DEVELOPMENTAL TRENDS OF STAND STRUCTURE AND TREE MORTALITY IN COASTAL WESTERN HEMLOCK FORESTS

by

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DEVELOPMENTAL TRENDS OF STAND STRUCTURE AND

TREE MORTALITY IN COASTAL WESTERN HEMLOCK FORESTS

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ABSTRACT

I examined forest structure and tree mortality in the Coastal Western Hemlock very wet maritime 1 variant (CWHvm1) of British Columbia, using data collected from 190 permanent sample plots representing stand ages from 13 to over 300 years old. I found that patterns of structural development of forest attributes in the CWHvm1 were similar to patterns observed elsewhere in the Pacific Northwest. For instance, percent cover of understory vegetation followed a so called "U" shaped curve with increasing stand age and, conversely, mean tree diameter, biomass of live stems and production of dead stem biomass were consistent with the so called "S" shaped or sigmoid curve. Overall stem density declined with age and in diameter distributions of live stems shifted from a "reverse-J" type distribution in young stands, to a near normal distribution in intermediate-aged stands, and back to a reverse-J distribution in old stands. Tree mortality and many size classes of live stems, for both stem density and stem biomass, followed an inverted "U" shaped trend over stand age.

My observations are consistent with other research demonstrating that old growth stands are structurally distinct from mature stands. Old growth stands were characterized by a wide range of tree diameters, high levels of understory cover, low density and high biomass of live stems, and a reverse-J diameter distribution. Further, tree mortality rates were low in old growth stands. In contrast, in intermediate-aged stands, the ranges of stem diameter, proportion of subcanopy stems, proportion of tree species other than hemlock, and understory cover were low. As well, stem diameter displayed a near-normal distribution and mortality rates were high.

Developmental trajectories in the CWHvm1 were influenced by site productivity and other factors such as aspect, elevation and geographic location. The rate of change in the density of different size classes of stems, percent cover of understory vegetation and degree of canopy closure increased on more productive sites. Therefore, the rate that a stand moves through developmental stages depends to some extent on the

productivity of the site. For example, a stand is likely to develop old growth characteristics more rapidly on more productive sites. Age, site productivity, aspect and geographic location do not explain all of the variation observed for the attributes examined in my study. When I examined the influence of these factors on density of live trees, I found that about 30% of the variation in stem density remained unexplained. It is possible that evaluating developmental trends at the site series level would eliminate much of this remaining variation, although I was unable to examine this with my data.

The structural dynamics of CWH forests require additional characterization. I was unable to examine trends in size and decay class distributions of standing and down dead wood, and differences in developmental trajectories resulting from different disturbance histories. Low sample sizes prevented me from exploring detailed developmental trends in stand structure during the transition from mature to old growth. Moreover I was unable to examine temporal trends among old growth CWH stands because ages of plots in these very old stands were not accurately determined.

New silvicultural prescriptions need to be developed if very large stems and elevated levels of understory cover are to be retained in managed landscapes. Further, regulations, guidelines and prescriptions based solely on the assumption that certain attributes are associated with a given age class are inappropriate because of substantial variation in structural characteristics of forest stands.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

1. INTRODUCTION

1.1 *Dynamics of forest development*

After a stand-initiating disturbance, substantial change occurs to forest ecosystems during subsequent stand development. For both live and dead overstory and understory vegetation, there are significant changes to structural characteristics such as the number, size and biomass of stems and abundance of understory herbs and shrubs (Spies and Franklin 1988). There are changes to function imposed by the new ecological regime (Peet and Christensen 1987). There are generally changes to the species composition of the forest stand (Oliver 1981), although in some forest ecosystems where there are few canopy species, stand composition may not be significantly altered (e.g. Franklin and Hemstrom 1981; Alaback 1984). Essentially all forests, however, undergo significant changes in structural characteristics during development; these structural components strongly influence the character and ecological function of the forest ecosystem.

1.2 *Trends in structural development*

Some of the most dramatic examples of structural development in forests occur in the long lived Douglas-fir (*Pseudotsuga menziesii*) forests of the Pacific Northwest (PNW) of North America. In these forests, the amount of biomass that accumulates in live and dead stems is nearly unsurpassed anywhere in the world (Franklin and Hemstrom 1981). These forests have been the focus of substantial research in recent decades and results show that some structural attributes of forests tend to follow specific trends through forest development after a stand initiating disturbance (e.g. Spies *et al.* 1988; Franklin and Spies 1991a; Huff 1995).

Based on their own observations and other research in Douglas-fir stands of the American PNW, Spies and Franklin (1988) proposed generalized patterns of structural change in forest stands. They present two general trajectories for structural attributes after a stand-initiating event of natural origin such as a fire, in the absence of further disturbances. The first is a so called "U" shaped pattern (Curve 1; Figure 1), where an ecosystem component exhibits a high abundance immediately after the disturbance, declining to low levels during intermediate stages of development and increasing again as the stand ages. Typically, large snags, down wood and understory vegetation follow the "U" shaped pattern (Figure 1). The pattern for standing and down dead stems is a consequence of general patterns of tree mortality and decay over time: a large stand initiating disturbance results in a large initial input of dead trees. Then decay reduces this dead material until, later in succession, mortality of individual trees produces new snags and logs.

The pattern for understory vegetation is similar to that of snags and down wood, but it occurs because of changes to canopy closure. Understory herbs, shrubs and saplings grow well in an open environment following a disturbance. Then, as the young forest develops, a dense overstory canopy forms, constrains resources to the understory and decreases plant life there. Eventually, tree mortality leads to gaps in the canopy and allows more light to reach the understory, reinitiating growth of herbs, shrubs and trees.

The second pathway is a so called "S" shaped or sigmoid trajectory (Curve 2; Figure 1), where an ecosystem component is at low levels during stand initiation and increases to a plateau in late successional forests. The "S" shaped pathway is primarily related to growth and development of live trees, and is exhibited by attributes such as mean tree diameter and stand biomass (Spies and Franklin 1988). These "S" and "U" shaped developmental pathways were based on observations for Douglas-fir forests of the American PNW, but Spies and Franklin (1988) expected that they would be relevant to other forest types as well. However, they remain essentially untested for many forest types and data are lacking that describe levels of various attributes and the lengths of time over which development occurs.

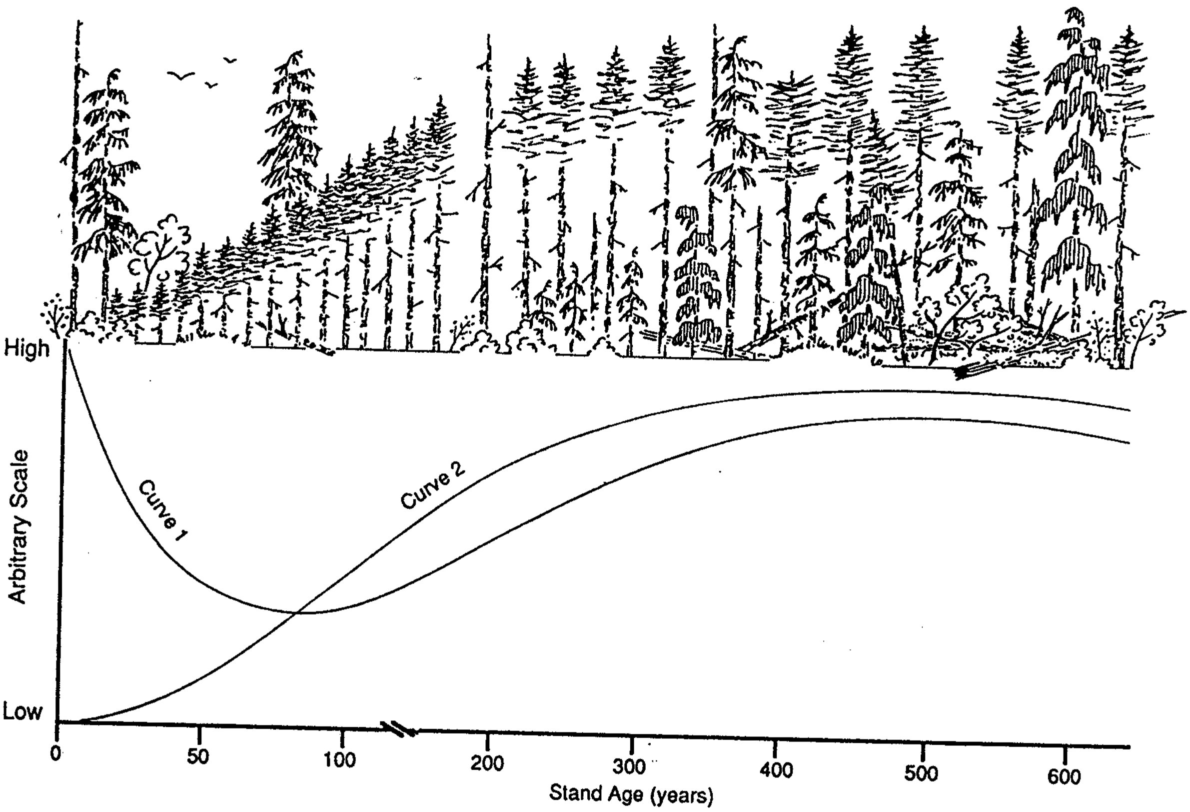


Figure 1: Generalized patterns of changes to ecosystem attributes with long recovery periods after disturbance in old-growth Douglas-fir forests. These patterns are expected to apply to other forest types, although trajectories will develop more rapidly in forests dominated by trees less long lived than Douglas-fir (modified from Spies and Franklin 1988).

Attributes following a "U-shaped" curve (Curve 1):

- Amount of understory vegetation
- Number of large snags
- Amount of down wood

Attributes following an "S-shaped" curve (Curve 2):

- Mean tree size
- Diversity of tree sizes
- Stand biomass

1.3 Stages of forest development

There is growing consensus that patterns of change observed in the structural characteristics of forest stands are related to distinct stages of forest development. A number of models of have been proposed (e.g. Day 1972; Bormann and Likens 1979; Oliver 1981; Peet and Christensen 1987; Spies and Franklin in press), most sharing common features. Oliver and Larson (1990) present a model of stand development based on Oliver (1981), but incorporate features of many of the other models, comprised of four stages: *stand initiation*, *stem exclusion*, *understory reinitiation* and *old growth* (Table 1). Oliver and Larson (1990) further divide the old growth stage into two components: "true" old growth where all canopy dominants have initiated under the forest canopy, and "transitional" old growth, where some canopy dominants are members of the original cohort.

Tree mortality is a primary process underlying the model. The initial disturbance that allows the new stand to initiate (*stand initiation*) kills most trees from the previous stand. In the *stem exclusion* stage, self thinning occurs and most stems die (see Peet and Christensen 1987 for a description of self-thinning) and closed canopies prevent vegetation from establishing in the understory. After this stage, mortality of overstory stems results in openings in the canopy that allow vegetation to establish in the understory (*understory reinitiation*). Finally, in the *old growth* stage, the death of large trees die and create canopy gaps, large snags, and down wood that characterize old growth stands.

Peet and Christensen (1987) present three patterns besides those presented in Figure 1, based on a general model of stand development equivalent to Oliver's (1981). They propose an inverted "U" shaped pattern of tree mortality, where mortality is low during stand initiation, then increases during self-thinning, and declines again as trees approach their maximum sizes and no longer compete for space. Peet and Christensen

Table 1: Stages of stand development (modified from Oliver and Larson 1990).

Stand initiation stage.	After a disturbance, new individuals and species continue to appear for several years.
Stem exclusion stage.	After several years, new individuals do not appear and some of the existing ones die due to competition as the stand undergoes self-thinning. The survivors grow larger and express differences in height and diameter; first one species and then another may dominate the stand.
Understory reinitiation stage.	Later, herbs and shrubs and shade tolerant trees appear on the forest floor and survive in the understory as tree mortality creates openings in the canopy.
Old growth stage.	Much later, overstory trees die in an irregular fashion allowing more resources to reach the understory. In these gaps, understory trees grow and eventually recruit to the overstory.

(1987) also describe the dramatic declines in density that stands exhibit during self-thinning. They further suggest that this decline in density will result in substantial changes to the diameter distributions of trees: initially a few trees will assume dominance, leading to a positively skewed distribution, then as self-thinning eliminates smaller trees, the distribution becomes more normal. As the stand ages, and understory reinitiation occurs, recruitment of small trees increases, until eventually, the distribution takes on a reversed-J shape (Leak 1965).

Spies and Franklin (in press) identified some limitations of Oliver's (1981) and other models (most notably the model proposed by Peet and Christensen 1987). Their major criticisms were that the models obscure the considerable structural change that occurs during the understory reinitiation and transitional old growth stages; that although tree mortality is one of the primary processes underlying model, the dynamics of dead trees are ignored; and that the structural dynamics of old growth are poorly described by the models, if at all.

These models remain inadequately tested for many forests types, including temperate conifer forests such as the Douglas-fir stands for which Spies and Franklin (1988) proposed their patterns of development. Moreover, as Spies and Franklin (in press) have noted, some aspects of the model likely require modification for some trends, particularly the structural dynamics of live and dead trees in older stands.

1.4 *Old growth*

Although Oliver and Larson (1990) define an old growth stage of stand development, I have noted that their description does not capture the unique structural, compositional and functional characteristics of these old forests. Old growth is generally characterized by large trees for species and site, wide variation in tree size and spacing, accumulations of large dead standing and fallen trees, multiple canopy layers, canopy gaps and understory patchiness (Franklin *et al.* 1981; Alaback 1984; Franklin and Spies 1991a and 1991b; Lertzman and Krebs 1991; Table 2). Further, these characteristics are thought to distinguish old growth forests from earlier stages of forest development (Alaback 1984; Hunter 1989; Franklin and Spies 1991a).

The structure and composition of old growth forest remains the subject of much research (e.g. Arsenault and Bradfield 1995; Lertzman *et al.* 1996) and debate remains over the characteristics and parameters that define old growth (Hunter 1989; Wells *et al.* 1994). For example, attempts to develop specific criteria based on selected structural components of old growth stands have been only partially successful in identifying other old growth stands in similar forest types (Franklin and Spies 1991a). As well, I have already noted that the transition from mature to old growth stages is poorly described; the same is true for temporal trends of development among old growth stands of varying age (Tyrrell and Crow 1994 provide a rare exception).

Table 2: Some structural characteristics of old growth forests (modified from Franklin and Spies 1991a).

- wide range of tree sizes with a "reverse-J" diameter distribution
- large trees for species and site conditions
- presence of large snags and down logs of various decay classes
- multiple canopy layers
- increased richness and productivity of understory plant communities
- canopy gaps

1.5 Limitations of current research

While some aspects of structural development have been well characterized for many forest types, many structural characteristics of forest stands remain poorly described, particularly for the latter stages of forest development. For example, growth and yield of young forest stands have been described in detail for many forest types, and the resulting yield tables are commonly used by forest companies. However, growth and yield tables only describe trends of overall biomass, and are generally confined to the first 80 to 100 years of stand development, the maximum length of typical timber rotations. As well, many studies of forest dynamics are often limited to such broad characteristics such as overall stand density and biomass (e.g. Day 1972; Peet and Christensen 1980). Moreover, these studies generally follow stands for relatively short periods of time because of the difficulty in collecting data over the very long periods associated with stand development (e.g. Peet and Christensen 1980). Where studies do examine trends over a wide range of ages by using a chronosequence of stands, the age classes tend to be few, with wide gaps between classes (e.g. Day 1972; Spies and Franklin 1991; Veblen *et al.* 1991; Arsenault and Bradfield 1995). Further, in most studies, old growth stands are grouped into one age class; very few studies examine trends in structural development within late successional forests.

1.6 Importance to management

Forest harvesting is causing significant changes to forests on a global scale (e.g. Wilson 1992). Growing public concern about the consequences of forest management has in part led policy makers to address a broad range of values, including biodiversity, in international agreements and in forest harvest regulations. For example, Agenda 21 of the UN Convention on Biodiversity includes "Guiding Principles on Forests" (UNCED 1992) and more locally, a new Forest Practices Code for British Columbia incorporates specific guidelines for the protection of biodiversity (BCMoF 1995b).

One significant way that forest harvesting affects biodiversity is by substantially altering habitat. Information on structural characteristics of forests has gained importance as researchers and managers try to improve understanding of the relationships between animal species and habitat components. For example, the importance of large snags to cavity nesters and down wood to small mammals and amphibians is well documented (Thomas 1979; Harmon *et al.* 1986; Dupuis *et al.* 1995) and research is now determining specific relationships between structural characteristics of forest stands and wildlife abundance. Carey and Johnson (1995) found significant relationships between the amounts of coarse woody debris and understory cover and abundance of some small mammals. Hansen *et al.* (1995) found strong associations between groups of bird species and specific tree and canopy characteristics. As well, current efforts to model habitat under different harvesting scenarios require detailed information about trends in stand structure, including specific size classes of live and dead stems (e.g. Hansen et al. 1995; Nelson and Wells 1996). Improved understanding of the dynamics of structural attributes is essential to allow information from studies such as these to be used by managers to examine and assess effects of forest practices.

1.7 Objectives

The coastal western hemlock (*Tsuga heterophylla*) forests of British Columbia are cooler and wetter than the Douglas-fir forests of Washington and Oregon that lead Spies and Franklin (1988) to propose the trends of development in Figure 1. Although the two regions share many tree species, in wetter variants of the Coastal Western Hemlock biogeoclimatic Zone of British Columbia (CWH; Meidinger and Pojar 1991), Douglas-fir is uncommon or absent (Green and Klinka 1994).

