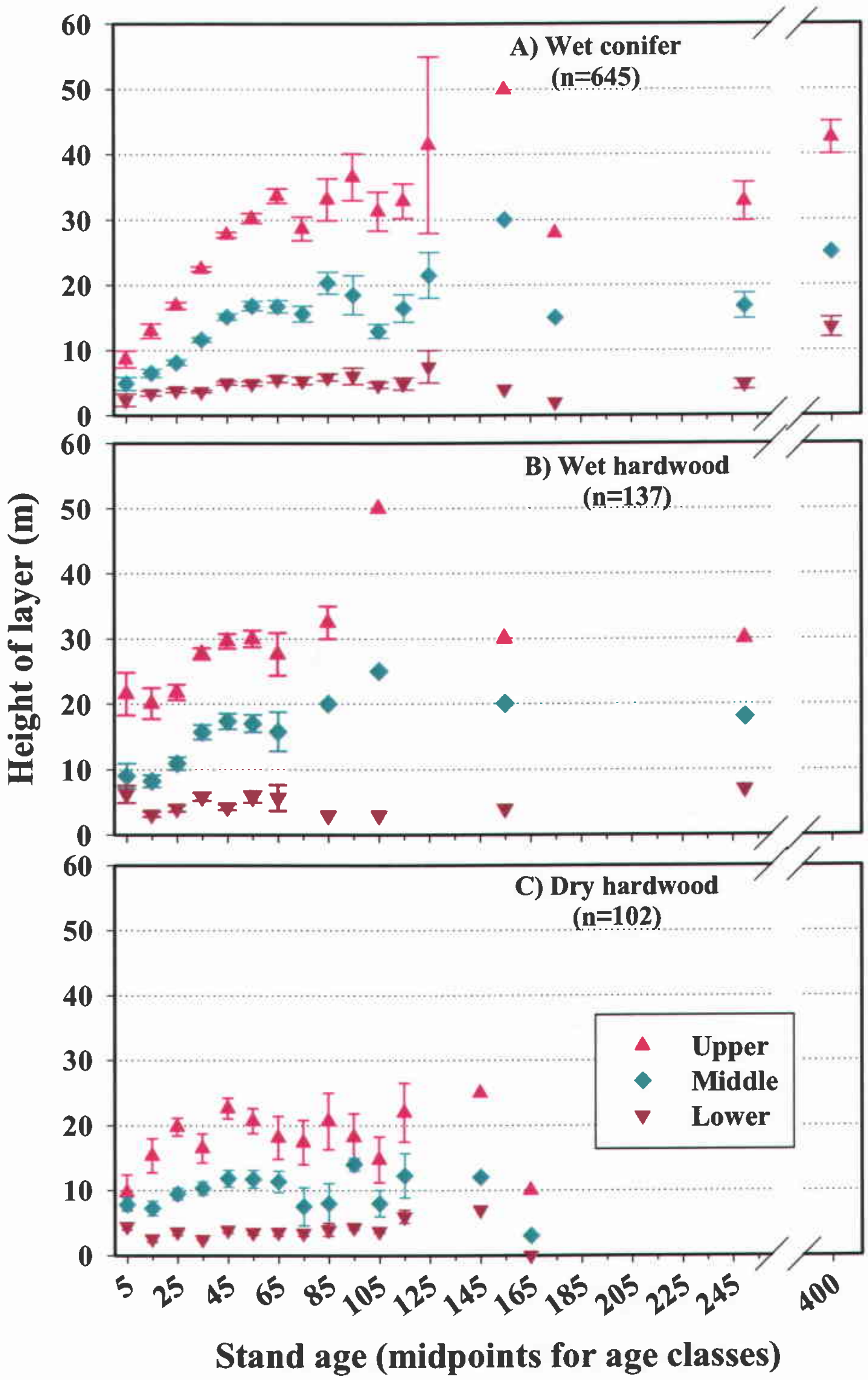

Fig. 2.6. Mean heights (± 1 SE) for three tree canopy layers across a chronosequence of stand ages by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

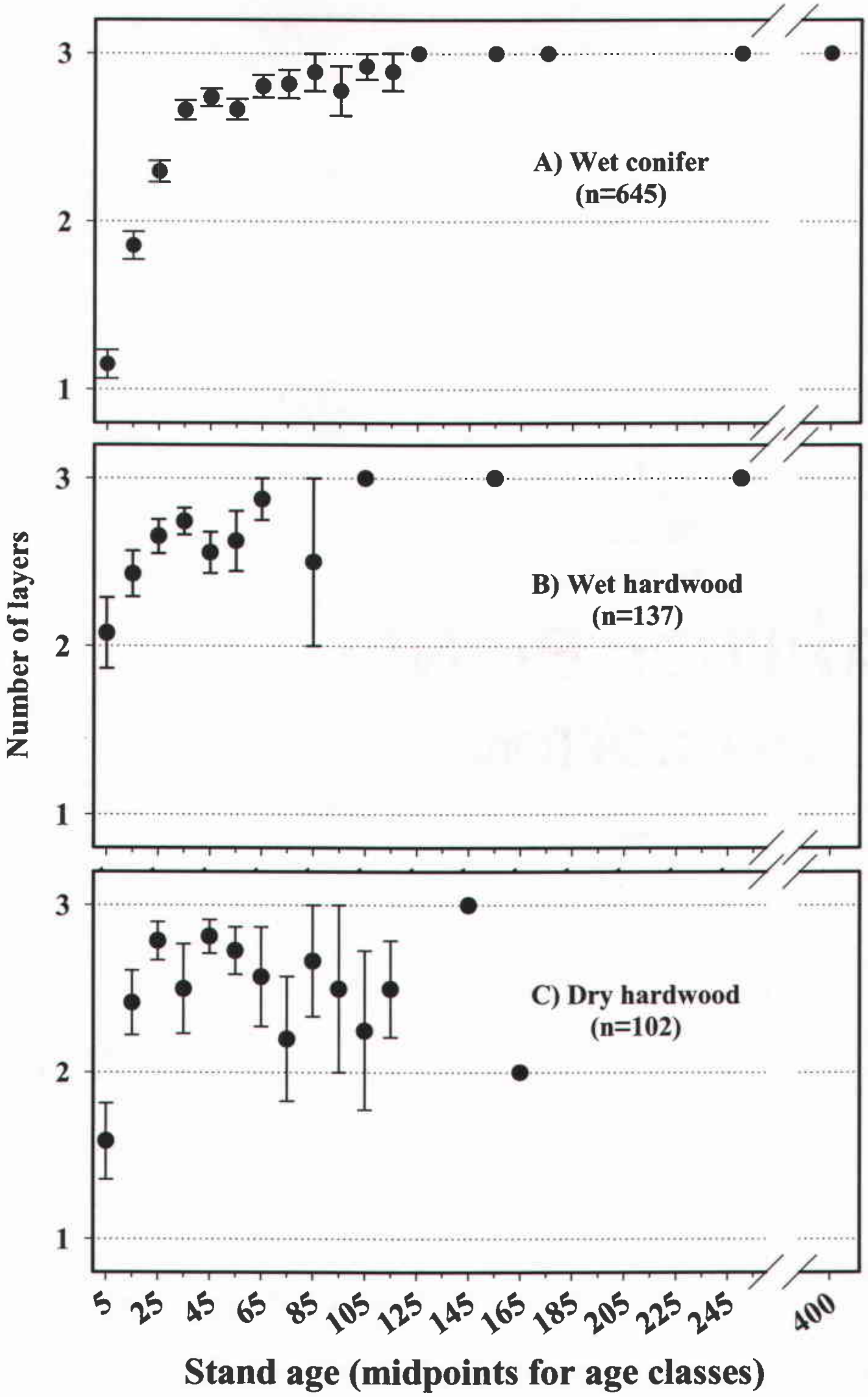

Fig. 2.7. Mean number of canopy layers (± 1 SE) across a chronosequence of stand ages by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

Understory cover

Shrub and forb cover did not exhibit expected patterns across stand ages (Fig. 2.8). For all forest types, percent cover of forbs dropped between ages 15 – 45 and then returned to higher levels similar to age 5. Percent cover of shrubs (39-52%) was consistent and similar between ages 5 and 115, except for slightly elevated levels at age 15. Beyond age 115 percent shrub cover was generally greater than percent forb cover. Shrub and forb cover patterns in wet-conifer stands were similar to all forest types, and beyond age 5 shrub cover was consistently greater than forb cover. For wet-hardwood stands, trends in understory cover were generally consistent with those of all forest types, but without the dip in percent forb cover from ages 15 to 45. In the dry-hardwood stands, patterns again followed all forest types, except that forb cover generally exceeded shrub cover in stands > 45 years.

For all forest groups, plots of individual understory species vs. total overstory cover indicated substantial scatter. Only 18 species of shrubs and 5 forb species met the criteria of minimum number of stands for plotting (Tables 2.8, 2.9). For these species there were no conclusive negative trends between total overstory cover and understory species cover (e.g. Fig. 2.9).

Only a few individual forb and shrub species exhibited a distinct shift in percent cover across stand ages associated with canopy closure (age 35,-Figs. 2.10, 2.11). In general *Rubus* spp., *Cirsium* spp., and *Pteridium aquilinum* decreased with canopy closure. *Corylus cornuta*, *Symphoricarpos* spp., *Toxicodendron diversilobum*, *Galium* spp., *Rosa gymnocarpa*, and *Polystichum munitum* increased with increasing stand age. Cover levels for many of the other species present tended to remain consistent across stand ages until beyond age 105, and only after that were changes in cover levels seen.

Mean shrub species richness dropped during canopy closure (age 35, Fig. 2.12). There was a local peak in richness in 15-yr stands. This was followed by a

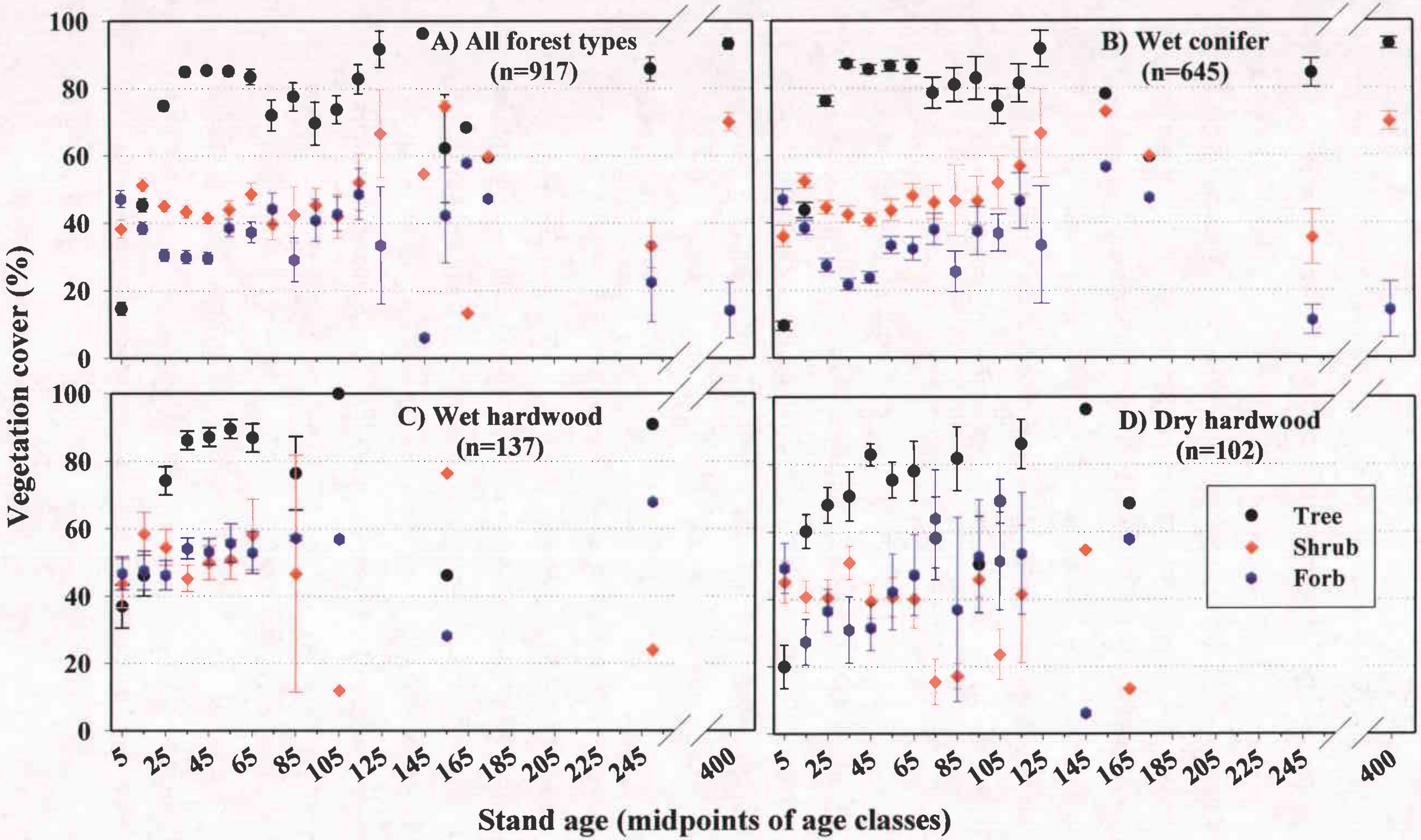

Fig. 2.8. Mean percent cover (± 1 SE) for total tree canopy, shrub, and forb across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

Table 2.8. Shrub species present in ≥ 20% of the FIA plots used in this study.

Code	Species	Common name	All forest types n	Percentage of plots
acci	*Acer circinatum* Pursh	Vine maple	482	51.6
coco	*Corylus cornuta* Marsh.	Hazelnut	398	42.6
frpu	*Frangula purshiana* (DC.) Cooper	Pursh's buckthorn	310	33.2
gash	*Gaultheria shallon* Pursh	Salal	495	53.0
hodi	*Holodiscus discolor* (Pursh) Maxim.	Oceanspray	396	42.4
lonic	*Lonicera* spp.	Honeysuckle	199	21.3
mane	*Mahonia nervosa* (Pursh) Nutt	Cascade Oregongrape	459	49.1
rogy	*Rosa gymnocarpa* Nutt.	Wood rose	379	40.6
rudi	*Rubus discolor* Weihe & Nees	Himalayan blackberry	192	20.6
rule	*Rubus leucodermis* Dougl. ex Torr. & Gray	Whitebark raspberry	189	20.2
rupa	*Rubus parviflorus* Nutt.	Thimbleberry	388	41.5
rusp	*Rubus spectabilis* Pursh	Salmonberry	350	37.5
ruur	*Rubus ursinus* Cham. & Schlecht.	California blackberry	694	74.3
salix	*Salix* spp.	Willow	191	20.4
sara	*Sambucus racemosa* L.	Elderberry	218	23.3
symph	*Symphoricarpos* spp.	Snowberry	342	36.6
todi	*Toxicodendron diversilobum* (Torr. & Gray) Greene	Poison oak	254	27.2
vapa	*Vaccinium parvifolium* Sm.	Red huckleberry	469	50.2

Table 2.9. Herb species present (with ≥ 3% cover in a stand) in ≥10% of the forested FIA stands used in this study.

Code	Species	Common name	All forest types n	Percentage of plots
cirs	*Cirsium* spp.	Thistle	93	10.0
gali	*Galium* spp.	Bedstraw	125	13.4
oxor	*Oxalis oregana* Nutt.	Oregon oxalis	265	28.4
pomu	*Polystichum munitum* (Kaulfuss) K. Presl	Swordfern	718	76.9
ptaq	*Pteridium aquilinum* (L.) Kuhn	Brackenfern	450	48.2

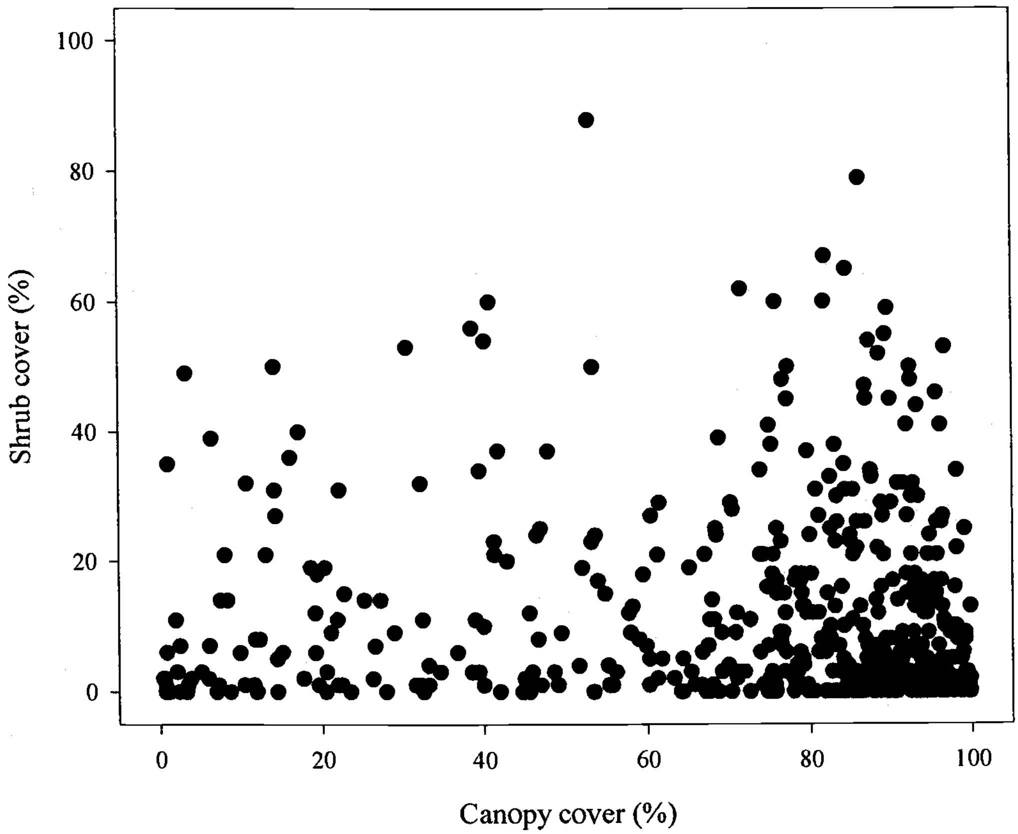

Fig. 2.9. Comparison of total overstory percent canopy cover and percent cover of *Gaultheria shallon* (salal) in the 488 stands from the 1995-97 FIA inventory of forested plots where salal was present.

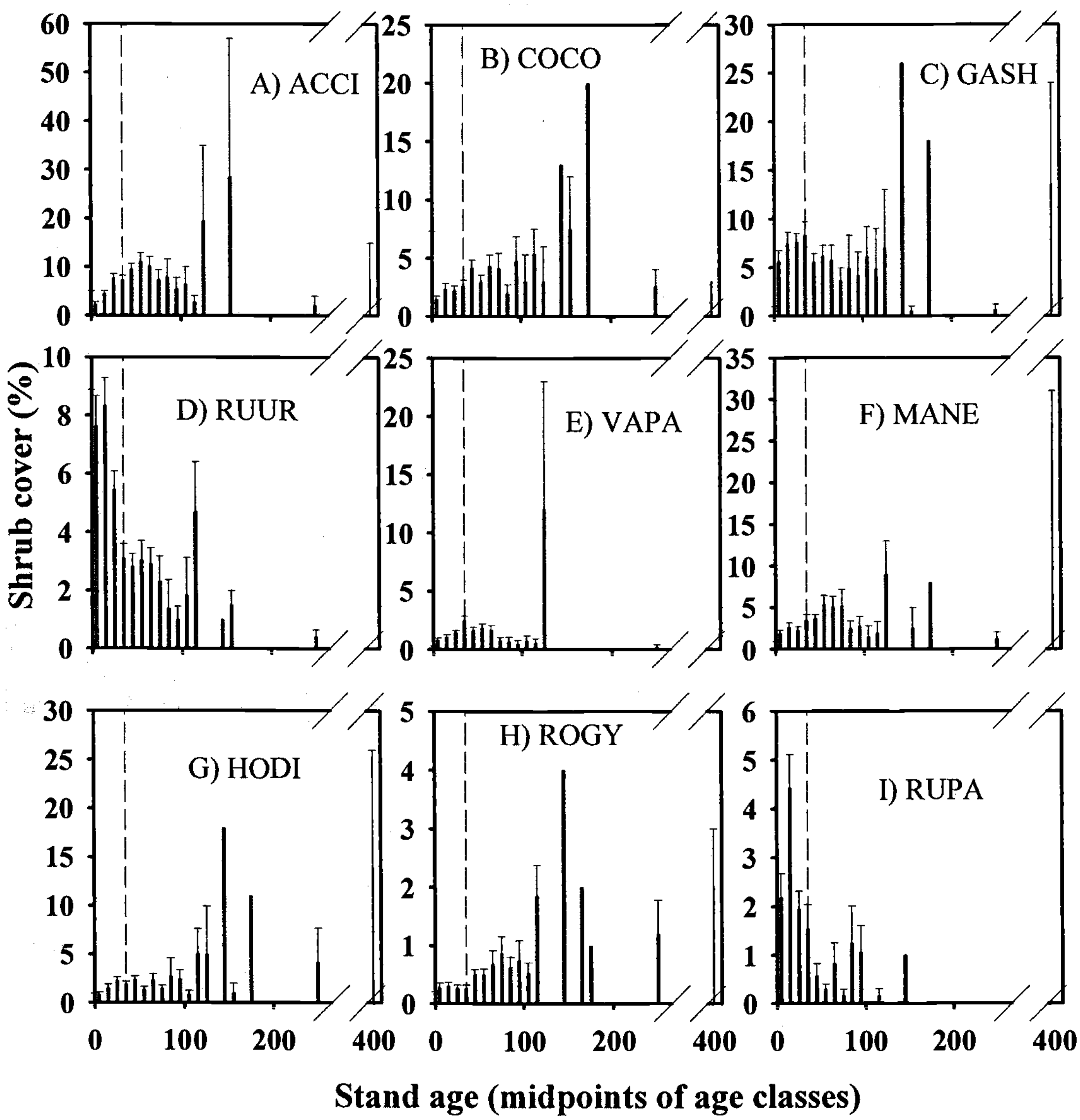

Fig. 2.10. Mean percent cover (± 1 SE) of the 18 most commonly occurring shrubs in 917 stands from the FIA inventory across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) in western Oregon. Sample sizes differed among stand ages (see Table 2.4). Codes for shrub species are provided in Table 2.8. The dashed line at age 35 represents canopy closure.

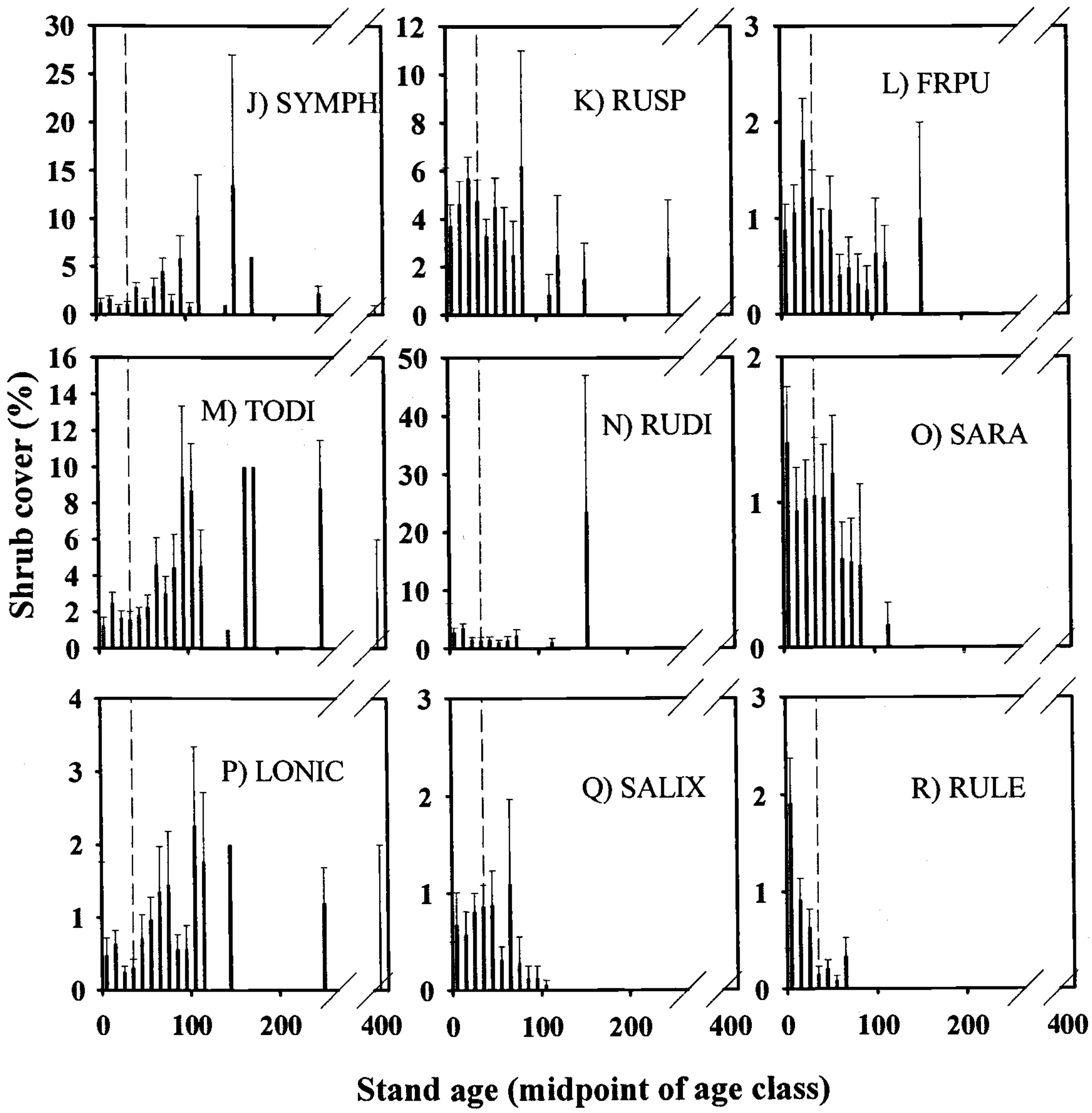

Fig. 2.10. Cont'd.

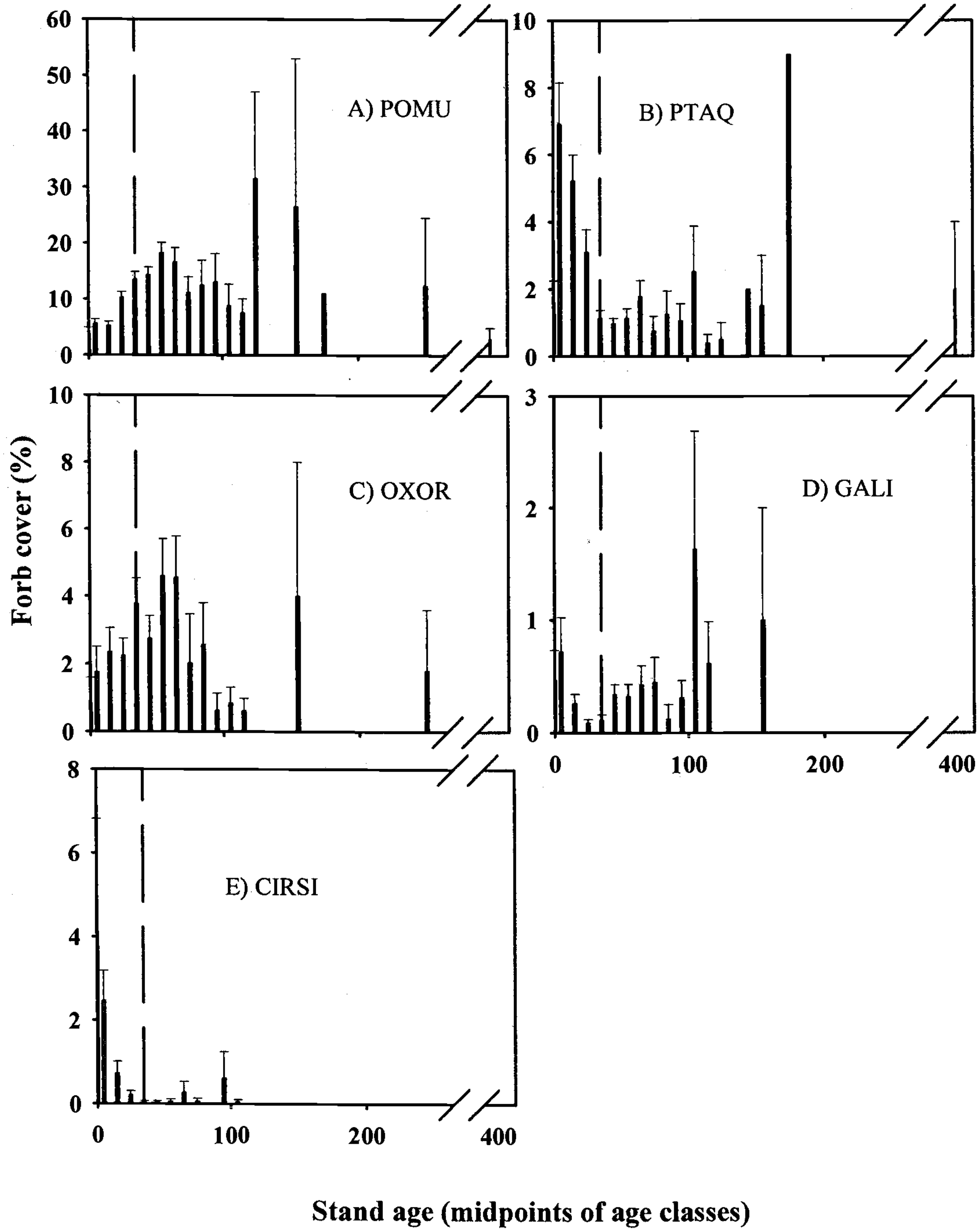

Fig. 2.11. Mean percent cover (± 1 SE) of the five most commonly occurring forbs in 917 stands from the FIA inventory across a chronosequence of stand ages (grouped into intervals and labeled using interval midpoints in western Oregon. Sample sizes differed among stand ages (see Table 2.4). Codes for forb species provided in Table 2.9. The dashed line at age 35 represents age of canopy closure.

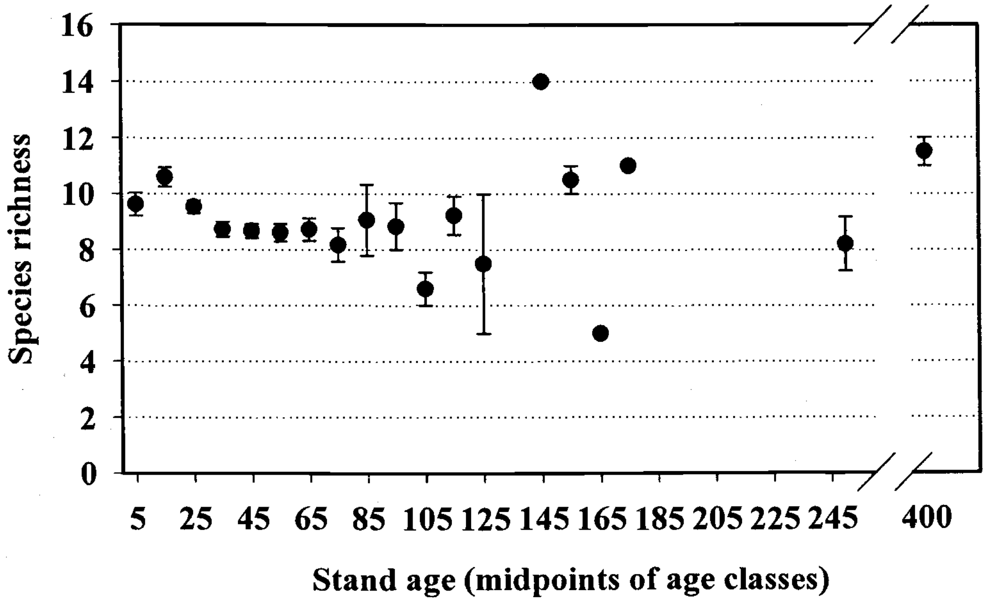

Fig. 2.12. Mean species richness of shrubs (± 1 SE) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

drop in richness to below age five levels. From ages 35 - 95 shrub richness was consistent at this reduced level. Beyond age 95, richness was highly variable.

Mean Simpson's diversity index measures revealed a small drop in diversity coincident with age of canopy closure at age 35 (Fig. 2.13). Simpson's diversity did not return to pre-canopy closure levels until age 115.

Shade-tolerance

Shade-tolerant percent cover was lower than expected for all three general forest groups (Fig. 2.14). The wet-conifer stands had the highest levels of shade-tolerant cover, with about 20% shade-tolerant cover between stand ages 35-85. Total shade-tolerant cover was unexpectedly low in the older stands. Shade-tolerant cover was primarily concentrated in the upper layer of cover. The wet-hardwood stands were even lower in shade-tolerant cover, with fairly consistent and similar cover levels for all three layers among stand ages, except in the older single samples. The dry-hardwood stands differed from the other two forest groups, with nominal total shade-tolerant cover in all layers for all stand ages.

As expected, the proportions of shade-tolerant cover were generally highest in the lower cover layer, compared with the middle and upper layers (Fig. 2.15). However, the proportion of shade-tolerant cover never exceeded shade-intolerant cover among the three vertical cover layers. In the wet-conifer stands, the proportions of shade-tolerant cover were consistently highest for the lower cover layer. The highest proportions of shade-tolerant cover occurred in stands aged 15-95. For the wet-hardwood stands, trends in the proportions of shade-tolerant cover were generally similar to wet-conifer stands. The dry-hardwood stands had minimal proportions of shade-tolerant cover, consistent with their low shade-tolerant cover levels.

Plots of shade-intolerant cover were excluded from the results. They were considered redundant, as they were the converse of the amount and proportions of shade-tolerant cover.

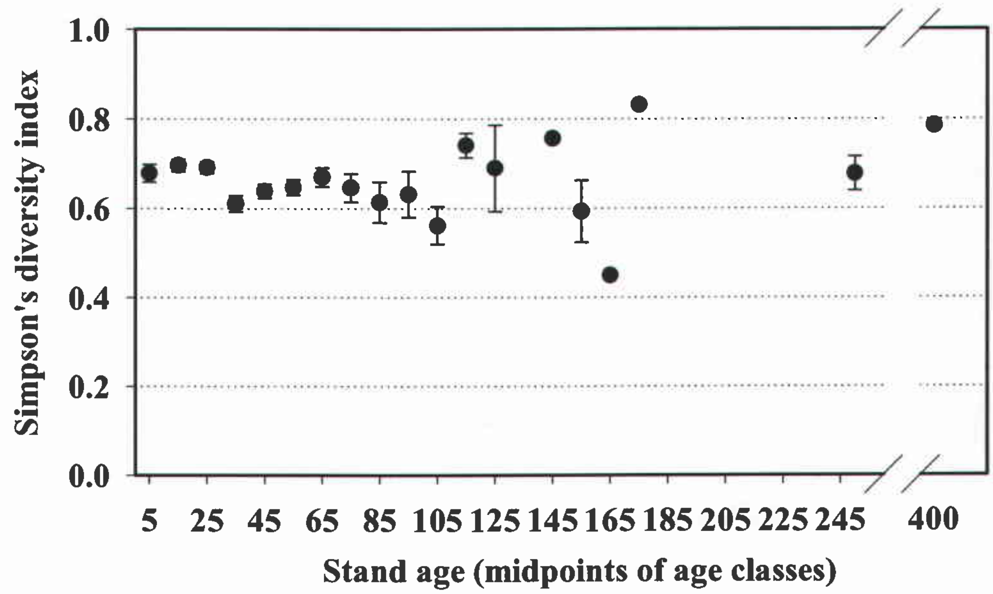

Fig. 2.13. Mean Simpson's diversity of shrubs (± 1 SE) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

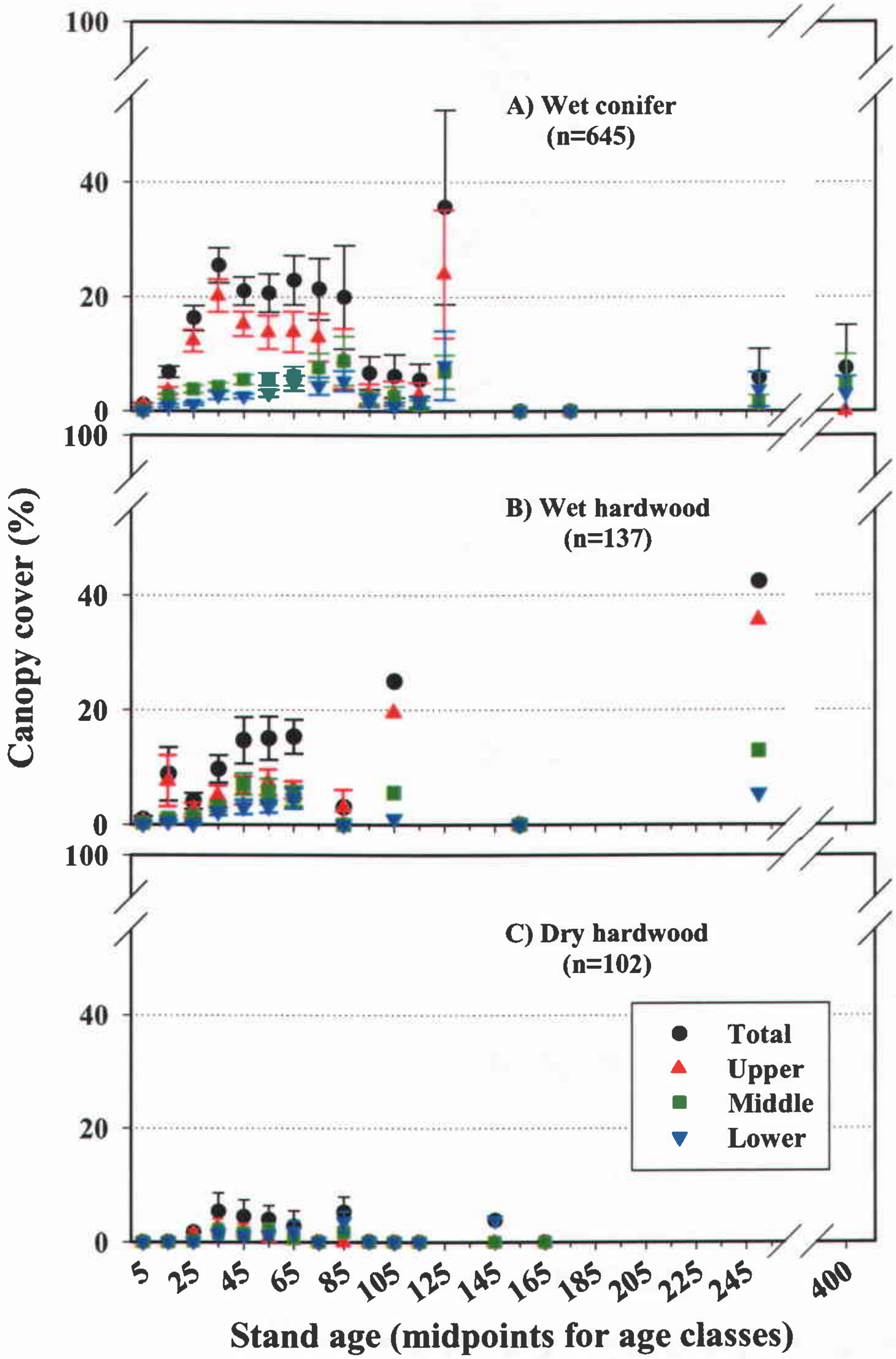

Fig. 2.14. Mean percent shade-tolerant canopy cover (± 1 SE) for three tree canopy layers and all layers combined across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

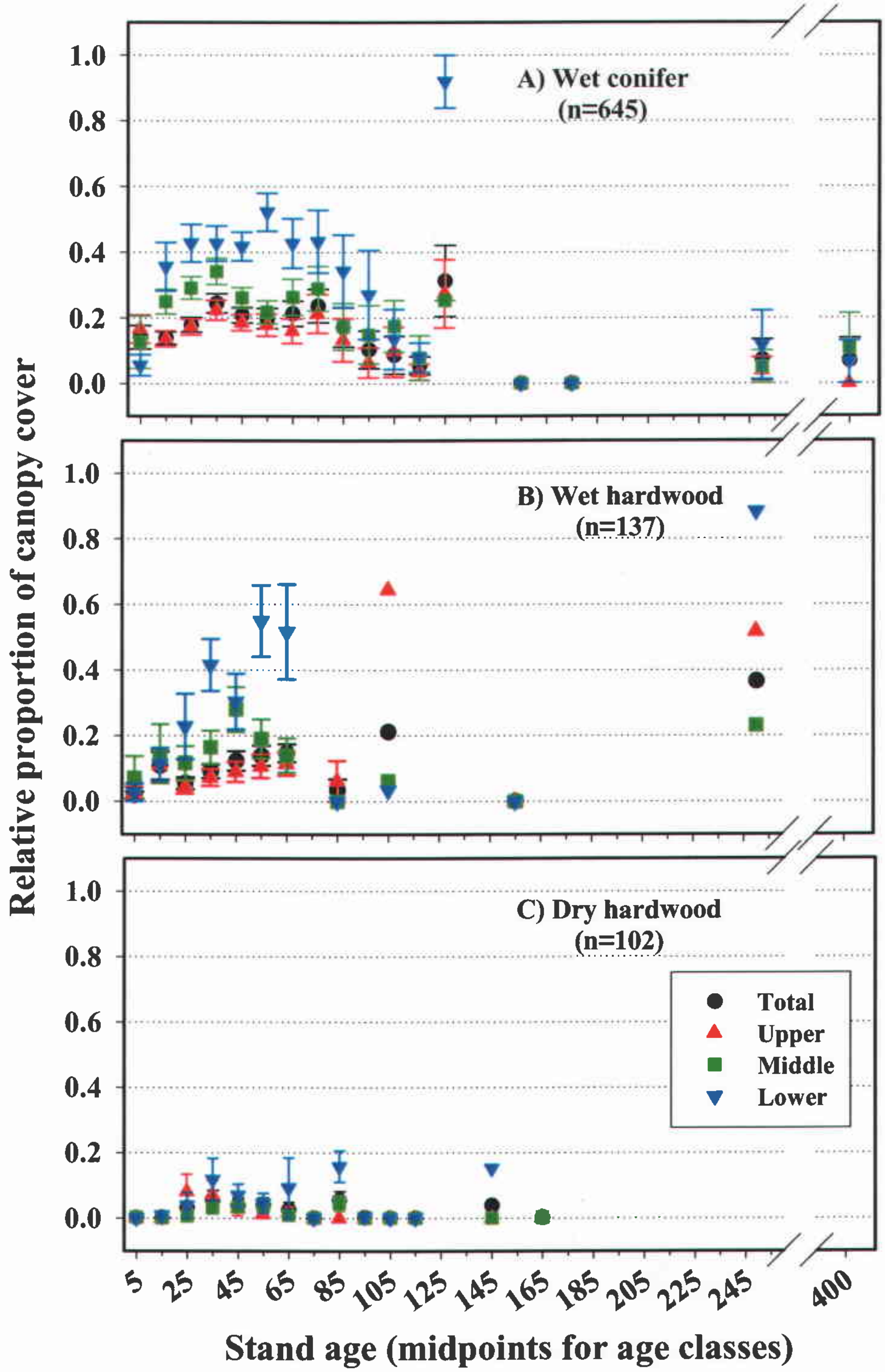

Fig. 2.15. Mean proportion (± 1 SE) of shade-tolerant percent canopy cover across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 2.5) in western Oregon. Sample sizes differed among stand ages (see Table 2.4).

Stand-Condition Class

Cover by layer

For the three forest groups, canopy cover generally increased with underlying age of stand-condition class (Fig. 2.16). An exception for all three forest-groups was mean percent cover for CSP stands. In the wet-conifer stands total cover of CSP stands was similar to that of large-sawtimber (LSAW) and old-growth (OG) stands, and greater than mean percent cover of open-sawtimber (OSAW) stands. Total cover of CSP exceeded all other stand conditions in the wet-hardwood forest group, but was lower than LSAW in the dry-hardwood stands. Mean percent cover of the upper layer mirrored trends for total percent cover, except for cover decreases in the wet-conifer OG stands and the dry-hardwood CSP stands. Cover of the middle layer gradually increased for the wet-conifer stands, with similar levels for CSP, OSAW, and LSAW. In both the wet- and dry-hardwood stands, cover of the middle layer was greatest in the CSP stand condition. Mean percent canopy cover for the lower layer was low, except for an increase in the wet-conifer OG stands.

In general, ground-based cover measures corresponded with the field criteria used to classify stand-conditions (see Table 2.1). The mean percent cover of the line- intercept values corresponded with ocular field assessments of percent cover for OSP and CSP. However for the OSAW stands the mean percent cover values were consistently >60% for OSAW stands. This did not correspond to the 'open' criteria of < 60% cover used to describe OSAW stands.

Height by vertical layer

For the three forest groups, mean heights for the vertical canopy layers were consistent with the development patterns shown for stand age. Thus they were not described in additional detail.

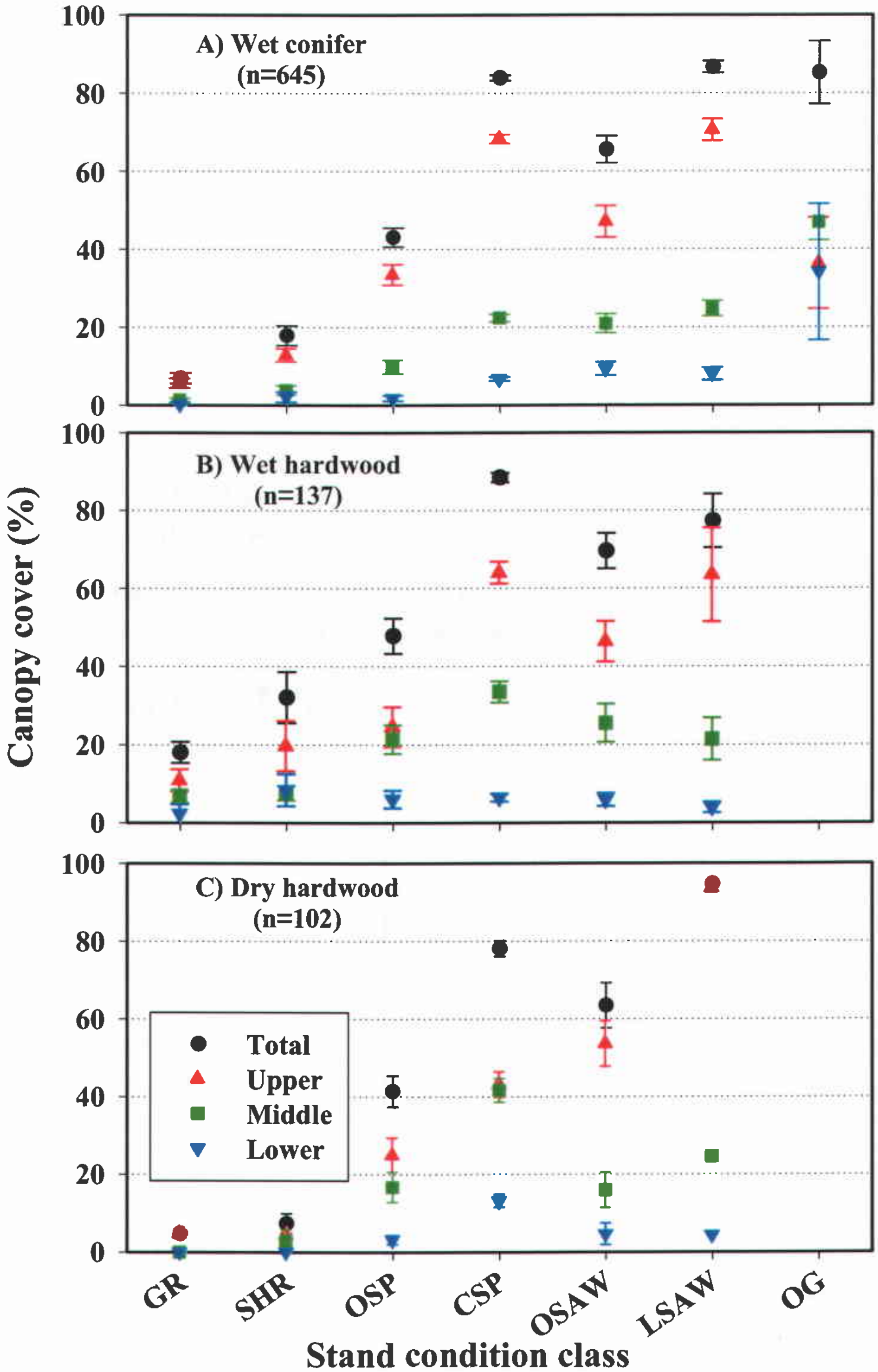

Fig. 2.16. Mean percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined among seven stand conditions by forest group (see Table 2.5) in western Oregon. Stand conditions and sample sizes are described in Table 2.1.

Number of vertical layers

The mean number of layers for stand condition classes mirrored patterns described using stand age to describe successional stage. Therefore, further descriptions of these trends were omitted.

Understory cover

For the three general forest groups, percent cover of forbs and of shrubs was generally consistent with the stand condition criteria (Fig. 2.17). As expected, in the grass (GR) stands forb cover was consistently higher than shrub and overstory cover. In the shrub (SHR) stands, shrub cover was consistently higher than forb and overstory cover, except in the dry-hardwood stands where forb and shrub levels were similar. The single dry-hardwood LSAW sample had nominal shrub cover. Otherwise, understory cover was similar to the patterns illustrated using stand age as a surrogate for stand succession stage.

Shade-tolerance

For the three forest groups, mean percent shade-tolerant cover was generally lower than expected across the development gradient, compared with shade-intolerant percent cover (Fig. 2.18). For the wet-conifer stands, total shade-tolerant cover was $\leq$ 20% across stand conditions. Except for shade-tolerant cover of the upper cover layer in CSP and LSAW, shade-tolerant cover was minimal across cover layers and stand conditions. Shade-tolerant cover of the wet-hardwood stands never exceeded 13%, and total shade-tolerant cover in the wet-hardwood stands was nominal except for CSP and LSAW. For the dry-hardwood stands, total shade-tolerant cover was negligible across development stages.

Proportions of shade-tolerant and shade-intolerant cover for the general forest groups generally followed the trends seen using stand age to describe stand development. They were not described further.

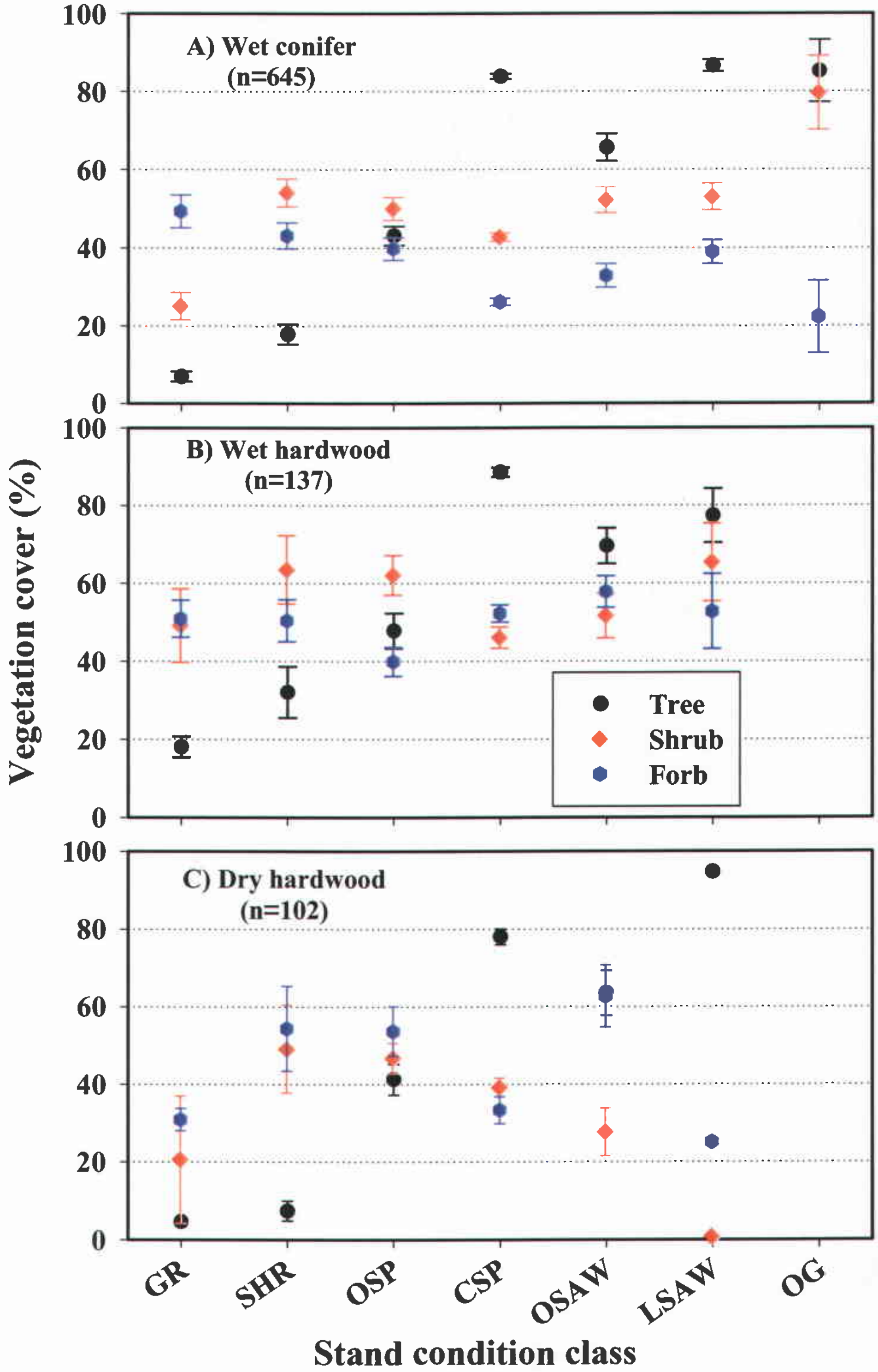

Fig. 2.17. Mean percent cover (± 1 SE) for total tree canopy, shrub, and forb among stand-condition classes by forest group (see Table 2.5) in western Oregon. Stand conditions and sample sizes are described in Table 2.1.

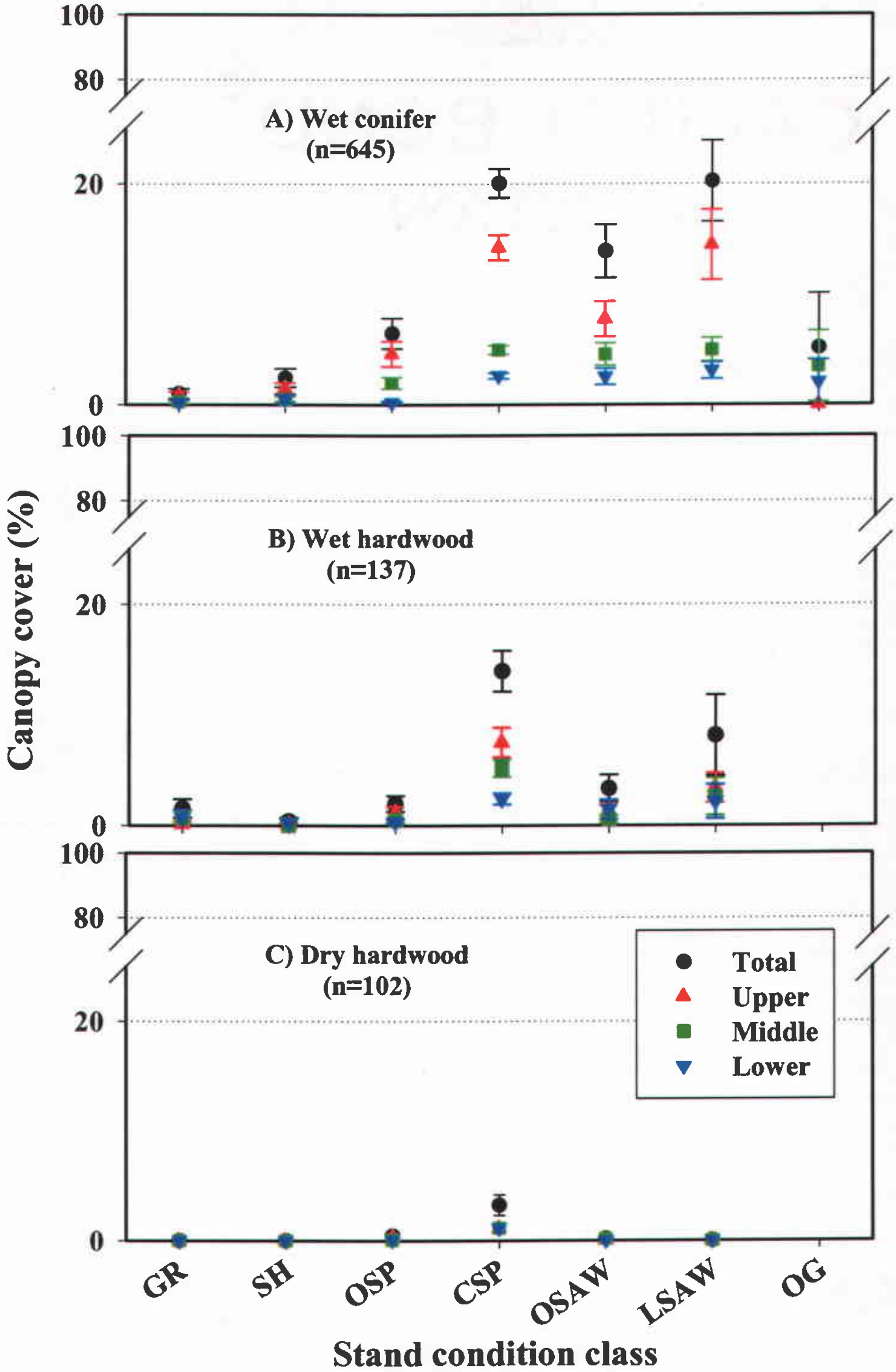

Fig. 2.18. Mean percent shade-tolerant canopy cover (± 1 SE) for three tree canopy layers and all layers combined among stand-condition classes by forest group (see Table 2.5) in western Oregon. Stand conditions and sample sizes are described in Table 2.1.

Stand-Size Class

Canopy cover attributes for wet-conifer forests exhibited little variance across the development gradient. In the size classes greater than seedling size, total canopy cover and cover in the three vertical layers were similar among the three size classes (Fig. 2.19). The remaining cover attributes varied little among the poletimber, small sawtimber, and large sawtimber classes and were not described in further detail.

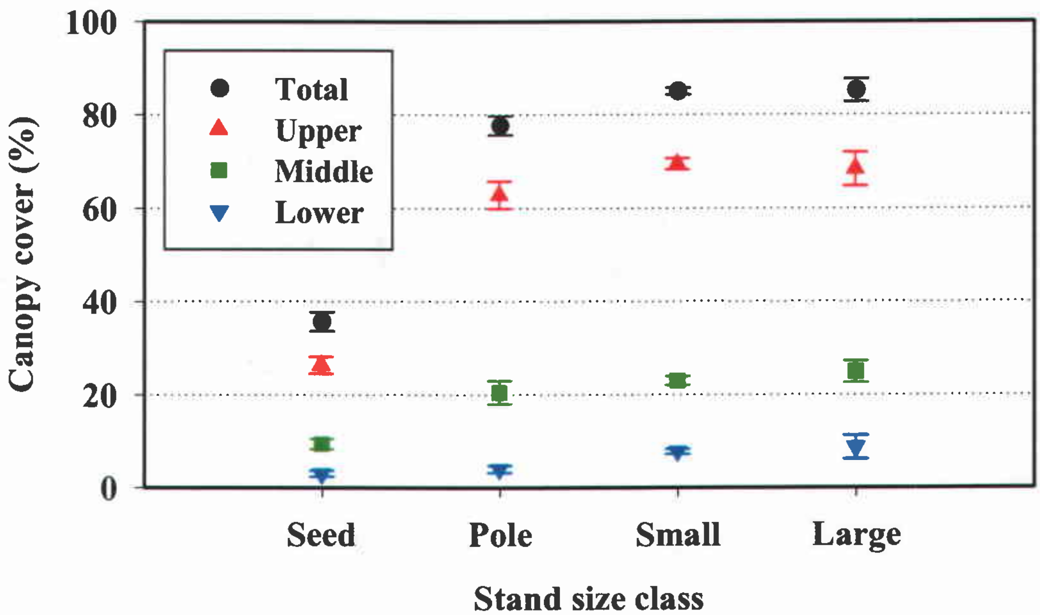

Fig. 2.19. Mean percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined for 917 stands in western Oregon. Stand-size classes and sample sizes are described in Table 2.3.

Thinning Intensity

Cover by vertical layer

Differences in canopy cover were exhibited across the levels of thinning (Fig. 2.20). Undisturbed (ND) and lightly thinned (LT) stands had similar (78-79%) total mean percent canopy cover, while cover was 62% in heavily thinned (HT) stands. Trends in canopy cover for the upper layer were similar to total percent cover. Mean percent canopy cover of the middle layer was lower in the HT stands than in the ND and LT stands. Mean percent cover of the lower canopy layer was nominal for all three thinning intensities.

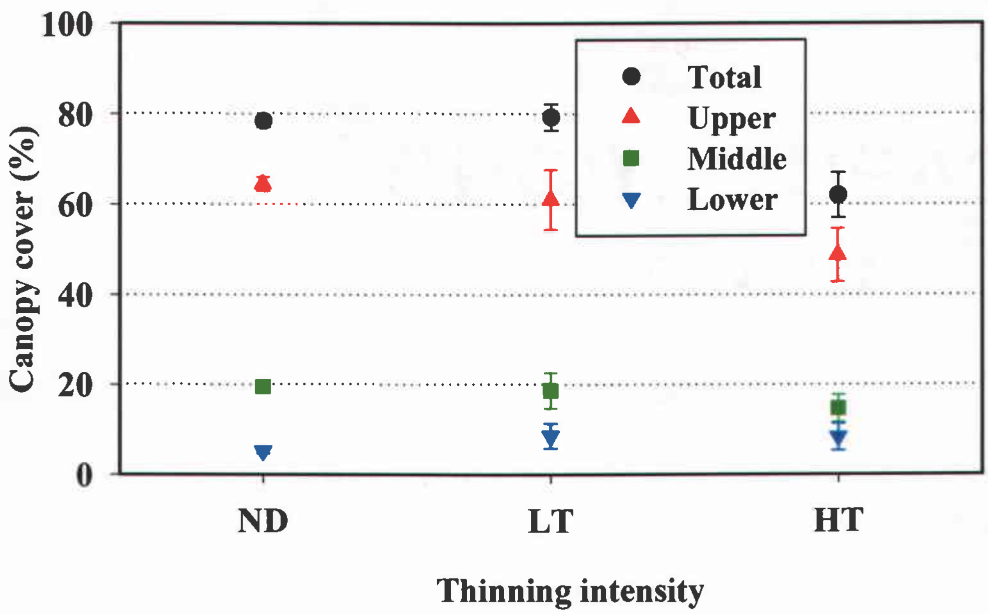

Fig. 2.20. Mean percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined among three thinning intensities in 295 Douglas-fir stands aged 15-45 in western Oregon. Thinning intensities and sample sizes are described in Table 2.6.

Height by vertical layer

Mean heights differed among the three levels of thinning (Fig. 2.21). The upper layer of the ND stands was on average shorter (20 m) than for thinned stands (24-25 m). The heights of the middle and lower layers were consistent across thinning intensities.

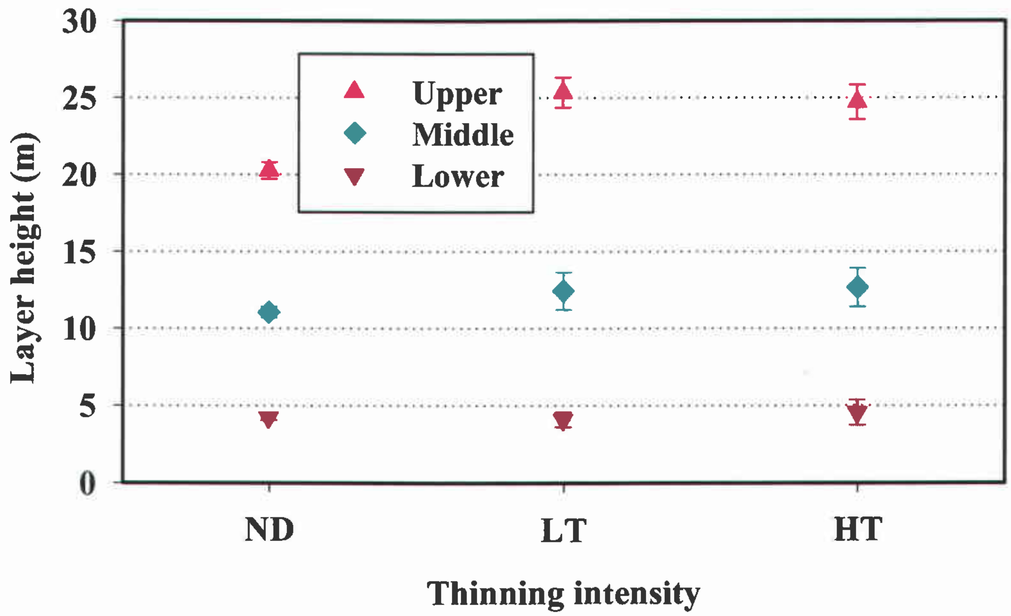

Fig. 2.21. Mean heights (+ 1 SE) for three tree canopy layers among three thinning intensities in 295 Douglas-fir stands aged 15-45 in western Oregon. Thinning intensities and sample sizes are described in Table 2.6.

Number of vertical layers

All three thinning levels had a mean of approximately 2.5 canopy layers.

Understory cover

There were no evident trends between understory cover and thinning history (Fig. 2.22). Both shrub and forb cover were fairly consistent and similar among the three thinning intensities.

