FOREST CANOPIES: FORM AND FUNCTIONAL RELATIONSHIPS

by

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# TABLE OF CONTENTS

<table>
<thead>
<tr>
<th>Chapter</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>ACKNOWLEDGEMENTS</td>
<td>ii</td>
</tr>
<tr>
<td>LIST OF TABLES</td>
<td>v</td>
</tr>
<tr>
<td>LIST OF FIGURES</td>
<td>vi</td>
</tr>
<tr>
<td>ABSTRACT</td>
<td>viii</td>
</tr>
<tr>
<td><strong>Chapter</strong></td>
<td></td>
</tr>
<tr>
<td><strong>I. ANALYSIS OF STAND DENSITY EFFECTS ON CANOPY STRUCTURE: A CONCEPTUAL APPROACH</strong></td>
<td></td>
</tr>
<tr>
<td>Summary</td>
<td>1</td>
</tr>
<tr>
<td>Introduction</td>
<td>2</td>
</tr>
<tr>
<td>Model Development</td>
<td>3</td>
</tr>
<tr>
<td>Methods</td>
<td>7</td>
</tr>
<tr>
<td>Results</td>
<td>11</td>
</tr>
<tr>
<td>Discussion</td>
<td>13</td>
</tr>
<tr>
<td>References</td>
<td>19</td>
</tr>
<tr>
<td><strong>II. RESPONSE OF LEAF AREA INDEX TO DENSITY: EFFECTS OF PLASTIC CROWN SIZE FOR TWO CONTRASTING TREE SPECIES</strong></td>
<td></td>
</tr>
<tr>
<td>Summary</td>
<td>27</td>
</tr>
<tr>
<td>Introduction</td>
<td>28</td>
</tr>
<tr>
<td>Material and Methods</td>
<td>32</td>
</tr>
<tr>
<td>Results</td>
<td>34</td>
</tr>
<tr>
<td>Discussion</td>
<td>36</td>
</tr>
<tr>
<td>References</td>
<td>42</td>
</tr>
</tbody>
</table>
III. FOREST PRODUCTION AND THE ORGANIZATION OF FOLIAGE WITHIN CROWNS AND CANOPIES

Abstract ................................................................. 53
Introduction .............................................................. 54
Material and Methods .................................................. 57
Results and Discussion .................................................. 61
References ............................................................... 67

IV. STRUCTURE, PRODUCTION AND CANOPY DYNAMICS: A COMPARISON OF LODGEPOLE PINE AND SUNFLOWERS

Abstract ................................................................. 81
Introduction .............................................................. 82
Material and Methods .................................................. 86
Results and Discussion .................................................. 90
Literature Cited .......................................................... 95

VITA .......................................................... 104
LIST OF TABLES

<table>
<thead>
<tr>
<th>Table</th>
<th>Description</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>Sample plot characteristics for overstory trees</td>
<td>23</td>
</tr>
<tr>
<td>1.2</td>
<td>Test results of model predictions by species</td>
<td>24</td>
</tr>
<tr>
<td>1.3</td>
<td>Revised predictions and results for mean crown volume</td>
<td>25</td>
</tr>
<tr>
<td>2.1</td>
<td>Sample plot characteristics for overstory trees</td>
<td>47</td>
</tr>
<tr>
<td>2.2</td>
<td>Regression results for $A_i \propto N^{a_1}$ where $A_i$ is mean leaf area, N is stand density, and $a_1$ is a regression parameter</td>
<td>48</td>
</tr>
<tr>
<td>2.3</td>
<td>Regression results for LAI $\propto N^{b_1}$ where LAI is leaf area index, N is stand density, and $b_1$ is a regression parameter</td>
<td>49</td>
</tr>
<tr>
<td>2.4</td>
<td>Regression results for LAI $\propto N^{b_1} \times L_c^{b_2}$ where LAI is leaf area index, N is stand density, $L_c$ is mean crown length, and $b_1$ and $b_2$ are regression parameters</td>
<td>50</td>
</tr>
<tr>
<td>3.1</td>
<td>Sample plot characteristics for overstory trees</td>
<td>75</td>
</tr>
</tbody>
</table>
## LIST OF FIGURES

<table>
<thead>
<tr>
<th>Figure</th>
<th>Page</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.1</td>
<td>(a) Mean crown width and (b) mean crown surface area versus absolute overstory density for lodgepole pine (squares) and subalpine fir (triangles)</td>
</tr>
<tr>
<td>2.1</td>
<td>Mean leaf area versus overstory density</td>
</tr>
<tr>
<td>2.2</td>
<td>Leaf area index versus overstory stand density</td>
</tr>
<tr>
<td>3.1</td>
<td>Mean volume increment plotted against (a) mean crown surface area and (b) mean crown volume</td>
</tr>
<tr>
<td>3.2</td>
<td>Estimated mean bare core volume versus overstory density</td>
</tr>
<tr>
<td>3.3</td>
<td>Ratio of mean bare core volume to mean crown volume ( (V_{bc}:V_c) ) versus mean crown volume</td>
</tr>
<tr>
<td>3.4</td>
<td>Estimated mean bare core volume plotted against the ratios of (a) mean crown surface area to volume ( (A_c:V_c) ), and (b) mean crown length to crown width ( (L_c:W_c) )</td>
</tr>
<tr>
<td>3.5</td>
<td>Stand volume increment versus overstory density for lodgepole pine (squares) and subalpine fir (circles)</td>
</tr>
<tr>
<td>4.1</td>
<td>Schematic representations of relationships between (a) mean leaf area and density; (b) mean stem volume increment and mean leaf area; and (c) ratio of foliage to total crown biomass versus mean leaf area</td>
</tr>
<tr>
<td>4.2</td>
<td>Mean leaf area as a function of overstory density for (a) lodgepole pine and (b) sunflowers</td>
</tr>
</tbody>
</table>
4.3 Mean stem volume increment versus mean leaf area for (a) lodgepole pine and (b) sunflowers ........................................... 101

4.4 Mean ratio of foliage to total crown biomass ($R_{F:C}$) as a function of mean leaf area for (a) lodgepole pine and (b) sunflowers .... 102

4.5 Average vertical distribution of $R_{F:C}$ for lodgepole pine and sunflowers ................................................................. 103
ABSTRACT

Forest Canopies: Form and Functional Relationships

by

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Forest canopy structure is strongly influenced by stand density due to changing competitive interactions among the individual trees and in turn directly influences stemwood volume production. The structure and dynamics of forest canopies, particularly in relation to the production of stemwood, were examined in unmanaged, even-aged stands of two dissimilar tree species, Pinus contorta var. latifolia Engelm. and Abies lasiocarpa (Hook.) Nutt. The analysis of structure-production relationships was guided by a conceptual model which generated hypotheses and led to examination of assumptions incorporated in the model.
Mean crown dimensions were related to stand density through a negative exponential function for both species, but because of differing shade-tolerances, mean crown size of lodgepole pine was affected more by increasing density than was mean crown size of subalpine fir. More importantly, examination of the model assumptions indicated that adequate characterization of canopy structure should account for the influence of both crown shyness and stand height.

Stand density also influenced the amount and distribution of leaf area in these forest stands. The more plastic mean leaf area of lodgepole pine led to a constant leaf area index over a range of density and, thus, was consistent with conventional wisdom which assumes closed canopied forest stands support stable leaf area indices across a wide range of densities. The less plastic mean leaf area of subalpine fir, however, led to positive correlation between leaf area index and density.

Changes in mean crown dimensions and mean leaf area influenced the production of stemwood volume such that large mean crown sizes were less efficient than small mean crown sizes. The decrease in efficiency was attributed to accumulation of large branch biomass in large crowns to support foliage far from the stem. Increased support costs were indicated by the increasing proportion of crown volume which was nonfoliated as mean crown size increased. The assumption that accumulated branch biomass was
responsible for the observed declines in efficiency for forest trees was reinforced by a comparison of structure-production relationships for lodgepole pine and the annual *Helianthus annuus* L.
Summary. A few assumptions were used to generate a series of specific, quantitative predictions for the relationships between stand density and various dimensional measures of canopy structure. The predictions, each indicating an increase in mean crown size as density decreased, appeared to be reasonable and intuitive. Predictions were compared to data for two conifer species with different crown forms, Pinus contorta var. latifolia and Abies lasiocarpa. Results of these comparisons were mixed—the linear, directly measured dimensions were consistent with predicted relationships, but dimensions calculated from the linear measures were not. Reexamination of the original assumptions indicated that the model should account for crown shyness (engagement/disengagement) to adequately reflect the influence of stand density on canopy structure. The results also indicated a strong association between stand height and measures of mean crown size. Mean crown size of lodgepole pine was altered much more by density than was mean crown size of subalpine fir, due primarily to the different relative shade tolerances of the two species. Some of the observed differences between
species may also reflect the range of densities examined and uneven spacing in the unmanaged natural stands.

Introduction

Foresters have long recognized that stand density affects measures of average tree size, including crown dimensions, as is evident in the attention to characteristics such as mean crown length, live crown ratio, mean crown diameter, and crown projection area. Many studies report relationships between measures of mean crown size and stand density (e.g., Assmann 1970; Beekhuis 1965; Curtis and Reukema 1970; Hamilton 1969; Stiell 1966). Much of this work has been concerned with the influence of canopy structure on stand production. Because many variables affect canopy development and, therefore, the production of stemwood, a conceptual approach would be useful in elucidating the processes and interactions underlying forest canopy development. Results could then be used to determine how canopy structure changes with stand development, to consider interactions between stand and canopy structure and forest production, and for applications such as simulation modeling.

We developed an \textit{a priori} conceptual model of the relationships between stand density and measures of crown size based on a mean tree approach and the following assumptions: 1) a size-density index based on mean top
height (average height of some proportion of the tallest trees in the stand) provides a valid measures of relative stand density; 2) this size-density index and live crown ratio are associated through a simple power function; 3) mean crown width is inversely related to the square root of stand density (crown width proportional to spacing); and 4) the shape of tree crowns can be approximated by a simple geometric solid.

Basic relationships between mean size and density were utilized to quantitatively predict how absolute density affects mean crown dimensions. These predictions were then compared with data from stands of two species with very different gross crown morphologies. With the simple assumptions used in developing the model, we did not expect the model to be completely accurate in all respects, but rather to identify changes necessary to bring predicted and observed values into closer agreement.

Model Development

Size-density relations reflect the predictable relationship between some measure of mean tree size and absolute stand density (trees per unit area). Examples of this type of function are stand density index (Reineke 1933), Wilson’s (1946) percent of height, and crown competition factor (Krajicek et al. 1961). Because these size-density indices are independent of stand age and
site quality, stands with the same index have similar site occupancy and competition, regardless of age or site quality (Long 1985).

The size-density index used in this model is a modification of one proposed by Czarnowski (1961) and is based on mean top height for the stand:

\[ \text{THD} = \frac{(H^2 \times N)}{10000} \]  

where THD (Top Height Density) is a size-density index, \( H \) is mean top height (meters), and \( N \) is absolute stand density (trees per hectare). THD thus represents the number of trees in a square area with sides of length \( H \).