Because few studies have examined the structural dynamics of CWH forests of British Columbia, it is not known if the trends observed by Spies and Franklin (1988) occur here. Arsenault and Bradfield (1995) undertook the only study that directly addresses structural variation among young, mature and old growth CWH forests in British Columbia, however their study is limited to three broadly defined age classes and broad structural characteristics. A few other studies compare some structural and compositional characteristics of mature and old growth western hemlock forests (e.g. Alaback 1984; Lertzman *et al.* 1996). However, no studies examine the transition from mature to old growth, and few studies examine structural characteristics on old growth in coastal hemlock forests, although Lertzman and Krebs (1991) investigate canopy gap structure in old growth mountain hemlock stands of the southern mainland coast.

To improve the understanding of the structural dynamics of CWH stands, I examined the structural changes of live overstory and understory vegetation and explored effects of tree mortality during development in the Very Wet Maritime variant of the CWH (CWHvm1; Green and Klinka 1994). I used a chronosequence approach, incorporating a large number of plots covering a wide range of ages to better elucidate the whole range of forest development. Thus, I was able to use a larger number of age classes than typical and treat age as a continuous rather than a categorical variable for some analyses. This allowed for a more complete description of stand development, including the transitional period between mature and old growth stands. My approach contrasts with the small number of categorical age classes common to many chronosequence studies (e.g. Arsenault and Bradfield 1995). In addition, trends in the structural development of size and canopy classes of stems have not been explored for CWH forests and were not typically examined in studies of other forest types.

My goal is to examine structural dynamics and tree mortality in the CWHvm1 through the full range of stand development. I will: *(i)* describe trajectories of stand structure and compare pathways to those hypothesized by Spies and Franklin (1988) and others (Table 3); *(ii)* explore trajectories of these attributes for evidence of stages of stand development and investigate the role of tree mortality as a primary process of stand development; *(iii)* examine old stands for differences that distinguish them from earlier developmental stages; and *(iv)* discuss the research and management implications of these developmental trends in stand structure and tree mortality.

Table 3: Predictions of trends in development of various structural characteristics for coastal western hemlock stands of British Columbia.

Structural Characteristic	Prediction	Source
Live stem biomass	"S" shape trajectory	Spies and Franklin 1988
Live stem density	Decreasing trend	Peet and Christensen 1987
Live stem diameter distribution	Skewed distribution in young and old stands; normal distribution in intermediate-aged stands	Peet and Christensen 1987
Mortality rate	Inverted "U" shaped trend	Peet and Christensen 1987
Input of dead stems (biomass)	"S" shape trajectory	Harcombe 1990, Sollins 1982
Understory vegetation (% cover)	"U" shape trajectory	Spies and Franklin 1988

2. METHODS

2.1 The database

MacMillan Bloedel Ltd. (Woodlands Services, Nanaimo, British Columbia) maintains a large database containing data on selected forest attributes. They collected data over a period of up to 40 years from nearly 2000 permanent sample plots (PSP), located primarily on Vancouver Island. MacMillan Bloedel established these plots to monitor growth and yield on their timberlands. Among data recorded by survey crews were species, diameter and canopy class of live stems as well as percent cover of understory vegetation by species (including herbaceous plants, shrubs and advanced regeneration of live stems) and abiotic site characteristics such as slope and aspect. During re-surveys of plots, which occurred approximately every five years, crews also recorded mortality of trees that had been alive on the previous census. For my study, MacMillan Bloedel Ltd. provided data collected from 190 plots for analyses of live stems and understory cover, and 163 plots for analyses of tree mortality.

2.2 Location of plots

All plots were located in the submontane, very wet maritime, coastal western hemlock (CWHvm1) biogeoclimatic variant (Meidinger and Pojar 1991; Green and Klinka 1994). The CWHvm1 has a wet, humid climate with cool summers and mild winters featuring relatively little snow (Green and Klinka 1994). Thus growing seasons are long. Precipitation is high, although rainfall varies throughout the region. Elevational limits of this variant range from sea level to about 600 m on Vancouver Island (Green and Klinka 1994). The CWHvm1 is the most expansive of 19 CWH variants, covering about 18.5% of the CWH (BCMoF 1996).

Most of the 190 plots analyzed in this study are clustered primarily on the northeastern and central-western regions of Vancouver Island (Figure 2). Five are

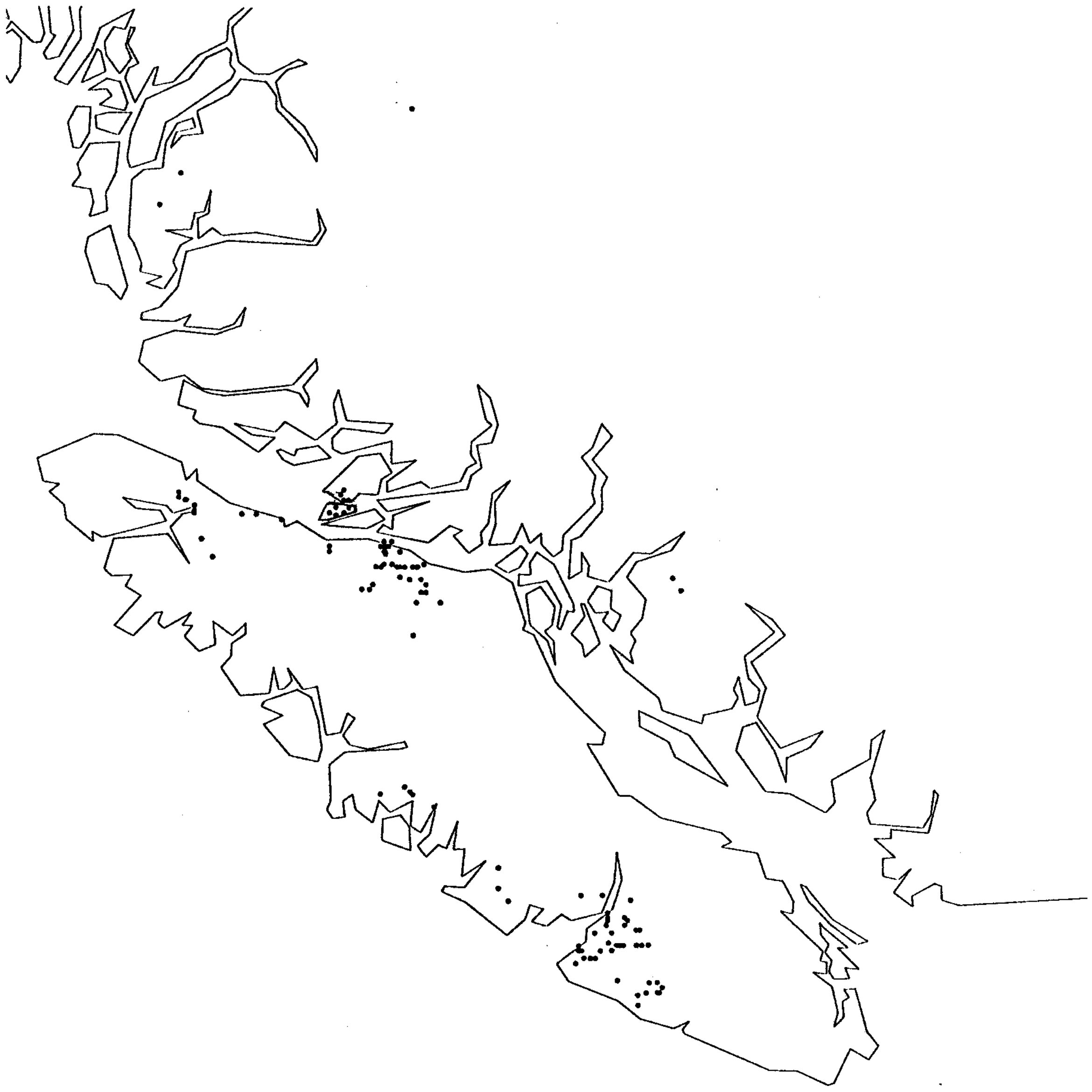


Figure 2: Approximate location of plots on Vancouver Island and the mainland coast of British Columbia (map scale 1:4,000,000).

located on the mainland coast, adjacent to Vancouver Island and nine are located on Turnour and Gilford Islands in Johnstone Strait (Figure 2). All plots are located between 48°38' and 52°11' latitude and between 124°23' and 127°68' longitude (Figure 2). Elevation ranges from 5 to 570 meters. Stand age for plots ranged from 9 years to over 400 years at the time of sampling. Plots represented a broad range of site index values (SI = 13 to 58 m). Site index is a measure of site productivity, based on estimates of the mean canopy height at a stand age of 50 years (Watts 1983).

Plots were not located randomly in the CWHvm1 (Figure 2). MacMillan Bloedel stratified plots by stand type and stand age across their timber holdings on Vancouver Island. Approximate locations were selected from forest cover maps and field crews determined final locations in the field. Generally, crews selected well stocked sites, and excluded locations in riparian zones, wetlands, or sites with significant unusual edaphic characteristics such as large rock outcroppings (Jim Loucks, pers. comm.).

2.3 Plot treatments and disturbance history

The plots examined in this study represented a range of disturbance histories (Table 4). Plots aged 62 years or younger (age classes 50 years and younger) all originated from harvesting. Plots between 64 and 87 years (75 year age class) originated after both natural disturbances and logging, and plots 90 years and older (age class 125 years and older) originated from natural disturbances only. It is likely that harvesting methods on older sites were different from those harvested more recently.

I used data from plots that had received no silvicultural treatments (i.e. they were not planted, thinned or fertilized). These plots were designated as "natural" or "control" in the PSP database. I used data from the most recent plot sampling date available to calculate trajectories of structural attributes and tree mortality except in old growth plots (>185 years) where data from the original sampling period were used. Based on preliminary examination of the data base I found that data from the original survey of the old growth plots were most reliable. In subsequent surveys, recruitment of new, small stems was not always measured, thus stem densities were sometimes underestimated. The original survey of the old growth plots occurred in 1973 and 1974.

Table 4: Age ranges and number of permanent sample plots for each age class.

Age Class (years)	Age Range (years)	Live Stems and Understory Cover n (# of plots)	CWD Production and Tree Mortality n (# of plots)	Stand Origin
15	10 to 24	15	9	harvested
30	25 to 37	32	28	harvested
50	38 to 62	35	33	harvested
75	64 to 87	36	34	harvested/natural origin
125	90 to 138	33	23	natural origin
175	159 to 185	10	9	natural origin
300	200 +	29	27	natural origin
	Total:	190	163	

2.4 Limitations of the dataset

There are some limitations of the data collected from the permanent sample plots. The minimum size class of stems included in the data varied among plot age classes. MacMillan Bloedel crews did not measure stems smaller than approximately 15 cm dbh (diameter measured at breast height) in old growth plots, and used a limit of approximately 5 cm dbh in the younger plots.

When establishing plots in young stands, crews estimated the age of plots by counting whorls of branches on young stems of appropriate tree species. In older plots they cored some canopy dominants. In old growth plots, although crews attempted to age some canopy dominants, a combination of heart rot and the large size of trees often prevented accurate measurement of tree ages. As a result, ages of many old growth plots were estimated subjectively, based on criteria such as tree size, and density (stems/ha).

Thus age estimates for old growth plots are unreliable. For most analyses this is not a problem because nearly all old growth plots were treated as one category (the 300 year age class). Some old growth plots with an estimated age of 185 years were included in the 175 year age class, but it is very unlikely these plots were older than the youngest plots in the 200 year age class because crews were able obtain good core samples in these plots (Bill Wilson, pers. comm.). However, results should be treated with caution where I present data in scatter plots for stands older than 200 years. Generally, there were no clear trends among old growth plots for most attributes I examined. The one exception where I observed a trend for biomass of very large stems, I discuss further in section 3.2.

Survey crews did not sample standing crops of snags and down wood during surveys of permanent sample plots so I was unable to examine trajectories of these attributes. However, I was able to examine production of standing and down wood because crews recorded mortality of individual trees during re-surveys of plots, which occurred approximately every five years. For my analyses of tree mortality, I used data from two surveys, generally 5 years apart (3-8 year range) for all plots except old growth plots. For old growth plots, I used data from three samplings, spanning 15 years, because many plots experienced no mortality over 5 years.

2.5 Statistical analysis

I chose seven age classes to represent trajectories and calculate statistics of some attributes (Table 4). I selected age classes subjectively, based on examination of scatter plots of live stem density (stems/ha) and percent understory cover. I attempted to match age classes to thresholds of attribute levels (e.g. thresholds in the number of stems/ha), and age gaps in the database. In general, I chose narrow age classes for younger plots, where attribute values change rapidly with stand development; and wider age classes for older plots, where attribute values change more slowly. Because plots were distributed over a wide geographic area, I examined scatterplots of location for each age class. Generally, plots in each age class were distributed over the full geographic area, although for the 125 and 175 year age class, no plots were located among the northernmost plots. Of the plots on the mainland coast, four were in the 300 year age class, one was in the 30 year age class. I had more plots available for analysis than I used for the 30, 50 and 75 year age classes. To maintain similar sample sizes among age classes, I used the RAND function in Excel (Microsoft 1994) to pseudo-randomly select plots from those available for analysis of these age classes.

I undertook a number of statistical analyses in my study. I calculated means and standard errors of stand attributes for each age class (in some cases stratified by site index) to examine trends. I used analysis of variance to compare attributes among age classes (SYSTAT; Wilkinson *et al.* 1992). I transformed proportional data from the canopy class, and tree mortality analyses using an arcsin transformation (Zar 1984) before statistical analysis to improve the normality of sample distributions. I used non-parametric tests for comparisons of understory cover and biomass of dead stems (SPSS; Norusis 1993) because I observed high heteroscedasticity in variance among age classes for these attributes. Where Mann-Whitney U tests were used to compare among multiple means, *P* values were checked for significance using the sequential Bonferroni correction (Rice 1989).

For some analyses, I stratified plots into "high" and "low" site index (SI) classes. Site index is a measure of site productivity based on estimates of the mean canopy height at a stand age of 50 years (Watts 1983). For plots younger than 185 years (age classes 125 and younger), I designated stands with an average site index of 30 m and greater as "high' and the remainder as "low". Strictly speaking, SI values above the low to mid twenties are not normally considered "low", but I was more concerned with relative than absolute differences among SI classes. Though I chose the site index cut-off of 30 m to provide the best balance of sample sizes between SI classes, plots under 50 years are biased to the low SI class and plots aged 50 to 80 years are biased to the high SI class. This bias in SI is likely due to the historical sequence of harvesting. Harvesting likely initially occurred on very productive sites and then moved to sites of decreasing productivity as the more productive sites were harvested.

For old growth plots (175 and 300 year age classes), I chose a SI cut-off of 25 m or greater for "high" sites rather then the SI cut-off of 30 m I used for younger stands. I used a different SI cut-off for old plots because the results of preliminary analyses suggested that SI values in these plots were underestimated compared to younger plots; for many attributes, trajectories showed an abrupt shift between the 125 and 175 year classes in (e.g. stem densities which had been declining would show an increase in the 175 year class and then decline again). When I used a SI cut-off of 25 m, this shift no longer occurred.

The consistent underestimation of SI in old growth stands of the CWH is recognized among foresters (Jeff Stone, pers. comm.). One reason that this occurs is because the older a stand becomes, the more difficult it is to estimate stand height at the 50 year index age. Old growth stands can be many centuries older than 50 years and mean tree height of the canopy in these stands will increase minimally if at all. In contrast, the growth curves commonly used to estimate SI assume mean canopy height continue to increase with stand age, so for very old stands, estimates tend to be low (Jeff Stone, pers. comm.). For example, a recent study demonstrated that SI values were underestimated by over 10 m for plots examined in the CWH wet submaritime variant (Nigh and Love 1996). Partly as a consequence of those results, there is a substantial effort underway to re-evaluate SI for old growth in the CWH (Gordon Nigh, pers. comm.).

I determined differences between SI classes for different age classes using a separate variances t-test (SYSTAT; Wilkinson *et al.* 1992). Because I tested for significant differences for multiple age classes, I determined appropriate *P* values for significance using a sequential Bonferroni correction (Rice 1989).

In Section 3.5.2, I present results of a multiple linear regression of stand density against age, site and geographic variables. For the regression, no independent variable with tolerances less then 0.1 were allowed to remain in the model to avoid collinearity among independent variables (Hair *et al.* 1992). The dependent variable (stem density, all stem diameters) was inverse transformed to improve linearity (Kleinbaum *et al.* 1988). I included aspect as an independent variable of the model. I converted aspect values whereby values greater than 180 were subtracted from 360 so that increasing aspect was equivalent to increasing southern exposure. I performed the multiple regression using SYSTAT (Wilkinson *et al.* 1992).

For many stand attributes, I present data plotted against stand age. I used LOWESS smoothing (Cleveland 1981; Wilkinson *et al.* 1992) to produce best fit lines of some attribute trajectories. LOWESS produces the best fit line by determining predicted values of Y for a given X based on a weighted average of local Y values.

2.6 Estimation of biomass

I used equations compiled by Means *et al.* (1994) to estimate the above ground portion of bole biomass from dbh for individual stems analyzed in this study. Means *et al.* (1994) compiled species specific and sometimes size specific equations used for estimating biomass that were developed from data collected in stands west of the Cascade mountains in Washington and Oregon. I chose biomass equations from Means *et al.* (1994) to match the species and ranges of dbh in the data that I analyze in my study. For western hemlock, Pacific silver fir (*Abies amabilis*) and Douglas-fir, diameter ranges of trees analyzed in my study were within the range of those used to develop the equations. For western redcedar (*Thuja plicata*) and Sitka spruce (*Picea sitchensis*), diameters were below the minimum used to develop the regression equations so my results may be biased for these species. Equations were not available for a few tree species such as western yew (*Taxus brevifolia*) and western white pine (*Pinus monticola*). Because the latter species were found in very small numbers and only in few plots, equations for other species were substituted. Appendix 1 lists the equations that I used.