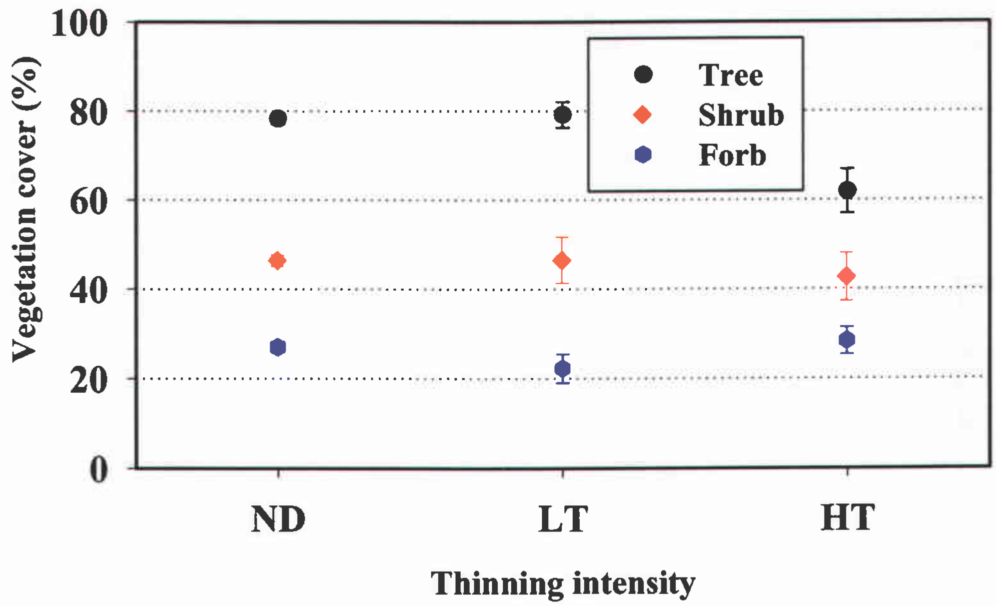

Fig 2.22. Mean percent cover (± 1 SE) for total tree canopy, shrub, and forb among three thinning intensities in 295 Douglas-fir stands aged 15-45 in western Oregon. Thinning intensities and sample sizes are described in Table 2.6.

Shade-tolerance

Shade-tolerant canopy cover of the layers was lower than anticipated (Fig. 2.23). The total and three vertical layers were consistently low in shade-tolerant cover for LT and HT stands. ND stands had slightly higher total and upper layer shade-tolerant cover.

Patterns in the proportions of shade-tolerant cover differed across the thinning intensities (Fig. 2.24). For ND and LT stands, shade-tolerant cover of the

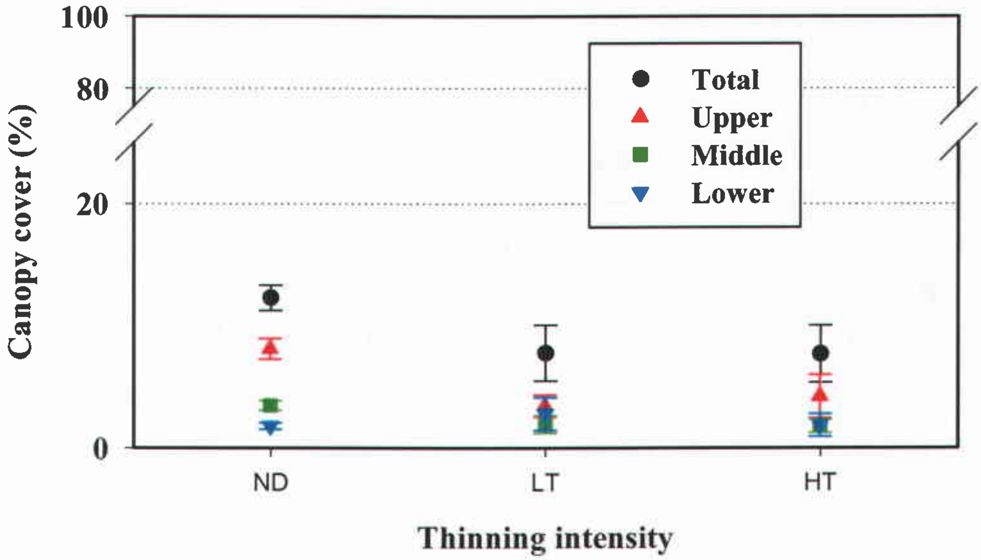

Fig. 2.23. Mean percent shade-tolerant canopy cover (± 1 SE) for three tree canopy layers and all layers combined among thinning intensities in 295 Douglas-fir stands aged 15-45 in western Oregon. Thinning intensities and sample sizes are described in Table 2.6.

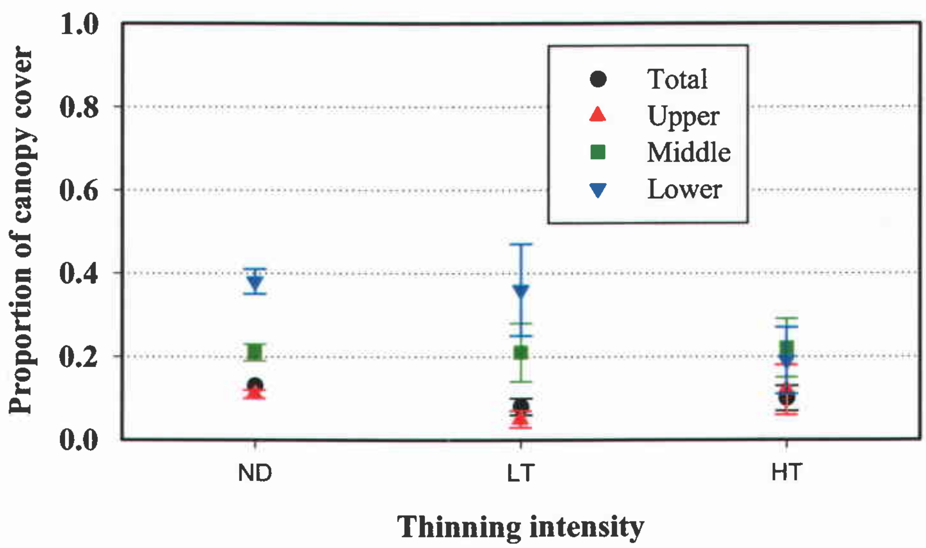

Fig. 2.24. Mean proportion of shade-tolerant percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined among thinning intensities in Douglas-fir stands aged 15-45 in western Oregon. Thinning intensities and sample sizes are described in Table 2.6.

lower layer consistently had the highest proportion of shade-tolerant cover compared with the other two cover layers. The HT stands had lower proportions of total shade-tolerant cover. The shade-tolerant proportion of the middle cover layer exceeded the lower layer for the HT stands.

Ownership

Canopy cover of the vertical layers differed among ownership categories (Fig. 2.25). Total canopy cover was highest (81%) in public lands, and lowest (67%) in private non-industrial forests. Canopy cover of the upper layer closely followed the trend for total cover. Canopy cover was more consistent across ownerships for both the middle (16-25%) and lower (6-7%) layers.

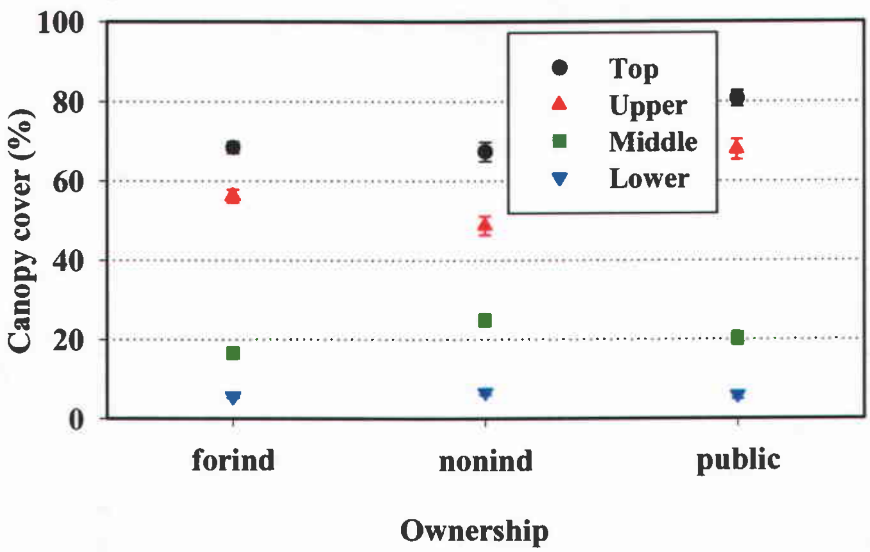

Fig. 2.25. Mean percent canopy cover (± 1 SE) for three tree canopy layers and all layers combined among three general ownership groups for 645 wet-conifer stands in western Oregon. Ownership classes and sample sizes are described in Table 2.7.

Beyond looking at total cover and cover by layer, there was minimal additional information gleaned from comparison of the three ownership groups, and additional results of analysis were excluded.

Discussion

Stand Development Canopy Structure Patterns

With several exceptions, canopy structure patterns seen across the chronosequence of stand ages and stand conditions were consistent with the stand development models of Oliver (1981) and Franklin et al. (2002). However, with some differences in canopy development between the two models, I further explored the differences among them as they related to the canopy structure data analyzed in this study.

The Oliver and Franklin et al. models propose different starting points for the initiation of stand development. The Oliver model generally describes stand development after a 'major' disturbance, whereby all living stems in an area are killed. Thus, it appears most relevant for evenaged stands where the cohort of trees all started at the same time. The Franklin et al. model is more flexible. It offers a gradient of starting points for a stand, from disturbance regimes in which large remnant trees remain in the overstory, through to the major stand-clearing disturbance described by Oliver. The recognition of variable starting points for establishment of a new cohort of trees appears more effective at describing unevenaged stands which may gradually regenerate after a disturbance. For the wet-conifer stands in western Oregon where clearcut harvesting is the dominant disturbance, both models suggest a similar starting point and are appropriate descriptors of stand initiation. However, for stands that originated from a disturbance that left legacy trees in the stand, or where tree seedlings naturally regenerated over a longer time frame, Oliver's major disturbance regime does not appear appropriate.

The young hardwood stands included in the inventory had unexpectedly high percent canopy cover. There were likely two main reasons for this. In some of the hardwood stands, the higher percent canopy cover likely resulted from the broad spreading form generally exhibited by hardwood species, compared with coniferous species. For example, bigleaf maple and Oregon white oak have short stout boles supporting spreading limbs, resulting in broad rounded crowns (Burns and Honkala 1990). This growth form differs from conifers, which tend to grow upwards forming narrow cylindrical crowns, expanding less horizontally than hardwood species (Burns and Honkala 1990). Also, many of the hardwood species (e.g. Pacific madrone, red alder, bigleaf maple, Oregon white oak) can vegetatively reproduce and undergo rapid juvenile growth (Burns and Honkala 1990). Thus, they can readily invade recently disturbed sites, leading to an initial flush of canopy cover in newly established hardwood stands. Also, some of the FIA inventory stands had residual tall canopy trees that were not removed during the stand-initiating disturbance. The stand-initiating disturbances were predominantly clear-cuts, but there were also incidences of partial harvest, incidental harvest, and wildfire. With reforestation practices focused on conifers in western Oregon, wet-hardwood and dry-hardwood stands tend to naturally regenerate post-disturbance. Therefore, given the varied starting points for the hardwood stands included in the FIA inventory, the Franklin model appears most suitable for describing the initial phases of hardwood stand development in western Oregon.

Both the Oliver and Franklin models proposed a stage of canopy closure after the new cohort of trees was established. In this stage the cohort of trees is primarily within a single height class. In this study mean canopy cover rarely exceeded 85% for the forest groups. The idea that full use of available growing space only occurs when adjacent plant crowns are touching can be an oversimplification, as it assumes that sunlight is the limiting factor in stands (Oliver and Larson 1996). Moisture and/or nutrients can be more limiting than light. With the wide range of site conditions encompassed in the FIA inventory, light may not necessarily be the limiting variable. Also, 10% of the area in fully-stocked stands on average can be accounted for by small gaps in immature Douglas-fir forests (~75 years) (Meyer 1930). These gaps may result from the round shape of crowns, gaps where shrubs dominate, presence of small creeks, 'rough' ground, and crown abrasion as trees grow taller. Therefore, the term closed-canopy may be misleading. While a stand may have attained 'canopy closure', in actuality gaps will still comprise 10% of the horizontal area.

While wet-hardwood and wet-conifer stands shared similar trends in early dominance of the upper layer of canopy, trends in the dry-hardwood stands differed. Unlike the other two forest groups, total canopy cover in the dry-hardwood stands was comprised of similar contributions from the upper and middle canopy cover layers across stand ages, excluding the OSAW and LSAW stands. The dry-hardwood stands were largely comprised of Oregon white oak and Pacific madrone forest types (see Table 2.5), which are not generally classified as shade-tolerant, but adequately reproduce under their own shade (Burns and Honkala 1990). Also, trees of dry hardwood stands retain few shade leaves (Oliver and Larson 1996) allowing more light penetration to reach the forest floor. These factors likely led to the lack of a dominant upper canopy layer.

Trends in total percent canopy cover in wet-hardwood and wet-conifer stands were consistent with Oliver's stem–exclusion phase and Franklin's biomass accumulation/competitive exclusion stage. This was demonstrated by leveling off of total canopy cover followed by slight decreases across older ages. These high canopy cover values likely resulted from the horizontal and vertical expansion of tree crowns. Crown-class differentiation followed, and eventually the shorter trees were over-topped by more dominant trees, leading to slight decreases in total canopy cover in older stands. This differentiation was demonstrated by the increase in number of canopy layers with increasing stand age among forest groups.

Trends in understory shrub and forb cover levels across stand ages were inconsistent with the expectation that understory cover would dramatically decrease during stem exclusion. Shrub levels are highly correlated with horizontal and vertical variation in canopy cover (Van Pelt and Franklin 2000). While the leaf-area-index (LAI) values of wet-conifer forests of the PNW are among the highest in the world, this cover is spread out over the vertical dimension of the stand (Van Pelt and Franklin 2000). This was shown in this study by the frequency of three vertical layers. Brown and Parker (1994) found photosynthetically-active radiation (PAR) was not strongly correlated with many simple measures of canopy structure, including canopy cover. Instead, they found PAR to be highly correlated with variables that described the vertical distribution of foliage. Studying trends of PAR with successional age, they found PAR transmittance increased during the first 50 years of stand development. These findings again suggest it is the vertical arrangement of foliage in a stand that influences light levels, rather than percent cover. In my study, the heights many of the stands attained, canopy closure occurrence at 85%, and the uneven vertical and horizontal distribution of the cover among the three vertical layers allowed for light penetration.

While the composition of shrubs and forbs may change from shade-intolerant to shade-tolerant species, the total understory percent cover varied little during stem-exclusion. Plants adapted to shaded habitats are less responsive to changes in light quality than those adapted to open habitats (Ross et al. 1986). There were only a few of the understory species that appeared to follow consistent trends of decreased cover associated with increasing age and corresponding high canopy cover levels (see Figs. 2.10, 2.11). Instead, many of the common understory species, including salal, Oregon grape, and vine maple were highly variable among stand ages. While there is limited literature that details the shade-tolerance of understory species, trends in cover of understory species seen here appear to indicate that with 85% canopy closure many species were still shade-tolerant enough to remain at consistent levels under these reduced light conditions.

While total percent cover of shrubs remained consistent, species richness and diversity did decrease with canopy closure (at age 35). This supported the concept that the species composition of the shrubs shifted. This likely resulted from the die-back of shrub species that were less-tolerant of the reduced light levels. The diminished percent cover of *Rubus* spp. and the increasing contribution of cover from hazelnut, snowberry, and poison oak demonstrated this. Diversity increased with age beyond canopy closure, likely related to shade-tolerant species replacing shade–intolerant species.

Indicative of Franklin's vertical diversification and Oliver's stem-reinitiation stages, the number of canopy layers increased with stand age. I expected the light-restricted middle and lower canopy layers to be dominated by shade-tolerant cover. Yet my results did not demonstrate a significant component of shade-tolerant trees in the lower and middle layers. In fact mean percent cover of shade-tolerant trees rarely exceeded 20% and even decreased in the oldest wet-conifer stands. However, while absolute quantities of shade-tolerant cover generally were low, the mean proportions of shade-tolerant cover in the lower and middle layers were higher than for the upper layer. This finding is indicative of the more dominant role that shade-tolerant species play below the upper layer of canopy.

In the wet-conifer forests I expected shade-tolerant species to be more prevalent in all the canopy layers. In the older stands, I anticipated higher amounts of western hemlock and western redcedar in the middle and upper cover layers than in young stands. This was because I expected shade-tolerant species to be released by horizontal differentiation. In a previous study of a 400-500 year old Douglas-fir, western hemlock stand in southwestern Washington, Ishii et al. (2000) suggested future forest canopy development would entail western hemlock and western redcedar slowly invading the upper canopy while Pacific silver fir and Pacific yew remained in the lower canopy. However, even the proportions of shade-tolerant cover dropped in the old-growth stands in my study. This was not expected given that western hemlock is generally the climax species in Douglas-fir forests. However, I was working with very small sample sizes in these older-aged stands. Therefore, shade-tolerant percent cover may have been lower in the set of old-growth stands because these older aged Douglas-fir stands were found in geographic areas with low precipitation levels (see Fig. 2.4). As shade-tolerant species like western hemlock do not generally do well on drier sites, Douglas-fir becomes a climax species at these drier sites (Burns and Honkala 1990). In the 400-500 year old stand studied by Ishii et al. Douglas-fir was likely to persist as the dominant in the upper canopy for a century or more. Therefore, the lack of increase in upper and middle layer shade-tolerant cover may also be a function of my chronosequence not going far enough out in time and/or not capturing the full range of site conditions for the oldest stands in this study.

Compared with the wet-conifer forests, I expected lower percent absolute shade-tolerant cover in the hardwood forests because of their dominant tree species generally being less shade-tolerant (see Table 2.2). While some species are partially shade-tolerant and able to regenerate successfully under their own canopies, they are intolerant of overtopping by conifers (e.g. Oregon white oak; Burns and Honkala 1990). With conifers present in many of the hardwood stands, I generally saw low percent and proportions of shade-tolerant cover in these forests. However, for the single wet hardwood stands at ages 105 and 250 some of the cover layers were predominantly shade-tolerant species. This resulted because western redcedar and western hemlock were also present in these stands.

Contributions from canopy layers generally corresponded with the development criteria of the stand-condition classes. Prior to old-growth in the wet-conifer and wet-hardwood stands, the upper canopy layer contributed the most to total canopy cover, except for similar percent canopy cover in the upper and middle layers of wet-hardwood OSP stands. The exception seen for the wet-hardwood OSP stands suggests the openness of the upper layer allowed for uneven vertical canopy layering. Also, given that wet-hardwoods naturally regenerate, it is more likely to have a multi-layered unevenaged cohort of trees, compared with artificially regenerated single-layer conifer forests. In later development stages the wet-hardwood upper canopy layer likely continued to spread horizontally with overtopping of the shade-intolerants of the middle layer leading to death and resulting in reduced canopy cover in the middle layer. Easter and Spies (1994) found canopies of mature stands in their study on the western slopes of the Cascade Range (ages 90-145) were monolayers of Douglas-fir with minimal amounts of shade-tolerant hardwoods and conifers in the lower story. This finding of a dominant single layer was expected because of the relative shade-intolerance of the dominant species (i.e. Douglas-fir and red alder) in these forest groups, and the lack of shade-tolerants in the understory. With a dominant cohort of trees in the upper layer, the crowns of the shade-intolerant trees in the lower layers were unable to develop. The canopy architecture of the wet-conifer stands also may contribute to the dominant upper layer of canopy. Stands of conical crowned trees have greater surface area per unit area than stands with rounded or flat crowned trees (Oliver and Larson, 1996). This larger growth in volume also can contribute to reduced light penetration to the middle and lower canopy layers.

In the three wet hardwood stands older than age 85, percent canopy cover for the upper layer was lower than percent cover of the middle layer. For these stands non-wet-hardwood tree species comprised the upper layer (i.e., Douglas-fir, Oregon white oak, western redcedar). Also, caution should be made in interpreting results of the age 250 stand. FIA calculated it as a 250-year hardwood stand but the alders present in the stand were around age 55, and all the trees >200 years were conifers. The upper layer of this stand was primarily legacy conifers, and thus the predominant alder trees in the middle canopy layer contributed the most to total canopy cover. In reality, the middle layer of these stands was comparable to the upper layer for the younger stands that lacked remnant trees.

Observed trends in canopy-layer heights across stand development stages were expected, but the lack of growth in the lower height layer across the general forest groups was surprising. For the later stages of stand development I expected horizontal heterogeneity and gap formation would lead to release of the lower layer trees and taller tree heights in this layer. This was not seen in the two hardwood forest groups, and was only evident in the stands > 250 years in the wet-conifer group. The lack of height development and low percent cover (< 20%) indicate this layer is spotty. A third layer may not be an appropriate descriptor for western Oregon hardwood forests. Thus, these stands may be better described as two-story forests. Alternatively, the FIA criteria of using 5-m vertical splits in the canopy to differentiate layers of cover may not be appropriate for shorter hardwood forests.

With their greater maximum height potentials, wet-conifer forests are more likely to have breaks in their canopy than hardwood forests.

Several of the wet-conifer stands in this study met the criteria of Franklin et al.'s horizontal diversification and pioneer-cohort loss phases and Oliver's old-growth stage. There was a sizeable increase in the percent cover and canopy height of the lower layer starting with the 250-year stands. This shift was consistent with gap formation releasing the shade-tolerant tree species found in the lower layer. The equal contribution of all three canopy layers in the 400-yr stands is likely related to the development of canopy gaps which opened up the understory and released advance regeneration trees in the middle and lower layers. The formation of larger gaps would also allow for establishment of less shade-tolerant species. My finding of distinct differences between the old-growth and earlier successional stages supports the important role the canopy plays in distinguishing the old-growth stage.

In the wet-hardwood forests, the height of the upper canopy layer was similar across stand age and condition classes. Most of these stands were red alder and bigleaf maple, which are species that experience rapid height growth when they are young (< 20 years; Burns and Honkala 1990). Instead growth in more developed stand conditions was likely limited to horizontal elongation, as the trees branched out laterally. This helps to explain the trend towards lack of vertical differentiation among later development stages. Therefore, arraying canopy heights by stand condition class may not adequately capture the quick vertical development occurring in the younger wet-hardwood stands.

Canopy layering was more variable in the dry-hardwood stands than in the other two forest groups. This is likely a function of the stressful environments these forest groups typically inhabit. In fact, Oregon white oak, the dominant species in many of the dry-hardwood stands is described as a climax species. Compared with other species, it has a superior ability to establish itself and persist in stressful environments, including sparse yearly or seasonal precipitation locales, where soils are droughty or shallow, and where fire is a natural repeated occurrence (Burns and

Honkala 1990). With the highly variable range of conditions where Oregon white oak establishes, I would expect the canopy cover to differ in response to the given site conditions. I expected stand development stage to play a less critical role than the site condition.

Comparison of ocular estimates made by field surveyors and line-intercept estimates provided conflicting results. Mean line-intercept canopy cover estimates were consistently >60% for OSAW stands, which contradicted the FIA criteria of < 60% that is used by the field crews. Cover estimates agreed for OSP (i.e. < 60%) but not for OSAW, which suggests that field personnel consistently underestimated canopy cover in the stands with larger diameter trees. It is unclear why this underestimation was inconsistent across tree-size distributions. It may be that taller tree heights in OSAW stands resulted in lower estimates of canopy cover than stands with similar canopy cover closer to the ground. This finding has implications for sampling methods. Coarse ocular estimates of canopy cover for younger, smaller stands appear adequate, but more detailed ground-based measures may be required for older and taller stands.

Stand-size class did not effectively differentiate canopy patterns. While tree size-class distributions provided detail on stand-scale structure, they did not differentiate among canopy attributes of young and old-growth stands. With the large number of small trees in old-growth forests, mean tree heights and diameters may be similar to those in young stands (Franklin and Spies 1991). The results of this study suggest canopy structure patterns along a stand development gradient correlate better with stand-condition and stand-age than with stand size.

Thinning Intensity

Only in the heavy-thin stands did total and upper canopy layer cover differ from undisturbed Douglas-fir stands. Commercial thinning generally coincides with crown closure to ensure steady radial log growth (Berg et al. 1996). With large gaps between trees in the heavy-thin stands, remaining trees could not use all of the newly available area in the time since thinning. Under light-thin conditions, the remaining trees could quickly fill in the newly available space through lateral branch development. This likely explains the lack of difference among ND and LT stands.

I expected differences in understory cover between the thinned and undisturbed stands. However, differences in overstory cover did not appear to have significant effects on understory development. Shrub and forb percent cover were consistent across all harvest levels. This supports my concept that light levels with all thinning intensities allow for consistent understory cover levels, although species composition may change. Although, this will depend on the pre-thinning cover levels.

Stand heights in the light- and heavy-thin stands were taller than the unthinned stands. The differences were likely due to higher site quality of thinned stand compared with the undisturbed sites. The mean age for the undisturbed stands was 31 years, while the two thinning levels both had mean ages of around 34 years. Thus, the difference may also be partially attributed to differences in mean ages among the three levels of management.

Reduction in shade-tolerant cover with thinning was observed. This decrease suggested thinning primarily targeted commercially undesirable shade-tolerant species. The shade-intolerant Douglas-fir were targeted for commercial timber production and so less Douglas-fir than shade-tolerant species were harvested during thinning activities.

Ownership

Canopy cover varied by ownership with highest cover levels on public lands. The public lands were primarily State-owned forest, including the Tillamook State Forest that was largely artificially regenerated after the Tillamook Burns (1933, 1939, 1945, and 1951). The majority of the public stands were $\geq$ 35 years (77%), while a greater proportion of the stands were younger in the private industrial (50%

< 35 years) and non-industrial (35% < 35 years) forests. The higher cover levels on public lands compared with private lands may be a result of the older ages of the public stands. Also, there may be less thinning and clearcutting employed on public lands, compared with more active management policies of the private-industrial forests. While breaking out ownership by stand age or stand condition may have revealed more apparent differences, the lack of sufficient sample units excluded my ability to do this.

I expected differences in understory cover among the three ownership classes. Higher levels of herbicide treatment on industrial forests would maximize seedling survival. However, ownership differences were not detected. A potential reason for this is all age classes were lumped together in this analysis. Youngest stands are managed more intensively. Thus, assessments across stand ages would better discern differences. Sample sizes were too limited, however, for such an assessment.

Limitations

There are nine factors that limit interpretation of the results of this study:

1) The inventory was depauperate of older aged stands, as the majority of older stands are located on federal land (Campbell et al. 2002) excluded from this study. Therefore, caution should be used in interpreting results for stand ages beyond age 115 for wet-conifer and dry-hardwood stands, and beyond age 65 for the wet-hardwood stands.

2) Predominant tree species were used to define forest types, but with stand age calculated using all species present. Other species present in less abundant quantities could still contribute large amounts of canopy cover. In the case of hardwood forests, there could be coniferous trees present which could potentially obscure hardwood species canopy patterns for the given forest type. This was demonstrated in the single age 250 'wet hardwood' stand where the hardwoods were only 65 yrs old.

3) I studied a chronosequence of stand ages, substituting space for time. This approach lumped stand with variations in site attributes, such as differences in mean precipitation levels, aspect, and elevation. Canopy structure changes based on a chronosequence approach may not reflect development trends of a stand.

4) Stand condition was classified on-site by surveyors and therefore was somewhat subjective. My calculated results demonstrated cover estimates made in the field were sometimes inaccurate. Therefore, there may be limited value in classifying stand conditions in the field using percent canopy cover as a selection criterion, especially for the stands with a few larger dbh trees, as seen in the OSAW stands.

5) The criteria for the old-growth stand condition included an average stand diameter of >53.3 cm. While the stand diameter criterion is relevant for conifer-dominated old-growth, it excluded hardwood-dominated forests in the PNW that did not meet this stand-diameter criteria. Old-growth deciduous forests have been described in other regions (e.g. Batista and Platt 1997; Tanner and Hamel 2002). With removal of the stand diameter criterion, the FIA old-growth stand condition could be used to describe hardwood old-growth in western Oregon. At present, the FIA criteria for old-growth tend to exclude hardwood-dominated forests. The FIA inventory's set of stand conditions were not effective for interpreting canopy cover results for hardwood forests.

6) The way disturbance history was determined in the field inventory limited detailed comparisons of management effects on canopy attributes. The surveyors, based on an ocular assessment, collected the disturbance history. Examining the disturbance criteria, heavy and light partial harvests were distinguishable, but the criteria included a percent crown cover. Thus, this was prone to errors associated with subjective estimates made by surveyors, compared with actual line-intercept calculated canopy cover. This combined with a lack of ample sample sizes for thorough analysis, restricted my ability to explore the scope of relationships between canopy structure and management history.

7) Sample sizes for the hardwood forests were much smaller, compared with the wet-conifer forests, and thus revealed relationships should be viewed with caution.

8) There were multiple factors that contributed to the variability of understory cover and shrub species richness among stand ages. First, the number of stands varied among stand ages. Second, the study sites encompassed a wide range of environment conditions. Understory species are generally found in locations that meet their individual habitat requirements (e.g. soil pH, elevation), rather than across the spectrum of environment conditions. So I would not expect species to be found in all of the stands used in this study. Therefore, trends in understory cover among stand ages were confounded by other sources of variability, and inferences about overstory - understory relationships should be made with caution.

9) The line-intercept layers were relative to the stand in which they were measured. As a result, while we examined trends among layers, the heights of layers weren't directly equitable among stands. Therefore, interpretations of results associated with layering should be viewed with caution.

Summary

1) I evaluated patterns of vertical and horizontal canopy structure and understory cover among stand ages, stand condition classes, and stand size classes, using 934 forested plots in western Oregon measured by the USDA Forest Service Forest Inventory and Analysis (FIA) program between 1995 and 1997 on private and non-federal public lands.

2) In general, overstory canopy cover increased with development stage for all of the forest groups analyzed. The upper tree canopy layer contributed the most to total cover except in the dry-hardwood stands, where the vertical distribution of tree cover was more evenly distributed.

3) Mean canopy cover rarely exceeded 85%, even in productive young conifer-dominated forests.

4) The upper and middle layers of canopy increased in height with stand development, while the lower layer remained short among forest groups. Forests in western Oregon appeared to be primarily two-layered until they reached old-growth stage.

5) The mean number of layers increased with development stage for wet-conifer and wet-hardwood stands, but was more variable for dry-hardwood stands.

6) Patterns in forb cover varied among the forest types. In the wet-conifer and dry-hardwood stands, forb cover decreased between ages 15-45. It did not decrease in the wet-hardwood forests. Forb cover generally exceeded shrub cover in dry-hardwood stands >45 years, while shrub cover generally exceeded forb cover in the other forest groups.

7) Contrary to expectations, cover of understory shrubs was not substantially lower in young closed-canopy stands than in other stands, although diversity did decrease.

8) Shade-tolerant species rarely made up more than 20% of canopy cover by age class, even in the lower canopy layers and in stands >100 yrs old.

9) The proportion of shade-tolerant cover was higher in the lower layer of cover, compared with the middle and upper layers among stand development stages. However, the proportions of shade-tolerant cover actually decreased in the oldest stands. This could be a result of gappiness and increased light levels leading to shade-intolerants invading the gaps.

10) Stand age was the best surrogate for stand development stage. Stand size-class was a poor differentiator of patterns in canopy structure

11) There were differences observed among the three thinning intensities. In heavy-thin stands, percent canopy cover was lower than in unthinned and light-thin stands. Unthinned stands had higher levels of shade-tolerant cover. This suggests that thinning activities selected for shade-tolerant species rather than the shade-intolerant species, which are primarily targeted for timber production.

12) Publicly-owned lands had higher percent cover than did the privately-owned lands.

13) Ocular field estimates of cover may not be adequate for stand-condition classification.

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PREDICTION OF CANOPY COVER FROM STANDARD FOREST INVENTORY MEASUREMENTS FOR THREE GENERAL FOREST GROUPS IN WESTERN OREGON

Abstract

Quantifying canopy cover is important for the management of public and private forests in the Pacific Northwest. However, sampling of canopy cover can be both labor and time-intensive. The prediction of canopy cover from other more readily measured stand attributes may reduce time and cost spent in the field. Alternatively, aerial photos may be used to estimate cover. Ground-based cover measures were compared with cover predicted by regression models from standard forest measurements, and with estimates from aerial photography and the forest vegetation simulator (FVS) program. Predictive models were developed for three general forest groups sampled by the Forest Inventory and Analysis (FIA) program in western Oregon: wet conifer, wet hardwood, and dry hardwood. Model predictions from inventory measurements were within 15 percent of measured cover for > 82% of the observations. Standard inventory estimates of cover using 1:40,000 scale aerial photos were poorly correlated with ground-measured cover, especially in wet-hardwood (r=0.58) and dry-harwood (r=0.61) stands. FVS tended to underestimate cover by up to 50% in wet-conifer and wet-hardwood stands. Thus, the aerial photos and FVS equations used in this study are not recommended as surrogates for ground-based measurements of cover. However, the level of accuracies of the predictive models may be adequate for some purposes.

Introduction

Quantifying canopy cover, the percent of the slope-corrected forest area occupied by vertical projection of tree crowns, is important for the management of public and private forests in the Pacific Northwest (PNW). Amount of cover and the vertical structure of forest canopies influence disease and insect susceptibility (Mathiasen 1996; Winchester and Ring 1996), fire hazard (Latham et al. 1998), atmospheric interactions (Rose 1996), microclimate (Yang et al. 1999), and habitat structure (Maguire and Bennett 1996). The canopy also plays multiple roles including roosting, nesting, foraging, and as thermal cover for numerous wildlife species (MacArthur and MacArthur 1961; Thomas and Verner 1986; Hayes et al. 1997; North et al. 1999; Johnson and O'Neill 2001). Canopy cover is one of the three parameters used in describing the California Wildlife Habitat Relationship (CWHR) classes (Mayer and Laudenslayer 1988). Canopy cover data are also used for predicting tree volume, potential forage production, and for the evaluation of forest pest damage (O'Brien 1989). Thus, reliable estimates of canopy cover are essential for the management of multiple objectives in forestlands.

Because ground sampling of canopy cover is labor and time-intensive, alternative approaches have been used to estimate canopy cover. Aerial photography is one such method. However, in multi-layered or high foliage density forests, measuring the outer/upper canopy surface may underestimate forest canopy cover (Van Pelt and North 1996). Ground-based measurements with the line-intercept method are considered more accurate than ocular estimates of intercepts from photos (O'Brien 1989). This is because individual crown areas recorded from overhead can miss portions of the canopy that extend below the upper surface of the canopy (Gill et al. 2000). Lund et al. (1981) demonstrated a relationship between aerial estimates of tree canopy cover and stocking. Bentley (1996) explored relationships between tree growth and stand parameters associated with canopy cover in northern Ontario white pine (*Pinus strobus* L.) forests. In ponderosa pine (*Pinus ponderosa* P.& C. Lawson) stands in the southern Rockies, Mitchell and Popovich (1997) evaluated the ability of multiple stand- and tree-level biotic and abiotic variables (e.g. elevation, basal area, tree height) to estimate canopy cover. Tree composition and cover were estimated from basal area and stand density by Cade (1997) in lodgepole pine (*Pinus contorta* Dougl. ex Loud.), Engelmann spruce (*Picea engelmanni* (D.C. Eat.) Gray), and subalpine fir (*Abies lasiocarpa* Ehrh.)

stands. Canopy height models were used to relate canopy-height characteristics to biometric measurements (e.g. basal area, stem volume, aboveground woody biomass) by Nelson et al. 1998. Buckley et al. (1999) investigated relationship of canopy cover and multiple other variables in Michigan oak and pine stands. Multiple studies have calculated crown radii using predictive equations (e.g. Paine and Hann 1982, Gill et al. 2000). The Pacific Northwest Regional Variant of the Forest Vegetation Simulator (FVS) has evolved from the Prognosis model of Moeur (1985), modeling overlap-corrected stand-level percent canopy cover by summing individual tree crown areas, using crown radii formulae of tree species specific to the region, and then correcting for overlap (Crookston and Stage 1999).

In general, very few previous studies have had success in predicting cover from other standard inventory measures and minimal attention has been given to estimating cover in hardwood forests. Aside from cover predicted using FVS, I am unaware of other equations that model canopy cover for the general forest groups of western Oregon. It is of interest to see how well predictive models and/or aerial photos can estimate canopy cover among conifer and hardwood-dominated forests. With creation of improved cover prediction models from either ground or aerial measurements, classifications of wildlife habitat suitability, stand fire hazard, etc. that are based on percent cover may potentially be improved, without expending the effort required for collection of ground-based cover measures.

In this study I addressed the research question: Can standard forest inventory measurements associated with forest development stage be used to predict total percent canopy cover, as an alternative to time-intensive canopy cover sampling for stands in western Oregon? I was also interested in whether aerial photography or FVS-predicted cover could be used as surrogates for ground-based canopy sampling. Because patterns in canopy structure differed among forest types in western Oregon (see Chapter 2), I addressed questions separately within forest types. I hypothesized that standard forest measurements could be used to estimate total percent canopy cover for wet-conifer, wet-hardwood, and dry-hardwood forests in western Oregon.

Methods

Study Area and Population of Interest

I used a subset of the western Oregon data collected by the USDA Forest Service Forest Inventory and Analysis (FIA) program from 1994-1997 (Azuma et al. 2002). Study sites of the FIA program consist of a permanent grid of plots located throughout western Oregon (Fig. 3.1). Western Oregon is defined as the area west of the crest of the Cascade Mountain Range, delimited by county boundary lines. The FIA study sites include all private and public forested lands, excluding Bureau of Land Management (BLM) and USDA Forest Service National Forest lands.

The study sites used in this study encompassed five physiographic provinces: The Oregon Coast Range, The Willamette Valley, Oregon Western Cascades, Klamath Mountains, and High Cascades (Franklin and Dyrness 1973). The forest zones included in the FIA inventory included the *Picea sitchensis*, *Tsuga heterophylla*, *Abies amabilis*, *Tsuga mertensiana*, *Quercus* woodland, Interior Valley, Mixed-Evergreen, Mixed-Conifer, *Abies concolor*, and *Abies magnifica shastensis* (Franklin and Dyrness 1973).

Sample Design

The FIA inventory design was based on a double sample for stratification (Cochran 1977). An exception was that permanently established primary photo-interpreted plots and secondary field plots were used for the design. In the first phase of sampling, conducted in 1994, 1:40000 scale black and white aerial photos at photo- points systematically distributed on a 1.36-km grid were used to estimate land use type, successional stage, and canopy cover. The second phase completed

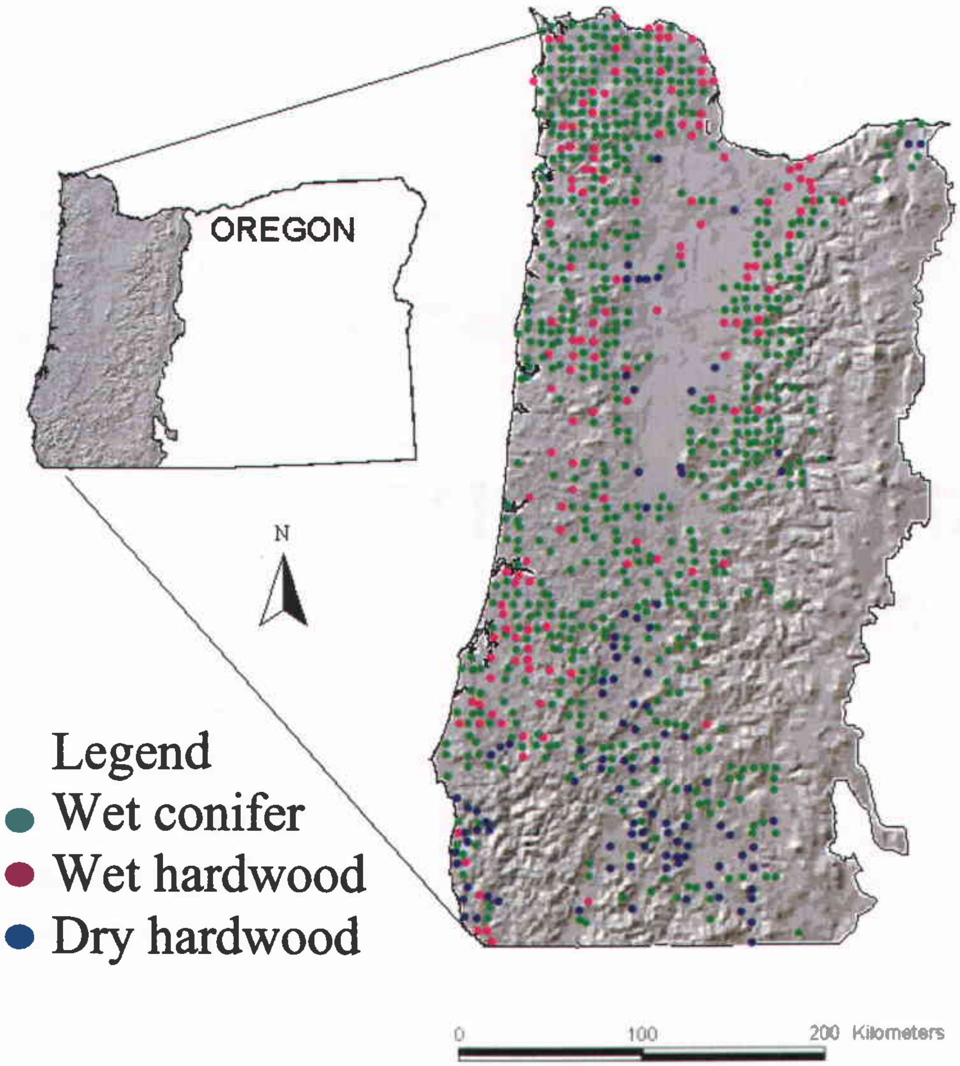

Fig 3.1. Locations of the 884 forested FIA 1995-97 inventory plots analyzed in this study.

from 1995-97 involved a ground plot sampling of approximately every 16th photo-point, with a grid density of 5.4-km. The systematic-grid design of this inventory allows for statistical inferences to the population from which the grid points were sampled. Information compiled and distributed from the FIA inventory is comprehensive, has minimal bias, is scientifically sound, and has known precision (Azuma and Hanson 2002). Therefore, results of analyses of the forested plots are representative of all non-federal forests in western Oregon.

All 1127 forested plots consisted of a systematically-arranged cluster of 5 0.09-ha subplots encompassed in a 2.5-ha area, regardless of stand boundaries or forest types (Fig. 3.2). Subplots were delineated into multiple condition classes to identify subplots that contained more than one forest type, stand-size class, management intensity category, or overlapped with non-forest land.

I only used plot information for the single forested condition class that comprised a minimum area of 0.27 ha (three subplots). A high degree of variability in canopy cover within a condition class was expected. I excluded cover data from the other condition classes in a plot because I felt areas < 0.27 ha could not adequately capture this variability. Out of the 1127 plots, there were 934 plots that met this criterion. Therefore, for each of these 934 plots the size of the experimental unit was the area of the plot contained in the single largest condition class. I will use the term stand throughout the remainder of this paper to refer to the experimental unit.

Data Collection

For each stand, multiple measurements were obtained. Composition, cover, and height of all shrubs, and forbs and grasses with > 3% cover were measured on 5-m fixed-radius plots around each subplot center (see Fig. 3.2). Trees were measured to a fixed-distance of 17 m from subplot centers in fixed-radius and variable-radius plots, using a 7-m2/ha basal area factor (BAF) prism. Age, dbh, compacted crown ratio, and height of all trees > 1.4 m tall were measured.

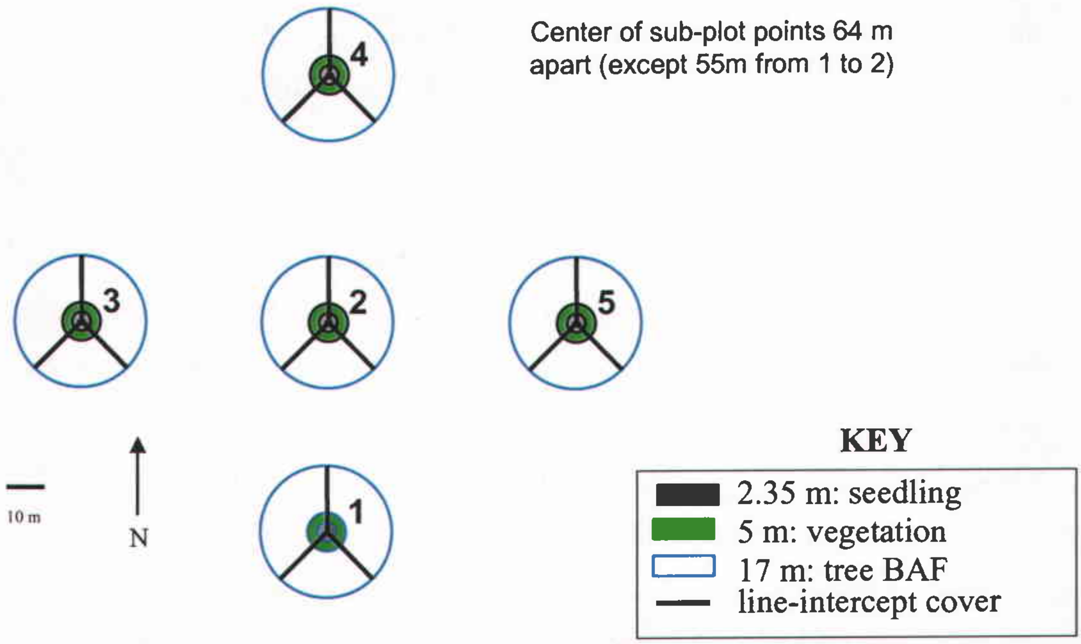

Fig 3.2. Design of the 1995-97 FIA inventory ground plot lay-out for western Oregon.

For each condition class, ground-based canopy cover estimates were collected. Trees were assigned to one of three canopy layers, with discrete layers differing by a minimum of 5 m in mean height. However, actual heights varied between stands, as canopy layers were relative to conditions within a stand. The line-intercept method was used to calculate percent canopy cover in each layer (Canfield 1941; O'Brien 1989). Canopy layers were classified as upper, middle, and lower based on relative stature. For every tree species within a canopy layer, crown boundaries were vertically projected onto transects. The distance along a transect line that the crown intercepted was recorded. Canopy cover was sampled on three 17-m long horizontal transects originating at subplot center and radiating out at 0, 135, and 225 degrees. The proportion of transect lengths that were intercepted by the crowns was the ground-estimated canopy cover.

Calculated FIA Variables

Multiple canopy cover values were calculated from the line-intercept data. Canopy transects that crossed condition classes were excluded because of errors assigning condition classes. Cover for individual tree species was calculated for each of the vertical layers. Cover by species by layer was vertically collapsed to calculate total cover. Thus cover never exceeded 100%.

Stand age and forest type were calculated for each stand. Stands were grouped into 10-yr age classes up to age 200, lumped into a 100-yr age class for ages 200-300, and stands > 300 yrs were all combined into a single age class (age 400). Stand age calculations distinguished between evenaged and unevenaged stands. Forest type was calculated in a two-step process. The first criteria determined whether hardwood or softwood trees dominated the stand. Then the forest type was assigned based on the stocking density of the predominant species of "mainstand" trees within the hardwood or softwood group.

Additional independent variables that could be used in my regression models to predict canopy cover were also calculated. Stocking density, the contribution of measured trees to a fully-stocked stand, based on normal yield tables, was calculated from multiple equations (Azuma and Hanson 2002). Stem density, basal area, mean annual increment, and quadratic mean diameters were also calculated from the tree data collected in the FIA inventory.

I calculated stem frequencies by size, crown-ratio, and tree-height classes. Three size classes were used (dbh $\leq$ 30 cm, 30-50, > 50). Crown classes only included dominant and co-dominant trees, as these were the trees expected to contribute most to total cover. Crowns were compacted crown ratios. Crown classes included: crown $\leq$ 10%, 10 < crown $\leq$ 40, 40 < crown $\leq$ 60, and crown > 60%. I used four tree height classes to divide stem density (tree height $\leq$ 5m, 5-20, 20-30, > 30). Divisions were kept broad enough that other datasets could be readily modified and incorporated into them (i.e. if I had selected narrower classes, this would limit the ability of other researchers with broader classifications to use them, whereas with the broad classes, finer classifications can easily be summed to the broader class level).

Each stand was assigned to one of four general forest groups. The forest groups were first clustered based on hardwood or softwood dominance. They were further divided based on the moisture levels characteristic of sites occupied by the dominant tree species in each forest group. Douglas-fir was the predominant species in the wet-conifer group; red alder (*Alnus rubra* Bong) was the dominant species in the majority of wet-hardwood stands, and Oregon white oak (*Quercus garryana* Dougl. ex Hook) and Pacific madrone (*Arbutus menziesii* Pursh) dominated in most of the dry-hardwood stands. I only performed analyses on the three most plentiful general forest groups: wet conifer, wet hardwood, and dry hardwood (884 stands; Table 3.1). The fourth possible forest group, dry conifer, had limited samples and was not analyzed.

Mean annual precipitation was estimated with the PRISM climate model (Daly et al. 1994). The mean annual precipitation by stand age was calculated in each of the four general forest groups and helped identify the transition between wet and dry forest types (Fig. 3.3).

Table 3.1. The three general forest groups included in the 1995-97 FIA ground inventory that met the criteria for inclusion in this study. Stands were grouped by hardwood and conifer type, and mean precipitation levels.

General forest group	n	Age range	Dominant tree species in the stand[a]
Wet conifer	645	5-400	*Pseudotsuga menziesii* (n=558), *Tsuga heterophylla* (n=57), *Picea sitchensis* (n=15), *Thuja plicata* (n=7), *Abies procera* Rehd. (n=4), *Abies amabilis* (n=2), *Chamaecyparis lawsoniana* (A. Murr.) Parl. (n=2)
Wet hardwood	137	5-250	*Alnus rubra* (n=99), *Acer macrophyllum* Pursh. (n=25), *Populus balsamifera* L. ssp. trichocarpa (Torr. & Gray) Brayshaw (Salicaceae) (n=5), *Salix* spp. (n=3), *Umbellularia californica* (Hook. & Arn.) Nutt. (n=3), *Fraxinus latifolia* Benth. Ore a. (n=2)
Dry hardwood	102	5-165	*Quercus garryana* (n=42), *Arbutus menziesii* (n=32), *Lithocarpus densiflora* (Hook. & Arn.) Rehd. (n=18), *Quercus kelloggii* Newb. (n=6), *Quercus chrysolepis* Liebm. (n=3), *Castanopsis chrysophylla* (Dougl.) DC. (n=1)

[a]The number in brackets is the number of plots in which the given species was dominant in the stand.

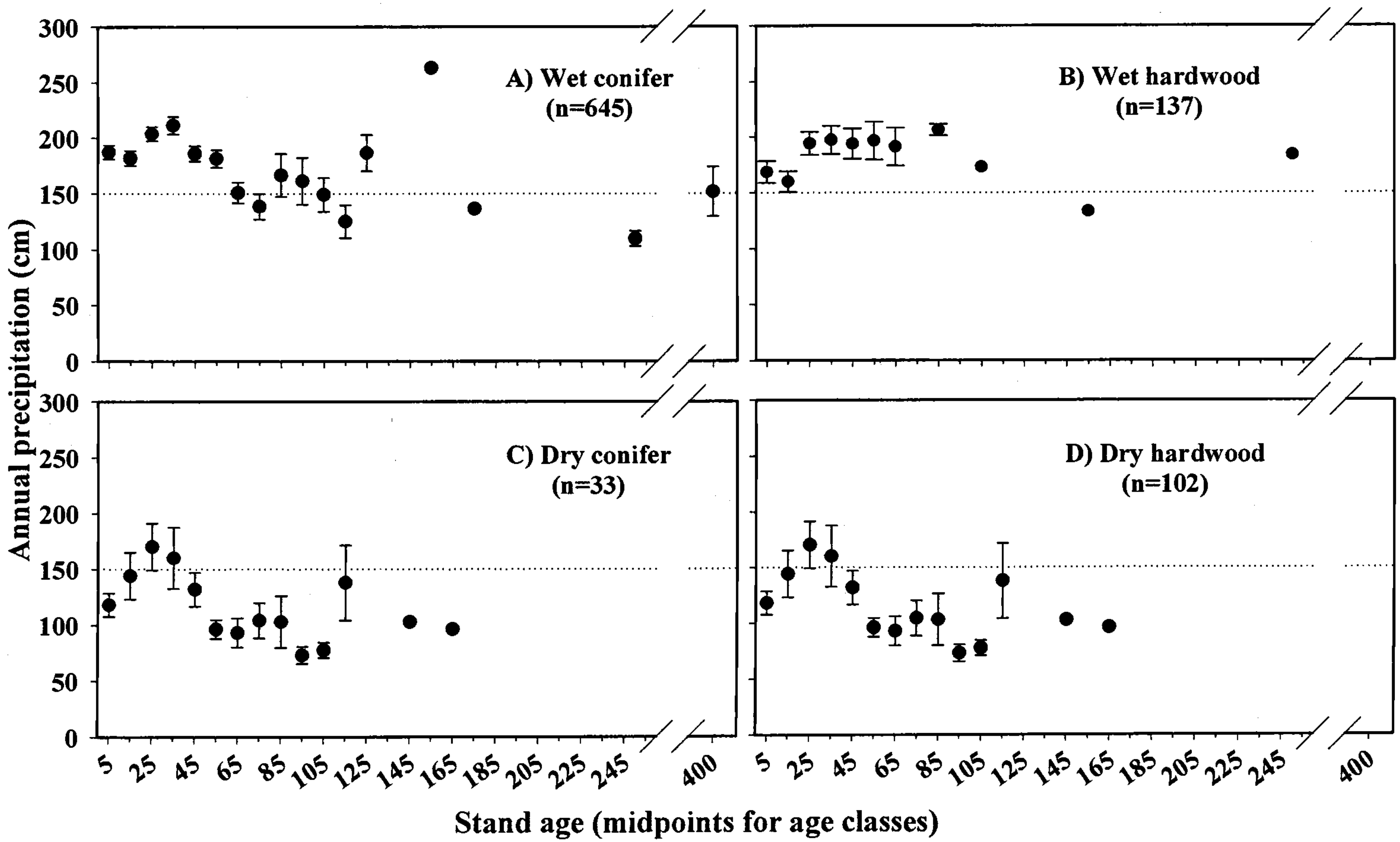

Fig 3.3. Mean annual precipitation (± 1 SE) estimated using the PRISM model (Daly et al. 1994) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 3.1) in western Oregon. Sample sizes differed among stand ages. Dotted line at 150 cm represents the division between wet and dry mean precipitation levels.

Aerial vs. Line-Intercept Canopy Cover

The line-intercept cover measurements were compared with the aerial photo interpreted cover estimates for the stands. Aerial photos were centered on subplot 1 (see Fig. 3.2). If the forested condition class used in the analysis did not include subplot 1, the stand was excluded from this analysis. For the three general forest groups, the remote cover estimates were plotted against the ground-based estimates, and Pearson correlation coefficients were used to determine level of agreement between ground and aerial estimates.

Comparison of FVS and Line-Intercept Cover

FVS is an individual tree, distance-independent growth and yield model (Donnelly and Johnson 1997). FVS can model a wide variety of forest types and stand structures. It is commonly used by the Forest Service as a forest management tool to compare alternative treatments. Variants of the simulator are specific to geographic areas. The Pacific Northwest Regional Variant models stand level percent canopy cover by summing individual tree crown areas, using tree species crown radii formulae specific to the region (Crookston and Stage 1999), fitting a standard equation to measurements made on Current Vegetation Survey trees generated the crown radii formulae. The original FVS canopy cover calculations did not account for overlap among tree crowns, and thus cover estimates could exceed 100%:

$$C' = 100(\Sigma pi\ ai\ )A^{-1} \qquad \text{(Eqn. 3.1)}$$

Where:

C' = percent canopy cover without accounting for overlap,
pi = trees per acre for the ith sample tree,
ai = projected crown area for the ith tree in ft 2 /acre,
A =ft^2 /acre (43560)

However, Crookston and Stage (1999) corrected for crown overlap with creation of an equation that accounts for the overlap by assuming random distribution of canopy elements:

$$C = 100\,[1 - \exp\,(-.01\,C')] \qquad \text{(Eqn. 3.2)}$$

Where:

C = percent canopy cover that accounts for overlap
C' = Equation 3.1

This modified equation provides cover estimates that are $\leq 100\%$.

I calculated overlap-corrected cover using the unpublished FVS Region 6 Variant crown radii formulae for each stand among the three general forest groups. The formulae used live tree species and dbh information for all trees within the stand. The crown radii were input into the FVS cover equations based on the area of the sample plot and the corresponding density represented by sampled trees.

FVS-generated cover estimates were compared with the line-intercept canopy cover values among the three forest groups. FVS-generated cover measures were plotted against the ground-based estimates. Pearson correlation coefficients were also used to determine level of agreement between ground and FVS cover estimates.

Prediction of Cover

Mean total cover and cover of the upper canopy layer changed more with age and stand-development than the middle and lower layers (see Chapter Two). However, given that the upper layer was relative to stand conditions, it could not be predicted. Thus, I only examined the ability of stand measurements to predict total canopy cover.

The three forest groups described in Chapter 2 have distinct compositions and environments and patterns of canopy structure development differed among them. Therefore, it was important to create predictive models for each of these forest groups independently.

I used an information-theoretic approach to predict canopy cover levels for forest stands in western Oregon. I developed a set of *a priori* hypotheses relating the amount of canopy cover to forest attributes measured in the FIA inventory. I expressed these hypotheses as multiple linear regression models that were fit to the inventory data.

I then used an objective model selection criterion, Akaike's information criterion for small sample sizes (AICc), to rank the models according to their ability to approximate the data (Burnham and Anderson 1998). This resulted in a "best approximating model" that was the most parsimonious explanation of the data. In addition a "good set" of approximating models was selected based on Akaike weights. Akaike weights can be interpreted as approximate probabilities that given models are really the closest to the unknown "true" model of canopy cover (Anderson et al. 2000). A general rule of thumb for differences in AIC score is a range of 4-7 as the practical cutoff for defining a 95% confidence model set (Burnham and Anderson 1998). However, instead of limiting good models to the 95% confidence set, I included all models with Akaike weights > 0 to ensure I did not exclude potentially biologically important models or variables. An important caution is that model selection is only as good as the set of models hypothesized.

I selected AICc as my model selection method because I was interested in multiple models that could potentially be used by forest managers to predict canopy cover. FIA stand structure measures are fairly exhaustive and multiple variables measured by FIA are not always measured in other forest and wildlife habitat studies. Therefore, multiple good models with different subsets of measurement variables would increase their ability to be applied across a wider spectrum of forest studies.

Model development

Prior to data analysis, I hypothesized biologically meaningful relationships between canopy cover and the forest variables measured or calculated in the FIA inventory (Table 3.2). I based hypotheses on my working knowledge of forest stand dynamics and relationships between stand structure and mensuration measures. I also considered variables based on their use in previous studies that modeled canopy structure features in other regions of North America (e.g. Paine and Hann 1982; Moeur 1986; Bentley 1996; Cade 1997; Mitchell and Popovich 1997; Nelson et al. 1998; Crookston and Stage 1999; Gill et al. 2000; Buckley et al. 1999). For all models, canopy cover was logit transformed. This was done to remove the inherent bounding of canopy cover from 0 to 100%. With the logit transformation, my response (logitcover) became more equal to a linear function of the explanatory variables. I used both linear and transformed forms of explanatory variables when hypothesizing *a priori* relationships with logitcover (see Table 3.2).

Hypothesized relationships resulted in a set of 43 models using single variables or combinations of variables (Table 3.3). In addition I included a null model that only included an intercept term to confirm that richer models were explaining more information than would be explained by chance. I was unable to fit a global model containing all important variables due to the high correlation between variables. Therefore, I assessed general fit of all of my models by checking assumptions of constant variance and normality.

The mathematical model demonstrating a hypothesized regression model is:

$$\text{Predicted logitcover}_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n Xn + \varepsilon_i + \varepsilon_j \qquad \text{(Eqn. 3.3)}$$

Where:

$\varepsilon_i \sim N(0,\sigma^2_\varepsilon)$ and where ε_i and $\varepsilon_{i'}$ are independent,

β's are regression coefficients for predictive model variables X_1 to X_n, which are the variables contained within a given AIC model,

Table 3.2. Descriptions of explanatory variables measured in the FIA plots in western Oregon that were used in models to predict canopy coverage in FIA plots in western Oregon.

Variable	Abbreviation	Units	Expected relationship[1]	Transformation
Basal area	ba	m^2/ha	linear or square root	$\sqrt{ba}$
Elevation	elev	m	linear	
Mean annual increment	mai	ft^3/acre/yr	linear or quadratic	$mai + mai^2$
Number of tree species in a plot	nspecies	n/a	linear	
Precipitation[2]	precip	cm	linear	
Quadratic mean diameter	qmd	cm	linear or quadratic	$qmd + qmd^2$
Remotely-sensed aerial photo estimated cover	photocov	%	logit	logit(photocov)
Stand age	age	years	linear or inverse	1/age
Stand height[4]	height	m	linear	
Stocking density[3] (percent of normal stand occupied by trees)	stock	%	linear or square root	$\sqrt{stock}$
Total trees per hectare	tph	trees/ha	linear or quadratic	$tph + tph^2$
Trees per hectare in crown class 1 (<10% compacted crown)	tphcrn1	trees/ha	linear	
Trees per hectare in crown class 2 (10-40%)	tphcrn2	trees/ha	linear	
Trees per hectare in crown class 3 (40-60%)	tphcrn3	trees/ha	linear	
Trees per hectare in crown class 4 (>60%)	tphcrn4	trees/ha	linear	
Trees per hectare in dbh class 1 (tree dbh<30 cm)	tphdbh1	trees/ha	linear	
Trees per hectare in dbh class 2 (30-50 cm)	tphdbh2	trees/ha	linear	
Trees per hectare in dbh class 3 (>50 cm)	tphdbh3	trees/ha	linear	
Trees per hectare in height class 1 (tree height <5m)	tphht1	trees/ha	linear	
Trees per hectare in height class 2 (5-20m)	tphht2	trees/ha	linear	
Trees per hectare in height class 3(20-30m)	tphht3	trees/ha	linear	
Trees per hectare in height class 4 (>30m)	tphht4	trees/ha	linear	

[1] Relationships are predicted relationships with logit-transformed canopy cover.
[2] The PRISM climate model (Daly et al. 1994) was used to estimate mean annual precipitation.
[3] Stocking equations which are specific to site productivity and forest type are provided in the appendix.
[4] Stand height was calculated as the mean height of the upper layer of canopy cover.

Predicted logitcover is the predicted logit of percent canopy cover in the i^{th} stand,
ε_i is the random effect of each sample that adds variability to value of logitcanopy cover, and
ε_j is the uncertainty associated with where the future value will be in relation to its mean.

Statistical analysis of models

Prior to the model fitting process, stands within each forest group were divided into two subsets (Table 3.4). Seventy-five percent of the data were used to generate the models (model dataset). This set was randomly selected from the total number of stands for each of the general forest groups. The remaining 25% were set

Table 3.3. Description of *a priori* models describing potential predictors of total canopy cover in FIA plots in western Oregon. Descriptions of abbreviated variables are described in Table 3.2.

Model	Hypothesis	Model structure
1	No effects (null model)	β_0
2	Positive effect of mai (linear)	$\beta_0 + \beta_1(\text{mai})$
3	Positive effect of mai (quadratic)	$\beta_0 + \beta_1(\text{mai}) - \beta_2(\text{mai}^2)$
4	Positive effect of species diversity	$\beta_0 + \beta_1(\text{nspecies})$
5	Positive effect of stand age (linear)	$\beta_0 + \beta_1(\text{age})$
6	Inverse effect of stand age (inverse)	$\beta_0 + \beta_1(1/\text{age})$
7	Positive effect of increasing stand height	$\beta_0 + \beta_1(\text{height})$
8	Positive effect of stocking (linear)	$\beta_0 + \beta_1(\text{stocking})$
9	Positive effect of stocking (square root)	$\beta_0 + \beta_1(\sqrt{\text{stocking}})$
10	Positive effect of ba (linear)	$\beta_0 + \beta_1(\text{baha})$
11	Positive effect of ba (square root)	$\beta_0 + \beta_1(\sqrt{\text{baha}})$
12	Positive effect of qmd (linear response)	$\beta_0 + \beta_1(\text{qmd})$
13	Positive effect of qmd (quadratic response)	$\beta_0 + \beta_1(\text{qmd}) + \beta_2(\text{qmd}^2)$
14	Positive effect of tph (linear)	$\beta_0 + \beta_1(\text{tph})$
15	Positive effect of tph (quadratic)	$\beta_0 + \beta_1(\text{tph}) + \beta_2(\text{tph}^2)$
16	Positive effect of tph in ht class 1	$\beta_0 + \beta_1(\text{tphht1})$
17	Positive effect of tph in ht class 2	$\beta_0 + \beta_1(\text{tphht2})$
18	Positive effect of tph in ht class 3	$\beta_0 + \beta_1(\text{tphht3})$
19	Positive effect of tph in ht class 4	$\beta_0 + \beta_1(\text{tphht4})$
20	Positive effect of tph in dbh class 2	$\beta_0 + \beta_1(\text{tphdbh2})$
21	Positive effect of tph in dbh class 3	$\beta_0 + \beta_1(\text{tphdbh3})$
22	Positive effect of tph in crown ratio 2	$\beta_0 + \beta_1(\text{tphcrn2})$
23	Positive effect of tph in crown ratio 3	$\beta_0 + \beta_1(\text{tphcrn3})$

Table 3.3 Cont'd.

Model	Hypothesis	Model structure
24	Correlation with remote photos	$\beta_0 + \beta_1$(photocov)
25	Positive effect of precipitation and negative effect of elevation	$\beta_0 + \beta_1$(precip) - β_3(elev)
26	Positive effect of precipitation and mai	$\beta_0 + \beta_1$(precipitation) + β_3(mai)
27	Positive effect of stocking and stand height	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$(height)
28	Positive effect of stocking and mai	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$ (mai)
29	Positive effect of stocking, stand height, and mai	$\beta_0+\beta_1(\sqrt{\text{stock}})+\beta_2$(height)+$\beta_3$(mai)
30	Positive effect of basal area and stand height	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height)
31	Positive effect of basal area and inverse effect of age	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(1/age)
32	Positive effect of ba and mai	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(mai)
33	Positive effect of ba, stand height and mai	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height) + β_3(mai)
34	Positive effect of qmd and stand height	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height)
35	Positive effect of qmd and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(mai)
36	Positive effect of qmd, stand height, and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height) + β_4(mai)
37	Positive effect of tph and stand height	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height)
38	Positive effect of tph and mai	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(mai)
39	Positive effect of tph, stand height, and mai	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(mai)
40	Positive effect of tph, depending on basal area	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + $\beta_3(\sqrt{\text{baha}})$ + β_4(tph*baha)
41	Positive effect of tph in dbh classes 1,2, 3	β_0 + β_1(tphdbh1)+β_2(tphdbh2)+β_3(tphdbh3)
42	Positive effect of tph in ht1, 2, 3, and 4	$\beta_0+\beta_1$(tphht1)+β_2(tphht2)+β_3(tphht3)+ β_4(tphht4)
43	Positive effect of tph in crown ratio classes 1,2, and 3. Negative effects of crown ratio class 4.	$\beta_0 + \beta_1$(tphcrn1) + β_2(tphcrn2) + β_3(tphcrn3) + β_4(tphcrn4)
44	Positive effect of ba, mai, and stand height, and inverse effect of stand age.	$\beta_0 + \beta_{1+}\beta_2$(baha) + β_3(baha^2) + β_4(mai) + β_5(stand height)- β_6(1/age)

Table 3.4. Sample sizes used in model-fitting and model-testing for each of the three general forest groups analyzed in this study.