Equation (1) can be rearranged to give

\[ H \propto \text{THD}^{1/2} \times N^{1/2}. \]  

Therefore, when THD is constant \( H \propto N^{1/2}. \) (2)

Long (1985) showed there is a relationship between average live crown ratio (LCR) for two conifer species in closed canopy stands and Reineke’s (1933) stand density index. Since THD is closely related to Reineke’s mean size-density measure, it is reasonable to assume that THD is also related to mean live crown ratio by

\[ \text{LCR} \propto \text{THD}^x \]

or

\[ \text{THD} \propto \text{LCR}^{1/x} \]  

where \( x \) is an unknown value. Thus, using equations (1) and (3)

\[ \text{LCR}^{1/x} \propto H^2 \times N \]  

Mean live crown ratio is defined as the ratio of mean live crown length \((L_c)\) to mean top height, so equation (4) can be rewritten as

\[
(L_c^{1/x} / H^{1/x}) \propto H^2 \ast N
\]

and

\[
L_c \propto H \ast H^{2x} \ast N^x.
\]

Equation (2) can substitute for \(H\) in this relationship. Therefore, when the index of mean size and density is constant

\[
L_c \propto N^{-1/2} \ast N^x \ast N^x
\]

which simplifies to

\[
L_c \propto N^{-1/2}.
\] (5)

A similar function characterizes the relationship between stand density and mean crown width if it is assumed that crown closure has occurred and that lateral expansion by crowns is restricted. The simplest assumption is that mean crown width, \(W_c\), is related to absolute stand density by

\[
W_c \propto N^{-1/2}
\] (6)

(i.e., mean crown width is directly related to average spacing). Unlike mean crown length in equation (5), this relationship is not constrained by constant THD.

Defining relationships for the basic mean crown dimensions of length and width (equations [5] and [6]) makes it possible to derive any number of additional mean crown characteristics. Many measures have been proposed, from simple to very complex, all of which can be calculated from crown length
and width. Predictions for three "derived" crown characteristics will be
developed here.

If it is assumed that a simple geometric solid adequately approximates
crown shape, mean crown volume, \( V_c \), can be calculated by

\[
V_c = k \times W_c^2 \times L_c
\]

where \( k \) is a shape-specific constant (e.g., \( \pi/12 \) for a cone and \( \pi/8 \) for a
paraboloid). If the relationships developed above are used

\[
V_c \propto W_c^2 \times L_c \propto N^{-1} \times N^{-1/2}
\]

\[
V_c \propto N^{3/2}
\]  \hspace{1cm} (7)

when at a constant size-density index. Formulae for mean lateral crown
surface area, \( A_c \), are more complicated than for mean crown volume, but for a
cone or a paraboloid the equations reduce to the form

\[
A_c \propto N^{-1},
\]  \hspace{1cm} (8)

again at constant THD.

Another structural index is the ratio of mean crown surface area to mean
crown volume, \( A_c:V_c \) (Assmann 1970). Using equations (7) and (8), it is
predicted that at a constant index of mean size and density,

\[
A_c:V_c = A_c/V_c \propto N^{-1}/N^{-3/2}
\]

\[
A_c:V_c \propto N^{1/2}.
\]  \hspace{1cm} (9)
Methods

Sample Species and Measurements

Sample plots were located at an elevation of approximately 2500 m in the Bear River Range of northern Utah, about 65 km northeast of Logan, UT. The climate is typical of the central Rocky Mountains, with approximately 104 cm annual precipitation, primarily as winter snow, and mean January and August temperatures of -11 and 17 °C, respectively. Further climatic and general ecological characteristics for the area can be found in Hart and Lomas (1979) and Schimpf et al. (1980).

The model predictions were tested with lodgepole pine (Pinus contorta var. latifolia Engelm.) and subalpine fir (Abies lasiocarpa (Hook.) Nutt.), two species with markedly different growth rates and crown morphologies. Subalpine fir is extremely shade tolerant with a long, narrow, spire-like crown. Conversely, lodgepole pine is very shade intolerant with a wider, more spreading crown (Fowells 1965). Subalpine fir also carries substantially more leaf area per tree than lodgepole pine for trees with equal sapwood area (Long and Smith 1989).

A total of 57 plots was used in these analyses, 34 pine and 23 fir. The sample plots were chosen such that one species contributed >75% of the plot basal area. Plot size varied with density to include an average of 34 live trees per plot for lodgepole pine and 35 for subalpine fir. At each plot
several measurements were recorded for all live trees taller than breast height (1.3 m): diameter at breast height (DBH), total height, and height to base of the live crown. In addition, trees were classified as either over- or understory (i.e., based on their position relative to the main canopy). The crown width of the overstory trees was measured along two perpendicular radii whose orientation was held constant within a plot. Those trees classified in the overstory included trees in the dominant, codominant, and upper intermediate crown classes, and on average represented 79% and 74% of all live trees in the pine and fir plots, respectively. Plot characteristics for the overstory trees are summarized in Table 1.1. Crown length and crown width were then used to calculate crown volume, crown surface area, and the ratio of crown surface area to crown volume using the assumption of paraboloid crown shape.

Only the overstory trees were used to calculate plot densities and mean tree values because the model assumes that the individual crowns interact within the canopy. Those trees classified as understory were below the main canopy, and their crowns did not appear to mechanically interact with those of the overstory. Mean top height for each plot was calculated as the average height of the upper 20% of the overstory trees on the plot.

Analysis

All of the predictions can be represented by an equation of the form
\[ Z = b_0 \cdot N^{b_1} \cdot \text{THD}^{b_2}. \]

THD is included as a second independent variable for those relationships which hold only at a constant size-density index. Including THD as a covariate accounts for this constraint.

The predicted relationships were tested with nonlinear iterative least squares regression using the Gauss-Newton method (SAS Institute Inc. 1987). Approximate $r^2$ values were calculated as the difference between the corrected total sum of squares and error sum of squares, divided by the corrected total. The $r^2$ values and residuals were used to assess the fit of the regression equations to the data and appropriateness of the model form.

Nonlinear regression was used rather than transforming logarithmically to use linear least squares regression or reduced major axis techniques (Leduc 1987) because the functional form of the relationships was of interest and transformation was not required to correct for heteroscedasticity. The least squares parameter estimates are not significantly biased, however, given the high correlation coefficient ($r \geq 0.7$) between the dependent and independent variables in all cases (Seim and Sæther 1983).

Bootstrap procedures with 100 replicates were used to estimate standard errors for the regression parameters (Efron and Tibshirani 1986). Because parameter estimates from nonlinear regression are highly correlated, the estimated standard error for the parameter of interest ($b_1$ in this case) is
inflated by letting both \( b_1 \) and \( b_2 \) vary together in each bootstrap regression. Two bootstrap procedures were therefore implemented to estimate the variance of \( b_1 \) when THD was included as a covariate. The first bootstrap procedure (100 replicates) allowed both \( b_1 \) and \( b_2 \) to vary. In the second bootstrap procedure (also 100 replicates) \( b_2 \) was fixed at the mean value from the first bootstrap run, which more accurately estimated the variance of \( b_1 \) when the size-density index was constant. The particular value at which \( b_2 \) is fixed changes the mean value of \( b_1 \) for the bootstrap samples, but does not change the estimate of standard error. The \( b_1 \) values from the original regressions were compared to the distribution of values generated by the second bootstrap procedure to test for statistical differences between the observed and postulated parameter values.

A probability value greater than 0.05 indicated support for the null hypothesis \( (H_0: b_1 = \text{prediction}, \text{where } b_1 \text{ is the exponent associated with density in the regression equation}) \). Additionally, the null hypothesis was rejected if the coefficient of variation (C.V.) was high (i.e., greater than 15%) even if the \( P \)-value was larger than 0.05 in order to avoid type II error (acceptance of the null hypothesis even when it is false). In such cases it was not possible to determine whether predicted and observed values were significantly different.
Results

Results of the comparisons are presented in Table 1.2. Though some of the model predictions are supported, more than half are not. In all cases, however, the $r^2$ values and lack of bias in the residuals indicate that the form of the regression function is appropriate.

The dimensions that were measured directly (i.e., crown width, crown length) agree most closely with predicted values, particularly for lodgepole pine (Table 1.2). The dimensions "derived" from these basic measurements, mean crown volume, mean crown surface area, and the ratio of the two (with the exception of $A_c:V_c$ for fir), differed most from the predictions. Such consistent discrepancies warrant closer examination of the assumptions used to predict these dimensional parameters, i.e., that crown shape can be approximated by a paraboloid, and mean crown width is proportional to spacing ($W_c \propto N^{1/2}$).

The assumption concerning crown shape is probably not the source of the discrepancies because formulae for calculating the volume of a cone or paraboloid differ only in the constant of proportionality, not in the exponents of the proportional relationship. As a further check, crown volumes were calculated with the relatively more complicated assumption of ellipsoid shape; this assumption changed the estimated crown volume of individual trees, but stand mean values were directly proportional to those based on paraboloid
shape. Thus, the proportional relationship between $V_e$ would not change if it was assumed that the crown is an ellipsoid rather than a paraboloid, and the particular shape assumed appears to have little effect on the tested relationship.

Derived crown dimensions were constrained to hold at constant THD due to the crown length-density relationship, while the $W_e$-N relationship was assumed to be independent of THD. The assumption $W_e \propto N^{1/2}$ used to predict derived measures of crown size may not be valid when THD remains constant. When we tested whether the crown width-density relationship changed at constant THD the relationships were different, especially for lodgepole pine (Table 1.3). The revised relationships ($W_e \propto N^{0.76}$ for lodgepole pine and $W_e \propto N^{0.38}$ for subalpine fir at a constant size-density index) imply that crowns were proportionally narrower for pine and wider for fir than originally assumed.

These results were used to revise predicted mean crown volume. As shown in Table 1.3, the modifications greatly improved prediction of the crown volume-density relationship. Similar revisions were not possible for mean crown surface area and the ratio of crown surface area to crown volume. This was due to the inability to reduce the complicated formula for surface area to a simple power function when the new crown width-density relationship were used.
Discussion

Canopy Structure

All of the dimensional characteristics showed a decrease in crown size as stand density increased, but only when THD was held constant. By definition (equation [1]) if two stands have equal THD but different absolute densities, the stand with more trees will have a lower top height. Therefore, in addition to the effect of density, there is also a strong association between total tree height and mean crown size, an association others have noted (e.g., Beekhuis 1965; Curtis and Reukema 1970; Kanazawa et al. 1985; Seymour and Smith 1987). This relationship must be considered when evaluating crown and canopy characteristics. Stand top height affects mean crown size because crowns expand to fill available volume rather than just expanding laterally as implied by the effect of stand density (Norberg 1988). Change in height is as important for filling this volume as lateral expansion, and greatly affects competitive interactions between individuals (Caldwell 1987).

The empirical $L_c$-$N$ results for both species were not statistically different from the predicted values, the only dimension for which this was the case. The observed exponents for the two species were significantly different from one another, however, indicating differences in response of crown length to changes in stand density. The differential species response is perhaps due to differences in crown shape which affect light penetration and self-shading.
(Kellomäki et al. 1986) in conjunction with their different relative shade tolerances, factors which have been noted by others to affect crown size (e.g., Krajicek et al. 1961). Also, Beekhuis (1965) found that live crown length was proportional to spacing for radiata pine in New Zealand, which is consistent with $L_c \propto N^{-1/2}$ as predicted by the model. He warns, however, that stand top height can affect the relationship and should be considered. THD, which is based on stand top height, was held constant in our tests and so accounts for the effect of stand height on the relationship.