2.7 Estimation of canopy closure

I used the following relationship to estimate mean canopy closure (MCC):

$$MCC = 1\text{-}e^{-0.2906RD^{0.8437}}$$
$$RD = BA/Dq^{0.5}$$
$$Dq = (BA*40{,}000/\pi*D)$$

RD = relative density; BA = basal area/ha (m^2/ha); Dq = estimate of quadratic mean of stem diameter/plot (cm); D = stem density (stems/ha).

MacMillan Bloedel Ltd. developed the equation (Smith 1989), based on a non-linear regression of RD (Curtis' relative density; Curtis 1982) against canopy closure measured with a "moosehorn" viewing device (Garrison 1949) which had an angle of view of 10.2°. For the regression, Smith (1989) used data collected from 49 plots with age ranges of 20 to 80 years. The regression was significant ($P<0.05$) and had a standard error of estimate (S_{yx}) of 0.095, or 9.5% mean canopy closure.

3. RESULTS

3.1 Species composition and canopy position of overstory trees

Western hemlock is the most common tree species found in the plots (Figure 3). Other common species include Pacific silver fir and western redcedar. Some species were not abundant (trees classified as 'other' in Figure 3), but present in some plots. Of these, Douglas-fir and Sitka spruce were the most common species. Yellow-cedar (*Chamaecyparis nootkatensis*) was observed in a few plots. Deciduous species were rarely observed, although red alder (*Alnus rubra*), broadleaf maple (*Acer macrophyllum*) and willow (*Salix spp.*) were present in a few plots. The presence of western hemlock, Douglas-fir and western redcedar is consistent with what is expected for the CWHvm1 variant as is the relative paucity of Douglas-fir, Sitka spruce, broadleaf maple and willow (Green and Klinka 1994; Meidinger and Pojar 1991). Green and Klinka (1994) found higher levels of red alder than I observed in some site series of the CWHvm1.

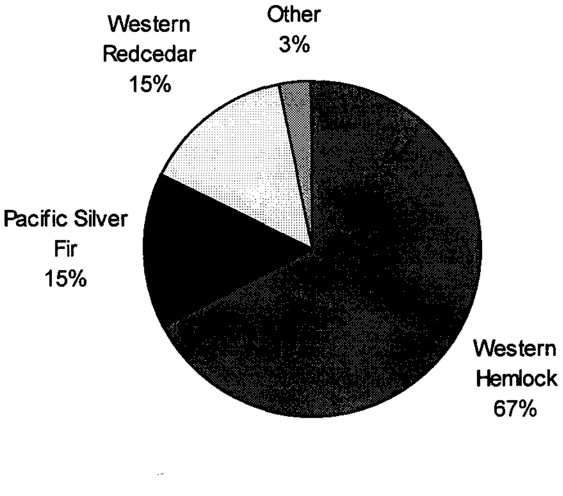


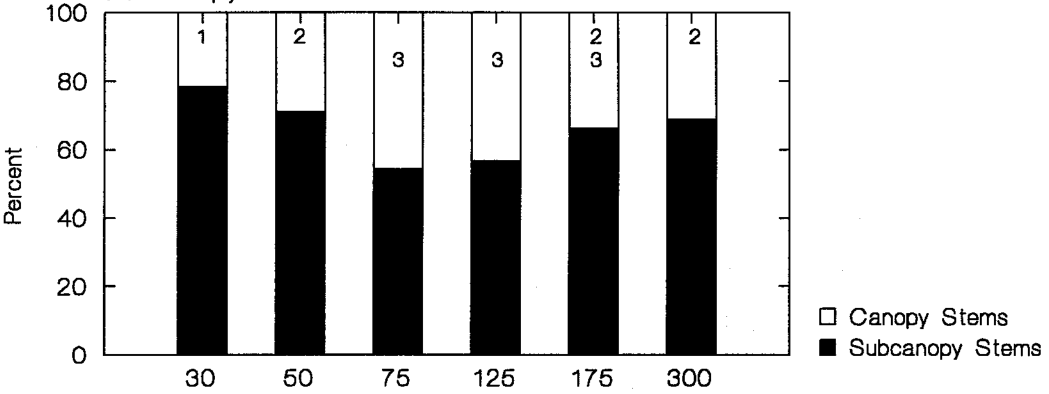
Figure 3: Species composition of 190 plots (over 12,000 trees) in the CWHvm1. Species included in "other" are Douglas-fir, Sitka spruce, yellow-cedar, red alder, broadleaf maple and willow.

I expected the proportion of live stems under the forest canopy to decrease relative to canopy stems during the stem exclusion stage of stand development (Oliver 1981; Table 1). The proportion of subcanopy stems relative to canopy stems did vary among age classes (ANOVA df=5, 176; F=16.00; $P < 0.001$). The proportion of subcanopy stems decreased in intermediate-age classes (Figure 4a; Tukey's HSD test for multiple comparisons) and declined in number as well (data not shown), suggesting that stem recruitment is constrained for these age classes. Proportions of species were similar between canopy classes with the following exceptions: in the 50, 75 and 125 age classes, the proportion of hemlock increases in the canopy relative to the subcanopy and redcedar is virtually absent from the canopy layer (Figures 4b and 4c).

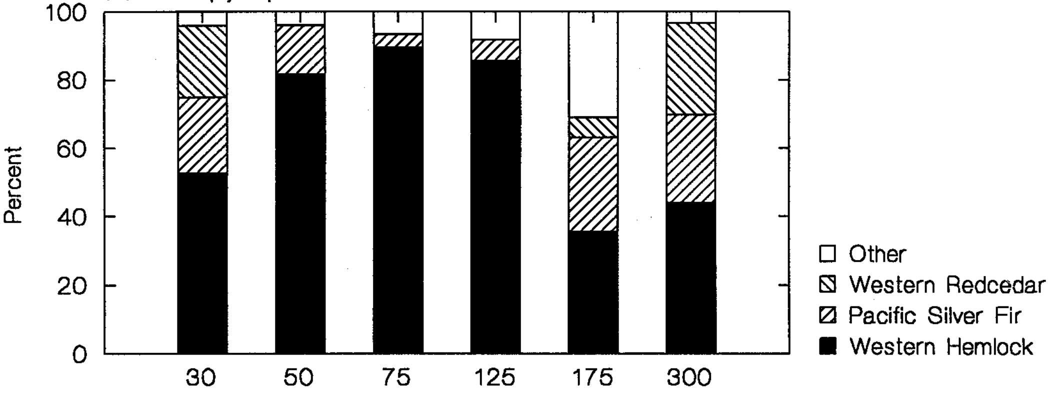
I predicted that the distribution of stem diameters would display the skewed "reverse-J" distribution typical of recruiting populations in young and old stands and display a more normal distribution in intermediate-aged stands (Table 3) because recruitment is suppressed during stem exclusion. Young and old stands had highly skewed and lepto-kurtotic size distributions, whereas the distributions in intermediate-aged stands were more normal in shape (Figures 5a to 5f). Although none of the distributions are truly normal (Kolmogorov-Smirnov test, $P < 0.01$, see Table 5 for sample sizes), skewness and kurtosis decrease as age classes increase from 30 to 125 years, and increase again though the 175 year and 300 year age classes (Table 5).

The distributions of stem diameters are consistent with the relative abundance between canopy and subcanopy stems (Figure 4): recruitment of small stems is constrained in intermediate-aged stands (50, 75 and 125 year age classes). Moreover, increases in recruitment require very long periods of time: an increase in abundance of the smallest size classes of stems did not occur until the 125 year age class. Further, the "reverse-J" shaped size distribution characteristic of very old stands (Leak 1965) did not appear until the 300 year age class (Figures 5a to 5f). The diameter distribution in the

(a) canopy classes



(b) canopy species



(c) subcanopy species

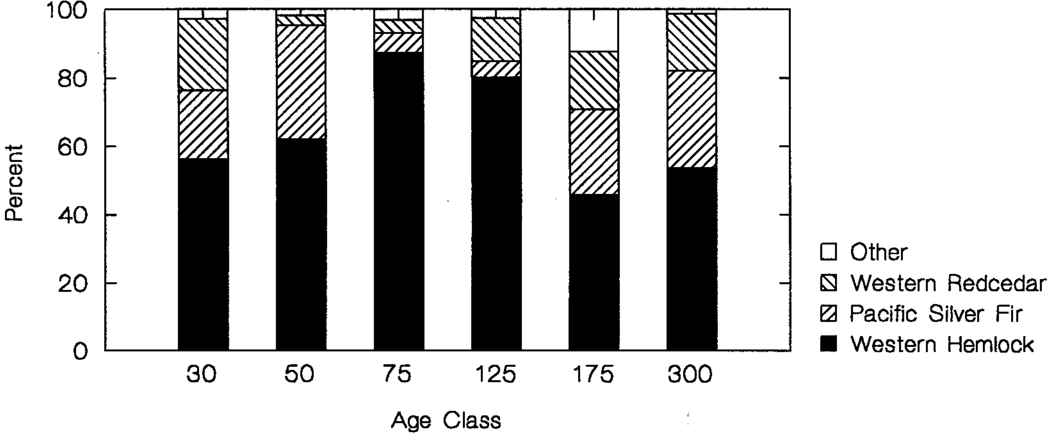


Figure 4: Mean proportional distribution of stem density by canopy class (a), canopy species (b) and subcanopy species (c). Numbers in (a) show statistically similar canopy classes (Tukey's HSD; $P > 0.05$ for significance).

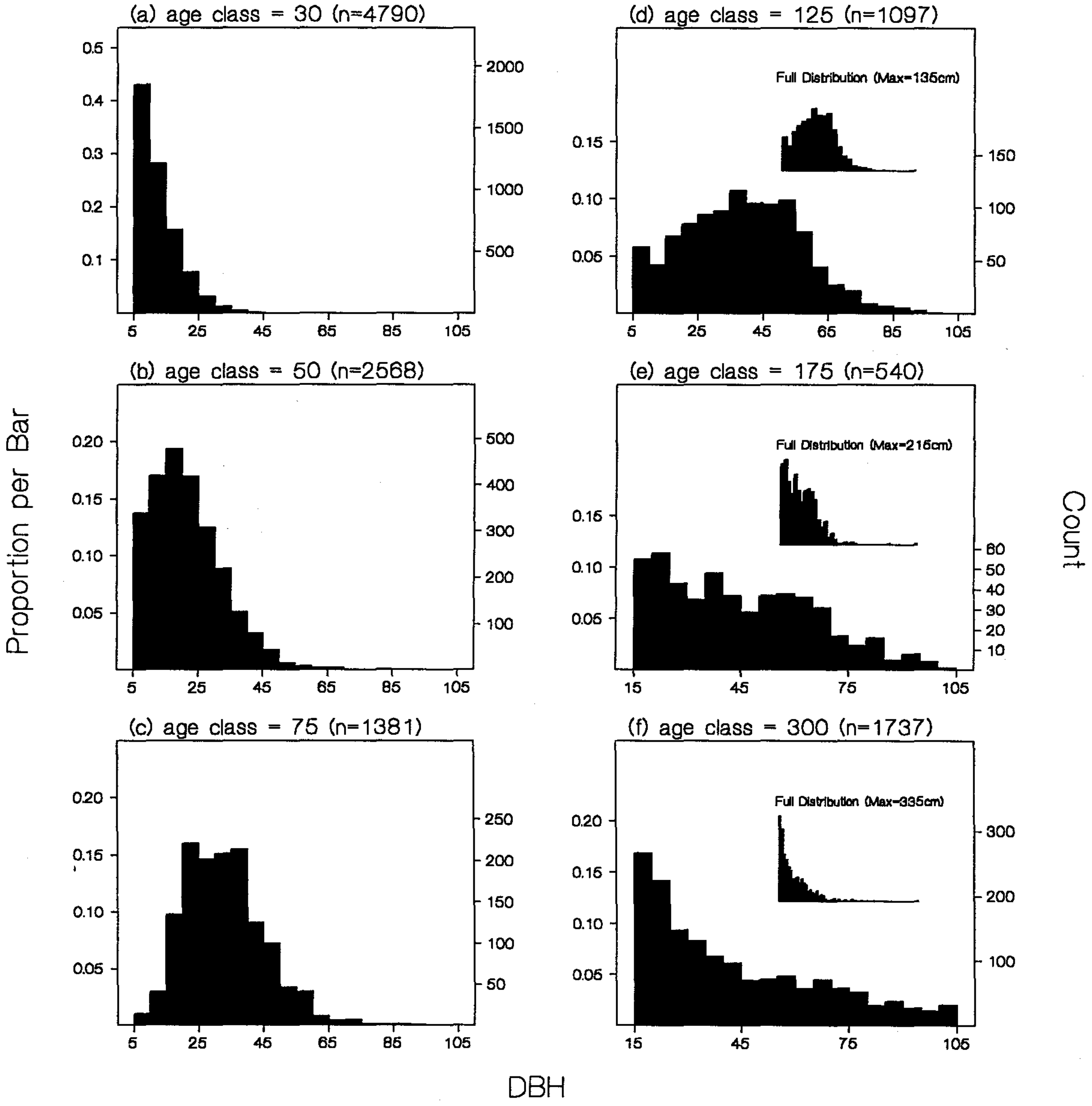


Figure 5: Diameter distributions of live stems. Insets show full distribution where maximum stem diameter exceeds 105 cm. Stems ≥ 5 cm dbh are shown for 30 to 125 year age classes, and stems ≥ 15 cm dbh are shown for 175 and 300 year age classes. n = total number of stems.

oldest age class (300 year) was significantly different than the next youngest class (Kolmogorov-Smirnov test, $P < 0.01$, see Table 5 for sample sizes).

Spies and Franklin (1988) predicted that as mean stem diameter increased with age, the variation in tree diameter would also increase. I observed increasing variation in standard deviation (SD) of dbh with stand age (Table 5). Alternatively, relative variation, as measured by the coefficient of variation (CV) displayed a "U" shaped trajectory, although the CV for the 300 year age class was greater than that observed in young age classes. Thus the shape of the distributions of stem diameter is similar in young and old stands, as is the relative variation in stem diameters, but not the size range of stem diameters.

Table 5: Variation in dbh of live stems (≥ 5 cm dbh). In 175 and 300 year age classes small stems (5-14 cm dbh) were not measured.

Age Class	Number of Stems	Mean dbh (cm)	SD	CV	Skewness	Kurtosis
30 years	4790	11.79	6.87	0.58	2.11	13.37
50 years	2568	20.88	11.39	0.54	1.15	4.21
75 years	1381	32.70	12.33	0.38	0.71	1.02
125 years	1097	38.42	18.48	0.48	0.33	0.33
175 years	540	45.13	24.61	0.55	1.38	5.11
300 years	1737	50.44	37.70	0.78	2.15	7.29

3.2 Trajectories of stand density and biomass

I predicted that stand density decreases (Table 3), and stand biomass increases with age ("S" shaped trajectory; Table 3). The density of live stems (stems/ha) initially declined exponentially with increasing plot age (Figure 6a). The rate of decline slowed in older age classes. Differences in stem density among younger age classes were

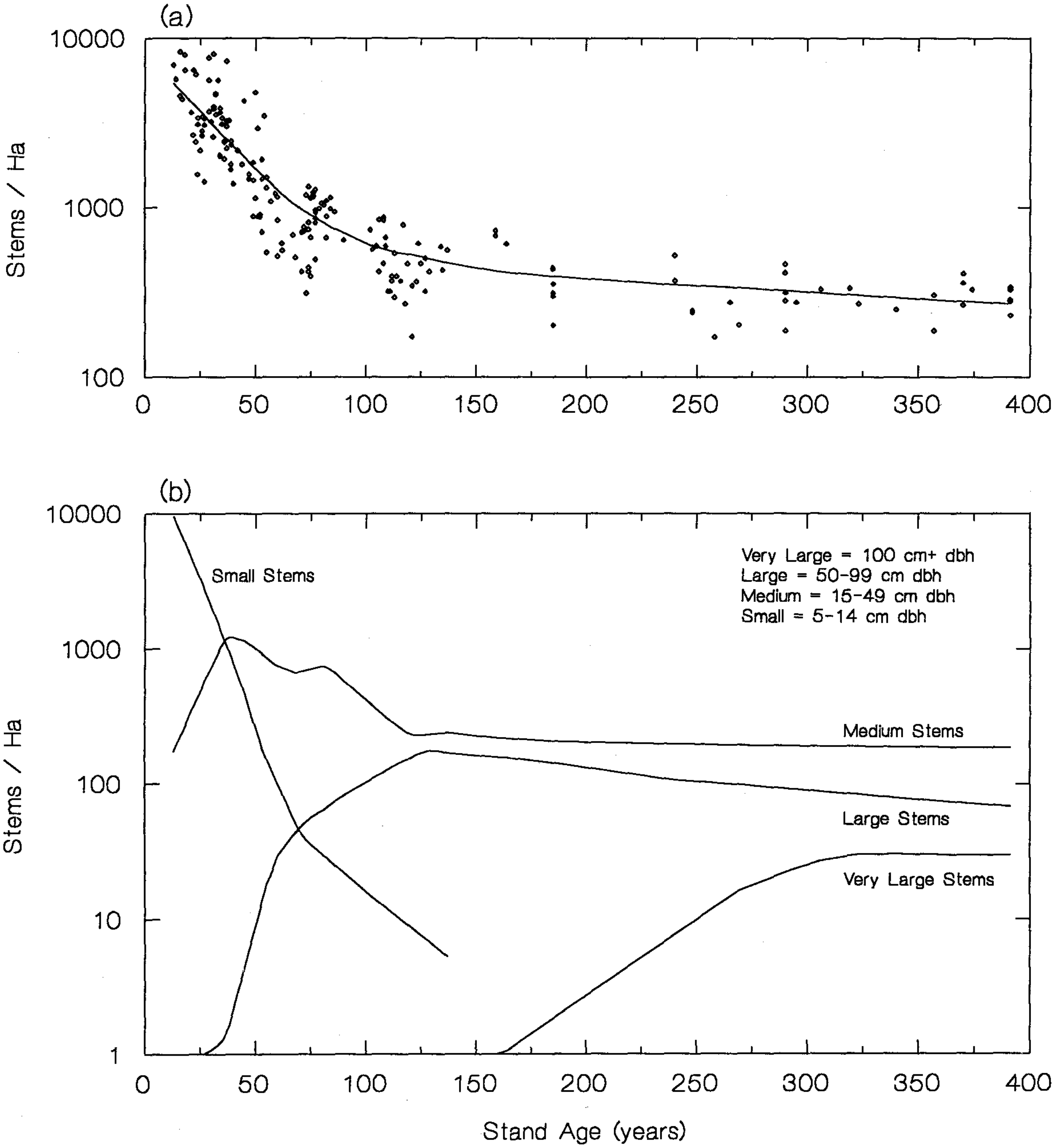


Figure 6: Total density of live stems (a; stems/ha; stems ≥ 5cm dbh), and stem density (b) by size class. The lines are distance-weighted least square smoothings of the data (Wilkinson *et al.* 1992).

significant (15, 30 and 50 year age classes; Tukey's HSD; $P \leq 0.009$). There was no significant decrease, however, in density for age classes 75 years and older (Tukey's HSD; $P > 0.30$), although means continued to decline.