Forest group	Model dataset (n)	Test dataset (n)
Wet-conifer	484	161
Wet-hardwood	103	34
Dry-hardwood	76	26
Total	663	221

aside to corroborate the fit of the model after it was completed (test dataset). Ranges of values for the explanatory variables were similar for the model and test datasets.

Models were fit using PROC MIXED (SAS Institute 1999). I evaluated the fit of the models by examining normality using PROC UNIVARIATE, and also checked residual plots. For models with poor fit, I applied transformations of explanatory variables that improved model fit. I then selected the best approximating models from my set of *a priori* models using AICc (Burnham and Anderson 1998). AICc values used the AIC score output from PROC MIXED where the lowest AIC score was the best model. Lastly, predicted percent cover was calculated by back-transforming Eqn 3.3:

$$\text{Canopy Cover} = \left(\frac{1}{1+\exp(-\beta_0-\beta_1(\text{Variable 1})\cdots-\beta_x(\text{Variable X})}\right)*100.5 \quad \text{(Eqn. 3.4)}$$

Where:

β_o is the intercept value,
β_1 is the coefficient for variable 1,
β_x is the coefficient for variable X, and
x is the number of variables included in a given model.

I examined the importance of the variables selected in the good model sets using importance weights. Importance weights were calculated by summing the Akaike weights for all models in which a given variable was present (p.141 Burnham and Anderson 1998).

Model corroboration

I was concerned that the model selection might be driven by the dominance of high canopy cover values (Table 3.5). Therefore, I randomly selected a subset of the stands so that numbers of points for stands with > 70% cover and lower levels of canopy cover were similar. I then reran the AICc model selection process with this reduced set of stands to ascertain whether the results would come out the same. I repeated this process with three subsets of high cover stands for each of the three forest groups.

Table 3.5. The number of stands within each of the three general forest groups that had cover levels $\geq$ 70% analyzed in this study. The percentage of total stands is given in the parentheses.

Forest group	Number of stands
Wet conifer	422 (65%)
Wet hardwood	93 (68%)
Dry hardwood	52 (51%)

The predicted sum of squares errors (predSSEs) from the test dataset were compared with the mean square errors (MSEs) of the model dataset. Similar predSSEs and MSEs suggested that the predictive model was not spurious. Using the square root of the predSSE ($\sqrt{\text{predSSE}}$) in place of the SE provided an estimate of the upper and lower confidence limits of these models for predicting canopy cover.

Canopy cover data are often incorporated into forest management as multiple broad cover classes (e.g. FIA stand condition criteria, Azuma and Hanson 2002). Therefore I also examined the performance of the predictive models using a classification scheme. I divided cover into 10% classes and used confusion matrices (Lillesand and Kiefer 1994) to quantify misclassification of model-predicted cover for each forest-group among the set of cover classes, using the test dataset.

Results

Remote vs. Ground Estimated Canopy Cover

Correspondence between ground-based and photo-interpreted cover measurements differed among the three general forest groups (Fig. 3.4). The strongest correlation between the two methods occurred in wet-conifer forests. For the wet-conifer and wet-hardwood groups, a consistent bias was not apparent. However, for dry-hardwood stands with < 60% cover (line-intercept), aerial photo cover measures tended to be higher.

Comparison of FVS and Line-Intercept Cover

Correspondence between FVS-generated cover and ground-based line-intercept measures differed among the three general forest groups (Fig. 3.5). For the wet-conifer and wet-hardwood stands there was consistent bias towards FVS underestimating cover. However, for the dry-hardwood stands there did not appear to be a bias between FVS and line-intercept cover.

Prediction of Cover

In general, model assumptions were satisfied. Residual plots showed constant variance and errors were normally distributed. There was high correlation among several of the variables (Pearson correlation coefficients > 0.60): stocking and basal area (r=0.91), and basal area and qmd (r=0.65). Therefore, these variables were not simultaneously included in a model.

An assumption of the AIC analytical approach is that the best approximating model for prediction of canopy cover was included in my 43 candidate models. The very high ΔAICc score of my null models for each of the forest types suggested at least one of the independent variables had explanatory capacity. Therefore, this assumption was supported.

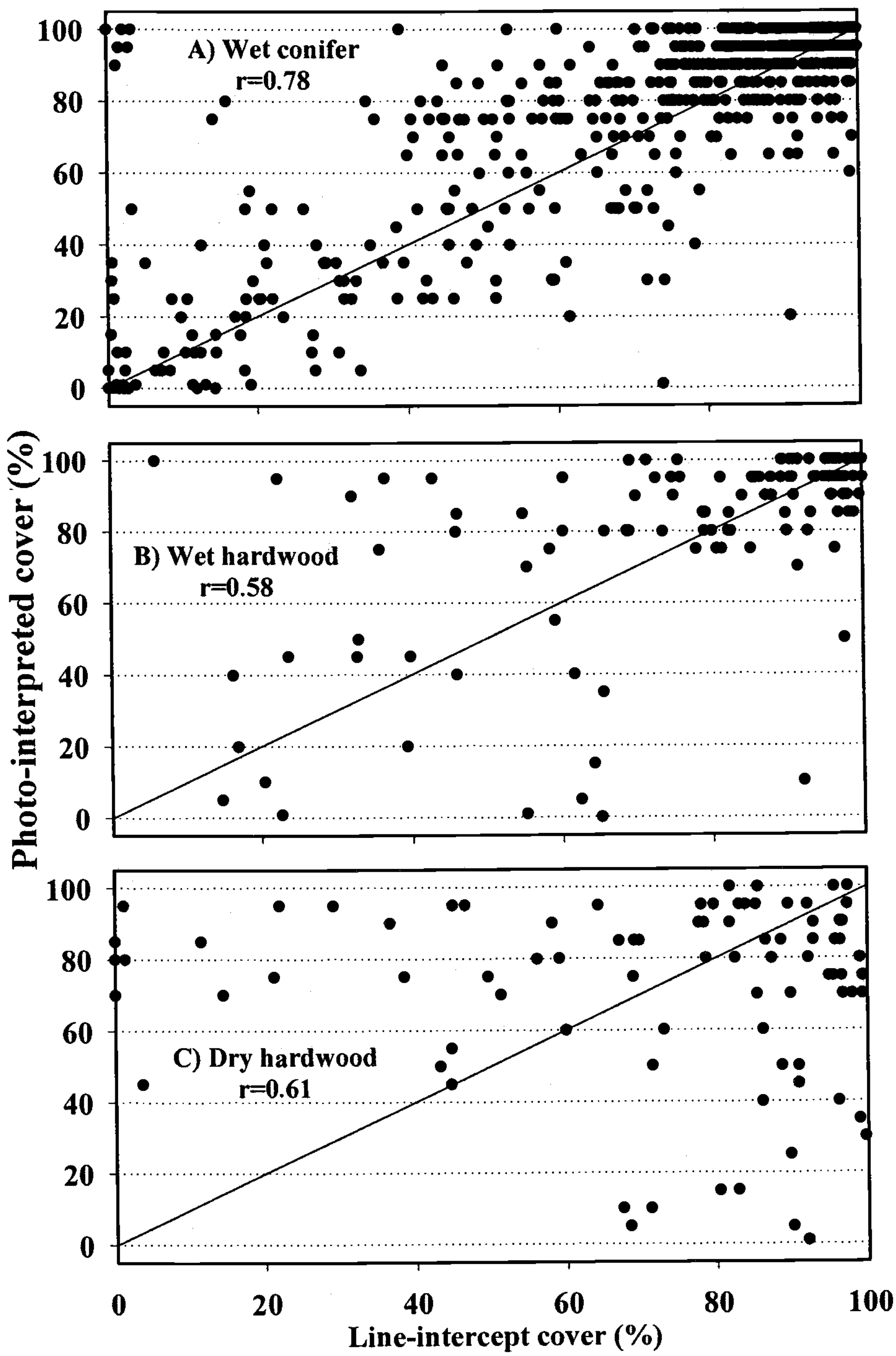

Fig 3.4. Comparison of 1:40000 aerial photo-interpreted canopy cover with ground-based line-intercept cover measures for three general forest groups (see Table 3.1) in western Oregon. The diagonal line represents a 1:1 relationship between the two cover estimates. The r-value is the Pearson correlation coefficient.

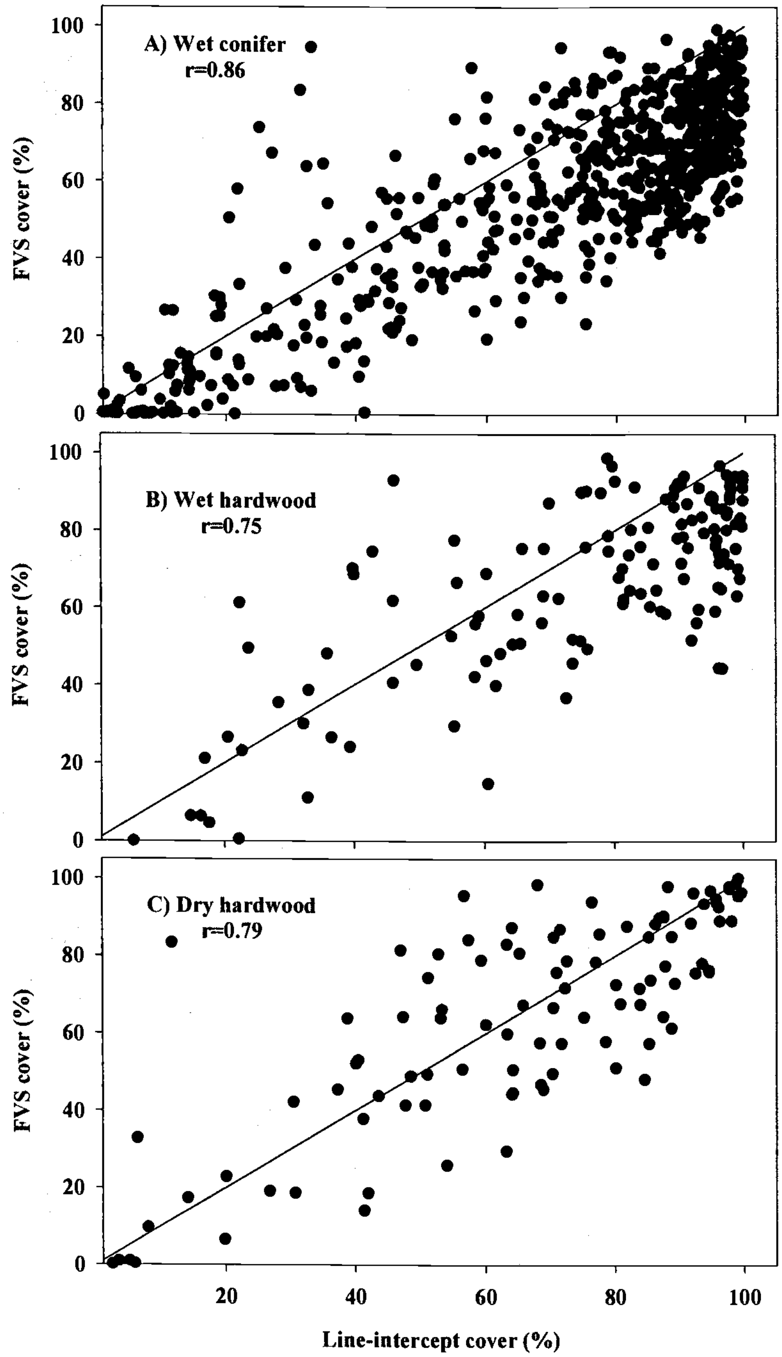

Fig. 3.5. Comparison of cover predicted by FVS equations and ground-measured line-intercept cover for three general forest groups (see Table 3.1) in western Oregon. The diagonal line represents a 1:1 relationship between the two cover estimates. The r-value is the Pearson correlation coefficient.

Repetition of the AIC model selection process with three subsets of high-cover stands resulted in the same set of good models for all three forest types. Thus, my full data regression results do not appear to be impacted by the skewed distribution of cover values.

Wet conifer

Model 28 was the best approximating model (ΔAICc=0, Table 3.6). There were three additional models with Akaike weights > 0 included in the good model set. For each good model of logitcover, parameter estimates were provided (Table 3.7). Importance weights for each of the variables in the good model set were calculated (Table 3.8).

In general, goodness of fit of the good model set was satisfactory (Table 3.9). The similar predSSEs and MSEs for the good models suggested the predictive models were not spurious. Rather, the predictive regression equations performed similarly with both the model and test datasets. Also, the adjusted-R^2 for all good models indicated that a high amount of variability was explained. Correspondence between predicted and ground-measured cover was inconsistent for the best model (Figs. 3.6, 3.7). Predicted values were within 10% cover of measured values for 73% of the observations for the best model, and within 15%, for 85% of the observations. Using √predSSE in place of the SE, the 95% confidence level predictive bands were > 20% across the majority of cover levels. Predictive bands narrowed at the upper and lower limits of cover, but this narrowing was an inherent function of the logit back-transformation.

The confusion matrix for the best model (28) demonstrated the predictive ability for 10% cover classes (Table 3.10). With 10% cover classes, only 47% of the test stands had cover estimates in the same 10% classes for measured and predicted cover. However, 83% of predictions were within one cover class of the measured cover class.

Table 3.6. Ranking of *a priori* models to predict canopy cover in 75% of the wet-conifer plots (n=484) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	*w*
28	√stock, mai	4	1286.42	0.00	0.7337
29	√stock, height, mai	5	1288.46	2.04	0.2652
9	√stock	3	1300.01	13.58	0.0008
27	√stock, height	4	1302.03	15.60	0.0003
44	1/age, √ba, mai, height	6	1323.85	37.43	0
31	1/age, √ba	4	1348.37	61.94	0
40	tph, tph^2, √ba, tph*ba	6	1399.70	113.27	0
33	√ba, mai, height	5	1417.83	131.41	0
32	√ba, mai	4	1419.93	133.50	0
30	√ba, height	4	1421.21	134.78	0
11	√ba	3	1423.74	137.32	0
8	stock	3	1472.78	186.36	0
6	1/age	3	1587.89	301.47	0
36	qmd, qmd^2, height, mai	6	1600.63	314.20	0
34	qmd, qmd^2, height	5	1603.40	316.98	0
35	qmd, qmd^2, mai	5	1613.96	327.53	0
13	qmd, qmd^2	4	1615.17	328.74	0
10	ba	3	1637.99	351.56	0
42	tphht1, tphht2, tphht3, tphht4	6	1643.49	357.06	0
41	tphdbh1, tphdbh2, tphdbh3	5	1765.18	478.75	0
39	tph, tph^2, height, mai	6	1789.24	502.82	0
37	tph, tph^2, height	6	1798.47	512.05	0
12	qmd	3	1822.94	536.51	0
7	height	3	1829.34	542.92	0
24	logit(photocov)	3	1832.92	546.50	0
20	tphdbh2	3	1833.82	547.40	0
18	tphht3	3	1902.65	616.23	0
16	tphht1	3	1909.42	623.00	0
43	tphcrn1, tphcrn2, tphcrn3, tphcrn4	6	1932.71	646.29	0
21	tphdbh3	3	1968.47	682.05	0
5	age	3	1972.48	686.05	0
19	tphht4	3	1977.28	690.85	0
4	speciestot	3	2004.88	718.46	0
17	tphht2	3	2009.28	722.85	0
3	mai, mai^2	4	2038.54	752.12	0
22	tphcrn2	3	2045.80	759.37	0
2	mai	3	2049.38	762.95	0
38	tph, tph^2, mai	6	2049.91	763.48	0
26	mai, precip	4	2050.30	763.87	0
14	tph	3	2051.81	765.38	0
1		2	2051.97	765.55	0
25	precip elev	4	2052.91	766.49	0
15	tph tph^2	3	2053.44	767.01	0
23	tphcrn3	3	2053.96	767.53	0

[1]Model numbers correspond to those in Table 3.3.
[2] Number of estimated parameters, including an error term.

Table 3.7. Coefficients (±SE) for estimating cover for the best models (Akaike weights > 0) for wet-conifer stands. Canopy cover is estimated using Eqn. 3.2.

Model[1]	Variable	Coefficient estimate
28	intercept	-3.6161 (0.1635)
	√stock	0.6200 (0.0144)
	mai	0.0032 (0.0008)
29	intercept	-3.6145 (0.1649)
	√stock	0.6211 (0.0199)
	mai	0.0032 (0.0008)
	height	-0.0004 (0.0051)
9	intercept	-3.1197 (0.1071)
	√stock	0.6210 (0.0146)
27	intercept	-3.1173 (0.1088)
	√stock	0.6227 (0.0202)
	height	-0.0006 (0.0052)

[1]Model numbers correspond to those in Table 3.3.

Table 3.8. Importance weights for the variables included in the good model set for wet-conifer stands (n=484).

Variable	Importance weight
√stock	1.0
mai	0.9989
height	0.2655

Table 3.9. Comparison of model statistics for the model dataset and the test dataset for wet-conifer stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=484). The predicted sum of squares error (PredSSE) was calculated for the set of wet-conifer stands that was used to test the fit of the model (n=161). Only models with Akaike weights > 0 were examined (ΔAICc< 16).

Model[1]	MSE	Adj. R^2	PredSSE
28	0.827	0.80	0.760
29	0.828	0.79	0.760
9	0.852	0.79	0.787
27	0.854	0.79	0.787

[1]Model numbers correspond to those in Table 3.3.

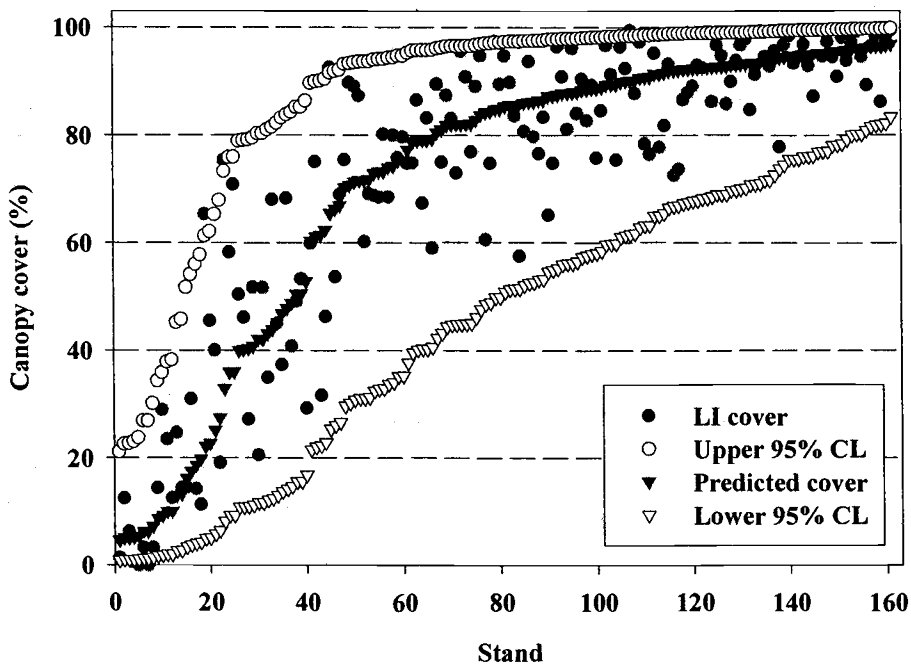

Fig 3.6. Comparison of line-intercept measured cover and canopy cover predicted using model 28 parameter estimates for wet-conifer stands. Comparison is for the 161 stands comprising the test dataset for wet-conifer stands (Table 3.7). The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

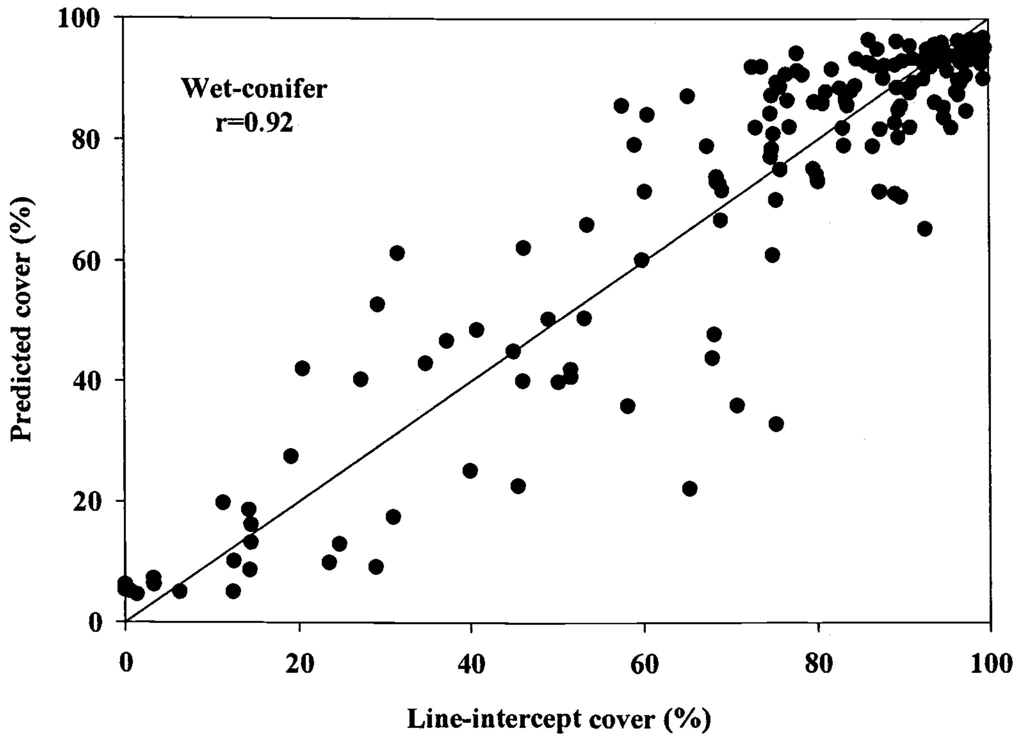

Fig 3.7. Comparison of line-intercept measured cover and canopy cover predicted using model 28 parameter estimates for 161 stands comprising the test dataset of wet-conifer stands (Table 3.7). The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 3.10. Confusion matrix for classification of wet-conifer test dataset stands (n=161) into ten equal cover classes. Columns represent the line-intercept cover classes. The rows represent the predicted cover classes, using model 28 (see Table 3.7). A perfect classification occurs when the matrix has zeros everywhere but on the diagonal. The diagonal is highlighted. A cell with a count > 0 that is not on the diagonal of the matrix signifies a stand in which the predicted cover was misclassified using the predictive model. The level of agreement between the measured and predicted cover is the percentage of stands that were correctly classified. For each canopy cover class, canopy values are greater than the lower value, and less than or equal to the larger value (which is in bold).

		Line-intercept canopy cover class										
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	Agreement (%)
Predicted cover class	0-10	7	2	2	0	0	0	0	0	0	0	63.6
	10-20	0	5	1	1	0	0	0	0	0	0	71.4
	20-30	0	1	0	0	2	0	1	0	0	0	0.0
	30-40	0	0	0	0	0	2	0	2	0	0	0.0
	40-50	0	0	2	2	3	2	2	0	0	0	27.3
	50-60	0	0	1	0	1	1	0	0	0	0	33.3
	60-70	0	0	0	1	1	2	1	1	0	1	14.3
	70-80	0	0	0	0	0	1	6	6	6	0	31.6
	80-90	0	0	0	0	0	1	2	9	14	13	23.1
	90-100	0	0	0	0	0	0	0	6	12	38	67.9
	Agreement (%)	100.0	62.5	0.0	0.0	42.9	11.1	8.3	25.0	43.8	73.1	46.6

Wet hardwood

Model 8 was the best approximating model (ΔAICc=0, Table 3.11). Nine additional models with Akaike weights > 0 were included in the good model set. For each good model of logitcover, parameter estimates were provided (Eqn. 3.3, Table 3.12). Importance weights for each of the variables in the good model set were calculated (Table 3.13).

Goodness of fit of the good model set was evaluated (Table 3.14). The adjusted-R^2 of the good models all demonstrated lower amounts of variability explained by the models, when compared with the other forest groups. The similar predSSEs and MSEs for the good models demonstrated that both datasets performed similarly.

Variability between the cover values of the line-intercept and predicted cover for model 8 was shown (Figs. 3.8, 3.9). Using the √predSSE in place of the SE, the 95% confidence level predictive bands were > 40% among most of the spectrum of cover levels. Predicted values were within 10% cover of measured values for 59% of the observations for the best model, and were within 15% for 82% of the observations.

The confusion matrix for the best model (8) demonstrated the predictive ability of the 10% canopy classes (Table 3.15). Sixty-eight percent of the stands were misclassified using the 10% cover classes. There were multiple cases where the measured and predicted cover classes were separated by > 2 classes. However, 85% of predictions were within one 10% cover class of the measured cover class.

Dry hardwood

Model 44 was the best approximating model (ΔAICc=0, Table 3.16). Five additional models with Akaike weights > 0 were included in the good model set. For each good model of logitcover, parameter estimates were provided (Eqn. 3.3,

Table 3.11. Ranking of a priori models to predict canopy cover in 75% of wet-hardwood plots (n=103) in western Oregon. Ranking is based on AICc values. W values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
8	stock	3	302.98	0.00	0.7512
9	√stock	3	307.27	4.29	0.0878
27	√stock, height	4	307.83	4.85	0.0664
28	√stock, mai	4	308.23	5.25	0.0545
29	√stock, height, mai	5	309.02	6.03	0.0368
11	√ba	3	315.61	12.63	0.0014
32	√ba, mai	4	317.22	14.24	0.0006
31	1/age, √ba	4	317.35	14.37	0.0006
30	√ba, height	4	317.76	14.78	0.0005
33	√ba, mai, height	5	319.42	16.44	0.0002
44	1/age, √ba, mai, height	5	321.08	18.09	0
40	tph, tph^2, √ba, tph*ba	6	321.69	18.71	0
10	ba	3	329.76	26.78	0
42	tphht1, tphht2, tphht3, tphht4	6	337.62	34.64	0
13	qmd, qmd^2	4	354.27	51.29	0
18	tphht3	3	354.39	51.41	0
34	qmd, qmd^2, height	5	354.80	51.82	0
35	qmd, qmd^2, mai	5	355.17	52.19	0
36	qmd, qmd^2, height, mai	6	356.02	53.04	0
41	tphdbh1, tphdbh2, tphdbh3	5	360.70	57.72	0
20	tphdbh2	3	361.66	58.68	0
6	1/age	3	374.21	71.23	0
12	qmd	3	380.46	77.47	0
16	tphht1	3	388.32	85.34	0
7	height	3	391.32	88.34	0
21	tphdbh3	3	391.48	88.50	0
5	age	3	391.80	88.82	0
24	logit(photocov)	3	392.37	89.39	0
43	tphcrn1, tphcrn2, tphcrn3, tphcrn4	5	392.61	89.63	0
37	tph, tph^2, height	5	395.15	92.17	0
19	tphht4	3	395.54	92.56	0
39	tph, tph^2, height, mai	6	396.73	93.75	0
23	tphcrn3	3	398.15	95.16	0
25	precip, elev	4	399.90	96.92	0
26	mai, precip	4	401.32	98.34	0
22	tphcrn2	3	404.41	101.43	0
4	speciestot	3	404.86	101.88	0
1		2	406.00	103.02	0
2	mai	3	406.84	103.86	0
14	tph	3	407.01	104.03	0
17	tphht2	3	408.04	105.06	0
3	mai, mai^2	4	408.48	105.49	0
15	tph, tph^2	3	409.18	106.19	0
38	tph, tph^2, mai	6	410.05	107.07	0

[1]Model number corresponds to those in Table 3.2.

[2] Number of estimated parameters, including an error term.

Table 3.12. Coefficients (±SE) for estimating cover for the best models (Akaike weights > 0) for wet-hardwood stands. Canopy cover is estimated using Eqn 3.2.

Model[1]	Variable	Coefficient estimate
8	intercept	-1.3934 (0.2516)
	stock	0.0493 (0.0037)
9	intercept	-2.9729 (0.3744)
	sqrtstock	0.6138 (0.0474)
27	intercept	-3.2261 (0.4245)
	√stock	0.5877 (0.0516)
	height	0.0173 (0.0138)
28	intercept	-3.3151 (0.4888)
	√stock	0.6108 (0.0474)
	mai	0.0022 (0.0021)
29	intercept	-3.5244 (0.5195)
	√stock	0.5866 (0.0516)
	height	0.01625 (0.0139)
	mai	0.0021 (0.0021)
11	intercept	-3.5244 (0.5195)
	√stock	0.5866 (0.0516)
	height	0.0163 (0.0139)
	mai	0.0021 (0.0021)
32	intercept	-2.1716 (0.4553)
	√ba	0.7317 (0.0610)
	mai	0.0016 (0.0022)
31	intercept	-1.6856 (0.4999)
	1/age	-1.7536 (2.7370)
	√ba	0.7023 (0.0798)
30	intercept	-1.9628 (0.3916)
	√ba	0.7308 (0.0701)
	height	0.0020 (0.0153)
33	intercept	-2.1903 (0.5028)
	√ba	0.7286 (0.0704)
	mai	0.0016 (0.0022)
	height	0.0014 (0.0153)

[1]Model number corresponds to those in Table 3.3.

Table 3.13. Importance weights for the variables included in the good model set for wet-hardwood stands (n=103)

Variable	Importance weight
stock	0.7512
√stock	0.2455
height	0.1039
mai	0.0921
√ba	0.0033

Table 3.14. Comparison of model statistics for the model fit dataset and the test dataset for wet-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2)were calculated for the stands used to fit the models (n=103). The predicted sum of squares error (PredSSE) was calculated for the set of wet-hardwood stands that was used to test the fit of the model (n=34). Only models with Akaike weights > 0 were examined (ΔAICc< 18).

Model[1]	MSE	Adj. R^2	PredSSE
8	1.065	0.64	1.229
9	1.110	0.62	1.086
27	1.104	0.62	1.056
28	1.108	0.62	0.975
29	1.104	0.62	0.958
11	1.204	0.59	1.106
32	1.209	0.59	1.027
31	1.211	0.59	1.089
30	1.215	0.58	1.105
33	1.221	0.58	1.027

[1]Model numbers correspond to those in Table 3.3.

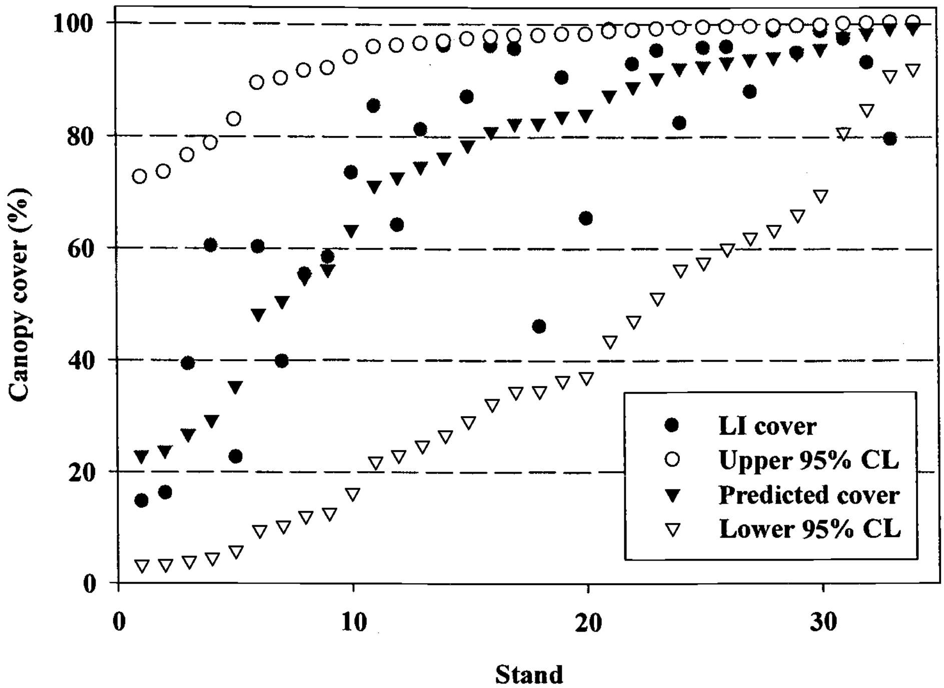

Fig. 3.8. Comparison of line-intercept measured cover and canopy cover predicted using model 8 parameter estimates for wet-hardwood stands. Comparison is for 34 stands comprising the test dataset of wet-hardwood stands (Table 3.12). The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

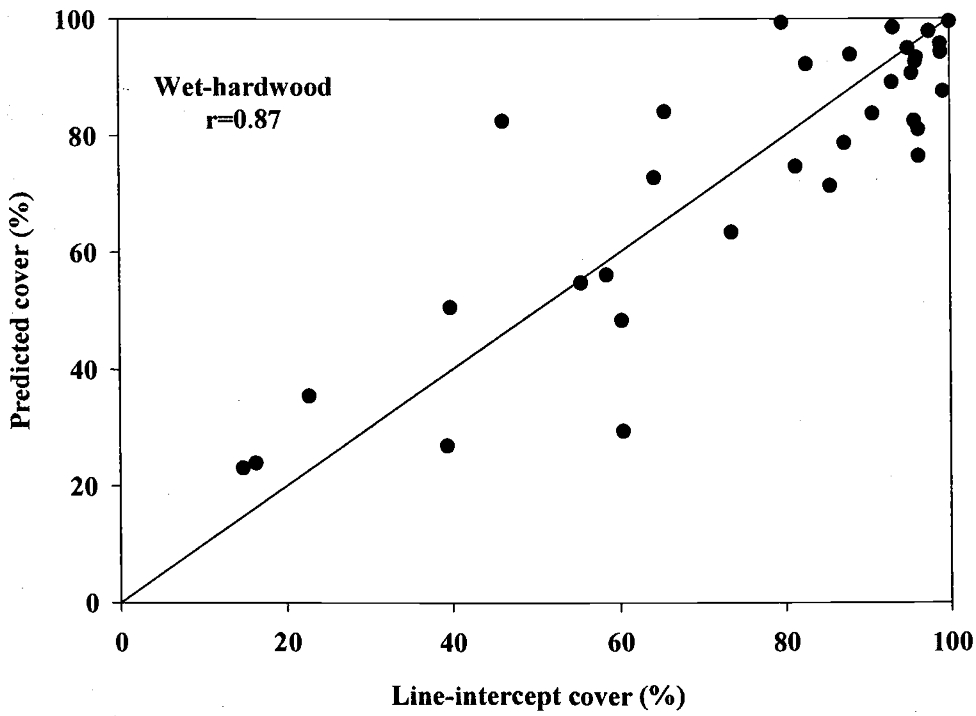

Fig 3.9. Comparison of line-intercept measured cover and canopy cover predicted using model 8 parameter estimates for 34 stands comprising the test dataset of wet-hardwood stands (Table 3.12). The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 3.15. Confusion matrix for classification of wet-hardwood test dataset stands (n=34) into ten equal cover classes (see Table 3.9). The predicted cover was calculated using model 8 (see Table 3.12).

		Line-intercept canopy cover class										
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	Agreement (%)
Predicted cover class	**0-10**	0	0	0	0	0	0	0	0	0	0	0.0
	10-20	0	0	0	0	0	0	0	0	0	0	0.0
	20-30	0	2	0	1	0	0	1	0	0	0	0.0
	30-40	0	0	1	0	0	0	0	0	0	0	0.0
	40-50	0	0	0	0	0	0	1	0	0	0	0.0
	50-60	0	0	0	1	0	2	0	0	0	0	66.7
	60-70	0	0	0	0	0	0	0	1	0	0	0.0
	70-80	0	0	0	0	0	0	1	0	3	1	0.0
	80-90	0	0	0	0	1	0	1	0	0	5	0.0
	90-100	0	0	0	0	0	0	0	1	2	9	75.0
	Agreement (%)	0	0	0	0	0	100.0	0.0	0.0	0.0	60.0	32.4

Table 3.16. Ranking of *a priori* models to predict canopy cover in 75% of dry-hardwood plots (n=76) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
44	1/age, √ba, mai, height	6	177.76	0.00	0.43
31	1/age, √ba	4	178.48	0.72	0.30
28	√stock, mai	4	179.78	2.01	0.16
29	√stock, height, mai	5	181.09	3.33	0.08
27	√stock, height	4	183.77	6.00	0.02
9	√stock	3	184.22	6.45	0.02
11	√ba	3	188.37	10.61	0.00
32	√ba, mai	4	190.21	12.44	0.00
30	√ba, height	4	190.55	12.79	0.00
33	√ba, mai, height	5	192.38	14.61	0.00
40	tph, tph^2, √ba, tph*ba	6	194.13	16.37	0.00
8	stock	3	196.44	18.68	0.00
10	ba	3	213.63	35.87	0.00
35	qmd, qmd^2, mai	5	240.94	63.18	0.00
36	qmd, qmd^2, height, mai	6	243.16	65.40	0.00
6	1/age	3	246.27	68.51	0.00
42	tphht1, tphht2, tphht3, tphht4	6	246.39	68.62	0.00
34	qmd, qmd^2, height	5	248.64	70.87	0.00
13	qmd, qmd^2	4	249.19	71.43	0.00
41	tphdbh1, tphdbh2, tphdbh3	5	254.50	76.73	0.00
20	tphdbh2	3	263.52	85.76	0.00
37	tph, tph^2, height	6	263.55	85.79	0.00
12	qmd	3	263.79	86.03	0.00
39	tph, tph^2, height, mai	6	265.68	87.91	0.00
7	height	3	267.41	89.65	0.00
17	tphht2	3	270.92	93.16	0.00
24	logit(photocov)	3	275.55	97.79	0.00
18	tphht3	3	275.81	98.05	0.00
43	tphcrn1, tphcrn2, tphcrn3, tphcrn4	6	277.81	100.04	0.00
5	age	3	280.37	102.60	0.00
21	tphdbh3	3	281.99	104.23	0.00
25	precip, elev	4	284.85	107.08	0.00
19	tphht4	3	288.45	110.68	0.00
16	tphht1	3	291.62	113.85	0.00
3	mai, mai^2	4	296.10	118.33	0.00
23	tphcrn3	3	296.38	118.62	0.00
2	mai	3	296.97	119.20	0.00
26	mai, precip	4	297.09	119.32	0.00
22	tphcrn2	3	297.15	119.38	0.00
14	tph	3	298.39	120.63	0.00
1		2	298.56	120.79	0.00
4	speciestot	3	299.30	121.54	0.00
15	tph tph^2	4	299.62	121.86	0.00
38	tph, tph^2, mai	6	299.73	121.97	0.00

[1]Model numbers correspond to those in Table 3.3.

[2] Number of estimated parameters, including an error term.

Table 3.17). Importance weights for each of the variables in the good model set were calculated (Table 3.18).

Goodness of fit differed among the set of good models (Table 3.19). The two top models (models 44, 31) had predSSEs that were higher than were the MSEs of these models. Thus, while these predictive models fit the model dataset best, they did a poorer job of fitting the test dataset. This suggested these predictive models could be spurious and may have overfit the data. Models 29, 28, 27, and 9 all had similar adjusted-R^2 to models 44 and 31, but in addition their predSSEs were lower than their MSEs. Therefore, this set of models did not over fit the data. Therefore I elected to further examine both the top model (model 44) and one of the good models that better fit the test dataset (model 29).

There was higher variability between the line-intercept and predicted cover for model 44, compared with the increased correlation between the two cover estimates for model 29 (Figs. 3.10-3.13). Using the $\sqrt{}$predSSE in place of the SE, the 95% confidence level predictive bands were narrower for model 29 than for model 44 across the spectrum of cover levels. Predicted values were within 10% cover of measured values only for 58% of the observations for both models. This increased to within 15% for 65% and 85% of the observations for models 44 and 29. Results suggest that model 29 had better predictive ability than model 44 at the stand level.

In general, the confusion matrices demonstrated the improved predictive ability of model 29, compared with model 44 (Tables 3.20-3.21). An exception was in the > 90% class, where model 44 consistently predicted the correct cover class. Only 39% of the test stands had cover estimates in the same 10% class for both models 44 and 29. However, 73% and 85% of predictions were within one class of the measured cover class for models 44 and 29 respectively.

Table 3.17. Coefficients (+SE) for estimating cover for the best models (Akaike weights > 0) for dry-hardwood stands. Canopy cover is estimated using Eqn. 3.2.

Model[1]	Variable	Coefficient estimate
44	intercept	-1.9002 (0.3449)
	1/age	-7.2584 (2.0069)
	√ba	0.6613 (0.0796)
	mai	0.0031 (0.0018)
	height	-0.0014 (0.0151)
31	intercept	-1.8872 (0.3443)
	1/age	-6.1006 (1.9047)
	√ba	0.6981 (0.0613)
28	intercept	-3.4753 (0.2663)
	√stock	0.5427 (0.0309)
	mai	0.0043 (0.0017)
29	intercept	-3.4969 (0.2675)
	√stock	0.5190 (0.0399)
	mai	0.0039 (0.0017)
	height	0.0132 (0.0140)
27	intercept	-3.2548 (0.2524)
	√stock	0.5093 (0.0408)
	height	0.0215 (0.0139)
9	intercept	-3.1707 (0.2488)
	√stock	0.5491 (0.0320)

[1]Model numbers correspond to those in Table 3.3.

Table 3.18. Importance weights for the variables included in the good model set for dry-hardwood stands (n=76).

Variable	Importance weight
1/age	0.73
√ba	0.73
mai	0.67
height	0.53
√stock	0.28

Table 3.19. Comparison of model statistics for the model dataset and the test dataset for dry-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj. R^2) were calculated for the stands used to fit the models (n=76). The predicted sum of squares error (PredSSE) was calculated for the set of dry-hardwood stands that was used to test the fit of the model (n=26). Only models with Akaike weights > 0 were examined (ΔAICc< 10).

Model[1]	MSE	Adj. R^2	PredSSE
44	0.597	0.81	0.802
31	0.605	0.81	0.798
28	0.590	0.81	0.438
29	0.591	0.81	0.420
27	0.625	0.80	0.466
9	0.636	0.80	0.512

[1]Model numbers correspond to those in Table 3.3.

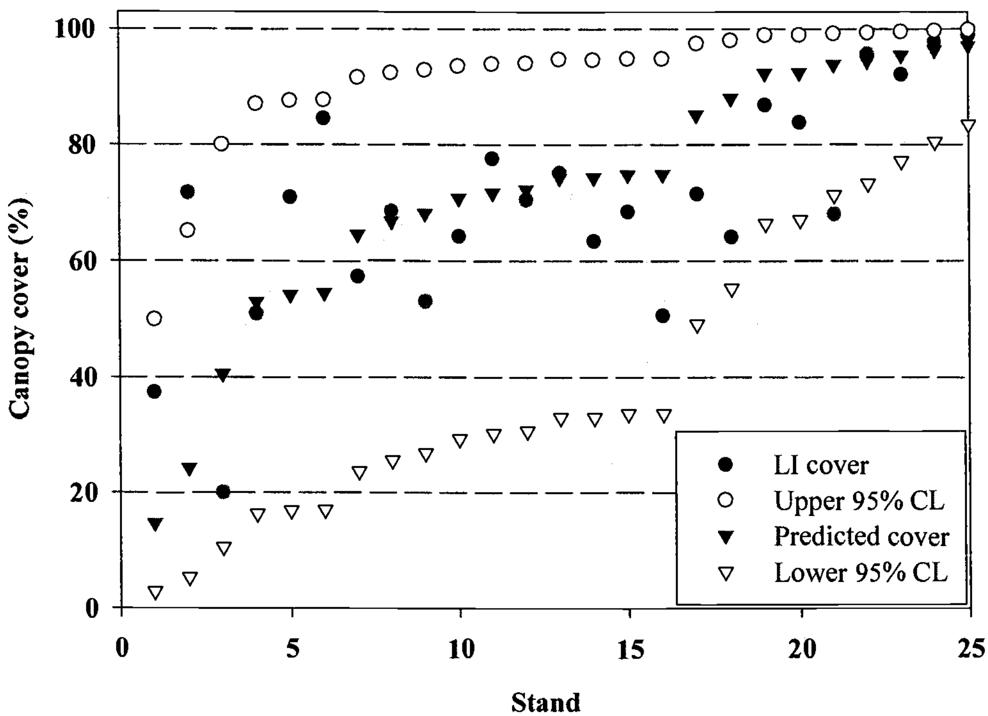

Fig 3.10. Comparison of line-intercept measured cover and canopy cover predicted using model 44 parameter estimates for dry-hardwood stands. Comparison is for 24 stands comprising the test dataset of dry-hardwood stands (Table 3.17). The 95% upper and lower confidence limits substituted the $\sqrt{\text{PredSSE}}$ in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

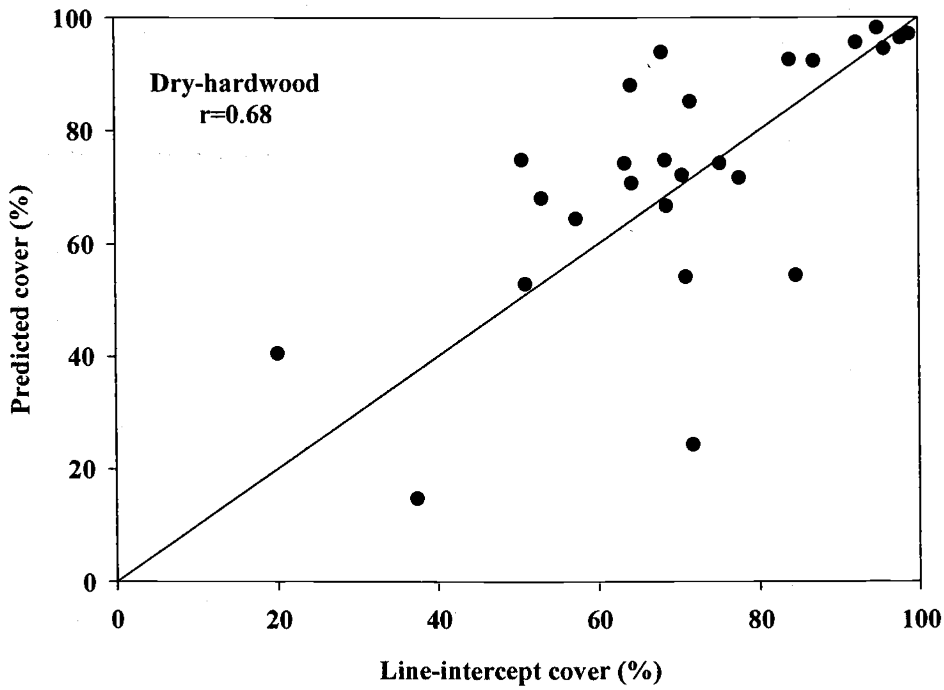

Fig 3.11. Comparison of line-intercept measured cover and canopy cover predicted using model 44 parameter estimates for 24 stands comprising the test dataset of dry-hardwood stands (Table 3.17). The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

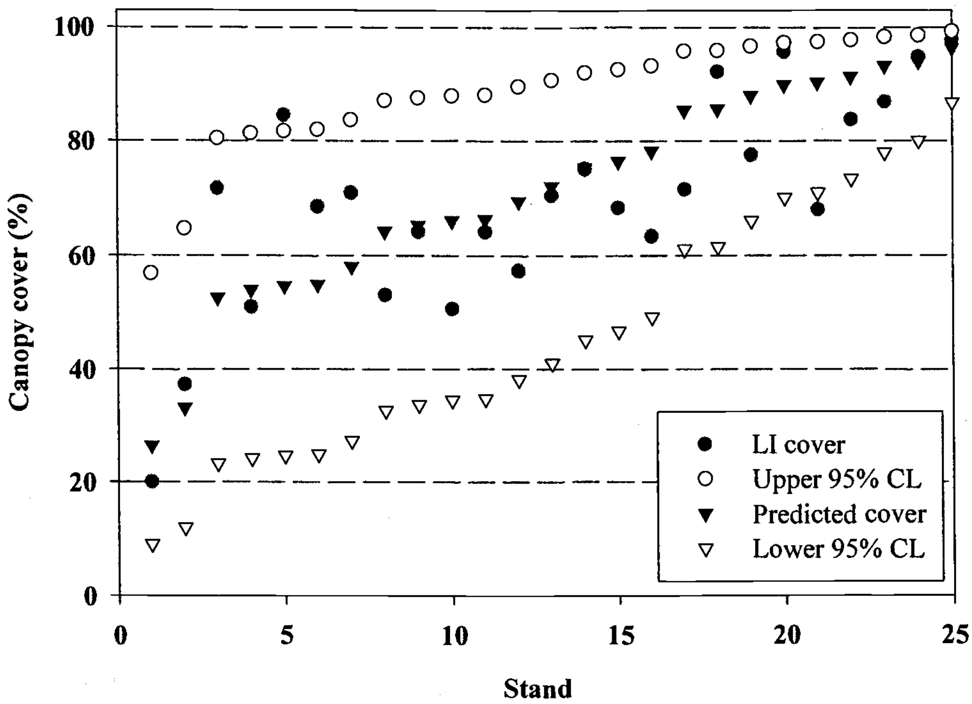

Fig. 3.12. Comparison of line-intercept measured cover and canopy cover predicted using model 29 parameter estimates for dry-hardwood stands. Comparison is for 24 stands comprising the test dataset of dry-hardwood stands (Table 3.17). The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

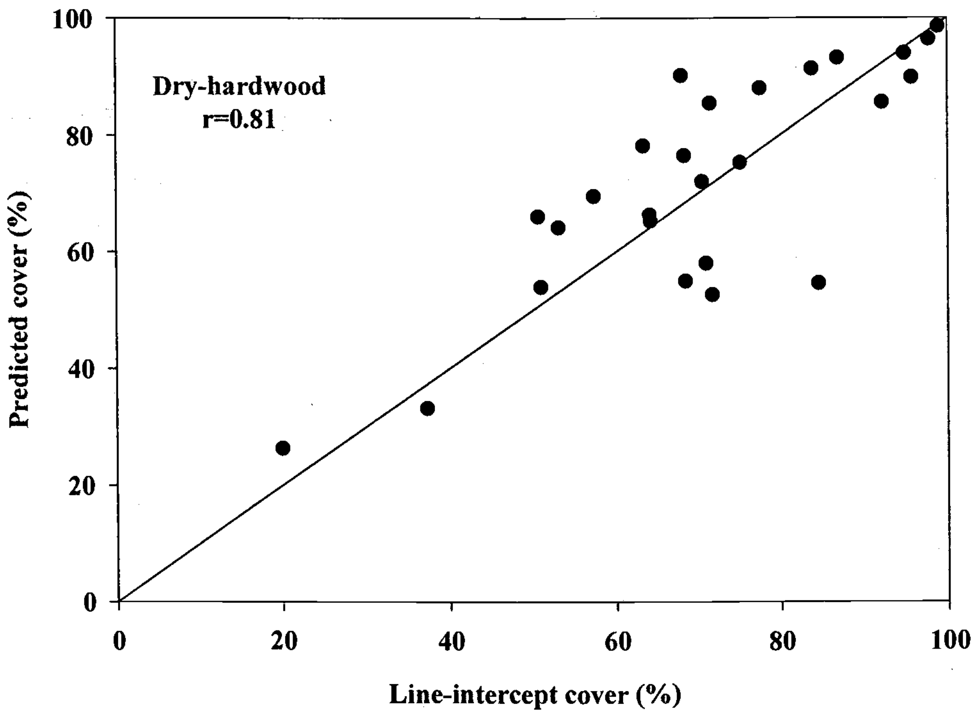

Fig. 3.13. Comparison of line-intercept measured cover and canopy cover predicted using model 29 parameter estimates for 24 stands comprising the test dataset of dry-hardwood stands (Table 3.17). The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 3.20. Confusion matrix for classification of dry-hardwood test dataset stands (n=26) into ten equal cover classes (see Table 3.9). The predicted cover was calculated using model 44 (see Table 3.17).

		Line-intercept canopy cover class										
		0-10	10-20	20-30	30-40	40-50	50-60	60-70	70-80	80-90	90-100	Agreement (%)
Predicted cover class	0-10	0	0	0	0	0	0	0	0	0	0	n/a
	10-20	0	0	0	1	0	0	0	0	0	0	0.0
	20-30	0	0	0	0	0	0	0	1	0	0	0.0
	30-40	0	0	0	0	0	0	0	0	0	0	n/a
	40-50	0	0	1	0	0	0	0	0	0	0	0.0
	50-60	0	0	0	0	0	1	0	1	1	0	33.3
	60-70	0	0	0	0	0	2	1	0	0	0	33.3
	70-80	0	0	0	0	0	1	3	3	0	0	42.9
	80-90	0	0	0	0	0	0	1	1	0	0	50.0
	90-100	0	0	0	0	0	0	1	0	2	5	62.5
	Agreement (%)	n/a	n/a	0.0	0.0	n/a	25.0	16.7	50.0	0.0	100.0	38.5

Table 3.21. Confusion matrix for classification of dry-hardwood test dataset stands (n=26) into ten equal cover classes (see Table 3.9). The predicted cover was calculated using model 29 (see Table 3.17).

		Line-intercept canopy cover class										
		0-10	10-20	20-30	30-40	**40-50**	**50-60**	60-70	**70-80**	**80-90**	**90-100**	Agreement (%)
Predicted cover class	**0-10**	0	0	0	0	0	0	0	0	0	0	n/a
	10-20	0	0	0	0	0	0	0	0	0	0	n/a
	20-30	0	0	1	0	0	0	0	0	0	0	100.0
	30-40	0	0	0	1	0	0	0	0	0	0	100.0
	40-50	0	0	0	0	0	0	0	0	0	0	n/a
	50-60	0	0	0	0	0	1	1	2	1	0	20.0
	60-70	0	0	0	0	0	3	2	0	0	0	40.0
	70-80	0	0	0	0	0	0	2	2	0	0	50.0
	80-90	0	0	0	0	0	0	0	2	0	2	50.0
	90-100	0	0	0	0	0	0	1	0	2	3	50.0
	Agreement (%)	n/a	n/a	100.0	100.0	n/a	25.0	33.3	33.3	0.0	60.0	38.5

Discussion

Remote vs. Ground Estimated Canopy Cover

There are likely multiple factors that contributed to the poor correlation of ground and aerial cover estimates for all of the forest groups. If the center of subplot one was incorrectly located on the remote photo, this could lead to gross inaccuracies between the ground and photo-based cover estimates. The remote photos were taken in 1994, while ground-based stand inventories were conducted between 1995 and 1997. With the lag between air and ground measurements, discrepancies among the methods may have resulted due to harvest activities or lateral branch development. Alternatively, given the coarse scale of the aerial photos, aerial photo interpreters may have misclassified shrubs as trees in young stands, and vice versa. This likely led to the lower correlation of the two cover measures for the hardwood forest groups, compared with the wet-conifer group. Also, the aerial photos did not always capture the full extent of cover in the middle and lower layers. This occurs because photos only show the portion of crown that extends above the intersection with its neighbors (Gill et al. 2000). Regardless of the source of error, my results suggest that the 1:40000 scale aerial photos used in this inventory are not adequate to describe canopy cover very accurately.

Comparison of FVS and Line-Intercept Cover

The Pacific Northwest Variant of FVS had a consistent bias towards underestimating cover in the wet-hardwood and wet-conifer stands. This finding supported previous research of another FVS variant used in Montana Douglas-fir/western larch (*Larix occidentalis* Nutt.) forests. Applegate (2000) compared cover predictions from the Northern Idaho variant of FVS with the densitometer and moosehorn and found FVS equations underpredicted cover in Douglas-fir stands, as well as in other cover types. This suggests that the overlap-corrected equation (Eqn. 3.2) overcompensates for overlap among cover of individual trees. Therefore, it does not appear that the existing FVS cover calculations should be used as management tools to estimate cover in wet-hardwood and wet-conifer stands in western Oregon. Instead, an improvement that re-adjusts the overlap-corrected equation, or ground-based estimates appear necessary to obtain estimates of percent cover for these forest groups.

Prediction of Cover

The best approximating models differed among the three general forest groups. This supported the findings of Chapter 2 that patterns of canopy structure differed among the three forest groups. The best model for wet-conifer stands included stocking and mean annual increment, while the best model for wet-hardwood stands only included stocking. The best model for dry-hardwood stands included basal area, mean annual increment, stand height and stand age. However, the dry-hardwood model that better fit the test dataset included stocking, mean annual increment and stand height. While basal area and stocking were highly correlated in the FIA inventory ($r=0.91$), it was stocking that was included in the models that best predicted canopy cover. Thus, it appears that stocking is a better predictor of canopy cover in these forest groups than basal area.

The hardwood forest groups had more variables with importance weights than did the wet-conifer stands. All of the important variables selected in the good model set for wet-conifer stands ($\sqrt{}$stock, mai, and height) were also included in the wet-hardwood and dry-hardwood groups. However, the wet-hardwood stands also included the linear form of stocking and $\sqrt{}$basal area, while dry-hardwood stands excluded the linear form of stocking, but did include the inverse of stand age. The selection of stand age as an important variable for predicting canopy cover in dry hardwood stands was surprising, because distinct patterns in canopy cover among stand ages were not evident in these stands (see Chapter 2 Fig. 2.5D).

My model selection results are generally in contrast to previous studies that predominately selected basal area as the best predictor of cover. Mitchell and

Popovich (1997) included stand density as a potential predictor, but found cover in Ponderosa pine stands was best predicted by basal area, and only for stands with canopy cover < 60%. Buckley et al. (1999) demonstrated regression of the square root of basal area could potentially be used to estimate canopy cover levels in Michigan oak and pine stands ($R^2 \geq 0.95$). Basal area, dbh, and stem density together were used as the best predictors of canopy cover in northern California stands (Gill et al. 2000, R^2=0.75 and 0.66 for test and model data sets). Cade (1999) recommended use of basal area to estimate cover when emphasis of larger-diameter uncommon trees was desired, such as in wildlife studies.

There are several potential reasons why stocking density was preferentially selected over basal area in this study. One potential reason is that, except for the study conducted by Mitchell and Popovich (1997), previous studies did not consider a measure of stocking. Also, previous studies have not explored the ability to model cover over such a large landscape as this one. Stocking density, calculated as the contribution of each measured tree to a fully-stocked stand based on normal yield tables, attempts to account for differences among individual stand site productivity, using site index. This study covered expansive ranges of variables including elevation, ownership, management, and stand ages. Therefore, stocking density was likely selected over basal area among most forest groups because, unlike stocking, basal area does not incorporate a stand's potential productivity. Therefore, with the diversity of stand attributes encompassed within each of the general forest groups, using a measure that was relative to a 'normal/fully-stocked' stand for a given site index did a better job than using an absolute measure, such as basal area. Regardless of the rationale, stocking density appears to better represent cover than basal area does.

For all three general forest groups there was a distinct trend towards tight 95% confidence intervals at the two extreme levels of cover (0 and 100%) and much wider bands at intermediate cover levels. It should be noted that this pattern is a direct consequence of the logit transformation that was employed during the model selection process. With canopy cover bounded from 0 to 100%, it was necessary to use the logit transformation to linearize the relationship between canopy cover and the explanatory variables. Therefore the differences in ranges of errors seen along the gradient of cover were unavoidable and a function of the transformation used.

Confusion matrices provided valuable information on the application of these predictive models at a coarser scale of cover classification. With 10% cover classes overall agreement was poor among the forest groups' best approximating models. But with the addition of error of the measured cover class within one 10% class, 83% of stands were within one cover class of the correct class among forest groups. Therefore, these predictive equations are useful for classification within 10% cover classes. Thus, if a manager/researcher's goal is simply to use a broad canopy cover class as a forest management criterion, then use of the 10% cover classes (± one 10% interval) studied here could be employed. These findings concur with Gill et al. (2000), who also reached the conclusion that their models should be used to classify forest stands into relatively broad cover classes.

Beyond classification within broad canopy cover classes, the predictive ability of these models is dependent on the forest group and the accuracy desired by the user. Stand-level predictions were within 10% of the measured cover for 70% of the observations for the best wet-conifer model. Predictions within 15% of measured cover improved to ≥ 82% for all three forest groups, except for the model 29 dry-hardwood model (which overfit the model dataset). These results suggest that in all forest types, if predicting cover within 15% is acceptable, these models can be used. However, if accuracy of 10% is needed, I would only cautiously recommend use of the wet-conifer model. With the scarcity of hardwood stands, especially in stands with < 75% cover, one should use the hardwood predictive models with caution.

As mentioned, the stands used to create these predictive models encompass a wide variation in multiple factors across the landscape of western Oregon. These variables include differing species compositions, spanning large environmental gradients, including precipitation and elevation, multiple types of ownerships, different intensities of management, wide-ranging stand ages, and varying site productivities. Therefore, it is impressive that these models perform as accurately as they do. However, model performance could potentially be improved further in the future through selection of a subset of stands that were of more uniform species composition and located in a more geographically localized region with similar environmental attributes.

Overall, the use of these predictive models is dependent on the objectives of a given study. If estimates of cover that are more accurate than were found in this study are desired, then the data collected by ground-based cover measurements cannot be substituted through the use of surrogate stand measures. However, in situations where the level of error described for these predictive equations is acceptable, the predictive models can be substituted for line-intercept ground-measured cover in the wet-conifer, wet-hardwood, and dry-hardwood forests of western Oregon.

Limitations

There are four factors that limit interpretation of the results of this study:

1) Sample sizes for the hardwood forests were limited, compared with the wet-conifer forests, especially in the test datasets. Thus, predictive models should be interpreted with caution.

2) The predominant tree species is used to define each forest type. However, other species present in less abundant quantities can still contribute large amounts of canopy cover. In the case of hardwood forests, there may still be coniferous trees present, including in the overstory. These trees can potentially obscure the ability to predict hardwood cover.

3) The distribution of canopy cover levels among the stands was skewed towards high cover levels. As a result, while we have a good understanding of the variability of error associated with high cover levels, the amount of variability in stands with lower cover levels is less certain. Ideally more stands with lower cover

levels would be necessary to get a better sense of the range of variability in these mid-cover level stands.

4) The inventory was depauperate of older aged stands, as the majority of older stands are located on federal land (Campbell et al. 2002) excluded from this study. Therefore, caution should be used in applying predictive models to stand ages beyond age 115 for wet-conifer and dry-hardwood stands, and beyond age 65 for the wet-hardwood stands (see Chapter 2, Table 2.4).

Summary

1) Ground-based cover measures were compared with cover predicted by regression models from standard forest measurements, and with estimates from aerial photography and the forest vegetation simulator (FVS) program on inventory plots.

2) Predictive models were developed for three general forest groups in western Oregon: wet conifer, wet hardwood, and dry hardwood.

3) Standard inventory estimates of cover using 1:40,000 scale black and white aerial photos were poorly correlated with ground-measured cover, especially in wet-hardwood ($r=0.58$) and dry-harwood ($r=0.61$) stands.

4) FVS generated cover underestimated cover by up to 50% in wet-conifer and wet-hardwood stands.

5) The best approximating models for estimating canopy cover predicted line-intercept measured cover within 15 percentage points of measured cover at the stand level among the general forest groups for > 82% of the observations.

6) If predicting cover within 15 percentage points is acceptable, the good model sets can be used. However, if accuracy of 10 percentage points is needed, only cautious use of the wet-conifer model is recommended.

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VERTICAL STRATIFICATION AND HEIGHT DIVERSITY OF WESTERN OREGON FORESTS

Abstract

Vertical canopy structure plays vital roles in forest ecosystems. This has motivated numerous attempts to describe vertical structure for comparison among different stands. In this paper, I compared fourteen measures of vertical structural diversity and stratification in the forests of western Oregon. I then attempted to predict selected vertical diversity measures from standard forest attributes. With increasing stand age, there was concurrent increase in vertical diversity and layering, consistent with expected crown patterns associated with stand dynamic models of succession. I developed predictive equations for SDI, Foliage Height Diversity (FHD), and Canopy Height Diversity Index (CHDI), which were based on basal area, standard deviation of dbh, and stem frequency within size classes as the best variables. Predicted SDI values were within 0.15 units of calculated SDI for $\geq$ 79% of the observations, predicted CHDI values were within 1.5 units for $\geq$ 91% of the observations, except for dry-hardwood stands (only 69%), and predicted FHD measures were within 0.2 units for $\geq$ 85% of the observations among forest groups.

Introduction

The vertical quantity and distribution of foliage of a stand are important components in forest ecosystems. The vertical canopy structure plays important functions for diverse community resources including wildlife (MacArthur and MacArthur 1961, Thomas and Verner 1986, Hayes et al. 1997, North et al. 1999, Johnson and O'Neill 2001, Shaw et al. 2002), insects (Humphrey et al. 1999), disease and insect susceptibility (Mathiasen 1996; Winchester and Ring 1996), fire hazard (Latham et al. 1998), atmospheric interactions (Monsi et al. 1973, Rose

1996), microclimate (Yang et al. 1999), and habitat structure (Maguire and Bennett 1996).

The vertical differentiation of canopy structure is an important feature of the successional stand dynamics described by Franklin et al. (2002) as demonstrated using natural stand development of the Douglas-fir – western hemlock sere in the PNW. Their newer model expands on Oliver's (1981) four-stage model of succession by incorporating changes in vertical forest structure. The model highlights eight commonly encountered developmental stages and includes canopy attributes of these stages. In the disturbance and legacy creation stage, the starting point for stand development varies by the intensity of the disturbance that initiated the stand. Canopy cover is provided by remnant trees in partial-stand disturbances (e.g. wildfire) or may be totally absent (e.g. clear-cut). In the cohort establishment phase a new generation of trees is established. Stands with below "normal" stocking levels undergo gradual canopy closure, while stands with normal to high stocking undergo intense self-thinning in short time periods. In the canopy closure phase, overlap among tree crowns leads to reduced light levels in the understory. The rate of canopy closure is dependent on tree regeneration density and site productivity. Low productivity sites may not achieve canopy closure. The biomass accumulation/competitive exclusion stage is where growth in both tree diameter and height, natural pruning of lower tree branches, and crown-class differentiation occur. In the maturation phase the original cohort of trees attains maximum height and crown diameter. During this phase the understory reestablishes as the mortality of overstory stems allows increased light penetration and frees up water and nutrients in the soil. High light levels promote establishment of previously suppressed shade-tolerant tree species. In the vertical diversification stage continuity of the canopy from the ground to the taller trees is reestablished. This vertical diversity results from the growth of shade-tolerant trees up into the middle and upper canopy layers and the development of epicormic branches along exposed boles for species with this trait. The horizontal diversification stage is characterized by mortality of individual or small clusters of stems (gap formation, etc.), and low variability in the upper and lower canopy levels, but high variability at the mid-canopy level. The final stage is pioneer-cohort loss where dominant shade-intolerant tree species in the overstory begin to die off and are replaced by a shade-tolerant overstory.

Vertical canopy structure can be described along a gradient (Whittaker 1967) or by separation into discrete layers or strata (Latham et al. 1998, Baker and Wilson 2000). While stratification is recognized as a useful tool for studying vertical distribution of animals and plants (Baker and Wilson 2000), it is a challenge to define vertical canopy stratification because of the subjective nature of the measures used to quantify it. Canopy profile diagrams, plotting leaf area along a vertical axis, have been used but are labor-intensive, spatially restricted, and their interpretation is subjective (Baker and Wilson 2000). Parker and Brown (2000) compared definitions of canopy stratification in multiple studies and found ten unique definitions for canopy stratification among them. These definitions included using it as a synonym for height, as a descriptor of vertical distribution of foliage, and as an index of vertical structure. This lack of a definitive description can result in one researcher concluding that a forest is multi-layered, while another concludes it is single-layered.