Unlike live crown length, the predicted relationship between mean crown width and stand density was supported only in lodgepole pine (Table 1.2). Modification of the original assumption constrained the $W_c - N$ relationship to hold at constant THD which led to more accurate prediction of observed crown volumes and had additional relevant consequences as well.

The revised crown width-density relationships indicate that, at a given $N$ and THD, fir will have a proportionally wider crown than pine. This difference between species may be due to the amount of crown engagement or disengagement (Assmann 1970). When $W_c \propto N^{-1/2}$, it is assumed that individual tree crowns expand to occupy only the average nominal area available to them and that adjacent crowns touch but do not intermingle. Lodgepole pine, however, exhibits crown shyness (disengagement or gaps between crowns) whereas subalpine fir crowns grow into one another. The
relationship $W_c \propto N^{0.78}$ for lodgepole pine implies that these crowns are narrower (disengagement) at a given density (and constant THD) than originally assumed, while $W_c \propto N^{0.38}$ for subalpine fir implies crowns are wider (engagement) than originally assumed. Observations of engagement or disengagement in forest canopies have been explained by differences in species tolerance and competitive strategy (Franco 1986) and, for disengagement, by mechanical damage between neighbors (Putz et al. 1984; Richards et al. 1962).

The revised crown width-density relationship also implies that crown shape, as indicated by the ratio of crown length to crown width ($L_c/W_c$), changes with stand density. Originally, when both $L_c$ and $W_c$ were assumed to be proportional to $N^{-1/2}$, the shape index remained constant as density changed (i.e., isometric growth). Others (e.g., Long and Smith 1984; Mohler et al. 1978; Norberg 1988; White 1981; Zeide 1987) have suggested that crown shape changes with density during stand development. When the relationship for crown width was revised, crown shape in both species changed with stand density, though the change was modest for subalpine fir.

The original predictions for the relationships between mean crown volume and mean crown surface area and stand density were also consistent with isometric growth (Norberg 1988) but were not supported by observation (Table 1.2). Instead, lodgepole pine mean crown volume decreased sharply
as stand density increased, more abruptly than was originally predicted, while fir crown volume decreased more gradually than originally predicted. Total crown surface area for several species is constant across a range of stand densities (Assmann 1970; Kajihara 1977), consistent with the original model prediction ($A_c \propto N^{-1}$). The total surface area was not constant across the range of densities for either species, however (Table 1.2)—it decreased with increased density for lodgepole pine and increased with stand density for subalpine fir (at constant THD).

Since crown volume diminishes more rapidly than surface area as stand density increases, the predicted relationship between $A_c:V_c$ and stand density was as expected, i.e., $A_c:V_c$ increased with density though there were differences between the two species. The ratio for lodgepole pine increased more abruptly than for subalpine fir because pine crown volume is more affected by density. Some of the difference is also due to the effect of overall crown form: the surface to volume ratio of the more rounded and spreading form of lodgepole pine crowns is inherently different from that of the narrower, elongated fir crowns.

Species Differences

The model assumed that species differed only in the constant of proportionality, not in the functional relationship between crown dimensions
and absolute density. The results in Tables 1.2 and 1.3, however, clearly indicate that stand density has different effects on the mean crown dimensions of lodgepole pine and subalpine fir. At a given N and THD fir trend to have a proportionally larger crown than pine (Fig. 1.1). Though the differences are not large, the species clearly differ at a given density for both a directly measured linear dimension ($W_c$, Fig. 1.1a) and a "derived" or calculated dimension ($A_c$, Fig. 1.1b). The extremely shade-tolerant subalpine fir will retain branches and foliage longer and at higher stand densities than the less shade-tolerant pine, leading to a relatively longer, wider crown in subalpine fir.

Some of the apparent differences in the effect of stand density may reflect the different ranges of density measured for the two species. Pure, low density fir stands are not common, and no fir plots had densities comparable to the lowest density pine plots (Table 1.1). The very low density pine plots have a great influence on the regressions, thus at least some of the apparent differences in species may be due to the lack of comparable density fir plots. Any influence due to different ranges of density in the data is not readily apparent in Fig. 1.1, however.

The variability in the data from these natural, unmanaged stands must also be considered. The model assumes a fairly even distribution of trees in the canopy, a condition which rarely occurred in these stands. Using only
overstory trees reduced the amount of variability because only trees considered active members of the main canopy were included, but there was still variation due to the uneven spacing. Subalpine fir stands are less uniform, which resulted in greater variability in crown sizes. The more uniform spacing and crown size of lodgepole pine increased the accuracy of prediction for mean crown dimensions of this species. The variability in crown size due to uneven spacing would primarily affect the mean values for individual stands and thus only indirectly affect the results presented here. The effect of tree spacing and high variability could be tested by analyzing plantation data where spacing is controlled.

The conceptual approach provided mixed results--some canopy structural characteristics were predicted fairly well while others were not. Discrepancies between predicted and observed values, however, indicated the need to modify some assumptions. For example, the effect of crown engagement/disengagement on mean crown width, and subsequently other dimensions, should be explicitly included to accurately model canopy structure. The approach and size-density index used also demonstrated how stand height influences canopy structure, an effect which others have observed. Finally, the canopy structures of the species considered in this study appear to be different at a given density, probably due to the different relative shade tolerances of lodgepole pine and subalpine fir in conjunction with changes in light environments with changing stand density.
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Reineke LH (1933) Perfecting a stand-density index for even-aged forests. J Agric Res 46:627-638


Stiell WM (1966) Red pine crown development in relation to spacing. Can Dept For Publ No 1145, Ottawa, Canada


Table 1.1. Sample plot characteristics for overstory trees. Numbers represent means and ranges.

<table>
<thead>
<tr>
<th>species</th>
<th>lodgepole pine</th>
<th>subalpine fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>number of plots</td>
<td>34</td>
<td>23</td>
</tr>
<tr>
<td>live trees per plot</td>
<td>25 (10-47)</td>
<td>24 (13-38)</td>
</tr>
<tr>
<td>density (trees/ha)</td>
<td>1868 (176-4800)</td>
<td>6322 (1111-12000)</td>
</tr>
<tr>
<td>quadratic mean</td>
<td>21.6 (10.9-36.7)</td>
<td>14.6 (8.9-22.1)</td>
</tr>
<tr>
<td>diameter (cm)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>mean top height (m)</td>
<td>22.8 (17.6-27.9)</td>
<td>17.0 (12.5-23.3)</td>
</tr>
<tr>
<td>top height density</td>
<td>63 (10-150)</td>
<td>112 (48-211)</td>
</tr>
<tr>
<td>(THD)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>age (yrs)</td>
<td>89 (67-134)</td>
<td>75 (66-98)</td>
</tr>
</tbody>
</table>
Table 1.2. Test results of model predictions by species. The symbol ** indicates agreement between predicted and observed values. "Pred. b1" is the original predicted exponent, "obs. b1" is the exponent observed from regression, SE is the standard error of the observed b1, C.V. is the coefficient of variation for the observed value, \( P \) is the probability that the predicted and observed exponents are equal, and \( r^2 \) is the coefficient of determination for the regression equation.

<table>
<thead>
<tr>
<th>Species</th>
<th>pred. b1</th>
<th>obs. b1</th>
<th>SE</th>
<th>C.V.</th>
<th>( P )</th>
<th>( r^2 )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Lodgepole pine</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( W_c \propto N^{b_1} )</td>
<td>-0.5</td>
<td>** -0.5</td>
<td>0.033</td>
<td>0.06</td>
<td>0.993</td>
<td>0.90</td>
</tr>
<tr>
<td>( L_c \propto N^{b_1}\cdot\text{THD}^{b_2} )</td>
<td>-0.5</td>
<td>** -0.55</td>
<td>0.032</td>
<td>0.06</td>
<td>0.128</td>
<td>0.79</td>
</tr>
<tr>
<td>( V_c \propto N^{b_1}\cdot\text{THD}^{b_2} )</td>
<td>-1.5</td>
<td>-2.45</td>
<td>0.177</td>
<td>0.07</td>
<td>(&lt; &lt; 0.001)</td>
<td>0.86</td>
</tr>
<tr>
<td>( A_c \propto N^{b_1}\cdot\text{THD}^{b_2} )</td>
<td>-1.0</td>
<td>-1.64</td>
<td>0.068</td>
<td>0.04</td>
<td>(&lt; &lt; 0.001)</td>
<td>0.88</td>
</tr>
<tr>
<td>( A_c:V_c \propto N^{b_1}\cdot\text{THD}^{b_2} )</td>
<td>0.5</td>
<td>0.61</td>
<td>0.017</td>
<td>0.03</td>
<td>(&lt; &lt; 0.001)</td>
<td>0.96</td>
</tr>
</tbody>
</table>

| **Subalpine fir** |          |         |      |      |        |        |
| \( W_c \propto N^{b_1} \) | -0.5     | -0.35   | 0.031| 0.09 | \(< < 0.001\) | 0.83   |
| \( L_c \propto N^{b_1}\cdot\text{THD}^{b_2} \) | -0.5     | ** -0.40| 0.050| 0.13 | 0.059  | 0.70   |
| \( V_c \propto N^{b_1}\cdot\text{THD}^{b_2} \) | -1.5     | -1.26   | 0.097| 0.08 | 0.022  | 0.88   |
| \( A_c \propto N^{b_1}\cdot\text{THD}^{b_2} \) | -1.0     | -0.78   | 0.063| 0.08 | 0.023  | 0.87   |
| \( A_c:V_c \propto N^{b_1}\cdot\text{THD}^{b_2} \) | 0.5      | ** 0.40 | 0.053| 0.13 | 0.074  | 0.74   |
Table 1.3. Revised predictions and results for mean crown volume. The symbol ** indicates agreement between predicted and observed values. Column headings are as in Table 1.2.

<table>
<thead>
<tr>
<th></th>
<th>pred. b1</th>
<th>obs. b1</th>
<th>SE</th>
<th>C.V.</th>
<th>P</th>
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<tr>
<td><strong>Lodgepole pine</strong></td>
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<td></td>
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<tr>
<td>$W_c \propto N^{b1}THD^{b2}$</td>
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<td><strong>-2.45</strong></td>
<td>0.177</td>
<td>0.07</td>
<td>0.057</td>
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<tr>
<td>$V_c \propto N^{b1}THD^{b2}$</td>
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<td>0.028</td>
<td>0.04</td>
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<tr>
<td><strong>Subalpine fir</strong></td>
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<tr>
<td>$W_c \propto N^{b1}THD^{b2}$</td>
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<td>-0.38</td>
<td>0.036</td>
<td>0.10</td>
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</tr>
<tr>
<td>$V_c \propto N^{b1}THD^{b2}$</td>
<td></td>
<td><strong>-1.26</strong></td>
<td>0.097</td>
<td>0.08</td>
<td>0.684</td>
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</tbody>
</table>
Fig. 1.1. (a) Mean crown width and (b) mean crown surface area versus absolute overstory density for lodgepole pine (squares) and subalpine fir (triangles). Lines were generated by regression equations for each species independently.
CHAPTER II

RESPONSE OF LEAF AREA INDEX TO DENSITY: EFFECTS OF PLASTIC CROWN SIZE FOR TWO CONTRASTING TREE SPECIES

Summary. It is commonly assumed that mature forest stands with closed canopies support constant amounts of foliage, independent of stand age or density. If foliage amounts are constant, mean leaf area must be plastic with respect to density. We examined the relationship between density and both leaf area index and mean leaf area for two contrasting tree species, *Pinus contorta* var. *latifolia* Engelm. (lodgepole pine) and *Abies lasiocarpa* (Hook.) Nutt. (subalpine fir). In lodgepole pine, leaf area index tended to be constant over a wide range of densities, but leaf area index of subalpine fir increased with density. Consistent with these results, mean leaf area of lodgepole pine was more plastic with respect to density than mean leaf area of subalpine fir. The presumption of stable foliage amounts independent of stand density is therefore not as general as usually assumed due to differential responses of mean leaf area to density. Differences in plasticity between the two species were attributed to differences in relative shade-tolerance and the effect of
shade on competitive interactions at high densities. Including an additional structural variable, mean crown length, with density increased the accuracy of leaf area index predictions for both species.