Total stem biomass (Mg/ha) increased with plot age (Figure 7a) as predicted (Table 3). Initially, the increase was rapid, but the rate of increase gradually declined as stands aged. Increases in biomass were significant among younger age classes (30, 50 and 75 year classes; Tukey's HSD; $P \leq 0.03$), although there was no significant difference between the 15 and 30 year classes (Tukey's HSD; $P = 0.18$). Biomass showed significant increases among older age classes as well: the 300 year age classes had significantly more biomass than 75 and 125 year age classes (Tukey's HSD; $P < 0.01$). Biomass did not appear to decline in very old stands although there was substantial variation among plots (Figure 7a).

I did not make *a priori* predictions about changes in the distribution of stem density and biomass among stems of different diameter classes with stand age. I did anticipate that the appearance of larger size classes of stems would be delayed as a consequence of the increasing time required for trees to grow to larger size classes. Further, my predictions about change in diameter distributions (Table 3; see previous section) led me to expect small sizes of stems to decline during intermediate-age classes, as recruitment becomes constrained during stem exclusion. Conversely, I expected smaller size classes of stems to be most abundant in very young and very old stands as a consequence of a reverse-J shaped diameter distribution.

Stem density for *small* stems (5-14 cm dbh) started at a very high initial densities of stems (Figure 6b). Unfortunately, small stems were not measured in old growth plots (>185 years), so I was unable to determine the trajectory of this size class in older stands. Density of *Medium* stems (15-49 cm dbh) initially increased, peaked around 50

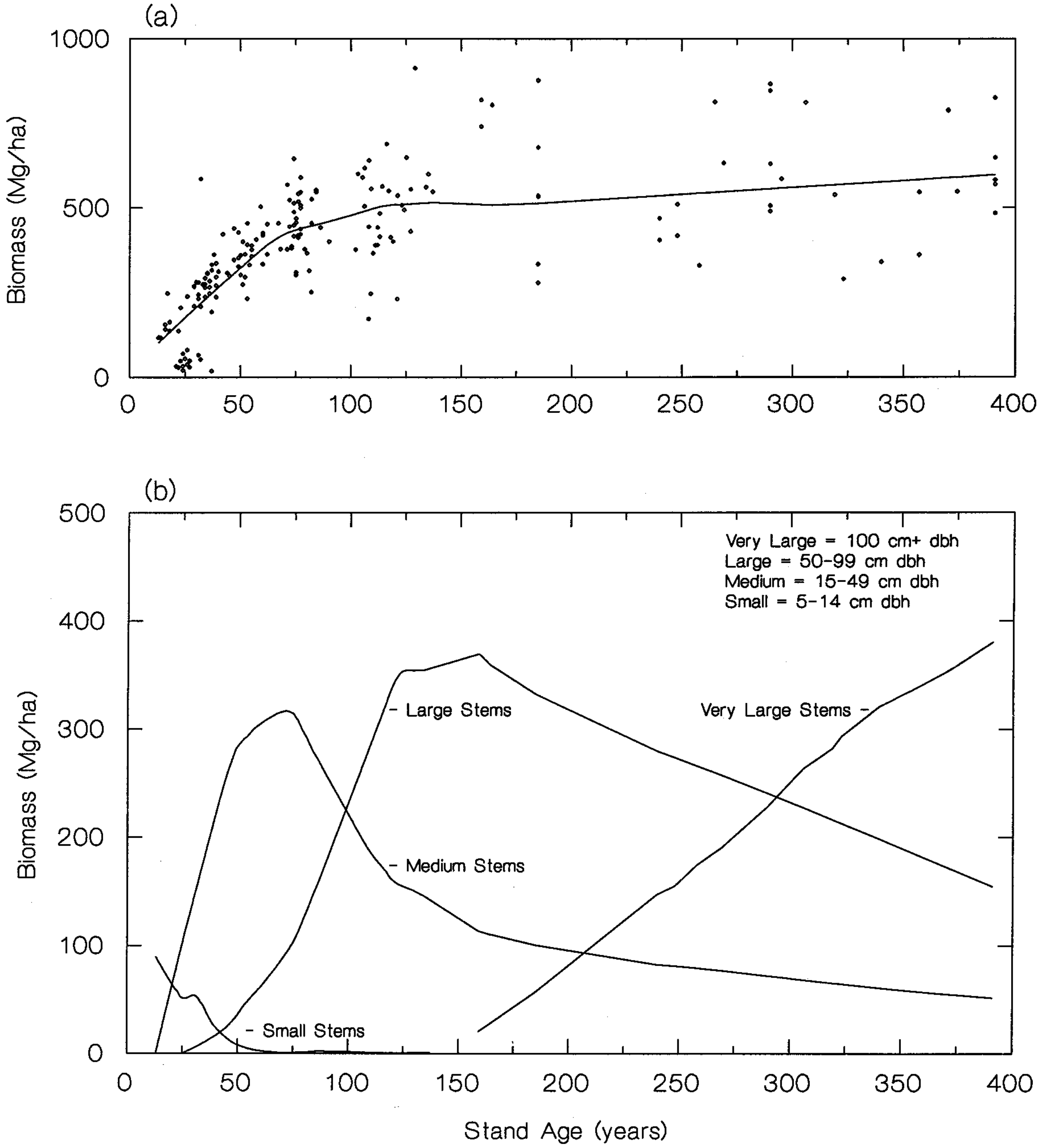


Figure 7: Total biomass of live stems (a; Mg/ha; stems ≥ 5cm dbh), and stem biomass (b) by size class. The lines are distance-weighted least square smoothings of the data (Wilkinson *et al.* 1992).

years, then declined rapidly until about 125 years, thereafter declining gradually. *Large* stems (50-99cm dbh) did not appear until 30 years, thereafter rapidly increasing in density, peaking around 125 years, then declining gradually.

In general, over the first 125 years, the change in density of stems is very dynamic for all size classes, thereafter change occurs much more gradually, with one exception: *very large* stems (100 cm + dbh) did not appear in plots younger than 185 years (the 175 year age class), with the exception of a few very large trees observed in a small number of younger plots (data not shown). Further, very large stems only become abundant in the oldest plots: significantly higher density of very large stems were found in the 300 year age class than any younger classes (Tukey's HSD; $P < 0.001$). Overall, medium stems remained more abundant than large stems, which in turn were more abundant than very large stems for all ages of plots. Only small stems declined to lower densities than stems of larger size classes. Small stems were not measured in the two oldest age classes, so it was not possible to determine if the density of this size class increased in those age classes.

Stem biomass (Mg/ha), like stem density (stems/ha), increased and then declined with stand age for medium and large stems (Figure 7b). Biomass of small stems was low initially and declined rapidly to very low levels and biomass of very large stems steadily increased after the stems of this size class first appear (with the exception of the few trees previously noted) in plots aged 185 years. As with stem density, I was unable to examine trends in the biomass of small stems in older stands.

While density of very large stems appeared relatively stable in very old stands, biomass was not (Figure 7b). For example, biomass of medium stems in the 50 and 75 year classes are significantly different than that in the 125 and older classes and biomass of medium stems in the 125 year class are significantly different than that in the 300 year age class (Tukey's HSD; $P < 0.001$). The same significant differences occurred among biomass of large stems, with additional significant differences between the 50 and 75 year classes, and between the 175 and 300 year classes (Tukey's HSD; $P \leq 0.006$). As with stem density, stem biomass of very large stems is significantly higher than any younger classes (Tukey's HSD; $P < 0.001$). Biomass of very large and large stems appears to undergo substantial change in the 300 year age class (Figure 7b). However, there is some uncertainty regarding the ages of plots in that age class (see Methods), so these results should be treated with caution.

3.3 Understory vegetation

I expected abundance of understory vegetation to follow a "U" shaped trajectory (Figure 1; Table 3), as initially vegetation cover declines during stem exclusion and then recovers during understory reinitiation (Oliver 1981; Table 2). I found that percent cover of understory vegetation (including herbaceous plants, shrubs and advanced regeneration of live stems) was significantly influenced by stand age (Figure 8; Kruskal-Wallis test; df = 6, 184; $H = 75.510$; $P < 0.001$). As predicted, cover was highest in the youngest and oldest stands, but low in the intermediate-age classes. Cover in the youngest age class (15 years) was significantly more than that in the 30, 50 and 75 year plots (Mann-Whitney U test; $P < 0.003$) and the 30 year age class was significantly less than that in the 50 and 300 year classes (Mann-Whitney U test; $P < 0.002$). The 50 year age class was significantly different from the three oldest age classes (125, 175 and 300; Mann-Whitney U test; $P \leq 0.009$) and the 75 year age class was significantly different from the 125, 175 and 300 year age classes (Mann-Whitney U test; $P < 0.003$). There were no significant differences in understory cover among the three oldest age classes (125, 175 and 300; Mann-Whitney U test; $P > 0.10$). Overall, these results indicate that recruitment of young stems, shrubs and herbs are constrained in stands of intermediate-age classes.

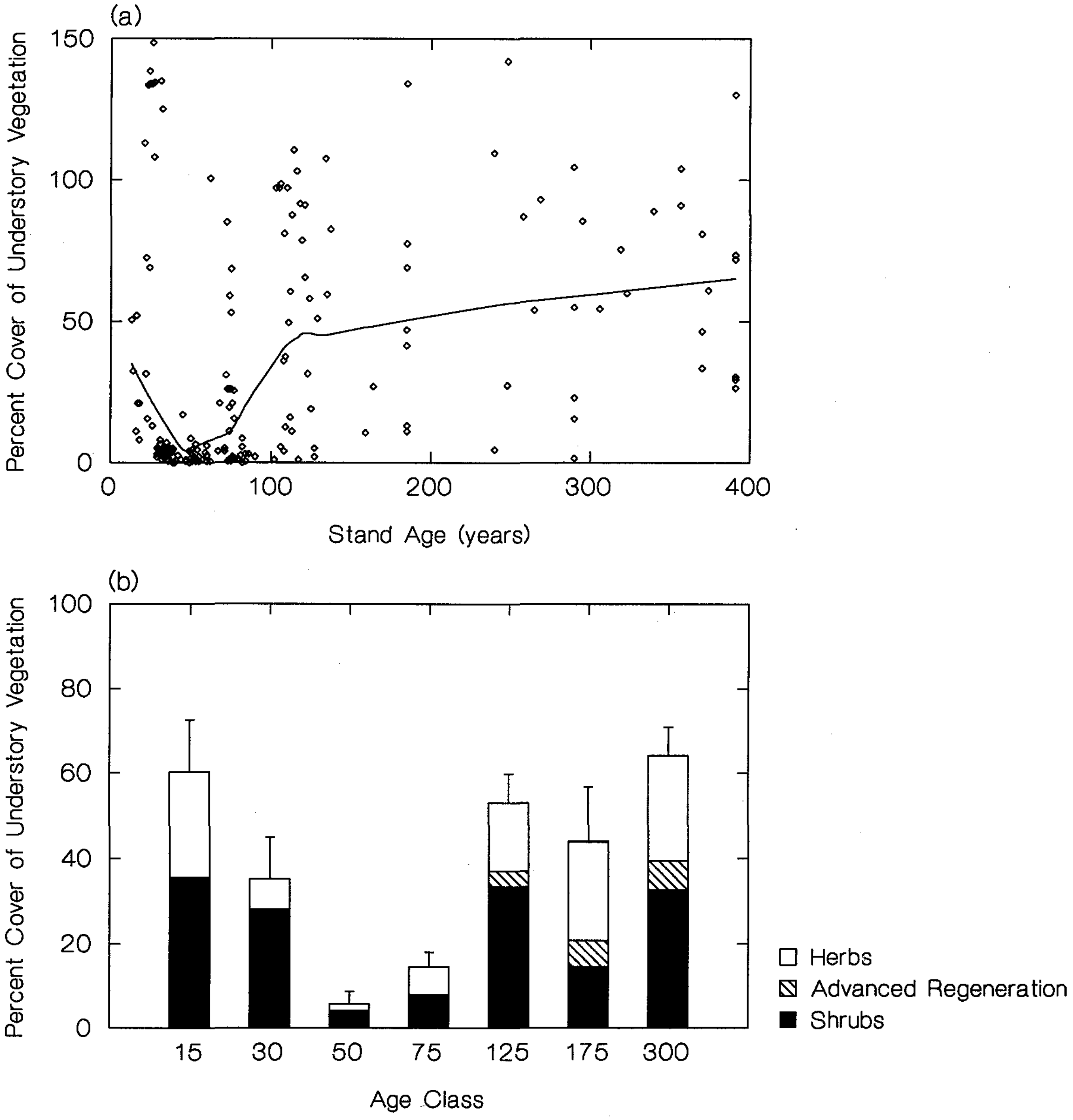


Figure 8: Percent cover of understory vegetation by age (a) and age class (b; Mean, SE). Advanced regeneration is an estimate of cover of live stem saplings. The line in (a) is a distance-weighted least square smoothing of the data (Wilkinson *et al.* 1992).

The degree of canopy openness is one factor thought to influence the abundance of understory vegetation, primarily by affecting the amount of solar radiation that reaches the forest floor (Alaback and Tappeiner 1991; Chazdon and Pearcy 1991; Halpern and Spies 1995). Canopy openness was not measured directly for the plots examined in this study, but I was able to estimate this characteristic from stand basal area and mean stem diameter (see Methods).

In general, for age classes 50 and older, where estimates of canopy closure were high, percent cover of understory vegetation was low (Figures 8 and 9). When I examined this relationship more directly, for plots 25 years or older (30 year age class), I found that there appeared to be a threshold at approximately 45 percent canopy closure, below which levels of understory cover appeared to be mostly independent of canopy closure (Figure 9), but above which appeared to be highly influenced by canopy closure. There also appeared to be high percent cover of understory vegetation on a few sites with very high canopy closure (Figure 10).

Understory cover appeared to follow a pattern of abundance that is roughly inverse to the density of medium sized stems (see Figures 15 and 16). I examined the relationship of this size class of stems with mean canopy closure. The two variables were strongly correlated and highly linear (Figure 11b; $r^2 = 0.70$, df = 1, 173; F = 400.33; $P > 0.001$), whereas the relationship between total stem density and mean canopy closure is clearly non-linear (Figure 11a). The strong linear relationship suggests that medium stems have a disproportional effect on canopy closure compared to other size classes. A few outliers can be seen in Figure 11, these may be plots where stems in the small size class influence the estimate of canopy cover.