With the current emphasis on biodiversity, including structural diversity, species diversity indices have been increasingly applied to describe patterns in forest structures (e.g. MacArthur and MacArthur 1961, Willson 1974, Aber 1979, Ambuel and Temple 1983, Freemark and Merriam 1986, Ashton and Hall 1992, Spies and Cohen 1992, Corona and Pignatti 1996, Dubrasich et al. 1997, Latham et al. 1998, Humphrey et al. 1999, Baker and Wilson 2000, Edgar and Burk 2001, Lindgren and Sullivan 2001, Neumann and Starlinger 2001, Staudhammer and LeMay 2001).

These measures of vertical structure can be used as tools in forest management. Stand structural diversity measures are important for predicting future stand growth (Staudhammer and Lemay 2001). Managing forests for biodiversity may be accomplished by managing for structural diversity (Onal 1997).

Quantification of vertical structure can also be used as a silvicultural tool for forest managers when planning harvest activities (Heuserr 1998, Lindgren and Sullivan. 2001, Sullivan et al. 2001).

Detailed crown measurements are required for calculating the measures of vertical diversity. As a result, alternate measures have been used to describe vertical forest structure. These methods include using one-dimensional stand parameters such as mean stand height or dbh, standard deviation of mean stand height or dbh (e.g. Neumann and Starlinger 2001), trees per hectare within height or diameter classes (e.g. Buongiorno et al. 1994, Lahde et al. 1999), and the coefficient of variation of tree heights (e.g. Edgar and Burk 2001) as substitutes. These surrogates for detailed crown measurements are often desirable because they are more readily obtained from standard stand exam measurements. However, it is uncertain how effectively these surrogate measures describe vertical diversity. Thus, further investigation of the use of surrogates to describe vertical canopy structure is warranted.

There are multiple criteria to be considered when selecting, using, and evaluating vertical structure measures and indices:

1) The index should be able to discriminate among subtle differences in diversity (Magurran 1988).

2) Given two populations with the same number of trees, the population with a greater range of tree heights or larger dbhs should have a higher diversity value (Staudhammer and LeMay 2001).

3) All other things equal, tall forests should have higher index values than shorter forests (Spies and Cohen 1992).

4) For forests of equal height, those with foliage or crowns found throughout the vertical space should have higher index values than those with foliage or crowns only at one or a few heights (Spies and Cohen 1992).

5) Interpretation of results is aided if the index is already widely understood and measured, or easy to use (Heuserr 1998, Magurran 1998). Slight modifications to understood diversity measures are more likely to be adopted by forest managers

than complex novel approaches. Good diversity measures are ones that are easy to measure in the field and not subject to observer bias (Spies and Cohen 1992).

As described, many indices have been introduced and applied in forest management and research to describe diversity in stand structure. However, it is unclear how well these measures discriminate among the vertical canopy structure of forests in western Oregon. Therefore, it is worthwhile to examine the vertical patterns of canopy structure data collected by the western Oregon Forest Inventory and Analysis program inventory of 1995-1997 to evaluate the differences among indices.

The main goal of this study was to evaluate measures of vertical canopy-structure diversity and stratification. The first objective was to compare the sensitivity of vertical diversity and stratification measures to gradients of vertical cover, structure, and stand development. The second objective was to assess whether diversity measures most sensitive to differences in vertical structure could be predicted from standard forest mensuration variables.

Methods

Study Area and Population of Interest

I used a subset of the data collected by the USDA Forest Service Forest Inventory and Analysis (FIA) program from 1994-1997 (Azuma et al. 2002). Study sites of the FIA program consist of a permanent grid of plots located throughout western Oregon (Fig. 4.1). Western Oregon is defined as the area west of the crest of the Cascade Mountain Range, delimited by county boundary lines. The FIA study sites include all private and public forest lands, excluding Bureau of Land Management (BLM) and USDA Forest Service National Forest lands.

The Current Vegetation Survey (CVS) program conducted an inventory using similar methodology to FIA, but on federal lands (Max et al. 1996). CVS

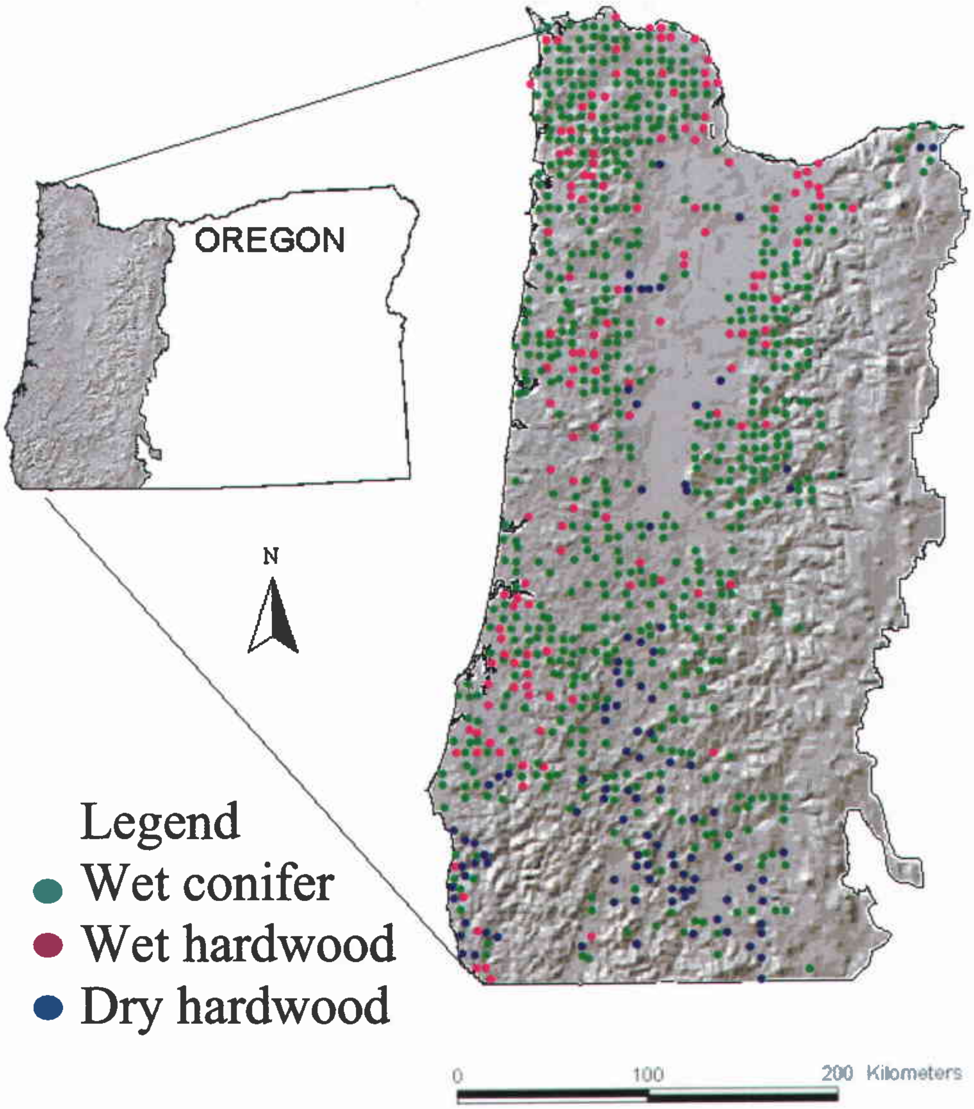

Fig 4.1. Locations of the 884 forested western Oregon FIA 1995-97 inventory plots analyzed in this study.

plots were 1-ha circular fixed-area plots systematically located on a 1.7-mile grid system (3.4 miles in designated wilderness areas). There were 5 systematically located subplots in each plot, with concentric fixed area vegetation plots within each subplot. Unlike the FIA inventory where tree heights and canopy cover were measured, cover measures were not collected and tree heights were only measured on a subset of trees, based on diameter classes. However, unlike FIA plots, crown widths were recorded for a set of growth sample trees. Therefore, the unpublished PNW FVS Variant equations to predict crown widths from dbh based on CVS tree data were used to estimate crown widths for the FIA trees.

The study sites used in this study encompassed five physiographic provinces: The Oregon Coast Range, The Willamette Valley, Oregon Western Cascades, Klamath Mountains, and High Cascades (Franklin and Dyrness 1973). The forest zones included in the FIA inventory included the *Picea sitchensis*, *Tsuga heterophylla*, *Abies amabilis*, *Tsuga mertensiana*, *Quercus* woodland, Interior Valley, Mixed-Evergreen, Mixed-Conifer, *Abies concolor*, and *Abies magnifica shastensis* (Franklin and Dyrness 1973).

Sample Design

The FIA inventory design was based on a double sample for stratification (Cochran 1977). An exception was that permanently established primary photo-interpreted plots and secondary field plots were used for the design. In the first phase of sampling, conducted in 1994, remotely sensed aerial photos at photo-points systematically distributed on a 1.36-km grid were used to estimate land use type, successional stage, and canopy cover. The second phase completed from 1995-97 involved a ground plot sampling of approximately every 16th photo-point, with a grid density of 5.4-km. The systematic-grid design of this inventory allows for statistical inferences to the population from which the grid points were sampled. Information compiled and distributed from the FIA inventory is comprehensive, has minimal bias, is scientifically sound, and has known precision (Azuma and Hanson

2002). Therefore, results of analyses of the forested plots are representative of similar forest types across western Oregon.

All 1127 - forested plots consisted of a systematically-arranged cluster of 5 0.09-ha subplots encompassed in a 2.5-ha area, regardless of stand boundaries or forest types (Fig. 4.2). Subplots were delineated into multiple condition classes to identify subplots that contained more than one forest type, stand-size class, management intensity category, or overlapped with non-forest land.

I only used plot information for the single forested condition class that comprised a minimum area of 0.27 ha (three subplots). A high degree of variability in canopy structure within a condition class was expected. I excluded cover data from the other condition classes in a plot because I felt areas < 0.27 ha could not adequately capture this variability. Out of the 1127 plots, there were 934 plots that met this criterion. Therefore, for each of these 934 plots the size of the experimental unit was the area of the plot contained in the single largest condition class. I will use the term stand throughout the remainder of this paper to refer to the experimental unit.

Data Collection

For each stand, multiple measurements were obtained. Composition, cover, and height of all shrubs, and forbs and grasses with $\geq$ 3% cover were measured on 5-m fixed-radius plots around each subplot center (see Fig. 4.2). Trees were measured to a fixed-distance of 17 m from subplot centers in fixed-radius and variable-radius plots, using a 7-m^2/ha basal area factor (BAF) prism. Age, dbh, compacted crown ratio, and height of all trees > 1.4 m tall were measured.

For each condition class, ground-based canopy cover estimates were collected. Trees were assigned to one of three canopy layers, with discrete layers differing by a minimum of 5 m in mean height. However, actual heights varied between stands, as canopy layers were relative to conditions within a stand. The mean height of each stand was defined as the average height of the uppermost

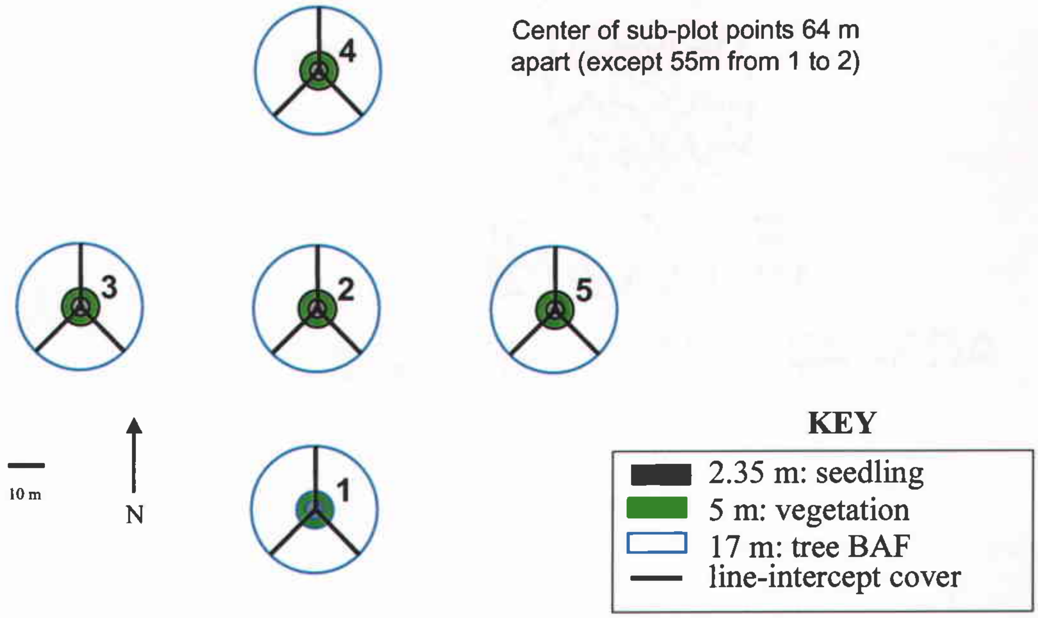

Fig 4.2. Design of the 1995-97 FIA inventory ground plot lay-out for western Oregon.

layer of canopy. The line-intercept method was used to calculate percent canopy cover in each layer (Canfield 1941; O'Brien 1989). Canopy layers were classified as upper, middle, and lower based on relative stature. For every tree species within a canopy layer, crown boundaries were vertically projected onto transects. The distance along a transect line that the crown intercepted was recorded. Canopy cover was sampled on three 17-m long horizontal transects originating at subplot center and radiating out at 0, 135, and 225 degrees. The proportion of transect lengths that were intercepted by the crowns was the ground-estimated canopy cover.

Calculated FIA Variables

Multiple canopy cover values were calculated from the line-intercept data. Canopy transects that crossed condition classes were excluded because of errors assigning condition classes. Cover was calculated for each of the vertical layers. Cover by layer was then vertically collapsed to calculate total cover. Thus cover never exceeded 100%.

Stand age and forest type were calculated for each stand. Stands were grouped into 10-yr age classes up to age 200, lumped into a 100-yr age class for ages 200-300, and stands >300 yrs were all combined into a single age class (age 400). Stand age calculations differentiated between evenaged and unevenaged stands. Forest type was calculated in a two-step process. The first criteria determined whether hardwood or softwood trees dominated the stand. Then the forest type was assigned based on the stocking density of the predominant species of "mainstand" trees within the hardwood or softwood group.

Additional independent variables that could be used in my regression models to predict vertical canopy diversity were also calculated. Stocking density, the contribution of measured trees to a fully-stocked stand, based on normal yield tables, was calculated from multiple equations (Azuma and Hanson 2002). Stem density, basal area, mean annual increment (mai), and quadratic mean diameter (qmd) were also calculated from the tree data collected in the FIA inventory.

I calculated stem frequencies by size, crown-ratio, and tree-height classes. Four size classes were used (dbh ≤ 30 cm, > 30, > 50, > 90). Crowns were compacted crown ratios. Crown classes included: crown ≤ 10%, 10.1-40, 40.1-60, and > 60%. I used four tree height classes to divide density (tree height ≤ 5m, 5.1-20, 20.1-30, > 30). Divisions were kept broad enough that other datasets could be readily modified and incorporated into them (i.e. if I had selected narrower classes, this would limit the ability of other researchers with broader classifications to use them, whereas with the broad classes, finer classifications can easily be summed to the broader class level).

Each stand was assigned to one of four general forest groups. The groups were first clustered based on hardwood or softwood dominance. They were further divided based on the moisture levels characteristic of sites occupied by the dominant tree species in each forest group. Douglas-fir was the predominant species in the wet-conifer group, red alder (*Alnus rubra* Bong) was the dominant species in the majority of wet-hardwood stands, and Oregon white oak (*Quercus garryana* Dougl. ex Hook) and Pacific madrone (*Arbutus menziesii* Pursh) dominated most of the dry-hardwood stands. I only performed analysis on the three most plentiful general forest groups: wet conifer, wet hardwood, and dry hardwood (884 stands; Table 4.1). The fourth possible forest group, dry conifer, had limited samples and was not analyzed. Mean annual precipitation was estimated with the PRISM climate model (Daly et al. 1994). The mean annual precipitation by stand age was calculated in each of the four general forest groups and helped identify the transition between wet and dry forest types (Fig. 4.3).

Table 4.1. The four general forest groups included in the 1995-97 FIA inventory that met the criteria for inclusion in this study. Stands were grouped by hardwood and conifer type, and mean precipitation levels.

General forest group	n	Age range	Dominant tree species in the stand[a]
Wet conifer	645	5-400[1]	*Pseudotsuga menziesii* (n=558), *Tsuga heterophylla* (n=57), *Picea sitchensis* (n=15), *Thuja plicata* (n=7), *Abies procera* Rehd. (n=4), *Abies amabilis* (n=2), *Chamaecyparis lawsoniana* (A. Murr.) Parl. (n=2)
Dry conifer	33	15-105	*Abies grandis* (n=9), *Calocedrus decurrens* (Torrey) Florin (n=9), *Pinus contorta* var. *murrayana* (Grev. & Balf.) Engelm. (n=6), *Abies concolor* (n=6), *Pinus ponderosa* var. ponderosa Dougl. (n=3)
Wet hardwood	137	5-250[1]	*Alnus rubra* (n=99), *Acer macrophyllum* Pursh. (n=25), *Populus balsamifera* L. ssp. *trichocarpa* (Torr. & Gray) Brayshaw (Salicaceae) (n=5), *Salix* spp. (n=3), *Umbellularia californica* (Hook. & Arn.) Nutt. (n=3), *Fraxinus latifolia* Benth. Ore a. (n=2)
Dry hardwood	102	5-165[1]	*Quercus garryana* (n=42), *Arbutus menziesii* (n=32), *Lithocarpus densiflora* (Hook. & Arn.) Rehd. (n=18), *Quercus kelloggii* Newb. (n=6), *Quercus chrysolepis* Liebm. (n=3), *Castanopsis chrysophylla* (Dougl.) DC. (n=1)

[a]The number in brackets is the number of plots in which the given species was dominant in the stand.
[1] Refer to Table 2.4 for number of stands associated with each stand-age class.

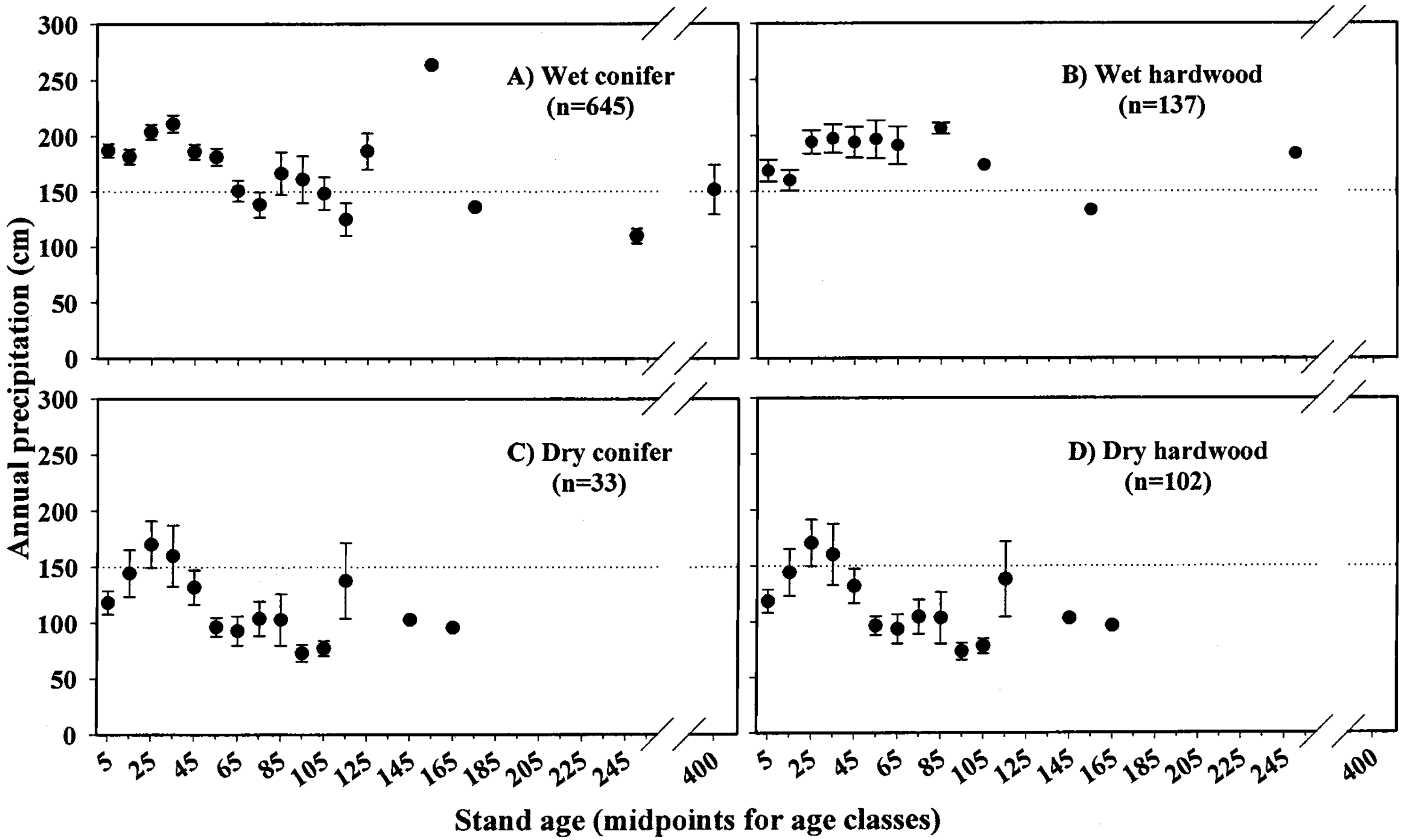

Fig 4.3. Mean annual precipitation ($\pm$ 1 SE) estimated using the PRISM model (Daly et al. 1994) across a chronosequence of stand ages (grouped into intervals and labeled using midpoints of intervals) by forest group (see Table 4.1) in western Oregon. Sample sizes differed among stand ages. Dotted line at 150 cm represents the division between wet and dry mean precipitation levels.

Vertical Measures

I calculated stem frequencies for trees taller than 1.4 m using tree height and base of live crown height intervals. Crown-base heights were calculated using the tree heights and compacted crown ratios. Unless alternate divisions were dictated by a given diversity measure, I vertically partitioned each stand into 5-m vertical intervals, and then classified trees into the 5 m height and crown-base height intervals. I selected 5-m intervals because this distance was a biologically meaningful value for wildlife or fire hazard. In addition, compacted crown ratios were only estimated to the nearest 10% and therefore smaller vertical intervals would have been too narrow to account for measurement error.

Variants of 11 diversity and two stratification measures (in addition to line-intercept layering) from the literature were calculated for each stand (Tables 4.2, 4.3). All indices referred to within-plot diversity (i.e. alpha diversity, Whittaker 1977). Structural diversity measures substituted height and crown-base height intervals for species, which are typically used when measuring diversity. Vertical structural richness was the number of height intervals occupied by tree heights, tree crowns, or crown-base heights (richness). The indices integrated the richness and the relative abundance of trees within each of these intervals (evenness).

Proportional measures (p_i) of trees are calculated by the frequency of stems (density) or basal area. In this study I used density and also density weighted by basal area. Proportions of total basal area were used because the number of stems gave higher weight to smaller sized trees. However, I expected the larger trees to be taller with larger crowns, and thus provide more vertical diversity than smaller trees. Previous studies have also used basal area instead of density to better represent the use of resources, recognizing that larger trees will have more influence (e.g. Staudhammer and Lemay 2001).

The foliage was not directly measured in the FIA inventory but was needed to calculate Foliage Height Diversity (see Table 4.2). I used basal area as a surrogate measure for the foliage cover. Within each height interval I weighted the

Table 4.2. Diversity measures and formulae and the context in which they were used in this study.

Measure	Formula	Variable descriptions	Classification	Interpretation
Berger-Parker Index (D, North et al. 1999)	$D=\frac{N_{total}}{N_{max}}$	N_{total} is the total basal area per hectare (baha) or total number of trees(tph) in the stand. N_{max} is the baha or tph of trees in the height interval with the most basal area.	Height intervals: Wet conifer: 1.4-4, 4-8, 8-16, 16-32, 32-48, 48-64, > 64m. Wet hardwood: 1.4-4, 4-8, 8-16, 16-32, 32-48, >48m Dry hardwood: 1.4-4, 4-8, 8-16, 16-32, > 32m	Decreased values suggest dominance of a single class. Increased values suggest evenness among classes.
Canopy Height Diversity Index (CHDI, Spies and Cohen 1992)	$CHDI=\sum_{i=1}^{N} Pi*H_i i$ Where: $P_i=\{C_i/0.3$ for $C<0.3$; Else 1 for $C\geq 0.3$ $Ci=\frac{\sum_{i=1}^{K} A_j}{AG}$	P_i is the height class cover score for the i^{th} height interval. H_i is the relative weight of height interval i. N is the number of height intervals. Ci is the horizontal crown area of a tree with height interval i. A_j is the horizontal crown area of the jth tree with height interal i. AG is the ground area of the sample. K is the number of trees in height interval i.	Height intervals: Wet conifer: 0-16, 16.1-32, 32.1-48, 48.1-64, > 64. Wet hardwood: 0-8, 8.1-16, 16.1-32, 32.1-48, > 48. Dry hardwood: 0-4, 4.1-8, 8.1-16, 16.1-32, and > 32 m.	Increases with increasing proportion of ground area covered by crown area. Taller stands will have higher diversity values than shorter stands with equivalent crown areas.
Coefficient of Variation (CV, Sokal and Rohlf 1981)	$CV=(SD/\overline{x})*100$	SD is the standard deviation of dbh, height, or base live crown (blc) height. $\overline{x}$ is the mean tree dbh, height, or blc height.		When the CV is small, the data scatter compared to the mean is small. When the CV is large compared to the mean, the amount of variation is large.

Table 4.2. Cont'd.

Measure	Formula	Variable descriptions	Classification	Interpretation
Diameter Diversity Index (DDI, McComb et al. 2002)	$DDI=\sum_{i=1}^{N} Pi*D_i i$	Pi is the index value of a diameter class (assigned using coefficients from a straight-line regression equation in which tree density is the independent variable). D_ii is the weighting for that class.	Diameter classes: 5–24 cm, 25–49 cm, 50–99 cm, and > 100	Increases with increasing amounts of large diameter trees. The DDI has a maximum value of 10.
Evenness Index (E, Pielou 1975)	E=H'/lnS	H' is Shannon diversity (see below). S is the number of height intervals occupied by tree heights.	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Measures evenness.
Foliage Height Diversity (FHD, MacArthur and MacArthur 1961)	$FHD=-\sum_{i}^{n}(\ln p_i)p_i$	P_i is the proportion of total foliage (using basal area as a surrogate) which lies in the i^{th} vertical layer/interval.	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Increases as the number of classes increases and/or the proportional distribution of the basal area among classes becomes more even. For a given number of classes, the maximum value of FHD is reached when all classes have the same basal area.
Height Class Richness (R)	R=N	N is the number of height or live crown base classes occupied by trees.	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Increases with the number of height classes occupied. It does not consider relative abundance.
Margalef Diversity (D_{mg}, Clifford and Stephenson 1975)	$D_{mg}=(S-1)/\ln N$	S is the number of height classes occupied by heights or blcs. N is the total baha or tph for all height classes	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Measures species richness.

Table 4.2. Cont'd.

Measure	Formula	Variable descriptions	Classification	Interpretation
Shannon Index of Diversity (SW, Shannon 1948)	$SW = -\sum_{i}^{n} (\ln p_i) p_i$	P_i is the proportion of trees or baha for trees with heights or blcs located in the i^{th} height interval.	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Increases as number of classes increases and/or the proportional distribution of trees among classes becomes more equitable. For a given number of classes, the maximum value is reached when all classes have the same basal area.
Simpson's Index of Diversity (SDI, Simpson 1949)	$SDI = 1 - \sum_{i}^{n} p_i^2$	P_i is the proportion of tph or baha for trees with heights or blcs located in the i^{th} height interval.	Height intervals: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, 30-35, 35-40, 40-45, 45-50, 50-55, 55-60, >60m	Increases with increasing diversity in tree heights. Tends to emphasize dominant classes.
Vertical Evenness (VE, Neumann and Starlinger 2001)	$VE = -\sum_{i}^{n} (\ln p_i) * \frac{p_i}{n}$	P_i is the relative baha or tph of all trees in the i^{th} height interval. Trees are stratified into four layers.	Height intervals: < 20% of maximum height, 20-50%, 50-80%, and 80-100%.	Low values characterize single-storied stands, while the theoretical maximum of one results for vertical equally distributed trees.

Table 4.3. Stratification measures and the context in which they were used in this study.

Measure	Approach	Variable descriptions	Classification
Stratification Algorithm (Baker and Wilson 2000)	1. If HT(tree2)+K_o is > mean base crown height (HBLC) of tree1 then tree2 is in the same stratum as tree1. 2. If Ht(tree2)+K_o < mean HBLC, then tree2 is in stratum below tree1.	Ko defines a threshold distance between mean HBLC and HT(tree2). K_o =1.5 m routinely identified levels of stratification consistent with the published accounts..	Layering increases when the heights of the next tallest trees are much shorter than the mean HBLCs of the next tallest strata.
TSTRAT (Latham et al. 1998)	Strata cut-off when tree height is <((0.40*CL) + HBLC)	CL is crown length HBLC is the height-to-base of the live crown for the tallest tree with longest crown in a given strata.	Layering increases when trees are shorter than than the strata cut-off.

basal area by the proportion of the height interval covered by crown. For example, if a given tree was 16 m tall with 1 m^2/ha of basal area and a crown ratio of 50% (thus crown-base height=8m), the foliage estimate would be calculated as 0.2*1 m^2/ha for the 15-20 m height interval, 1*1 m^2/ha for the 10-15 m height interval, and 0.4*1 m^2/ha for the 5-10m height interval.

The different roles the foliage and the space below the crowns might play in the forest community were considered. For example, from a wildlife viewpoint, a forest with adjacent crowns of equal lengths would not provide the same amount of open space for foraging by spotted owls compared to a forest with unequal crown lengths. From a fire perspective, the positioning of crowns in the forest influences active crown fires. If two stands with equal tree heights were compared (Fig. 4.4), both would receive equal values of diversity when only considering tree heights. However, if the diversity of crown length was included (using crown-base height as a surrogate), Fig 4.4B would have higher diversity. From an ecological standpoint, I would consider the forest in Fig. 4.4B to be more diverse than Fig. 4.4A, as it is providing more vertical 'niche differentiation'. Thus, ignoring the total length of foliage, this ecological information would have been lost.

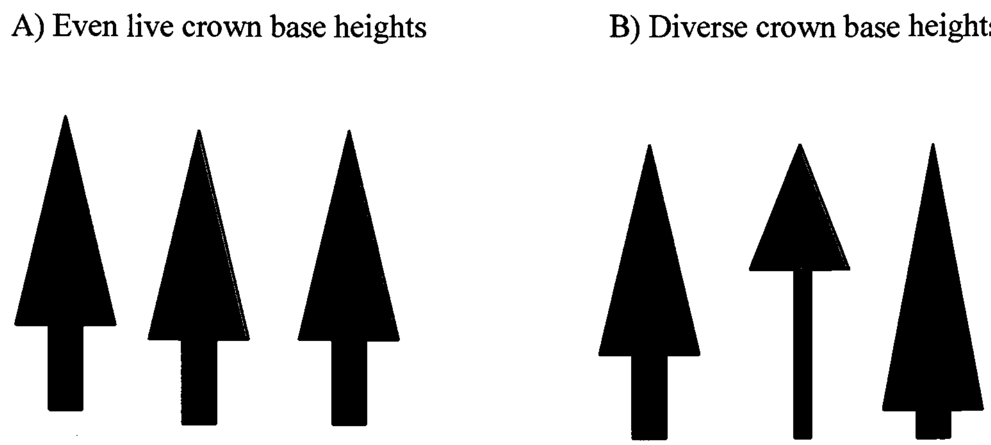

Fig. 4.4: Comparison of stands with even heights of live crown bases and stands with diverse live crown base heights.

Therefore, in addition to measuring height and crown-base height diversity independently, I also integrated tree heights and crown-base heights in diversity index measures. I did this in two ways. First I summed the calculated diversity values for the height and crown-base intervals, and second, I calculated the mean of the two diversity values (similar to Staudhammer and LeMay 2001). This could then be compared with estimates of FHD.

For several diversity metrics it was necessary to modify the height intervals for different forest groups. I modified the CHDI index for wet and dry hardwood stands. Spies and Cohen (1992) originally developed CHDI for wet-conifer forests. However, there were very few trees taller than 48 m and 32 m respectively in the wet- and dry-hardwood stands. Thus, it did not make sense to differentiate among the trees taller than these heights. However, I still wanted to maintain a total of five height intervals because of the relative weightings assigned to the different height intervals to achieve a maximum CHD of 15. For the wet-hardwood stands I used : 1.4-8, 8.1-16, 16.1-32, 32.1-48, and > 48 m, while for the dry-hardwood stands I used: 1.4-4, 4.1-8, 8.1-16, 16.1-32, and > 32 m. For the Berger-Parker index I used the seven height interval divisions of North et al. (1999) for the wet-conifer stands, but for the wet- hardwood stands I used six intervals (1.4-4, 4.1-8, 8.1-16, 16.1-32, 32.1-48, and > 48 m), and only five intervals (1.4-4, 4.1-8, 8.1-16, 16.1-32, 32.1-48, and > 48 m) for the dry-hardwood stands.

The CHDI equation (see Table 4.2) requires crown area estimates. However, these were not calculated in the FIA inventory. Therefore crown areas were calculated from crown width equations (Moeur 1985) created by the FVS programmers using CVS plot data. In addition to the FIA stands, CHDI was also calculated for a set of CVS plots as a baseline with which to compare FIA results.

The Diameter Diversity Index (DDI, see Table 4.2) serves as a surrogate for CHDI (Thomas Spies and Robert Pabst, personal communication). DDI is based on densities of trees among dbh classes. There are two sets of coefficients that have been derived for DDI, based on the ecoregion in which they were used (Coast Range or Cascades). DDI is essentially a relative measure and similar DDIs can result from different stem frequency distributions. However, it is thought that DDI can be used for general characterization of a stand. Stands with all trees < 5 cm dbh will have a DDI value of 0. For stands that were estimated to be within the vicinity of the cascade ecoregion, I calculated DDI values using the Cascade coefficients (n=339). For the remaining stands I used the Coast Range DDI coefficients.

Selection of stands for measuring vertical diversity

I calculated vertical diversity measures for the wet-conifer, wet-hardwood, and dry-hardwood groups independently and then combined them together. While Chapter 2 provided evidence for different vertical patterns among the forest groups, I thought differences in species composition and vertical growth potential among the forest groups might already be captured by different patterns in crown elongation and shade-tolerance which would be incorporated within the vertical diversity measures. In addition some forest groups (especially dry hardwood) had very limited stands for some of the vertical height intervals. Therefore, looking at forest groups as a whole was also warranted. I also examined a subset of stands with minimum mean stand heights of 20 m. I assumed that the height of a stand would influence the vertical diversity measure. A taller stand inherently would be more diverse because it had more height intervals. Therefore, I compared diversity patterns with and without stands < 20 m tall to explore whether the dominance of a height class could be an artifact of the limited number of 5-m height intervals present in shorter stands.

Sensitivity of vertical measures

To evaluate the sensitivity of the multiple measures to changes in vertical structure, individual stands were assigned to vertical cover and structure groups. I used two methods to assign stands to vertical groups. The first approach involved creating vertical cover groups based on the relative distribution of cover among the three layers of line-intercept cover. I plotted stand-level graphs using heights and crown-base heights for all measured trees. In addition the total percent cover, cover within each of the three line-intercept layers of cover, and heights of the three cover layers were overlaid on the plot of heights and crown-base heights (e.g. Fig. 4.5). I visually examined plots of vertical cover present to determine overall variation. Based on these stand-level plots, I determined there were eight potential cover groups that could be used to differentiate among the vertical diversity of stands. These groups were based on the relative proportions of total cover contained within each of the three layers of cover (Table 4.4). For the second approach I used rank abundance graphs of individual stands to create vertical structure groups (e.g. Fig. 4.6). Stand-level rank abundance graphs assigned each measured tree to vertical intervals. Each tree was then weighted by the basal area per hectare it represented. I then established criteria that assigned each stand to one of the five vertical structure groups based on its rank-abundance measures (Table 4.5).

I examined box-whisker plots that plotted the distribution of diversity index values against each of the cover and structure groups. I then plotted the mean ($\pm$ 1 SE) number of layers calculated using stratification indices (see Table 4.3). Box-whisker plots and mean plots revealed which metrics were giving results expected based on relative diversity of the vertical groups. General patterns of increasing diversity and layering with increasing proportions of cover , heights, and crown-base heights located among multiple layers of cover were expected.

Correlation analyses among the vertical diversity and layering measures, using Spearman's rho, were calculated to examine similarity among diversity measures calculated using density versus using density weighted by basal area.

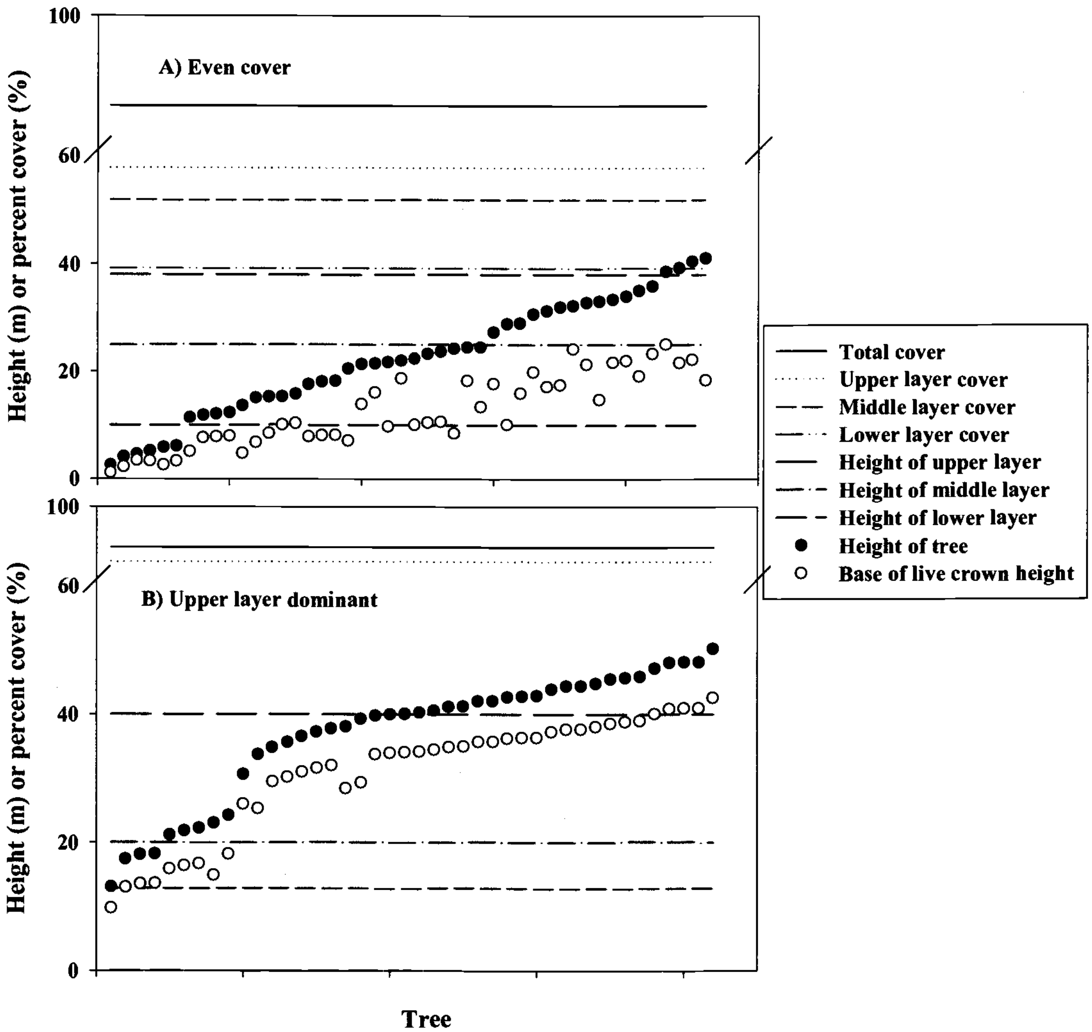

Fig. 4.5. Example plots of tree heights, live crown bases, and information on canopy cover layering used to create criteria distinguishing among vertical cover classes for A) a stand with even distribution of cover among layers, and B) a stand with a dominant upper layer of cover. Vertical cover classes are described in Table 4.4.

Table 4.4. Description of the vertical cover groups using line-intercept canopy cover data.

		Sample size (n)				
Cover Group	Abbreviation	Wetcon	Wethar	Dryhar	Total	Description
Minimal cover	Mincov	43	1	6	50	Total canopy cover is ≤ 10%.
Layer 1 Dominant	Lyr1dom	395	65	31	491	Upper layer cover is ≥ 2.2 times cover of middle and lower layers. Total canopy cover is > 10%.
Layer 2 Dominant	Lyr2dom	32	17	24	73	Middle layer cover is ≥ 2.2 times the percent cover for the upper and lower layers. Total canopy cover is >10%.
Layer 3 Dominant	Lyr3dom	3	1	0	4	Lower layer cover is ≥ 2.2 times the percent cover both the upper and and middle layers.
Layers 1-2 Dominant	Lyr12dom	57	21	9	87	Upper or middle layer of cover is ≥ 40% of total canopy cover. Then the two layers of cover must be within 14% of each other. The lower layer of cover must be ≤ 30% of total cover. Total cover must be > 10%.
Layers 2-3 Dominant	Lyr23dom	6	2	1	9	Middle or lower layer of cover is ≥ 40% of total canopy cover. Then the two layers of cover must be within 14% of each other. The upper layer of cover must be ≤ 30% of total cover. Total cover must be > 10%.
Equally Dominant	Evencov	12	3	3	18	All three cover layers have cover ≥ 20% of total cover. Each of the three cover layers are within 14% of the other layers of cover. Total cover is > 10%.
Unclassified	Interm	97	27	28	152	Stands where the allocation of cover among the three layers does not meet the criteria for the seven other vertical classes.

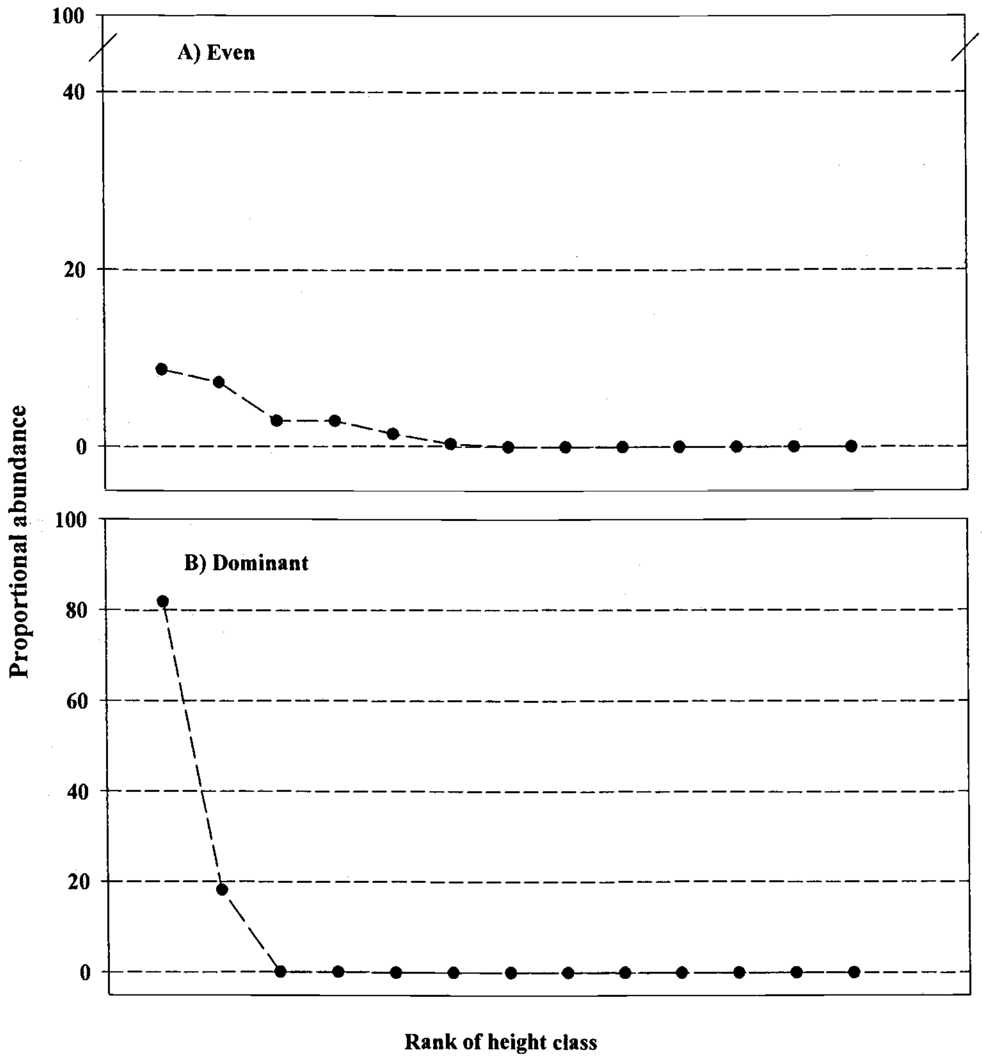

Fig. 4.6. Comparison of rank abundance graphs for two stands that represent the two extremes of the vertical height classes: A) even distribution and B) dominant distribution. The proportional abundance is the number of trees with heights within the given height interval, weighted by basal area. Dividing basal area within each 5-m interval by the total basal area for the vertical cover class standardized abundance of basal area among vertical cover classes (range from 0–100%). Vertical height classes are described in Table 4.5.

Table 4.5. Description of the vertical height groups created based on rank abundance data for 5-m height intervals.

	Sample size (n)				
Cover Group	Wetcon	Wethar	Dryhar	Total	Description
Dominant	71	12	9	96	The most abundant height class has ≥ 80% of the total basal area of the stand.
Sub-dominant	96	16	17	131	The most abundant height class has ≥ 60% and < 80% of the total basal area of the stand.
Intermediate	238	48	43	349	The most abundant height class has ≥ 40% and < 60% of the total basal area of the stand.
Sub-even	197	58	29	299	The most abundant height class has ≥ 20% and < 40% of the total basal area of the stand.
Even	2	1	0	3	The most abundant height class has < 20% of the total basal area of the stand.

Diversity Along a Successional Gradient

The diversity measure(s) that best differentiated among the vertical structure and cover groups were used to describe patterns in vertical diversity across a successional gradient. Regardless of its performance, I explored successional patterns of CHDI for the wet-conifer FIA stands to compare them with CVS stands. I did this to compare the primarily private lands included in the FIA inventory with the baseline of public federal lands included in the CVS inventory. For the diversity measures, I used the chronosequence of the FIA data to examine vertical diversity patterns along a successional gradient. Evenaged and unevenaged stands were combined for analysis, as only 11% of the samples were unevenaged.

Prediction of Vertical Diversity

The ability to use standard forest measurements to predict canopy diversity measures was evaluated. Predicted models were attempted for the diversity measure(s) that best differentiated among the vertical structure and cover groups. Because the three general forest groups have distinctive developmental patterns of canopy structure, predictive models were pursued for each of the forest groups.

I used an information-theoretic approach to predict vertical diversity levels for forest stands in western Oregon. I developed a set of *a priori* hypotheses relating the amount of vertical structural diversity to forest attributes measured in the FIA inventory. I expressed these hypotheses as multiple linear regression models that were fit to the inventory data. I then used an objective model selection criterion, Akaike's information criterion for small sample sizes (AICc), to rank the models according to their ability to approximate the data (Burnham and Anderson 1998). I used AICc as my model selection method because I was interested in evaluating multiple models that potentially could be used by forest managers to predict vertical structural diversity. The AIC method results in a "best approximating model" that is the most parsimonious explanation of the data. In addition a "95% confidence/good set" of approximating models can be selected based on Akaike weights. Akaike weights can be interpreted as approximate probabilities that given models are really the closest to the unknown "true" model of vertical diversity of structure (Anderson et al. 2000). A general rule of thumb for differences in AIC score is a range of 4-7 as the practical cutoff for defining a 95% confidence model set (Burnham and Anderson 1998). The importance of the variables included in this 95% confidence model set can be assessed by summing the Akaike weights for all models in which a given variable is present (p. 141 Burnham and Anderson 1998)

Model Development

Prior to data analysis, I hypothesized biologically meaningful relationships between vertical structural diversity and the forest variables measured or calculable from the FIA inventory (Table 4.6). I considered variables based on their use in previous studies, or potential utility in future models, that model canopy structure features (e.g. Aber 1979, Paine and Hann 1982, Bentley 1996, Cade 1997, Mitchell and Popovich 1997, Nelson et al. 1998, , Buckley et al. 1999, Crookston and Stage 1999, Garman and Cole 1999, Gill et al. 2000).

Hypothesized relationships resulted in models that used single variables or combinations of variables (Tables 4.7-4.9). Three sets of models were required because three diversity measures used required different transformations to meet model assumptions. I included null models that only included an intercept term to confirm that richer models were explaining more information than would be explained by chance. I was unable to fit a global model containing all variables due to the high correlation between several variables. Therefore, I assessed general fit of all models by checking assumptions of constant variance and normality.

The mathematical model demonstrating a hypothesized regression model is:

$$\text{Preddiversity}_i = \beta_0 + \beta_1 X_1 + \beta_2 X_2 + \ldots + \beta_n Xn + \varepsilon_i + \varepsilon_j \qquad \text{(Eqn. 4.1)}$$

Where:

$\varepsilon_i \sim N(0,\sigma^2_\varepsilon)$ and where ε_i and $\varepsilon_{i'}$ are independent,
β's are regression coefficients for predictive model variables X_1 to X_n, which are the variables contained within a given AIC model,
Preddiversity is the predicted diversity of vertical stand structure in the i^{th} stand,
ε_i is the random effect of each sample that adds variability to value of preddiversity, and
ε_j is the uncertainty associated with where the future value will be in relation to its mean.

Table 4.6. Descriptions of explanatory variables measured in the FIA plots in western Oregon that were used in models to predict vertical structural diversity in FIA plots in western Oregon.

Variable	Abbreviation	Units	Expected relationship[1]	Transformation
Basal area	baha	m^2/ha	linear or square root	$\sqrt{baha}$
Elevation	elev	m	linear	
Mean annual increment	mai	ft^3/acre/yr	linear or quadratic	mai - mai^2
Number of tree species in a plot (richness)	nspecies	n/a	linear	
Precipitation[2]	precip	cm	linear	
Quadratic mean diameter	qmd	cm	linear or quadratic	qmd - qmd^2
Stand age – evenaged and unevenaged stands combined	age	years	linear or inverse	1/age
Stand height – height of tallest tree in the stand	height	m	linear	
Standard deviation of dbh	sdofdbh	cm	linear, natural log, square root	ln(sdofdbh) $\sqrt{sdofdbh}$
Stocking density[3] (percent of normal stand occupied by trees)	stocking	%	linear or square root	$\sqrt{stock}$
Total trees per hectare	tph	trees/ha	linear or quadratic	tph + tph^2
Trees per hectare in crown class 1 (<10% compacted crown)	tphcrn1	trees/ha	linear	
Trees per hectare in crown class 2 (10-40%)	tphcrn2	trees/ha	linear	
Trees per hectare in crown class 3 (40-60%)	tphcrn3	trees/ha	linear	
Trees per hectare in crown class 4 (>60%)	tphcrn4	trees/ha	linear	
Trees per hectare in dbh class 1 (tree dbh<30 cm)	tphdbh1	trees/ha	linear	
Trees per hectare in dbh class 2 (>30 cm)	tphdbh2	trees/ha	linear	
Trees per hectare in dbh class 3 (>50 cm)	tphdbh3	trees/ha	linear	
Trees per hectare in dbh class 4 (>90 cm)	tphdbh4	trees/ha	linear	
Trees per hectare in height class 1 (tree height <5m)	tphht1	trees/ha	linear	
Trees per hectare in height class 2 (5-20m)	tphht2	trees/ha	linear	
Trees per hectare in height class 3(20-30m)	tphht3	trees/ha	linear	
Trees per hectare in height class 4 (>30m)	tphht4	trees/ha	linear	

[1]Relationships are predicted relationships with logit-transformed canopy cover.
[2]The PRISM climate model (Daly et al. 1994) was used to estimate mean annual precipitation.
[3]Stocking equations which are specific to site productivity and forest type are provided in appendix I.

Table 4.7. Description of *a priori* models describing potential predictors of SDI (See Table 4.2) in FIA plots in western Oregon. Descriptions of abbreviated variables are described in Table 4.6.

Model	Hypothesis	Model structure
1	No effects (null model)	β_0
2	Positive effect of species richness	$\beta_0 + \beta_1$(nspecies)
3	Positive effect of stand age (linear)	$\beta_0 + \beta_1$(age)
4	Inverse effect of stand age (inverse)	$\beta_0 + \beta_1$(1/age)
5	Positive effect of increasing stand height	$\beta_0 + \beta_1$(height)
6	Positive effect of stocking (linear)	$\beta_0 + \beta_1$(stocking)
7	Positive effect of stocking (square root)	$\beta_0 + \beta_1$(√stock)
8	Positive effect of ba (linear)	$\beta_0 + \beta_1$(baha)
9	Positive effect of ba (square root)	$\beta_0 + \beta_1$(√baha)
10	Positive effect of tph (linear)	$\beta_0 + \beta_1$(tph)
11	Positive effect of species richness and large trees	$\beta_0 + \beta_1$(nspecies)+ β_2(tphdbh4)
12	Positive effect of tph in ht classes 3 and 4	$\beta_0 + \beta_1$(tphht3)+ β_2(tphht4)
13	Positive effect of tph in dbh class 2	$\beta_0 + \beta_1$(tphdbh2)
14	Positive effect of tph in dbh class 3	$\beta_0 + \beta_1$(tphdbh3)
15	Positive effect of tph in dbh class 4	$\beta_0 + \beta_1$(tphdbh3)+ β_2(tphdbh4)
16	Positive effect of tph in crown ratio 2	$\beta_0 + \beta_1$(tphcrn2)
17	Positive effect of tph in crown ratio 3	$\beta_0 + \beta_1$(tphcrn3)
18	Negative effect of tph in crown ratio 4	$\beta_0 - \beta_1$(tphcrn4)
19	Positive effect of precipitation and negative effect of elevation	$\beta_0 + \beta_1$(precip) - β_3(elev)
20	Positive effect of stocking and stand height	$\beta_0 + \beta_1$(√stock) + β_2(height)
21	Positive effect of stocking and qmd	$\beta_0 + \beta_1$(√stock) + β_2 (qmd)
22	Positive effect of stocking, stand height, and mai	β_0+β_1(√stock)+β_2(height)+β_3(mai)
23	Positive effect of basal area and stand height	$\beta_0 + \beta_1$(√baha) + β_2(height)
24	Positive effect of basal area and inverse effect of age	$\beta_0 + \beta_1$(√baha) + β_2(1/age)
25	Positive effect of ba and qmd	$\beta_0 + \beta_1$(√baha) + β_2(qmd)
26	Positive effect of ba, stand height and mai	$\beta_0 + \beta_1$(√baha) + β_2(height) + β_3(mai)
27	Positive effect of qmd and stand height	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height)
28	Positive effect of qmd and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(mai)
29	Positive effect of qmd, stand height, and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height) + β_4(mai)
30	Positive effect of tph and stand height	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height)
31	Positive effect of tph, stand height, and mai	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(mai)
32	Positive effect of tph, stand height, and qmd	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(qmd)
33	Positive effect of tph, depending on basal area	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(√baha) + β_4(tph*baha)
34	Positive effect of tph in height classes 1,2,3,4	$\beta_0 + \beta_1$(tphht1) + β_2(tphht2) + β_3(tphht3)+ β_4(tphht4)

Table 4.7. Cont'd.

Model	Hypothesis	Model structure
35	Positive effect of tph in crn classes 1,2, 3,4	$\beta_0 + \beta_1(\text{tphcrn1}) + \beta_2(\text{tphcrn2}) + \beta_3(\text{tphcrn 3}) + \beta_4(\text{tphcrn4})$
36	Positive effect of ba, stand height,and mai, inverse effect of age	$\beta_0 + \beta_1(\text{baha}) + \beta_2(\text{height}) + \beta_3(\text{mai}) + \beta_4(1/\text{age})$
37	Positive effect of stand height and species richness	$\beta_0 + \beta_1(\text{height}) + \beta_2(\text{nspecies})$
38	Positive effect of sd of dbh (linear)	$\beta_0 + \beta_1(\text{sdofdbh})$
39	Positive effect of sd of dbh (natural log)	$\beta_0 + \beta_1(\ln(\text{sdofdbh}))$
40	Positive effect of sd of dbh (ln)	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height})$
41	Positive effect of sd of dbh (ln), stand height (ln), and ba (square root)	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\sqrt{\text{baha}})$
42	Positive effect of sd of dbh (ln), stand height (ln), and tph	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\text{tph})$
43	Positive effect of sd of dbh (ln), stand height (ln), and tph among size classes	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\text{tphdbh1}) + \beta_4(\text{tphdbh2})$
44	Positive effect of sd of dbh (ln) and tph among size classes	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{tphdbh1}) + \beta_3(\text{tphdbh2})$
45	Positive effect of sd of dbh (ln) and ba (square root)	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\sqrt{\text{baha}})$

Table 4.8. Description of *a priori* models describing potential predictors of CHDI (See Table 4.2) in FIA plots in western Oregon. Descriptions of abbreviated variables are described in Table 4.6.

Model	Hypothesis	Model structure
1	No effects (null model)	β_0
2	Positive effect of species richness	$\beta_0 + \beta_1$(nspecies)
3	Positive effect of stand age (linear)	$\beta_0 + \beta_1$(age)
4	Inverse effect of stand age (inverse)	$\beta_0 + \beta_1$(1/age)
5	Positive effect of increasing stand height	$\beta_0 + \beta_1$(height)
6	Positive effect of stocking (linear)	$\beta_0 + \beta_1$(stocking)
7	Positive effect of sd of dbh (linear)	$\beta_0 + \beta_1$(sdofdbh)
8	Positive effect of ba (linear)	$\beta_0 + \beta_1$(baha)
9	Positive effect of tph (linear)	$\beta_0 + \beta_1$(tph)
10	Positive effect of species richness and large trees	$\beta_0 + \beta_1$(nspecies)+ β_2(tphdbh4)
11	Positive effect of tph in ht classes 3 and 4	$\beta_0 + \beta_1$(tphht3)+ β_2(tphht4)
12	Positive effect of tph in dbh class 2	$\beta_0 + \beta_1$(tphdbh2)
13	Positive effect of tph in dbh class 3	$\beta_0 + \beta_1$(tphdbh3)
14	Positive effect of tph in dbh class 4	$\beta_0 + \beta_1$(tphdbh3)+ β_2(tphdbh4)
15	Positive effect of tph in crown ratio 2	$\beta_0 + \beta_1$(tphcrn2)
16	Positive effect of tph in crown ratio 3	$\beta_0 + \beta_1$(tphcrn3)
17	Negative effect of tph in crown ratio 4	$\beta_0 - \beta_1$(tphcrn4)
18	Positive effect of precipitation and negative effect of elevation	$\beta_0 + \beta_1$(precip) - β_3(elev)
19	Positive effect of stocking and stand height	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$(height)
20	Positive effect of stocking and qmd	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$ (qmd)
21	Positive effect of stocking, stand height, and mai	$\beta_0+\beta_1(\sqrt{\text{stock}})+\beta_2$(height)+$\beta_3$(mai)
22	Positive effect of basal area and stand height	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height)
23	Positive effect of basal area and inverse effect of age	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(1/age)
24	Positive effect of ba and qmd	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(qmd)
25	Positive effect of ba, stand height and mai	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height) + β_3(mai)
26	Positive effect of qmd and stand height	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height)
27	Positive effect of qmd and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(mai)
28	Positive effect of qmd, stand height, and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height) + β_4(mai)
29	Positive effect of tph and stand height	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height)
30	Positive effect of tph, stand height, and mai	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(mai)
31	Positive effect of tph, stand height, and qmd	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(qmd)
32	Positive effect of tph, depending on basal area	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + $\beta_3(\sqrt{\text{baha}})$ + β_4(tph*baha)
33	Positive effect of tph in height classes 1,2,3,4	$\beta_0 + \beta_1$(tphht1) + β_2(tphht2) + β_3(tphht3)+ β_4(tphht4)
34	Positive effect of tph in crn classes 1,2, 3,4	β_0 + β_1(tphcrn1)+β_2(tphcrn2)+β_3(tphcrn3) +β_4(tphcrn4)

Table 4.8. Cont'd.

Model	Hypothesis	Model structure
35	Positive effect of ba, stand height,and mai, inverse effect of age	$\beta_0 + \beta_1$(baha)+ β_2(height) + β_3(mai)+ β_4(1/age)
36	Positive effect of stand height and species richness	$\beta_0 + \beta_1$(height)+ β_2(nspecies)
37	Positive effect of sd of dbh (square root)	$\beta_0 + \beta_1$(√sdofdbh)
38	Positive effect of sd of dbh (square root) and stand height	$\beta_0 + \beta_1$(√sdofdbh)+ β_2(height)
39	Positive effect of height, ba, inverse effect of age.	$\beta_0 + \beta_1$(height) + β_2(baha) + β_3(1/age)
40	Positive effect of stocking, height, inverse effect of age	$\beta_0 + \beta_{1+}\beta_2$(stocking) + β_2(height) +β_3(1/age)
41	Positive effect of sd of dbh (square root), stocking (natural log)	$\beta_0 + \beta_1$(√sdofdbh)+β_2(ln(stock))
42	Positive effect of sd of dbh (square root), ba	$\beta_0 + \beta_1$(√sdofdbh)+β_2(baha)
43	Positive effect of sd of dbh (square root), tph	$\beta_0 + \beta_1$(√sdofdbh)+β_2(tph)
44	Positive effect of sd of dbh (square root), ba, height	$\beta_0 + \beta_1$(√sdofdbh)+β_2(baha)+ β_3(height)
45	Positive effect of sd of dbh (square root), tph, height	$\beta_0 + \beta_1$(√sdofdbh)+β_2(tph)+ β_3(height)
46	Positive effect of sd of dbh (square root), tph among size classes, heights	$\beta_0 + \beta_1$(√sdofdbh)+β_2(height) + β_3(tphdbh1) + β_4(tphdbh2)
47	Positive effect of sd of dbh (square root), tph among size classes	$\beta_0 + \beta_1$(√sdofdbh)+ β_2(tphdbh1) + β_3(tphdbh2)

Table 4.9. Description of a priori models describing potential predictors of FHD (See Table 4.2) in FIA plots in western Oregon. Descriptions of abbreviated variables are described in Table 4.6.

Model	Hypothesis	Model structure
1	No effects (null model)	β_0
2	Positive effect of species richness	$\beta_0 + \beta_1$(nspecies)
3	Positive effect of stand age (linear)	$\beta_0 + \beta_1$(age)
4	Inverse effect of stand age (inverse)	$\beta_0 + \beta_1$(1/age)
5	Positive effect of increasing stand height	$\beta_0 + \beta_1$(height)
6	Positive effect of stocking (linear)	$\beta_0 + \beta_1$(stocking)
7	Positive effect of stocking (square root)	$\beta_0 + \beta_1(\sqrt{\text{stocking}})$
8	Positive effect of ba (linear)	$\beta_0 + \beta_1$(baha)
9	Positive effect of ba (square root)	$\beta_0 + \beta_1(\sqrt{\text{baha}})$
10	Positive effect of tph (linear)	$\beta_0 + \beta_1$(tph)
11	Positive effect of species richness and large trees	$\beta_0 + \beta_1$(nspecies)+ β_2(tphdbh4)
12	Positive effect of tph in ht classes 3 and 4	$\beta_0 + \beta_1$(tphht3)+ β_2(tphht4)
13	Positive effect of tph in dbh class 2	$\beta_0 + \beta_1$(tphdbh2)
14	Positive effect of tph in dbh class 3	$\beta_0 + \beta_1$(tphdbh3)
15	Positive effect of tph in dbh class 4	$\beta_0 + \beta_1$(tphdbh3)+ β_2(tphdbh4)
16	Positive effect of tph in crown ratio 2	$\beta_0 + \beta_1$(tphcrn2)
17	Positive effect of tph in crown ratio 3	$\beta_0 + \beta_1$(tphcrn3)
18	Negative effect of tph in crown ratio 4	$\beta_0 - \beta_1$(tphcrn4)
19	Positive effect of precipitation and negative effect of elevation	$\beta_0 + \beta_1$(precip) - β_3(elev)
20	Positive effect of stocking and stand height	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$(height)
21	Positive effect of stocking and qmd	$\beta_0 + \beta_1(\sqrt{\text{stock}}) + \beta_2$ (qmd)
22	Positive effect of stocking, stand height, and mai	$\beta_0+\beta_1(\sqrt{\text{stock}})+\beta_2$(height)+$\beta_3$(mai)
23	Positive effect of basal area and stand height	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height)
24	Positive effect of basal area and inverse effect of age	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(1/age)
25	Positive effect of ba and qmd	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(qmd)
26	Positive effect of ba, stand height and mai	$\beta_0 + \beta_1(\sqrt{\text{baha}}) + \beta_2$(height) + β_3(mai)
27	Positive effect of qmd and stand height	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height)
28	Positive effect of qmd and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(mai)
29	Positive effect of qmd, stand height, and mai	$\beta_0 + \beta_1$(qmd) + β_2(qmd^2) + β_3(height) + β_4(mai)
30	Positive effect of tph and stand height	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height)
31	Positive effect of tph, stand height, and mai	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(mai)
32	Positive effect of tph, stand height, and qmd	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + β_3(height) + β_4(qmd)
33	Positive effect of tph, depending on basal area	$\beta_0 + \beta_1$(tph) + β_2(tph^2) + $\beta_3(\sqrt{\text{baha}})$ + β_4(tph*baha)
34	Positive effect of tph in height classes 1,2,3,4	$\beta_0 + \beta_1$(tphht1) + β_2(tphht2) + β_3(tphht3)+ β_4(tphht4)

Table 4.9. Cont'd.

Model	Hypothesis	Model structure
35	Positive effect of tph in crn classes 1,2, 3,4	$\beta_0 + \beta_1(\text{tphcrn1}) + \beta_2(\text{tphcrn2}) + \beta_3(\text{tphcrn3}) + \beta_4(\text{tphcrn4})$
36	Positive effect of ba, stand height,and mai, inverse effect of age	$\beta_0 + \beta_1(\text{baha}) + \beta_2(\text{height}) + \beta_3(\text{mai}) + \beta_4(1/\text{age})$
37	Positive effect of stand height and species richness	$\beta_0 + \beta_1(\text{height}) + \beta_2(\text{nspecies})$
38	Positive effect of sd of dbh (linear)	$\beta_0 + \beta_1(\text{sdofdbh})$
39	Positive effect of sd of dbh (natural log)	$\beta_0 + \beta_1(\ln(\text{sdofdbh}))$
40	Positive effect of sd of dbh (natural log) and stand height	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height})$
41	Positive effect of sd of dbh (natural log), stand height and tph	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\text{tph})$
42	Positive effect of sd of dbh (natural log), stand height and tph among size classes	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\text{tphdbh1}) + \beta_4(\text{tphdbh2}))$
43	Positive effect of sd of dbh (natural log), stand height and ba (square root)	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\text{height}) + \beta_3(\sqrt{\text{baha}})$
44	Positive effect of stocking, height	$\beta_0 + \beta_1(\text{stocking}) + \beta_2(\text{height})$
45	Positive effect of stocking, tph among size classes	$\beta_0 + \beta_1(\text{stocking}) + \beta_2(\text{tphdbh1}) + \beta_3(\text{tphdbh2})$
46	Positive effect of sd of dbh (natural log), ba (square root)	$\beta_0 + \beta_1(\ln(\text{sdofdbh})) + \beta_2(\sqrt{\text{baha}})$

Statistical Analysis of Models

Prior to the model fitting process, stands within each forest group were divided into two subsets (Table 4.10). Seventy-five percent of the data were used to generate the models (model dataset). This set was randomly selected from the total number of stands for each of the general forest groups. The remaining 25% were set aside to corroborate the fit of the model after it was completed (test dataset). Ranges of values for the explanatory variables were similar for the model and test datasets.

Table 4.10. Sample sizes used in model-fitting and model-testing for each of the three general forest groups analyzed in this study.

Forest group	Model dataset (n)	Test dataset (n)
Wet conifer	484	161
Wet hardwood	103	34
Dry hardwood	76	26
Total	663	221

Models were fit using PROC MIXED (SAS Institute 1999). Linear and transformed explanatory variables were used to test *a priori* relationships with vertical diversity (see Table 4.6). I evaluated the fit of the models by examining normality using PROC UNIVARIATE (SAS Institute 1999), and also by checking residual plots. For models with poor fit, I applied transformations of response and/or explanatory variables that improved model fit.

I then selected the best approximating models and 95% confidence model sets from my set of *a priori* models using AICc (Burnham and Anderson 1998). AICc values used the AIC score output from PROC MIXED where the lowest AIC score was the best model.

Model Corroboration

For models included in the 95% confidence set, the predicted sum of squares errors (predSSEs) from the test datasets were compared with the mean square errors (MSEs) of the model datasets. Similar predSSEs and MSEs suggested the predictive models were not spurious. Using the square root of the predSSE ($\sqrt{\text{predSSE}}$) in place of the SE provided an estimate of the upper and lower confidence limits of these models for predicting canopy cover.

Results

Computed Diversity Measures

There were a maximum of 13 height intervals, and 11 crown-base height intervals for the FIA plots examined in this study. Height intervals were 5-m intervals up to 60 m and with the very limited number of trees taller than 60 m these trees were lumped together into a single height interval.

Selection of stands

Applying diversity formulae by density, or weighted by basal area did not generally influence results (Table 4.11). Three exceptions were the Evenness, Vertical Evenness, and Berger-Parker indices, which were less highly correlated than the other measures ($r_s < 0.75$). Recognizing that larger rather than smaller diameter trees for a given height would generally contribute more cover, I opted to further examine calculated diversity measures that were weighted by basal area.

Overall, diversity measures calculated among the three general forest groups revealed similar results. In addition, these patterns remained fairly consistent when comparing all stands with stands taller than 20m. Therefore I have elected only to describe the patterns for all forest groups combined.

Table 4.11. Correlation between diversity formulae calculations using trees per hectare and using trees per hectare weighted by basal area for the stands used in this study.

Variable	Correlation
Berger-parker	0.48
Evènness index (Neumann)	0.54
MacArthur (5-m)	0.90
Margalef (5-m)	0.84
Pielou (5-m)	0.10
Shannon (5-m) height	0.83
Shannon (5-m) crown-base height	0.88
Shannon (5-m) base and height combined	0.87
Simpson height	0.75
Simpson base height	0.83
Simpson base and height combined	0.81

Sensitivity of vertical groups

The use of cover groups for comparison with vertical diversity estimates was problematic. Instead of increasing diversity with decreasing dominance of a single line-intercept cover layer, there were no clear patterns (e.g. Figs. 4.7, 4.8). The diversity measures were generally similar for stands with cover evenly distributed among the three layers versus those with cover primarily in a single layer. Rank-abundance plots of basal area within height intervals and plots of standard deviations of tree sizes and tree heights within stands, provided evidence for the lack of sensitivity of the vertical cover groups (Figs. 4.9-4.11). In stands with a dominant layer, I expected lower standard deviations compared with even distribution of cover stands and steeper rank-abundance curves, but this was not seen. Therefore, patterns in diversity along the vertical cover group gradient were not further analyzed because this gradient was not biologically meaningful.

Structure groups proved to be a better set of criteria for distinguishing patterns in vertical diversity. Rank-abundance plots of basal area within structure groups revealed desired patterns of decreasing dominance of one or a few structure groups with a shift from the dominant to even vertical structure groups (Fig. 4.12).

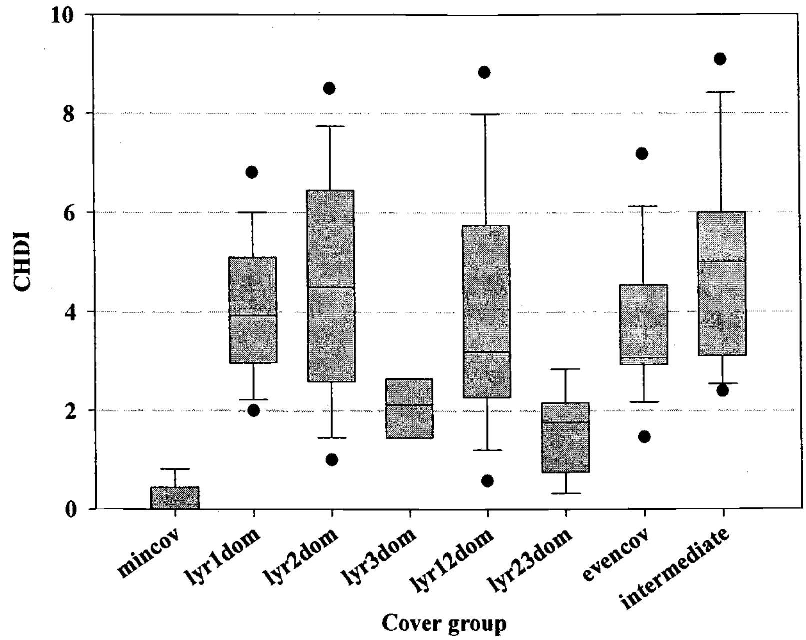

Fig. 4.7. Box-whisker plots comparing canopy height diversity index (CHDI, See Table 4.2) among eight cover groups for the three general forest groups in western Oregon analyzed in this study. Cover groups are described in Table 4.4. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean CHDI, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

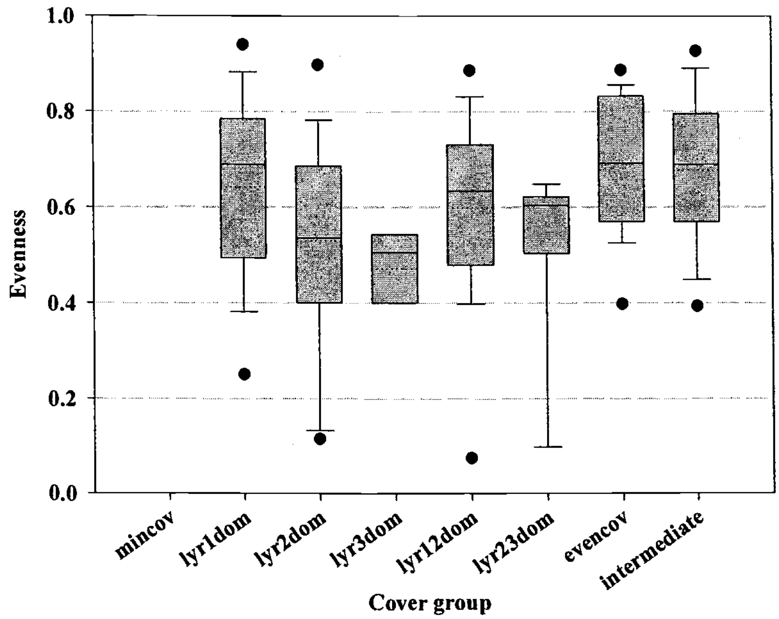

Fig. 4.8. Box-whisker plots comparing vertical evenness (Starlinger and Neumann 2001) among eight cover groups for the three general forest groups in western Oregon analyzed in this study. Cover groups are described in Table 4.4. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean vertical evenness, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

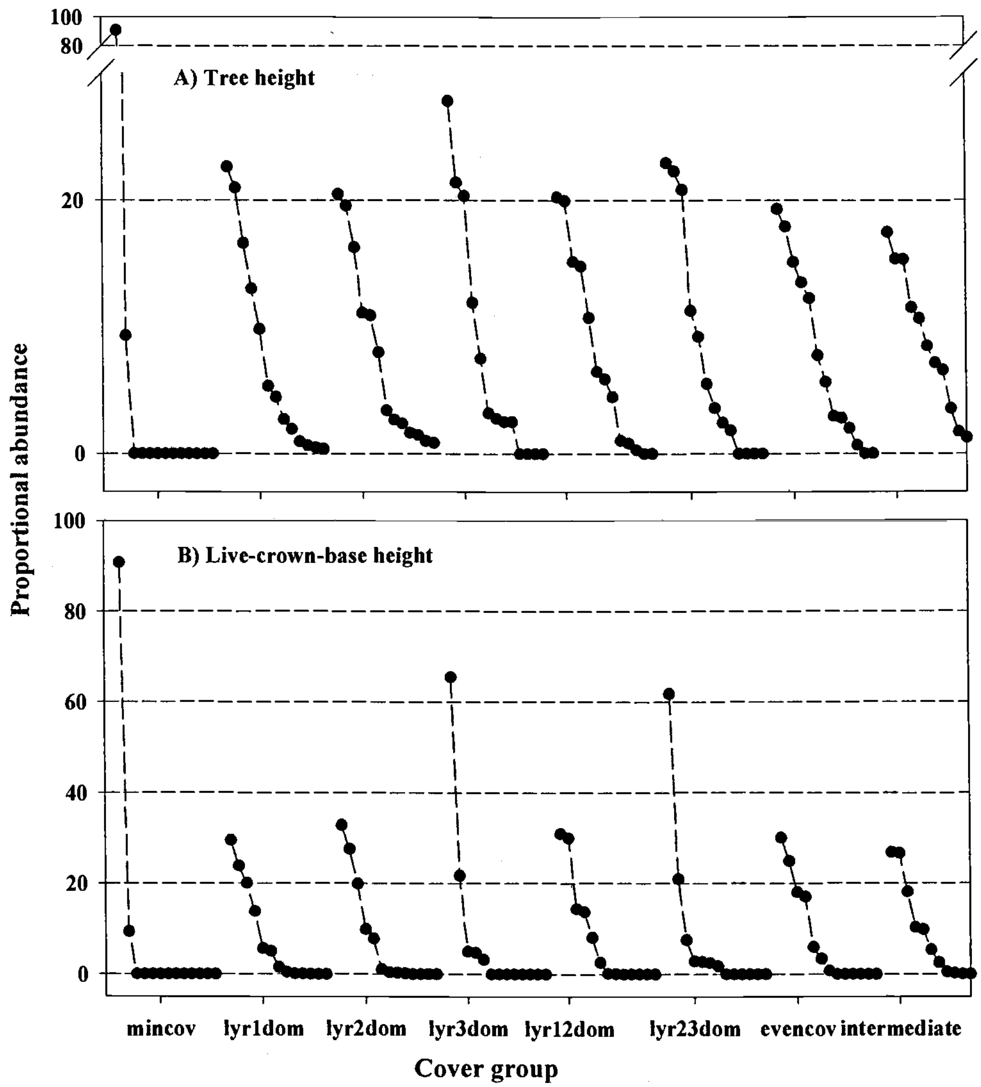

Fig. 4.9. Rank abundance plots for the wet-conifer, wet-hardwood, and dry-hardwood stands examined in this study. The proportional abundance is the number of trees with heights (A) and live-crown-base heights (B) within the given height interval, weighted by the basal area of the trees. Dividing basal area within each 5-m interval by the total basal area for the cover group standardized abundance of basal area among cover groups (range from 0–100%). This provided a more direct comparison between the cover groups with different numbers of stands measured for each of them. Cover groups are described in Table 4.4.

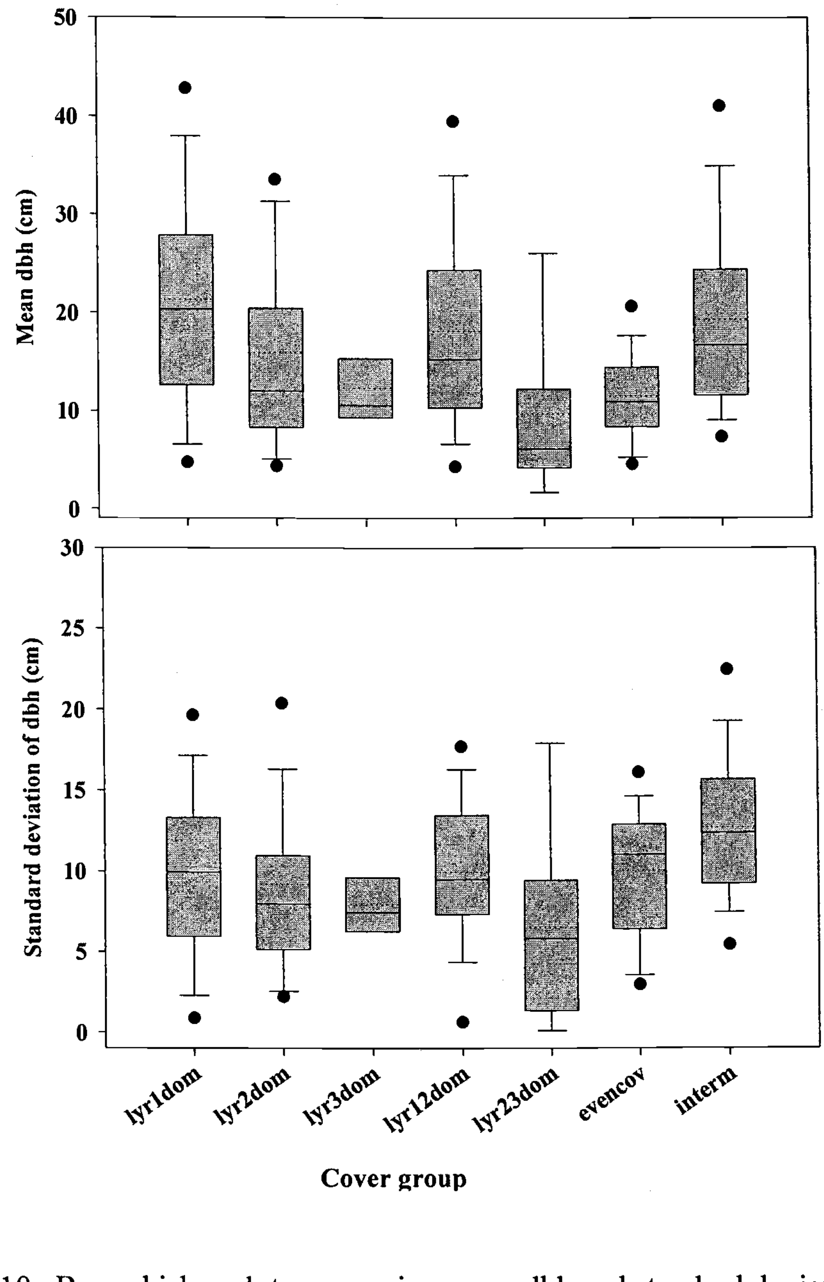

Fig. 4.10. Box-whisker plots comparing mean dbh and standard deviation of dbh among seven cover groups for the three general forest groups in western Oregon analyzed in this study. Cover groups are described in Table 4.4. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean dbh, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

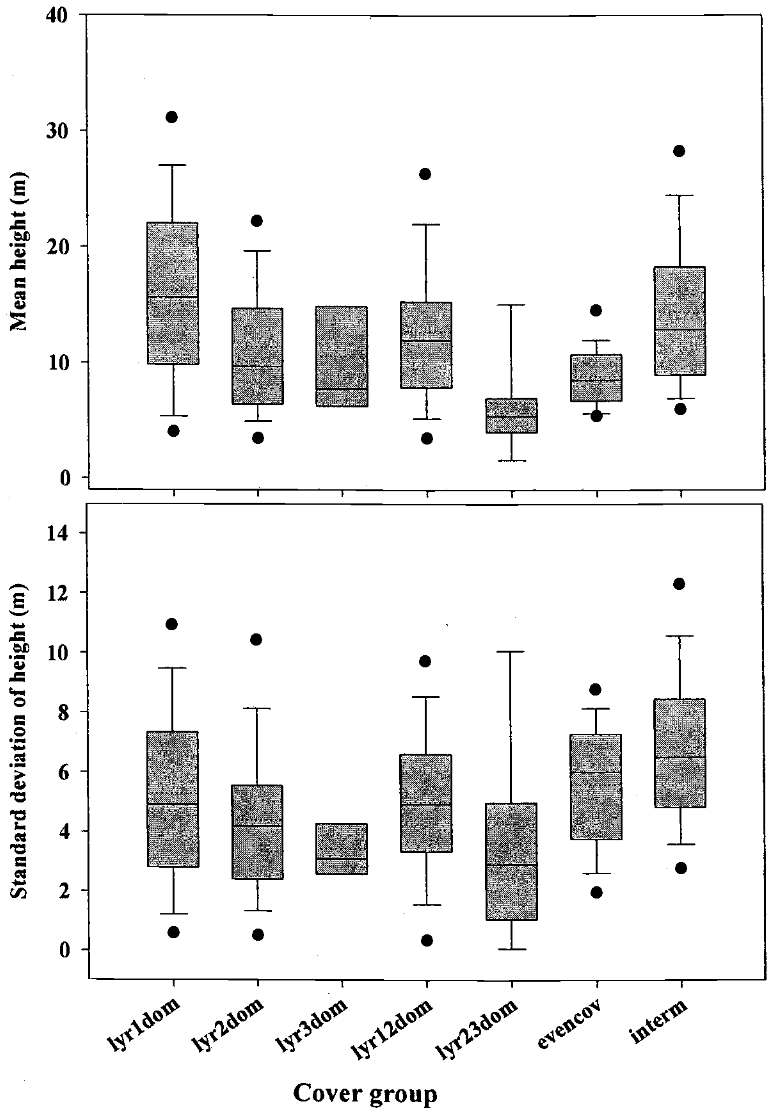

Fig. 4.11. Box-whisker plots comparing mean height and standard deviation of height among seven cover groups for the three general forest groups in western Oregon analyzed in this study. Cover groups are described in Table 4.4. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean height, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

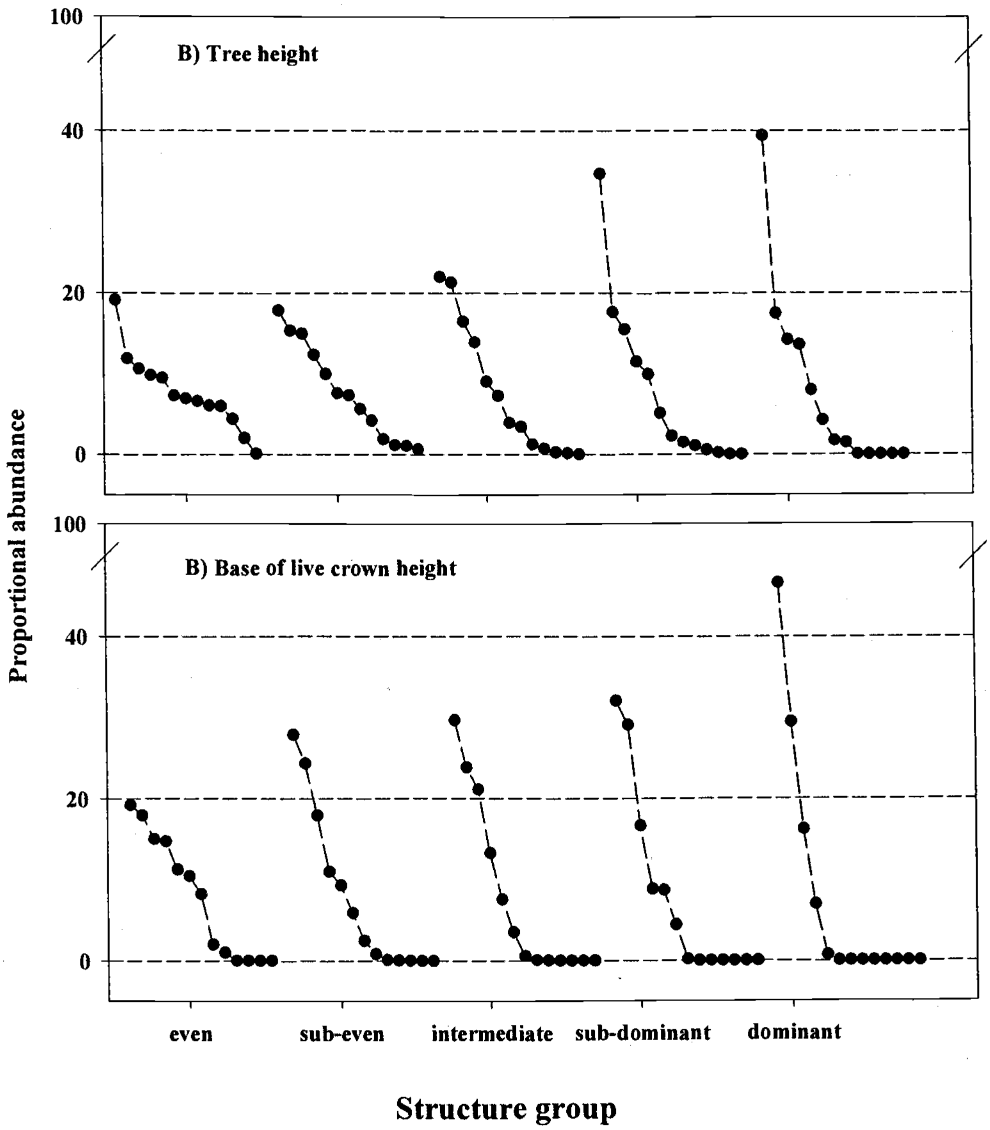

Fig. 4.12. Rank abundance plots for the wet-conifer, wet-hardwood, and dry-hardwood stands examined in this study. The proportional abundance is the number of trees with A) heights and B) live-crown-base heights within the given height interval, weighted by the basal area of the trees. Dividing basal area within each 5-m interval by the total basal area for the cover group standardized abundance of basal area among cover groups (range from 0–100%). This provided a more direct comparison between the cover groups with different numbers of stands measured for each of them. Structure groups are described in Table 4.5.

In stands with a dominant layer, lower standard deviations, compared with even distribution of cover stands, were evident (Figs. 4.13, 4.14). Therefore, further analyses examined patterns of diversity measures along the vertical structure gradient.

Sensitivity of diversity measures among structure groups

Diversity calculations of the eleven measures were generally consistent with expected patterns (e.g. Figs. 4.15-4.22). Diversity tended to increase for groups with decreased dominance of one or few height intervals. Among the diversity measures, Simpson's Diversity Index based on tree height (SDI) was most sensitive to changes among the vertical structure groups (i.e. had lowest overlap among structure groups, see Fig. 4.15). Diversity measures that incorporated both crown and crown-base heights did not differentiate as well as those based on height classes among the vertical structure groups (e.g. 4.15).

Sensitivity of stratification measures among vertical structure groups

The mean number of layers calculated using TSTRAT, line-intercept, and the stratification algorithm generally decreased with increasing dominance of a single layer (Fig. 4.23). The stratification algorithm consistently had the lowest numbers of layers.

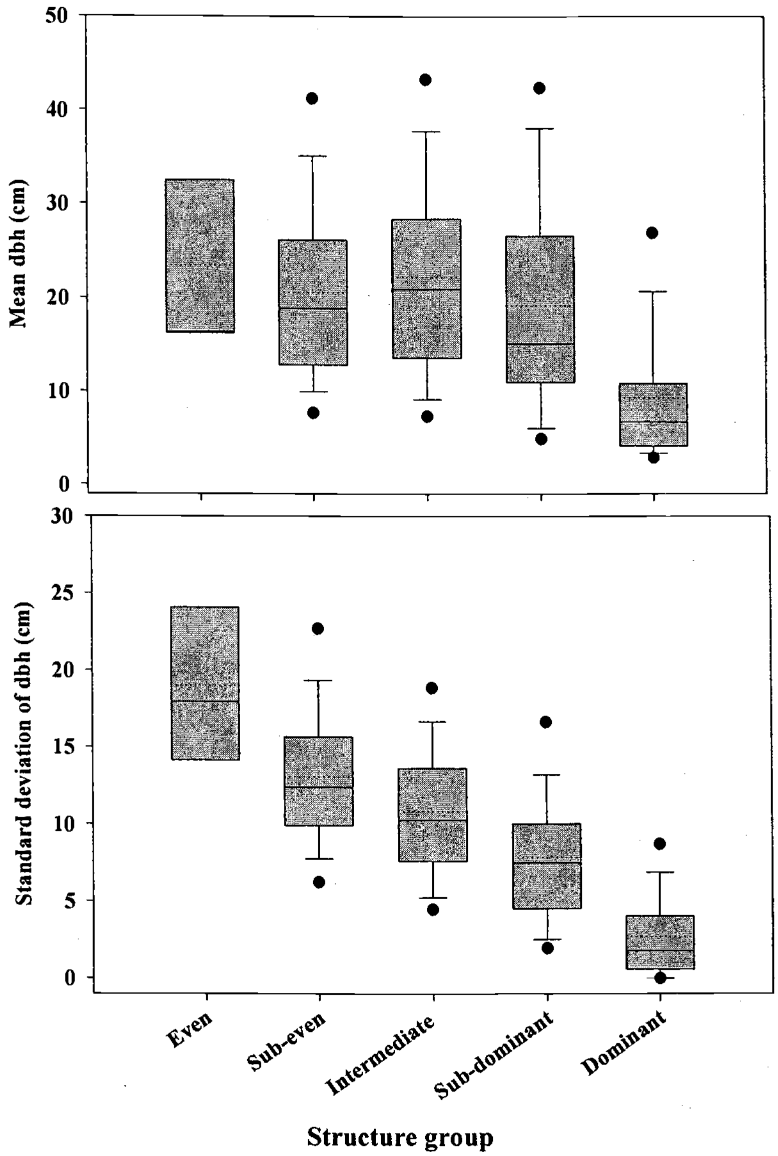

Fig. 4.13. Box-whisker plots comparing mean dbh and standard deviation of dbh among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean dbh, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

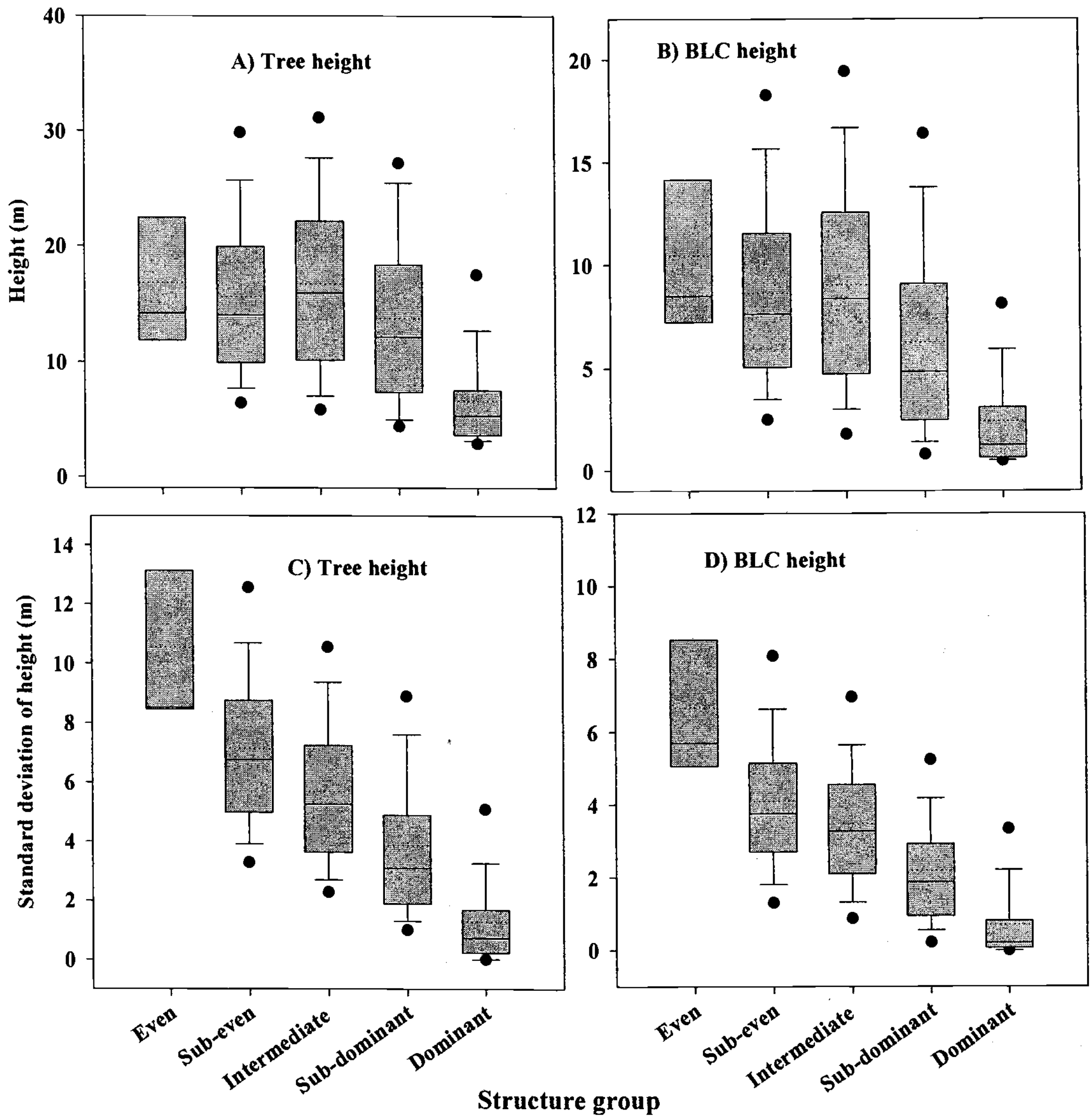

Fig. 4.14. Box-whisker plots comparing mean height of A) trees and B) BLC heights, and standard deviation of C) height and D) BLC height among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

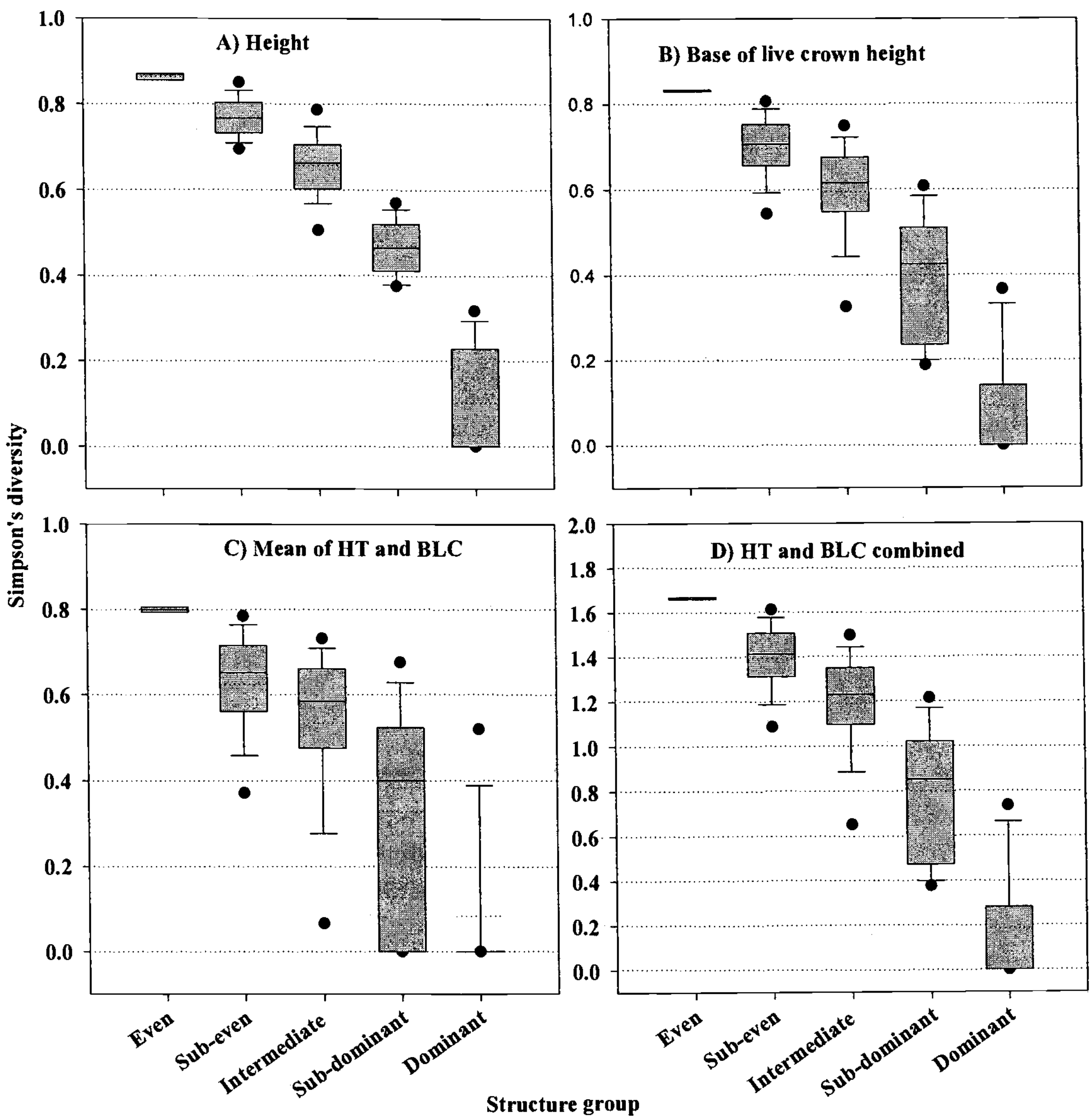

Fig. 4.15. Box-whisker plots comparing Simpson's Diversity (see Table 4.2) of A) height (HT) B) base of live crown (BLC), C) mean of HT and BLC, and D) HT and BLC combined, among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

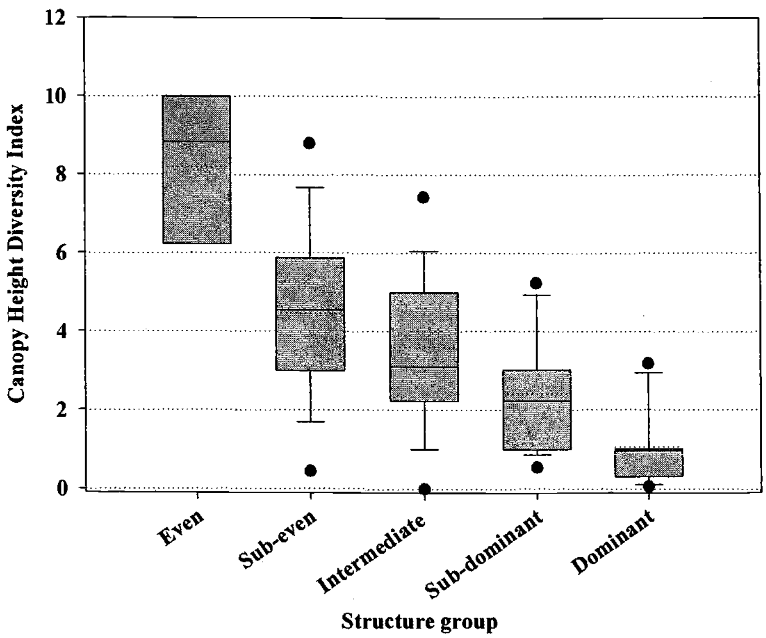

Fig. 4.16. Box-whisker plots comparing CHDI (see Table 4.2) values among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

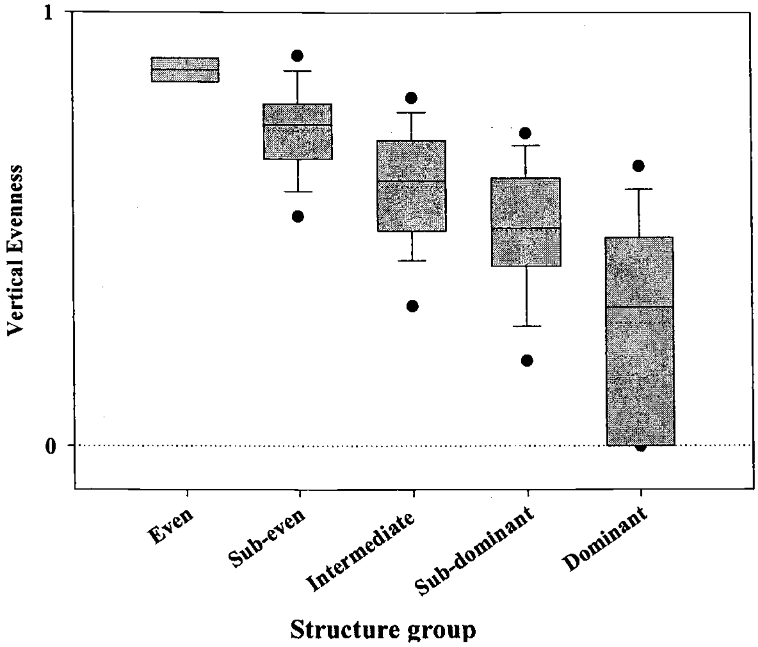

Fig. 4.17. Box-whisker plots comparing Vertical Evenness (see Table 4.2) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

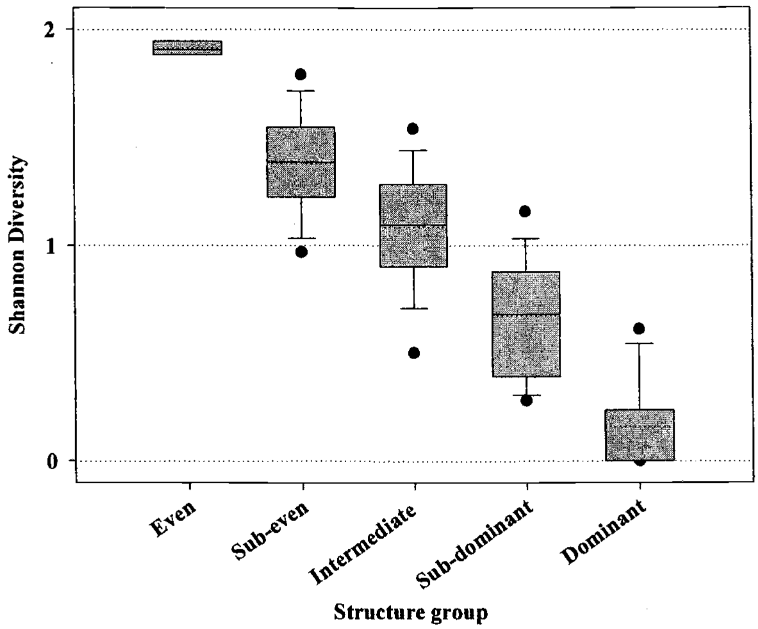

Fig. 4.18. Box-whisker plots comparing Shannon Diversity (see Table 4.2) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

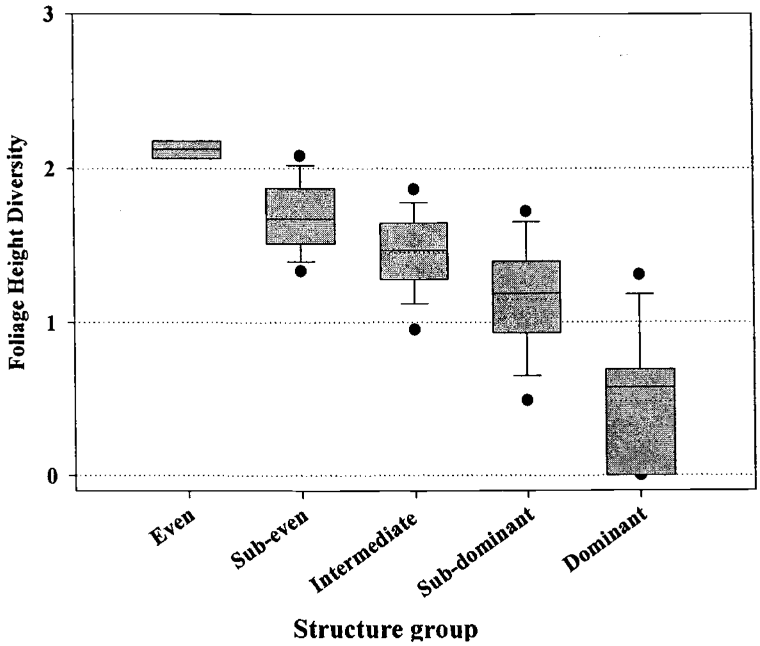

Fig. 4.19. Box-whisker plots comparing Foliage Height Diversity (see Table 4.2) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

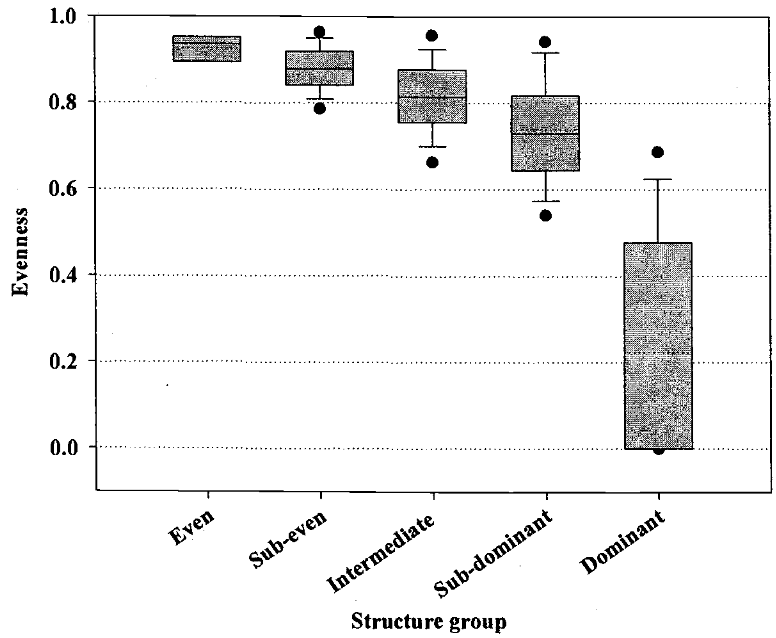

Fig. 4.20. Box-whisker plots comparing Evenness (see Table 4.2) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

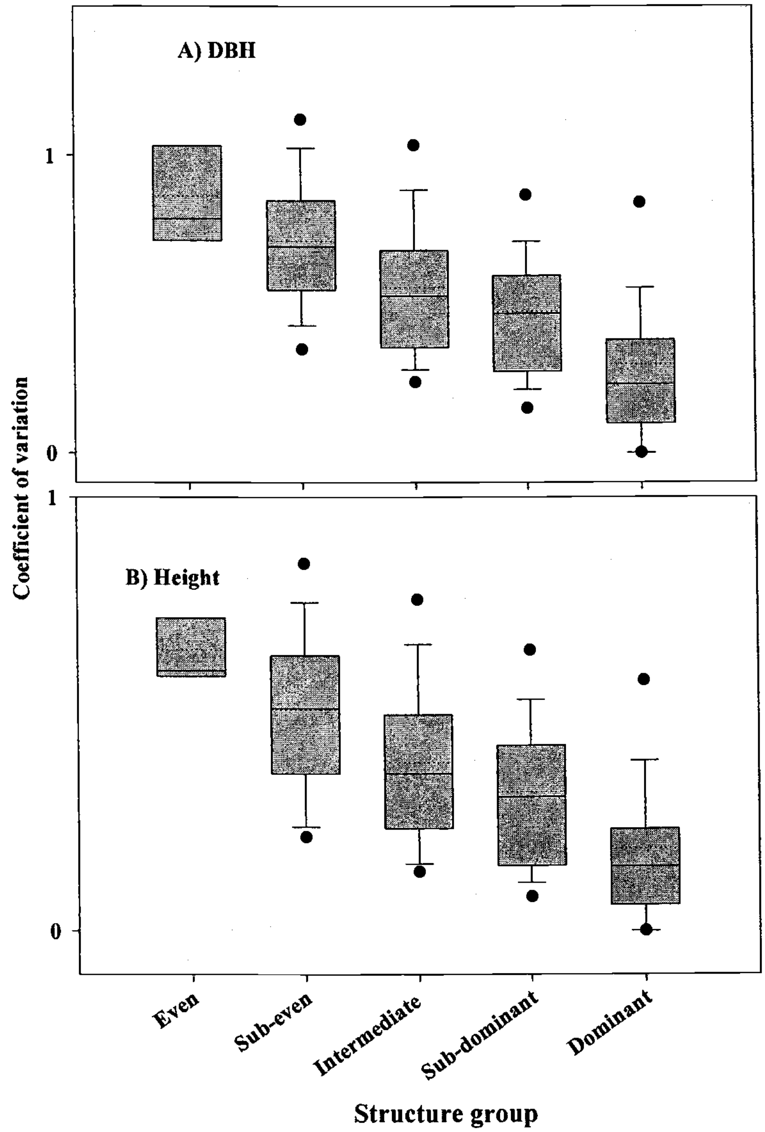

Fig. 4.21. Box-whisker plots comparing the coefficient of variation (see Table 4.2) of A) DBH and B) Height among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

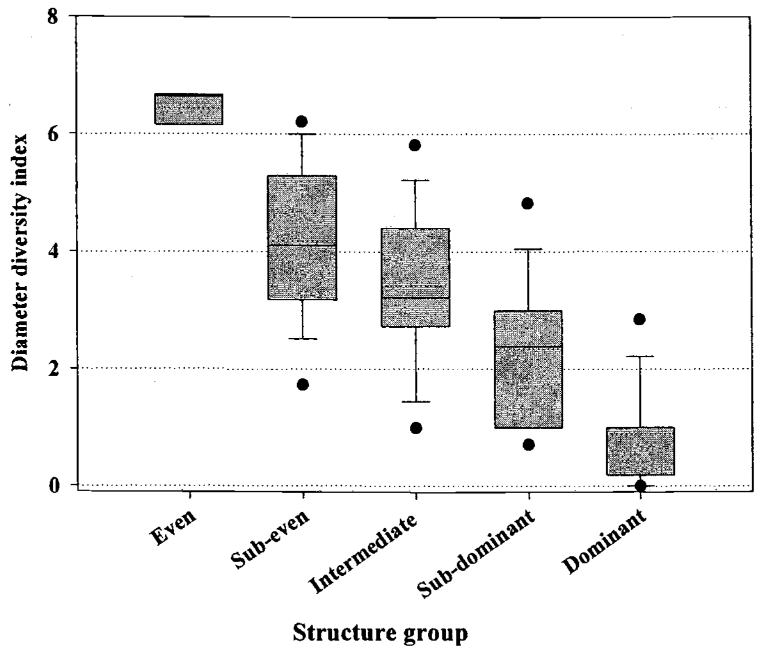

Fig. 4.22. Box-whisker plots comparing Diameter Diversity Index (see Table 4.2) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5. Each box represents the interquartile range (25th-75th percentiles), with the inside line showing the median, the dotted line representing the mean, whiskers showing the 5th and 95th percentiles, and dots representing outliers.

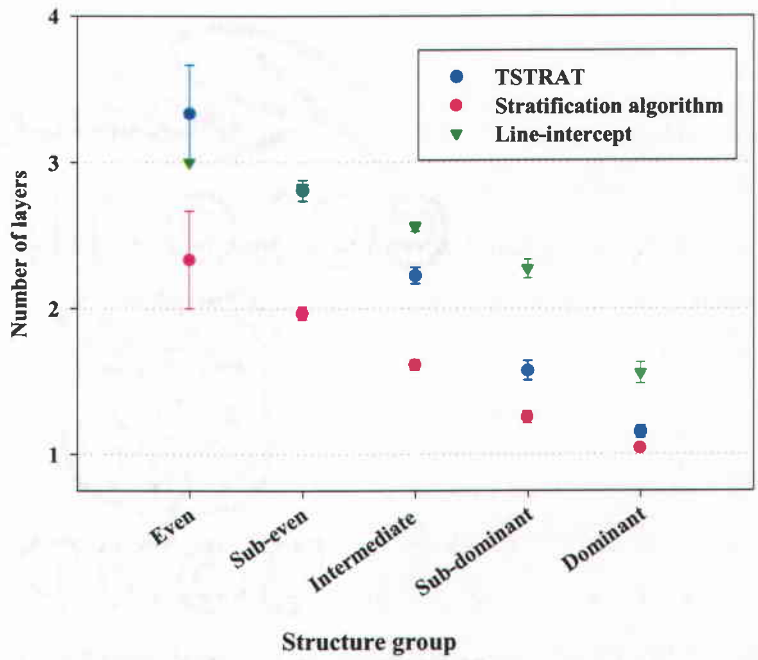

Fig. 4.23. Comparison of the mean number of layers (± 1 SE) calculated using the three different stratification methods (see Table 4.3) among five structure groups for the three general forest groups in western Oregon analyzed in this study. Structure groups are described in Table 4.5.

Successional gradient patterns

SDI

Both Simpson's Index of Diversity using height and crown-base height intervals increased across age classes in western Oregon (Fig. 4.24). As expected, diversity increased during stand initiation, remained somewhat constant during the stem-exclusion phase, and was highest in the old-growth stands.

CHDI

CHDI increased with increasing stand age up to age 155. This increase with stand age was steeper for the FIA wet-conifer stands than for the CVS stands (Fig. 4.25). However, CVS stands leveled off at age 105, with CHDI values fluctuating around six, while FIA stands leveled off at age 55 with reduced levels around five.

Stratification

Layering generally increased with stand age in all forest groups for the three methods of stratification (Fig. 4.26). The relative increases differed among the groups, with TSTRAT consistently assigning the lowest number of layers. The number of layers delineated by line-intercept increased the most rapidly along the chronosequence and then leveled off, while TSTRAT and the stratification algorithm generally continued to increase up to the oldest-aged stands.

Prediction of Vertical Diversity

I attempted to create predictive models for three diversity measures. I chose SDI because it was the most sensitive to changes in vertical dominance. I selected CHDI because it has been used in wildlife habitat models (Garman and Cole 1999) and it was worthwhile to see whether it could be applied to additional wildlife

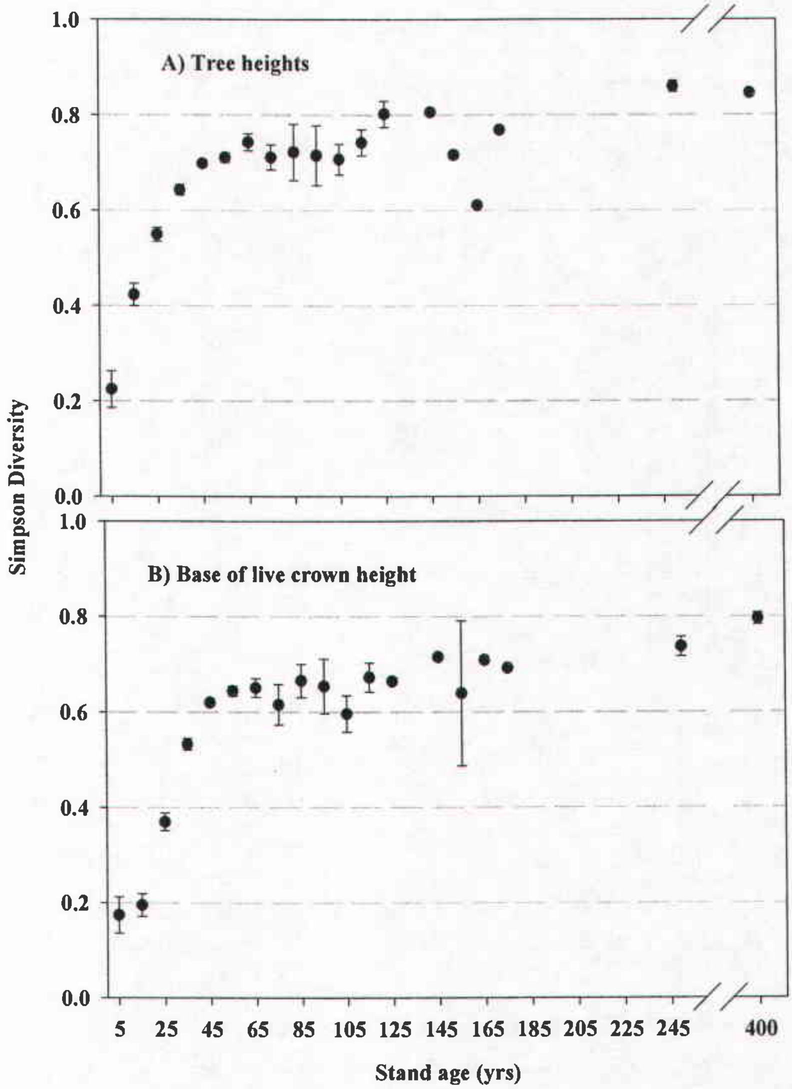

Fig. 4.24. Mean Simpson Diversity (± 1 SE) of A) heights and B) base of live crown heights among a chronosequence of stand ages for the three general forest groups in western Oregon (see Table 4.2). Sample sizes differed among stand ages (see Table 2.4).

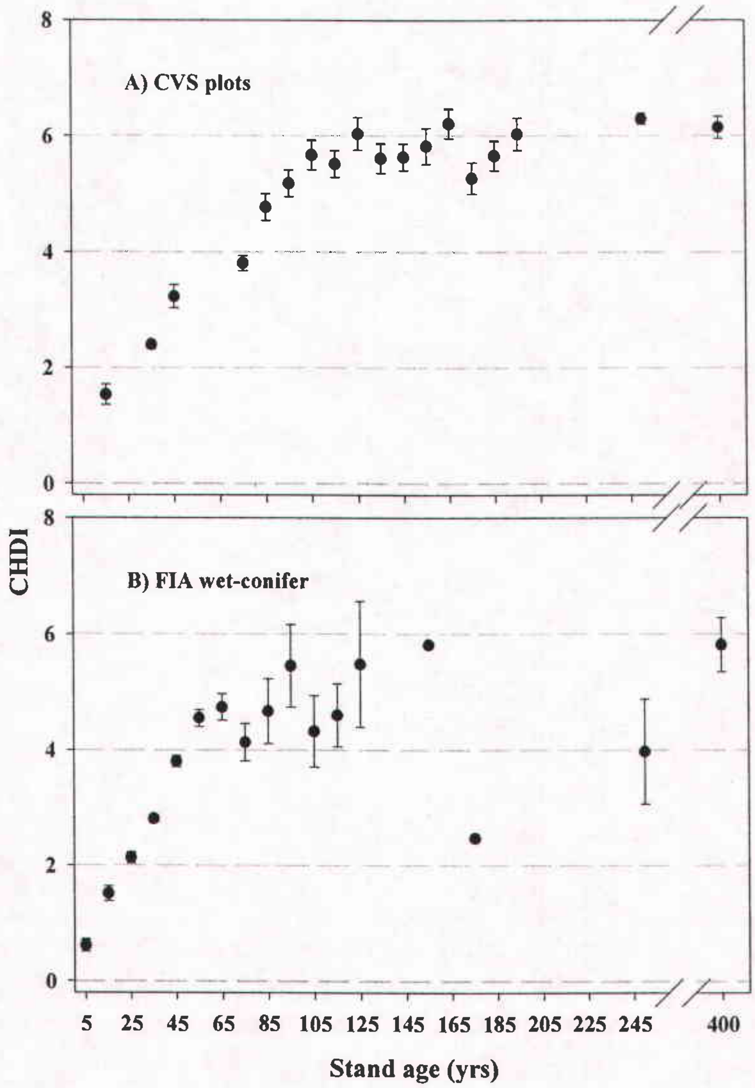

Fig. 4.25. Comparison of mean CHDI (± 1 SE) of A) CVS stands and B) FIA wet-conifer stands among a chronosequence of stand ages.

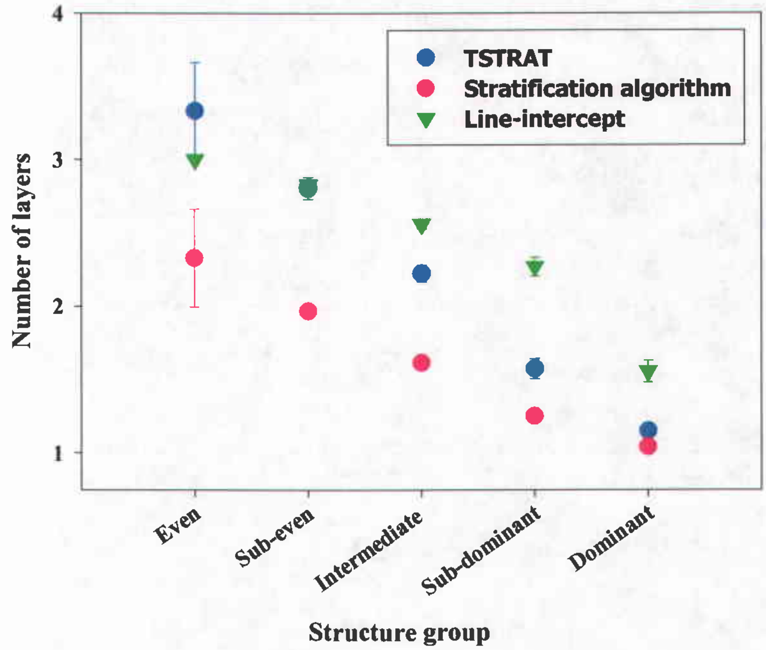

Fig. 4.26. Mean number of layers (± 1 SE) calculated using the three different stratification methods across a chronosequence of stand ages for the three general forest groups in western Oregon (see Table 4.3). Sample sizes differed among stand ages (see Table 2.4).

datasets that lacked crown width measurements. I selected FHD because it emphasized relative positioning of foliage, rather than relative positioning of tree heights.

SDI was logit transformed and CHDI was square root transformed, while no transformation of FHD was necessary. In these forms, model assumptions for the three measures were generally satisfied, although residual plots showed some non-constant variance and there was some long-tailedness in the data. Predicted diversity was calculated using equations 4.2-4.4:

$$\text{Predicted Simpson's} = \left(\frac{1}{1+\exp(-\beta_0-\beta_1(\text{Variable 1})\cdots-\beta_x(\text{Variable X})}\right)*1.05 \qquad \text{Eqn. 4.2}$$

$$\text{Predicted CHDI}=(\beta_0+\beta_1X_1+\beta_2X_2+\ldots+\beta_xX_x)^2 \qquad \text{Eqn. 4.3}$$

$$\text{Predicted FHD}=(\beta_0+\beta_1X_1+\beta_2X_2+\ldots+\beta_xX_x) \qquad \text{Eqn. 4.4}$$

There was high correlation among several of the variables (Pearson correlation coefficients > 0.60): stocking and basal area (r=0.91), and basal area and qmd (r=0.65). Therefore, these variables were not simultaneously included in a model.

An assumption of the AIC analytical approach is that the best approximating model for prediction of canopy cover was included in my set of candidate models. The very high ΔAICc score of my null models for each of the forest types suggested at least one of the independent variables had explanatory capacity. However, in several cases I determined that my model set did not always include the most parsimonious approximating model. For several model sets the standard error of one variable within the best approximating model was larger than the parameter estimate. This suggested that my *a priori* model included an unnecessary variable that was adding noise to the model. From this I inferred that a more parsimonious model with that variable removed would have improved model fit. Therefore, I reran my analyses to include the more parsimonious models and added these models to my model sets (see Tables 4.7-4.9). While these additional models were not strictly '*a priori*', they were subsets of *a priori* models. Thus I determined this approach was justified, especially given a test dataset was used to corroborate model selection. I was then confident that my 95% confidence model sets included the most parsimonious best approximating models.

Wet conifer

SDI

Model 41 was the best approximating model (ΔAICc=0, Tables 4.12-4.13). There were no additional models included in the 95% confidence model set. The model explained 91% of the variance in SDI.

Table 4.12. Ranking of *a priori* models to predict SDI (see Table 4.2) in 75% of the wet-conifer plots (n=484) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
41	ln(sdofdbh) height √baha	5	758	0	1.00
43	ln(sdofdbh) height tphdbh1 tphdbh2	6	769.7	11.72	0
44	ln(sdofdbh) tphdbh1 tphdbh2	5	791.3	33.29	0
45	ln(sdofdbh) √baha	4	798.4	40.44	0
42	ln(sdofdbh) height tph	5	801.5	43.51	0
40	height ln(sdofdbh)	4	828.5	70.50	0
39	ln(sdofdbh)	3	856.3	98.31	0
36	invage √baha mai height	6	866.6	108.62	0
20	√stock height	4	899.3	141.34	0
22	√stock height mai	5	901	143.03	0
23	√baha height	4	945.4	187.43	0
26	√baha mai height	5	947.4	189.46	0
24	invage √baha	4	949.8	191.80	0
27	qmd qmd2 height	5	970.2	212.21	0
29	qmd qmd2 height mai	6	972.2	214.18	0
21	√stock qmd	4	988.7	230.67	0
33	tph √baha tph*baha	5	1010.8	252.82	0
7	√stock	3	1012.6	254.61	0

Table 4.12. Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
32	tph height qmd	5	1036.4	278.42	0
31	tph height mai	5	1067.5	309.48	0
37	speciestot height	4	1068.3	310.35	0
30	tph height	4	1068.9	310.94	0
5	height	3	1076.7	318.75	0
25	√baha qmd	4	1078.8	320.81	0
9	√baha	3	1079.5	321.55	0
4	invage	3	1118.7	360.68	0
28	qmd qmd2 mai	5	1126.6	368.64	0
6	stocking	3	1235.3	477.34	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	1264.0	506.00	0
16	tphcrn2	3	1279.3	521.30	0
18	tphcrn4	3	1296.1	538.10	0
17	tphcrn3	3	1303.4	545.40	0
8	baha	3	1328.9	570.91	0
34	tphht1 tphht2 tphht3 tphht4	6	1346.6	588.64	0
38	sdofdbh	3	1351.4	593.41	0
13	tphdbh2	3	1478.8	720.77	0
12	tphht3 tphht4	4	1496.2	738.17	0
3	stndage	3	1550.6	792.66	0
14	tphdbh3	3	1559.3	801.35	0
11	speciestot tphdbh4	4	1569.7	811.68	0
2	speciestot	3	1573.7	815.70	0
15	tphdbh4	3	1635.2	877.24	0
19	modelprecip elev	4	1640.8	882.82	0
1		2	1642.3	884.33	0
10	tph	3	1643.8	885.79	0

[1]Model numbers correspond to those in Table 4.7.
[2] Number of estimated parameters, including an error term.

Table 4.13. Coefficients (± 1 SE) for estimating SDI (See Table 4.2) for the best model for wet-conifer stands. SDI is estimated using Eqn 4.1.

Model[1]	Variable	Coefficient estimate
41	intercept	-2.207 (0.079)
	ln(sdofdbh)	0.890 (0.058)
	height	-0.013 (0.003)
	√baha	0.192 (0.022)

[1]Model numbers correspond to those in Table 4.7.

In the assessment with the test data, the predSSE of predictions was similar to the MSE of the model (Table 4.14). Correspondence between predictions and calculated diversity was similar for predicted diversity > 0.20 (Figs. 4.27, 4.28). Predicted diversity values were within 0.1 units 73% of the time and this increased to 85% when predicted diversity was within 0.15 units.

Table 4.14. Comparison of Simpson's (See Table 4.2) statistics for the model and test datasets for wet-conifer stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=484). The predicted sum of squares error (PredSSE) was calculated for the set of wet-conifer stands that was used to test the fit of the model (n=161). Only the best model was examined (ΔAICc=0).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
45	0.310	0.357	0.91

[1]Model numbers correspond to those in Table 4.7.

CHDI

Model 40 was the best approximating model (ΔAICc=0, Tables 4.15-4.16). There were no additional models included in the 95% model set. The model explained 86% of the variance in CHDI.

In the assessment of the test dataset, the predSSE of predictions was similar to the MSE of the model (Table 4.17). Correspondence between predictions and calculated diversity values was similar (Figs. 4.29, 4.30). Predicted diversity values were within one unit for 86% of the observations for the best model and this increased to for 96% of the observations when predicted diversity was within 1.5 units.