Introduction

Foliage is the primary site of photosynthesis, gas exchange and transpiration in forest stands and thus is a major factor in many biotic processes. Not surprisingly, the amount of foliage in forest canopies has been related to stand production (e.g., Tadaki 1986; Waring 1983), and also has been used as a measure of site occupancy (Long and Dean 1986; Waring et al. 1980) and to assess the effects of silvicultural practices (Binkley and Reid 1984; Ford 1985; Long and Smith in press a; Waring et al. 1981). Therefore, the amount and distribution of foliage in forest stands, measured as either leaf biomass or leaf area, has received extensive study.

A common observation is that closed canopy forest stands of many different species appear to maintain fairly stable amounts of foliage biomass or area over time (Gholz 1986; Grier and Running 1977; Marks and Bormann 1972; Pook 1984; Tadaki 1966, 1986) and across a wide range of stand densities (Møller 1947; Mohler et al. 1978; Stiell 1966; Turner and Long 1975). Because the phenomenon has been reported for many species and many
different site conditions, the concept of constant foliage amounts following canopy closure has become widely accepted.

The commonly applied term "foliage equilibrium" is used most correctly to describe the maintenance of constant foliage amounts over time. That is, a stand has an equilibrium foliage amount if, following canopy closure, the amount of foliage present in the canopy remains at nearly constant levels for many years. The equilibrium is dynamic, with the fixed amount of foliage being distributed among fewer trees over time due to self-thinning, resulting in an increase in mean leaf area (Dean and Long 1985; Long and Smith 1984; Westoby 1984). Equilibria are usually confirmed through a chronosequence approach (examination of several stands of different ages but with assumed similar site conditions and early stand development) or, more rarely, by determining foliage amounts for a single stand through time. The results of most such studies show that stands achieve and maintain an equilibrium, though some show that foliage amounts slowly decline over time (e.g., Tadaki 1986).

The phenomenon of constant amounts of foliage in stands with widely different densities is similar, but not directly comparable, to an equilibrium over time. A comparison of this type involves different stands of similar age that contain different numbers of trees per hectare. If the foliage amount is measured as leaf area and if total leaf area or leaf area index (LAI, m²m⁻²) is
constant, then mean leaf area ($A_i$) should be inversely proportional to stand density, i.e., $A_i \propto N^{-1}$ where $N$ is trees per hectare. This relationship for mean leaf area implies that stands with different densities but similar leaf area indices must differ in the distribution of foliage among individuals.

The phenomena of equilibrium foliage amounts over time and constant foliage amounts across a range of stand densities are not independent: each stand in the foliage-density relationship has an individual pattern of stand development, and each probably also has reached a stand-level foliage equilibrium. Although the amount of foliage may be unaffected by density after equilibrium is reached, the time required to achieve the equilibrium is dependent on initial density (Jarvis 1975; Long and Smith 1984; Turner and Long 1975). This interdependence between total foliage amounts, time, and stand density is illustrated by Turner and Long (1975).

Stand density is thus a factor common to the two phenomena. To maintain constant LAI over time, the mean leaf area in individual stands must change during stand development to compensate for foliage lost through self-thinning. Similarly, to maintain nearly equal leaf area indices in stands of different densities, the mean leaf area in stands of lower density must be larger to compensate for fewer individuals. Therefore, mean leaf area plasticity is fundamental to maintaining constant LAI over time or density.
We examined two species whose mean crown dimensions respond quite differently to density: lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). Long and Smith (in press b) reported that the LAI of lodgepole pine is independent of stand density, indicating that changes in mean leaf area closely compensate for changes in tree number. Further, Jack and Long (in press) reported that mean crown dimensions of lodgepole pine were more responsive to density than mean crown dimensions of subalpine fir (i.e., lodgepole pine crown dimensions are more plastic). If the relationships between mean leaf area and density are similar to those between mean crown dimensions and density, then the mean leaf area of subalpine fir will also be less responsive to density. If so, subalpine fir may not maintain constant LAI across time or density, thus providing an exception to conventional wisdom. Such an exception would challenge the presumed generality of constant leaf area index during a considerable portion of stand development, and possibly also explanations for processes which assume that the amount of foliage remains constant. Our objective was therefore to examine the relationship between leaf area index and density for lodgepole pine and subalpine fir, and to investigate the effect of plastic mean leaf area on these relationships.
Material and Methods

Lodgepole pine and subalpine fir differ in their crown morphologies and growth rates. Lodgepole pine is an extremely shade-intolerant, early successional species with spreading crown form, while subalpine fir is exceedingly shade-tolerant and has a long, narrow, spire-like crown form (Fowells 1965). In trees of equal sapwood area, subalpine fir supports substantially more leaf area than does lodgepole pine (Long and Smith 1989).

Study plots were located in the Bear River Range of northern Utah (42° N, 111° W), about 65 km northeast of Logan, UT, U.S.A. The plots were situated on a broad plateau-like ridge at an elevation of approximately 2500 m. The climate is typical of the central Rocky Mountains with mean January and August temperatures of -11 and 17 °C, respectively, and 104 cm average annual precipitation, primarily as winter snow. Further climatic information and general ecological characteristics are found in Hart and Lomas (1979) and Schimpf et al. (1980).

The 57 sample plots, 34 dominated by lodgepole pine and 23 dominated by subalpine fir, were located in unmanaged natural stands with a range of densities (Table 2.1). The dominant species in a plot was considered to be one that contributed at least 75% of the plot basal area (cumulative cross-sectional area of all stems at height of 1.3 m). Plot area varied to include 30-40 live trees per plot. At each plot, several measurements were recorded for
all live trees taller than breast height (1.3 m), including diameter at breast height (DBH), total height and height to the base of the live crown. Additionally, two increment cores were taken at right angles to each other at breast height on each tree, and the boundary between sapwood and heartwood was marked. Sapwood cross sectional area was calculated using the average width of sapwood from the two cores by assuming circular cross section. Projected leaf area was estimated for each tree utilizing the equations of Dean and Long (1986) for lodgepole pine and Long and Smith (1989) for subalpine fir. LAI was calculated as the sum of the individual tree leaf areas divided by plot area.

All live trees on each plot were classified either as members of the overstory or understory based on their position relative to the main canopy. The crowns of those trees classified as understory did not appear to be mechanically interacting with the crowns of the overstory trees. The overstory trees on average represented 79% and 74% of all live trees on the pine and fir plots, respectively. Plot characteristics for the overstory trees are summarized in Table 2.1. Plot averages were calculated using only the overstory trees in order to consider just those trees comprising the main canopy. Stand top height was calculated as the average height of the tallest 20% of the overstory trees on each plot.
A nonlinear, iterative least squares regression procedure (SAS Institute 1987) was used to examine the relationships of mean leaf area and leaf area index to stand density. The function regressed was \( L = a_0 + N^{a_1} \) where \( L \) is either leaf area index or mean leaf area, \( N \) is absolute stand density, and \( a_0 \) and \( a_1 \) are regression parameters. Estimated \( r^2 \) values were calculated as the difference between the corrected total and error sums of squares divided by the corrected total. Error estimates for the individual regression parameters were generated by bootstrap techniques (Efron and Tibshirani 1986). The \( a_1 \) values from the original regressions were compared to the distribution of values generated by the bootstrap routines to test for statistical differences from the expected values (-1 for the \( A_i-N \) relationship, 0 for the \( LAI-N \) relationship). Appropriateness of the model form was assessed using the \( r^2 \) values and examination of residuals.

Results

Mean leaf area of lodgepole pine is apparently more plastic with respect to density than is mean leaf area of subalpine fir (Table 2.2 and Fig. 2.1). In the regression function \( A_i = a_0 + N^{a_1} \), \( a_1 \) was not significantly different from -1 for lodgepole pine but was significantly different for fir (Table 2.2). These results imply that the lodgepole pine stands maintain constant leaf area index
over a range of densities, while the value of $a_1$ for subalpine fir suggests that leaf area index should increase with density.

The regressions of leaf area index against absolute stand density (Table 2.3 and Fig. 2.2) show that lodgepole pine LAI was independent of density while LAI of subalpine fir did increase with density. The regression equation for lodgepole pine (Fig. 2.2) indicates that LAI decreased slightly with density, a finding consistent with LAI decreases for some species with age (e.g., Tadaki 1986); the decline was not statistically significant, however (Table 2.3). Though the regressions were significant ($\alpha < 0.01$), much of variation was not explained by the functions (low $r^2$ values).

In an attempt to account for the large amount of variation in the relationship between leaf area index and stand density, and because there was some bias in the residuals when plotted against stand top height, a second variable, mean crown length ($L_c$), was used in the regressions for LAI. The inclusions of $L_c$ substantially increased the $r^2$ values for both species (Table 2.4) and also removed the bias in the residuals with stand height.

Though the regressions shown in Tables 2.2, 2.3 and 2.4 are based on only the overstory trees, including data from understory trees did not change the general conclusions, and only slightly changed the regression parameters. This is because the understory trees add very little to the stand total leaf area and primarily affect stand density.
Discussion

Lodgepole pine, which maintained constant leaf area index independent of stand density, had very plastic mean leaf area. In comparison, the mean leaf area of subalpine fir was less responsive to density and its leaf area index was positively correlated with density. Figure 2.1 illustrates this difference between the species. Mean leaf area of lodgepole pine varied considerably, from 7 to $222 \text{ m}^2$ over the range 4800 to 176 overstory trees ha$^{-1}$, whereas mean leaf area of subalpine fir varied only from 8 to 46 m$^2$ over the larger range of 12000 to 1111 overstory trees ha$^{-1}$.

The greater variation in mean leaf area for lodgepole pine is partially due to the greater range of mean tree sizes for this species (Table 2.1), primarily due to the very low densities in the lodgepole pine data. Though the two species overlap over a considerable range of densities, their different silvical characteristics mean that there are densities beyond the range of overlap. The separation by species at the extremes of the combined data range leads to the requirement of separate regression equations for the two species; although a single regression function appears to fit the combined data (not shown), the resulting residuals are strongly biased by species.

Therefore, greater numbers of subalpine fir trees pack more foliage into the canopy, more than offsetting any small decrease in mean crown size resulting from the higher density. But because mean crown size is not
plastic, subalpine fir does not readily alter its mean size to make use of all available growing space at lower densities. Thus LAI of subalpine fir declines at low densities, and may result in less than full site occupancy. In contrast, the crown size of lodgepole pine increases to utilize all available growing space at low densities, and its mean crown size is strongly diminished at high densities where growing space and available light are reduced. These species differences can be interpreted in two ways: lodgepole pine is much more sensitive than subalpine fir to the increased competition at high densities, or, alternatively, lodgepole pine is better able to compensate for changes in density by altering mean leaf area to maintain a constant LAI.