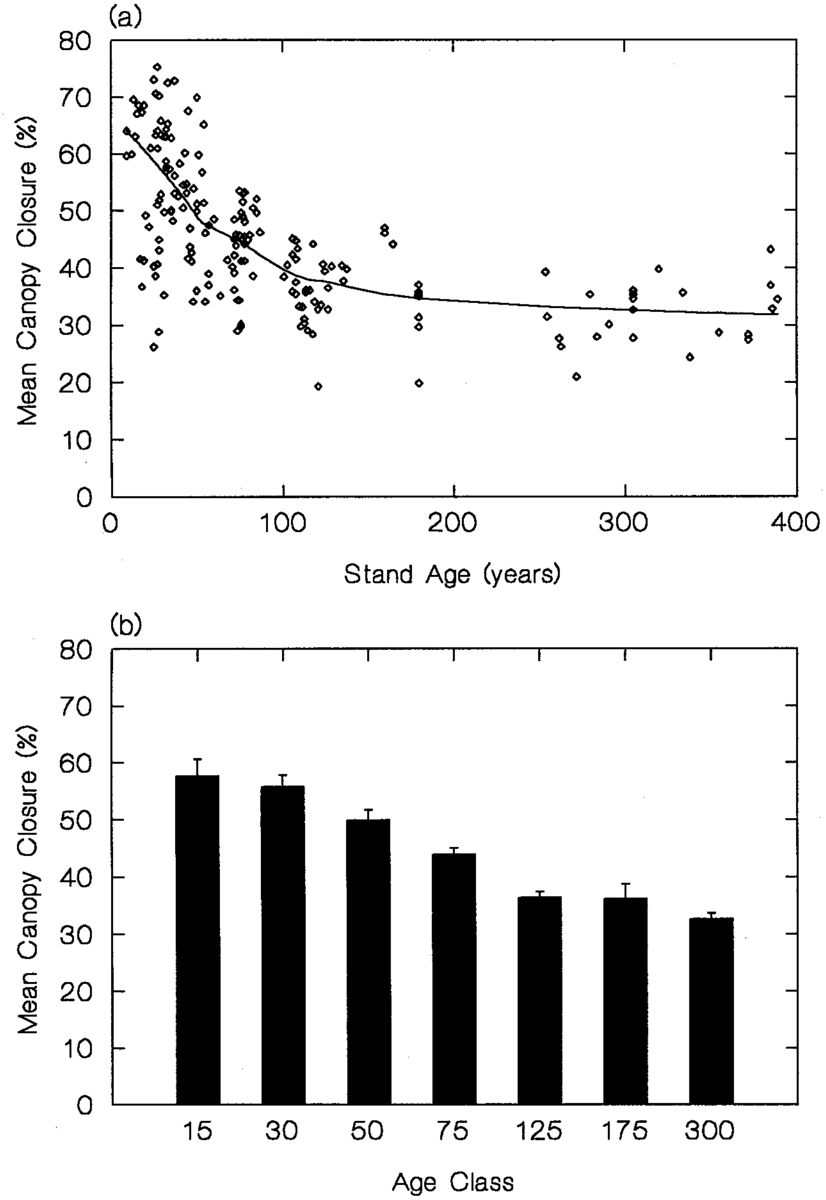


Figure 9: Estimate of mean canopy closure by age (a) and age class (b; Mean, SE). The line in (a) is a distance-weighted least square smoothing of the data (Wilkinson *et al.* 1992).

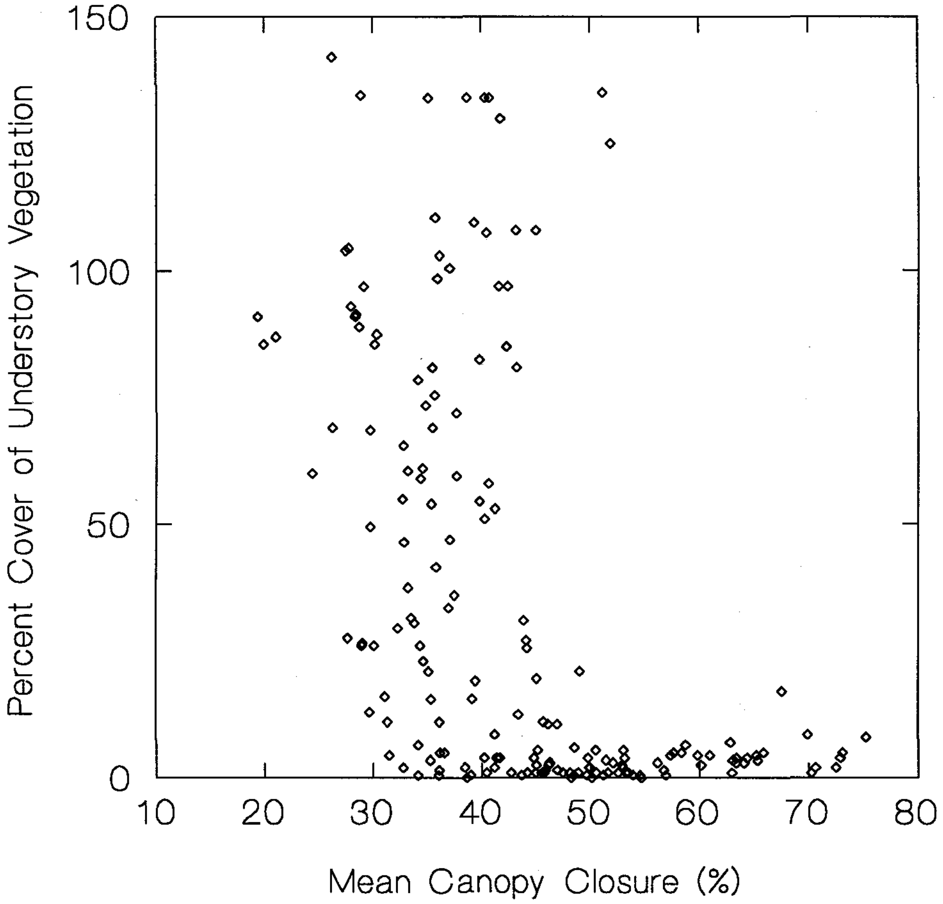
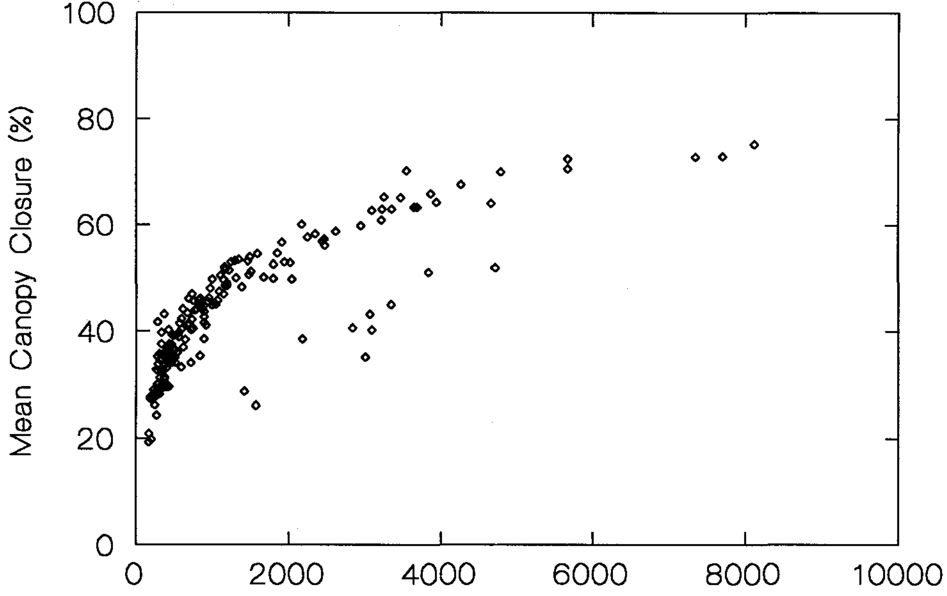
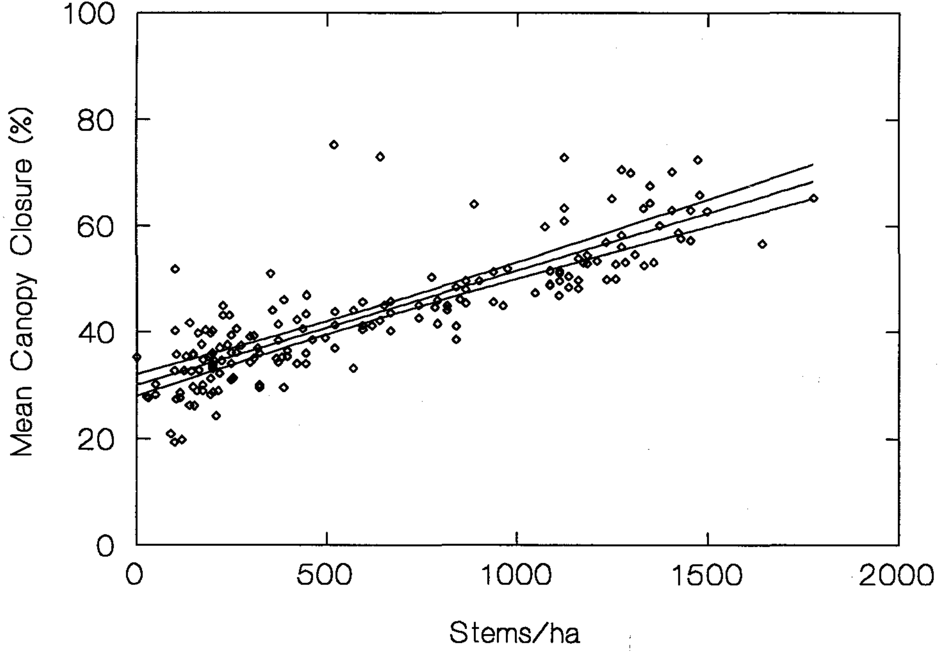


Figure 10: Percent cover of understory vegetation and mean canopy closure. The figure shows plots aged 25 years (30 year age class) or older.



(a) all stems



(b) medium size stems

Figure 11: Mean canopy closure for all stems (a; ≥ 5 cm dbh) and medium size stems (b; 25-49 cm dbh). The figure shows plots aged 25 years (30 year age class) or older.

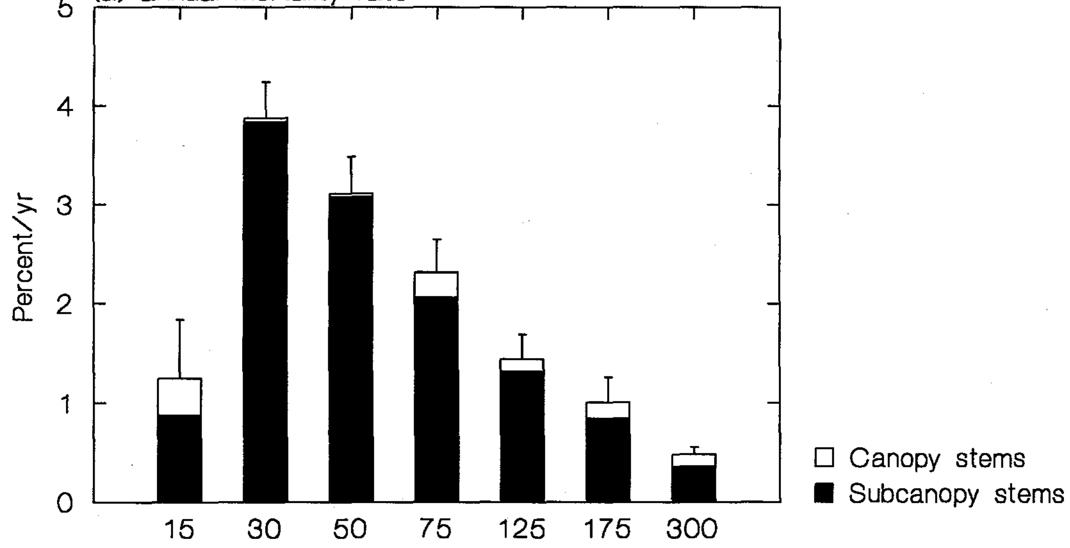
3.4 Tree mortality

I expected an inverted "U" shaped trajectory for mortality rates of trees (Table 3) as rates initially increased during stem exclusion, then declined during understory reinitiation (Table 2). Mortality rates did vary among age classes (ANOVA df = 6, 162; F = 18.45; $P < 0.001$) following an inverted "U" shaped trajectory as predicted (Figure 12). For the 15 year age class, mortality was significantly lower than in the 30 and 50 year age classes (Tukey's HSD; $P \leq 0.009$) and the 30 year class was significantly higher than in the 75 and older classes (Tukey's HSD; $P \leq 0.005$). Mortality in the 50 year class was significantly higher than in 125 and older classes (Tukey's HSD; $P \leq 0.003$) and the 125 year class was significantly higher than in the 300 year class (Tukey's HSD; $P \leq 0.02$).

I also examined the proportion of mortality that occurred among canopy trees relative to understory trees. As stands aged, I expected an increase in mortality among understory trees relative to canopy trees as stands moved from initiation to stem exclusion stages and a decline in mortality from understory trees to canopy trees as stands moved from stem exclusion to understory reinitiation. I found that the proportion of stems in each canopy class did change with age (ANOVA df = 6, 162; F = 4.67; $P < 0.001$; Figure 12b). The proportion of stems in each canopy class in the 300 year age class were significantly different than plots in the 30, 50 and 75 year age classes (Tukey's HSD; $P \leq 0.003$). Most of the shift in proportion of mortality between canopy classes was due to changes in mortality rate among subcanopy stems. There was also a decrease in mortality rate among canopy trees between 15 and 30 year age classes, and an increase between the 50 and 75 year age classes (Figure 12a).

Annual production of dead stems (stems/ha-yr; Figure 13) followed a similar pattern to tree mortality rates (percent per annum), although the increase in the 30 year

(a) annual mortality rate



(b) percent mortality by canopy class

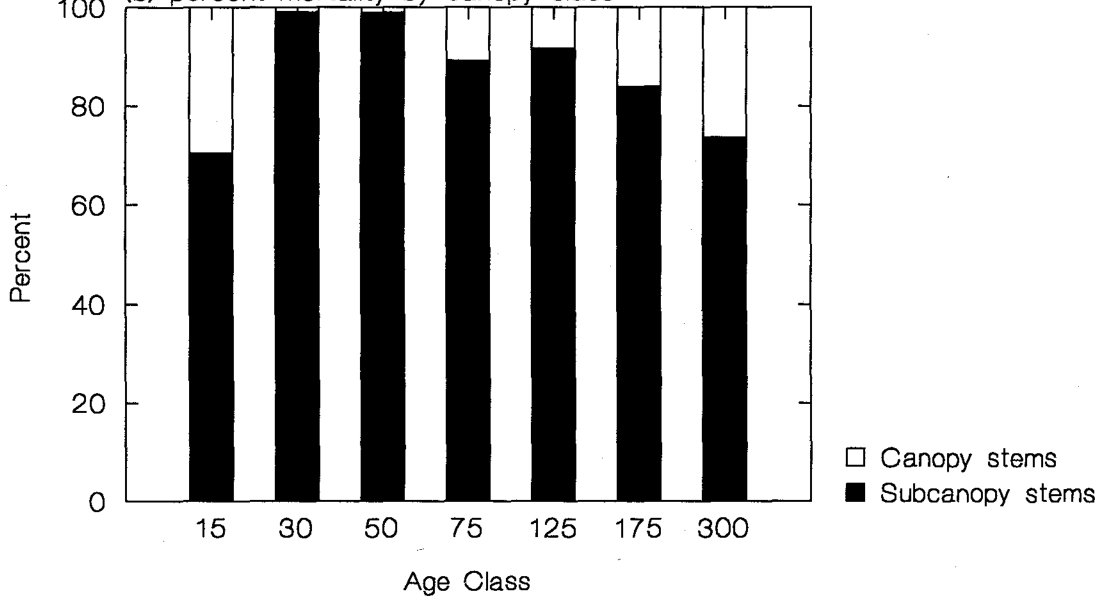
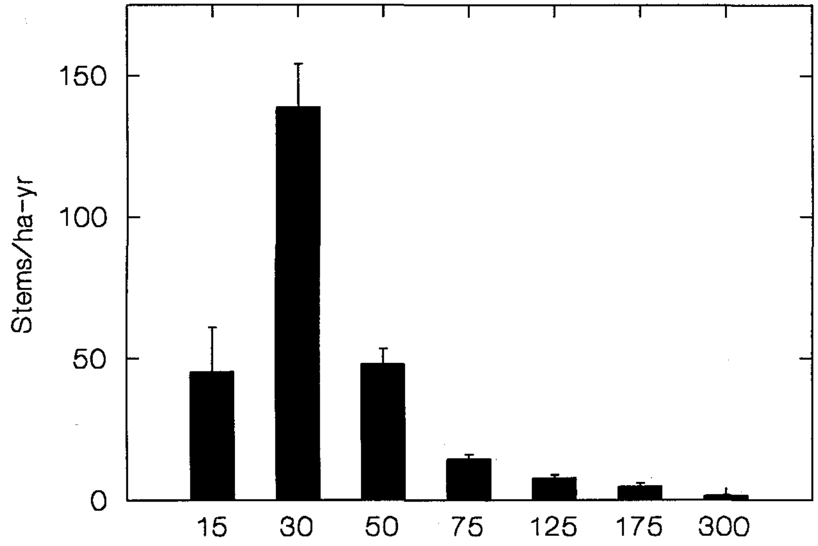


Figure 12: Annual mortality rate and percent mortality among canopy classes for all stems (≥ 5 cm dbh). In 175 and 300 year age classes small stems (5-14 cm dbh) were not measured.