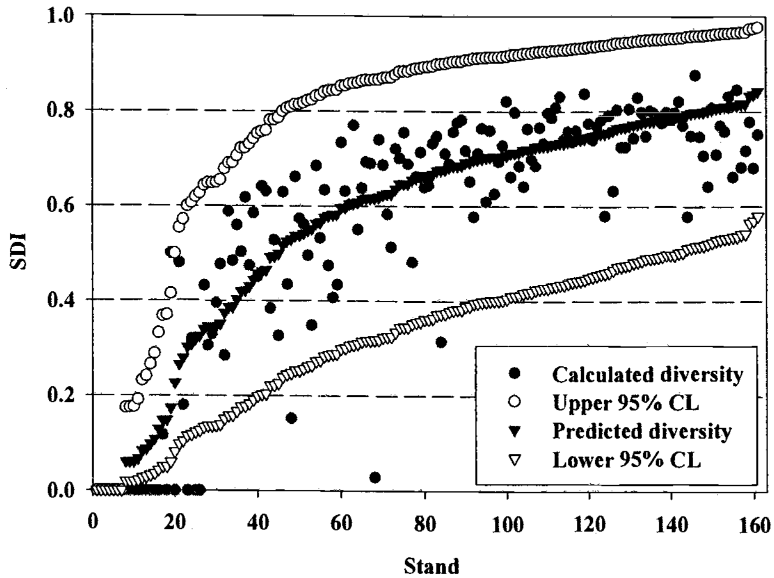

Fig. 4.27. Comparison of Simpson's height diversity (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates for wet-conifer stands (Table 4.13). Comparison is for the 161 stands comprising the test dataset for wet-conifer stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

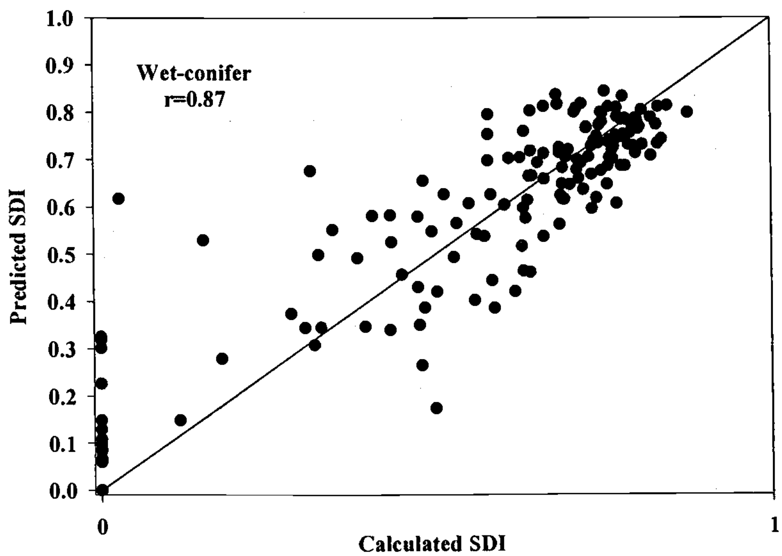

Fig 4.28. Comparison of Simpson's height diversity (see Table 4.2) calculated from stand data and predicted using model 41 parameter estimates (Table 4.13) for 161 stands comprising the test dataset of wet-conifer stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 4.15. Ranking of *a priori* models to predict CHDI (see Table 4.2) in 75% of the wet-conifer plots (n=484) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
40	1/age stocking height	5	-167.6	0.00	1.00
44	√sdofdbh height baha	5	-148.1	19.44	0
39	1/age baha height	5	-147.5	20.10	0
35	1/age baha mai height	6	-145.8	21.71	0
19	stocking height	4	-139.9	27.62	0
21	stocking height mai	5	-138	29.52	0
22	baha height	4	-97.3	70.22	0
25	baha mai height	5	-95.3	72.21	0
46	√sdofdbh height tphdbh1 tphdbh2	6	-31.6	135.95	0
42	dbh baha	4	-27.1	140.41	0
45	√sdofdbh height tph	5	25.3	192.86	0
31	tph height qmd	5	29.9	197.44	0
38	height √sdofdbh	4	43.5	211.02	0
41	√sdofdbh logstock	4	45.4	212.96	0
26	qmd height	4	73.4	240.96	0
28	qmd height mai	5	75	242.54	0
30	tph height mai	5	78.9	246.48	0
29	tph height	4	79.9	247.48	0
36	speciestot height	4	83.5	251.09	0
5	height	3	87.1	254.69	0
47	√sdofdbh tphdbh1 tphdbh2	5	132.8	300.32	0
23	1/age baha	4	175.3	342.90	0
20	stocking qmd	4	176.8	344.40	0
43	√sdofdbh tph	4	220.5	388.06	0
37	√sdofdbh	3	244	411.58	0
24	baha qmd	4	275	442.58	0
32	tph baha tph*baha	5	345.2	512.76	0
6	stocking	3	375.8	543.41	0
8	baha	3	379.9	547.49	0
7	sdofdbh	3	502.1	669.69	0
4	1/age	3	518	685.54	0
27	qmd mai	4	533	700.57	0
33	tphht1 tphht2 tphht3 tphht4	6	551.1	718.66	0
34	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	579.8	747.38	0
17	tphcrn4	3	619.1	786.67	0
15	tphcrn2	3	656.5	824.06	0
11	tphht3 tphht4	4	695.7	863.23	0
16	tphcrn3	3	700.8	868.36	0
13	tphdbh3	3	705.3	872.88	0
12	tphdbh2	3	767.3	934.88	0
3	stndage	3	791.2	958.80	0
10	speciestot tphdbh4	4	854.8	1022.36	0

Table 4.15. Cont'd

Model[1]	Model variables	k^2	AICc	ΔAICc	w
2	speciestot	3	903.1	1070.67	0
14	tphdbh4	3	919.5	1087.05	0
1		2	971.3	1138.85	0
9	tph	3	972.5	1140.10	0
18	modelprecip elev	4	975.3	1142.83	0

[1]Model numbers correspond to those in Table 4.8.
[2] Number of estimated parameters, including an error term.

Table 4.16. Coefficients (+ 1 SE) for estimating CHDI (See Table 4.2) for the best model (ΔAICc=0) for wet-conifer stands. CHDI is estimated using Eqn. 4.3

Model[1]	Variable	Coefficient estimate
40	intercept	0.683 (0.038)
	1/age	-1.716 (0.311)
	stocking	0.0065 (0.0005)
	height	0.022 (0.001)

[1]Model numbers correspond to those in Table 4.8.

Table 4.17. Comparison of CHDI (See Table 4.2) model statistics for the model and test datasets for wet-conifer stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=484). The predicted sum of squares error (PredSSE) was calculated for the set of wet-conifer stands that was used to test the fit of the model (n=161 Only the best modelwas examined (ΔAICc=0).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
40	0.040	0.043	0.86

[1]Model numbers correspond to those in Table 4.8.

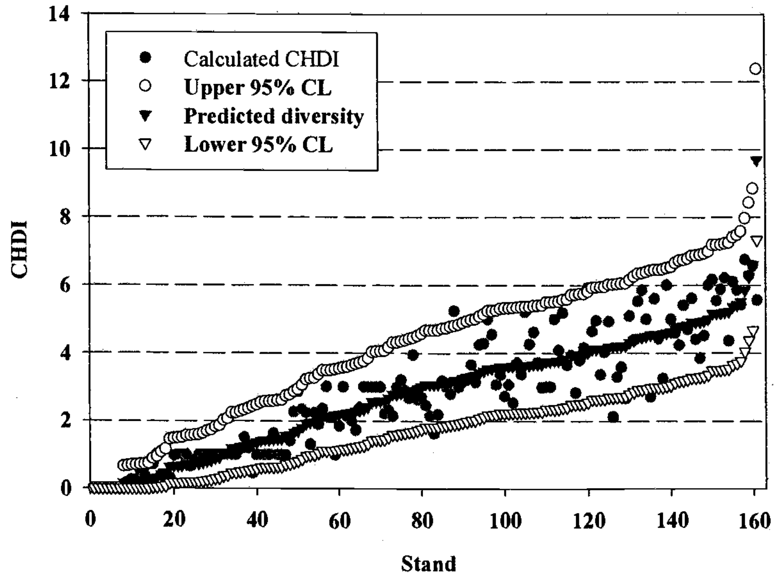

Fig. 4.29. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates for wet-conifer stands (Table 4.16). Comparison is for the 161 stands comprising the test dataset for wet-conifer stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error.

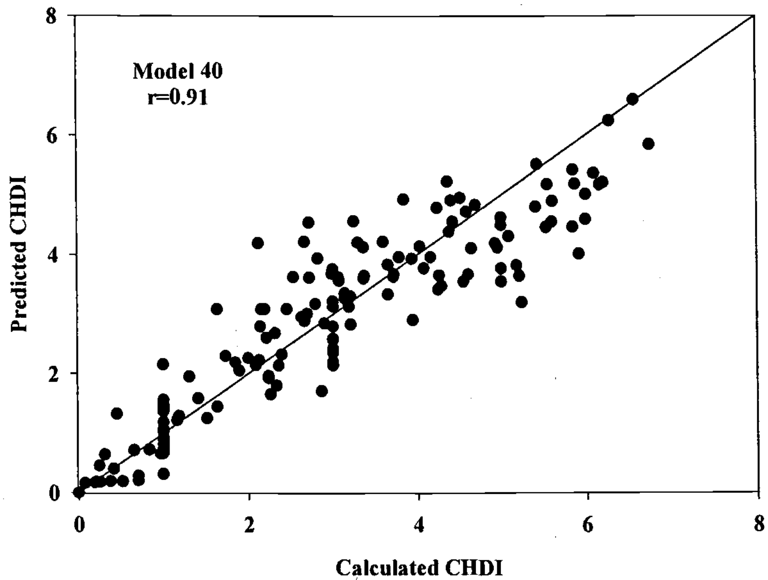

Fig. 4.30. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates (Table 4.16) for 161 stands comprising the test dataset of wet-conifer stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

FHD

Model 42 was the best approximating model (ΔAICc=0, Tables 4.18-4.19). There was one additional model included in the 95% confidence model set. The models explained 91% of the variance in FHD.

In the assessment of the test data, the predSSEs of predictions were similar to the MSEs of the best models (Table 4.20). Correspondence between predictions and calculated diversity values was similar between the two models (Figs. 4.31, 4.32). Predicted diversity values were within 0.15 units for 79% of the observations for the best model and this increased to for 89% of the observations when predicted diversity was within 0.2 units.

Wet hardwood

SDI

Model 41 was the best approximating model (ΔAICc=0, Tables 4.21-4.22). There were three additional models included in the 95% model set.

In the assessment of the test data, the predSSEs of predictions were generally ~1.5 to 2 times greater than the MSEs for the best models, demonstrating that the fit and test datasets fit the data differently (Table 4.23). Correspondence between predictions and calculated diversity was low for the best model using the test dataset (Figs. 4.33, 4.34), with similar results among the good model set. Predicted diversity values were within 0.1 units only for 56% of the observations for the best model and increased to 79% when predicted diversity was within 0.15 units.

CHDI

Model 40 was the best approximating model (ΔAICc=0, Tables 4.24-4.25). Three additional models were included in the 95% model set. In the assessment with the test data, the predSSEs of predictions were similar to the MSEs of the best

Table 4.18. Ranking of *a priori* models to predict FHD (See Table 4.2) in 75% of the wet-conifer plots (n=484) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
42	ln(sdofdbh) height tphdbh1 tphdbh2	6	-435.4	0	0.78
41	ln(sdofdbh) height tph	5	-432.9	2.53	0.22
40	height ln(sdofdbh)	4	-418.8	16.61	0
43	ln(sdofdbh) height √baha	5	-417.2	18.24	0
36	invage √baha mai height	6	-257.6	177.77	0
20	√stock height	4	-226.1	209.34	0
22	√stock height mai	5	-224.9	210.51	0
23	√baha height	4	-196.5	238.87	0
26	√baha mai height	5	-195.4	240.06	0
37	speciestot height	4	-195	240.4	0
44	stocking height	4	-186.4	248.97	0
30	tph height	4	-181.2	254.25	0
32	tph height qmd	5	-180.1	255.33	0
31	tph height mai	5	-179.1	256.29	0
5	height	3	-178.5	256.9	0
27	qmd height	4	-176.7	258.74	0
29	qmd height mai	5	-174.7	260.71	0
46	ln(sdofdbh) √baha	4	-96.6	338.78	0
45	ln(sdofdbh) tphdbh1 tphdbh2	5	-51.3	384.08	0
39	ln(sdofdbh)	3	-47.6	387.83	0
21	√stock qmd	4	227.5	662.91	0
33	tph √baha tph*baha	5	239.1	674.49	0
25	√baha qmd	4	241.6	676.99	0
24	invage √baha	4	245.5	680.91	0
9	√baha	3	296	731.37	0
38	sdofdbh	3	331.3	766.76	0
7	√stock	3	356.9	792.36	0
28	qmd mai	4	461.7	897.07	0
4	invage	3	463.5	898.93	0
6	stocking	3	509.7	945.16	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	567.4	1002.80	0
18	tphcrn4	3	581.5	1016.90	0
8	baha	3	522.3	957.72	0
34	tphht1 tphht2 tphht3 tphht4	6	602.6	1037.97	0
16	tphcrn2	3	629.0	1064.40	0
17	tphcrn3	3	651.2	1086.60	0
14	tphdbh3	3	685.3	1120.74	0
3	stndage	3	688.8	1124.24	0
12	tphht3 tphht4	4	715.4	1150.77	0
13	tphdbh2	3	732.9	1168.3	0
11	speciestot tphdbh4	4	743.9	1179.32	0
15	tphdbh4	3	820.4	1255.81	0

Table 4.18. Cont'd.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
10	tph	3	872.4	1307.82	0
1		2	873.7	1309.1	0
2	√speciestot	2	873.7	1309.1	0
19	modelprecip elev	4	877.3	1312.74	0

[1]Model numbers correspond to those in Table 4.9

[2] Number of estimated parameters, including an error term.

Table 4.19. Coefficients (± 1 SE) for estimating FHD (See Table 4.2) for the 95% confidence model set for wet-conifer stands. FHD is estimated using Eqn. 4.4.

Model[1]	Variable	Coefficient estimate
42	intercept	0.122 (0.025)
	ln(sdofdbh)	0.271 (0.015)
	height	0.022 (0.001)
	tphdbh1	0.00004 (0.00001)
	tphdbh2	0.0001 (0.00009)
41	intercept	0.126 (0.025)
	ln(sdofdbh)	0.268 (0.015)
	height	0.021 (0.001)
	tph	0.00004 (0.00001)

[1]Model numbers correspond to those in Table 4.9.

Table 4.20. Comparison of FHD (See Table 4.2) statistics for the model and test datasets for wet-conifer stands. The fitted Mean Square Error (MSE) and adjusted R^2 were calculated for the stands used to fit the models (n=484). The predicted sum of squares error (PredSSE) was calculated for the set of wet-conifer stands that was used to test the fit of the model (n=161). Only the 95% confidence models were examined (ΔAICc< 7).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
42	0.022	0.021	0.91
41	0.022	0.019	0.91

[1]Model numbers correspond to those in Table 4.9.

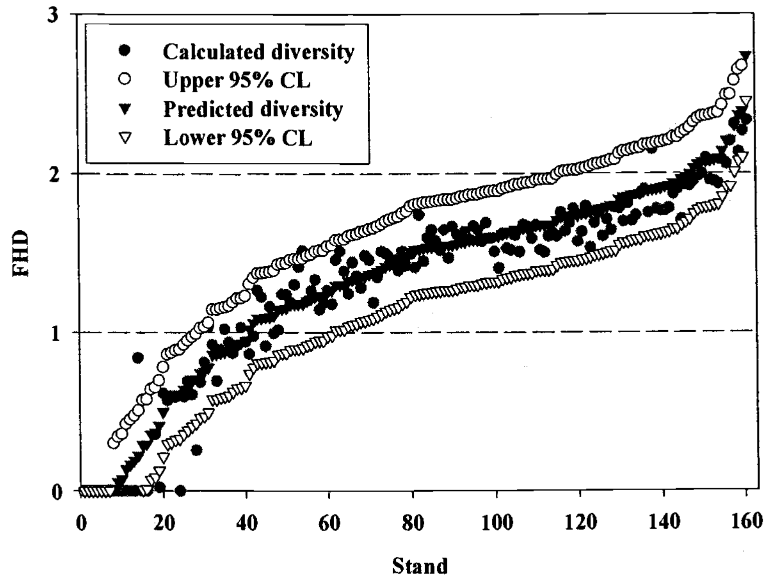

Fig. 4.31. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 42 parameter estimates for wet-conifer stands (Table 4.19). Comparison is for the 161 stands comprising the test dataset for wet-conifer stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error.

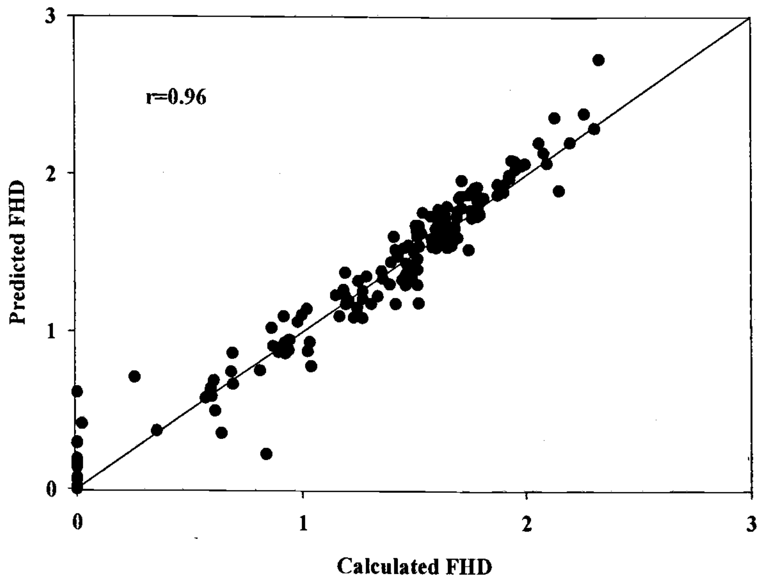

Fig. 4.32. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 42 parameter estimates (Table 4.19) for 161 stands comprising the test dataset of wet-conifer stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 4.21. Ranking of *a priori* models to predict SDI (See Table 4.2) in 75% of wet-hardwood plots (n=103) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
41	ln(sdofdbh) height √baha	5	142.5	0.00	0.61
43	ln(sdofdbh) height tphdbh1 tphdbh2	6	144.4	1.94	0.23
44	ln(sdofdbh) tphdbh1 tphdbh2	5	145.6	3.09	0.13
45	ln(sdofdbh) √baha	4	149	6.49	0.02
42	ln(sdofdbh) height tph	5	150.9	8.39	0.01
40	height ln(sdofdbh)	4	152.4	9.96	0
39	ln(sdofdbh)	3	156.3	13.79	0
36	invage √baha mai height	6	166.6	24.07	0
27	qmd qmd2 height	5	171.2	28.72	0
29	qmd qmd2 height mai	6	173.5	30.98	0
23	√baha height	4	174.7	32.20	0
20	√stock height	4	175	32.49	0
26	√baha mai height	5	176.9	34.40	0
22	√stock height mai	5	177.2	34.69	0
5	height	3	188.9	46.42	0
32	tph height qmd	5	189.8	47.31	0
30	tph height	4	190.5	48.00	0
37	speciestot height	4	190.8	48.30	0
31	tph height mai	5	192.6	50.14	0
24	invage √baha	4	193.1	50.63	0
28	qmd qmd2 mai	5	194.2	51.67	0
21	√stock qmd	4	194.5	51.96	0
25	√baha qmd	4	200.4	57.89	0
9	√baha	3	200.6	58.13	0
33	tph √baha tph*baha	5	200.7	58.19	0
7	√stock	3	200.7	58.22	0
18	tphcrn4	3	212.3	69.80	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	5	215.4	72.90	0
4	invage	3	217.7	75.25	0
16	tphcrn2	3	224.5	82.00	0
17	tphcrn3	3	225.5	83.01	0
38	sdofdbh	3	225.5	83.01	0
6	stocking	3	225.7	83.21	0
8	baha	3	229.5	87.05	0
13	tphdbh2	3	239.2	96.71	0
34	tphht1 tphht2 tphht3 tphht4	6	241.1	98.62	0
12	tphht3 tphht4	4	244.3	101.80	0
14	tphdbh3	3	250.3	107.82	0
3	stndage	3	250.9	108.36	0
2	speciestot	3	256.4	113.90	0
11	speciestot tphdbh4	4	258.3	115.85	0
10	tph	3	262.9	120.46	0

Table 4.21. Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
1		2	263.4	120.88	0
15	tphdbh4	3	264.2	121.69	0
19	modelprecip elev	4	264.8	122.32	0

[1]Model numbers correspond to those in Table 4.7.
[2] Number of estimated parameters, including an error term.

Table 4.22. Coefficients (± 1 SE) for estimating SDI (See Table 4.2) for the good model set (ΔAICc < 7) for wet-hardwood stands. SDI is estimated using Eqn. 4.2.

Model[1]	Variable	Coefficient estimate
41	intercept	-1.698 (0.184)
	ln(sdofdbh)	0.760 (0.121)
	height	-0.011 (0.007)
	√baha	0.139 (0.039)
43	intercept	-1.896 (0.247)
	ln(sdofdbh)	0.923 (0.130)
	height	0.0064 (0.007)
	tphdbh1	0.00017 (0.00007)
	tphdbh2	0.0023 (0.0007)
44	intercept	-2.108 (0.185)
	ln(sdofdbh)	0.915 (0.073)
	tphdbh1	0.00020 (0.00006)
	tphdbh2	0.0022 (0.0007)
45	intercept	-1.899 (0.157)
	ln(sdofdbh)	0.730 (0.088)
	√baha	0.115 (0.037)

[1]Model numbers correspond to those in Table 4.7.

Table 4.23. Comparison of SDI (See Table 4.2) statistics for the model and test datasets for wet-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=103). The predicted sum of squares error (PredSSE) was calculated for the set of wet-hardwood stands that was used to test the fit of the model (n=34). Only the 95% confidence models were examined (ΔAICc< 7).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
41	0.225	0.346	0.57
43	0.227	0.411	0.56
44	0.226	0.400	0.69
45	0.236	0.350	0.68

[1]Model numbers correspond to those in Table 4.8.

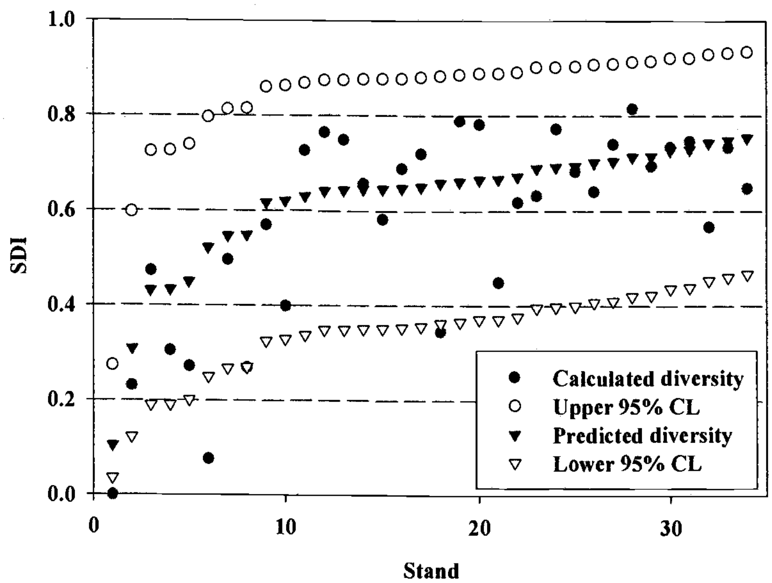

Fig. 4.33 Comparison of Simpson's height diversity (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates for wet-hardwood stands (Table 4.22). Comparison is for the 34 stands comprising the test dataset for wet-hardwood stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

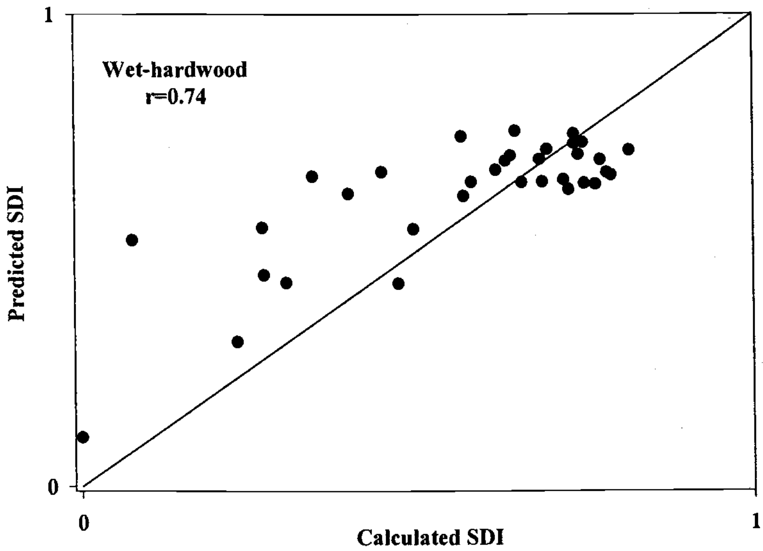

Fig. 4.34. Comparison of Simpsons' height diversity (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates (Table 4.22) for 34 stands comprising the test dataset of wet-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 4.24. Ranking of *a priori* models to predict CHDI (See Table 4.2) in 75% of the wet-hardwood plots (n=103) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
40	1/age stocking height	5	27.2	0.00	0.53
21	stocking height mai	5	28.6	1.37	0.27
19	stocking height	4	29.4	2.17	0.18
41	√sdofdbh logstock	4	33.6	6.35	0.02
35	1/age baha mai height	6	48.4	21.19	0
39	1/age baha height	5	50.6	23.33	0
25	baha mai height	5	54.1	26.82	0
22	baha height	4	54.8	27.52	0
44	√sdofdbh height baha	5	57	29.73	0
46	√sdofdbh height tphdbh1 tphdbh2	6	68.7	41.43	0
31	tph height qmd	5	77.6	50.36	0
45	√sdofdbh height tph	5	78.8	51.58	0
20	stocking qmd	4	79.2	51.97	0
30	tph height mai	5	79.3	52.04	0
29	tph height	4	80.1	52.90	0
6	stocking	3	83.6	56.33	0
42	√sdofdbh baha	4	85.2	57.96	0
5	height	3	86.5	59.25	0
28	qmd height mai	5	86.8	59.58	0
36	speciestot height	4	88.3	61.04	0
38	height √sdofdbh	4	88.6	61.32	0
26	qmd height	4	88.7	61.42	0
47	√sdofdbh tphdbh1 tphdbh2	5	89.7	62.49	0
23	1/age baha	4	95.6	68.39	0
8	baha	3	104.5	77.21	0
24	baha qmd	4	104.6	77.36	0
32	tph baha tph*baha	5	105.8	78.60	0
43	√sdofdbh tph	4	106	78.73	0
37	√sdofdbh	3	124.9	97.71	0
33	tphht1 tphht2 tphht3 tphht4	6	126	98.80	0
4	1/age	3	138.1	110.91	0
11	tphht3 tphht4	4	143.1	115.83	0
15	tphcrn2	3	143.4	116.14	0
34	tphcrn1 tphcrn2 tphcrn3 tphcrn4	5	145.8	118.56	0
17	tphcrn4	3	146.4	119.17	0
7	sdofdbh	3	147.7	120.45	0
16	tphcrn3	3	148.3	121.11	0
27	qmd mai	4	149.3	122.02	0
12	tphdbh2	3	154.5	127.25	0
13	tphdbh3	3	155.7	128.47	0
3	stndage	3	158.7	131.46	0
10	speciestot tphdbh4	4	169.9	142.71	0
2	speciestot	3	172.9	145.70	0

Table 4.24. Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
14	tphdbh4	3	174.6	147.40	0
18	modelprecip elev	4	178.6	151.33	0
1		2	180.8	153.56	0
9	tph	3	182.9	155.68	0

[1]Model numbers correspond to those in Table 4.8.
[2] Number of estimated parameters, including an error term.

Table 4.25. Coefficients ($\pm$ 1 SE) for estimating CHDI (See Table 4.2) for the good model set (ΔAICc < 7) for wet-hardwood stands. CHDI is estimated using Eqn. 4.3.

Model[1]	Variable	Coefficient estimate
40	intercept	1.133 (0.122)
	1/age	-1.358 (0.654)
	stocking	0.0096 (0.001)
	height	0.015 (0.003)
21	intercept	0.823 (0.114)
	mai	0.00095 (0.0006)
	stocking	0.010 (0.001)
	height	0.016 (0.003)
19	intercept	0.952 (0.087)
	stocking	0.011 (0.001)
	height	0.016 (0.003)
41	intercept	-0.022 (0.120)
	√sdofdbh	0.108 (0.037)
	lnstock	0.460 (0.038)

[1]Model numbers correspond to those in Table 4.8.

models (Table 4.26). Correspondence between predictions and calculated diversity was similar for the four good models (e.g. Figs. 4.35, 4.36). Predicted diversity values were within one unit for 53% of the observations for the best model but this increased to 91% when predicted diversity was within 1.5 units.

Table 4.26. Comparison of CHDI (See Table 4.2) model statistics for the model and test datasets for wet-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=103). The predicted sum of squares error (PredSSE) was calculated for the set of wet-hardwood stands that was used to test the fit of the model (n=34). Only the 95% confidence models were examined (ΔAICc< 7).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
40	0.072	0.078	0.70
21	0.073	0.085	0.70
19	0.074	0.081	0.69
41	0.077	0.069	0.77

[1]Model numbers correspond to those in Table 4.8.

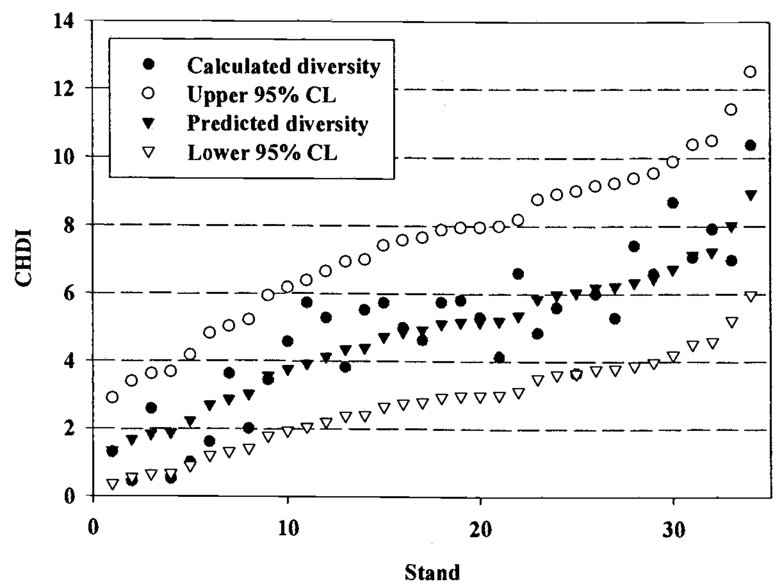

Fig. 4.35. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates for wet-hardwood stands (Table 4.25). Comparison is for the 34 stands comprising the test dataset for wet-hardwood stands. The 95% upper and lower confidence limits substituted the $\sqrt{\text{PredSSE}}$ in place of the standard error.

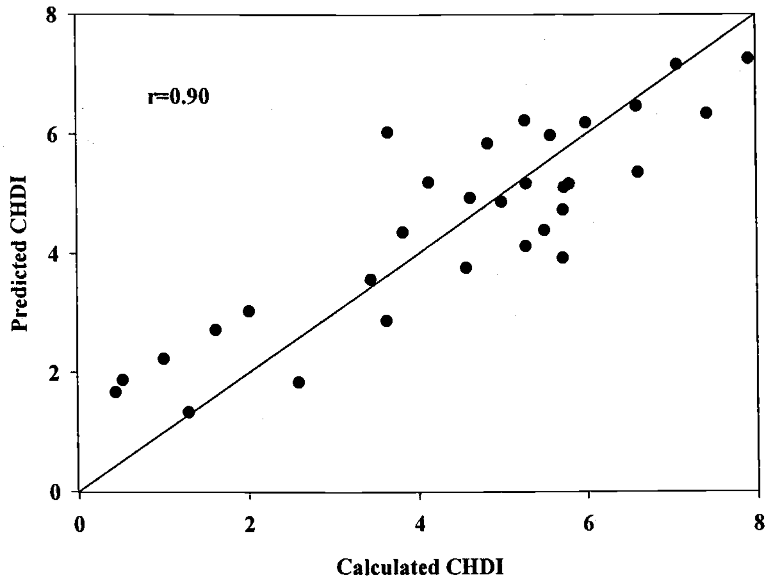

Fig. 4.36. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates (See Table 4.25) for 34 stands comprising the test dataset of wet-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

FHD

Model 42 was the best approximating model (ΔAICc=0, Tables 4.27-4.28). There was one additional model included in the 95% confidence model set.

Assessment of the test data revealed the predSSEs of predictions were similar to the MSEs of the models (Table 4.29). Correspondence between predictions and calculated diversity values was similar (e.g. Figs. 4.37, 4.38). Predicted diversity values were within 0.15 units for 79% of the observations for the best model and this increased to 91% of the observations when predicted diversity was within 0.2 units.

Dry hardwood

SDI

Model 41 was the best approximating model (ΔAICc=0, Tables 4.30-4.31). There were three additional models included in the 95% model set. A fourth model with ΔAICc < 7 was excluded because it was less parsimonious and the standard error of the inverse of age was a magnitude greater than the parameter estimate.

Assessment of the test data revealed the predSSEs of predictions were similar to the MSEs of the best models (Table 4.32). Correspondence between predicted and calculated diversity was similar for the best model, with the exception of three stands (Figs. 4.39, 4.40). Predicted diversity values were within 0.1 units for 69% of the observations for the best model and this increased to 81% when predicted diversity was within 0.15 units.

CHDI

Model 41 was the best approximating model (ΔAICc=0, Tables 4.33-4.34). There were no additional models included in the 95% model set.

Table 4.27. Ranking of *a priori* models to predict FHD (See Table 4.2) in 75% of the wet-hardwood plots (n=103) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
42	ln(sdofdbh) height tphdbh1 tphdbh2	6	-148.1	0	0.96
41	ln(sdofdbh) height tph	5	-141.7	6.453	0.04
40	height ln(sdofdbh)	4	-114.6	33.477	0
43	ln(sdofdbh) height √baha	5	-114.1	33.995	0
30	tph height	4	-92.3	55.802	0
31	tph height mai	5	-91.4	56.763	0
32	tph height qmd	5	-90.3	57.831	0
27	qmd height	4	-90.2	57.885	0
5	height	3	-89.8	58.326	0
29	qmd height mai	5	-89.3	58.786	0
20	√stock height	4	-88.8	59.267	0
37	speciestot height	4	-88.5	59.646	0
23	√baha height	4	-87.6	60.48	0
44	stocking height	4	-87.6	60.494	0
22	√stock height mai	5	-87.5	60.572	0
36	invage √baha mai height	6	-86.7	61.438	0
26	√baha mai height	5	-86.1	61.979	0
45	ln(sdofdbh) tphdbh1 tphdbh2	5	-19.6	128.473	0
46	ln(sdofdbh) √baha	4	-19.4	128.669	0
39	ln(sdofdbh)	3	-15.4	132.698	0
38	sdofdbh	3	42.4	190.477	0
21	√stock qmd	4	57.8	205.899	0
25	√baha qmd	4	58.7	206.858	0
33	tph √baha tph*baha	5	65.5	213.641	0
24	invage √baha	4	66.6	214.713	0
9	√baha	3	66.9	214.988	0
7	√stock	3	77	225.153	0
28	qmd mai	4	83.2	231.27	0
14	tphdbh3	3	91.7	239.787	0
8	baha	3	92.5	240.63	0
6	stocking	3	96.1	244.231	0
4	invage	3	98.8	246.89	0
18	tphcrn4	3	98.8	246.90	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	5	101.3	249.40	0
17	tphcrn3	3	107.3	255.40	0
16	tphcrn2	3	107.3	255.40	0
3	stndage	3	107.3	255.439	0
11	speciestot tphdbh4	4	108.9	256.995	0
34	tphht1 tphht2 tphht3 tphht4	6	111.1	259.169	0
12	tphht3 tphht4	4	112.3	260.432	0
15	tphdbh4	3	113.3	261.459	0
13	tphdbh2	3	115.5	263.615	0

Table 4.27. Cont'd.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
10	tph	3	128.7	276.841	0
1		2	130.6	278.687	0
2	√speciestot	2	130.6	278.687	0
19	modelprecip elev	4	134.2	282.327	0

[1]Model numbers correspond to those in Table 4.9.
[2] Number of estimated parameters, including an error term.

Table 4.28. Coefficients (± 1 SE) for estimating FHD (See Table 4.2) for the 95% confidence model set for wet-hardwood stands. FHD is estimated using Eqn. 4.1.

Model[1]	Variable	Coefficient estimate
42	intercept	0.066 (0.058)
	ln(sdofdbh)	0.261 (0.030)
	height	0.025 (0.002)
	tphdbh1	0.00008 (0.00002)
	tphdbh2	-0.0004 (0.0002)
41	intercept	0.062 (0.060)
	ln(sdofdbh)	0.254 (0.032)
	height	0.024 (0.002)
	tph	0.000091 (0.00002)

[1]Model numbers correspond to those in Table 4.9.

Table 4.29. Comparison of FHD (See Table 4.2) statistics for the model and test datasets for wet-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=103). The predicted sum of squares error (PredSSE) was calculated for the set of wet-hardwood stands that was used to test the fit of the model (n=34). Only the 95% confidence model set was examined (ΔAICc< 7).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
42	0.0125	0.042	0.92
41	0.0135	0.023	0.92

[1]Model numbers correspond to those in Table 4.9.

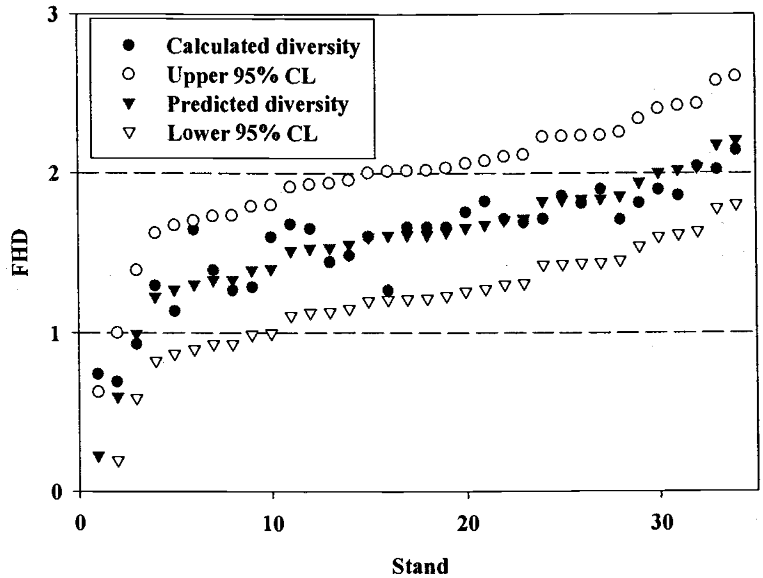

Fig. 4.37. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 42 parameter estimates for wet-hardwood stands (Table 4.28). Comparison is for the 34 stands comprising the test dataset for wet-hardwood stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error.

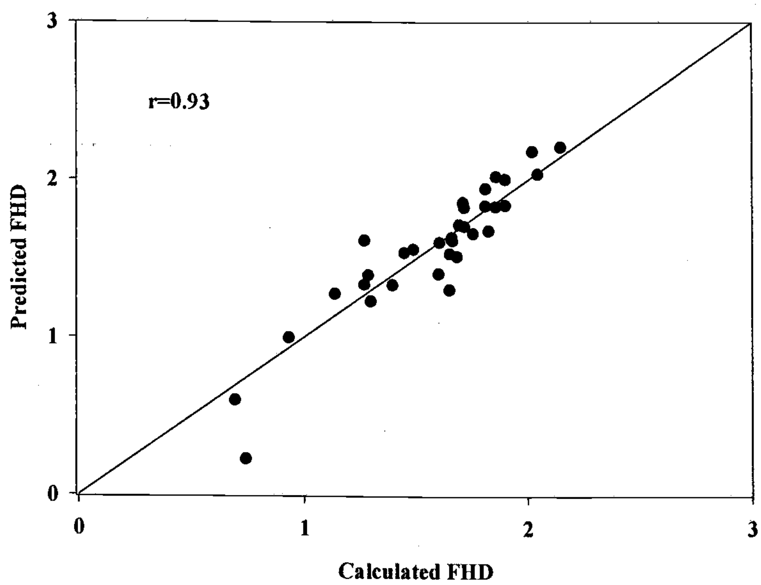

Fig. 4.38. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 42 parameter estimates (Table 4.28) for 34 stands comprising the test dataset of wet-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 4.30. Ranking of *a priori* models to predict SDI (See Table 4.2) in 75% of dry-hardwood plots (n=76) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
41	ln(sdofdbh) height √baha	5	154.8	0.00	0.55
23	√baha height	4	156.5	1.71	0.23
45	ln(sdofdbh) √baha	4	158.6	3.82	0.08
26	√baha mai height	5	158.8	4.01	0.07
36	invage √baha mai height	6	161.1	6.37	0.02
20	√stock height	4	162.1	7.31	0.01
43	ln(sdofdbh) height tphdbh1 tphdbh2	6	163.6	8.81	0.01
22	√stock height mai	5	164.2	9.42	0.01
40	height ln(sdofdbh)	4	164.2	9.43	0.01
27	qmd qmd2 height	5	164.9	10.11	0
42	ln(sdofdbh) height tph	5	165.3	10.53	0
29	qmd qmd2 height mai	6	165.7	10.93	0
44	ln(sdofdbh) tphdbh1 tphdbh2	5	167.4	12.66	0
32	tph height qmd	5	170.4	15.61	0
39	ln(sdofdbh)	3	170.6	15.84	0
9	√baha	3	171.5	16.68	0
33	tph √baha tph*baha	5	171.8	17.00	0
25	√baha qmd	4	171.9	17.15	0
24	invage √baha	4	172.9	18.15	0
21	√stock qmd	4	174.3	19.55	0
37	speciestot height	4	174.5	19.73	0
5	height	3	174.8	20.05	0
30	tph height	4	176.5	21.70	0
28	qmd qmd2 mai	5	177.9	23.10	0
31	tph height mai	5	178.6	23.80	0
7	√stock	3	179.9	25.12	0
8	baha	3	195.6	40.78	0
16	tphcrn2	3	196.9	42.10	0
17	tphcrn3	3	197.1	42.30	0
18	tphcrn4	3	197.1	42.30	0
6	stocking	3	199.5	44.70	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	201.9	47.10	0
38	sdofdbh	3	205.4	50.60	0
34	tphht1 tphht2 tphht3 tphht4	6	208.8	54.04	0
4	invage	3	212.6	57.80	0
13	tphdbh2	3	216.8	62.01	0
12	tphht3 tphht4	4	224.6	69.86	0
11	speciestot tphdbh4	4	230.1	75.31	0
3	stndage	3	230.2	75.45	0
14	tphdbh3	3	230.3	75.53	0
2	speciestot	3	231.3	76.56	0
15	tphdbh4	3	234.9	80.14	0

Table 4.30. Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
19	modelprecip elev	4	236.4	81.64	0
1		2	236.5	81.74	0
10	tph	3	238.5	83.70	0

[1]Model numbers correspond to those in Table 4.7.
[2] Number of estimated parameters, including an error term.

Table 4.31. Coefficients (± 1 SE) for estimating SDI (See Table 4.2) for the 95% confidence model set (ΔAICc < 6) for dry-hardwood stands. SDI is estimated using Eqn. 4.2.

Model[1]	Variable	Coefficient estimate
41	intercept	-2.058 (0.291)
	ln(sdofdbh)	0.393(0.199)
	height	0.0056 (0.010)
	√baha	0.245 (0.071)
23	intercept	-1.728 (0.243)
	height	0.014 (0.010)
	√baha	0.307 (0.064)
45	intercept	-2.348 (0.198)
	ln(sdofdbh)	0.579 (0.145)
	√baha	0.250 (0.064)
26	intercept	-1.723 (0.249)
	mai	-0.00018 (0.002)
	height	0.014 (0.010)
	√baha	0.308 (0.065)

[1]Model numbers correspond to those in Table 4.7.

Table 4.32. Comparison of SDI (See Table 4.2) statistics for the model and test datasets for dry-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=76). The predicted sum of squares error (PredSSE) was calculated for the set of dry-hardwood stands that was used to test the fit of the model (n=26). Only 95% confidence models were examined (ΔAICc< 7).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
41	0.457	0.346	0.46
23	0.476	0.416	0.43
45	0.439	0.329	0.65
26	0.483	0.417	0.43

[1]Model numbers correspond to those in Table 4.8.

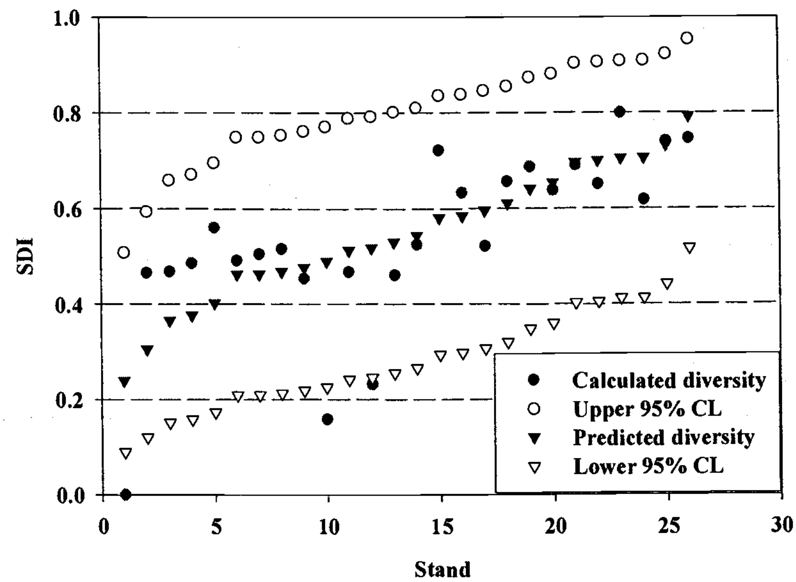

Fig. 4.39. Comparison of Simpson's height diversity (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates for dry-hardwood stands (Table 4.31). Comparison is for the 26 stands comprising the test dataset for dry-hardwood stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error. Error bars are uneven because they are back-transformed from the logit scale.

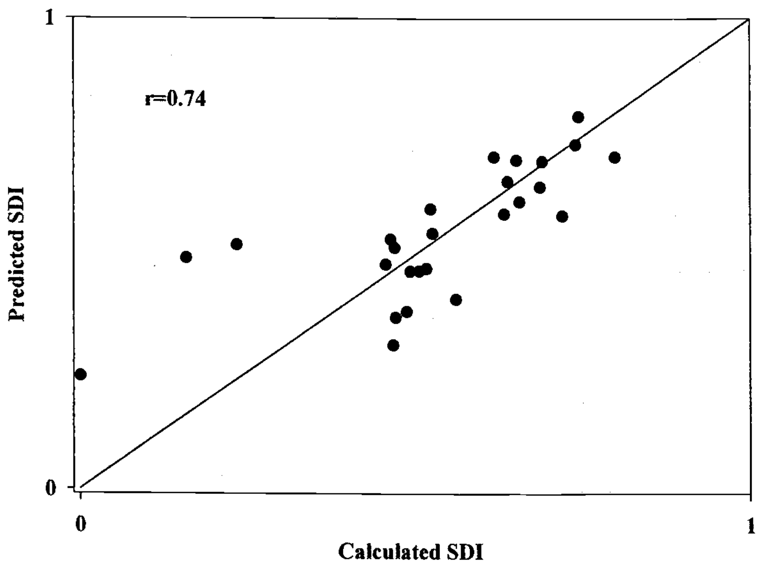

Fig. 4.40. Comparison of Simpson's height diversity (See Table 4.2) calculated from stand data and predicted using model 41parameter estimates (Table 4.31) for 26 stands comprising the test dataset of dry-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

Table 4.33. Ranking of *a priori* models to predict CHDI (See Table 4.2) in 75% of dry-hardwood plots (n=76) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
41	√sdofdbh logstock	4	40.1	0.00	1.00
35	1/age baha mai height	6	55.4	15.28	0
40	1/age stocking height	5	56.4	16.29	0
21	stocking height mai	5	58.8	18.69	0
39	1/age baha height	5	59.3	19.24	0
19	stocking height	4	62.6	22.52	0
44	√sdofdbh height baha	5	63.2	23.09	0
22	baha height	4	68.2	28.06	0
25	baha mai height	5	68.3	28.21	0
46	√sdofdbh height tphdbh1 tphdbh2	6	74.3	34.20	0
45	√sdofdbh height tph	5	76.2	36.16	0
47	√sdofdbh tphdbh1 tphdbh2	5	77.6	37.51	0
43	√sdofdbh tph	4	78.7	38.57	0
42	√sdofdbh baha	4	80.2	40.14	0
31	tph height qmd	5	89.2	49.14	0
38	height √sdofdbh	4	92	51.94	0
23	1/age baha	4	94.3	54.20	0
28	qmd height mai	5	96.1	56.00	0
26	qmd height	4	99.1	59.02	0
30	tph height mai	5	101.5	61.46	0
5	height	3	101.9	61.79	0
36	speciestot height	4	102	61.89	0
20	stocking qmd	4	102.1	62.06	0
29	tph height	4	102.3	62.18	0
37	√sdofdbh	3	110.2	70.10	0
6	stocking	3	114.1	73.98	0
24	baha qmd	4	116.4	76.27	0
32	tph baha tph*baha	5	118.9	78.78	0
8	baha	3	119.3	79.18	0
15	tphcrn2	3	134.5	94.40	0
16	tphcrn3	3	135.2	95.10	0
4	1/age	3	138.1	98.00	0
17	tphcrn4	3	139.8	99.70	0
34	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	140.4	100.3	0
7	sdofdbh	3	143	102.94	0
27	qmd mai	4	146.4	106.26	0
33	tphht1 tphht2 tphht3 tphht4	6	149.6	109.48	0
12	tphdbh2	3	163.9	123.77	0
18	modelprecip elev	4	173.8	133.73	0
11	tphht3 tphht4	4	174.1	133.98	0
3	stndage	3	174.5	134.42	0
13	tphdbh3	3	176	135.88	0
10	speciestot tphdbh4	4	176.3	136.26	0

Table 4.33. Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
2	speciestot	3	179.2	139.10	0
14	tphdbh4	3	181.4	141.27	0
9	tph	3	183.1	142.99	0
1		2	184.5	144.43	0

[1]Model numbers correspond to those in Table 4.8.
[2] Number of estimated parameters, including an error term.

Table 4.34. Coefficients (± 1 SE) for estimating CHDI (See Table 4.2) for the best model for dry-hardwood stands. CHDI is estimated using Eqn. 4.3.

Model[1]	Variable	Coefficient estimate
41	intercept	0.037 (0.110)
	√sdofdbh	0.130 (0.060)
	lnstock	0.493 (0.046)

[1]Model numbers correspond to those in Table 4.8.

Evaluation of the test data revealed the predSSE of the prediction was similar to the MSE of the best model (Table 4.35). Correspondence between predicted and calculated diversity was similar (Figs. 4.41, 4.42). Predicted diversity values were within one unit only for 38% of the observations for the best model and this increased to 69% when predicted diversity was within 1.5 units.

Table 4.35. Comparison of CHDI (See Table 4.2) statistics for the model and test datasets for dry-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=76). The predicted sum of squares error (PredSSE) was calculated for the set of dry-hardwood stands that was used to test the fit of the model (n=26). Only the best model was examined (ΔAICc=0).

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
41	0.092	0.069	0.86

[1]Model numbers correspond to those in Table 4.9.

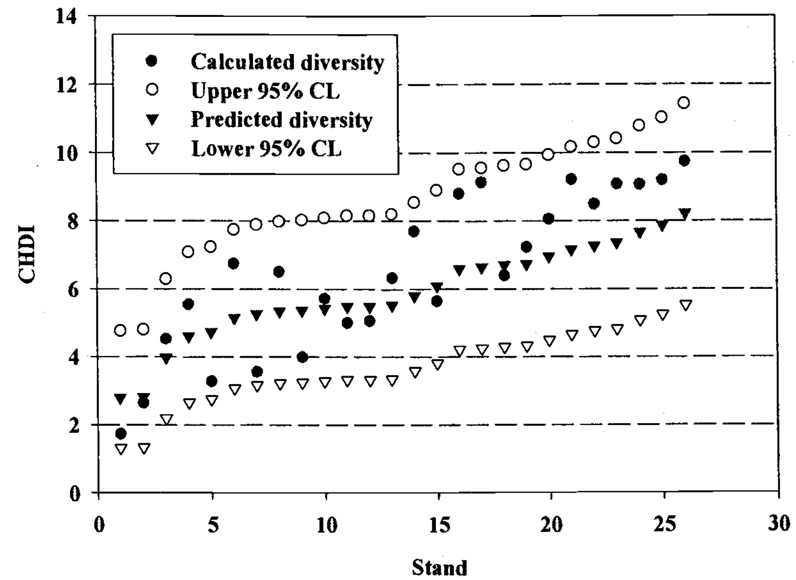

Fig. 4.41. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates for dry-hardwood stands (Table 4.34). Comparison is for the 26 stands comprising the test dataset for dry-hardwoodr stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error.

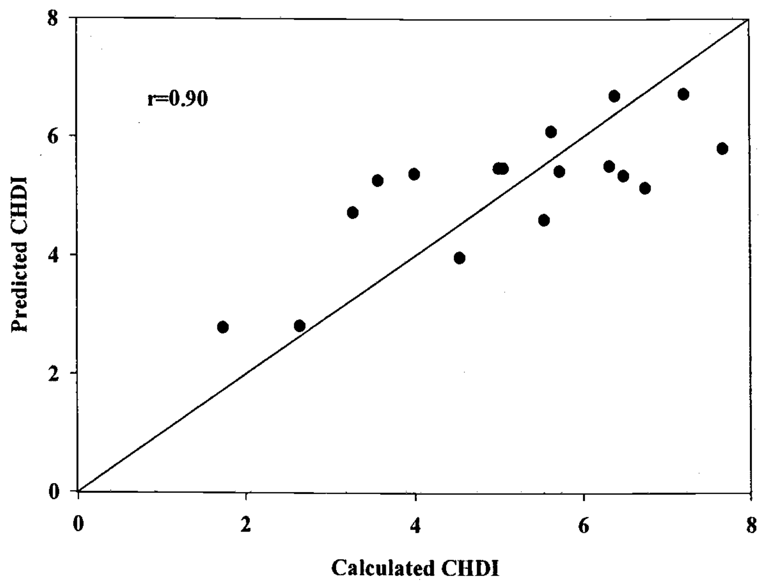

Fig. 4.42. Comparison of CHDI (See Table 4.2) calculated from stand data and predicted using model 41 parameter estimates (Table 4.34) for 26 stands comprising the test dataset of dry-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient

FHD

Model 40 was the best approximating model (ΔAICc=0, Tables 4.36-4.37). There were two additional models included in the 95% confidence model set. Model 42 was excluded from the good model set because model 41 provided better fit and was more parsimonious (i.e. tph=tphdbh1+tphdbh2).

In the assessment with the test data, the predSSEs of the predictions were similar to the MSEs of the models (Table 4.38). Correspondence between predicted and calculated diversity values was similar (e.g. Figs. 4.43, 4.44). Predicted diversity values were within 0.15 unit for 69% of the observations for the best model and this increased to 85% of the observations when predicted diversity was within 0.2 units.

Discussion

Criteria for Selecting and Using Diversity Measures

The diversity measures I used met the criteria for selecting useful diversity indices (Heuserr 1998, Magurran 1998). I used measures that were relatively easy to understand and interpret and that were cited in the ecology literature. Also, given the similar patterns seen among the diversity measure, it didn't appear that more complicated measures provided more information than simple measures in this study.

I agreed with the criteria of Spies and Cohen (1992) that; 1) an index should be easy to measure in the field, 2) all other things equal, tall forests should have higher index values than shorter forests, and 3) for forests of equal height, those with foliage or crown throughout the vertical space should have higher index values than those with foliage or crowns only at one or a few heights. However, I thought the CHDI metric failed to accomplish the first criterion because it requires

Table 4.36. Ranking of *a priori* models to predict FHD (See Table 4.2) in 75% of the dry-hardwood plots (n=76) in western Oregon. Ranking is based on AICc values. *w* values are Akaike weights.

Model[1]	Model variables	k[2]	AICc	ΔAICc	w
40	height ln(sdofdbh)	4	-51.2	0.00	0.42
43	ln(sdofdbh) height √baha	5	-50.8	0.40	0.34
41	ln(sdofdbh) height tph	5	-49	2.19	0.14
42	ln(sdofdbh) height tphdbh1 tphdbh2	6	-48.4	2.75	0.11
36	invage √baha mai height	6	-31.1	20.08	0
30	tph height	4	-30.2	21.01	0
37	speciestot height	4	-28.7	22.51	0
5	height	3	-28.5	22.67	0
20	√stock height	4	-28.4	22.77	0
31	tph height mai	5	-27.9	23.32	0
32	tph height qmd	5	-27.9	23.32	0
27	qmd height	4	-27.5	23.66	0
23	√baha height	4	-27.3	23.84	0
44	stocking height	4	-26.5	24.73	0
22	√stock height mai	5	-26.2	24.95	0
29	qmd height mai	5	-25.3	25.90	0
26	√baha mai height	5	-25.3	25.90	0
45	ln(sdofdbh) tphdbh1 tphdbh2	5	23.1	74.25	0
46	ln(sdofdbh) √baha	4	23.4	74.55	0
39	ln(sdofdbh)	3	24.6	75.77	0
38	sdofdbh	3	50.7	101.86	0
25	√baha qmd	4	59.3	110.46	0
9	√baha	3	59.7	110.91	0
24	invage √baha	4	60.6	111.77	0
33	tph √baha tph*baha	5	61.7	112.91	0
21	√stock qmd	4	62.2	113.37	0
7	√stock	3	68.8	120.01	0
28	qmd mai	4	79.2	130.37	0
8	baha	3	81.6	132.79	0
6	stocking	3	85.8	136.98	0
18	tphcrn4	3	89.3	140.50	0
16	tphcrn2	3	89.3	140.50	0
17	tphcrn3	3	89.5	140.70	0
34	tphht1 tphht2 tphht3 tphht4	6	90.5	141.64	0
4	invage	3	91.3	142.46	0
11	speciestot tphdbh4	4	95.5	146.71	0
35	tphcrn1 tphcrn2 tphcrn3 tphcrn4	6	95.7	146.90	0
14	tphdbh3	3	97	148.18	0
13	tphdbh2	3	100.8	151.98	0
12	tphht3 tphht4	4	103.2	154.38	0
15	tphdbh4	3	104.2	155.35	0
3	stndage	3	109.3	160.52	0

Table 4.36 Cont'd.

Model[1]	Model variables	k^2	AICc	ΔAICc	w
19	modelprecip elev	4	112.7	163.89	0
1		2	114.8	165.97	0
2	√speciestot	2	114.8	165.97	0
10	tph	3	116.7	167.93	0

[1]Model numbers correspond to those in Table 4.9.
[2] Number of estimated parameters, including an error term.

Table 4.37. Coefficients (± 1 SE) for estimating FHD (See Table 4.2) for the best models for dry-hardwood stands. FHD is estimated using Eqn. 4.4.

Model[1]	Variable	Coefficient estimate
40	intercept	0.088 (0.069)
	ln(sdofdbh)	0.229 (0.043)
	height	0.028 (0.002)
43	intercept	0.103 (0.070)
	ln(sdofdbh)	0.258 (0.048)
	height	0.029 (0.003)
	√baha	-0.023 (0.017)
41	intercept	0.070 (0.089)
	ln(sdofdbh)	0.237 (0.049)
	height	0.027 (0.003)
	tph	0.000007 (0.00002)

[1]Model numbers correspond to those in Table 4.9.

Table 4.38. Comparison of FHD (See Table 4.2) statistics for the model and test datasets for dry-hardwood stands. The fitted Mean Square Error (MSE) and adjusted R^2 (Adj R^2) were calculated for the stands used to fit the models (n=76). The predicted sum of squares error (PredSSE) was calculated for the set of dry-hardwood stands that was used to test the fit of the model (n=26). Only the 95% confidence models were examined.

Model[1]	MSE	PredSSE	Adj. R^2 (fit)
40	0.027	0.020	0.86
43	0.026	0.020	0.86
41	0.027	0.020	0.86

[1]Model numbers correspond to those in Table 4.9.

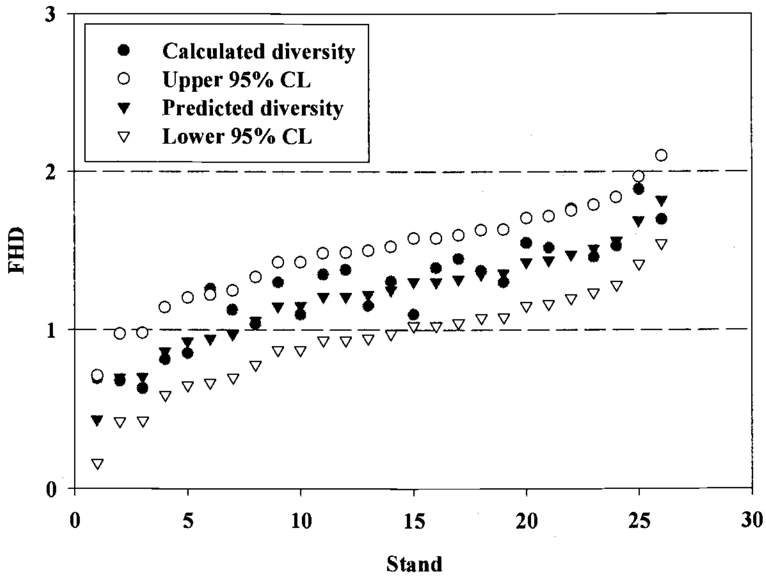

Fig. 4.43. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates for dry-hardwood stands (Table 4.37). Comparison is for the 26 stands comprising the test dataset for dry-hardwood stands. The 95% upper and lower confidence limits substituted the √PredSSE in place of the standard error.

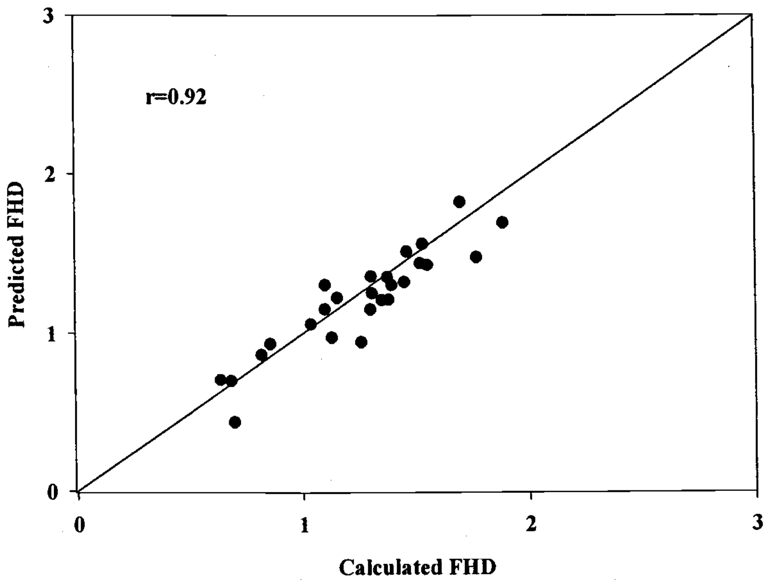

Fig. 4.44. Comparison of FHD (See Table 4.2) calculated from stand data and predicted using model 40 parameter estimates (Table 4.37) for 26 stands comprising the test dataset of dry-hardwood stands. The diagonal line represents a 1:1 relationship between the predicted and measured cover. The r-value is the Pearson correlation coefficient.

measurement of individual crown widths, which are not a standard forest measurement. Instead, as in this study, crown widths must often be estimated from dbh using crown diameter equations. However, Spies and Pabst (personal communication) created DDI as a surrogate for CHDI in stands where crown widths were not measured. In this study, DDI did not appear to perform any better than using CHDI. The diversity measures based on proportions of cover, tree heights, or base-crown heights located within height intervals (e.g.Shannon, Simpson, FHD) did not produce higher values for taller forest than for shorter-stature forests. However, values increased with the height of a stand because of the increasing number of occupied height intervals. Also, the majority of these measures did give higher diversity values in stands with a greater range of tree heights or larger diameters, as proposed by Staudhammer and LeMay (2001). Unlike CHDI, which gave higher weight to taller trees, a measure of relative positioning of trees among the height classes was not used in other measures. Therefore, in stands with low diversity estimates the 5-m intervals with the highest relative proportion can not be determined. This is also the case for stands with low CHDI values, as these low values can result from a variety of vertical structure distributions of foliage. This is a potential shortcoming of these approaches. Forest managers often are interested in information other than vertical diversity, such as the dominant height class. Thus, providing additional measures such as stand height or the mean and standard deviation of tree heights or diameters can supplement descriptors of height diversity.

Crown ratio is not included in the calculation of CHDI. Yet CHDI still discriminated among the various structure groups. This likely resulted because taller trees have greater weight. However, the proportion-based measures that did not weight by height interval, but incorporated crown lengths, produced results similar to those of the CHDI. This suggests that weighting crown widths by tree heights has a similar function as weighting by basal area.

Sensitivity of diversity measures

Species diversity measures that substituted height intervals for species were generally effective at capturing richness and evenness. Structural diversity assigned the data to vertical intervals, giving the data upper and lower bounds, whereas with species diversity the maximum number of species is usually unknown. Therefore, there is less uncertainty associated with interpreting vertical diversity measures, compared with species diversity measures.

The selection of cover groups proved to be very poor at discriminating among the calculated diversity measures. These criteria were based on the relative proportions of cover among layers defined by the line-intercept method. Thus it appears the line-intercept criteria for separating layers were problematic for use in differentiating among vertical diversity measures. With the way that the line-intercept layers in my study are defined, a break of at least 5 m between tree heights must occur in order for a new layer to be defined. If the canopy strata truly are discrete within a stand, then this definition would succeed in differentiating among dominance and diversity. However, my findings suggest that instead of a discrete break in the canopy, there are also stands where tree heights are more continuous (e.g. Edgar and Burk 2001). In these stands where this is not a separation of at least 5 m, one ends up with a single-layered canopy, based on the line-intercept criteria. This discrepancy can be illustrated by comparing two hypothetical stands that have similar levels of total cover. Both stands have a mean height of 20 m. In the one stand there is a cohort of trees that are around 10 m and another cohort of trees that are 30 m tall (i.e. two-layer canopy). In a second stand there is a continuous gradient of trees with individual tree heights differing by a maximum of 4 m (i.e. single-layer). The problem arises because both stands will be classified as having a single dominant cover layer. While these two stands have distinctive vertical patterns, this would be muted using the line-intercept criteria, which would treat the two stands as equitable.

The variability among methods for assigning layers of cover should also be considered. If I had alternatively used the number of layers of strata described by the stratification algorithm or by TSTRAT then the criteria for cover groups would have aggregated different stands. The assessments of diversity measures would likely have been different. Thus, the use of cover groups based on fixed classes versus adjustable layers is relative to individual stands and the method used. Cover based on layering should not be used to describe vertical structure in western Oregon forests.

The use of vertical structure groups based on height and crown-base height intervals was effective at differentiating vertical patterns. Using height intervals worked better than relative proportions of cover among layers because the height intervals were fixed. This is in contrast to the layers of cover that were relative to each stand and thus varied among stands. Fixed intervals allowed for more direct comparisons among stands.

The slight overlap in diversity measures among the five structure groups was expected, as these structure groups were somewhat 'fuzzy', with arbitrary divisions. They were arbitrary because two 14-m and 16-m tall trees might provide similar ecological functions in a stand, and yet with 5-m intervals, they are assigned to separate vertical height classes. This can be compared with two 12-m and 14-m tall trees that would be assigned to the same class. Thus, I would anticipate stands in the sub-even and even vertical structure groups with similar diversity values. The relative similarity among structure groups would be even higher if trees were aggregated into larger height classes. This is because more trees would be included within a height interval.

While all diversity measures provided a pattern of decreasing diversity with increasing dominance, SDI was most discriminating. Unlike the Shannon index, which is sensitive to rarer height intervals, the SDI emphasizes more dominant height intervals. Therefore, it was not surprising that it did the best job of discriminating among the vertical structure groups, given the 5-m intervals used in this study. With narrower height intervals I would expect reduced dominance of a height interval. Thus Simpson's index would likely be a poorer discriminator of diversity with smaller intervals, compared with Shannon, owing to the increase in rarer height intervals.

Patterns Along a Successional Gradient

SDI

A single height interval dominated in young stands, while dominance sharply declined as the canopy developed taller trees and larger crowns. Diversity remained fairly consistently high during the stem exclusion ages. Vertical diversity and layering were highest in the old-growth stands, consistent with the 'gappy' multi-layered characteristics of them that allowed for multiple size classes of trees to occur in a community. Aber (1979) proposed two potential successional pathways for hardwood stands of northeastern USA beyond age 30. He suggested that either (1) the canopy would continue to grow upwards in a concentrated form or (2) the canopy would grow taller but elongate as it grew, with a more evenly distributed canopy. In stands of western Oregon it appears that the second pathway, with decreased dominance of a single vertical interval, is the more likely scenario, and the use of SDI aids in ascertaining this.

CHDI

In this study I used the CVS data as a baseline with which to compare the FIA wet-conifer stands. I only included wet-conifer stands, as this was the predominant forest group of the CVS plots. I expected CVS plots to be more representative of natural stands that initiated after natural disturbances (e.g. fire). The higher maximum value of CHDI calculated for the CVS plots was indicative of the higher diversity of heights associated with natural stands, compared to the managed stands dominating the FIA dataset. This is because managed stands tend to have a single dominant layer resulting from partial-harvest activities (i.e.

thinning) during the stand-initiation phase. The steeper increase in CHDI seen in the FIA stands is likely because they are primarily industrial forest lands, that tend to be located on high-productivity sites. Therefore, they are more likely to grow taller more quickly compared with CVS plots that tend to be on less productive (e.g. higher elevation) sites. Thus, with the increased height weighting in the CHDI calculation more productive sites would attain higher CHDI values at younger ages. Overall, mean CHDI values only reached just over half of the theoretical maximum CHDI value of 15 for wet-conifer forests . This suggests that either the CVS and FIA datasets have not captured the full range of CHDI present in the landscape, or that CHDI values nearer to 15 are only theoretically attainable.

Stratification

The concept of vertical canopy stratification lacks clarity and agreement. For the FIA inventory, stratification referred to a maximum of three canopy layers differing in their average heights by at least 5 m. Using this criterion, an increase in canopy layering along diversity and successional gradients were supported. Alternate definitions of stratification, such as the use of a fixed proportion of the crown length of the tallest tree in a stratum (TSTRAT), or a threshold of overlap between the height of a shorter tree and the moving average of mean base crown height of all taller trees (Stratification algorithm) lead to similar conclusions, but different absolute numbers of layers. This suggests defining the number of layers in a stand is somewhat arbitrary. Therefore, it is crucial for researchers to clearly define their interpretation of a forest community as multi-layered or not, clearly describing the method of stratification they used.

Prediction of Diversity

A potential drawback of using Simpson's index is that there are multiple interpretations of an index value of zero. Simpson's index ranges from zero to one, with zero being maximum dominance of a given height interval. In addition, zero values can also mean that there are no trees in a stand. Therefore, if one selects SDI to describe vertical structure of a stand, additional information, such as stem density should also be provided to better interpret index values.

Among the three forest groups, calculated SDI diversity was consistently zero in stands where predicted diversity was < 0.20. This suggested that there was total dominance of a single height interval in these stands. However, this dominance of a single height interval was not captured using the predictive models. This occurred because the variables in the 95% model sets for all of the forest groups included basal area, the natural logarithm of standard deviation of dbh, and the height of the stand. While all three variables were expected to increase with increasing diversity, none of these variables could adequately distinguish among height intervals. Two stand scenarios with the same variation in heights, using my selection of 5-m height intervals, demonstrate this. In the first stand, trees are 9-m and 11-m tall, while in the second stand they are 11 and 13 m tall. In the first stand the two sets of trees will be assigned to different height intervals, while in the second stand they will be assigned to the same height interval. Thus, the first stand will have a single dominant layer, while the second stand will have a more diverse vertical structure. However, using the predictive models, this distinction among the two stands is not directly captured. Thus, with the 5-m height intervals, the use of surrogates to predict SDI was problematic for stands with predicted diversity < 0.2.

An alternative theory is that the predicted SDI diversity is really more representative of the stand diversity. If the heights of trees differ by 2-m in both stands then maybe these two stands should have the same level of diversity, rather than different degrees of dominance. Thus, the two described stand scenarios demonstrate how condensing continuous variables to intervals can dilute or change interpretation of the data. When using continuous data, the problem of multiple interpretations of a zero value of SDI is removed, as only stands without trees will have a value of zero. However, in reality, this interpretation is not always the correct one, because a total dominance of a given tree height is precluded by the use of continuous variables.

In stands with predicted diversity > 0.2 correlation between predicted and calculated SDI diversity was generally good among the three forest groups. An exception was in wet-hardwood stands, where the correlation between predicted and calculated diversity was lower than for other forest groups ($r=0.74$). This suggested that wet-hardwood predictive models captured less of the variability in the wet-hardwood dataset than the other forest groups did. However, examining all plots comparing predicted and calculated SDI, accuracy of predicted diversity within 0.15 units of calculated diversity occurred in $\geq$ 79% of stands. Therefore, all these predictive models can be used to approximate vertical structural diversity, recognizing that when SDI is predicted as < 0.2, dominance of a single 5-m height interval is likely to be greater than predicted.

Except for stand height, the variables included in the 95% model sets among forest groups generally differed for CHDI, compared with SDI and FHD. Among all the forest groups, stand age, and stocking were selected as important variables in the 95% model set. This is in contrast to the selection of basal area and density of trees for FHD and SDI. This likely resulted because unlike SDI and FHD, CHDI directly accounted for positions of tree heights within a stand. Recall that CHDI gave higher weight to taller, larger trees with wider crown widths. The selection of stocking rather than basal area as good predictors of CHDI suggests that CHDI is better described using a measure that is relative to the potential density of stems for a given site index, rather than using an absolute measure, such as basal area. The calculations of FHD and SDI incorporated measures of basal area or density because the original calculations of these measures weighted stem densities by their respective basal areas.

There was generally good correspondence between calculated and predicted diversity of CHDI and FHD, except for in the dry-hardwood stands. There were 96% of wet-conifer stands and 91% of wet-hardwood stands within 1.5 units of calculated CHDI using the best models. However, this number decreased to only 69% for the best model in dry-hardwood stands. It appears that all models included in the 95% model sets for the forest groups have a good ability to model CHDI, except for the diminished capability of the dry-hardwood stand models. With ≥ 85% of stands predicting FHD within 0.2 units of calculated FHD, these models can be used. Therefore, if the accuracy of predictions measured in this study are adequate to meet a researcher's objectives, I recommend the use of these predictive models in stands that lack detailed crown measures.

Overall, in the absence of detailed crown measures, I think that the good set of predictive models formulated in this study can be used to assess the vertical diversity of forested stands in western Oregon. Even the models with reduced accuracies of prediction can still provide information on relative trends in diversity, and will likely distinguish among highly dominant and highly diverse vertical structural compositions. The selection of which diversity measure to predict may be based on the availability of standard forest data. For example, for stands with information on age, stocking, and stand height, CHDI can be best predicted. These CHDI, FHD, and SDI models can be applied among wet-conifer, wet-hardwood, and dry-hardwood forests similar to those used in this study, across the landscape of western Oregon.

Limitations

There are eight factors that limit interpretation of the results of this study:

1) The inventory was depauperate of older aged stands, as the majority of older stands located on federal land (Campbell et al. 2002) were excluded from this study. Therefore, caution should be used in interpreting results for stand ages beyond age 115 for wet-conifer and dry-hardwood stands, and beyond age 65 for the wet-hardwood stands.

2) I studied a chronosequence of stand ages, substituting space for time. This approach lumped stands with variable site attributes, such as mean precipitation levels, aspect, and elevation. Vertical canopy structure changes based on a chronosequence approach may not reflect true developmental trends of a stand.

3) Sample sizes for the hardwood forests were limited, and thus revealed relationships should be viewed with caution.

4) The FIA inventory lacked detailed information on the vertical distribution of foliage. Compacted crown ratios were assigned to 10 percentage point classes. Therefore, I had to assume that the crown was continuous from the top of the tree in order to calculate the crown-base height. Also, I used basal area as a surrogate when estimating foliage cover within height intervals. While basal area has been previously used to give larger trees more weight than smaller trees (e.g. Staudhammer and Lemay 2001), I was unable to use the methods of MacArthur and MacArthur (1961) to estimate foliage among height intervals. Therefore, caution should be used when interpreting the calculated results of the vertical foliage diversity measures.

5) Only three sample units for the vertical cover group with all height intervals with < 20% of cover were available.

6) While I opted to use 5-m height intervals, the selection of height intervals is somewhat arbitrary. The values of diversity measures would have differed if I had selected different sized height intervals. If I had selected 2-m intervals then, overall, trees would have been assigned to more intervals, leading to increased diversity, whereas with larger intervals (e.g. 10-m), there would have been increased dominance for a given interval. Therefore, the choice of height intervals directly impacts the values of diversity measures. With the 5-m height intervals, trees that are 4 m and 6 m tall (for example) would be assigned to different vertical intervals, even though they are similar. Thus, there is potential for slight overlap among the diversity measures calculated by each of the methods among structure groups.

7) The SDI predictive models in this study should only be used to interpret the relative diversity of heights among 5-m intervals.

8) The CHDI predictive models in this study should only be used to interpret the relative diversity using the height intervals described in Table 4.2.

Also, crown widths were estimated from CVS crown width equations, rather than directly measured.

Summary

1) I compared thirteen measures of vertical structural diversity and layering on 884 FIA inventory plots among vertical and successional gradients. I then attempted to predict selected vertical diversity indices from standard forest variables.

2) Weighting by density or basal area made little difference in patterns of diversity among the majority of diversity measures.

3) Vertical diversity measures performed similarly among forest groups, and thus patterns in diversity were only described for all forest groups combined.

4) Cover groups were poor at distinguishing vertical patterns of diversity and stratification, while structure groups effectively distinguished vertical diversity and layering patterns.

5) With increasing evenness among height intervals and increasing stand age, there was concurrent increase in canopy height and crown-base height diversity and canopy layering consistent with expected height and live crown patterns associated with dominance and succession. SDI best differentiated among vertical structure groups.

6) Predictive models for CHDI, FHD, and SDI were created using an objective model selection approach.

7) Predicted SDI values were within 0.15 units for $\geq$ 79% of the observations. Predicted CHDI values were within 1.5 units for $\geq$ 91% of the observations, except for only in 69% of the dry-hardwood stands. Predicted FHD measures were within 0.2 units for $\geq$ 85% of the observations among forest groups.

8) In the absence of detailed crown measurements, FHD, SDI and CHDI can be predicted using the formulated predictive models included in the 95%

confidence model sets, assuming that the accuracies of prediction are sufficient to attain the objectives of a given study.

9) The information that the diversity measures used in this study are providing has practical use for describing vertical forest structure across the stand succession gradient in western Oregon.

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COMPARISON OF PREDICTABILITY OF BIRD-HABITAT ASSOCIATION MODELS FOR THREE VERTICAL CANOPY DIVERSITY INDICES

Abstract

Wildlife associated with forest canopies, including numerous bird species, are a key concern of current forest management in the Pacific Northwest. As a result, greater attention is being given to evaluating measures of canopy structure as predictors of wildlife habitat. Two indices of vertical canopy diversity, Foliage Height Diversity (FHD) and Simpson's Index of Height Diversity (SDI) were used to determine if existing models using the Canopy Height Diversity Index (CHDI) to predict presence of bird species could be improved on. The proportions of bird models with higher classification efficiencies than CHDI were 33% and 66% in the Coast Range using FHD and SDI, respectively, and 18% for models with the two canopy measures in the Cascade Range. Improvements generally were less than six percentage points. Given their strength of prediction, future use of the majority of these models is warranted where data are available to calculate estimates of FHD or SDI but not CHDI.

Introduction

Wildlife associated with forest canopies are a key concern of current forest management in the Pacific Northwest (PNW). Canopy associated wildlife are included in the Northwest Forest Plan Survey and Manage Program (USDA, USDI 1994). Societal concerns for biodiversity, as demonstrated by the first criterion of the Montreal Process (The Montreal Process 1999) are also forcing land managers to focus on the impacts of forest management on wildlife. The first criterion of the Montreal Process highlights the need for conservation of biological diversity for the conservation and sustainable management of temperate and boreal forests. The Oregon Board of Forestry's *Forestry Program for Oregon* mission and vision statements are incorporating the seven Montreal Process Criteria and Indicators, including biodiversity, as their central goals. Thus, the need to focus on the effects of forest management on wildlife and their habitat diversity is of increasing importance.

The vertical structure of the forest canopy is a critical habitat component for numerous bird species. With increase in tree height, there is a concurrent increase in vertical profiling and discriminatory use of the canopy by birds (Sharpe 1996). Macarthur and Macarthur (1961) found species diversity of birds was highly correlated with vertical and horizontal foliage complexity, including layering and gaps. Airola and Barrett (1985) studied an insect-gleaning guild of birds in a Sierran mixed-conifer forest. Their comparisons of proportional availability and use of foliage height classes and tree species demonstrated the birds' selectivity among tree species and heights within the forest. In a simulation study of impacts of multiple silvicultural treatment scenarios, Hansen et al. (1995) found bird species tended to fall into four habitat-use guilds, with their levels of canopy cover and structural complexity characterized these guilds. Shaw et al. (1996) divided the canopy of an old-growth Douglas-fir forest into three zones; bright, transition, and dim. They detected 15 small bird species significantly more often in one zone of the canopy than in the others. McComb et al. (2002) found that a surrogate of canopy heterogeneity typically explained the most variability in habitat capability indices for nest sites of the northern spotted owl (*Strix occidentalis*).

Other taxa also use the canopy in PNW forests. Eleven bat species regularly roost, forage, and reproduce in the canopy (Wunder and Carey 1996). The Oregon red tree vole (*Aborimus longicaudus*) is dependent on coniferous tree canopies for foraging, nesting, travel routes, refugia cover, and moisture (Carey 1991) and is an important food source of the northern spotted owl. Carey et al. (1999) found that captures of northern flying squirrels (*Glaucomys sabrinus*) were correlated with foliage height diversity as measured by the Berger-Parker index.

With cost often limiting field-based investigations of forest fauna (Thomas and Verner 1986), a challenge in numerous studies is to develop relationships that can be applied to predicting change in abundance and fitness of wildlife over time, for various management alternatives (Cade 1997). Models that estimate wildlife-habitat associations can be used to assess management impacts on species' habitats. Models that include canopy structure variables are especially pertinent for wildlife species that use the forest canopy.

Wildlife species are associated with certain features of vertical structure. For example, bark-gleaning bird species, which feed in furrowed older bark, favor lower older portions of the canopy (Sharpe 1996) and thus focus on the region below the live crown. Meanwhile, the distribution of foliage is likely important for foliage gleaners. Therefore, vertical diversity variables describing varied aspects of the vertical structure, including the distribution of foliage and the relative positioning of tree heights (see Chapter Four), are important to consider when constructing wildlife habitat-association models.

The Vertebrate Habitat Relationships Databank (VHRDB; Garman and Cole 1999) combined results from 23 wildlife studies spanning a wide range of forested conditions and management treatments in western Oregon. Logistic regression models developed using the VHRDB relate vegetation parameters such as shrub cover, tree density, vertical height diversity, and relative conifer-hardwood abundance, to the presence/absence of various groups of wildlife species including breeding birds. The VHRDB models demonstrated the importance of the vertical canopy height diversity to numerous bird species.

The objective of this study was to compare existing VHRDB habitat models for bird species associated with vertical forest structure with new models using alternative descriptors of canopy features. Two additional indices of vertical diversity were applied to existing wildlife-habitat datasets to see how well they predicted the distribution (presence/absence) of bird species in western Oregon, compared with the existing models.

Methods

The Canopy Height Diversity Index (CHDI; Spies and Cohen 1992) was included in a subset of models that predicted bird-species occurrence (Garman and Cole 1999). CHDI was included in models for 15 species in the Coast Range and 11 species in the Cascade Range (Table 5.1, also see Tables 4 and 14 in Garman and Cole 1999).

Table 5.1. Acronym, common name, and scientific name for bird species from the Vertebrate Habitat Relationships Data Bank (VHRDB) used in this study.

Code	Common Name	Scientific Name
AMGO	American Goldfinch	*Carduelis tristis*
BGWA	Black-throated Gray Warbler	*Dendroica nigrescens*
BHGR	Black-headed Grosbeak	*Pheucticus melanocephalus*
BTPI	Band-tailed pigeon	*Columba fasciata*
BRCR	Brown Creeper	*Certhia americana*
CBCH	Chestnut-backed Chickadee	*Parus rufescens*
EVGR	Evening Grosbeak	*Coccothraustes vespertinus*
GCKI	Golden-crowned Kinglet	*Regulus satrapa*
GCSP	Golden-crowned Sparrow	*Zonotrichia querula*
GRJA	Gray Jay	*Perisoreus canadensis*
HETH	Hermit Thrush	*Catharus guttatus*
HEWA	Hermit Warbler	*Dendroica occidentalis*
MGWA	MacGillivray's Warbler	*Oporornis tolmiei*
NOFL	Northern Flicker	*Colaptes auratus*
OCWA	Orange-crowned Warbler	*Vermivora celata*
PISI	Pine Siskin	*Carduelis pinus*
PSFL	Pacific Slope Flycatcher	*Empidonax difficilis*
RBNU	Red-breasted Nuthatch	*Sitta canadensis*
SOSP	Song Sparrow	*Melospiza melodia*
SPTO	Spotted Towhee	*Pipilo maculatus*
VATH	Varied Thrush	*Ixoreus naevius*
WCSP	White-crowned Sparrow	*Zonotrichia leucophrys*
WETA	Western Tanager	*Piranga rubra*
WIWR	Winter Wren	*Troglodytes troglodytes*

Vertebrate Habitat Relationships Data Bank

In this study I used three bird study datasets from the Coast Range and five bird datasets from the western side of the Cascade Range (Table 5.2). These datasets constituted 100 stands in the Cascade Range and 143 stands in the Coast Range. Studies were conducted during a variety of seasons and years, beginning in April 1984, with the final study completed in November 1993. Size classes by which trees were sampled varied among studies (see Table 5.2). All bird observations were $\leq$ 50-m distance from the observation-station center. Observation methods differed among studies and included variable circular plots and spot mapping. The combining of the studies for analyses allowed for the most complete datasets for the study areas.

Diversity Indices

My comparison of eleven vertical diversity measures including CHDI, revealed that Simpson's diversity of height index (SDI; Simpson 1949, see also Chapter 4 Table 4.2) best discriminated among five structural groups. In addition to height diversity measures I also examined Macarthur and Macarthur's (1961) index of foliage height diversity (FHD, see also Chapter 4 Table 4.2). SDI and FHD weight trees by their basal area and focus on relative positioning of tree heights and foliage, respectively, within 5-m height classes. CHDI focuses on tree heights and volumes among 16-m height classes and weights trees based on their positioning within height classes. Only FHD differentiates between the ecological space of the crown and the space located below the crown of a tree. Thus, CHDI, FHD, and SDI describe the diversity of the vertical canopy, with each emphasizing slightly different aspects.

Vegetation data included in the VHRDB generally were measured by size classes (see Table 5.2). Also, detailed crown measurements were not typically recorded. Thus, the coarseness of these datasets limited the ability to directly calculate vertical diversity measures. The predictive models from Chapter Four

Table 5.2. Field studies in the Vertebrate Habitat Relationships Data Bank (VHRDB) used in this study. Stands were predominately Douglas-fir dominated forests.

Study id	Source	Size classes used to record trees[a]	Survey method[b]	Stand types	Duration
Oregon Coast Range					
we002	Hansen et al. 1990	2-10, 11-30, 31-50, 51-90, > 90	TRPL	Open canopy plantations, closed-canopy plantations, mature conifer stands	January-February 1989, May-June 1989, 1990
we006	McGarigal and McComb 1995	2.54-12.6, 12.7-22.8, 22.9-332.9, 32.9-43.1, 43.2-53.2, 53.3-63.4, 63.5-73.6, 73.7-81.3, >81.3 cm	TRPL	Stands captured within the Central Oregon Coast Range, Drift Creek, Lobster Creek and Nestucca River Basins	May-July 1990-1992
we052	Carey et al. 1991	actual diameter	TRPL	Young, mature and old-growth conifer forests	April-June 1985, 1986
Oregon Cascade Range					
we001	Hansen et al. 1995	2-10, 11-30, 31-50, 51-90, > 90	TRPL	Mature, clearcut, and shelterwood conifer stands	May-June 1989, 1990
we004	Hansen et al. 1995	22-30, 31-40, 41-50, 51-60, 61-90, 91-121	TRPL	Harvest units with variable snag retention levels	May –July 1991
we008	Hagar 1996	actual diameter	PT	Pre-harvest young Douglas-fir stands	May-June 1992-1993
we009	Vega 1993	2-10, 11-20, 21-30, 31-40, 41-50, 51-60, 61-70, 71-80, 81-90, ≥ 91	PT	Clearcut, green-tree retention and mature conifer stands	May-August 1992
we062	Huff et al. 1991 (Southern Oregon Cascades)	actual diameter	PT	Chronosequence of Douglas-fir stands aged 35 to 500 yrs	April – July 1984
we063	Huff et al. 1991 (Central Oregon Cascades)	actual diameter	PT	Chronosequence of Douglas-fir stands aged 35 to 500 yrs	April – July 1984

[a] Frequency of stems was recorded by species, except in we006 which recorded trees by hardwood or conifer.
[b] TRPL=transect with plots, PT=Point counts

were formulated to circumvent this problem. Predictive models developed in Chapter Four were used to predict canopy measures for the VHRDB datasets. The VHRDB sites used in this study were dominated by wet-conifers so I used the best-approximating wet-conifer predictive equations from Chapter Four for the two diversity measures:

pFHD=0.122+(0.271*lnsdofdbh+(0.022*ht)+(0.00004*tphdbh1)+(0.0001*tphdbh2)

where:

pFHD is the predicted foliage height diversity.
sdofdbh is the standard deviation of dbh.
ht is the height of the tallest tree within the stand.
tphdbh1 is the density of stems $\leq$ 30 cm dbh.
tphdbh2 is the density of stems > 30 cm dbh.

$$pSDI = \left(\frac{1}{1 + \exp(2.207 - (0.89 * \ln(sdofdbh) + (0.013 * ht) - (0.192 * (\sqrt{baha})}\right) * 1.05$$

where:

pSDI is the predicted Simpson's diversity of tree heights.
sdofdbh is the standard deviation of dbh.
ht is the height of the tallest tree within the stand.
baha is the basal area per hectare.

Estimates of FHD and SDI were based on assumptions of diameter distributions and used modeled tree heights. Estimates of standard deviation of dbh were based on assumptions of tree sizes, especially for the uppermost size class. Midpoints of size classes were used to calculate means and SDs of dbh for each study. The uppermost size class was assigned a conservative 'midpoint' of 110 cm because this was previously used in the VHRDB to estimate CHDI. This is a conservative estimate for large trees in conifer-dominated forests of western Oregon. As a relatively low upper diameter estimate it likely underestimated stand height and standard deviation of dbh for the study sites that did not record individual tree measures. This in turn would decrease diversity measures. However, if a strong connection between bird species and vertical diversity existed, this conservative estimate was still likely to discern these relationships. Whereas, if I had opted to use a much larger upper diameter 'midpoint' then the revealed relationships would more likely be an artifact of the high diameter size. Tree heights were predicted from dbh using empirically based equations (Garman et al. 1995). When there were multiple equations for a tree species, I selected the one with closest proximity to the study area. I selected equations for elevations < 1000 m, as the majority of the study sites were located below this elevation. The stand height used in this study was the modeled height of the tallest tree.

Model Generation

Logistic regression was performed using the LOGISTIC procedure (SAS Institute 1999). The number of stations with species present and absent weighted logistic regression models. I used the logistic models that were previously derived by Garman and Cole (1999) as the starting points for my model generation. Garman and Cole used a manual stepwise procedure to derive their models, which included the most parsimonious set of habitat variables to best predict the probability of occurrence for a species. Therefore, I assumed that their models were the best available to describe species' associations with vertical habitat. In their models Garman and Cole excluded the intercept term for models in which the intercept was not significant (alpha=0.05). For consistency, I used the same set of habitat parameters and only included significant intercept terms. I substituted the estimates of FHD and SDI in place of CHDI to create the new logistic models.

Model Evaluation

I calculated the probability of occurrence for individual bird species within each study site using the generated logistic models. The logistic models returned a probability scaled from 0 to 1. For probabilities < 0.5, I assumed the species was absent and for probabilities ≥ 0.5 I assumed the species was present.

I compared the classification efficiencies (i.e. percentage of correct prediction rates) of the CHDI logistic models with the 'new' generated models that substituted SDI and FHD for CHDI. I was interested in whether the alternative models improved upon the classification efficiency of the CHDI-based models. In addition, I compared the omission errors (i.e. percentages of stands that were predicted to be absent of a species, even though the species was present) and commission errors (i.e. the percentage of stands in which a species was predicted to be present, even though it was absent) among the three indices. Following the procedures of Garman and Cole (1999), I used Cohen's kappa for a chance-corrected classification rate (Titus et al. 1984) to test the significance of this classification rate for individual FHD and SDI species' models. Cohen's kappa compared the observed classification rate with that expected by chance.

Results

Logistic models predicting presence/absence of the bird species using the two vertical diversity indices were calculated (Tables 5.3-5.4). Performance of the species' models among the indices differed between the Coast and Cascade Ranges. Therefore, model results from these two regions are presented separately.

Oregon Coast Range

Classification efficiencies for models using FHD and SDI were significant (alpha=0.05) for all species except the northern flicker (Table 5.5). Classification efficiencies of FHD and SDI improved for 33.3% and 66.7% of species' models, respectively. Of the models improving classification efficiency, the improvement ranged from 0.7 to 7.7 percentage points for FHD models, compared with 1.3 to 8.4 percentage points for SDI models. There were 26.7% of species' models with lower efficiencies for FHD than CHDI, compared to 40% for SDI. Of the models

Table 5.3. Logistic regression models of species occurrence for bird species included in this study, Oregon Coast Range. Definitions of species acronyms are in Table 5.1.

Species	Measure	Model[a] (Logit(p)=)[b]
AMGO	CHDI	(0.0155 * Ptot1)+(-1.8772 *CHDI)
	FHD	(0.0188 * Ptot1)+(-0.4305 *FHD)
	SDI	(0.0195 * Ptot1)+(-1.4137 *SDI)
BTPI	CHDI	-1.447+(0.0042 * CT2-5)+(1.4439 * CHDI)+(-0.00643*HT2-5)
	FHD	-3.1438+(0.00354 * CT2-5)+(1.2305 * FHD)+(-0.00339*HT2-5)
	SDI	-2.9084+(0.00327 * CT2-5)+(3.138 * SDI)+(-0.00276*HT2-5)
CBCH	CHDI	-1.2163+(1.6085 * CHDI)+(0.0338 * CT4-5)
	FHD	-3.5475+(2.3692 * FHD)+(0.00599 * CT4-5)
	SDI	-3.2435+(6.1925 * SDI)+(0.00467 * CT4-5)
EVGR	CHDI	-1.644+(1.3413 * CHDI)+(0.018 * CT4-5)
	FHD	-1.8824+(0.5398 * FHD)+(0.0168 * CT4-5)
	SDI	-3.0644+(3.6535 * SDI)+(0.00879 * CT4-5)
GCKI	CHDI	-2.0566+(0.0423 * Ptot2-5)+(-0.3461 * CHDI)
	FHD	-4.5331+(-0.00565 * Ptot2-5)+(3.0072 * FHD)
	SDI	-4.3738+(- 0.0332 * Ptot2-5)+(11.0495 * SDI)
HEWA	CHDI	-1.3089+(0.7867 * CHDI)+(0.0325 * CT4-5)
	FHD	-3.8806+(2.0987 * FHD)+(0.00926 * CT4-5)
	SDI	-3.7488+(5.8716 * SDI)+(0.00563 * CT4-5)
MGWA	CHDI	(0.00225 * Tot1)+(-1.7586 * CHDI)
	FHD	(0.00293 * Tot1)+(-0.4895 * FHD)
	SDI	(0.00301 * Tot1)+(-1.5046 * SDI)
NOFL	CHDI	0.6118+(-2.8453 * CHDI)+(0.0119 * CT4-5)
	FHD	0.685+(-0.5039 * FHD)+(0.00542 * CT4-5)
	SDI	1.5735+(-3.8169 * SDI)+(0.0193 * CT4-5)
OCWA	CHDI	1.281+(-1.3516 * CHDI)+(-0.0333 * PTot4-5)
	FHD	0.8386+(0.0366 * FHD)+(-0.0512 * PTot4-5)
	SDI	1.9054+(-1.9211 * SDI)+(-0.0326 * PTot4-5)
PSFL	CHDI	-2.8547+(56.1575 * CHDI)
	FHD	-10.1348+(7.0635 * FHD)
	SDI	-9.2963+(18.565 * SDI)
SOSP	CHDI	2.2104+(-0.0245 * CT4-5)+(-1.1743 * CHDI)+(-0.00112 * Tot1-5)
	FHD	3.0957+(-0.0169 * CT4-5)+(-1.0035 * FHD)+(-0.0009 * Tot1-5)
	SDI	5.2438+(-0.00643 * CT4-5)+(-6.0903 * SDI)+(-0.00139 * Tot1-5)
SPTO	CHDI	(0.00177 * Tot1)+(-0.8574 * CHDI)
	FHD	(0.00243 * Tot1)+(-0.407 * FHD)
	SDI	(0.00246 * Tot1)+(-1.2711 * SDI)
VATH	CHDI	-1.6882+(0.0274 * Tot4-5)+(1.4139 * CHDI)
	FHD	-4.5385+(0.0114 * Tot4-5)+(2.2334 * FHD)
	SDI	-4.091+(0.0117 * Tot4-5)+(5.5183 * SDI)
WCSP	CHDI	3.5165+(-3.6177 * CHDI)+(-0.0163 * Tot2-5)
	FHD	3.7819+(-0.778 * FHD)+(-0.0179 * Tot2-5)
	SDI	4.2486+(-3.8867 * SDI)+(-0.0138 * Tot2-5)

Table 5.3. Cont'd.

Species	Measure	Model[a] (Logit(p)=)[b]
WIWR	CHDI	-2.2144+(39.9558 * CHDI)
	FHD	-5.7035+(4.1782 * FHD)
	SDI	-5.448+(12.294 * SDI)

[a] Probability of occurrence = Exp[logit(p)]/[1+Exp(logit(p))]
[b] Variable definitions:
CT# = density (no./ha) of conifer stems; HT# = density (no./ha) of hardwood stems; Tot# = total density (no./ha); PTot# = percentage of total stem density; where # = size class 1 to 5; 1(2-10 cm dbh), 2 (11-30 cm dbh), 3 (31-50 cm dbh), 4 (51-90 cm dbh), 5 (> 90 cm dbh) [combined size classes noted by lower-upper classes; e.g., CT3-4 = density of conifer stems 31-90 cm dbh]
CHDI - Canopy Height Diversity Index
FHD – Foliage Height Diversity Index
SDI – Simpson's Diversity Index of Tree Heights

Table 5.4. Logistic regression models of species occurrence for bird species included in this study, Oregon Cascade Range. Definitions of species acronyms are in Table 5.1

Species	Measure	Model[a] (Logit(p)=)[b]
BGWA	CHDI	-2.1157+(0.49840 * CHDI)+(0.01760 * HT2-5)
	FHD	-1.5729+(0.4582 * FHD)+(0.0246 * HT2-5)
	SDI	-2.9504+(3.2109 * SDI)+(0.0244 * HT2-5)
BHGR	CHDI	-1.5023+(-0.03110 * SnagL)+(0.59300 * CHDI)
	FHD	-0.959+(-0.0151 * SnagL)+(0.5575 * FHD)
	SDI	-1.5348+(-0.0233 * SnagL)+(2.6172 * SDI)
BRCR	CHDI	(-1.26530 * CHDI)+(0.12650 * CT4-5)+(0.11680 * SnagL)
	FHD	(-1.7967 * FHD)+(0.1333 * CT4-5)+(0.0841 * SnagL)
	SDI	(-6.7049 * SDI)+(0.1615 * CT4-5)+(0.1157 * SnagL)
CBCH	CHDI	-4.4883+(4.09320 * CHDI)
	FHD	-2.9931+(1.5514 * FHD)
	SDI	-7.4455+(11.8145 * SDI)
GCKI	CHDI	-2.3034+(0.84720 * CHDI)
	FHD	-2.7729+(1.3662 * FHD)
	SDI	-4.9027+(7.2285 * SDI)
GRJA	CHDI	-1.4413+(0.02920 * Tot5)+(0.31510 * CHDI)
	FHD	-2.3628+(0.0202 * Tot5)+(0.9644 * FHD)
	SDI	-3.1514+(0.0136 * Tot5)+(4.0429 * SDI)
HETH	CHDI	-5.4019+(1.20440 * CHDI)+(0.00659 * Tot2)
	FHD	-5.4368+(1.5579 * FHD)+(0.0102 * Tot2)

Table 5.4. Cont'd

Species	Measure	Model[a] (Logit(p)=)[b]
	SDI	-6.638+(6.2426 * SDI)+(0.00957 * Tot2)
PISI	CHDI	-1.3958+(0.43060 * CHDI)
	FHD	-1.8333+(0.8625 * FHD)
	SDI	-1.739+(2.433 * SDI)
RBNU	CHDI	(0.45240 * CHDI)+(0.00267 * SnagL)+(-0.03060 * Shrub)
	FHD	(0.4758 * FHD)+(0.0178 * SnagL)+(-0.0274 * Shrub)
	SDI	(1.6501 * SDI)+(0.0117 * SnagL)+(-0.0286 * Shrub)
WETA	CHDI	(-0.40860 * CHDI)+(0.02410 * CT4-5)
	FHD	(-0.308 * FHD)+(0.0142 * CT4-5)
	SDI	(-1.3673 * SDI)+(0.0185 * CT4-5)
WIWR	CHDI	-3.6725+(0.55060 * CHDI)+(0.03620 * PTot2-5)
	FHD	-4.5168+(0.6602 * FHD)+(0.0489 * PTot2-5)
	SDI	-6.2827+(5.5649 * SDI)+(0.0375 * PTot2-5)

[a] Probability of occurrence = Exp[logit(p)]/[1+Exp(logit(p))]

[b] Variable definitions:

CT# = density (no./ha) of conifer stems; HT# = density (no./ha) of hardwood stems; Tot# = total density (no./ha); PTot# = percentage of total stem density; where # = size class 1 to 5; 1(2-10 cm dbh), 2 (11-30 cm dbh), 3 (31-50 cm dbh), 4 (51-90 cm dbh), 5 (> 90 cm dbh) [combined size classes noted by lower-upper classes; e.g., CT3-4 = density of conifer stems 31-90 cm dbh] PHT1-5 - hardwood stem-density percentage (all sizes combined)

CHDI - Canopy Height Diversity Index

FHD – Foliage Height Diversity Index

SDI – Simpson's Diversity Index of Tree Heights

Shrub - percent shrub cover

SnagL - density (no./ha) of all snags > 50-cm dbh, > 3-m tall

Table 5.5. Logistic regression model statistics for species occurrence of bird species, Oregon Coast Range. Definitions of species acronyms are in Table 5.1.

	No. of stands		Classification efficiency[a] (%)			Omission error (%)			Commission error (%)		
Species	absent	present	CHDI	FHD	SDI	CHDI	FHD	SDI	CHDI	FHD	SDI
AMGO	124	19	74.8^{2}	71.3^{1}	74.8^{2}	5.6	5.6	5.6	19.6	23.1	19.6
BTPI	103	40	70.0^{5}	65.7^{4}	62.9^{3}	7	8.4	7.7	23.1	25.9	29.4
CBCH	14	129	74.1^{3}	81.8^{4}	82.5^{3}	25.2	16.1	14.7	0.7	2.1	2.8
EVGR	80	63	65.8^{5}	69.2^{5}	70.6^{5}	13.3	11.2	7	21	19.6	22.4
GCKI	25	118	82.5^{5}	83.2^{5}	86^{5}	13.3	13.3	11.2	4.2	3.5	2.8
HEWA	32	111	75.6^{5}	79^{5}	81.8^{5}	19.6	15.4	13.3	4.9	5.6	4.9
MGWA	111	32	78.4^{5}	77.6^{5}	79.7^{5}	7.7	9.1	9.1	14	13.3	11.2
NOFL	116	27	62.9^{2}	61.5^{0}	65.7^{0}	5.6	11.2	9.1	31.5	27.3	25.2
OCWA	81	62	72.1^{5}	67.8^{5}	71.3^{5}	14	11.2	14.7	14	21	14
PSFL	22	121	96.6^{5}	90.2^{5}	95.1^{5}	3.5	9.1	4.2	0	0.7	0.7
SOSP	86	57	68.6^{5}	67.8^{5}	72^{5}	14	14	15.4	17.5	18.2	12.6
SPTO	88	55	74.1^{4}	76.9^{5}	79^{5}	7.7	8.4	8.4	18.2	14.7	12.6
VATH	45	98	81.9^{5}	81.8^{5}	81.8^{5}	11.9	6.3	11.2	6.3	11.9	7
WCSP	124	19	93.8^{5}	93^{5}	97.2^{5}	1.4	1.4	1.4	4.9	5.6	1.4
WIWR	15	128	91.7^{5}	90.9^{5}	93^{5}	7.7	8.4	6.3	0.7	0.7	0.7

[a] $^{0}P>0.05$ $^{1}P<0.05$, $^{2}P<0.025$, $^{3}P<0.01$, $^{4}P<0.001$, $^{5}P<0.0001$

lowering classification efficiency, the decrease ranged from 0.8 to 6.3 percentage points for FHD models, compared with 0.8 to 7.1 percentage points for SDI models. Improvement in omission error varied between FHD and SDI species' models. For FHD models, omission error was higher for 40% and lower for 40% of the species' models. Improvements in omission error were from 2.1 to 9.1 percentage points, while increases in error ranged from 0.7 to 5.6 percentage points. Omission error increased for 46.7% of the SDI models, and decreased for 40%. Improvements in omission error were from 0.7 to 10.5 percentage points, while increases in error ranged from 0.7 to 3.5 percentage points.

Improvement in commission error also differed between FHD and SDI species' models. Commission error increased for 60% of the FHD models, while it decreased for 33.3% of the models. Improvements in commission error varied from 0.7 to 4.2 percentage points, while increases in error spanned from 0.7 to 7 percentage points. SDI model commission error was higher for 33.3% of models, and declined for 40% of models. Improvements in commission error varied from 1.4 to 6.3 percentage points, while increases in error ranged from 0.7 to 3.5 percentage points.

Oregon Cascade Range

Classification efficiencies were generally lower using the new diversity indices, compared with CHDI models (Table 5.6). There were four species for FHD and one for SDI without significant (alpha=0.05) classification efficiencies. Classification efficiencies of FHD and SDI only improved for 18.2% of species' models. Of the models improving classification efficiency, the improvements were only between 2-4 percentage points for FHD models, and 1 to 3 percentage points for SDI models. There were 72% of species' models with lower classification efficiencies for FHD and SDI. Of the models lowering classification efficiency, the decrease spanned from 3 to 32 percentage points for FHD models, compared with 2 to 11 percentage points for SDI models.

Table 5.6. Logistic regression model statistics for species occurrence of bird species, Oregon Cascade Range. Definitions of species acronyms are in Table 5.1.

	No. of stands		Classification efficiency[a] (%)			Omission error (%)			Commission error (%)		
Species	absent	present	CHDI	FHD	SDI	CHDI	FHD	SDI	CHDI	FHD	SDI
BGWA	64	36	66^{3}	70^{4}	62^{1}	13	16	16	21	14	22
BHGR	63	37	66^{4}	55^{0}	61^{2}	9	14	11	25	31	28
BRCR	32	68	88^{5}	90^{5}	91^{5}	2	7	6	10	3	3
CBCH	17	83	98^{5}	66^{0}	87^{5}	2	25	11	0	9	2
GCKI	28	72	84^{5}	65^{0}	77^{5}	7	22	19	9	13	9
GRJA	60	40	67^{4}	67^{4}	68^{4}	15	12	12	18	21	20
HETH	43	57	81^{5}	78^{5}	76^{5}	8	13	12	11	9	12
PISI	57	43	63^{3}	58^{0}	58^{0}	11	29	12	26	13	30
RBNU	42	58	73^{5}	70^{5}	71^{5}	11	16	16	16	14	13
WETA	59	41	67^{4}	64^{3}	67^{4}	10	12	13	23	24	20
WIWR	21	79	91^{5}	86^{5}	87^{5}	6	8	6	3	6	7

[a] $^{0}P>0.05$ $^{1}P<0.05$, $^{2}P<0.025$, $^{3}P<0.01$, $^{4}P<0.001$, $^{5}P< 0.0001$

Omission error generally increased for FHD and SDI species' models, compared with CHDI. For FHD models, omission error was higher for 90.9% and lower for only 9.1% of the species' models. Improvements in omission error only increased classification efficiency by 3 percentage points, while increases in error spanned from 3 to 25 percentage points. Omission error increased for 81.8% of the SDI models, while it only decreased for 9.1% of models. The improvement in omission error was only 3 percentage points, while increases in error ranged from 2 to 12 percentage points among models.

Improvement in commission error differed between FHD and SDI species' models. Commission error increased for 54.5% of the FHD species' models, while it decreased for 45.5% of the models. Improvements in commission error varied from 2 to 13%, while increases in error spanned from 3 to 9 percentage points. SDI model commission error was higher for 63.6% of models, and declined for 27.3% of models. Improvements in commission error varied from 3 to 7 percentage points, while increases in error ranged from 1 to 4 percentage points.

Discussion

In the Cascade Range there were three species whose classification efficiencies declined by more than five percentage points for FHD models, compared with CHDI models. This decrease was generally accompanied by large increases in both commission and omission error. Thus these models are simultaneously underestimating and overestimating individual species occupancy among stands. This suggests that these FHD models are poorly fitting the datasets as a whole. There are some stands in which the birds may be differentiating among the space within and below the crowns, but in many other stands they are not. Therefore, it may be worthwhile to re-evlaluate studies independently to see whether patterns among stand types are being muted by the presence of other stand types.

Bird species, for which FHD models lowered classification efficiency more than five percentage points, also had low classification efficiencies when using SDI in the Cascade Range. However, decreases in their classification efficiency were generally associated with steep increases in omission error. Thus, habitat use was being underestimated by only examining the diversity of tree heights. This suggests that additional habitat parameters in conjunction with SDI are needed to capture the same habitat importance that is being described by CHDI. Stands with taller trees appear to be more important than the relative positioning of tree heights for these species.

Improvements in classification efficiency greater than five percentage points only occurred in the Coast Range. The classification efficiencies of the models for the chestnut-backed chickadee improved when using FHD and SDI, while the model for the hermit's warbler improved for SDI. All of these increases in efficiency resulted from decreases in omission error, without concomitant increase in over-prediction of occupancy. Therefore, these habitat models appeared to better explain the habitat-relationships of these species, compared with CHDI. This suggests that these species are more strongly associated with the relative distribution of tree heights and foliage within narrow height classes, rather than with the absolute stand height emphasized by CHDI.

It was surprising that there were improvements in models for the chickadee in the Coast Range, given the large decreases in classification efficiency for this species in the Cascade Range. These conflicting findings suggest regional differences in important habitat features. In addition to geographic location, there is variation in attributes such as age, aspect, slope and elevation between the Coast and Cascade Range studies. Evidence of these regional differences was previously demonstrated by the different habitat attributes included in the best original VHRDB models. Both vertical diversity and the density of conifer stems 31-90 cm dbh were included in the Coast Range, whereas only vertical diversity was included in the Cascade Range CHDI model. These findings suggest that habitat associations can be confounded by many attributes. Thus, it is evident that the relationships found for a species in the region are not necessarily transferable to other geographic areas within a species' range.

For the remainder of bird species analyzed in this study, there was only nominal improvement or decline in classification efficiency by substituting FHD and SDI for CHDI (i.e. classification within 5 percentage points of CHDI). These findings suggest that while the three diversity indices may be emphasizing different aspects of the vertical canopy, the measures are not different enough for the majority of bird species to discriminate among the features emphasized by them. While many bird species are associated with the canopy, it is likely that many species are able to survive along a gradient of habitat. The gradient of vertical habitat is likely to overlap among the three diversity measures, thus leading to similar classification efficiencies. For the majority of species, any of these diversity indices provides similar classification efficiencies for predicting the probability of occurrence of a species.

My analyses were limited to the use of existing logistic models, with substitution among vertical diversity indices. This was done to directly compare the classification efficiency for the two new diversity indices with the CHDI index. However, these two new indices may correlate differently with the other habitat variables included in the manual stepwise process, compared with how CHDI did. Therefore, in order to confirm the best models for vertically associated bird species it may be more appropriate to rerun the stepwise logistic model technique employed by Garman and Cole (1999), substituting FHD and SDI for CHDI. A potential example would be inclusion of the proportion of stems that are large in addition to FHD. This process could potentially result in a different set of parameters being included in the most parsimonious and biologically meaningful models using FHD and SDI. These new models may improve classification efficiencies compared with the models that merely substituted FHD and SDI for CHDI.

Overall, in studies that survey wildlife populations it is important to recognize that the density or presence of a species doesn't necessarily indicate habitat quality (O'Brien 1990). This can be explained by the concepts of sink and source habitat (Pulliam and Danielson 1991). Conditions in source habitats enable population growth, while sink habitat represents sub-optimal dispersal habitat where a species may survive in the short-term, but persistence over longer periods requires emigration from source habitats. Presence of a species in a given environment may be a function of an induced scarcity of 'good' (source) habitat for that species. This may result in a species seeking out alternate habitat that can only partially meet its needs (sink). For example, if a forest is clear-cut, then a canopy-associated species will be forced to seek temporary refuge in an adjacent un-harvested stand, even if this alternate stand is of a different age or species composition than its' typical habitat. Alternatively, competition for finite resources within and among species may force some individuals to seek out alternate habitat sources. Therefore, caution must generally be used when interpreting the results of wildlife-habitat association models. However, the datasets used in this study were based on studies of breeding adult birds, and as they would be expected to need optimal habitat for reproduction, these bird observations are more likely to be indicators of source habitat than sink habitat.

There was a wide diversity and large number of stands included in this study. In cases where the majority of stands are of similar type, the selection of logistic models may be driven by the predominant stand type or study. With increased sample sizes and diversity of sites, it is less likely that habitat-association models will tend to be misleading. Thus, for this study it is unlikely that habitat associations are artifacts of sample size or predominance of a stand type.

In conclusion, the new FHD and SDI–based wildlife habitat models provided similarly (within five percentage points) valuable information on the importance of vertical habitat for multiple bird species, and improved by > five percentage points for three bird models. Future exploration of these wildlife habitat models is warranted. Especially for bird species with decreased classification efficiencies, it may also be worthwhile to proceed with manual stepwise logistic regression for the new diversity indices. This would ensure that the models in this study are in fact the best available predictive models. It would also be informative to test these logistic models with additional independent sets of stands to see whether species are found in other stands consistent with the habitat parameters included in these habitat-association models.

This study also demonstrates a need for consistency in the types of vegetation data that are collected during studies of wildlife associated with the forest canopy. There were numerous studies in the VHRDB that were excluded from analyses based on a lack of suitable vegetation data. If detailed canopy measurements will not be recorded in a study, I recommend the collection of vegetation attributes that can be substituted to estimate canopy diversity (see equations 4.2-4.4). I selected the stand height to be the height of the tallest tree. Therefore, it would be relatively straightforward and beneficial for wildlife researchers to measure the height of the tallest tree in a stand. In addition, estimates of tree diameters, at least within size classes are needed in ordered to estimate the standard deviation of dbh. It would also be useful to measure the diameter of the widest tree in the stand to have an upper limit of dbh. An estimate of basal area using a basal area factor prism would be relatively quick and easy to collect. With this habitat information, estimates of vertical diversity can be readily calculated, as demonstrated in this study.

Limitations

There are three factors that limit interpretation of this study:

1) An unknown amount of variation exists in the dataset because of differences among observers among studies, geographic locations, sampling effort, habitat sampling methods, and years in which surveys took place. Therefore, caution must be used when interpreting results.

2) FHD and SDI calculations were based on estimates of standard deviation and modeled tree heights, which introduced additional error to results. Given that the same approach was used among diversity indices, the overall trends in the classification efficiencies of the indices should still be meaningful.

3) The mixing of studies with different degrees of accuracy can potentially introduce additional variability into results. It may be worthwhile to further examine studies with tree-level data and studies with class-level diameter and tree height data separately to confirm that the same habitat variables are emerging as important for the various bird species. Alternatively, it may be useful to aggregate stands with tree-level data to the class-level, such that all studies have consistent calculations of FHD and SDI. With the current analyses, it was more likely that the stands with tree-level data would inherently have higher standard deviations of dbh, and thus higher FHD and SDI diversity values. This was because if all trees had different diameters but fell within a given diameter class, then the standard deviation was zero because only the frequency of stems within a given diameter class was recorded. Yet, for a set of trees that had individual dbh measures in addition to their frequency within a diameter class, their standard deviation was greater than zero. Thus, the use of diameter classes potentially reduced estimates of vertical diversity. While this is a limitation of this assessment, it's also a limitation of the Garman and Cole equations using CHDI. Therefore, this additional error should not have interfered with my ability to compare results using the three canopy diversity measures.

Summary

1) This study compared 26 existing habitat models for bird species associated with vertical forest structure, with new models using alternative vertical descriptors that emphasized different canopy features. Two additional indices of vertical canopy diversity, Foliage Height Diversity (FHD) and Simpson's Index of Height Diversity (SDI) were used to determine if existing models using CHDI to predict presence of bird species could be improved on.

2) The proportions of new bird models with higher classification efficiencies than CHDI were 33% and 66% in the Coast Range for FHD and SDI, respectively, and 18% for both new models in the Cascade Range. Improvements in

classification efficiencies among models were generally less than six percentage points.

3) Given the high classification efficiencies of the majority of the models used in this study, future use of the majority of these models is warranted.

4) To confirm that these are the best models for vertically associated bird species, it may be appropriate to rerun the stepwise logistic model technique employed by Garman and Cole (1999), substituting FHD and SDI for CHDI

5) In studies of fauna associated with the canopy where detailed canopy measurements are not recorded, I recommend collecting vegetation attributes that can be used to estimate canopy diversity, such as stand height and basal area.

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COMPARISONS AMONG FIVE CANOPY-COVER ESTIMATING METHODS IN FIVE DOUGLAS-FIR/WESTERN HEMLOCK STRUCTURE TYPES IN THE WESTERN OREGON CASCADES

Abstract

Estimates of forest canopy cover are widely used in forest research and management. Yet there is no single method commonly used to quantify canopy cover. Four ground-based techniques for estimating forest overstory cover —line-intercept, spherical densiometer, moosehorn, and hemispherical photography—and estimates generated using FVS were compared in five different Douglas-fir/western hemlock structure types located in western Oregon. Variability of the methods among plots and among forest-structure types was examined. Among the ground-based methods there was no significant interaction of method and structure type, suggesting their canopy cover estimates did not depend on the structure type in which they were measured. However, comparing cover estimates made with FVS with the ground-based methods revealed differences among methods depended on the forest-structure type in which they were measured. With increasing angle of view, an increase in cover was expected. Differences among ground-based methods were primarily related to differences in angle of view. Although the line-intercept had the narrowest angle of view, the moosehorn provided the most conservative estimates of overstory cover. Variability in cover estimates among methods generally followed expected patterns consistent with cover levels and angles of view. The moosehorn had the highest variability in cover estimates. Cover estimates were least variable in unthinned young stands among all methods. Regression equations were derived to allow conversion among canopy cover estimates developed with the four ground-based methods. These equations can be used by forest managers to transpose MCC values among the four methods examined in this study for similar Douglas-fir/western hemlock forests in the western Oregon Cascades. The FVS calculated cover should not be used as a

substitute for ground-based measures in these forest types given that it was consistently much lower than ground-based estimates. Ultimately, the ground-based method selected for estimating cover should depend on the observers' objectives.

Introduction

Estimates of forest canopy cover are widely used in forest research and management. Current regulations for some wildlife species provide for maintenance of certain levels of canopy cover (e.g., Weiss et al. 1991). In California, the USDA Forest Service (Forest Service) designated a series of Spotted Owl Habitat Areas (SOHAs) managed to sustain suitable owl habitat (Verner et al. 1992). These SOHAs included guidelines requiring mature timber stands with multi-storied canopies of at least 70 percent cover, with greater than 40 percent of the total canopy in trees 21 inches or more in dbh (Verner et al. 1992). Percent canopy cover is often also used as a criterion when classifying stand structure (e.g., Azuma and Hanson 2002, Widsom et al. 2000). When monitoring stream temperatures canopy cover is used as a surrogate for shade (OWEB 1999). In addition, cover estimates are used to measure penetration of light to the understory (e.g., Canham et al. 1990, Lieffers et al. 1999, Englund et al. 2000). Thus, quantifying cover is an important management tool.

There are a wide variety of ground-based techniques used to estimate overstory tree cover. Commonly used methods include ocular estimates, the moosehorn (Robinson 1947), spherical densiometers (concave and convex; Lemmon 1956), the densitometer (Stumpf 1993), hemispherical photography (Evans and Coombe 1959), point counts, and the line-intercept method (Canfield 1941; O'Brien 1989). Less commonly cited methods include stem and crown mapping, the vertical tube (Johansson 1985), and gimbal sight (Walters and Soos 1962).

Multiple terms have been used to describe the measures of overstory tree crowns estimated using these various canopy measurement methods. I followed Bunnel et al.'s (1985, p. 181) definition of crown completeness: "...the proportion of the sky obliterated by tree crowns within a defined angle (or determined with a described instrument) from a single point. It combines reduction in cover resulting from both the absence of tree crowns and from holes within tree crowns". Mean crown completeness (MCC) is the stand-level crown completeness. As the angle of MCC reduces to zero, only measuring the area directly overhead, MCC becomes equivalent to vertical canopy cover. Measurement of MCC is dependent on the angle of view, and angle of view varies among the methods of measurement. The larger the angle of view the higher the estimate of MCC will be. This occurs because canopy gaps visually "close" as the angle of view is lowered from the zenith towards the horizon (Fig. 6.1). Devices with large viewing angles tend to over-measure canopy cover because they are less likely to count holes without canopy (Kirchoff and Schoen 1987; Fig. 5.1 Bunnell and Vales 1990). Thus, as angle is reduced, more accurate, less-biased estimates most representative of vertical canopy cover are achieved (Bunnell and Vales 1990). The line-intercept method, with theoretical zero width, is the least biased most accurate estimator of vertical canopy cover. However, the line-intercept method includes all area within the outline of a crown as cover, regardless of presence of small gaps inside the outline of the crown. Therefore, it is a special case of crown completeness whereby holes in individual tree crowns are ignored.

There is no particular method mandated for quantification of cover in forest research and management activities. There can be a great degree of variability among measurement methods used, which can lead to high variability in the estimates of percent cover derived. This discrepancy among methods can have serious management implications. Two examples illustrate potential consequences: 1) SOHAs where minimum cover of 70% is required and 2) Pacific Northwest riparian areas mandated to have a minimum percent cover to prevent elevated summer stream temperatures (Belt et al. 1992). There is the potential for managers in these situations to select a method with known bias towards higher cover estimates, in order to attain targeted cover levels. Meanwhile the 'true' target value

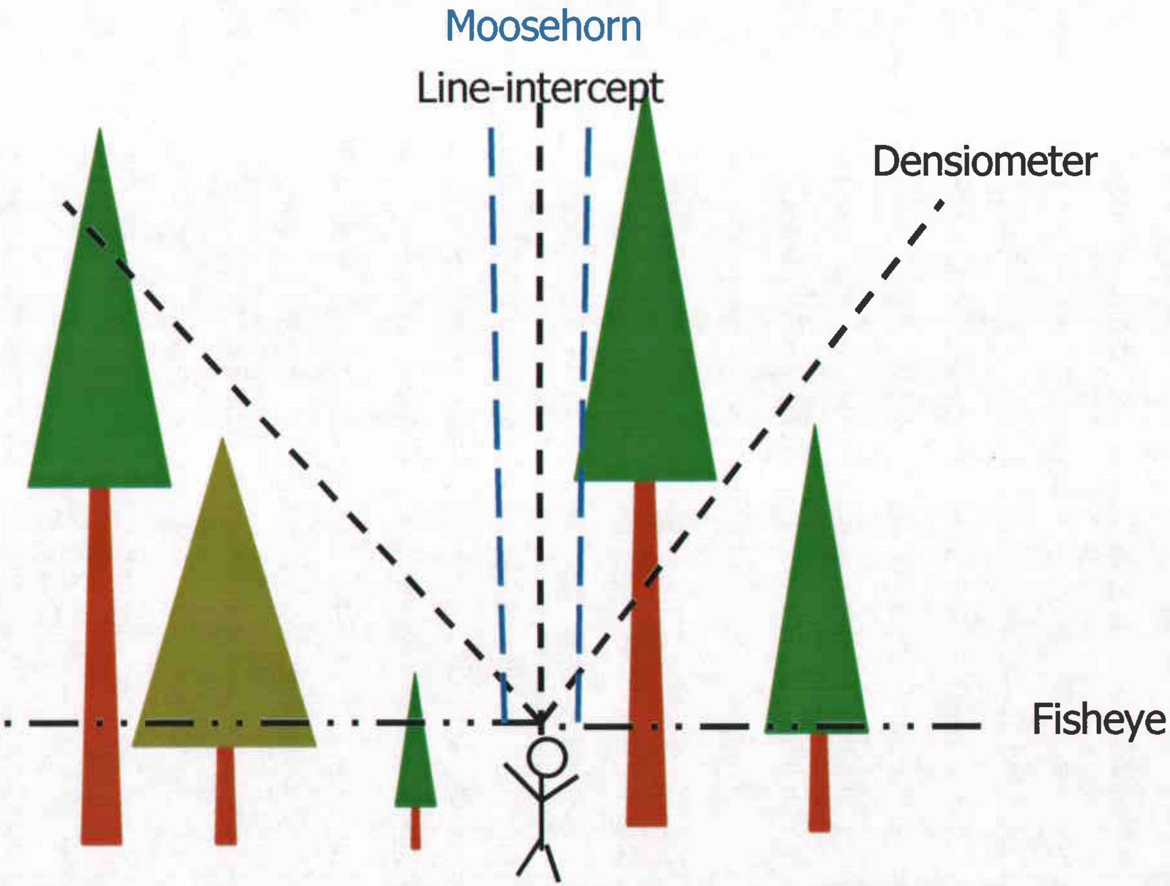

Fig. 6.1. Comparisons of effects of angle of view for four methods for estimating canopy cover on the amount of cover estimated by a given technique. Different methods will provide different estimates of percent cover in this illustration.

that is required for habitat or temperature purposes may not be reached, leading to loss of the needed habitat. Thus, improved understanding of the relationship among estimates of cover made by various techniques is critical to ensure that forest management guidelines are being adequately met.

Multiple studies have compared methods of measuring MCC and canopy cover. Bunnell and Vales (1990) compared ocular estimates, the gimbal sight, spherical densiometers, the moosehorn, and hemispherical photography methods. The vertical tube and densiometer were compared by Ganey and Block (1994). Cook et al. (1995) compared the convex and concave spherical densiometers. Fisheye, densiometer and LAI-2000 were used to estimate light under broadleaf canopies by Comeau et al. (1998). Laymon (1988) compared an inverted monocular, the sighting tube, spherical densiometer, 35 mm camera with a 28 mm lens, and ocular estimates. Coates (1995) compared canopy closure estimates obtained using the convex spherical densiometer, moosehorn, Cover extension of the Stand Prognosis model, and light transmittance using a Sunfleck ceptometer. Applegate (2000) compared the moosehorn and GRS ™ densitometer with a variant of the FVS model for estimating canopy cover. Differences between digital and film fisheye photographs also have been examined (Englund et al. 2000; Frazer et al. 2001; Hale and Edwards 2002). Many of these studies have suggested that cover estimates differ among techniques. I am unaware of any previous studies comparing the line-intercept method with other methods for estimating canopy cover and MCC. Given that the line-intercept method has the narrowest vertical projection among methods, further research is warranted to better evaluate the relative effectiveness of the line-intercept method compared to other measurement techniques across a variety of seral stages.

I hypothesize that cover estimates will differ among canopy measurement methods. As demonstrated in previous studies, I expect methods with wider angles of view will tend to overestimate canopy cover. Methods with similar angles of view should provide similar overstory cover estimates. Further, I expect differences among the methods within different stand-structure types. In stand-structure types with a very high percentage of canopy cover, cover values obtained using the various methods will be more similar than in stands with moderate cover levels.

The main objective of this study was to compare canopy cover estimates of the line-intercept method with MCC estimates from three other cover measurement techniques commonly used. The line-intercept method was compared with hemispherical photography (fisheye), the moosehorn, and the convex spherical densiometer. A second objective was to compare these four ground-based cover-estimating methods with estimates of canopy cover generated by the Forest Vegetation Simulator overlap-corrected cover equations. A final objective was to compare the variability in the estimates of cover obtained by the techniques among individual stands and among forest structure types. The cover-estimating methods were compared in five *Pseudotsuga menziesii* (Mirb.) Franco / *Tsuga heterophylla* (Raf.) Sarg. (Douglas-fir/western hemlock) structure types in the western Oregon Cascade Range.

Methods

Study Area and Population of Interest

The study was conducted in 52 stands located in the Mt. Hood and Willamette National Forests of the Oregon Western Cascades during June – September 2001 (Fig. 6.2). Plots were located in the *Tsuga heterophylla* forest zone (Franklin and Dyrness 1973) and represented a range of Douglas-fir/western hemlock stands. Stand-structure types included: young stands (38-52 years old) that were unthinned, lightly thinned, heavily thinned; mature (120-180 years); and old-growth (> 250 years).

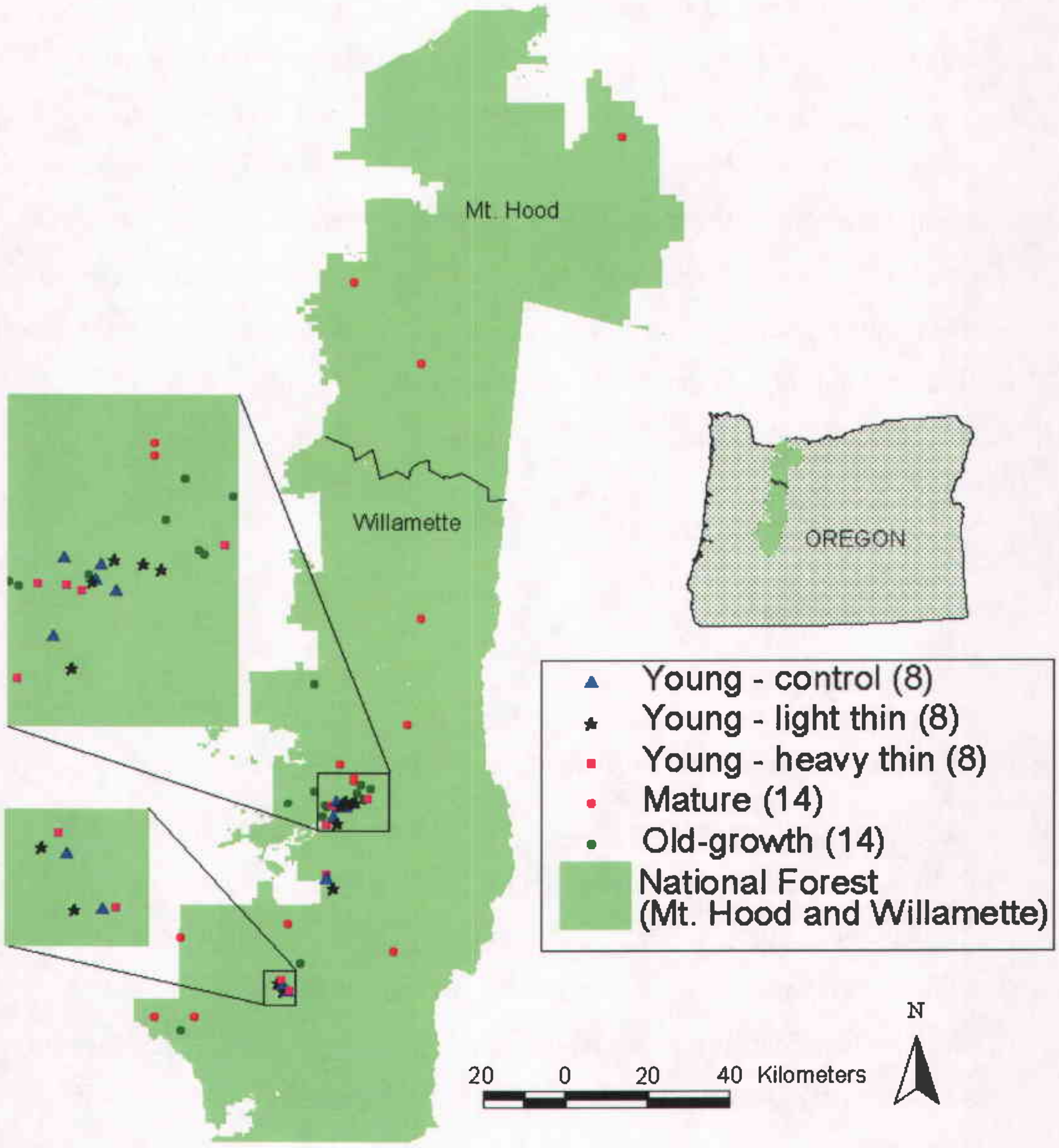

Fig. 6.2. Locations of the 52 stands located in the Willamette and Mt. Hood National Forests used in this study.

Young stands

Eight stands were sampled for each of the three types of young stands, for a total of 24 stands (Table 6.1). Half of these stands were from the Young Stand Thinning Diversity Study (YSTDS; CCEM 1996): control (unthinned, n=4), light thin (n=4), and heavy thin (n=4). There were three Uneven-Aged Management Project (UAM; CCEM 1999) treatments sampled in this study: control (no thin, n=4), multi-storied stand (which I classified as light thin based on relative density, n=4), and single-tree selection (which I classified as heavy thin based on relative density, n=4). I randomly selected five of the subplots from each of the stands for this study, with the exception of one stand where only five subplots were available (UA5, see Table 6.1).

Mature and old-growth stands

The mature and old-growth stand-structure types each had 14 replicates in this study (Table 6.2). The plots were comprised of Forest Service Region 6 Current Vegetation Survey plots (CVS; CVS 2002) and Permanent Sample Plots (PSP; Dyrness and Acker 1999). CVS plots were 1-ha circular fixed-area plots systematically located on a 1.7-mile grid system (3.4 miles in designated wilderness areas). There were five systematically located subplots in each plot (Fig. 6.3). PSP plots were a group of 1-ha square stem-mapped plots dominated by Douglas-fir. The PSP plots were located in the region around the HJ Andrews Experimental Forest (44.2°N, 122.2°W) to represent different community types of mature and old-growth Douglas-fir dominated forests. The mature stands in this study were randomly selected from 35 PSP and CVS plots that were between the ages of 120-180 years. The old-growth stands were randomly selected from 73 CVS and PSP stands that were > 250 years. I used the five-subplot arrangement established by the CVS program for all the PSP and CVS plots used in this study.