There is some upper limit to the amount of leaf area which can be supported at a given site, so LAI of subalpine fir obviously cannot continue to increase indefinitely with density. This is indicated by the nonlinear relationship between LAI and density (Table 2.3 and Fig. 2.2). The plot of the regression function (Fig. 2.2) shows that the LAI of subalpine fir continues to increase over the range of density included in these data, but with only modest increases at high densities (e.g., greater than 5000 trees ha⁻¹). The flattening of the curve at high densities could be interpreted as an indication that LAI is approaching some constant value, and the failure to reach a constant LAI attributed to the range of densities measured. This is probably not the case, however, because relative densities (SDI, Reineke 1933) were
also calculated for these stands, and values for the stands with the highest densities were comparable to the maximum SDI values reported for subalpine fir (Long and Smith in press a). Stands at high relative densities represent near maximum combinations of mean size and density, and LAI for such stands should be at the maximum for a species in a given environment (Long and Smith 1984; Smith 1986). Thus, it is unlikely that there would be higher density subalpine fir plots in which LAI would be greater and constant.

Though speculative, the species' differences in ability to alter crown size with density might be associated with two interdependent factors: shade-tolerance and successional status. At high stand densities relative shade-tolerance is a dominant factor affecting mean leaf area plasticity. At low light levels, the extremely shade-tolerant subalpine fir is able to maintain foliage and lower branches, whereas the intolerant pine sheds lower branches. Mean crown size of subalpine fir is therefore reduced less as density increases than is the mean crown size of lodgepole pine (Jack and Long in press). On the other hand, the ability to expand mean crown size at low absolute densities is related to the species' successional status and competitive strategy (Boojh and Ramakrishnan 1982; Horn 1971). In the study area both species form extensive, even-aged stands, but lodgepole pine is strictly an early successional species which invades sites opened by disturbance, while subalpine fir is a late successional species which establishes most often
beneath the canopies of other tree species (Schimpf et al. 1980). Lodgepole pine’s ability to rapidly increase mean crown size to utilize available growing space and exclude competitors is thus an important adaptation. Subalpine fir, however, dominates a site through numbers and persistence in the understory, and eventually shades less tolerant competitor species by forming a dense canopy of many individuals. Most reports of equilibria or constant foliage amounts across density concern relatively shade-intolerant species of commercial importance, which may explain why constant LAI is assumed to be a general phenomenon (e.g., Stiell 1966 (Pinus resinosa); Tadaki 1966 (Cryptomeria japonica, Pinus densiflora); Turner and Long 1975 (Pseudotsuga menziesii); but see also Möller 1947 (Fagus sylvatica); Mohler et al. 1978 (Abies balsamea)).

Though the relationships between LAI and absolute stand density clearly differ for the two species (Fig. 2.2), both regression equations leave much variation unexplained. This variation is similar to that found in data cited to support the concept of equilibrium foliage amounts over time (e.g., Kira and Shidei 1967; Tadaki 1986). Since stand density alone did not account for all of the observed variability in LAI, we included a second structural variable in the regression function.

The additional variable considered was mean crown length (Lc), a simple index of canopy structure with intuitive appeal. Many studies have shown the
importance of including measures of canopy structure when examining relationships between structure and production in forest stands. Mean crown length is a measure of canopy depth, and therefore provides the third dimension to an idealized spatial volume occupied by the canopy: stand density accounts for lateral dimensions, and crown length accounts for the vertical dimension. Therefore, at constant density an increase in mean crown length would be expected to increase canopy leaf area.

When mean crown length was a covariate, leaf area index at a given density increased with canopy depth (Table 2.4, positive exponent on crown length). Including mean crown length also removed bias in the residuals associated with stand top height, a result which reflects the correlation between stand height and crown length (Beekhuis 1965; Jack and Long in press). The similar values of the exponent on crown length for the two species (Table 2.4) apparently indicates that when the effect of density (which differs for the two species) is accounted for, LAI tends to be directly proportional to canopy depth for both species.

These results indicate that not all closed canopied forest stands maintain constant levels of leaf area index independent of stand density, a result which may be relevant to explanations of biotic processes which assume foliage amounts remain stable. Constant leaf area index independent of stand density necessarily implies that mean leaf area be exceedingly plastic with
respect to density. In lodgepole pine, LAI was independent of density, and mean leaf area was very responsive to density. In subalpine fir, however, mean leaf area was not as plastic with respect to density and LAI increased with the number of trees. For the species in this study, mean crown size plasticity may be related to shade-tolerance, i.e., shade-tolerant species are less affected by increased competition at higher densities. Finally, including mean crown length as a simple measure of canopy structure greatly increased the amount of variation in leaf area index explained by the regression equations, regardless of the relationship between LAI and stand density.
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### Table 2.1. Sample plot characteristics for overstory trees. Values are means with ranges in parentheses.

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<tr>
<th></th>
<th>Lodgepole Pine</th>
<th>Subalpine Fir</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Number of plots</strong></td>
<td>34</td>
<td>23</td>
</tr>
<tr>
<td><strong>Live trees per plot</strong></td>
<td>25 (10-47)</td>
<td>24 (13-38)</td>
</tr>
<tr>
<td><strong>Density (trees ha⁻¹)</strong></td>
<td>1868 (176-4800)</td>
<td>6322 (1111-12000)</td>
</tr>
<tr>
<td><strong>Quadratic mean diameter (cm)</strong></td>
<td>21.6 (10.9-36.7)</td>
<td>14.6 (8.9-22.1)</td>
</tr>
<tr>
<td><strong>Mean top height (m)</strong></td>
<td>22.8 (17.6-27.9)</td>
<td>17.0 (12.5-23.3)</td>
</tr>
<tr>
<td><strong>Leaf area index (m² m⁻²)</strong></td>
<td>3.13 (1.40-4.71)</td>
<td>7.58 (4.82-12.83)</td>
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<tr>
<td><strong>Age (years)</strong></td>
<td>89 (67-134)</td>
<td>75 (66-98)</td>
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Table 2.2. Regression results for $A_i \propto N^{a_1}$ where $A_i$ is mean leaf area, $N$ is stand density, and $a_1$ is a regression parameter.

<table>
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<tr>
<th>species</th>
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<th>subalpine fir</th>
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<td>$r^2$</td>
<td>0.91</td>
<td>0.86</td>
</tr>
<tr>
<td>observed $a_1$ value</td>
<td>-1.16</td>
<td>-0.64</td>
</tr>
<tr>
<td>standard error of $a_1$</td>
<td>0.10</td>
<td>0.052</td>
</tr>
<tr>
<td>Probability ($a_1 = -1$)</td>
<td>0.14</td>
<td>$&lt;&lt; 0.0001$</td>
</tr>
</tbody>
</table>


Table 2.3. Regression results for \( \text{LAI} \propto N^{b_1} \) where LAI is leaf area index, \( N \) is stand density, and \( b_1 \) is a regression parameter.

<table>
<thead>
<tr>
<th>species</th>
<th>lodgepole pine</th>
<th>subalpine fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>( r^2 )</td>
<td>0.01</td>
<td>0.43</td>
</tr>
<tr>
<td>observed ( b_1 ) value</td>
<td>-0.020</td>
<td>0.29</td>
</tr>
<tr>
<td>standard error of ( b_1 )</td>
<td>0.047</td>
<td>0.076</td>
</tr>
<tr>
<td>Probability ((b_1 = 0))</td>
<td>0.67</td>
<td>0.0012</td>
</tr>
</tbody>
</table>
Table 2.4. Regression results for $\text{LAI} \propto N^{b_1}L_c^{b_2}$ where LAI is leaf area index, N is stand density, $L_c$ is mean crown length, and $b_1$ and $b_2$ are regression parameters.

<table>
<thead>
<tr>
<th>species</th>
<th>lodgepole pine</th>
<th>subalpine fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>$r^2$</td>
<td>0.36</td>
<td>0.86</td>
</tr>
<tr>
<td>observed $b_1$ value</td>
<td>0.36</td>
<td>0.68</td>
</tr>
<tr>
<td>standard error of $b_1$</td>
<td>0.12</td>
<td>0.064</td>
</tr>
<tr>
<td>observed $b_2$ value</td>
<td>1.02</td>
<td>1.19</td>
</tr>
<tr>
<td>standard error of $b_2$</td>
<td>0.27</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Fig. 2.1. Mean leaf area versus overstory density. Squares represent lodgepole pine plot means, circles subalpine fir plot means. Lines generated by the regression equations $A_i = 84677N^{1.16}$ for lodgepole pine and $A_i = 3826N^{0.94}$ for subalpine fir.
Fig. 2.1. Mean leaf area versus overstory density. Squares represent lodgepole pine plot means, circles subalpine fir plot means. Lines generated by the regression equations $A_i = 84877N^{-1.16}$ for lodgepole pine and $A_i = 3926N^{-0.64}$ for subalpine fir.
Fig. 2.2. Leaf area index versus overstory stand density. Squares and circles as in Fig. 2.1. Lines generated by the regression equations $\text{LAI} = 3.61 \times N^{-0.020}$ for lodgepole pine and $\text{LAI} = 0.71 \times N^{0.29}$ for subalpine fir.
CHAPTER III
FOREST PRODUCTION AND THE ORGANIZATION OF FOLIAGE
WITHIN CROWNS AND CANOPIES

Abstract

A nonfoliated area (or "bare inner core") develops in the interior of tree crowns as the size of the crown increases during stand development. We examined the relationship between mean bare core volume and both stand density and mean crown volume, and its association with the production of stemwood volume for two conifer species, *Pinus contorta* var. *latifolia* and *Abies lasiocarpa*. Mean bare core volume decreases with absolute stand density and increases with mean crown volume for both species. The bare core volume occupies an increasing proportion of total crown volume with increasing crown size. Small bare core volumes are associated with small, efficient crown sizes, and large bare core volumes with large, less efficient crown sizes. These relationships are examined in the context of tree crop ideotypes and the influence of differing density regimes on stand production.
Introduction

As mean crown size increases during forest stand development, canopy structure and competitive interactions among the individual crowns progressively change (Assmann, 1970; Ford, 1982; Oliver and Larson, 1990). One result of the increase in crown size is the development of a nonfoliated area in the central portion near the stem; i.e., the foliage is arrayed in a mantle or shell at the edge of the crown, with the inner portions bare of foliage (Assmann, 1970; Mitchell, 1975; Schulze et al., 1977; Ford, 1985; Magnussen et al., 1986; Smith and Long, 1989). Assmann (1970) termed this central region without foliage the "bare inner core". The bare core develops because the foliage at the edge of the crown absorbs most of the incident radiation, causing light levels in the inner crown to fall below the light compensation point (Schulze et al., 1977; Oker-Blom and Kellomäki, 1982; Kurachi et al., 1986; Magnussen et al., 1986); consequently, the foliage nearer the stem dies and is not replaced.

The formation of a bare core in the individual crowns comprising a forest canopy is of morphological and structural interest, particularly in light of reports that stemwood production per unit crown projection area (Kramer, 1966; Assmann, 1970; O'Hara, 1989) or per unit leaf area (Ryan, 1989; Long and Smith, 1990; Smith and Long, in press) decreases with increasing crown size, i.e., larger crowns are less efficient. The presence of a bare inner core
is germane to observed declines in efficiency because these declines are usually explained in terms of the increased costs associated with constructing and maintaining a larger crown (Cannell, 1979; Mäkelä, 1986; Ryan, 1989; Smith and Long, 1989; Long and Smith, 1990; Smith and Long, in press).