(a) all stems



(b) large stems (50-99 cm dbh)

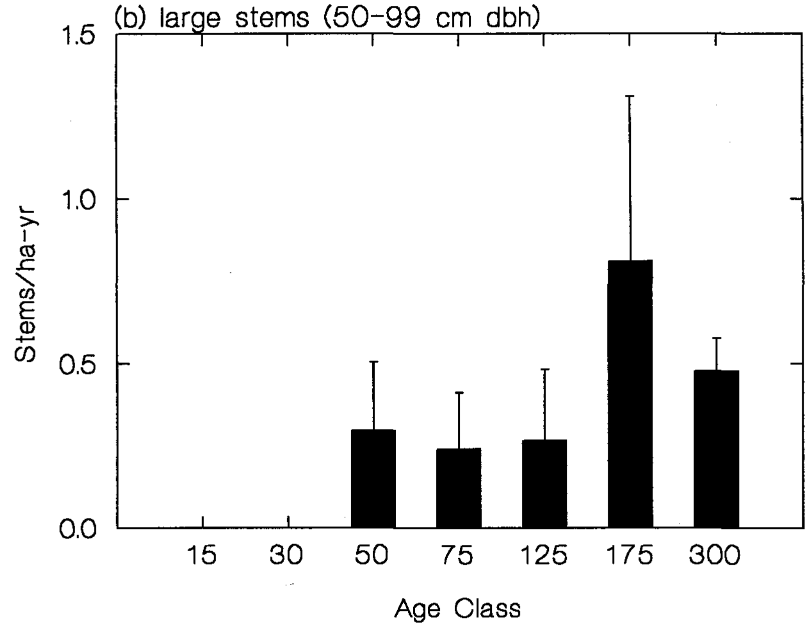


Figure 13: Annual production of dead stems for all stems (a; ≥ 5 cm dbh) and large stems (b; 50-99 cm dbh). In 175 and 300 year age classes small stems (5-14 cm dbh) were not measured.

age class relative to 15 and 50 year classes is marked compared to changes in mortality rate for the same age classes. The differences in annual production of dead stems among age classes was significant (ANOVA df = 6, 162; F = 36.11; $P < 0.001$). The trajectory was an inverted "U" shape: mortality for the 15 year age class was significantly different than that for the 30 year class (Tukey's HSD; $P < 0.001$); the 30 year class was significantly different from all older classes (Tukey's HSD; $P < 0.001$); and the 50 year class was significantly different than all older classes except the 125 year class (Tukey's HSD; $P \leq 0.03$).

Production of large (50-99 cm dbh) and very large dead stems (≥ 100 cm dbh) was largely restricted to older age classes. For the 50, 75 and 125 year age classes, mortality of large stems was sporadic: many stands had no mortality of large stems, a few had rates well above the mean (between 1-5 stems/ha-yr). For stands in the 175 and 300 year classes, mortality of large stems was more normally distributed among plots. No very large stems died in stands younger than in the 300 year age class, and even in the 300 year age classes, mortality of very large stems was very rare: mean annual production of dead stems was 0.044 (SE = 0.021) stems per hectare-year, or 1 very large stem per year for every 23 hectares.

I expected production of dead stem biomass (Mg/ha-yr) to follow an "S" shaped trajectory (Figure 1; Table 3). Annual production of dead stem biomass did, in fact, follow an "S" shaped trajectory (Figure 14; Kruskal-Wallis test; df = 6, 184; $H = 18.731$; $P = 0.005$), although production appeared to decline somewhat in older age classes. Production of dead stem biomass in the 15 year age class was significantly different than in the 30, 50, 75, 125 and 300 age classes (Mann-Whitney U test; $P < 0.003$).

In general, most mortality occurred among stems that were small and below the canopy (Figures 12-14). Although the mortality of canopy stems and larger sized stems was very low by comparison, these stem classes contribute noticeably to production

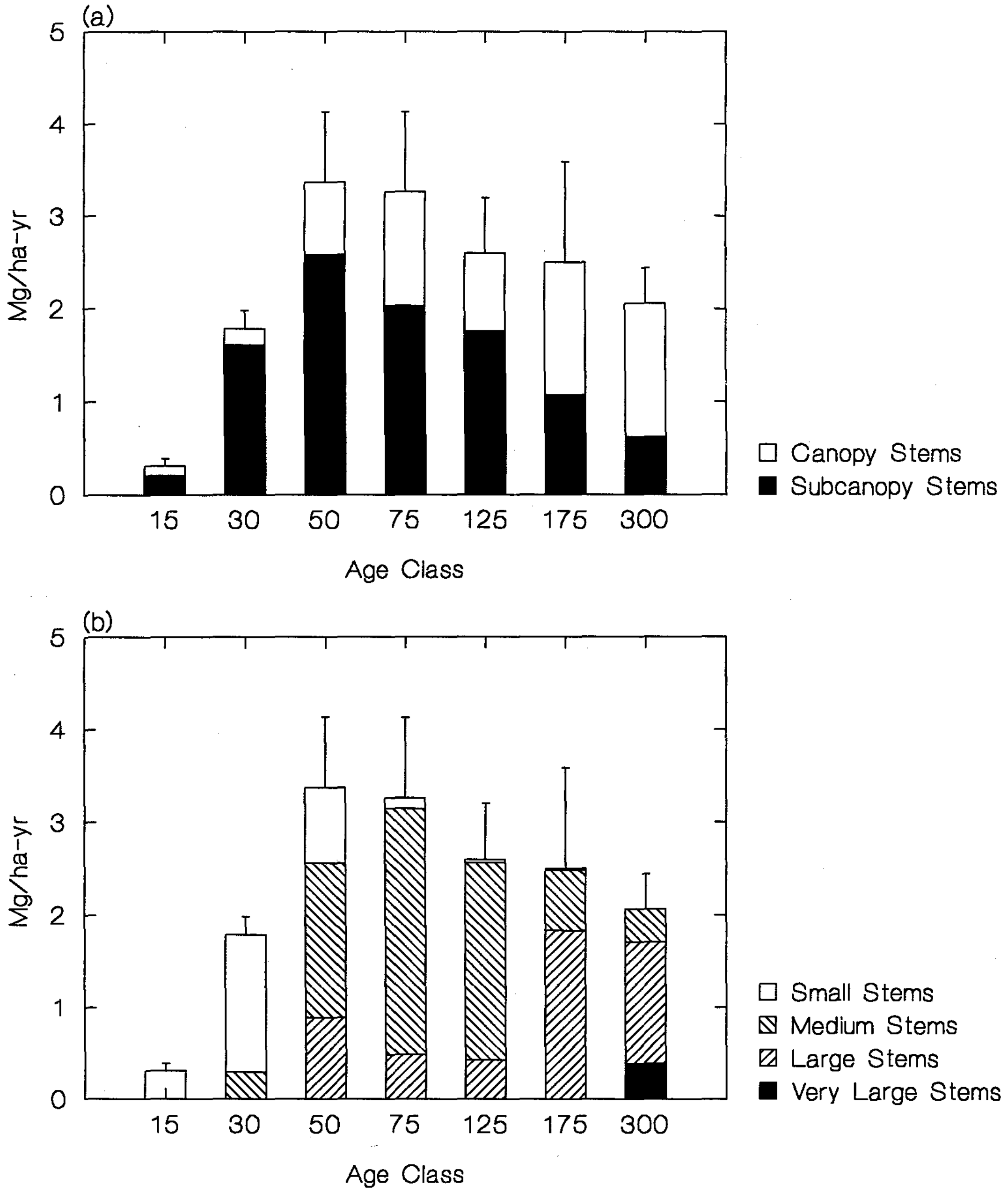


Figure 14: Annual production of dead stem biomass by canopy class (a) and size class of stems (b). In 175 and 300 year age classes small stems (5-14 cm dbh) were not measured.

of biomass (Figures 12-14). As well, I did not confirm patterns of differences among age classes for size classes of stems statistically as I did for live stems. Variance was high, and for individual size and canopy classes, no mortality occurred in many plots over the periods that I calculated mortality. These factors limited statistical power.

3.5 Factors influencing stand development

The characteristics of stand structure that I examined all showed considerable variation with age. Many characteristics also displayed significant variation independent of age. For example, total biomass, especially in older stands (Figure 7a), understory cover (Figure 8a); and production of dead stem biomass (Figure 14) varied substantially among plots of similar age.

Site productivity can vary significantly with location, changing with soil moisture and nutrient levels, for example. Other factors that may effect tree growth include site attributes such as slope or aspect and factors influenced by geography such as the length of growing season. In this section I examine some of these factors, including site index, slope, aspect and geographic location (longitude and latitude).

3.5.1 Influence of site productivity

Site index, a measure of site productivity, is based on the actual growth rate of trees (tree height relative to stand age; Watts 1983). It is a good measure of site productivity, although it reveals nothing about the specific factors that influence growth rate. I used estimates of site index to examine the influence of site productivity on stand structure. I stratified plots into high and low site index classes and compared differences of stem density and percent understory cover.

Site index influenced the density of live stems and percent understory cover. Live stem density was measurably delayed in stands with low site index values. For example, medium stems reached maximum abundance by the 30 year age class on high sites but not until the 50 year age class on low sites (Figure 15). Further, the density of medium stems appears to stabilize by the 125 year class on high sites, but did not reach similar low levels until the 175 year class on low sites. Stems in the largest size class were present in low densities (at a mean value of 1.6 stems/ha) in the 125 year class on high sites, but did not appear until the 175 year class on low sites (Figure 16). Further, in the 175 year age class all very large stems were on sites with a site index value of more than 24 m (generally considered to be productive sites); on sites with site index values lower than 24 m, very large stems did not appear until the oldest age class. These data reveal a substantial delay in developmental trajectories on low site index sites.

The developmental trajectory of understory cover was also influenced by site productivity. On low sites, declines in percent cover of understory vegetation with stand age were delayed relative to high sites as were later increases (Figure 17). There were also differences in production of biomass of dead stems (Mg/ha-yr). In general, production of biomass was higher on high SI sites, although the difference was significant for the 50 year age class only (Figure 18), mean differences were often large between the two site index classes, but detection of significant differences was hampered by low statistical power. I detected no significant differences of production of stem/ha-yr between SI classes for any age classes (separate variances t-test, $P > 0.05$). Thus it appears that trees dying on high SI sites are generally larger, contributing more dead stem biomass than those on low sites, because similar numbers of stems appear to be dying in the two SI classes.

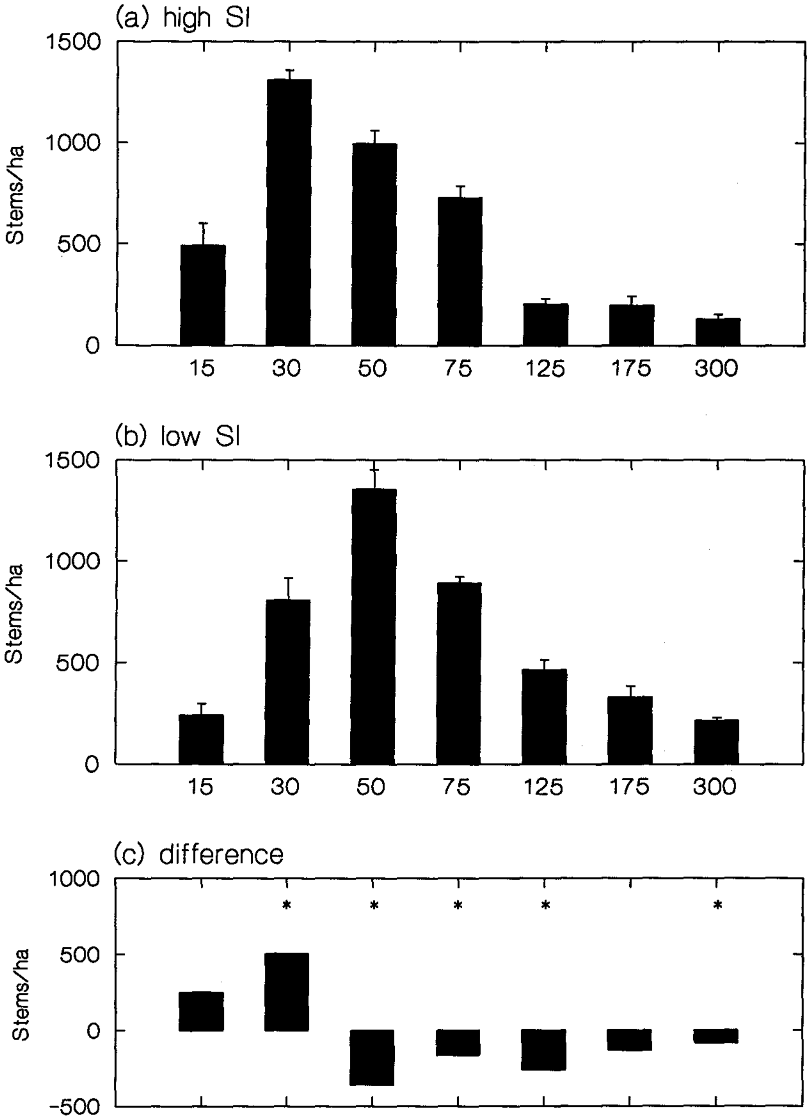


Figure 15: Medium stems (25-49 cm dbh) for high (a) and low site index classes (b). Significant differences in stems/ha for each age class (c) are noted by a "*" (separate variances t-test, $P < 0.05$, using sequential Bonferroni correction for significance).

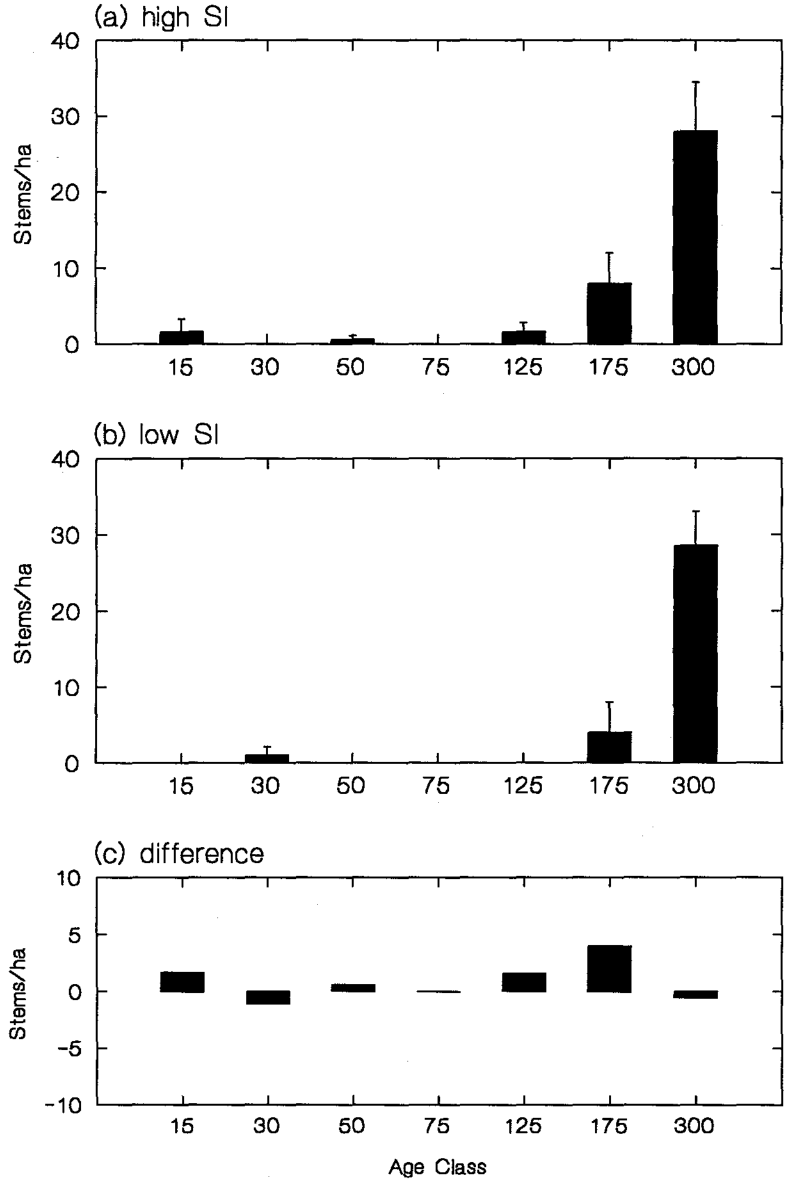


Figure 16: Very large stems (≥ 100 cm dbh) for high (a) and low site index classes (b). No differences in stems/ha for each age class (c) are significant (separate variances t-test, $P < 0.05$, using sequential Bonferroni correction for significance).