Table 6.1. Description of the young stands used in this study.

Plot ID[1]	Thinning treatment[2,3]	Elevation (m)	Subplots (n)	Stand size (ha)	Stand age[4]
Unthinned					
TAC1	None	805	23	30	49
TAC13	None	634	18	51	46
TAC5	None	902	25	52.6	51
TAC9	None	878	23	30.8	48
UA1	None	853	9	11.7	45
UA13	None	608	6	8.2	42
UA5	None	577	5	9.4	42
UA9	None	911	8	8	38
Light thin					
TAC11	321 tph	902	22	32	48
TAC15	247 tph	646	15	22.3	42
TAC3	303 tph	610	26	37.2	47
TAC7	375 tph	524	27	37.2	52
UA12	RD 30	731	7	11.6	41
UA16	RD 30	577	7	10.9	46
UA4	RD 30	760	8	16.1	42
UA8	RD 30	608	7	10.4	46
Heavy thin					
TAC10	145 tph	905	15	20.2	45
TAC14	114 tph	652	13	19	44
TAC2	126 tph	792	13	19.4	49
TAC6	200 tph	658	24	34.8	51
UA11	RD 20	610	10	12.8	41
UA15	RD 20	850	7	14.3	39
UA3	RD 20	850	7	18.4	45
UA7	RD 20	730	12	17.9	44

[1]Plot IDs that begin with TAC are Young Stand Thinning Diversity Study (CCEM 1996) stands, and plot IDs that begin with UA are Uneven-Aged Management Project (CCEM 1999) stands.

[2] TAC harvest treatments occurred between 1994 and 1996. UA stands harvest treatments occurred between 1999 and 2000.

[3] RD is relative density (Davis and Johnson 1987).

Table 6.2. Details of mature and old-growth 1-ha stands used in this study.

Plot ID[1]	Elevation (m)	Stand age[2]
Mature		
RS26	720	150
RS35	460	130
1080116	366	141
1086120	549	174
1110156	884	176
2080122	884	139
2085152	945	122
2087136	914	125
2098146	914	127
2099144	975	169
2102154	1067	177
2129156	1097	132
2135146	610	159
2146186	1036	121
Old-growth		
RS1	510	460
RS2	520	460
RS3	950	460
RS20	700	450
RS21	1190	450
RS28	1060	459
RS29	800	450
RS30	870	450
2097140	792	394
2105140	1036	357
1096136	1189	508
2079120	427	337
2084138	1097	525
1096144	701	331

[1]Plot IDs that are eight digit numbers are Forest Service Region 6 Current Vegetation Survey plots (CVS 2002) and plot IDs beginning with RS are Permanent Sample Plots (Dyrness and Acker 1999).
[2]Stand ages were estimates provided by CVS and Permanent Sample Plot data.

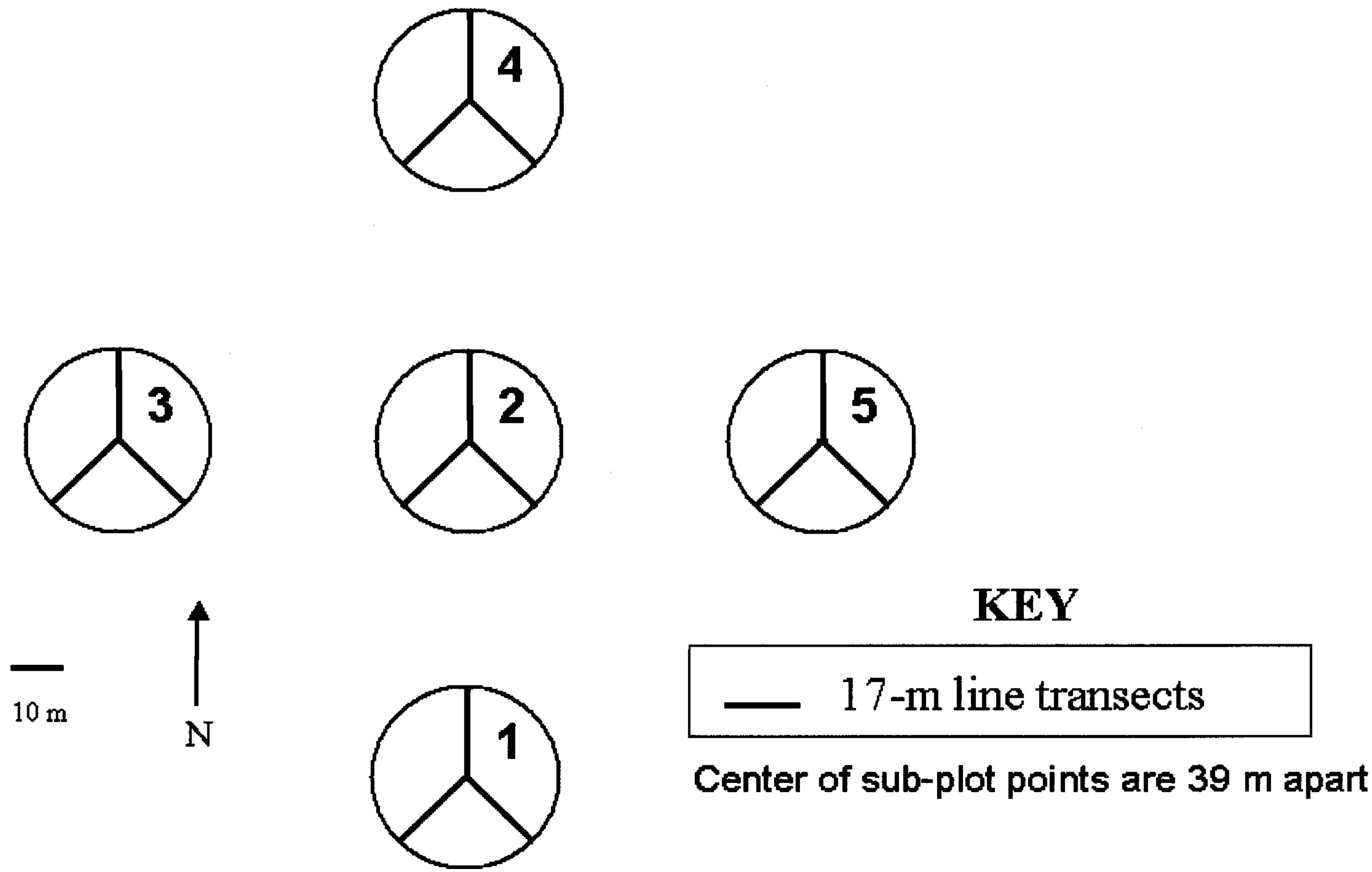

Fig. 6.3. Lay-out of the subplots for the mature and old-growth stands in this study.

Techniques for Estimating Cover Used in This Study

Line-intercept

The line-intercept method measures canopy cover by recording horizontal distance covered by live crown along a line-transect. It assumes that all area within the outline of a crown is cover. This technique is considered one of the most accurate methods because it measures intercepts on the ground, rather than ocularly estimating them from aerial photos (O'Brien 1989).

Canopy cover data were collected for individual tree species in a maximum of three vertical canopy layers. In each stand, trees were assigned to one of three canopy layers, with discrete layers differing by a minimum of 5 m in mean height. However, actual heights varied among stands, as canopy layers were relative to conditions within a stand. Intercept measures were taken along the length of 3 17-m long horizontal transects in each subplot. Canopy cover was measured for all live trees and shrubs $\geq$ 1.4 m tall. Shrub species were included because the other three methods could not distinguish between taller shrub and overstory tree cover. For every species and canopy layer, the distance along each transect line where the crown first intercepted the line to the point where the crown (or multiple contiguous crowns of the same species) last intercepted the line was recorded (to the nearest dm), using a clinometer to verify crown interception directly overhead. The proportion of transect lengths that were intercepted by crowns was the ground-estimated canopy cover. This cover was measured for individual canopy layers and then cover for the three layers was combined to provide an estimate of total overstory cover. Cover by species by layer was vertically collapsed to calculate total cover so cover could not exceed 100%. The mean of the 15 line-intercept transects per stand provided an estimate of the stand-level canopy cover.

Moosehorn

The moosehorn measures crown closure and has been shown to simply quantify MCC (Demarchi and Bunnell 1993). It employs a square grid similar to the spherical densiometer. With the aid of an angled mirror at 45 degrees, canopy cover is reflected through an aperture in the side of the instrument, through which the observer records the amount of canopy cover contained within the dots or cross-hairs of squares (Robinson 1947, Bonnor 1967). This technique measures both individual crown holes and gaps between crowns. The angle of view incorporated with this technique is up to 5.1 degrees from the vertical (Jennings et al. 1999), as not all moosehorns have a standardized angle of view.

The moosehorn I used in this experiment viewed an average angle of 6.3 degrees from the vertical. It was modified to remain level when measuring canopy cover. The grid consisted of 25 squares (maximum 36 cross-hair intersections). The number of cross-hairs intersected by cover divided by 36 provided an estimate of crown completeness. There were 65 moosehorn measurements collected in each stand. The mean of these measurements was the MCC of the stand.

Convex spherical densiometer

The convex spherical densiometer is comprised of a convex spherical shaped mirror engraved with a graticule (Lemmon 1956). The observer assumes each square has four evenly-spaced dots, and counts how many of these dots intercept with the reflection of the canopy while the densiometer is held horizontally. This process is repeated for each of the four cardinal directions at each measuring location (Lemmon 1956, Jennings et al. 1999). The curved reflecting surface of the densiometer results in both lateral and overhead position readings, which leads to overlap in canopy cover measurements recorded in each of the four directions (Strickler 1959, Cade 1997). Thus, a modification of the original densiometer technique removes overlap from measurements by estimating from 17 points in a wedge-shaped area of the densiometer grid for each of the four directional measurements (Strickler 1959). Use of the wedge-shaped area is not biased by point duplication, and results in an easier to maintain eye position. This modified technique has been used with success (e.g., Cook et al. 1995).

I used the convex spherical densiometer with the modified method proposed by Strickler (1959). The densiometer was placed on a tripod at approximately 1.4 m above the forest floor in order to ensure consistent level positioning. To calculate crown completeness for a given point, I summed the points intersected by cover for each of the four cardinal directions and divided by 68 (maximum possible intersected points). Thirty-five densiometer measures were collected for each stand and averaged to estimate MCC.

Hemispherical photography (Fisheye)

Hemispherical photography is a common means of quantifying plant cover and sub-canopy radiation regimes (Canham et al. 1990, Demarchi and Bunnell 1993, Englund 2000). It provides a wide-angle view of the forest canopy from a given site, using a 180-degree lens. A limitation with hemispherical photography is that its resolution varies depending on sunlight, cloud cover, and wind. This is because it requires good contrast between the canopy and the sky (Jennings et al. 1999). MCC is calculated from digitization of the developed film negatives using specialized software.

I used an AE-1 Canon camera with a Canon fisheye lens (7.5 mm focal length) to estimate MCC. Hemispherical photographs were taken approximately 1.4 m above the forest floor, with the top of the photo oriented towards True North. The camera was mounted on a tripod with levels to ensure horizontal positioning. The fisheye lens used in this camera had a built-in filter, so a hand-held lightmeter was needed to determine appropriate shutter speeds. I used Kodak Tmax-100 print black and white film for all pictures. At each photo point, a photograph was taken at the shutter speed suggested by the hand-held light meter, and then an additional photo at one shutter speed higher was taken. Hemispherical photos were taken under a variety of sky conditions that occurred throughout the summer, including both overcast and bright sunny days. I felt that only taking the photos during ideal overcast sky or dawn conditions would not be representative of the potential use of this method by many forest managers. It was of more interest to see how the method performed regardless of given sky conditions in order to allow for more widespread future use of this method without restriction of time of day or overstory sky conditions. A total of 20 photo points were measured for each stand.

Canopy photographs were analyzed using the CANOPY (Rich 1989) software program. Data were summarized using corrected indirect sun factor (ISF), the proportion of indirect radiation received in an open site (Rich 1989). The corrected ISF corrected for angle of incidence and for the different amounts of sky the pixels represented depending on proximity to horizon or zenith. A single researcher analyzed all photos. The analysis was somewhat subjective, as depending on the presence and positioning of sun, boles and leaves could appear to be sky. Thus, a toggle function allowed manual adjustment of the threshold values that differentiated canopy from sky. To assure consistent analysis among plots, I followed a protocol of recalculating and comparing ISF estimates from several previously analyzed photos each time I analyzed new fisheye photos. The corrected ISF calculated by CANOPY was subtracted from 100 to obtain an estimate of crown completeness. The mean of all these estimates provided a measure of MCC for each stand.

Forest Vegetation Simulator (FVS) equations

The FVS is an individual tree, distance-independent growth and yield model (Donnelly and Johnson 1997). FVS can model a wide variety of forest types and stand structures. It is commonly used by the Forest Service as a forest management tool to compare alternative treatments. Variants of the simulator are specific to geographic areas. The Pacific Northwest Regional Variant models stand level percent canopy cover by summing individual tree crown areas, using tree species crown radii formulae specific to the region (Crookston and Stage 1999). Fitting a standard equation to measurements made on CVS trees generated the crown radii formulae. The original FVS canopy cover calculations did not account for overlap among tree crowns, and thus cover estimates could exceed 100%. However, Crookston and Stage (1999) corrected for crown overlap with creation of an equation that accounts for the overlap by assuming random distribution of canopy elements:

$$C = 100\,[1 - \exp(-.01*C')] \qquad \text{(Eqn. 6.1)}$$

Where:

C = percent canopy cover that accounts for overlap
C' = Equation 3.1

This modified equation provides cover estimates that are $\leq$ 100%.

I calculated overlap-corrected cover using the unpublished FVS Region 6 Variant crown radii formulae for each stand. The formulae used live tree species and dbh information for all subplots in each of the stands. Individual tree dbh and species information that was previously recorded in each of the study stands was used. The crown radii were input into the FVS cover equations based on the stand area in which the tree data were collected. However, in the PSP stands trees between 5-15 cm were only measured on a subset of the area, and this area could not be determined. Therefore, these tree sizes were omitted when calculating FVS percent cover for the PSP stands.

Study Design

Canopy measurements for the four ground-based methods were collected for five subplots in each of the 52 stands. In each subplot, canopy measurements were recorded along 3 17-m slope-corrected line transects radiating out from the center of each subplot (azimuth 0°, 120° and 240°; Fig. 6.4). The numbers and locations of

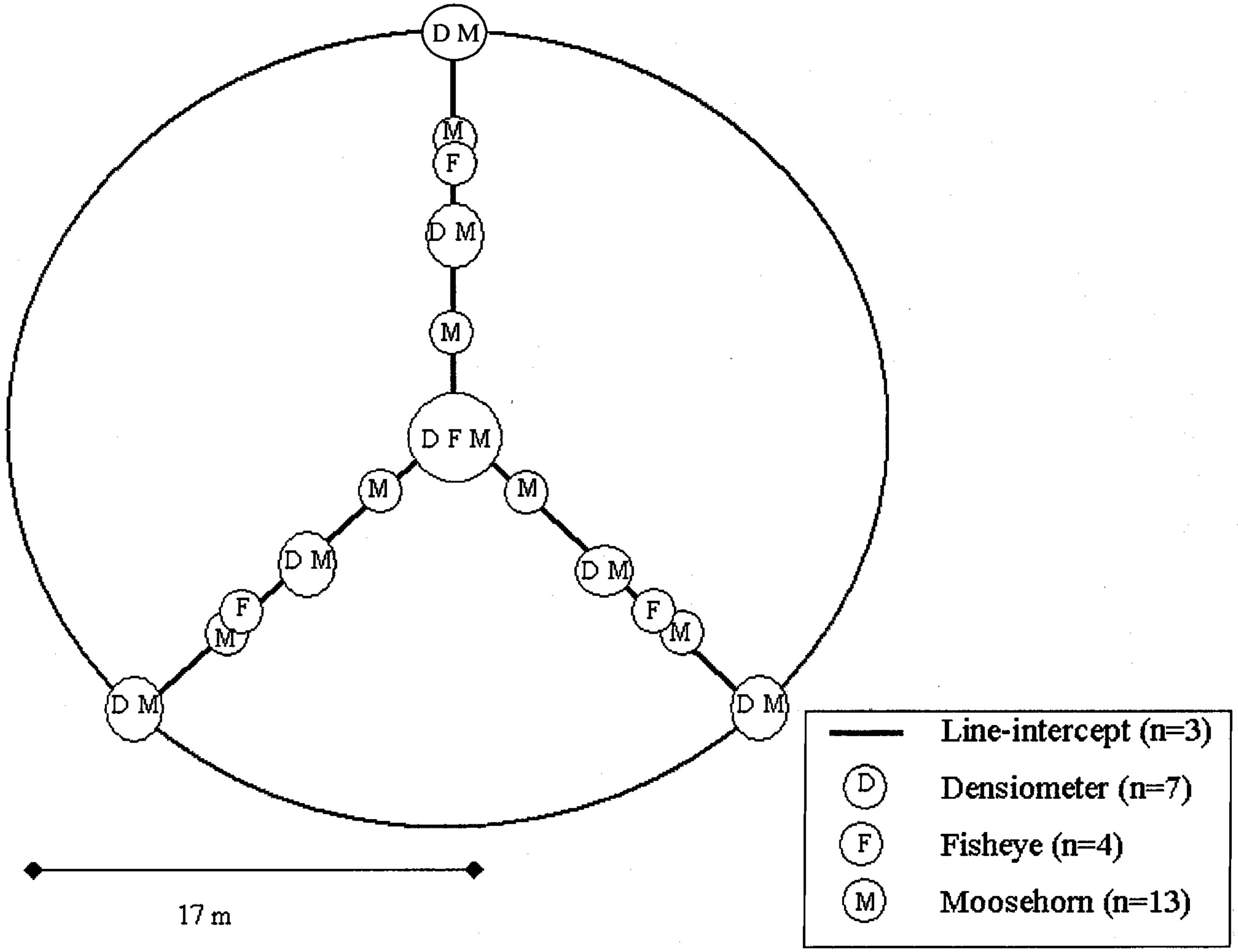

Fig. 6.4. Locations of measurements for each of the four ground-based techniques compared in this study within individual 0.09-ha subplots.

canopy measurements differed for the four methods being compared.

It was important to replicate previously described techniques and sample sizes for each of the methods. This ensured that the results were relevant to forest managers and easy to replicate in future field studies. It was also important to have higher numbers of measures for methods with narrower angles of view in order to capture a similar total area of crown closure within each stand. Previous use of fisheye photography suggested a minimum of 6-10 photographs per stand should be measured (e.g. Canham et al. 1990; Easter and Spies 1994), and I took photos at 20 photo points per stand. Originally, Robinson (1947) recommended 20 or 40 measurements should be taken with the moosehorn on a quarter-acre plot, and suggested, in a multi-tiered canopy, that multiple canopy layers should never be combined. However, the moosehorn has since been used in multi-layered stands with previous studies taking a range of measurements including 10, 16 and 50 per plot (e.g. Garrison 1949, Cook 1995, North et al. 1999), while Bonnor (1967) suggested 100 measurements were required with the Hilborn moosehorn to obtain +/- 5% canopy cover with 95% confidence. Previous studies using the densiometer have ranged from 4 measures per subplot to 30 measures per stand (e.g. Lemmon 1956, Cook 1995, Vales et al. 1988, Englund et al. 2000). The Forest Service Forest Inventory and Analysis program used 15 17-m line transects to collect line-intercept canopy data during the 1995-1997 inventory (Azuma and Hanson 2002).

In each subplot, replicate measures for the same technique were located to minimize overlap (see Fig. 6.4). Densiometer measurements were recorded at the center of each subplot, and at slope-corrected distances of 8.5 and 17 m along each of the three transects. Moosehorn measurements were recorded at the center of the subplot, and at 4.25-meter slope-corrected horizontal intervals along each of the three transects. With the widest angle of view, the fisheye required the fewest points. Photo-points were located at the center of the subplot, and at distances of 11.3 m along each transect. Point locations for measurements along individual transects were consistent across the five subplots for each method.

Two observers collected measurements. To ensure consistency, at the beginning of the study, observers practiced recording cover estimates using all techniques except the hemispherical photography. Observers took turns measuring cover with the various methods to minimize potential bias associated with inter-observer variability.

Analysis of Findings

This study was a split-plot design with stand-structure type as the whole-plot level treatment and the technique for estimating cover as the sub-plot treatment. The split plot approach was appropriate because the multiple canopy method measures were all taken in the same stand. The model is described by the equation:

$$Y_{ijk} = \mu + \alpha_i + d_{jk} + \beta_j + (\alpha\beta)_{ij} + e_{ijk} \qquad \text{(Eqn. 6.2)}$$

Where:

Y_{ijk} is the percent canopy cover for a given stand and method
μ is the overall mean
α_i is the fixed effect of stand-structure type (i=1,2,3, 4, 5)
d_{jk} is the experimental error for the whole plot
βj is the fixed effect of method (j=1,2,3,4,5(for FVS comparisons))
$(\alpha\beta)_{ij}$ is the interaction effect between method and stand-structure type
e_{ijk} is the experimental error for the subplot level

Differences between canopy measures using the different techniques within stands and among different stand-structure types were statistically tested. These tests were first conducted for the four ground-based methods, in order to explore differences solely among ground-based methods that differed based on angle of view. The tests were then re-run with FVS cover estimates included, to test for differences between modeled cover and ground-based method estimated cover. Mixed-effects ANOVAs (PROC MIXED, SAS Institute 1999) were used to test for significant differences among methods, among stand-structure types, and for interactions between method and stand-structure type. For significant (α=0.05) ANOVA results, paired contrasts (using Scheffe family-wise correction and Bonferroni multipliers where appropriate) were used to explore significant differences in MCC estimates among methods. The line-intercept was considered the least-biased method and was used as the basis for comparisons. Comparisons among the other methods, however, were also performed. For each different pairs of methods, x was regressed on y to translate relationships among the methods:

$$Y=\beta_o + \beta_1 X_j \qquad \text{(Eqn. 6.3)}$$

Where:

Y_i is the percent canopy cover of a given method for estimating cover,
β_o is the coefficient of the intercept,
β_1 is the coefficient for the canopy cover estimating method being transposed, and
X_j is the percent canopy of the cover estimating method being transposed.

I primarily used the line-intercept and moosehorn methods as the response variable as they were assumed to be the least-biased estimators of cover, and thus it would be of most interest to translate measurements from the other methods into these estimates.

Analysis of Variability

The stand-level standard deviations for each of the cover-estimating methods were calculated to assess the variability of the cover estimates made by each of the methods. The differences in standard deviations were visually compared among individual stands for the ground-based cover-estimating methods. Standard deviations were then aggregated to the level of Douglas-fir/western hemlock structure type to compare the variability of all five cover-estimating methods among varying levels of cover.

Results

Analysis of residuals and normal probability plots revealed non-constant variance and lack of normality for all measures. To meet the assumptions of constant variance and normality, a logit transformation of percent canopy cover was performed (Shapiro-wilk $W=0.992$, $p=0.37$).

Comparison of Ground-Based Methods

The split-plot ANOVA design demonstrated that there was no significant interaction between method and stand-structure type ($F_{12, 188}=1.14$, $p=0.33$). Therefore, only the main effects of stand-structure type and method were examined. Mean percent cover values differed among stand-structure types ($F_{4, 188}=62.55$, $p<0.0001$) and among methods ($F_{3, 188}=35.78$, $p<0.0001$). In this paper I will focus on the specific differences among the ground-based methods, because the differences in MCC among stand-structure types were expected and were not of interest in this study.

Multiple linear comparisons of cover estimated by the various methods demonstrated differences among most methods (Table 6.3, Figs. 6.5 and 6.6). The densiometer and fisheye did not significantly differ ($\alpha=0.05$, Scheffe-adjusted $p=0.59$), nor did the fisheye and line-intercept methods ($\alpha=0.05$, Scheffe-adjusted $p=0.30$). However, based on visual comparison of the fisheye and line-intercept (see Figs. 6.5 and 6.6) it appears that, at reduced cover levels fisheye cover is greater than line-intercept cover. The remaining pair-wise comparisons of cover estimates were significant. The moosehorn was generally the most conservative estimator of cover, while the densiometer and fisheye generally had higher cover estimates.

Linear regression coefficients and equations were derived to describe the differences among the methods (Table 6.4; Eqn. 6.3). Regression relationships among the methods demonstrated the consistent bias towards overestimation of

Table 6.3. Differences of least square means for logit-transformed cover estimates among ground-based methods compared in this study. Significant pair-wise comparisons are highlighted in bold.

Methods compared	Difference Estimate	SE	t value	Scheffe–adjusted p-value
Densiometer vs fisheye	0.1556	0.11	1.38	0.59
Densiometer vs line-intercept	0.3726	0.11	3.31	**0.0135**
Densiometer vs moosehorn	1.0771	0.11	9.58	**<0.0001**
Fisheye vs line-intercept	0.2169	0.11	1.93	0.29
Fisheye vs moosehorn	0.9214	0.11	8.19	**<0.0001**
Line-intercept vs moosehorn	0.7045	0.11	6.26	**<0.0001**

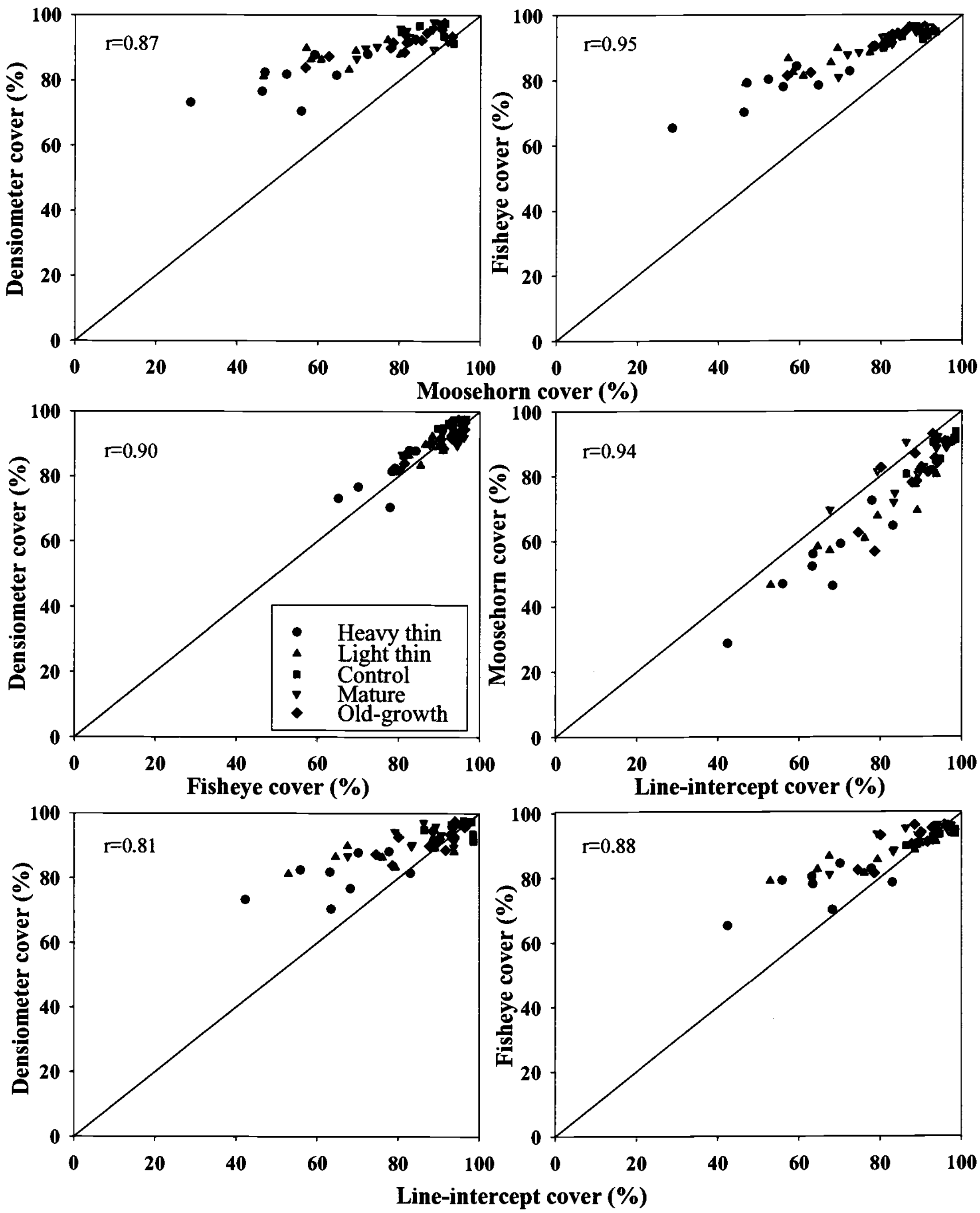

Fig 6.5. Comparisons of the four ground-based canopy estimation methods in this study. There were no significant differences among forest-structure types among the methods. The r-values are the Pearson correlation coefficients between each set of two methods.

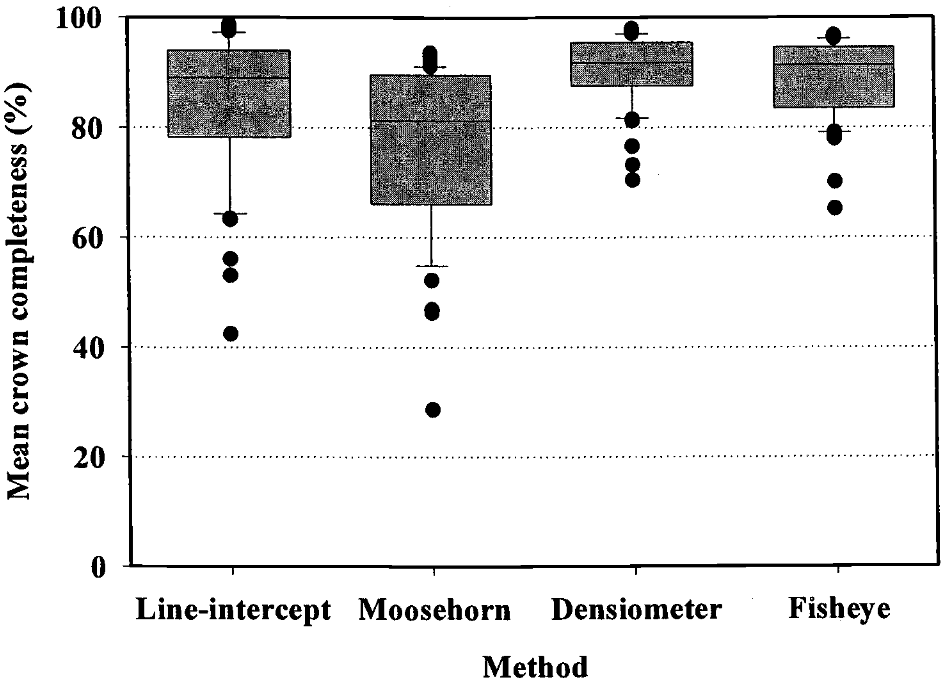

Fig. 6.6. Box-whisker plots comparing four methods for estimating mean crown completeness of five Douglas-fir/western hemlock stand-structure types. Stand structure types are described in Tables 1 and 2. Each box represents the interquartile range (25th-75th percentiles), with the inside showing the median, and whiskers showing the 5th and 95th percentiles. Observed data were from stands throughout the west-central Oregon Cascades at elevations ranging from 350-1200 m (see Tables 1 and 2). Each of the cover methods was measured in 52 stands.

Table 6.4. Regression equation coefficient estimates (SE) for the models that describe each of the combinations of cover-estimate techniques. These regression coefficients can be used in Equation. 4 to transpose percent cover among methods.

Response variable	Explanatory variable	Intercept	Slope estimate	Adj. R^2	Explanatory variable valid range
Line-intercept cover	Moosehorn cover	22.94 (3.34)	0.81 (0.04)	0.87	Moosehorn cover = 29-94%
Line-intercept cover	Densiometer cover	-69.77 (15.89)	1.71 (0.17)	0.65	Densiometer cover = 70-98%
Line-intercept cover	Fisheye cover	-60.32 (11.10)	1.62 (0.12)	0.77	Fisheye cover = 65-97%
Moosehorn cover	Fisheye cover	-104.41 (8.78)	2.03 (0.10)	0.89	Fisheye cover = 65-97%
Moosehorn cover	Densiometer cover	-116.41 (15.31)	2.13 (0.17)	0.76	Densiometer cover = 70-98%
Fisheye cover	Densiometer cover	-3.58 (6.39)	1.03 (0.07)	0.81	Densiometer cover = 70-98%

cover by the fisheye and densiometer, with reduced line-intercept cover, and the moosehorn having the overall lowest estimates of MCC.

Ground-Based Methods Compared with FVS

Cover calculations made with FVS corrected and uncorrected calculations greatly differed. Without overlap correction FVS calculated cover ranged from 14 to 265%. After correcting for overlap among crowns, FVS cover decreased to between 13 and 93%.

The split-plot ANOVA design demonstrated that cover readings estimated by a given technique were dependent on the stand-structure type and vice versa for at least one of the five methods ($F_{16, 235}=3.46$, $p<0.0001$). Therefore, I compared ground-based methods with FVS modeled cover within each stand-structure type.

In general, cover calculated using FVS was consistently much lower than estimates from the ground-based methods within each forest-structure type (Tables 6.5-6.6; Fig. 6.7). FVS cover estimates were significantly lower than densiometer estimates among all forest-structure types. Fisheye and FVS estimates were significantly different except in young unthinned stands. Aside from light-thin stands, line-intercept cover estimates were significantly higher than FVS estimates. Compared with the moosehorn, FVS cover estimates were only significantly lower in mature and old-growth stands. FVS cover calculations were consistently much lower than cover estimates for the ground-based methods within each forest-structure type (see tables 6.5-6.6; Fig. 6.7).

Variability Among Stands and Structure Types

As expected, with increasing area of cover measured, there was generally a decrease in the variability of ground-based cover measurements for individual stands (see Table 6.6). With its narrow angle of view, the moosehorn generally had the highest within stand variability. The densiometer and fisheye, with their large areas of view, had the lowest within stand variability.

Table 6.5. Differences of least square means among the logit-transformed FVS-modeled cover and the four ground-based method cover estimates.

Stand structure type	Methods compared	Difference estimate	SE	t-value	Bonferroni–adjusted p-value
Control	**FVS vs densiometer**	-1.0264	0.28	-3.67	**0.0012**
	FVS vs fisheye	-0.6683	0.28	-2.39	0.0712
	FVS vs line-intercept	-1.23	0.28	-4.39	**<0.0001**
	FVS vs moosehorn	-0.1494	0.28	-0.53	1.0
Light thin	**FVS vs densiometer**	-1.2293	0.28	-4.39	**<0.0001**
	FVS vs fisheye	-1.1084	0.28	-3.96	**<0.0001**
	FVS vs line-intercept	-0.6566	0.28	-2.35	0.0792
	FVS vs moosehorn	0.04812	0.28	0.17	1.0
Heavy thin	**FVS vs densiometer**	-1.583	0.28	-5.65	**<0.0001**
	FVS vs fisheye	-1.397	0.28	-4.99	**<0.0001**
	FVS vs line-intercept	-0.8399	0.28	-3.00	**0.012**
	FVS vs moosehorn	-0.2922	0.28	-1.04	1.0
Mature	**FVS vs densiometer**	-2.1054	0.21	-9.95	**<0.0001**
	FVS vs fisheye	-1.9427	0.21	-9.18	**<0.0001**
	FVS vs line-intercept	-1.6669	0.21	-7.88	**<0.0001**
	FVS vs moosehorn	-1.0669	0.21	-5.04	**<0.0001**
Old-growth	**FVS vs densiometer**	-2.4187	0.21	11.43	**<0.0001**
	FVS vs fisheye	-2.4682	0.21	-11.66	**<0.0001**
	FVS vs line-intercept	-2.1066	0.21	-9.95	**<0.0001**
	FVS vs moosehorn	-1.5173	0.21	-7.17	**<0.0001**

Table 6.6. Percent cover estimated by each of the five methods in each of the 52 stands compared in this study. SD is the within stand standard deviation.

Plot ID[1]	Line-intercept (SD)	Moosehorn (SD)	Densiometer (SD)	Fisheye (SD)	FVS
Unthinned					
TAC1	98.55 (2.36)	91.07 (14.06)	93.53 (3.88)	93.50 (2.07)	89.31
TAC13	93.17(10.86)	90.34 (15.51)	96.30 (4.12)	92.45 (4.53)	87.85
TAC5	98.65 (4.97)	93.55 (5.08)	91.30 (2.86)	94.76 (2.06)	88.52
TAC9	97.51(8.16)	90.38 (12.03)	97.35 (1.88)	95.03 (2.43)	89.33
UA1	98.23 (4.61)	91.45 (14.10)	97.40 (2.79)	93.71 (4.19)	88.58
UA13	86.55 (14.20)	80.60 (26.79)	94.79 (4.95)	89.77 (4.51)	77.91
UA5	96.54 (5.14)	90.64 (17.72)	95.55 (3.70)	95.93 (1.52)	86.71
UA9	94.84 (5.18)	85.13 (20.72)	96.68 (3.61)	93.24 (4.40)	92.96
Light thin					
TAC11	53.08 (25.59)	46.62 (35.45)	81.22 (8.34)	79.13 (7.75)	55.56
TAC15	76.21 (19.78)	60.85 (34.03)	86.30 (8.81)	81.33 (8.07)	58.89
TAC3	79.43 (18.24)	67.74 (30.04)	83.32 (8.42)	85.55 (3.94)	65.88
TAC7	93.95 (12.82)	80.34 (17.94)	88.03 (3.41)	91.06 (2.4)	82.72
UA12	88.70 (9.64)	77.27 (30.11)	92.44 (4.12)	88.44 (6.41)	76.13
UA16	89.17 (13.16)	69.32 (31.46)	89.16 (9.22)	89.90 (4.88)	66.27
UA4	64.69 (29.32)	58.29 (34.72)	86.45 (11.18)	82.57 (9.03)	60.55
UA8	67.62 (18.96)	57.14 (32.29)	89.87 (4.22)	86.71 (4.30)	60.72
Heavy thin					
TAC10	42.41 (27.15)	28.63 (33.82)	73.19 (6.03)	65.28 (5.24)	42.35
TAC14	68.28 (19.28)	46.28 (41.75)	76.60 (12.47)	70.17 (11.65)	50.34
TAC2	63.48 (31.48)	55.94 (39.82)	70.46 (25.12)	77.97 (13.32)	46.92
TAC6	83.08 (17.25)	64.57 (27.10)	81.47 (6.32)	78.45 (6.60)	69.87
UA11	63.28 (25.94)	52.22 (42.08)	81.81 (13.13)	80.33 (10.64)	51.59
UA15	56.03 (26.51)	46.92 (39.32)	82.44 (7.95)	79.14 (10.95)	12.95
UA3	77.89 (23.46)	72.27 (33.68)	87.98 (9.13)	82.72 (9.35)	49.31
UA7	70.24 (23.74)	59.19 (35.30)	87.82 (7.53)	84.33 (8.4)	53.59

[1]Plot IDs that begin with TAC are Young Stand Thinning Diversity Study (CCEM 1996) stands, plot IDs that begin with UA are Uneven-Aged Management Project (CCEM 1999) stands, plot IDs that are eight digit numbers are Forest Service Region 6 Current Vegetation Survey plots (CVS 2002), and plot IDs beginning with RS are Permanent Sample Plots (Dyrness and Acker 1999).

Table 6.6. Cont'd.

Plot ID	Line-intercept (SD)	Moosehorn (SD)	Densiometer (SD)	Fisheye (SD)	FVS
Mature					
RS26	94.29 (10.15)	92.09 (10.66)	91.97 (3.22)	96.29 (2.33)	51.41
RS35	93.88 (13.61)	88.72 (16.05)	89.50 (4.34)	94.64 (2.47)	34.38
1080116	96.44 (10.16)	88.68 (16.59)	97.90 (1.90)	96.71 (1.65)	63.66
1086120	86.50 (26.57)	90.34 (19.13)	97.10 (2.86)	95.26 (3.30)	59.59
1110156	89.50 (17.02)	80.47 (30.03)	95.92 (4.68)	93.16 (3.38)	83.73
2080122	97.76 (4.76)	90.77 (12.18)	96.97 (2.17)	96.14 (2.37)	70.35
2085152	94.02 (10.15)	88.50 (18.55)	95.80 (3.60)	96.04 (2.62)	72.56
2087136	97.14 (5.20)	90.43 (16.63)	96.26 (3.03)	94.00 (3.42)	72.23
2098146	83.72 (25.51)	74.66 (32.03)	90.25 (12.08)	88.53 (12.33)	70.45
2099144	83.47 (20.86)	71.84 (33.34)	89.83 (7.34)	87.89 (8.88)	58.93
2102154	79.41 (26.85)	81.37 (26.58)	94.20 (4.34)	93.51 (3.70)	77.72
2129156	90.84 (16.12)	82.86 (25.13)	93.28 (6.09)	90.99 (7.54)	71.71
2135146	93.25 (12.22)	82.05 (25.27)	95.29 (5.99)	91.60 (7.04)	53.38
2146186	67.74 (22.13)	69.62 (36.94)	86.68 (9.37)	81.04 (12.85)	65.25
Old-growth					
RS1	87.76 (19.75)	77.91 (27.47)	89.87 (6.49)	90.33 (7.84)	38.88
RS2	88.87 (13.52)	78.42 (24.73)	91.55 (5.31)	90.33 (4.03)	38.79
RS3	93.45 (8.38)	85.51 (25.02)	92.23 (3.52)	94.54 (3.51)	36.39
RS20	91.71 (9.69)	81.24 (22.71)	88.61 (9.27)	91.00 (5.26)	37.50
RS21	90.13 (11.33)	82.69 (24.42)	92.14 (9.44)	93.97 (2.55)	37.93
RS28	92.87 (10.14)	92.95 (14.28)	93.40 (2.79)	95.31 (1.86)	45.91
RS29	89.71 (11.80)	81.84 (25.61)	91.60 (3.34)	93.20 (2.27)	33.69
RS30	93.98 (9.85)	84.02 (24.93)	92.56 (4.77)	94.31 (2.43)	42.24
2097140	80.11 (22.28)	82.65 (28.07)	92.65 (3.66)	93.11 (4.69)	56.45
2105140	78.59 (19.57)	56.84 (42.39)	83.91 (17.32)	81.42 (11.59)	71.04
1096136	74.53 (26.76)	62.61 (39.04)	87.27 (8.54)	82.38 (9.01)	48.88
2079120	95.87 (10.08)	90.68 (11.73)	96.72 (2.26)	96.37 (2.49)	61.06
2084138	93.99 (6.06)	91.11 (15.82)	97.52 (2.01)	94.76 (2.19)	81.90
1096144	88.53 (11.85)	86.84 (18.90)	94.54 (5.90)	96.23 (2.65)	70.93

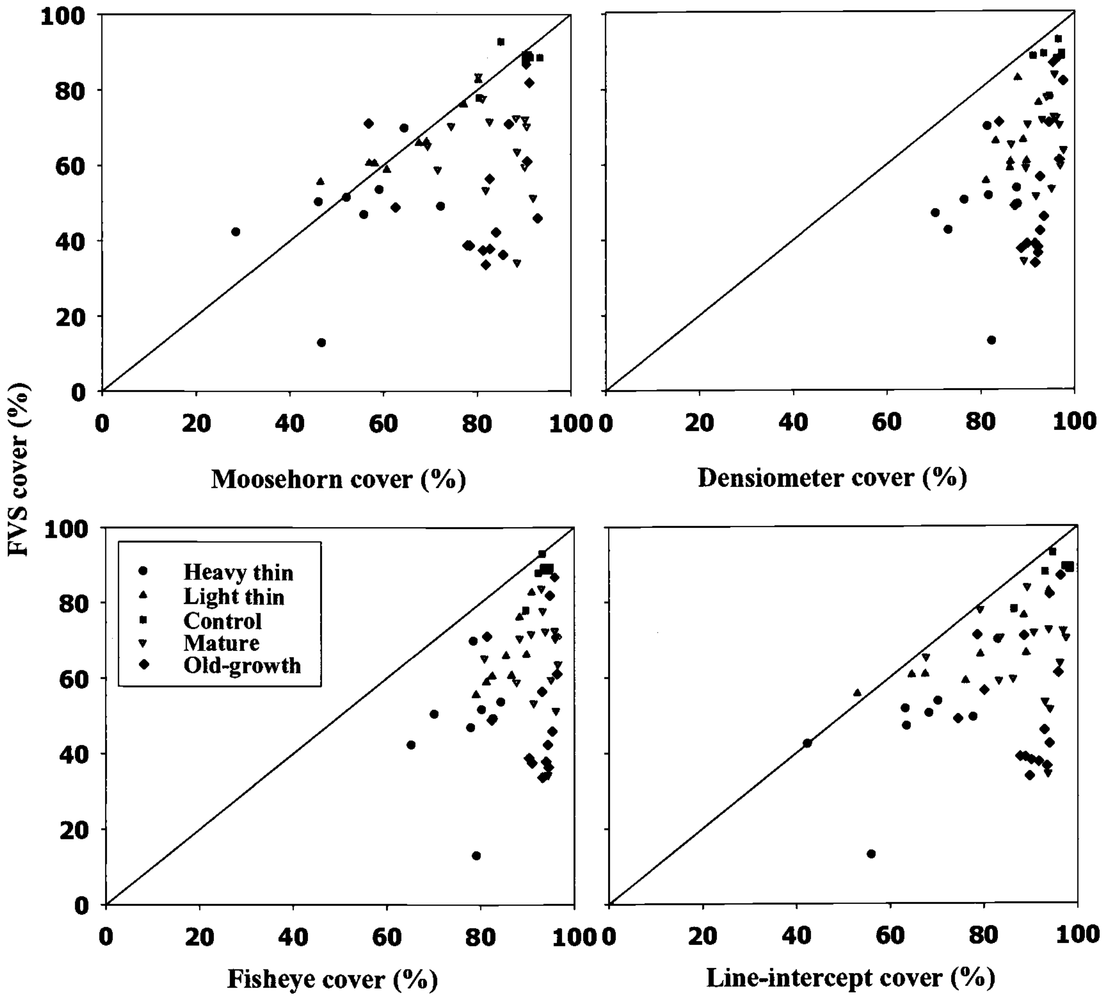

Fig 6.7. Comparisons of FVS-calculated cover with canopy estimates from the four ground-based methods measured in this study. Relationships between FVS and the other four methods differed depending on the forest-structure type in which they were measured (see Table 6.5).

As expected, cover measurements of methods were more variable in forest-structure types with reduced levels of mean percent cover (Table 6.7). For all methods the unthinned young stands had the highest percent cover concurrent with the lowest amount of variability. Except for the line-intercept method, the heavy-thin stands were lowest in percent cover but with the highest degree of variability.

Discussion

The four methods used in this study had different angles of view. As such I expected them to have different estimates of overstory cover. Bunnell and Vales (1990) illustrated the differences associated with angle of view using basic trigonometry. In general, the moosehorn, densiometer, and fisheye photography all followed the expected patterns of increasing cover with increasing angle of view. However, the line-intercept did not follow the expected pattern.

Even though the line-intercept method had the narrowest angle of view, in general it did not have the lowest percent cover among stands. Instead, the next narrowest-angled method, the moosehorn, usually had the lowest percent cover. This may be attributed to the differing definitions of crown completeness applied to the line-intercept versus the other methods. Unlike the other methods, for the line-intercept technique all the horizontal space contained within the outline of the crown was considered as cover. Therefore within crown gaps captured by the moosehorn were ignored by the line-intercept method. This omission of within-tree crown gaps impacted the estimates of MCC. I expect this difference primarily resulted from the presence of tree species in the stands that lacked dense canopies. For example, the 'low-density' spreading form characteristic of *Acer macrophyllum* Pursh, and *Acer circinatum* Pursh likely contributed to the moosehorn's lower cover estimates compared with the line-intercept, as these species were abundant in many of the stands. This crown form is in contrast to species like Douglas-fir and western hemlock that have dense crowns with high leaf area index (LAI) values. I would

Table 6.7. Percent cover estimated by each of the five methods in each of the five forest-structure types. SD is the between stand variation.

Forest Structure Type	Line-intercept (SD)	Moosehorn (SD)	Densiometer (SD)	Fisheye (SD)	FVS (SD)
Unthinned	95.50 (4.10)	89.15 (4.19)	95.36 (2.10)	93.55 (1.89)	87.65 (4.33)
Light thin	76.61 (14.09)	64.70 (11.17)	87.10 (3.61)	85.59 (4.26)	65.84 (9.25)
Heavy thin	65.59 (12.68)	53.25 (13.24)	80.22 (6.38)	77.30 (6.42)	47.12 (15.97)
Mature	89.14 (8.35)	83.74 (7.46)	93.64 (3.46)	92.55 (4.34)	64.67 (12.56)
Old growth	88.58 (6.42)	81.09 (10.18)	91.76 (3.57)	91.95 (4.68)	50.11 (15.55)
All Plots	84.42 (13.24)	76.24 (15.36)	90.33 (6.28)	89.12 (7.17)	61.76 (18.22)

anticipate that in other stand-structure types with even more numerous low-LAI tree and shrub species, the difference between line-intercept and moosehorn might be even more exaggerated. This is a potential area for future study.

While the line-intercept method and fisheye were not statistically different, examination of the regression equation that equated the two methods, and examining the graph comparing the two methods demonstrated differences among them were biologically significant. The Scheffe multiplier used in this study is conservative and guarantees at least 95% confidence for all family-wise comparisons. As such, it decreases potential for Type I errors, but as a consequence the probability of a Type II error is increased. Therefore, while the Scheffe-adjusted p-value did not show significant differences between these two methods, biologically the two methods were clearly distinct at lower cover levels. Thus, the regression equation (see Table 6.4) should be used to transpose cover estimates between these two methods.

The FVS cover calculations were consistently biased towards underestimating cover compared with the four ground-based methods. This finding supports previous research in Montana Douglas-fir/western larch (*Larix occidentalis* Nutt.) forests (Applegate 2000). Applegate compared cover predictions from the Northern Idaho variant of FVS with the densitometer and moosehorn and found FVS equations underpredicted cover in the Douglas-fir stands, as well is in various other cover types. Therefore, it does not appear that the FVS cover calculations should be used as management tools to estimate cover in Douglas-fir/western hemlock stands. Instead, it appears that ground-based estimates are necessary to obtain estimates of percent cover.

Patterns in variability among methods and between stand types were generally expected. Given the small area of the canopy that is captured by individual moosehorn measures, I expected the very high within stand variability. The converse was expected and seen for the wider-angle, and thus wider area of canopy coverage, methods. The only surprising result was that line-intercept cover measures had lower variability than did moosehorn cover measures. However, I think this resulted from the mean and standard deviations being condensed to the level of the 15 17-m transects in each stand. There may have been a lot of variability in canopy coverage along individual transects. However by calculating mean and standard deviation of the stand using transect level data, this variability was not captured in these calculations.

No direct measures of efficiency associated with collection of canopy data by the four methods were recorded. However, in the field it was evident the line-intercept method was the most time consuming of the four. This was especially true in stands with a wide variety of species in all three canopy layers. Looking up overhead with the clinometer to ascertain start and end points of cover intercepts and then verifying these to the nearest dm on the transect tape was definitely challenging. The densiometer also was time-intensive because of the challenges of positioning it on the tripod in the correct direction on sloping ground and then assuring proper positioning of the observer. Also, recording measurements in each of the four directions took extra time. The fisheye also required some effort in order to set it up on the tripod and correctly position it. But with fewer measures required per stand, the fisheye was still much faster than the densiometer. The self-leveling moosehorn was definitely the quickest and easiest to use instrument.

With the line-intercept being more time-intensive and less conservative in its cover estimates than the moosehorn, the current line-intercept method may not be the best standard by which to compare other methods. Instead, it may be appropriate to modify the method to include gaps of a minimum size within individual crowns. However, this could become an even more labor- and time-intensive process than the line-intercept already is. Given the consistent relationship between the line-intercept and the moosehorn, and the moosehorn's ease of use, the moosehorn may actually be the better method to use in the field. This may be especially true in stands with low-LAI tree crowns, where conservative estimates are desired.

However, a benefit of the line-intercept method not to be overlooked is that it provides forest managers with additional information lacking with the other methods. Information on the number of layers of cover, the species composition, and the percent cover by species were collected for individual layers and then combined to form an estimate of total combined cover. Using the densiometer and fisheye, breaking out cover by species, shade-tolerance, etc. would be impossible. All these other methods can effectively do is differentiate between open sky and cover. With the moosehorn it may be possible to glean limited information about cover by species or layer, but this would be challenging due to overlap among species and the difficulty of identifying individual species cover when multiple species are clumped together. Also overlap among cover layers, with lower layers obstructing cover of higher layers would impede the ability of the moosehorn to identify cover among multiple layers of cover, especially in stands with high levels of cover in multiple layers. If detailed canopy structure information is desired then I recommend the line-intercept method. However, to avoid conflicting interpretations of layering among stands, I recommend modifying the line-intercept method so cover is measured within heigh intervals that are fixed distances (e.g. 10-m height classes).

Hemispherical photographs appeared effective at estimating overstory cover regardless of sky conditions and times of day when they were taken. All hemispherical photographs taken in the 52 stands were used to estimate MCC, and none were excluded from analysis based on sub-optimal sky conditions. The only difference was that more manual manipulation of threshold levels between light and dark were required when the sun was present in photos. Therefore, it appears forest managers may employ this method to obtain ISF values even when the sun is present and the sky is not uniformly overcast.

As previously demonstrated (Bunnell and Vales 1990) the densiometer and fisheye both overestimated cover. This overestimation was exaggerated with lower cover levels. If accurate estimates of vertical overstory cover are desired, these methods are not effective.

However, Nuttle (1997) raised an interesting point about the densiometer and fisheye when he suggested wide-angle MCC estimators may provide unbiased estimates of what he referred to as the true variable of interest: angular cover or light interception. From a wildlife perspective, Nuttle argued that an animal's perception of cover was likely to encompass general cover overhead, not just cover directly vertical overhead. If a researcher is more interested in assessing the overall light reaching a point from all directions from the zenith towards the horizon, then the densiometer and fisheye photography are actually more appropriate techniques than the moosehorn or line-intercept. Therefore, the method selected for estimating cover should depend on the observer's objectives, and the observer should clearly define the portion of the canopy they are quantifying.

In this study the standard was the line-intercept method because it was assumed to be most representative of true vertical cover, the variable I was interested in measuring. Yet the results suggest the alternative that the moosehorn, even with its wider angle of view, may serve as the most conservative estimator of vertical cover.

Limitations

There are two main limitations of this study:

1) The scope of inference of this study is limited to stands with a minimum level of 50% vertical cover, assuming the line-intercept as the standard. All of my study stands had mean percent cover of at least 42%, using the line-intercept method as the standard. The moosehorn minimum MCC value among stands was 29%, the fisheye MCC minimum was 65%, and the densiometer minimum MCC was 70%. However, even using the moosehorn and line-intercept techniques, the majority of stands had > 50% cover, and thus overall results are generally applicable in stands with > 50% line-intercept cover.

2) The stands used in this study also limited the scope of inference. The interpretation of results should be limited to Douglas-fir/western hemlock dominated stands that share characteristics similar to those of the stands used in

this study. Further research is needed to assess the use of these cover-estimation methods in other forest structure types with differing crown characteristics.

Summary

1) I compared four ground-based techniques for estimating forest overstory cover —line-intercept, spherical densiometer, moosehorn, and hemispherical photography—and estimates generated using FVS in five different Douglas-fir/western hemlock structure types in western Oregon.

2) There was no significant interaction between method and structure type, suggesting differences in canopy cover estimates for the four ground-based methods did not depend on the structure type in which they were measured.

3) Comparisons of the cover calculated by FVS and the ground-based cover estimates differed depending on the forest structure types in which they were compared; i.e., the interaction term was significant.

4) The moosehorn provided the most conservative estimates of ground-measured MCC. Compared to the moosehorn, the line-intercept method overestimated cover because it included gaps in individual tree crowns as cover.

5) The moosehorn may actually be a preferred standard to the existing line-intercept method, given its most conservative estimates of MCC.

6) Regardless of actual overstory cover, observers' will achieve high cover estimates when using the fisheye or convex densiometer.

7) Using Strickler's modified method (estimating from 17 points in a wedge-shaped area of the densiometer grid for each of the four directional measurements) did not remove the convex densiometer's bias to overestimate cover.

8) The FVS-calculated cover estimates should not be used as a substitute for ground-based measures in these forest types given that they were consistently much lower than ground-based measures within each forest-structure type.

9) Variability in cover estimates among methods generally followed expected patterns consistent with cover levels and angles of view. The moosehorn

had the highest variability in cover estimates. Cover estimates were least variable in unthinned young stands among all methods.

10) Regardless of overstory sky conditions, fisheye negatives were successfully analyzed for ISF and used to estimate MCC.

11) The line-intercept method provided the most detailed information on the forest canopy, even though this degree of information could not be used when comparing the line-intercept method with the other three ground-based methods. A modification whereby cover is recorded among fixed height classes (e.g. 10-m intervals) may be preferable to the existing approach for ease of comparison of layering among stands.

12) Regression equations among the four ground-based methods (see Table 6.4) provided a means of standardizing measurements recorded with different techniques. These equations can be used by forest managers to transpose MCC values among multiple estimation methods in Douglas-fir/western hemlock dominated forests in the western Oregon Cascades.

13) The method selected for estimating cover should depend on the researcher's objectives. Researchers' must clearly define the aspect of the canopy they are interested in quantifying. If angular interception of cover is the true variable of interest then the densiometer and fisheye are the most appropriate methods. If cover directly overhead is of interest, the moosehorn should be used.

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CONCLUSIONS

This study examined canopy-cover attributes for western Oregon, including using 934 forested plots in western Oregon from the Forest Service Forest Inventory and Analysis 1995-1997 inventory. Results provide forest managers with new information and tools that can be applied across the forested landscape of western Oregon. The most pertinent findings from this study include:

Based on patterns of vertical and horizontal canopy structure and understory cover along a successional gradient, the upper tree canopy layer contributed the most to total cover except in the dry-hardwood stands, where the vertical distribution of tree cover was more evenly distributed. However, mean canopy cover rarely exceeded 85%, even in productive young conifer forests. Shade-tolerant species rarely made up more than 20% of canopy cover by age class, even in the lower canopy layers and in stands > 100 yrs old. Contrary to expectations, cover of understory shrubs and herbs was not substantially lower in young closed-canopy stands than in other stands.

Regression models to predict canopy cover on inventory plots from standard forest measurements were within 15 percent of measured cover for > 82% of the observations. However, standard inventory estimates of cover using 1:40,000 scale aerial photos were poorly correlated with ground-measured cover, especially in wet-hardwood (r=0.58) and dry-harwood (r=0.61) stands, and estimates using FVS underestimated cover by up to 50% in wet-conifer and wet-hardwood stands. The aerial photos and FVS equations used in this study are not recommended as surrogates for ground-based measurements of cover. The levels of accuracies of the predictive models may be adequate for some purposes.

Comparisons of fourteen vertical measures of diversity and stratification revealed that with increasing evenness among height intervals and increasing stand age, there was concurrent increase in vertical diversity and layering, consistent with expected crown patterns associated with dominance and succession. Predictive equations for Simpson's height diversity index (SDI), Foliage Height Diversity (FHD), and Canopy Height Diversity Index (CHDI), used combinations of stand height, basal area, standard deviation of dbh, and stem frequency within size classes as the best variables. Predicted SDI values were within 0.15 units of calculated SDI for ≥ 79% of the observations, predicted CHDI values were within 1.5 units for ≥ 91% of the observations, except for in dry-hardwood stands (only 69%), and predicted FHD measures were within 0.2 units for ≥ 85% of the observations among forest groups. The formulated models within the 95% confidence model sets can be applied among similar wet-conifer, wet-hardwood, and dry-hardwood forests in western Oregon lacking detailed crown measurements.

Predictive equations for FHD and SDI were applied to a wildlife-habitat database for western Oregon to determine if existing models using CHDI to predict presence of bird species could be improved on. Models with the three vertical measures generally revealed similar (within 5 percentage points) classification efficiencies among the three measures. The proportions of new bird-habitat association models with higher classification efficiencies than CHDI were 33% and 66% in the Coast Range for FHD and SDI, respectively, and 18% for both new models in the Cascade Range. Although improvements in classification efficiency were less than six percentage points, future use of these diversity indices is warranted.

Comparison of four ground-based techniques and estimates generated using FVS revealed differences among the methods. Differences among ground-based methods were primarily related to differences in angle of view. Although the line-intercept had the narrowest angle of view, the moosehorn provided the most conservative estimates of overstory cover. Thus, the moosehorn is recommended for estimating canopy cover, assuming detailed information on cover by species, etc. is not needed. Regression equations allow for conversion among canopy cover estimates developed with the four ground-based methods. The FVS generated cover should not be used as a substitute for ground-based measures in these forest types given that the FVS cover was consistently much lower than estimates from the ground-based methods within each forest-structure type.

Limitations and Future Research Needs

This study only briefly examined relationships between management activities and canopy structure. In current management practices, retention of canopy trees is meant to better represent patterns of disturbance and structural complexity of natural forests, with the objective of maintaining canopy complexity over the entire rotation cycle (Hansen et al. 1995). However, the way disturbance history was determined in the FIA inventory limited detailed comparisons of management effects on canopy attributes. Thus, there is still a need for further research on patterns of canopy structure associated with variable silvicultural prescriptions and management regimes.

The concept of vertical canopy stratification still lacks clarity and agreement. For the FIA inventory, stratification referred to a maximum of three canopy layers differing in their average heights by at least 5 m. Using this criterion, increases in canopy layering along diversity and successional gradients were supported. Alternate definitions of stratification lead to similar conclusions, but different absolute numbers of layers. For example, the TSTRAT algorithm uses a fixed proportion of the crown length of the tallest tree in a stratum (TSTRAT), while Baker and Wilson's stratification algorithm assigns a threshold of overlap between the height of a shorter tree and the moving average of mean base crown height of all taller trees. These findings suggest defining the number of layers in a stand is somewhat arbitrary. Therefore, it is crucial for researchers to clearly define their interpretation of a forest community as multi-layered or not, clearly describing the method of stratification they used to reach this conclusion.

A limitation of the use of the line-intercept layer, as implemented by FIA, was revealed. Because the layers were relative to the stand in which they were measured, the heights of layers and the distribution of cover among layers weren't directly equitable among stands, i.e. the line-intercept method did not differentiate between the upper layer of a young 10-m tall stand and an old-growth 80-m tall stand. Yet, from an ecological standpoint, we would not expect the upper layer of these two stands to be directly comparable. This example suggests that the concept of layering has not been resolved in this study. Therefore, using line-intercept delineated layers to describe the forest canopy can be ambiguous and subject to multiple interpretations.

I propose an alternative to the existing line-intercept method be used. Instead of quantifying line-intercept cover among three layers which are relative to the stand conditions, I propose segmenting the canopy into fixed height classes, e.g. 2.5-10 m, 10.1-30 m, etc.. Cover data can then be recorded within each of these height intervals. Fixed intervals will allow for more meaningful comparisons among stands, compared with the relative layering system currently in place. This modification would still allow for a total estimate of cover to be calculated through collapsing of cover among the height classes. In addition it would provide information on stratification of cover among the canopy that could be directly compared among stands. This modificatin is likely to be much more time intensive than the three-layer technique. Therefore, it is only suggested for studies where detailed canopy structure data is needed. For studies that desire less-detailed information, stands could be treated as 'single-layered' (lumping all trees together), with all intercepts combined into a single estimate of line-intercept cover. This would still provide information on cover by species not provided by other traditional methods of estimating cover, but without the complications of describing layers.

Owing to budgetary constraints, after completion of the 1995-1997 FIA inventory, the line-intercept ground-based sampling of canopy cover was again removed from the FIA inventory. Yet long-term patterns in canopy structure within individual stands are more meaningful than the patterns I demonstrated using chronosequences of the stands in western Oregon because they remove a lot of the variability inherent in a chronosequence. Given the utility of canopy structure measurements demonstrated in this study, collection of canopy data should continue in the future. However, as a balance between time and level of canopy information desired, I would recommend adoption of the single-layered line-intercept approach. If budgetary constraints do not allow for further collection of detailed canopy data, then the predictive models from this study can be used to estimate canopy structure attributes.

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APPENDICES

Appendix 1

Table A1.1 Stocking equations used in the western Oregon FIA inventory[1]

Softwood equations	Eq. 1	$PN = 0.00073722 \times DBH^{1.54385} \times TPHS$
	Eq. 2	$PN = 0.00036526 \times DBH^{1.675} \times TPHS$
	Eq. 3	$PN = 0.00028275 \times DBH^{1.6757} \times TPHS$
	Eq. 4	$PN = 0.00035001 \times DBH^{1.7} \times TPHS$
	Eq. 5	$PN = 0.00036590 \times DBH^{1.73} \times TPHS$
	Eq. 6	$PN = 0.00026889 \times DBH^{1.734} \times TPHS$
	Eq. 7	$PN = 0.00036592 \times DBH^{1.73} \times TPHS$
Hardwood equations	Eq. 8	$PN = 0.00183402 \times DBH^{1.4057} \times TPHS$
	Eq. 9	$PN = 0.00107420 \times DBH^{1.153} \times TPHS$
	Eq. 10	$PN = 0.00310100 \times DBH^{1.13} \times TPHS$
	Eq. 11	$PN = 0.00157244 \times DBH^{1.39} \times TPHS$
	Eq. 12	$PN = 0.00099100 \times DBH^{1.63} \times TPHS$

[1] For further information please refer Azuma and Hanson 2002.

TPHS= trees per hectare not yet divided by the number of subplots, DBH in CM, PN= percent of normal stand

Appendix 2

Table A2.1 Comparison of cover among the five different stand types examined in Chapter Five. Stand types that significantly differed are highlighted in bold.

Variables compared	Difference Estimate	SE	t value	Scheffe–adjusted p-value
Control vs light-thin	1.3186	0.14	9.55	**<0.0001**
Control vs heavy-thin	1.8669	0.14	13.52	**<0.0001**
Control vs mature	0.4071	0.12	3.33	**0.0289**
Control vs old-growth	0.5841	0.12	4.77	**0.0002**
Heavy- vs light-thin	-0.5482	0.14	-3.97	**0.0043**
Heavy-thin vs mature	-1.4598	0.12	-11.92	**<0.0001**
Heavy-thin vs old-growth	-1.2828	0.12	-10.48	**<0.0001**
Light-thin vs mature	-0.9115	0.12	-7.44	**<0.0001**
Light-thin vs old-growth	-0.7345	0.12	-6.00	**<0.001**
Mature vs old-growth	0.1770	0.10	1.69	0.5804