Large branch biomass is associated with a large crown because lower branches must be strong enough to array foliage at a considerable distance from the stem, but a high proportion of this branch biomass does not contribute to the pool of photosynthates because it is nonfoliated. Branches do, however, use carbohydrates for both growth and maintenance respiration, and therefore are a net carbon sink. Because respiration demands are met first (Mooney, 1972) and stem diameter growth has a relatively low priority (Lanner, 1985; Waring and Schlesinger, 1985), high allocation to branches means proportionally less carbohydrate is available for the production of stemwood (Kaufmann and Ryan, 1986; Ryan, 1989). Higher stemwood production efficiencies should therefore result when the foliage shell is arrayed closer to the stem, thereby reducing the size of the bare core within a given crown or canopy volume (Hamilton, 1969; Assmann, 1970; Ford, 1985).

The presence and extent of the bare inner core is usually measured only for individual trees (e.g., Burger, as cited in Assmann, 1970; Schulze et al., 1977), and despite its intuitive importance to production processes, little is known about how the size of the bare core varies with absolute crown size or
with stand and canopy structure. Recent work to characterize the vertical and horizontal distributions of leaf area density for use in process-based simulation models (e.g., Wang et al., 1990) indirectly indicates the presence of a bare core, but such work is also done for individual trees using a limited range of stand structures. On a stand basis, there are reports that the average ratio of foliage weight to total crown weight decreases with increasing mean crown size (Satoo et al., 1955; Lavigne, 1985; Long and Smith, 1990; Smith and Long, in press), but this work is also only suggestive of the formation of a nonfoliated, bare inner core.

Our objectives were therefore to consider how an estimate of the size of the bare core varies with changes in stand and canopy structure such as might occur during stand development or following silvicultural treatments. Additionally, we wished to examine the relationship between the size of the bare core and the production of stemwood volume, and whether the size of the bare core is associated with changes in efficiency as some have suggested. Finally, the results based on an analysis of the mean tree will be extended to the design of efficient canopy structure for stand-level volume production.
Material and Methods

Sample plots were located in the Bear River Range of northern Utah, approximately 65 km northeast of Logan, UT, USA. The Utah State University Forest (42° N, 111°30' W) is located on a broad, plateau-like ridge with moderate topographic relief, ranging in elevation from 2500 to 2700 m. The climate is typical of the central Rocky Mountains: mean January and August temperatures are -11 and 17 °C, respectively, and average annual precipitation is 104 cm, primarily from winter snow. Hart and Lomas (1979) and Schimpf et al. (1980) describe further climatic and general ecological characteristics.

The two contrasting tree species used in this study were lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.). These species differ in gross crown morphology, growth rate, and relative shade-tolerance (Fowells, 1965). Subalpine fir is exceptionally shade-tolerant with a long, narrow, spire-like crown form. In contrast, lodgepole pine is an extremely shade-intolerant, early successional species possessing a more rounded, spreading crown form. Additionally, for trees of equal sapwood area subalpine fir supports substantially more leaf area than lodgepole pine (Kaufmann and Troendle, 1981; Long and Smith, 1989).

Fifty-seven sample plots, 34 classified as lodgepole pine plots and 23 as subalpine fir plots, were located across a range of absolute and relative stand densities (Table 3.1). A plot was classified as dominated by one species
when that species contributed more than 75% of the plot basal area (cumulative cross-sectional area of all stems at a height of 1.3 m). Plot area varied from 17.5 to 750 m² to include 30-40 live trees per plot. At each plot, all trees taller than breast height (1.3 m) had diameter at breast height (dbh, cm), height (m), and height to the base of the live crown (m) recorded. Each tree also had two increment cores removed from breast height at right angles to each other. The boundary between sapwood and heartwood was marked on these cores, and the average sapwood radius used to calculate sapwood area at breast height. The calculated sapwood areas were used to estimate leaf area per tree by applying the equations of Dean and Long (1986) for lodgepole pine and Long and Smith (1989) for subalpine fir. These equations account for the effects of sapwood taper and density on estimates of leaf area. Leaf area index (LAI) for each plot was calculated as the sum of the individual tree leaf areas divided by plot area. The two cores were also used to measure radial increment for the last five years, and species-specific local volume equations used to estimate current annual increment as described in Long and Smith (1990) and Smith and Long (in press).

Each live tree on each plot was additionally classified as a member of either the understory or overstory. Understory trees were those whose crowns did not appear to be mechanically interacting with the crowns of the overstory trees. The overstory trees thus were primarily from the dominant,
codominant, and upper intermediate crown classes, and on average represented 79% and 74% of all live lodgepole pine and subalpine fir trees per plot, respectively. Stand top height was calculated as the average height of the tallest 20% of the overstory trees on a plot. Two measurements of crown diameter were taken for each overstory tree; the two diameters were perpendicular to each other and their orientation was kept constant within a plot. The average of the two diameter measurements was used with the measured crown length to calculate crown volume and crown surface area for each tree by assuming paraboloid crown shape. Canopy structure for a plot was indicated by the mean crown dimensional characteristics of only the overstory trees, i.e., those trees comprising the main canopy.

Leaf area density (LAD, m\(^2\)/m\(^3\)) is usually calculated by dividing leaf area by the estimated crown or canopy volume (e.g., Kira et al., 1969; Whitehead, 1986). Since foliage is often arrayed in a shell, we instead assumed that the effective leaf area density (ELAD, the actual density within the foliated region) per tree is constant for a given species, regardless of crown size. Because we had estimates of crown volume (CRV) and leaf area (LA) for each tree, we could calculate by subtraction the bare core volume (BCV) that yielded the species-specific ELAD for each crown (i.e., \(BCV = CRV - LA/ELAD\)). This approach using concentric shells within the crown is similar to those used by
Mitchell (1975), Rook et al. (1985) and Grace et al. (1987a,b), though we have used only two shells, the outer being foliated and inner nonfoliated.

To estimate the species specific ELAD values, leaf area density was first calculated for each tree in the common manner, i.e., leaf area divided by crown volume. All trees of a given species (842 lodgepole pine trees and 563 subalpine fir trees) were then pooled across all plots and the 95th percentile value for LAD calculated and assumed to be the effective leaf area density for that species. The 95th percentile value was used because it represented values of LAD for trees with very small crowns, which we assumed did not have an appreciable bare inner core, yet at the same time avoided extreme values. The ELAD values, 4.39 m²/m³ for lodgepole pine and 5.26 m²/m³ for subalpine fir, were used as outlined above to estimate BCV for each overstory tree, and the average bare core volume \( V_{bc} \) calculated for each plot.

An iterative, nonlinear regression procedure (SAS Institute, 1987) was used to characterize relationships between the variables of interest. Estimates of \( r^2 \) for these regressions were calculated as the difference between the error and corrected total sum of squares divided by the corrected total. Standard error estimates for the individual regression parameters were generated using bootstrap techniques (Efron and Tibshirani, 1986).
Results and Discussion

The relationship between stemwood volume increment and the mean crown dimensions of surface area and volume (Fig. 3.1) are similar to those found for other measures of crown size: a larger crown produces more absolute growth, but the nonlinear form of the relationship indicates that the unit increase in growth per unit increase in mean crown size is proportionally smaller at large mean crown sizes. Therefore, as mean crown size increases, production of stemwood becomes less efficient. The surprising result is that the relationships between mean crown size and stemwood production do not separate by species, a result also found by Smith and Long (in press) for the same two species using mean leaf area as the measure of crown size. Apparently, a given mean crown size produces a given mean stem volume increment independent of species (at least for these two conifers). It should be remembered, however, that a particular mean crown size will occur at very different densities for these two species (Jack and Long, in press). Thus, even though mean increment is the same, canopy structures and per hectare productivities will vary greatly.

Our estimate of bare core volume was determined by assuming that the effective leaf area density is independent of stand or canopy structure. Although we calculated separate ELAD values for the two species, the estimate of $V_{bc}$ is not sensitive to the particular value of ELAD used for
computation. Use of a single ELAD for the two species combined did not substantially affect estimates for $V_{bc}$, and did not change conclusions based upon these estimates. Also, though the ELAD values used are considerably greater than reported leaf area density values in forest stands (e.g., Kira et al., 1969; Smith and Long, 1989), the larger values result from differing assumptions of the volume occupied by foliage, i.e., use of the foliated mantle volume versus the entire crown volume for calculation of leaf area density.

When the effective leaf area density is used to estimate mean bare core volume, $V_{bc}$ varies with density ($N$) as shown in Fig. 3.2. Large values of $V_{bc}$ are associated with low stand density and thus also with large mean crown size (Jack and Long, in press). Because low $N$ and large mean crown size have also been associated with reduced efficiencies (Fig. 3.1; Kramer, 1966; Long and Smith, 1990; Smith and Long, in press), these results provide circumstantial evidence that the size of the bare core is negatively associated with stemwood production efficiency.

There is a nonlinear relationship between $V_{bc}$ and mean crown volume ($V_c$) because the exponent in the nonlinear regression function is statistically different from 1 ($P=0.001$, $V_{bc} = 0.6096 \times V_c^{1.064}$, $n=57$, $r^2=0.99$). Thus, for each unit increase in mean crown volume the volume of the bare core increases by a proportionally greater amount, and the bare core occupies an increasingly greater proportion of the total crown volume as the crown
increases in size. Thus the ratio of $V_{bc}:V_c$ increases with $V_c$, but eventually reaches an upper limit or plateau when the ratio is approximately 80% (Fig. 3.3). The asymptotic form of the relationship is perhaps indicative of some functional limit to the amount of respiring, structural biomass which can be supported by a given amount of foliage.

The proportion of the crown volume which is bare of foliage can influence the partitioning of carbon in trees. A large $V_{bc}:V_c$ ratio implies that the majority of the foliage is necessarily amassed at considerable distance from the stem. Theoretical calculations (Ford, 1985; Cannell and Morgan, 1990) indicate that arraying foliage far from the stem is more costly in terms of carbohydrates than displaying foliage on smaller, higher order branches near the stem. Maintenance of foliage on small lateral branches close to the stem, which reduces the proportion of the crown volume that is nonfoliated, thus affords a greater surplus of assimilates which can be exported from the branches for stemwood production (Cannell and Morgan, 1990).

Based on similar considerations, Assmann (1970) reasoned that crown forms with high surface to volume ratios should minimize the size of the bare core and thus increase the efficiency of stemwood production. Comparable suggestions are found in proposals for crop tree ideotypes meant to maximize harvest index and production per hectare. In general, the best crop ideotype for temperate conifers is thought to be a tree with a long, narrow, pointed
crown and few short, thin branches (Cannell et al., 1983; Pulkkinen et al., 1989). Because both of these suggested crown forms entail the arrangement of foliage close to the stem (i.e., minimized bare core size), we examined the relationships between $V_{bc}$ and both the ratio of crown surface area to crown volume ($A_c:V_c$) and a measurement of crown slenderness, the ratio of crown length to crown width ($L_c:W_c$).