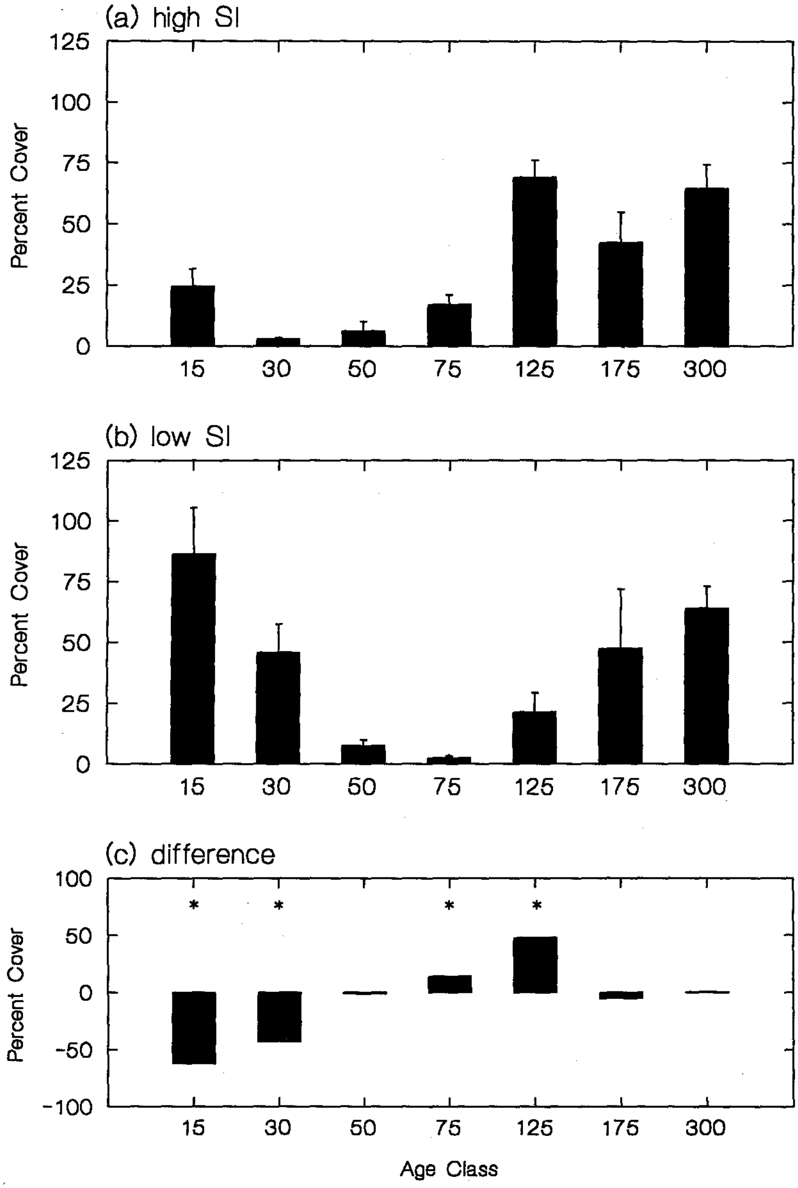
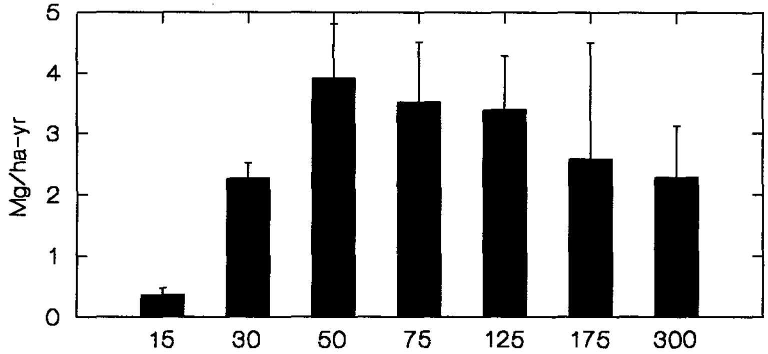
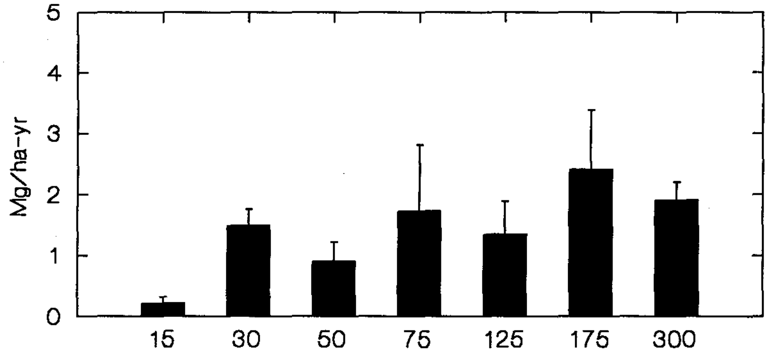


Figure 17: Percent cover of understory vegetation for high (a) and low site index classes (b). Significant differences in percent cover for each age class (c) are noted by a "*" (separate variances t-test, $P < 0.05$, corrected by sequential Bonferroni for significance).

(a) high SI



(b) low SI



(c) difference

Figure 18: Production of dead stem biomass for high (a) and low site index classes (b). Significant differences in Mg/ha-yr for each age class (c) are noted by a "*" (separate variances t-test, $P < 0.05$, corrected by sequential Bonferroni for significance). In 175 and 300 year age classes small stems (5-14 cm dbh) were not measured.

3.5.2 *Influence of other site and geographic factors*

The plots examined in this study were spread over a wide geographic area (Figure 2). I expected that developmental trajectories might vary geographically within the range of sampling. I also expected some other site characteristics, such as slope and aspect to influence stand development. I used regression analysis to test the influence of factors available in the data (Table 6).

Age, site index, latitude, elevation and aspect had a significant influence on stem density (Adjusted Multiple $r^2 = 0.71$; ANOVA df = 5, 183; F = 92.79; $P < 0.001$). Longitude and slope did not. Increases in age and site index decreased total stem density (negative coefficients; Table 6), consistent with trends observed in my previous analyses (Figure 6a for age; Figures 15 and 16 for site index). Increasing southerly aspect also decreased stem density, whereas increasing latitude and elevation lead to increased stem density (positive coefficients; Table 6). In general, increasing age, site index and southerly aspect all advanced stand development, while increasing latitude and elevation delayed stand development.

Table 6: Results of regression analysis of total stems/ha[1] against various site and geographic factors.

Variable	Coefficient	Std. Error	Tolerance	*P*	(r^2)[3]
Constant	-0.0115947	0.0032930		0.001	
Age	-0.0000110	0.0000015	0.91	<0.001	0.60
Average SI	-0.0000371	0.0000082	0.82	<0.001	0.06
Latitude	0.0002431	0.0000655	0.95	<0.001	0.01
Elevation	0.0000018	0.0000004	0.82	<0.001	<0.01
Aspect[2]	-0.0000019	0.0000009	0.96	0.050	0.03
Slope				0.833	
Longitude				0.949	

[1] Inverse transformed, see methods.
[2] Converted aspect, see methods.
[3] Additional r^2, after entering the model.

3.5.3 Effect of disturbance history

The plots that I examined experienced different disturbance histories. Plots younger than 70 years almost exclusively originated from harvesting, and most older plots originated from natural disturbances. However, there was some overlap in the 60 to 80 year age range, allowing me to test for differences between stands of natural and anthropogenic origin.

I examined differences between plots in each disturbance type for each of the previous analyses for live stems (size classes of live stem density and biomass), understory vegetation (% cover) and tree mortality (mortality rate and dead wood production of stems and biomass). The mean age of the plots originating after the two disturbance types (n = 10 for each group) were similar, but significantly different (61 years for the harvested group, and 71 years for the natural origin group; separate variances t-test; $P < 0.001$). I found no significant differences between the logged and naturally disturbed plots for *any* of 14 attributes that I examined (separate variances t-test; $P > 0.06$ for all attributes; $P > 0.1$ for most attributes), although means differed in the direction expected based on the age difference (i.e. stem density was slightly lower and understory cover was slightly higher in the older group). Although I failed to detect a statistical difference between disturbances types, statistical power was low for all tests ($\beta = 0.53$ or greater), so it is very likely that there are real differences between some attributes for logged sites compared to naturally disturbed sites.

4. DISCUSSION

4.1 Trends in stand development

Stands of the CWHvm1 display distinct trends of structural change through developmental time. In general, the patterns of structural development of forest attributes that I observed support the patterns proposed by Spies and Franklin (1988). Specifically, the pattern of understory cover and the proportion of subcanopy stems to canopy stems in the CWHvm1 follow the "U" shaped developmental curve hypothesized by Spies and Franklin (1988; Figure 1) and the increases in mean tree diameter and stand biomass seen in the analysis are consistent with the "S" shaped curve of Figure 1. I also confirmed predicted trends for the decline in overall stem density with age and the shift in diameter distributions of live stems from a reverse-J distribution in young stands to a near normal distribution in intermediate-aged stands and back to a reverse-J distribution in old stands (Table 3). As predicted (Table 3), tree mortality followed a "U" shaped trend in and production of dead stem biomass followed an "S" shaped trajectory. Finally, many size classes of live stems in the CWHvm1 followed an inverted "U" shaped trajectory for, for both stem density and stem biomass.

Few studies have explicitly tested the trends in structural development as proposed by Spies and Franklin (1988), so it is difficult to compare these patterns to those occurring elsewhere. One exception is a study by Lee *et al.* (1995) in aspen mixed wood stands of northern Alberta. They observed "S" shaped trajectories for tree height and diameter, and "U" shaped trajectories for understory cover, snags and down wood, although over very compressed time frames compared to the western hemlock stands that I examined and the Douglas-fir stands examined by Spies and Franklin (1988). The results of Lee *et al.* (1995) are consistent with the basic patterns proposed by Spies and Franklin (1988) for Douglas-fir forests and with my results. Thus the patterns of development proposed by Spies and Franklin (1988) appear to be valid for these markedly different forest types.

There has been some question whether biomass eventually declines in very old stands as losses due to mortality outweigh gains due to recruitment and growth (e.g. Franklin *et al.* 1981). Declines in biomass with stand age have been observed in some forest types. Pare and Bergeron (1995) reported declines for a boreal mixedwood forest in southern Quebec and Schulze *et al.* (1995) reported declines in larch (*Larix gmelinnii*) stands in eastern Siberia. However, I detected no decline in biomass in old CWHvm1 stands. Nor does biomass appear to decline with age in Douglas-fir stands of Washington and Oregon. Spies and Franklin (1988) noted that no declines through 900 years of stand development were observed in one unpublished study and Huff (1995) reported that basal area continued to increase with stand age through 500 years of development in old Douglas-fir stands. Thus, declines in biomass do not appear to be typical of old conifer stands in western Washington and Oregon and coastal British Columbia.

My results for production of dead wood biomass are of interest because few studies have examined this characteristic in coastal forests of Washington and Oregon and British Columbia (reviewed by Harmon *et al.* 1986 and Caza 1993). Of two studies that did, Harcombe *et al.* (1990) reported biomass inputs increasing from about 2 Mg/ha-yr for 37 year old stands to about 6 Mg/ha-yr for 138 year old plots in Sitka spruce - western hemlock stands. Sollins (1982) reported biomass inputs 2 - 4 Mg/ha-yr in mature Douglas-fir stands and 3 - 5 Mg/ha-yr in old growth Douglas-fir stands. Based on those two studies, I expected that biomass production would follow an "S" shaped trajectory. I observed an "S" shaped trajectory for dead wood biomass in the CWHvm1 and the levels of production of biomass that I report (mean values of between 3 - 4 Mg/ha-yr in mature plots and between 2 - 3 Mg/ha-yr in old growth plots) are similar to values reported by Harcombe *et al.* (1990) and Sollins (1982) for stands of similar ages.

Spies and Franklin (1988) suggested amounts of snags and down wood would follow a "U" shaped trajectory. I was unable to examine trajectories for snags and down wood in the CWH, but I did examine the density of large live stems among age classes. Like snags and down wood, large live stems will also survive natural disturbance as "biological legacies" (Franklin and Hemstrom 1981). These "veterans" of natural disturbances are often observed in post disturbance stands. For example, Huff (1995) observed a number of overstory trees that survived stand initiating fires in Douglas-fir stands. Such remnants have also been observed in the forests of coastal British Columbia (Ken Lertzman, pers. comm.). A portion of these veterans will die as the new stand ages before new large stems can recruit to the canopy. Therefore, like snags and down wood, large live stems should follow a "U" shaped trajectory in stands initiating from natural disturbances.

I did not see a "U" shaped trajectory for large live stems. I observed stems of this size class in only a few young plots (30 year age class or younger), and than only in small numbers. Large live stems were not intentionally retained under the harvesting regime that initiated the young plots that I examined. However, one young plot (9 years; not included in this analysis) sampled after a fire retained many large live stems. Snags, like veteran trees, were not normally retained under the harvesting regimes which initiated the stands that I studied (in fact, they were actively removed because of safety regulations). Therefore, while veterans and snags may follow a "U" shaped trajectory under natural disturbance regimes, they are unlikely to do so under harvesting regimes that do not explicitly retain some veterans and snags.

4.2 Stages of stand development

Overall, my results support the general model of stand development proposed by Oliver (1981). The reduced density of small stems and percent cover of understory vegetation that I observed as stands shift from young to intermediate ages are consistent with a shift from the initiation to the stem exclusion stage described in the model. Recovery in levels of understory cover, an increase in the proportion of subcanopy stems and the emergence of a reverse-J diameter distribution are indicative of understory reinitiation. My results also demonstrate an old growth stage that is structurally distinct from other stages of stand development (Section 4.3).

Oliver's (1981) model is also characterized by a successional shift in the composition of tree species populating the canopy from shade intolerant to shade tolerant species. This shift in species composition does not occur in the western hemlock stands examined in this study. Western hemlock is the dominant species in all age classes for both subcanopy and canopy stems. However, as stands age beyond 75 years, the relative abundance of other species such as western redcedar and Pacific-silver fir increases, suggesting that recruitment of these species could be another indicator of the understory reinitiation stage.

Tree mortality is one of the primary processes driving stand development (Peet and Christensen 1987), thus I expected changes in tree mortality to indicate changes among developmental stages. The dramatic increase in mortality that I observed between the 15 and 30 year age class indicates that the onset of the stem exclusion stage occurred during the latter age class. The mortality rate continues to decline thereafter (primarily among subcanopy stems). An increase in mortality rate among overstory stems occurs between the 50 and 75 year age classes, but it is difficult to relate this shift to reinitiation of understory vegetation and small stems which did not occur until the 125 year age class. I did not observe a threshold in mortality rate that clarified the distinction between understory reinitiation old growth stages of development.

More generally, my results demonstrate that there are limits to delineating one developmental stage from another. For most attributes, change occurred gradually among age classes, although more rapidly in younger stands and more slowly in older stands. I rarely observed thresholds, and with few exceptions, the attributes I examined were not exclusive to any one age class. Our ability to discriminate among developmental stages is also limited because changes with stand development are asynchronous. For example, percent cover of understory vegetation changed more rapidly with changes in age class than did characteristics associated with live stems. Understory cover decreased substantially by the 30 year class, and regained abundance by the 125 year class whereas shifts in patterns of stem diameter distributions occur much later: small stem abundance was lowest in the 75 year class and did not regain abundance until the 175 year class. This is likely because young trees in the small stem size class persist longer into the stem exclusion stage than do herbs shrubs and saplings, but also take longer to recruit as the stand begins understory reinitiation.

4.3 Characteristics of old stands

My observations are consistent with other research demonstrating that old growth forests are structurally distinct from mature stands (Franklin and Spies 1991b; Alaback 1984; Arsenault and Bradfield 1995). Old stands were characterized by a wide range of tree diameters, high levels of understory cover, low density and high biomass of live stems, and a reverse-J diameter distribution. Further, tree mortality rates were low. In contrast, in intermediate-aged stands, range of stem diameter, proportion of subcanopy stems, proportion of non-hemlock tree species, and understory cover were low. As well, stem diameters displayed a near-normal distribution and mortality was high.

Different attributes attained levels similar to those observed in the oldest age class at different times. For example, overall density of live stems was similar to old stands by the 75 year age class. By the 125 year age class, understory cover was similar to older stands, and canopy proportion, biomass of live stems and tree mortality by the 175 year age class. Densities of very large stems, mortality of very large stems and the reverse-J diameter distribution in the 300 year age class were unique to these old plots. Some trends continued into the oldest age class (e.g. mortality rate and biomass for total, medium and large stems), but were not statistically different from the 175 or sometimes younger age classes. Some of these trends may be real, but my ability to detect them was constrained due to insufficient statistical power.

Some authors have proposed an index approach to defining old growth (Franklin and Spies 1991a; Spies and Franklin 1988; Alaback 1982). In an indexed based system, "old growthness" is determined by scores related to the magnitude of a number of forest attributes associated with old growth, such as large trees, snags and down logs. They recommend this approach because of the variability in the structural characteristics of old growth stands and the times at which different attributes attain levels associated with old growth. My results support this assessment: many variables that I examined showed substantial variation; as did the time when attributes attained levels at or close to those in the oldest age class. Therefore, use of an index based system is an appropriate approach to evaluating stands for levels of "old growthness".

I also noted that young stands displayed some characteristics similar to old stands, but distinct from intermediate-aged stands, including high levels of understory cover and a reverse-J distribution of stem diameters. However, these characteristics are transient and change rapidly as the stand ages. In contrast, the attributes which distinguish very old stands from younger stands do not begin to emerge until well into the first century of development and often remain for at least several centuries thereafter.

4.4 Other aspects of stand dynamics

4.4.1 Dynamics of understory vegetation

Recruitment of young stems and percent cover of understory vegetation is highly constrained in stands of intermediate-age classes. Recruitment also appears to decrease disproportionally for Pacific silver fir and western redcedar relative to western hemlock among subcanopy stems. This pattern of development of understory vegetation is consistent with patterns observed in other similar forest types. Alaback (1982) noted that understory biomass peaked 15 - 25 years after overstory removal and then dropped dramatically following canopy closure in spruce-hemlock forests of southwest Alaska. Understory biomass remained low until 140-160 years, after which herb and shrub biomass increased. Similar patterns were also observed for understory vegetation following forest harvesting in CWH stands in southern Vancouver Island and the Fraser Valley (Klinka *et al.* 1985). Alaback (1982) and Klinka *et al.* (1985) also noted changes in the composition of understory species with changes in plot age.

Factors limiting recruitment under the forest canopy may change with time over stand development. There appears to be a threshold around 45% the amount of canopy closure I estimated, below which understory vegetation is consistently suppressed, but above which levels of understory vegetation vary widely. Canopy openness influences understory vegetation by influencing the amount of photosynthetically active radiation (PAR) available to the understory (Alaback 1982; Chazdon and Pearcy 1991). The threshold that I observed may thus be related to changes in levels of PAR reaching the understory. Below some point, PAR will be insufficient to allow most plants to reach their photosynthetic compensation point, limiting growth and above that point, plants will respond strongly to increasing levels of PAR (Kramer and Kozlowski 1979). However, at some point increasing levels of PAR will no longer result in increase plant growth. For example, Canham (1988) found that saplings responded strongly to increases in PAR due to canopy gaps compared to closed canopy, but showed little response to further increases of light in canopy gaps.

Studies have shown that a number of factors other than light can be limiting for understory vegetation: including soil moisture and nutrients (Riegel *et al.* 1992); characteristics of the forest floor substrate, such as the pit and mound microtopography and nurse trees created by tree falls (Christy and Mack 1984); and herbivory (Schreiner *et al.* 1996). Factors such as these could explain variations in understory vegetation levels that I observed where canopy openness is high. Further, I expect changes in factors limiting understory vegetation to be related to stages of stand development. Understory vegetation may be primarily light limited in stands due to the dense overstory canopies that form during stem exclusion, and primarily limited by other factors in the other stages of stand development, where canopies are more open.

Estimates of canopy closure used in my study should be treated with caution because they are not a direct measure of canopy openness; rather they are based on other parameters (basal area and stand density) of live trees. As well, I did not show results from the youngest age class (15 years) because the ages of plots in this class mostly fall below the minimum age of plots sampled to develop the algorithm. The very high levels of canopy closure the algorithm generates for this age class likely have little relationship with percent cover of understory vegetation (which was high in this age class).

Even where estimates of closure are accurate they do not describe how that openness is distributed in space. Understory plants may respond differently to similar levels of canopy openness produced by a few large openings compared to that found in many small ones. Direct measurements such as those provided by hemispherical canopy photographs (Chazdon and Field 1987; Canham *et al.* 1990) would reduce uncertainty associated with estimates such as those used in my analysis and provide a more complete description of canopy openness.

4.4.2 Effect of site productivity

Developmental trajectories in the CWHvm1 are dependent on site productivity and other factors such as aspect, elevation and geographic location. The rate of change in the density of different size classes of stems, percent cover of understory vegetation and degree of canopy closure increases on more productive sites. Therefore, the rate that a stand moves through developmental stages depends to some extent on the productivity of a site. For example, a stand is likely to develop old growth characteristics more rapidly on more productive sites.

Age, site productivity, aspect and geographic location do not explain all of the variation observed for the attributes examined in my study. For example, when I examined the influence of these factors on density of live trees, I found that about 30% of the variation in stem density remained unexplained. Many factors combine to influence stand development, including factors such as soil moisture and nutrient status (Riegel *et al.* 1992), genetics of individual trees (Namkoong and Conkle 1976), local edaphic conditions (Lertzman *et al.* 1996), and small scale mortality events such as windthrow that provide canopy openings (e.g. Lertzman *et al.* 1996). The biogeoclimatic ecosystem classification system in British Columbia allows for classification at the site series level, a finer scale of classification than the variant level of classification that I used for my study (Meidinger and Pojar 1991). Stands are classified to site series by an edaphic grid of soil moisture and nutrient status or by indicator species of plants (see for example Green and Klinka 1994 for site series of the CWHvm1). It is possible that evaluating developmental trends at the site series level would eliminate much of the variation I observed in my study, although I was unable to evaluate this with my data.

4.5 Limitations of study

4.5.1 Limitations of permanent sample plot data

The trends that I describe for the CWHvm1 apply to the upland forested portion of the landscape because plots were not randomly located. Riparian zones and wetlands and sites with significant edaphic characteristics such as large rock outcroppings were excluded, as were sites with atypically low densities of trees. Thus, for example, I underestimate canopy openness - edaphic openings in the CWHvm1 contribute substantially to canopy openings (Lertzman *et al.* 1996 reported about 16% of the openings in CWHvm1 plots were in edaphic gaps). Further, the paucity of deciduous species that I observed can partly be explained by the lack of plots in riparian zones. As well, plots were clustered geographically on timberlands of MacMillan Bloedel Ltd. although it is difficult to know what biases might result from this. In general, statistical results that I present in this study allow inferences to be made for more productive sites on the upland forested portions of the landscape, but not the CWHvm1 as a whole.

I was unable to describe the full scope of variation in structural characteristics found in the CWHvm1 because some data were not collected in the permanent plot surveys. Some important components of forest stands such as snags and down logs were not measured in the growth and yield plots and so could not be described in this study. As well, I was unable to describe the structure of young stands in the CWHvm1 that initiated after natural disturbances and therefore I was unable to compare them with young stands initiated after harvesting. For example, I was unable to determine if snags and down wood compare to "U" shaped trajectories proposed under natural disturbance regimes by Spies and Franklin (1988) and observed in Douglas-fir forests (Spies *et al.* 1988).

4.5.2 Limitations of the chronosequence approach

My study is based on the chronosequence approach of "substituting space for time." The very old stands in my study began their development at least 250 years ago and in some cases substantially longer. Thus it is possible that older plots are on different developmental trajectories than younger ones. Climatic conditions have changed significantly over that length of time, and these changes may influence stand development. For example, Lertzman (1995) found that forest composition of mountain hemlock forests of southeast British Columbia are likely in a state of compositional disequilibrium due to climatic changes over the past few centuries.

Disturbance history has also varied among plots that I examined. All of the late successional stands are of natural origin, while younger plots initiated after harvesting. I was not able to detect differences between stands of natural origin and stands of anthropogenic origin, at least for stands in the 60 - 80 year age range. For this age class, stands of natural origin did not differ significantly from those resulting from harvesting. However, I caution that although I failed to detect a statistical difference between disturbances types, statistical power was very low for all tests ($\beta = 0.53$ or greater), so it is very likely that there are real differences between some attributes for logged sites compared to naturally disturbed sites. Further, because I was unable to examine standing crops of snags and down wood in this study I could not test if these attributes were different in stands originating from the two different disturbance types. As well, harvesting practices were likely different 60 to 80 years ago, so my results may not apply to more recent harvesting practices.

4.6 Implications for research and management

Models of stand development such as those proposed by Oliver (1981), Peet and Christensen (1987) and Spies and Franklin (1988) provide a useful conceptual framework for understanding stand dynamics. However, as Spies and Franklin (in press) point out, these conceptual models need corroboration and refinement. I have clarified some aspects of the stand dynamics of the CWH but other aspects remain poorly described and require further study.

Understanding the dynamics of forest structure is of fundamental importance to forest managers. Information about forest structure is critical to understanding the implications of harvesting on habitat and will facilitate the development of alternative silvicultural prescriptions that maintain vital habitat components (e.g. Hopwood 1991). Maintenance of habitat quality has gained importance as local concerns and international accords, such as the United Nations Convention on Biological Diversity (UNCED 1992), have lead to increased commitment to biodiversity in forest planning in British Columbia and elsewhere. Retention of stand level habitat attributes is considered a vital part of maintaining habitat in a managed landscape (Thomas 1979; Bunnell and Kremsater 1990; Hansen *et al.* 1991; Franklin 1993; Clayoquot Sound Scientific Panel 1995) and new regulations and guidelines in British Columbia reflect this approach (BCMoF 1995a).

Based on the results of my study, I identify a number of recommendations for researchers and managers.

4.6.1 Recommendations for researchers

1. *The structural dynamics of CWH forests require additional characterization.*

Some aspects of the structural development of CWHvm1 forests remain poorly described. These include trends in size and decay class distributions of standing and down dead wood and, more generally, differences in developmental trajectories resulting from different disturbance histories. Further, differences in developmental trajectories among different subzones of the CWH have not been explained.

The transition from mature to old growth stands and temporal trends of development in old growth CWH stands are also poorly characterized. I have described asynchronous trends in development among some attributes through this transition period, but I was not able to determine trajectories for snags and down wood, or examine factors influencing tree mortality, canopy openness and understory reinitiation. Further, because of uncertainty of the ages of old growth plots, I was unable to follow trends of development in old growth stands of the CWHvm1. However, in one of the few studies to examine old growth for developmental trends, Tyrrell and Crow (1994) found changes in snags and down wood, density of large trees and canopy gap structure with age in hemlock-hardwood forests of the American mid-west. Their results suggest that trends occur in other forest types. These remain untested in the CWH and elsewhere in the PNW.

2. *Improved information on mortality rates and decay rates of trees in CWH forests are required to understand the dynamics of coarse woody debris.*

Data on tree mortality and decay rates are required to model the dynamics of snags and down wood in the CWH. My results provide mortality rates for the CWHvm1 during development, but information on decay rates remain sparse, as do data on rates of transition of snags to down wood (Caza 1993). Models of coarse woody debris dynamics are important because they provide the only method to estimate future impacts of harvesting on coarse woody debris levels.

3. *Studies are required to better understand the factors that influence the growth and development of understory vegetation.*

My results suggest the dominant factors affecting growth and development of understory vegetation may change depending on the developmental stage of the surrounding stand. During stem exclusion, canopy openness and the amount of PAR available to the understory may be the primary factor influencing abundance of understory vegetation. During other stages of stand development, other factors may play a larger role. Some possible factors include soil type, moisture and nutrient quality, characteristics of the forest floor substrate, (e.g. pit and mound microtopography and nurse trees created by tree falls), and herbivory. To my knowledge, no studies in the CWH have examined factors influencing the abundance of understory vegetation across a range of stand ages.

4. *Descriptions of the structural characteristics of younger stands in the CWH that originated from natural disturbance are required.*

Young stands that initiate after natural disturbance often have biological legacies such as snags and down wood (e.g. Spies *et al.* 1988) originating from the pre-disturbance stand. These legacies are not expected to be present in young stands initiated from forest harvesting (Spies *et al.* 1988; Franklin 1993) but are thought to play important roles in ecological function and as habitat in forest ecosystems (Thomas 1979; Harmon *et al.* 1986). Hansen *et al.* (1991) reviewed many studies of plant and animal composition and found similarities in species distribution among different age classes of PNW forests of natural origin. They felt that a primary reason for those similarities was directly related to the legacies that contribute to the structural diversity of the younger stands. Data are required from younger stands that initiated after natural disturbances in the CWH if we are to understand how these stands differ structurally, and ultimately functionally, from those initiated after harvesting.

5. *Better understanding of the role stand level structural components play as animal habitat is needed.*

A description of stand structure facilitates the ability of managers to assess habitat quality for a wide range of species of terrestrial vertebrates. Data on different size classes of stems and understory cover are among the variables required to determine habitat suitability for various species of terrestrial vertebrates (Daust *et al.* 1993). However, habitat has been traditionally been associated with forest age classes or developmental stages (e.g. Thomas 1979; Brown 1985). The importance for habitat of some structural forest components such as snags and down wood (Harmon 1986) is well known, but details of those relationships and many others are not. Some recent studies have addressed this information gap (e.g. Hansen *et al.* 1995 for birds and Carey and Johnson 1995 for small mammals), but for many species and many structural attributes the relationships remain unclear. A better understanding of these relationships is critical to allow development of silvicultural options that are designed to retain some structural components such as large snags, shrubs or a diverse canopy structure for habitat.

4.6.2 Recommendations for managers

1. *Regulations, guidelines and prescriptions based solely on the assumption that certain attributes are associated with a given age class are inappropriate.*

Current forest practice guidelines for biodiversity recommend maintaining a certain proportion of stands across a range of age classes including old growth (BCMoF 1995b). Part of the rational for maintaining full range of age classes is to retain important structural attributes such as snags or understory vegetation. Age-based guidelines designed, for example, to retain some minimum level of understory cover might be appropriate on productive sites but not on unproductive sites. I observed substantial variation, some of which is related to site productivity, in levels of different attributes on plots of similar ages. Therefore age-based regulations, guidelines and prescriptions should be sensitive to the inherent variation found in forests. One way to achieve this is to utilize site index values, which are often evaluated for managed stands, in addition to age class as criteria for achieving management objectives. Alternatively it may be more appropriate to set guidelines at the site series level of ecosystem classification, although I was unable to evaluate variation with my data by site series. My results suggest that geographic location also influences stand development, and should be considered when setting management objectives. Finally, the pervasive variation in attribute levels observed in my study argue against setting fixed endpoints for maintaining levels of attribute abundance; for many attributes a range of values would be more appropriate.

2. *New silvicultural options need to be developed if very large stems and a productive forest understory are to be retained in managed landscapes.*

In the CWHvm1, levels of understory cover are significantly depressed in mid-seral stands relative to young and old stands, and the very large stems abundant in old stands are rarely found in younger stands. Because current rotation ages are less than the age that these attributes begin to emerge, silvicultural options need to be developed that retain very large stems and elevate levels of understory cover in managed stands.

Some results of my analyses suggest the direction some silvicultural prescriptions might take. For example, improved understanding of the relationship between stem density of particular size classes of stems, canopy closure and understory initiation may yield thinning regimes designed to enhance levels of understory cover in mid-seral stands. Nonetheless, development of thinning regimes designed to enhance levels of understory vegetation is likely to be challenging in the CWH, because western hemlock is able to quickly dominate the understory after thinning. For example, in western hemlock forests of southeast Alaska, Alaback and Herman (1988) found that understory herbs and shrubs were often out-competed by young hemlock trees in thinned stands by the first decade after thinning. They also found that the most extensive ingrowth of hemlock saplings occurred on the most heavily thinned sites. They therefore recommended periodic light to moderate thinnings over less frequent, but heavier thinnings. Thus the timing, intensity and location of thinnings require careful planning to maintain a productive shrub and herb layer in the otherwise depauperate understory found in mid-seral stands.

3. *Government agencies and forest companies should expand inventory and mapping to include a broader range of attributes and a more detailed description of the landscape.*

The British Columbia Ministry of Forests and many forest companies maintain standard growth and yield inventories and forest cover mapping that contain limited information outside of upland forested areas. Riparian and poorly stocked areas are generally inadequately described. Managers now require information representative of the landscape in which they are found to develop effective prescriptions that maintain important habitat characteristics. Data sets which only describe a portion of the landscape, such as the growth and yield data analyzed in my study, are inadequate for biodiversity planning. Inventory efforts need to be expanded to include important habitat characteristics such as snags and down wood and mapping to include information collected from stands other than those located on upland forested sites, including riparian zones, wet lands, edaphic gaps and sites dominated by vegetation that does not have commercial value. Further, determining the site series classification of PSP plots would allow managers to evaluate structural characteristics at a more appropriate scale of resolution than is provided by classifying plots to the variant level.

4. *Managers should consider the effects on carbon storage of converting old stands to younger plantations in CWH forests.*

Forests play a significant role in mediating CO^2 levels in the atmosphere because of the substantial quantity of carbon these forests accumulate (Harmon *et al.* 1990; Kurz and Apps 1991). In the CWHvm1, I observed trends of biomass accumulation that showed that while biomass increased most rapidly in young stands, old stands stored substantially more biomass than did younger stands. Under current harvesting rotations for CWHvm1 (60 - 80 years), stands will not accumulate the amount of biomass found in pre-harvest stands, which were typically well over 200 years in age (Beese and Sanford 1992). Moreover, the average age of forest plantations will be younger than the rotation age, thus the amount of biomass stored in managed forests will be substantially less than the historical amounts stored in the CWHvm1. The mean biomass of stands was just over 300 Mg/ha for stands aged 10 to 90 years compared to over 600 Mg/ha in stands older than 200 years in the CWHvm1 stands I studied. This represents a substantial net reduction in stored carbon, and potentially a net increase in CO^2 in the atmosphere, depending on the fate of the wood fiber removed by harvesting. While my results apply to the CWHvm1, they are similar to those observed elsewhere in the PNW (Harmon *et al.* 1990), suggesting that a net reduction of carbon storage in managed landscapes is likely typical for many forests of the PNW.

Older stands may store carbon longer than younger stands of equivalent biomass in the CWHvm1. While overall levels of biomass remained relatively stable after 120 years, the allocation of that biomass appeared to shift to fewer, larger trees as stands aged (see Figure 7). If this shift in biomass to larger trees is typical of the CWHvm1, older stands may store carbon longer than younger stands of equivalent biomass, because larger stems tend to decay slower than smaller stems after they die (Harmon *et al.* 1986).

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APPENDIX

Equations used to estimate stem and bark biomass (BST) from diameter at breast height (DBH; Means *et al.* 1994).

Species	Eqn. No[1].	Equation	Dbh (cm) Min	Dbh (cm) Max	N	r^2	Mse
Western Hemlock	374	ln(BST) = 4.635161 + 2.3938 * ln(DBH)	19.3	121.6	41	0.98	0.027
Western Hemlock	130	ln(BST) = 4.82286 + 2.3275 * ln(DBH)	2.1	13.4	9	0.99	0.011
Pacific Silver Fir	250	ln(BST) = 3.897953 + 2.5867 * ln(DBH)	8.1	109.3	143	0.95	0.092
Western Redcedar	332	ln(BST) = 4.077376 + 2.4024 * ln(DBH)	11.8	168.5	17	0.99	0.032
Yellow-cedar	326	ln(BST) = 3.800163 + 2.5616 * ln(DBH)	18.9	109.1	26	0.97	0.041
Sitka Spruce	311	ln(BST) = 4.871437 + 2.3320 * ln(DBH)	35.4	283.0	41	0.95	0.044
Douglas-fir	256	ln(BST) = 4.660412 + 2.4247 * ln(DBH)	17.0	212.7	215	0.97	0.058
Douglas-fir	300	ln(BST) = 4.63891 + 2.11972 * ln(DBH)	1.4	13.4	18	0.97	0.059
Lodgepole Pine	413	ln(BST) = 4.710428 + 2.3363 * ln(DBH)	12.2	48.3	30	0.95	0.042
Red Alder	266	ln(BST) = 3.97 + 2.56 * ln(DBH)	6.0	20.0	12	0.98	0.013
Broadleaf Maple	34	ln(BST) = 3.4148 + 2.723 * ln (DBH)	7.6	35.3	18	0.99	0.014

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[1] Equation number in Means et al. (1994).