Bare core volume is strongly and inversely associated with $A_c:V_c$ (Fig. 3.4a), but there is no predictable relationship between $V_{bc}$ and $L_c:W_c$ (Fig. 3.4b). Therefore, while maintaining a high surface to volume ratio does appear to minimize the size of the bare core, the same cannot not be said (based on these two species) for crowns which are relatively long and narrow. It has been suggested that on theoretical grounds, a longer crown should be more efficient at gathering light (Jahnke and Lawrence, 1965; Kira and Shidei, 1967), and there are results showing that a relatively narrow crown produces stemwood more efficiently (Hamilton, 1969; Kuuluvainen, 1988; Pulkkinen et al., 1989). Others, though, have found that long crowns are less efficient at producing stemwood (Kellomäki, 1986; Sheppard and Ford, 1986; Smith and Long, 1989), thus the relationship between stemwood production efficiency and crown length or slenderness is not clear. Long narrow crowns do allow more trees per unit area, however, and therefore can increase per hectare production through greater numbers of trees (Kellomäki, 1986).
It has been reported that the maximum annual stemwood volume increment per hectare of a given stand occurs at about the time of canopy closure, presumably before a substantial bare inner core develops in the individual trees (Metzger, 1893, cited in Assmann, 1970; Kira, 1975; Ford, 1982, 1985). Because a greater proportion of mean crown volume is foliated at small mean crown size (Fig. 3.3), and because mean crown size is strongly inversely related to stand density (Jack and Long, in press), a larger proportion of total canopy volume should be foliated at higher densities. Thus, high density stands should have higher stand volume increments. This is in fact the case for the two species in this study (Fig. 3.5). High stand densities lead to greater annual production of stemwood volume per hectare, though of course the size of the individual trees will on average be smaller (Long, 1985).

The results of this study indicate the tradeoffs to be considered when making decisions about how best to meet particular management objectives for the production of stemwood volume (Kramer, 1966; Assmann, 1970; Ford, 1984; Long, 1985; Kellomäki, 1986; Smith and Long, 1989). A stand composed of many small-crowned individuals will be more efficient at producing stemwood volume because of relatively small bare cores, and per hectare volume production will be high. This is the concept which has led to the development of crop tree ideotypes, i.e., maximizing stand production.
Under such a system, however, the size of the individual stems will be small and of low value. Conversely, a stand composed of few trees with large mean crown size, and thus large bare core volumes, will be less efficient and less total volume will be produced per hectare, but the value of the larger individual stems will be considerably greater.

Clearly, the choice of density regime must be made in light of specific objectives and the product of interest. Stands with smaller but more efficient trees will not necessarily meet the same objectives as a stand with a few large and vigorous individuals. In practice, management of forest stands often involves a compromise of intermediate tree size and median efficiency (Long, 1985; Kellomäki, 1986), thereby striking a balance between stand production and individual value.
References


Table 3.1
Sample plot characteristics for overstory trees. Numbers represent means and ranges.

<table>
<thead>
<tr>
<th>species</th>
<th>lodgepole pine</th>
<th>subalpine fir</th>
</tr>
</thead>
<tbody>
<tr>
<td>number of plots</td>
<td>34</td>
<td>23</td>
</tr>
<tr>
<td>density (trees ha⁻¹)</td>
<td>1868 (176-4800)</td>
<td>6322 (1111-12000)</td>
</tr>
<tr>
<td>quadratic mean diameter (cm)</td>
<td>21.6 (10.9-36.7)</td>
<td>14.6 (8.9-22.1)</td>
</tr>
<tr>
<td>mean top height (m)</td>
<td>22.8 (17.6-27.9)</td>
<td>17.0 (12.5-23.3)</td>
</tr>
<tr>
<td>leaf area index (m² m⁻²)</td>
<td>3.13 (1.40-4.71)</td>
<td>7.58 (4.82-12.83)</td>
</tr>
<tr>
<td>age (yrs)</td>
<td>89 (67-134)</td>
<td>75 (66-98)</td>
</tr>
</tbody>
</table>
Fig. 3.1. Mean volume increment plotted against (a) mean crown surface area and (b) mean crown volume. Squares represent lodgepole pine plot means, circles subalpine fir plot means. Lines generated by the following regression equations for the 57 plots combined across species: (a) \( I_v = 0.01663 \times (1 - e^{-0.007562 \times A_c}) \) \( (r^2=0.89) \), and (b) \( I_v = 0.01180 \times (1 - e^{-0.02130 \times V_c}) \) \( (r^2=0.86) \) where \( I_v \) is mean volume increment, \( A_c \) is mean crown surface area and \( V_c \) is mean crown volume.
Fig. 3.2. Estimated mean bare core volume versus overstory density.
Squares and circles as in Fig. 3.1.
Fig. 3.3. Ratio of mean bare core volume to mean crown volume \((V_{bc}:V_c)\) versus mean crown volume. Plotted regression line: 
\[
V_{bc}:V_c = 0.7697 \times (1 - e^{-0.2103 \times V_c}) \quad (n=57, r^2=0.58).
\]
Fig. 3.4. Estimated mean bare core volume plotted against the ratios of (a) mean crown surface area to volume \((A_c : V_c)\), and (b) mean crown length to crown width \((L_c : W_c)\). Squares and circles are as defined in Fig. 3.1.
Fig. 3.5. Stand volume increment versus overstory density for lodgepole pine (squares) and subalpine fir (circles). The regression lines were generated by the equations: $T_{lv} = 0.5547 \times N^{0.3149}$ ($n=34$, $r^2=0.53$) and $T_{lv} = 0.6246 \times N^{0.3511}$ ($n=23$, $r^2=0.48$) for lodgepole pine and subalpine fir, respectively, where $T_{lv}$ is stand volume increment and $N$ is overstory density.
CHAPTER IV

STRUCTURE, PRODUCTION AND CANOPY DYNAMICS: A COMPARISON OF LODGEPOLE PINE AND SUNFLOWERS

Abstract

Populations of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.) and sunflower (*Helianthus annuus* L.) were examined to compare the influence of stand density on canopy structure and the association between canopy structure and the production of stem volume. The two types of populations exhibited both similarities and differences. Structural dynamics, as indicated by comparable plastic responses of canopy structure to competitive interactions with increasing density, were similar for lodgepole pine and sunflowers. The influence of canopy structure on the production of stem volume, however, was fundamentally different: the similar responses of canopy structure to changes in density resulted in a decrease in efficiency with increasing mean crown size for lodgepole pine populations, but not in populations of sunflower. This intrinsic difference between the two species was attributed to the large accumulation of branch biomass required to...
effectively display foliage in the canopies of the perennial lodgepole pine, accumulation which does not occur in the annual sunflower.

Introduction

Forest stand structure undergoes many changes during stand development due to changing competitive interactions among the individual trees comprising the stand (Assmann, 1970; Ford, 1982; Oliver and Larson, 1990). These changes in structure are particularly evident within the forest canopy. Early in the development process, the individual crowns are free to expand into available growing space. Eventually, however, a point is reached where lateral growth is restricted by neighbors (Long and Smith, 1984), and crown length and leaf area are limited by the light environment (i.e., growth is restricted by competition for space and light). Both the ultimate size of the individual crowns and the timing of lateral growth restriction depend on the absolute density of the stand: small mean crown size is associated with high densities (Assmann, 1970; Curtis and Reukema, 1970; Hamilton, 1969; Jack and Long, 1991), and competition between crowns begins sooner at high densities (Long and Smith, 1984). The distribution of stand leaf area among individuals is also strongly determined by stand density (Dean and Long, 1985; Long and Smith, 1990).
Concomitant with the changes in stand and canopy structure, production of stemwood volume also changes. Mean stem volume increment increases with increasing mean crown size, but the relationship is nonlinear so that increases in stem growth at large mean crown sizes are proportionally less than at small mean crown sizes (Ryan, 1989; Smith and Long, 1989; Long and Smith, 1990; Smith and Long, 1991). Large crowns are, therefore, less efficient than small crowns at producing stemwood volume.

The change in efficiency with crown size is usually attributed to the increased costs of constructing and maintaining a larger crown (Cannell, 1979; Ryan, 1989; Long and Smith, 1990). Mean crown dimensions and mean leaf area are increased at low densities primarily through the retention of branches in the lower portions of the crown (Beekhuis, 1965; Stiell, 1966; Jack and Long, 1991). The foliage on these lower branches is arrayed at great distance from the stem due to low light levels in the interior of the crown, thus a high proportion of the total branch length is nonfoliated resulting in low ratios of foliage to wood biomass.

Branch biomass in a large crown, due predominately to large lower branches, therefore entails a considerable respirational cost because the woody portions of these large branches do not photosynthesize yet are important carbohydrate sinks. Because respiration needs are met first (Mooney, 1972) and radial stem growth is a relatively low priority (Lanner,
1985; Waring and Schlesinger, 1985), the large basal branches export little assimilate for stem growth. One indicator of the large respiration costs inherent in constructing and maintaining a large crown is the ratio of foliage to total crown biomass which decreases with increasing mean crown size (Satoo, Nakamura and Senda, 1955; Lavigne, 1985; Long and Smith, 1990; Smith and Long, 1991).

A general conceptual model for the effect of stand and canopy structure on forest production can therefore be outlined as follows:

1) Stand density influences canopy structure and the distribution of leaf area due to the plastic response of individual crowns within the canopy to competition for space and light (Fig. 4.1a).

2) Changes in canopy structure have considerable influence on both absolute stem growth and on the efficiency of this growth due to the influence of crown and canopy structure on the allocation of carbon within the trees (Fig. 4.1b). Though larger crowns produce more stem growth in absolute terms, the growth is produced less efficiently.

3) The assumed mechanism for this decline in efficiency is the increased respiration costs associated with supporting the accumulated branch biomass in large crowns. The decline in the mean ratio of foliage to total crown biomass \(R_{F,C}\) with increasing crown size in forest trees (Fig. 4.1c) is consistent with this assumption.
This model for structure-production relationships was developed based on information from conifer forests where structural characteristics are clearly important (Oliver and Larson, 1990) and are known to affect carbon partitioning and production. The model, however, is not necessarily specific to forest systems; the relationships incorporated in the model, and the associated assumptions, may also apply to other types of developing plant populations.

We therefore examined structure-production relationships in stands of sunflower (*Helianthus annuus* L.) established across a range of densities, and compared these relationships to those found for stands of lodgepole pine (*Pinus contorta* var. *latifolia* Engelm.). Sunflowers provide a potentially useful analog to trees because they are single stemmed and because they, like trees, exhibit considerable plastic responses to competition (Clements, Weaver and Hanson, 1929). The objective of these comparisons was to examine whether the influence of canopy structure on stem volume production, presumably due to the costs of displaying foliage in large crowns, is similar for populations of a woody perennial (lodgepole pine) and an annual (sunflower).
Material and Methods

The sunflower plots were located on the Utah State University Greenville Experimental Farm, Logan, Utah, USA. Plots with seven different approximate densities (10, 25, 50, 100, 200, 300 and 400 plants m$^{-2}$) were established in freshly tilled soil on 10 and 13 June 1988. For the two lowest densities, seeds were placed in furrows and spaced to approximate the desired density. For all other densities the appropriate amount of seed, determined by weight (1480 seeds per 100 g), for the desired density was spread evenly within the plot. Due to the method of seeding and incomplete germination, spacing between plants within the subplots and subplot densities within the larger plots were not uniform for either planting method. The uneven spacing and range of densities, however, is not unlike the variable spacing and densities of the naturally established lodgepole pine to which these data were compared.

The plots were large enough to allow the establishment of six square subplots at random within the larger plot (except in the 50 plants m$^{-2}$ plot where 4 subplots were established due to poor germination within the plot). The subplots were located such that there was a buffer strip at least two plant heights wide between them. The dimensions of the subplots varied with density (15 cm to 1 m on a side). Approximately 25 days after germination, each plant within a subplot was tagged to aid identification throughout the experiment.
Each tagged plant on each subplot had several measurements recorded on 4 and 5 August 1988, 52 to 55 days after planting. At this time the plants were mature and the canopy fully developed, but there was not yet significant flower development. The measurements included basal diameter (cm, at 2.5 cm above groundline), total height (cm), height to the lowest live leaf (cm), and two measurements of crown diameter (cm) oriented N-S and E-W. Each plant was also characterized as a member of the over- or understory based on whether or not it appeared to be mechanically interacting with the main canopy. Only overstory plants were used in the calculations of mean values for comparison to lodgepole pine because these were the individuals comprising the canopy.

All plants in the subplots were subsequently harvested. Plants were sectioned into 10 cm lengths (starting from groundline), and fresh weight of the leaf and stem components for each section measured in the field using a portable electronic balance. Three plants from each subplot, representing the range of plant sizes, also had diameter at the base of each section measured with calipers, then were returned to the lab for determination of leaf area (LiCor optical planimeter) and component dry weights. Regression equations with fresh weight as the independent variable were developed from this subsample to estimate leaf area and dry weight by section and component for all tagged plants. Stem volume was calculated for the subsample of
plants by using the sectional diameter measurements and applying Smalian's formula (Husch, Miller and Beers, 1972), and a regression equation developed to predict stem volume from basal diameter and height.

Total leaf area for each plant was calculated by summing the sectional leaf areas estimated from the regression equation, and an average calculated for the overstory plants in a subplot. The estimated component dry weights were used to calculate the ratio of leaf to total biomass (leaf + stem) by section and for the entire crown for all plants. The mean ratio of foliage to total biomass within the crown ($R_{F:C}$) for each subplot was calculated as the average of the values for the overstory plants. Mean stem volume increment was estimated as the average volume of the stems of overstory plants divided by the number of days since planting.

Data for lodgepole pine, an extremely shade-intolerant pioneer species, were gathered from 34 sample plots established in the Utah State University Experimental Forest in the Bear River Range of northern Utah, about 65 km northeast of Logan, UT, USA. Elevation ranged from approximately 2550 to 2750 m. General ecological characteristics of the area were described by Schimpf, Henderson and MacMahon (1980).

Sampling procedures and the measurements taken for lodgepole pine were essentially the same as those described for sunflowers. Sample plots were located in stands with a wide range of stand densities, and plot size
varied with density to include 30 to 40 live trees per plot. Each tree taller than breast height (1.3 m) had diameter at breast height (cm), height (m), and height to the base of the live crown (m) recorded. Additionally, each tree had two increment cores removed at right angles to each other from breast height. The boundary between the translucent sapwood and opaque heartwood was marked on each core by holding it in sunlight. Sapwood cross sectional area was calculated from the average width in the two cores by assuming circular cross section. Sapwood area was then used to estimate leaf area for each tree using the equation of Dean and Long (1986), an equation which accounts for sapwood taper and density effects. Stem volume increment was estimated by measuring radial growth during the last five years from the increment cores, and employing a local volume equation developed by Long and Smith (1990). As for sunflowers, only trees classified as members of the overstory were used in the calculation of plot means.

Relationships between variables of interest were characterized using either linear least-squares regression or iterative nonlinear least-squares regression procedures (SAS Institute, 1987). Approximate $r^2$ values for the nonlinear regression equations were estimated as the difference between error and corrected total sums of squares divided by the corrected total.
Results and Discussion

Despite their vastly different longevities and stature, sunflowers have, in fact, been used as an analog for forest trees in other studies (e.g., Kuroiwa, 1960). Sunflowers were chosen for this study because of their single stem and the documented influence of density on mean crown size for the species (Clements et al., 1929). Though the absolute units of measurement differ for the two types of populations, the range of densities for both include nearly open-grown to self-thinning populations and thus represent similar ranges of site occupancy and competition. Additionally, the range of leaf area index measured for the two types of populations was very similar (LAI ranged from 1.4 to 4.7 and 0.5 to 4.9 m$^2$ m$^{-2}$ for lodgepole pine and sunflowers, respectively). Stands of lodgepole pine and sunflower, therefore, appear to have structural similarities so that valid comparisons can be made between the population types.

The relationship between mean leaf area and overstory density for both lodgepole pine and sunflowers (Fig. 4.2) indicate the plastic response of mean crown size to competition. Relationships (not shown) between dimensional measures of mean crown size (e.g., mean crown volume) and density exhibit similar negative exponential relationships for both population types.

As with forest trees, competition limits mean crown size at high densities. The particular exponents in the regression equations describing the
relationships between mean leaf area and overstory density differ \( A_i \propto N^{-0.60} \) and \( A_i \propto N^{-1.12} \) for sunflowers and lodgepole pine, respectively, where \( A_i \) is mean leaf area and \( N \) is overstory density), thereby indicating differing degrees of plasticity in response to changes in density. The basic form of the relationships is the same, however: large mean leaf areas are found at low absolute densities, while small mean leaf areas result at high densities. Mean leaf area is larger in each instance primarily through greater retention of lower branches or leaves at low densities. This retention of foliage low in the crown is reflected by the strong negative correlation between mean live crown length and density for both species \( (r = -0.76, P = 0.0001 \) for lodgepole pine; \( r = -0.57, P = 0.0001 \) for sunflowers).  

In contrast to these similarities, stem volume production as a function of mean leaf area is fundamentally different for lodgepole pine and sunflowers (Fig. 4.3). For populations of lodgepole pine, the nonlinear relationship between mean volume increment and mean leaf area indicates a decrease in efficiency with increasing crown size. In contrast, the mean increment-mean leaf area relationship for sunflowers is linear. Therefore, for sunflowers a larger crown leads to proportionally more absolute stem growth with no loss of efficiency.  

The usual explanation given for the decrease in efficiency with increasing crown size observed in trees, and the assumption incorporated into our
conceptual model, involves the increased structural biomass found in large
tree crowns where foliage is arrayed in a shell surrounding a "bare core" of
woody branches (Assmann, 1970). The nonfoliated interior within the foliated
shell increases in size as the crown increases in size; hence the branches,
which live for several years, must continue to elongate and thicken in order to
support foliage at ever greater distances from the stem. Respiration
associated with accumulating branch biomass thus represents a large cost for
displaying foliage far from the stem. Nothing directly comparable to a bare
core develops in sunflowers where the leaves and entire plant survive for only
one growing season. Instead, the individual leaves grow to a determinant
size (which is dependent on density) and are supported by a petiole which
grows to a size sufficient to support the attached leaf blade, but with no
subsequent growth.

The structural differences resulting from the accumulation of branch
biomass are clearly shown in Figure 4.4: while \( R_{F:C} \) in the crowns of
lodgepole pine is strongly and negatively associated with increasing mean leaf
area, there is no such negative correlation between a similar ratio and mean
leaf area in sunflowers. Thus, sunflowers increase mean leaf area and crown
size with no associated increases in support costs, and efficiency does not
decrease with increasing crown size as is the case for lodgepole pine.
The mean vertical distributions of $R_{F:C}$ at relative heights for 58 lodgepole pine and 119 sunflower plants (Fig. 4.5) illustrate the different distributions of leaf area in the perennial and annual plant populations. Decreasing proportions of assimilating biomass with increasing crown size in trees results from the presence of long, thick branches at the bottom of large crowns and their very low ratios of foliage to total section biomass. Figure 4.5 shows that the ratio of foliage to total biomass for lodgepole pine is greatest in the upper crown where branches are smallest, and decreases monotonically towards the base of the crown. Thus, branches in the lower crown have a profound effect on $R_{F:C}$ values for the entire crown. In contrast, the distribution for sunflowers is modal with the maximum ratio occurring near mid-crown, and the overall variation with crown depth is much smaller (Fig. 4.5).

Differences in the mean $R_{F:C}$ ratios for the entire crown and by crown section indicated in Figures 4.4 and 4.5 are largely attributable to the difference between perennial and annual plants. Since tree branches generally live for several years, branch biomass increases each year as crown size increases, and therefore represent an increasing sink for assimilates (Kira and Shidei, 1967). In sunflowers, there is not the same accumulation of non-photosynthetic biomass as is found in trees.

Even though the structure-production relationships differed for lodgepole pine and sunflowers, the differences reinforce rather than diminish the validity
of the assumptions incorporated into the conceptual model of forest production. No decrease in efficiency with increasing crown size was evident for sunflowers, but there was also no relationship between $R_{F:C}$ and mean leaf area for the species. Because both efficiency and $R_{F:C}$ decrease with increasing mean leaf area for lodgepole pine, the comparison between the two types of plant populations provides circumstantial support for the assumption that an increase in the respiratory load on foliage in large crowns is responsible for the observed declines in efficiency with increasing mean crown size in forest trees.
Literature Cited


FIG. 4.1. Schematic representations of relationships between (a) mean leaf area and density; (b) mean stem volume increment and mean leaf area; and (c) ratio of foliage to total crown biomass versus mean leaf area.
FIG. 4.2. Mean leaf area as a function of overstory density for (a) lodgepole pine and (b) sunflowers. Lines were generated by the regression functions \( A_i = 84877 \times N^{-1.12} \) (n=34, \( r^2=0.91 \)) for lodgepole pine and \( A_i = 2617 \times N^{-0.60} \) (n=40, \( r^2=0.77 \)) for sunflowers, where \( A_i \) is mean leaf area and \( N \) is overstory density.
FIG. 4.3. Mean stem volume increment versus mean leaf area for (a) lodgepole pine and (b) sunflowers. Regression equations are $I_v = 0.015 \times (1 - e^{-0.012 \times A_l})$ (n=34, $r^2=0.89$) and $I_v = -0.13 + 0.0038\times A_l$ (n=40, $r^2=0.98$) for lodgepole pine and sunflowers, respectively, where $I_v$ is mean stem volume increment.
FIG. 4.4. Mean ratio of foliage to total crown biomass ($R_{F:C}$) as a function of mean leaf area for (a) lodgepole pine and (b) sunflowers.
FIG. 4.5. Average vertical distribution of $R_{F:C}$ for lodgepole pine and sunflowers. Height is expressed on a relative basis to facilitate averaging of sectional ratios between individuals.
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NR 360 "Quantitative Analysis for Natural Resource Management" (USU): team taught undergraduate course covering quantitative decision making methods; designed and presented lectures and assignments covering topics such as FORTRAN programming and simulation models in natural resources (3 quarters)

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RECENT RESEARCH ACTIVITIES:

Relationships between stand and canopy structure and forest productivity: dissertation research tests a conceptual model derived from a few basic assumptions to relate changes in stemwood production to changes in stand structure and canopy architecture

Density management: translation of basic research results on effects of manipulating stand structure to applied management context

Fertilization of southern pines: work with CRIFF (Cooperative Research in Forest Fertilization), a university-industry cooperative; masters research project used stem analysis techniques to examine the effect of fertilization on stem form

Spatial patterns in a northern Utah juniper woodland

Generation of site index curves for Norway spruce in New York and ponderosa pine in the southwest
REFEREED PUBLICATIONS:


OTHER PUBLICATIONS AND PRESENTATIONS:


