AN ABSTRACT OF THE DISSERTATION OF

Mark L Hanus for the degree of Doctor of Philosophy in Forest Resources, presented on February 3, 2003. Title: Modeling Light Competition in the Forests of Western Oregon.

Signature redacted for privacy.

Abstract approved:

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A plant's immediate neighborhood reflects its realized level of competitive stress, since competition and natural selection act at the individual level. In stands with continuous canopies competition for light is the dominant spatial interaction. Over 100 spatially explicit indices have been used to characterize the local competitive environment in models of individual tree growth. These indices can be divided into those that indirectly characterize the light environment and those that directly characterize the light environment. The three classes of indirect measures are: size-distance, competitive influence zones, growing space and the two classes of direct measures are open sky views and light-interception methods.

Studies that have compared the ability of the indirect indices of the light environment have failed to identify a universally superior measure of competition. However, the two direct measures of the light environment have not been included in the comparisons. An examination of the comparative studies showed that most of them identify indices characterizing competition from larger neighbors as superior. This finding leads to the conclusion that competition for light is the dominant spatial interaction in the stands examined. Thus, spatial indices that directly quantify light should explain more variation than those that quantify both above and below ground competition.

Light intensity is modeled with the radiation transport equations. SEALS is a program for calculating light intensity in forest stands. It uses the radiation transport equations to model seasonal quantum light flux (SAL). It uses simulated hemispherical photographs to model direct beam light intensity (PCSHS). SAL and PCSHS were compared to three indirect measures of light competition in a planted western hemlock understory and 11 managed Douglas-fir plots. It was found that SAL reduced the residual variation in height growth of understory western hemlock by 48% over a model including only a power of tree height and PCSHS reduced the residual variation by 40%. SAL also reduced residual variation by 48% for overstory Douglas-fir and 18% for understory Douglas-fir while PCSHS reduced the residual variation by 15% and 14% respectively. These reductions were significantly better than those from the indirect classes of spatially explicit index.

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ACKNOWLEDGMENTS

This research was self funded but that does not mean that I do not recognize the firm foundations upon which it was built. I would like to acknowledge the support and assistance of Midori, my bride of 19 years, without whom I should never have set foot on this path. Thank you dear, its finally done!

I am most honored to recognize the guidance, mentoring and challenging of professor David Hann. I have not been the easiest graduate student you have had to tolerate and it has been a long time. I owe you a large debt of gratitude for your persistence in pushing me to attend to details and showing me the art of statistical modeling. Thank you for your time and efforts, I have really grown under your watch.

I also recognize the great shadows of the past surrounding this project. The efforts of Dr. Allan Berg who established the research plots used in my study. The efforts of Dr. David Marshall in rescuing his project from the trash heap of progress and believing in it so much that he stole time and resources to continue measuring the plots and updating the data, thank you. Thank you Dr. John Tappeiner for supporting the development of the visualization software that formed the basis of this project. Thank you also to Dr. Juhan Ross for encouraging me to continue my studies of radiation transport and the Russian language.

I am especially grateful to Dr. William Ripple who helped me more than he knows, thank you. It has been a real pleasure working with you on our other projects. And thanks also to Louis Beer who measured the understory vegetation for his masters thesis.

In the pages that follow, I invite you to partake in what has been for me a consuming project of nearly ten years. However, they reflect only a small portion of the effort required to complete this study. A count of the characters in this dissertation (omitting white space, punctuation and equations) reveals that it comprises slightly less than two-thirds of the characters (omitting white space,

comments and semicolons) in the source code for the models developed to do the work. I hope that I have captured the essence of the computer models in the following pages.

Modeling Light Competition in the Forests of Western Oregon.

By
Mark L. Hanus

A Dissertation

Submitted to

Oregon State University

In partial fulfillment of
the requirements for the
degree of

Doctor of Philosophy

Presented February 3, 2003
Commencement June 2003

CHAPTER 1

GENERAL INTRODUCTION

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February 17, 2003

For submission to: Not for submission

GENERAL INTRODUCTION

This dissertation is presented in the form of four distinct manuscripts. While each manuscript may stand alone, together they take the reader through the development of a spatially explicit direct index of the light environment. The goal of this combined work is to reduce the gulf between models of individual tree growth based upon ecophysiological processes and those based upon empirical relationships.

Competition is the mechanism by which plants influence the growth of their neighbors and are affected by their neighbors. In plant communities forming continuous canopies, competition for light is the prevailing limitation to growth. Spatially explicit indices use an indirect approach to characterize competition as a measure of crowding. They were developed to quantify the general competitive environment among trees growing in forest stands, and have been implied to depict competition for light. Spatially explicit indices have been divided into three classes: (1) size-distance (SD) relationships, (2) competitive influence zones (CIZ) and (3) growing space (GS) measures.

It is also possible to characterize the directly competitive environment of the tree by measuring available light. Two methods of light characterization have shown promise of characterizing the light environment in forest stands: hemispherical photographs and light meters. These direct methods however share the disadvantage of requiring the presence of measuring equipment in the field. Some progress has been made in constructing computer analogs of these measurements. Computer graphics offer an opportunity to approximate the light environment from past stand measures as well as projected future conditions. A graphics image of the upwards hemispherical view from a point in a stand can be analyzed in a manner similar to a hemispherical photograph to yield a index of the open sky above a point in the stand. A graphics image can form the basis for a solution of the equations describing light intensity within the stand. These two methods of directly characterizing the light environment represent members of two more classes of spatially explicit index: open sky view (OSV) and light interception (LI) indices. They can be characterized as direct measures of the light environment.

The objective of Chapter 2 is to examine past studies comparing spatially explicit indices of competition. The results of these studies are collected and the techniques used are compared. The past studies were mostly conducted in even aged stands and included members of four of the five classes of spatially explicit index. They have also failed to identify any class of spatially explicit index as consistently superior to all others. This failure may be due to insufficient growth models, given that these comparison studies have used a single equation form to represent the impact of competition on growth,.

The transport of light through stationary media has a long history of physical exploration. Methods for solving the differential equations for light intensity have been extended from stellar and planetary atmospheres to forest stands. The objective of Chapter 3 is to describe the development of a new direct index of the intensity of light available to each tree. A new method for solving these equations using a graphics image of the forest stand is presented. The calculation of an LI index of available light (SAL) is described along with the methods used to represent the forest canopy. The same graphics image is used to construct an OSV index from a simulated hemispherical view of the open sky above each tree (PCSHS).

The objective of Chapter 4 is to describe the application of three indirect indices, SAL and PCSHS to explaining the height growth of understory western hemlock growing planted beneath an overstory of Douglas-fir. The planting of the understory trees on a regular lattice placed trees in situations where they would not be naturally regenerated giving the indices a more powerful test. The competition indices are allowed to enter models of individual tree height growth in alternative model forms preselected by the developers of the index. The models are compared to a nonlinear function of tree size using a ratio of mean squared residual.

The objective of Chapter 5 is to extend the comparison of the indices from the two-storied stand used in Chapter 4 to Douglas-fir growing in managed plots. It is likely that the stand used to develop SAL and PCSHS may have conditions that are not commonly encountered in other situations. Chapter 5 seeks to replicate the Chapter 4 results in stands that represent conditions more common to the managed forests of the coastal Pacific Northwest. It also extends the investigations detailed in Chapter 4 to another species and to a broader range of stand conditions including overstory trees.

CHAPTER 2

SPATIALLY EXPLICIT MEASURES OF INTER-INDIVIDUAL COMPETITION FOR EMPIRICAL MODELS OF TREE DEVELOPMENT

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February 17, 2003

For submission to: The Forest Research Laboratory
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Abstract

A plant's immediate neighborhood reflects its realized level of competitive stress. This, coupled with the observation that plants exhibit similar strategies for dealing with limited resources has inspired the use of spatially explicit measures of competition to modify predictions in models of tree growth. Over 100 spatially explicit indices have been used to characterize the local competitive environment of the tree in models of tree development. These indices have been divided into five classes; (1) size-distance measures, (2) competitive influence zones, (3) growing space measures, (4) open sky views and (5) light-interception methods.

In plant communities forming continuous canopies light has been identified as the major growth limiting factor. The Douglas-fir forests of western Oregon are communities of this type. Therefore indices that quantify the light environment should perform much better than those quantifying below ground competitive pressure.

Studies that have compared the ability of size-distance, competitive influence zones and growing space measures have failed to identify a universally superior measure of competition. However, two additional classes, open sky views and light interception, have not been included in the comparisons. An examination of the comparative studies showed that most of them identify indices characterizing competition from larger neighbors as superior. This finding leads to the conclusion that competition for light is the dominant spatial interaction in the continuous canopy forests examined. Thus, spatial indices that quantify light should explain more variation than those that quantify below ground competition in stands with continuous canopies.

Introduction

Tilman (1988) suggested that the central goal of ecology is to understand the causes behind the patterns observed in nature. Patterns of species frequency and location are explained as the result of the reactions of organisms to the environmental constraints which they experience. The primary mechanism of plant interaction is competition. Competition and natural selection act at the individual level. Thus, a plant's immediate neighborhood should reflect its realized level of competitive stress. This, coupled with the observation that plants exhibit similar strategies for acclimating to limited resources has inspired the use of spatially explicit measures of competition to modify predictions in models of tree growth.

Competition among plants is summarized as action on, and reaction to, their living environment (Ford and Sorrensen 1992). As they grow, plants compete with each other through modification of their environment by altering their neighbors ability to acquire resources. They do this by over-topping neighbors, by increasing soil occupancy and by spreading chemical growth inhibitors (Chapin 1991). It is difficult to quantify competition between individuals since the competitive effect differs, in rate and content, between species and, perhaps, between individuals of a species. Plants also adjust to environmental change by responding to competition and by altering the nature of that competition. Spatial interaction has been identified as the primary mechanism of competition and mortality as the result of growth reduction attendant to resource depletion.

Munro (1974) identified two major classes of competition measures used in models of tree growth: distance-dependent and distance-independent measures. Since then, distance-dependent measures have been generalized into spatially explicit competition measures. In general, spatially explicit measures require more complete knowledge of the physical relationship between a subject tree and its competitors. These measures seek to include the competitive stresses due to competition for light, nutrients and available water.

Tomé and Burkhart (1989) identified three components of competition: (1) the general environment of the tree, (2) micro-environmental and genetic influences, and (3) the influence of local neighbors. They felt that the general environment of competition was accounted for by stand level measures of competition such as total stand basal area or stand density index. Micro-environmental and genetic influences were accounted for by species differences and the ratio of the size of the subject tree to the average or maximum size of trees in the stand. Spatially explicit indices quantify the influence of local neighbors by modifying the mean response of the first two levels of competition. This goal is complicated because the competitive effect may be confounded with local physical barriers to growth and genetic variation of individuals (Weiner 1984). It is also assumed that the total competitive pressure experienced by a subject tree is the sum of the individual pressures exerted by each of the competitors.

Spatially explicit indices of competition were divided into four classes by Vanclay (1994): (1) competitive influence zone, (2) area potentially available, (3) size-distance, (4) sky view / light-interception. Extensions to area potentially available have been added and form growing space indices. Sky view measures were separated from light-interception measures to reflect their increasing variety and the difference in methods of calculation. The resulting classification scheme yields five classes of spatially explicit measures: (1) size-distance (SD) relationships, (2) competitive influence zones (CIZ), (3) growing space (GS) measures, (4) open sky view (OSV) and (5) light-interception (LI) methods.

Size-distance relationships depict competition as proportionate to the size of the competing plant reduced by a function of its distance from the subject plant (L). Competitive influence zones view competition as proportionate to the fraction of the target plant's free to grow influence zone occupied by its neighbors. Growing space measures view competition as reflected by the area or volume surrounding the plant that is not occupied by its neighbors. Open sky view measures quantify competition by the fraction of overhead space not occupied by neighboring plants. Light-interception measures view competition as being proportionate to the amount of light falling on a plant over the course of a growing season.

Some species primarily respond to competition from larger competitors while others respond to competition from both larger and smaller neighbors (Weiner 1990, Hann and Larsen 1991, Ford and Sorrensen 1992). The classes of spatially explicit competition measures describe different aspects of the local competitive environment of the plant. SD and weighted GS indices can differentiate competition from smaller plants from competition from large plants, OSV and LI methods do not include any plants shorter than the subject plant. The competitive environment of plants sensitive to competition from all neighbors will be better quantified by SD or weighted GS measures than by OSV or LI methods. However, the competitive environment of plants more sensitive to competition from larger individuals over competition from smaller individuals is better quantified by an OSV or LI method.

A significant barrier to the use of spatially explicit indices is the identification of competitors. The number of competitors and the magnitude of their competitive effect can not be predicted at the time of stand initiation (Ford and Sorrensen 1992). The area over which individual trees compete has not been identified, which may result in significant competitors being missed or insignificant competitors included. Missing significant competitors for some trees results in the estimated competitive pressure for these trees to be underestimated.

All spatially explicit measures of competition are also susceptible to bias due to edge effects (Monserud and Ek 1974), because, in most conditions, there is no definite or known barrier to the influence of competition. In these cases the edge trees are under the influence of unsampled individuals and a calculated index for them would be underestimated. Measuring and locating the trees in an area surrounding the subject trees can correct for this bias; however, it is generally not possible to determine how many additional trees to measure. Several methods of edge correction have been proposed, depending on the physical situation and the type of index (Upton and Fingleton 1985, Cressie 1990). Martin et al. (1977) suggest use of a linear expansion to correct for plot edge bias; however, use of this index assumes that competitors are equally likely to be found in all directions of the subject tree and that the spatial distribution of size is stationary.

Over one hundred variations of spatially explicit indices have been applied to tree growth. Following are descriptions of the five classes of indices and examples from each class. Limits on the application of the classes are explored as well as their susceptibility to bias from edge effects. Finally the classes are compared to each other and opportunities for future research are explored.

Classes of Spatially Explicit Indices

The goal of spatially explicit indices is to explain the differences in local competitive pressure felt by individual plants. Tree species are sensitive to different aspects of competition which may vary with environment (Ford and Sorrensen 1992). Some species experience competition only from larger individuals while others are sensitive to all of the individuals on the plot. Since spatially explicit measures quantify different aspects of competitive pressure it is important to match the index to the species and stand structure. If competition is for water and nutrients, an index that captures the light environment may not provide sufficient information. Conversely, if light competition dominates then an index that weights shorter individuals equally with taller individuals may not reflect the competitive environment. Additionally computational and available data limit the application of some indices.

Identification of competitors is also important for the successful implementation of spatially explicit competition indices. Including too many neighbors reduces its utility as a descriptor of the influence of local neighbors. Conversely, including too few neighbors understates the competitive stress felt by the subject tree.

SIZE-DISTANCE

Size-distance relationships characterize competition with a function of the size of each competitor and its distance from the subject tree. The indices in this class all include a function of tree size and a function of distance between the subject and each competitor. They are distinguished from one another by the size and distance functions used. They can also differ in the method of competitor selection and how those competitors enter the index. Competitors are selected with fixed or variable competition horizons and may enter the index as a function of relative size, absolute size or size difference. The most common function of size is diameter at breast height (D), while the most common function of L is its inverse (L^{-1}). In general, any function of tree size and any declining function of distance can be used. Weiner (1984) postulated that when competition is for light, the influence of a competitor will decline linearly with increasing distance and when the competition is for water or nutrients, competitive influence will decline by the square of distance.

Point density (PD) is different from other SD measures in that distance enters the index by the angle subtended by the bole of the competitor. PD is the sum of the angles subtended by the boles of the competitors of the subject tree (Spurr 1962). A fixed number of competitors may be specified or a variable number depending on the fixed or variable radius limit of competition. The influence of each competitor is made proportionate to the ratio of the competitor's D (D_C) to the subject's D (D_S). Two types of PD were defined, one that included the basal area of the tree and one that did not.

Opie (1968) used PD to identify competitors and adjust basal area growth in Eucalyptus. In that study a function of D_S was used to select the sampling angle. Lemmon and Schumacher (1962) and Daniels et al. (1986) applied PD to modify predictions of diameter growth in ponderosa pine and loblloly pine, respectively.

In SD relationships, weighting of competition effects are usually a function of D, since it is the most common size measurement of trees. The index of Hegyi (1973) sums the ratio of D_C to D_S scaled by the inverse of L. The index of Martin and Ek (1984) sums the ratio of D_C to D_S scaled by a negative exponential function of L divided by the sum of D_C and D_S ($e^{-\frac{16L}{(D_C+D_S)}}$). Other measures of size such as bole volume (Weiner 1982) or crown volume (Biging and Dobbertin 1992) may be used in SD indices.

DeLong (1991) introduced an SD index that he named light interception. DeLong's (1991) goal was to explain the amount of light intercepted by a subject tree which was accomplished by scaling percent crown closure of the competing tree by the ratio of its height and its distance from the subject tree. Given that DeLong's (1991) light interception used the competitors percent crown closure multiplied by its height as a function of size and L^{-1} as the function of distance, it is a size-distance measure.

Identification and selection of competitors in SD indices can widely alter the observed correlation of the index to individual tree growth (Lemmon and Schumacher 1962, Alemdag 1978). Opie (1968) identified competitors using various fixed area and variable radius plots which allowed the competition horizon to vary with the tree's D. Hegyi (1974) used all trees within a fixed distance of the subject tree. Daniels (1976) extended Hegyi's (1974) index to use a variable competition horizon. Studies have concluded that the optimal competition horizon for SD measures includes as large an area as possible (Opie 1968, Alemdag 1978) perhaps indicating that for the species examined, local competition is less important than overall competition.

Lin (1974) selected a single competitor in each quadrant and compared their subtended angles to two standard angles, one from an open grown tree and the other from a suppressed tree. The function of size is the sum of D_C and D_S divided by twice D_S. The function of distance is the angle subtended by D_C when viewed from the subject tree. An additional scaling was applied to the subtended angle, by scaling it to range between the angle expected from an open-grown tree (2.15°) and that expected of a tree growing in extreme competition (5.25°).

Biging and Dobbertin (1992) evaluated three methods of selecting competitors for 38 SD indices: (1) all trees taller than a cone of 50° whose apex is located at the base of the subject tree, (2) all trees taller than a cone of 60° whose apex is located at the base of the subject tree, (3) the apex of the cone was located at the base of the live crown and the angle of the cone was selected to preserve its volume. They used the sum of the fraction of a competitor's cross-sectional crown area within the cone of competition as the function of size and L^{-1} as explicit function of distance. Analogs that did not include an explicit function of size were also compared. In these measures distance entered the relationship only through the physical relationship between the location of the competitor's crown and the cone of competition.

COMPETITIVE INFLUENCE ZONES

Competitive influence zones are based on two ideas: (1) the area over which an individual experiences competition and exerts influence is proportionate to its size, and (2) the magnitude of competitive pressure is proportionate to the degree of overlap between the influence zone of the subject tree and the influence zones of its competitors. Staebler (1951) suggested that the size of the influence zone be set at the maximum extent of the crown of an open-grown tree of the same size as the subject tree. Influence zones of this size would approximate the area of the maximum extent of a fully developed crown and/or root system. The degree to which the zones of neighboring trees overlapped that of the subject tree would provide a measure of its competitive pressure. Any surrounding tree whose influence zone overlays the subject tree's influence zone is considered a competitor.

Opie (1968) described zone count (ZC) as a weighted CIZ index. ZC was calculated in two ways: (1) using an explicit count of area from a scale drawing of the influence zones of the competitors and (2) using an angle count of the number of competitors measured at the four cardinal points, two-third's the radius of the influence zone away from the subject tree.

Arney (1972) introduced a CIZ measure based on the overlap of open-growth crown widths. The open grown crown width is the expected width of the crown of an open-growth tree with the same species and D as the subject tree. The hypothesis guiding the development of this index was that the exposed crown of a tree grows at the same rate as the same sized crown of an open-grown tree. Competition is calculated by the influence zone overlap at each whorl estimated from open-grown crown size and shape equations.

Bella's (1971) index weighted competitive pressure proportionate to the relative size of D_S and D_C. This weighting ensured that small nearby neighbors did not exert a disproportionately large competitive influence on the subject tree. To achieve a similar result, Arney (1974) scaled the area of open-grown crown overlap by the crown ratio of the subject tree and Ek and Monserud (1974) scaled the area of overlap by crown volume, measured as the product of the tree's crown radius and its height.

Where the competitive influence from larger neighbors is dominant, competition is more accurately modeled by weighting the influence zone overlap by the relative size of the individuals (Ek and Monserud 1974). In two-sided competition the magnitude of competition is related strictly to the amount of overlapping area and not to the number of individuals involved. In these cases, the same competitive pressure is derived from one large tree as from many small trees so weighting of the influence zone overlaps is not as important.

In CIZ measures competitor selection is determined by the size of the influence zone of the subject tree. The prediction equation selected for calculation of the influence zone width determines the area from which competitors will be selected. In this region smaller competitors may be excluded from a CIZ to reflect competition from larger neighbors.

GROWING SPACE

Growing space measures are based on the assumption that resource availability and hence, competitive pressure is related to the area or volume available to each plant. This assumes that resources are homogeneously distributed in the area or volume in which the plant lives. One method of GS calculation is area potentially available (Brown 1965). Area potentially available (APA) is a rediscovery of a long explored mathematical concept variously attributed to Peter Gustav Dirichlet (1850) and Georgy Voronoï (1907). Voronoi diagrams are a more general mathematical construct than are Dirichlet tessellations (Okabe et al. 2000). Dirichlet tessellations partition the entire stand area among individual trees based upon their location. This is done by assigning to each individual that area which is closer to it than to any other individual. APA assumes that the area of the polygon containing the subject is inversely proportional to the amount of competition experienced by the subject. Since every portion of the stand is apportioned to only one individual, the resulting polygons constitute a tessellation. APA is the area of the subject trees polygon resulting from a Dirichlet tessellation of the stand. Two additional properties of Dirichlet polygons might serve as measures of competition: the number of sides, or the length of the perimeter (Upton and Fingleton 1985).

A Dirichlet tessellation is constructed by bisecting the lines connecting a point with each of its nearest neighbors. Segments perpendicular to the connecting segments are constructed and extended until they cross other segments or reach the boundary of the region. The resulting mosaic (Rogers 1964) is complete in that it apportions all of the area in the region to non-overlapping cells. Methods for constructing Voronoi diagrams are introduced and discussed by Okabe et al. (2000).

Mead (1966) also rediscovered the Dirichlet tessellation naming the resultant diagram plant polygons. In addition to using the area of the polygon, Mead (1966) introduced the notion that the shape and position of the individual within the polygon are important in describing its growth. Two measures of describing the shape of the polygon were presented: (1) eccircularity, a measure of the extent to which the polygon is elliptical and (2) abcentricity, the degree to which the plant is displaced from the center of the area. It was observed that two trees with the same polygon area, one growing in a circle and the other growing in an ellipse, experience different levels of competition. Trees located near the center of the polygon experience a lower level of competition than trees with the same available growing space but located near its edge.

APA should only be applied in stands where all individuals are close to the same physical size (Wimberley and Bare 1996). Since APA includes the nearest individuals without regard to their size, it fails to describe the competitive environment in stands where there is a significant difference in tree size or with multiple stories. APA polygons are non-overlapping thus only a single competitor, the nearest, is represented in any one direction regardless of the number or attributes of other individuals in that direction (Stohlgren 1993). This results in all competitors, regardless of size, contributing an equal amount to the index. To allow larger individuals to apply greater competitive pressure than small individuals Moore et al. (1973) modified the polygon definition of the available area so that the distance from the subject tree to the bisector defining the cell boundary was weighted by the relative sizes of the two trees. Okabe et al. (2000) identify four methods of weighting the polygons: (1) multiplicatively weighted, (2) additively weighted, (3) compound weighted and (4) power weighted. Since each weighting scheme results in deviations from the unweighted tessellation pattern, care should be exercised in the selection of the weighting scheme. Weighting however fails to account for potentially larger competitive effects due to larger neighbors shielded by nearer small neighbors.

Wimberley and Bare (1996) describe another method of explaining one-sided competition in multilayered stands which they called layered APA. Layered APA consists of calculating separate tessellations for the competitors in each crown class. APA for the suppressed trees was calculated based on all trees on the plot. APA for the intermediate trees was calculated from a tessellation of the intermediate, co-dominant and dominant trees. APA for the co-dominant and dominant trees was based on a tessellation of only the co-dominant and dominant trees.

Pelz (1978) also sought to account for differences in competitive pressure exhibited by larger trees by weighting the bisectors of the APA. Polygons were created by weighting the bisector in one of three ways: (1) a function of total tree height (H), (2) a function of the product of D and H or (3) a function of D^2H. Three-dimensional analogs of the two-dimension indices were created by multiplying the area of the polygon by H. It was concluded that in a 23 year old tulip tree (*Liriodendron tulipifera*) stand the three-dimensional indices correlated better with individual tree basal area growth than did their two-dimensional analogs. Pelz (1978) also found that both the two-dimensional and three-dimensional versions weighting horizontal growing space by D^2H performed best.

Alemdag (1978) introduced two weighted APA measures, the first weighted the bisector by D_C divided by the sum of D_S and D_C. This index did not perform as well as did a second index in explaining diameter increment in white spruce (*Picea glauca*) plantations. The second method assumed a small tree close to the subject tree exerts the same pressure as a large tree far from the subject tree. Competitors were identified using an angle gauge centered at the subject tree. The index was constructed as the sum of the area of circular sectors from each competitor. The radius of each circular sector was L weighted by D_C divided by the sum of D_S and D_C. The angle subtended by each sector is the fraction of a circle proportionate to the competitors contribution to the sum of D_C divided by L. Angles from 1° to 3° were tested for competitor identification, an angle of about 2° provided the best correlation to diameter increment in white spruce.

Asymmetric division of intertree distances resulting from weighting by tree size can lead to areas of the plot not contributing to the available growth area of any tree. In this case, the total of the areas available for growth no longer represent the total area. A mosaic based on differentially weighted polygon boundaries may result in polygons totally enclosed by other polygons or polygon boundaries interrupted by small slivers (Okabe et al. 2000).

The edges of weighted and unweighted APA polygons are straight segments. However, the use of a curved boundary mosaic to represent the area of competition was proposed by Nance et al. (1987). The curved boundaries resulted from APA polygons that were constrained in low density stands by maximum crown width. In this type of mosaic, cells are constructed as non-overlapping circular zones centered on the subject tree proportionate to its size. These circular zones are truncated upon contacting other zones. The truncation distance was proportionate to the difference in size of the plants. Upton and Fingleton (1985) report that little is known of the properties of this type of mosaic although it was investigated by Evans (1945) in the context of metallic corrosion centers. Evans also explored a similar mosaic where either the ease of growth in a particular direction is spatially dependent such as might occur where light originates from one direction, or where additional centers are added when additional plants become established over time in the growth region.

Another type of growing space index that produces a similar spatial pattern is the crown stand model (Mitchell 1969a, 1969b, 1975; Arney 1972). Crown stand models extend branches and height into the space surrounding the tree. Branch growth is stopped when the branches from the subject tree meet the branches of its neighbors. Tree growth is reduced when the volume of living foliage dips below the optimum level for the species and the tree dies when it is over topped by a neighbor. The mosaic resulting from a horizontal projection of crowns grown with a crown stand model is a rounded mosaic similar to a constrained APA until crown closure when it resembles a weighted Dirichlet tessellation. Older or faster growing trees occupy more horizontal space than a Dirichlet tessellation predicts. Younger or slower growing trees occupy less horizontal space than a Dirichlet tessellation predicts. If small trees are allowed to grow under the crowns of taller trees, doubly occupied polygons might result. However, if the horizontal extension of all trees is equal and the horizontal projection of the crowns fills the entire area then the projection becomes a Dirichlet tessellation.

OPEN SKY VIEW

Open sky view methods are based on the observation that the dominant restrictions to plant growth are the effect of light competition (Horn 1965). Botanical theory predicts that if the light environment of the plant is known then the competitive environment is fully described by the crown environment until soil nutrients or water become limiting (Tilman 1988). OSV methods determine the amount of unobscured sky seen from the position of the subject tree. Construction of OSV indices require a three-dimensional model of all of the subject tree's competitors. Three methods have been used to generate OSV measures: (1) tracing paths through the foliage into the sky similar to the grid in a spherical densiometer and counting the fraction of paths free from obstruction (Brunner 1998), (2) processing hemispherical photographs taken from the location of the tree (MacDonald et al. 1990) or (3) simulating the fraction of open sky seen from the location of the tree and counting the pixels free from obstruction (Van Pelt and North 1996).

Since not all free areas of the sky have the same potential to contribute equally to photosynthetically significant incident light, unobstructed access to the portions of the sky yielding the most significant light intensity may be given more weight (Chan et al. 1986). OSV indices are sensitive to height above the ground since canopy foliage is not distributed uniformly with height. The location from which the sky is viewed need not be the base of the tree; OSV values calculated from the top of the tree show a larger amount of unobscured sky than the same index calculated from ground level. An OSV calculated from the tip of the tree effectively weights competition to larger individuals (one-sided competition) while an OSV calculated from the base of the tree will include both larger and smaller neighbors (two-sided competition). To reflect differences in crown architecture, OSV might also be located at the centroid of the crown, perhaps calculating the centroid by weighting crown volume by local foliage photosynthetic efficiency (Vanclay 1994).

Competitors are selected by the differential weighting of portions of the sky and by selecting the height at which the index is calculated.

LIGHT-INTERCEPTION

Light-interception methods were motivated by the same observations as the OSV measures. They are calculated in one of four ways: (1) determine the fraction of the crown exposed to direct sunlight, (2) ray trace light paths through obstructing vegetation, (3) project obstructing objects onto the surface of the crown, or (4) solving the radiation transport equations for the stand. LI methods seek to quantify the amount of light striking the subject tree by incorporating the aboveground environment of the tree and its competitors. This requires the construction of a three-dimensional model of all of the trees in the volume containing the subject tree. The complexity of the indices in this class varies with the application. They have been calculated using geometric solids to represent the crowns of individual trees (Hatch 1971, Hatch et al. 1975, Ross 1981, Grace et al. 1990) or specific vegetative relationships giving structure to the crown (Ross 1981, Myneni et al. 1986).

The least complicated LI index determines the fraction of the crown surface area exposed to direct sunlight (Hatch 1971). The altitude of the sun was fixed and a parabola representing the track of the sun at the fixed altitude was used to determine which of the eight closest trees cast shade upon the subject tree. The amount of the subject crown shaded by each of the competitors was subtracted from the total crown surface area to the subject tree. Since the light environment was simplified this value was felt to represent the minimum crown surface area exposed to the sun (Hatch 1971).

Determining the fraction of the crown exposed to direct sunlight may also be achieved by tracing the outline of neighboring crowns onto the surface of the subject crown. Graphics routines for projecting three-dimensional shapes have made projection methods very efficient. The projection of obstructing objects results in the accumulation of shade depth instead of light exposure.

Kuuluvainen and Pukkala (1981) use projection of the obstructing objects onto the crown of the subject tree to calculate the amount of light exposure for the subject tree. Light is attenuated by a probability that is a negative exponential function of the depth of the projected crown. The resulting light exposure is the sum of the probabilities. Kuuluvainen and Pukkala (1981) averaged instantaneous light exposure from six minute increments during daylight hours into a single daily value. Daily values were recalculated at 10 day intervals during the growing season. The sum of the resulting probabilities is the average shade projection area of the crown. Light exposure at a specific point can be calculated as 1.0 minus the average shade projection.

Granberg (1988) suggested the use of bit-mapped graphics to project shade from the crowns. The resulting shade intensity is constant but the methodology can be extended to produce variable intensity shade with greater computational efficiency than the method of Kuuluvainen and Pukkala (1981). The key to this increase in efficiency was the use of graphics memory along with efficient projection routines. Since that work, the refinement of projection routines has continued (Woo et al. 1997).

Ray tracing has been used to quantify the amount of light impinging on the crown of the subject tree. This is done by tracing paths from the sun to the subject tree reducing light intensity as it passes through the crown of competing trees (Jahnke and Lawrence 1965, Grace et al. 1987, Kuuluvainen and Pukkala 1987). Computational intensity of this method has been mitigated by the use of a simplified crown structure (Ross 1981) and by reducing the number of ray traced paths by using average light intensity values for daily, weekly or monthly sun exposure (Vanclay 1994). The intensity of competition is calculated as the difference between the amount of light received by the subject tree and either the maximum potential sun exposure or the average sun exposure in the stand. In these indices the structure of the crown was assumed to be random. A random foliage distribution yields light attenuation that is characterized by a negative exponential function of the length of the light path through the crown.

Jahnke and Lawrence (1965) constructed a LI index to examine the relation between the shape of a tree and daily light interception. They represented the crown of the tree by cones of varying height and width. Horn (1965) generalized their model to more species by varying the geometric shape of the crown. His method slices the tree crown parallel to the incident radiation path. Each of these two-dimensional slices are projected onto a one-dimensional vector parallel to the surface of the earth. Shade intensity was modeled as a function of the number of slices at a distance. The vectors resulting from all of the slices are added together to form a two-dimensional surface of "shade". The light environment of the tree is the inverse of the projection of the shade surface upon its crown. Using this method Horn (1965) was able to model the light intercepted by hardwood trees of varying shapes.

Tracing light paths through a three-dimensional model of the stand to the subject tree yields a measure of the shade intensity experienced by the subject tree during the growing season. Oker-Blom and Kellomäki (1982) present a method of estimating light extinction within and between conical crowns with internal structure. They assumed that within each crown, shoots were distributed randomly and the average orthogonal projection area of a shoot was independent of the direction of the incident light. Under these conditions the probability of the ray being absorbed by the crown assuming a negative exponential function of the density of shoots, average orthogonal projection of the shoot area and the distance through the crown. The intensity of shade is the sum of these probabilities in the same manner as Kuuluvainen and Pukkala (1987) used for projected crowns.

Foliage within crowns is known to be clumped at several scales (Baldocchi and Collineau 1994). Exploration of the effects of crown structure on light attenuation has found that nonrandom distributions of foliage yielded significantly different light intensity patterns than do random foliage distributions (Oker-Blom and Kellomäki 1983). The negative and positive binomial probability distributions for light extinction have been used to characterize clumped and dispersed foliage distributions (Baldocchi and Collineau 1994). Accounting for the spatial distribution of plant foliage increases the ability to discern the amount of light available to plants in non-homogeneous canopies (Ross 1981, Myneni et al. 1986). In non-homogeneous canopies distribution models are used to describe the size and location of the canopy elements at each level of grouping.

Penumbral effects have also been found to account for a significant fraction of diffuse radiation within and below the canopy (Denholm 1981, Oker-Blom 1985). Penumbra is the partial shade that results from the light cast by opposite edges of the sun's disk. Penumbral effects are most substantial in coniferous forests since the distance where the sun's disk is obscured by each leaf is very small (Oker-Blom 1985). Inclusion of penumbra in a LI index significantly complicates its calculation. However, since penumbra tends to extinguish shadows cast on objects far from the shading obstruction, ignoring penumbral effects will result in an underestimation of the amount of light falling on objects below the canopy. This underestimation increases with the distance between the understory tree and the obscuring foliage.

Radiation transport theory provides a method to calculate the intensity and spectral quality of light at any point within a stand (Ross 1981). To do this, the entire stand volume is divided into small volume elements (voxels) on whose boundaries the differential equations for radiation transport can be solved. The solutions to the equations are then accumulated parallel to the direction of the incident radiation to constitute a solution for the entire stand. As long as the equations can be solved over the sides of the voxel, its size is arbitrary. If the atmosphere within the stand can be assumed transparent then all empty voxels simply pass the light within them without change and the light intensity on one side of the voxel is translated to the other side. At the other extreme, voxels totally filled by solids attenuate all light that is not reflected. Voxels partially filled with canopy elements may be classed into a series of pre-solved canopy classes (Myneni et al. 1986), or classes solved for their contents based on a canopy reconstruction (Ross 1981, Myneni et al. 1986).

Diurnal pattern of solar radiation intensity received at a single point on the surface of the earth, barring atmospheric effects, is described by a peaking function centered at local noon (Brock 1981). Solar radiation intensity is affected by the physical attributes of zenith angle, latitude, season, local slope and aspect. It is also affected by weather and haziness of the atmosphere. To fully characterize the radiation environment at ground level, a diffuse radiation component, arising from the interactions of sunlight with the gas molecules of the atmosphere and with dust and smoke particles, must be added to the direct radiation component (Gates 1980). Prediction of environmental factors affecting incident light intensity further complicate the calculation of LI. Cumulative seasonal light intensity flux varies with the amount of cloud cover and dust. To counter these effects the periodic cumulative light intensity can be reduced if the average light attenuation by weather can be estimated.

The LI index for a subject tree is the sum of the amount of projected light incident on its crown for the entire growth season. LI methods have been criticized for their complexity and the difficulty of their calculation. Assumptions of canopy structure and simplifications in incident light regime can dramatically affect the magnitude of the LI index (Ross 1981, Oker-Blom and Kellomäki 1983, Myneni et al. 1986). LI indices based upon a solution of radiation transfer equations have the promise of quantifying both intensity and spectral qualities of the incident light stream.

Discussion

The development of spatially explicit indices of competition was founded on the theory of zone of influence (Aaltonen 1926) and first parameterized with local measures of stand density (Smith 1959). Spatially explicit measures struggle to balance the scale of competition through sizing the area of competitive effect to capture variation in local competitive environment. It has been observed that the more individuals included in the measure of competition, the better the correlation of the index with growth (Opie 1968, Alemdag 1978). This might indicate that for the species and conditions examined, stand level competition is more intense than local competition. The goal of spatially explicit indices however, is capturing the variation in competitive stress felt by individual trees not accounted for by stand levels measures of competition. Including too many competitors fails to differentiate between local and stand level competition.

The classes of spatially explicit indices seek competitors in different ways and thus quantify different aspects of competition. The ability to describe the competitive environment of a tree with a single index varies with the growth environment of the tree. SD measures can be tailored to weight the competitive influence of each competitor in an wide number of ways and modify their impact on the subject tree. LI and OSV measures quantify competition in only larger individuals. In contrast, GS indices such as APA or plant polygons place equal importance on all competitors regardless of their size. Weighting of the bisectors (Nance et al. 1987) and adjusting for abcentricity and eccentricity (Mead 1966) have been proposed to account for differences in the importance of competitors.

INDEX COMPARISONS

Studies have sought to identify the best spatial index for a species and growing condition. They have compared the indices to in a variety of species. However, most of these comparisons have been conducted in even-aged pure species stands. No clear trends in superiority of the individual or classes of indices have emerged.

Alemdag (1978) examined one SD index, five CIZ indices, and two GS measures and found that they provided poor explanatory power for characterizing diameter increment in thinned and unthinned plantations of white spruce (*Picea glauca*). The index of Bella (1971) showed the most consistent explanatory power among the indices tested. The stands were described as regularly spaced with closed canopies and high survival. The poor performance of the spatial indices was attributed to the lack of differentiation in the plantation trees, or possibly due to root grafting (Alemdag 1978). It was also noted that the more competitors included in the computation of any of the indices the greater the correlation with diameter increment. White spruce is tolerant of low light levels (U.S.D.A. 2001).

Noone and Bell (1980) examined three SD indices and five CIZ indices. They found that an SD measure constructed with the four nearest competitors (Lin 1974) was the most highly correlated with diameter increment in thinned and unthinned even-aged stands of Douglas-fir (*Pseudotsuga menziesii*) in Oregon. However, the authors noted that none of the indices was clearly superior to the others. This study used a fixed width buffer to correct for edge effects. Douglas-fir is moderately tolerant of low light levels (U.S.D.A. 2001).

Lorimer (1983) examined the effects of altering the competition horizon on the performance of five SD indices in three even-aged hardwood stands. Competitors were defined as all trees within a fixed distance of the subject tree. He found that a competition horizon of 3.5 times the mean crown width of the overstory trees best defined competition in these stands. A size-distance index computed as the sum of the diameter ratios (D_C / D_S) weighted by the square root of the ratio of L to the competition horizon was best correlated with diameter growth.

Martin and Ek (1984) examined two SD measures and one CIZ measure and found that an SD index using a negative exponential function of L (e^{-L}) explained slightly more variation in diameter and height growth of plantation red pine (*Pinus resinosa*) than an SD using L^{-1} and the CIZ method. Red pine is intolerant of low light levels (U.S.D.A. 2001). They found, however, that none of the spatially explicit indices performed as well as stand basal area. Competitors were identified as all trees within ((D_S + D_C) / 8) meters of the subject tree. The data were corrected for edge bias using the linear correction factor of Martin et al. (1977).

Weiner (1984) examined ten SD indices and the number of neighbors within two meters of the subject. The competition horizon exceeded the maximum crown extent of the trees in the stand. Edge correction was accomplished by excluding all trees within two meters of the edge of the plots. The study was conducted in an even-aged stand of pitch pine (*Pinus rigida*) which had regenerated by sprouting following a fire. Pitch pine is intolerant of low light levels (U.S.D.A. 2001). A size function including the sum of competitors D_C^2H yielded better correlation with bole volume increment than functions of H, D_C^2, mean competitors D_C^2H or number of neighbors. The sum of competitors D_C^2H paired with a distance function of the inverse of L yielded the best correlation with bole volume increment.

Daniels et al. (1986) examined three SD, two CIZ and two GS measures. The study was conducted on loblolly pine (*Pinus taeda L.*) plantations in northern Louisiana. Edge correction was achieved by a fixed width buffer. All of the measures tested were significantly correlated to basal area and diameter growth, however weighted APA explained more variation in both diameter and basal area growth than the other indices tested. They further found that weighted APA was still significant in the presence of tree size, stand density, crown ratio and size ratio. The CIZ and SD indices tested showed greater correlation with diameter growth than with basal area growth, however the correlation of the GS measures was higher with basal area growth than with diameter growth. Explanatory power of the GS measures was not significantly improved by the addition of abcentricity and eccentricity. This was attributed to the lack of variation in these measures in the even-aged stand used in the study. Loblolly pine is moderately tolerant of shading (U.S.D.A. 2001).

Pukkala and Kolström (1987) examined the ability of 11 SD indices and one CIZ index to explain variation in the radial increment of Scots pine (*Pinus sylvestris*) trees, growing in three naturally regenerated stands in Finland. Scots pine is intolerant of shading (U.S.D.A. 2001). They found that the sum of the angles subtended by the competitor's boles best explained the variation in radial growth among all of the stands. Competitors were selected as those trees where D_C was larger than D_S and L was less than five meters. Edge correction was accomplished using a five meter buffer. They also found that further extension of the competition horizon failed to improve the explanatory power of the indices. This was attributed to the minor contributions by trees from a further distance. When growth was expressed as a fraction of potential growth the best index was the sum of the angles subtended by the height of competitors above the subject tree. It was noted that crown dimensions did not explain significant variation in radial increment in these stands. However, crown length and width were measured on a subset of the trees and predicted for the remainder.

Tomé and Burkhart (1989) conducted an extensive examination of 34 SD, 24 CIZ and four GS spatially explicit indices. The comparison was conducted on data from young, widely spaced plantations of *Eucalyptus globulus*, which is intolerant of low light levels (U.S.D.A. 2001). The SD indices were indices constructed with four different competition horizons, two size functions (D_C, D_C^2) and four distance functions (L^{-1}, L^{-2}, $e^{-f(L)}$ and $1 - e^{-f(L)}$). To these were added the two versions of PD. The CIZ indices were calculated with six radii of influence and four exponents in the size function. The GS indices were calculated with four different bisector weighting exponents. An analog was created for each of these indices. The modified analog weighted the index by competitor status, larger trees increased the competitive effect while suppressed and dead neighbors decreased it. It was found that, in all classes, the modified analogs performed better than the standard versions. The unmodified analog of D_C^2 weighted APA explained the most variation in diameter growth. The modified analog of SD including D_C as the function of size and L^{-1} as the function of distance was the best performing index examined.

MacDonald et al. (1990) compared three SD and five OSV measures to each other and to seven distance-independent indices including canopy fractal (Mandelbrot 1967) dimension. The comparison was conducted in plantation black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) seedlings in Ontario, Canada. Black spruce is tolerant of low light levels and jack pine is intolerant of low light levels (U.S.D.A. 2001). The SD indices were constructed with size measures of basal area, volume and H and a distance measure of L^{-1}. They found that total canopy fraction, an OSV measure, correlated best with height and diameter increment. Total canopy fraction and canopy fractal dimension were measured from seedling centered hemispherical photographs. Canopy fractal dimension correlated weakly with diameter or height increment. The total amount of competition was more important in explaining variation in height and diameter growth than was the spatial distribution of the trees in the young plantations tested.

Holmes and Reed (1991) compared five SD indices, 16 CIZ and six GS indices to each other. They used correlation values to conclude that a crown weighted CIZ was most highly correlated to annual diameter growth in northern red oak (*Quercus rubra* Michx. f.) and red maple (*Acer rubrum* L.). Two different SD indices were more highly correlated with annual diameter growth in aspen (*Populus* spp.) and paper birch (*Betula papyrifera* Marsh.). The authors noted that indices including a ratio of competitor to subject diameter were more highly correlated to diameter growth than those that did not.

Biging and Dobbertin (1992) examined 38 SD, four CIZ and four GS measures. They found that all of the crown based SD and CIZ indices explained significant variation in basal area and height increment in white fir (*Abes concolor*), Douglas-fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) growing in California mixed conifer stands. Douglas-fir and ponderosa pine were found to display similar levels of explained variation while white fir showed a very different response. In white fir spatial competition indices explained more variation in D^2 growth than in height growth, just the opposite was found in ponderosa pine and Douglas-fir. These differences were attributed to the relative light tolerance of the species which were ranked in increasing tolerance to low light levels as: ponderosa pine, Douglas-fir and white fir. In contrast to other comparison studies, stand basal area performed worse than the spatially explicit indices and the explanatory power of the spatial indices was not improved by increasing the competition horizon. The best measures of competition were the crown based measures, both the spatially explicit and their distance-independent analogs.

Biging and Dobbertin (1995) included the best performing spatial indices of Biging and Dobbertin (1992): five SD and one CIZ index, in a comparison with distance-independent measures of competition. It was found that in white fir (*Abies concolor*) and ponderosa pine (*Pinus ponderosa*) growing in California mixed conifer stands, none of the spatially explicit measures explained more variation in height growth and diameter-squared growth than did the distance-independent measures. There were also no clear trends in explanatory power among the classes of spatially explicit index for either diameter-squared growth or height growth for either species.

Wimberly and Bare (1996) examined one SD, one CIZ and two GS measures. This study used data on growth of Douglas-fir (*Pseudotsuga menzeisii*) and western hemlock (*Tsuga heterophylla*) from thinned and unthinned, even-aged, mixed species stands on the British Columbia coast. Douglas-fir is moderately tolerant of low light levels while western hemlock is very tolerant of low light levels (U.S.D.A. 2001). It was found that one GS measure, layered APA, explained more variation in basal area growth than the other indices evaluated. They also found that layered APA made only a marginal contribution to the overall model. It was concluded that the regular spatial distribution of the thinned stands limited the utility of the spatially explicit measures, especially the SD measure, to quantify competition.

Most of the studies summarized above tested indices from only the SD, CIZ and GS classes. These studies have failed to identify a clear superiority in the explanatory power of any individual or class of spatially explicit index. SD indices with a distance function proportionate to the inverse of L proved superior slightly more frequently than the other tested classes. However, GS measures slightly edged SD measures more frequently in explaining basal area increment. These studies also failed to show the superiority of spatially explicit methods over distance-independent measures. In addition, most of the studies found that the spatial indices did not significantly account for local competition in the absence of tree size. These observations are consistent with a smaller magnitude of variation in growth attributable to local environment than to stand level and genetic influences. Tome and Burkhart (1989) suggest that a ratio of tree size to the stand mean or stand maximum of that measure serves as an indication of the micro-environmental and genetic influences on a tree. A complete model of competition would include a measure of stand level competition, a measure of tree size and a measure of the local competitive environment. Spatially explicit indices are not replacements for stand level competition measures or tree size measures, rather they are supplemental measures of competition.

INDEX ASSUMPTIONS

Each of the classes of spatially explicit indices have specific assumptions that can guide the selection and calculation of the appropriate index. SD indices use a measure of tree size to represent the difference in magnitude of the plants involved. These indices also differentially weight the area over which competition occurs. Most CIZ and GS indices assume that the spatial component of competition on any area of the influence zone is constant. The difference in competitive weight comes from the relative size of the subject and competitor.

Holmes and Reed (1991) weighted the CIZ of their root-crown indices in a manner that yielded increasing pressure in areas closer to the tree than those areas at the edges of the zone. OSV and LI indices weight competitive pressure by measures of available light. However, since above-ground competition is confounded with below-ground competition information about one provides information about the other.

Another assumption is that the effects modeled by the indices are strictly inhibitory, plants inhibit the growth of other plants. Tomé and Burkhart (1989) tested this assumption. In their study, they created modified analogs for each of the spatially explicit measures of competition tested. These analogs included the contribution of larger trees as an increase in the value of the index while smaller or dead trees decreased the value of the index. They found that regardless of index class, the modified analogs were superior to the standard indices. Since in their study the spatial indices tested were used to modify stand level competition the resulting measure was the local competition from larger trees. The finding that measures giving greater weight to competition from larger trees is consistent with the findings from the other comparison studies that measures quantifying light competition are superior in explaining the variation of growth in canopy forming ecosystems. Pukkala (1987) asserted that in thinned, young Scots pine stands removal of a neighbor can offset the competitive effects of another neighbor of the same size.

Measures of crown size have been found superior to other measures of competition (Biging and Dobbertin 1992). While crown size is directly related to light competition, crown size has also been found to be related to the amount of water running down the stem in Sitka spruce (*Picea sitchens*) (Ford and Deans 1978) and to the amount of transpiration. Competition measures weighted by crown size will confound crown size and competitive pressure. Other measures that quantify competition by light exposure will depend only on the level of light exposure.

INDEX SELECTION

The basic limitation to the use of a class of indices is the availability of data. Some indices require specific information that is not commonly collected in stand examinations. The application of OSV and LI indices is limited since the required knowledge of foliage distributions is not available for all species. The developmental overhead as well as the required computer processing power might not be justified by all applications.

The process of selecting a spatially explicit index should include consideration of the expected form of competition and the conditions under which the trees are growing. Indices that quantify the light environment should not be expected to perform well in situations where the competition is for below ground resources. Unfortunately it is not always possible to know in advance what the significant mechanism of competition will be (Ford and Sorrensen 1992).

Weiner (1982) concluded that where competition is for light, the effect of a competitor should fall off as L^{-1} and where competition is for below ground resources the effect should fall off as L^{-2}. In most of the comparison studies it was found that SD indices with distance functions utilizing L^{-1} were superior to those that utilized other distance functions. In addition, the growing space indices that sought to characterize light competition, either layered APA or by weighting by crown size were superior to other configurations. The only comparison study that included an OSV index (MacDonald et al. 1990) found it superior to the other spatial indices tested. Tomé and Burkhart (1989) found that indices calculated in a manner such that dead and suppressed neighbors reduced the level of competition on the subject tree performed better than their analogs that increased with all competitors. In their comparison model they utilized the spatial index to modify stand level crowding. This method resulted in a local measure of the competition in larger trees. All of these results are consistent with competition for light being the primary mechanism of local competition.

Trees growing in high density stands show a reduction in crown length. Hanus et al. (2000) reported that the prediction of height to crown base in Douglas-fir was slightly improved by the use of local competition measures ($R_a^2 = 0.5170$), instead of a stand level competition measure ($R_a^2 = 0.5019$). In that case, knowledge of the local competitive environment, while a slight improvement over the stand level measures, was not sufficient to explain significantly more variation in the plants stress reaction. Hann (1997) found that 73% of the variation in largest crown width in Douglas-fir was explained by crown length and diameter-height ratio. It was also found that the amount of variation explained by the same equation was greater for intolerant ponderosa pine (88%) but less for tolerant grand fir (*Abies grandis*) and white fir (61%). In tolerant species, the tree might be responding to light stress by altering crown characteristics thereby buffering density effects (Maguire and Bennett 1996). An analogous situation is expected to occur with roots in below ground competition. If measures of foliage or diameter are used to represent the micro-environmental and genetic influences in models of tree growth, then spatial information may not add significant explanatory power.

All spatial indices require some form of edge correction (Martin et al. 1977). In situations where competitors are uniformly distributed around the subject tree and the angles to them are independent of the size and distance to competitors, an unbiased edge correction for SD indices can be calculated. GS indices can be buffered such that any tree whose cell shares an edge with the plot is dropped. CIZ indices can be buffered in a similar manner if the zone of influence of the largest tree can be predicted. OSV and LI indices can be adjusted for edge bias if the range of shadows from obstructing vegetation or physical features can be predicted. A common method of edge correcting LI indices is to use a fixed height obscuring ridge which is a feature that blocks all light from below a fixed angle from the horizontal (Ross 1981). An obscuring ridge prevents additional light from entering the plot from the direction of the ridge. The obscuring ridge can be constructed such that light striking it from the plot is reflected back into the plot or attenuated.

AREAS FOR FUTURE RESEARCH

The comparisons of spatially explicit indices have been conducted on even-aged stands that are mostly single species. Many of these comparisons conclude that there was insufficient variation in the indices calculated using data from even-aged stands to identify a correlation (Martin and Ek 1984, Weiner 1984, Daniels et al. 1986). The trends in competition might be more visible in situations where the interaction has occurred undisturbed for a longer period of time.

Plants react to competition by modifying their growth patterns. Crown size is strongly affected by density; under heavy competitive pressure, a tree will increase crown width and decrease crown length (Oliver and Larson 1990). Spatially explicit indices should be useful in explaining variation in crown recession rates since, the height to the base of the live crown is better modeled using local competition measures (Hanus et al. 2000).

Only one of the comparisons included an OSV index (MacDonald et al. 1990) and none included LI indices. Since competition for light is primary in some environments there is opportunity to test the utility of spatial indices in these environments.

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CHAPTER 3

SEALS: SPATIALLY EXPLICIT AMBIENT LIGHT SIMULATOR

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February 17, 2003

For Submission to: Ecological Modeling
Elsevier Science Publishers, New York, NY

Abstract

In continuous canopy stands light limits plant growth. However, due to the physical nature of light, constructing an index of competition based upon the light available to a plant is very complicated. Its direct prediction is affected by the changing influences on the incident light stream and the complex nature of the forest canopy. Light is described by it intensity and spectrum and is quantified by radiation transport equations. The solution to the radiation transport equations for the large volume of aerial space occupied by canopy structures is complicated by the intensity of data collection and the intensity of processing required. Discrete ordinates is a boundary value, time discrete method of solving the radiation transport equations for a portion of the aerial volume at a point in time and aggregating the solution to arrive at an approximation of light intensity and quality.

A computer program, Spatially Explicit Ambient Light Simulator (SEALS), was developed that combined a three-dimensional graphics image of the stand with an efficient data structure for holding spatially explicit values of light intensity. SEALS uses sample data and empirical estimates of crown structure to represent the three dimensional locations of the canopy elements. This image is used to describe the contents of canopy space. SEALS calculates light intensity values at each location for moments in time during the growing season. The light intensity values are then aggregated over the crown surface of each tree and expressed as an average per unit of surface area to determine the amount of light available for growth. Light intensity is also calculated by counting the amount of open sky in a simulated hemispherical scene viewed from the tip of each tree.

Since SEALS uses data collected from a stand examination it can estimate available light for past stand conditions for which light measurements were not taken. It can also estimate the available light in canopy locations that are not easily reached with instrumentation.

Introduction

Solar radiation is important to plant growth since it provides the only source of energy for the process of photosynthesis. Its absence limits both shoot and whole plant growth (Horn 1971). Light arrives at the plant in a radiation field which may be described by three components: (1) solar radiation incident from the sun, (2) diffuse radiation scattered from the incident radiation stream by the atmosphere and (3) complementary radiation resulting from scattering of radiation from foliage and the ground. The first two components penetrate the stand through openings while the third is created by the interaction of the light stream with canopy components. The theory of light transport through plant communities has a long history of study (Myneni and Ross 1991).

Predictions of light transport have been used to describe the fraction of the incident radiation that penetrates a canopy (Ross 1981, Myneni and Ross 1991), the quantity and quality of light reflected back into the atmosphere from the surface of the canopy (Balick 1987) and the amount of light available to each plant for photosynthesis (Grace et al. 1990, Brunner 1998). Each of these classes of application have different requirements on both the information required to generate the light and the information provided on the light environment.

Direct characterization of the light environment under plant canopies was first attempted through the application of Beer's law which predicts light intensity as an exponential function of the depth below the canopy surface. Beer's law assumes that the canopy volume can be represented as a turbid medium. This means that all of the occluding elements are: (1) small in cross-sectional area when compared to the volume of interest, (2) randomly distributed in volume of interest, (3) uniformly oriented in space and (4) are numerous (Chandrasekhar 1950). Since leaves, shoots and branches are not arranged randomly in space, solutions from application of Beer's law differ in fundamental ways from the light environment observed in natural stands (Ross 1981).

Canopy foliage is clumped at several scales. Branches and their corresponding leaves are grouped into plants while shoots may be grouped into whorls or other architectural forms and within a shoot the leaves may be arranged into groups yielding spatial distributions far from uniform (Hallé et al. 1978). The clumping of foliage yields greater actual light penetration between tree crowns than predicted by Beer's law when the incident radiation is nearly vertical (Ross 1981) and when it is far from the zenith in coniferous crowns (Oker-Blom and Kellomäki 1983).

Modeling the grouping of shoots into whorls and whorls into trees has improved the correspondence between predictions of light intensity and observations (Norman and Jarvis 1975, Oker-Blom and Kellomäki 1983, Oker-Blom et al 1991). Modeling the non-uniform angular distributions of the leaves within shoots has also led to better predictions (Ross 1981). Additional improvements to predicted light intensity was realized by including models of differential surface scattering and the nonrandom direction of incident radiation (Ross 1981). Since the sun is not a point light source, rays from one side of its disk partially illuminate areas shaded by rays from the other side of the disk. This partial illumination is known as penumbra. Penumbra has been found to make a significant contribution to the available light both within and below the crown especially in coniferous stands (Denholm 1981, Oker-Blom 1985). While these improvements have resulted in superior predictions of light intensity in and under plant canopies, they have come at the cost of ever increasing model complexity.

Predicting the light environment in stands that are not well represented by Beer's law is much more complex. It requires knowledge of the location, orientation and size of the foliage throughout the volume of the stand, which has proven to be a daunting task requiring the modeling of shadows from many arbitrarily sized small bodies arranged non-randomly in space. The method of discrete ordinates has been advanced as a heuristic for directly estimating light intensity (Chandrasekhar 1950).

In the method of discrete ordinates, space is divided into volume cubes of arbitrary size on the sides of which the differential equations describing the light environment can be solved. Four light attributes must be quantified for each volume element: emission, absorption, reflection and transmission (Chandrasekhar 1950). A solution to the radiation transport equations consists of jointly solving these four differential equations for the six faces of each cubic volume element for every moment in time.

Storing the location, size and orientation of the thousands of canopy elements expected within a typical stand requires an efficient data structure. A spatially explicit ambient light simulator (SEALS) was developed to predict the light available to the plants in the stand. It combines a rendering program with an efficient data structure for storing the light intensity at locations within the stand. In combination these routines are used to solve the radiation transport equations at a single point in time via the method of discrete ordinates. SEALS makes it possible to describe the light environment of fairly complex canopy structures on a personal computer.

SEALS starts with data from a sampled stand and renders a graphics image of the stand using a special OpenGL (Woo et al. 1997) version of VIZ4ST (Hanus and Hann 1997). VIZ4ST takes the species, outside bark diameter at breast height, total tree height, the height to the base of the live crown (HCB) and the spatial location of each tree and renders an image of the stand using empirical equations for crown structure. The canopy space as defined by the sampled stand is subdivided into small cubes and the predicted light intensity and distribution on each face of each cube are stored in an octtree that is expanded only if the cube contains foliage. The solution is repeated for changes in solar position during the growing season and the predicted light intensity values are aggregated. The simulated available light (SAL) for each tree is calculated by dividing the aggregated light reaching the crown surface by the area of the surface. A pixel counted simulated hemispherical photograph (PCSHS) is also calculated by counting the fraction of open sky visible from the tip of each tree.

Tree Images

The basis of SEALS is an OpenGL (Woo et al 1997) generated graphic image of the forest stand, OpenGL is a library of efficient graphics routines available for many programming languages. Trees in the sampled stand are rendered as three-dimensional images built from the OpenGL graphics primitives and scaled to their measured size. The tree images were designed to capture the structural attributes of the species while minimizing extraneous visual details. The relative placement of the trees is determined by measured locations and local topography.

Plants consist of roots, stems, branches, leaves, flowers and fruits, each component having its own form, texture, size, and color, and varying by species and by individuals within species. Computer rendering of plant group requires the reduction of natural complexity to essential structural elements without compromising species differences. To accomplish this, essential structural elements must be determined and then replicated in proper relation to one another.

Characterizing the light environment requires renditions of trees that include stems, branches, and leaves, each with attributes measured directly in the field or predicted indirectly with empirical relationships. Plant stems can be characterized by size, form, bark color and texture (Harlow & Harrar 1969), and by the degree of sinuosity and swelling of the stem. Realistic rendering of branches requires information on the number and placement of primary branches on the main stem, and on the size, degree of sinuosity, and angle of insertion into the main stem of each primary branch. Characteristics for describing higher order branches are size, frequency, and branching pattern (Horn 1971). Leaves are characterized by their size, shape, color, and placement on branches (Harlow & Harrar 1969).

In nature, patterns of branching may change with time and with location on the plant (Hallé et al. 1978). Some conifer species maintain their conical shape for hundreds of years, while other species have different architectures in different habitats, or under different growing conditions (Horn 1971). Still others may change from one architectural form to another during their life span, such that knowledge of plant age is required for their rendering (Fisher & Honda 1979). It has been noted that in some conifer species crown form changes with geographic latitude and social position in the stand (Koch 1987, Hann 1999). The number of branches in a whorl and their lateral extent is related to the competitive environment in Douglas-fir but not in lodgepole pine (Williams et al. 1999).

In their work on tropical plants Hallé et al. (1978) used physiological characteristics, growth form and reproductive structures to identify 23 types of plant architectures. The majority of these architectural forms are restricted to tropical regions (Kuuluvainen 1992). Trees in Pacific northwest forests exhibit only five of the basic architectural forms. SEALS utilizes only the structural elements of these architectures and measures of size, texture, color, orientation and placement of the stems, branches and leaves to characterize tree species.

Lindenmayer (1968) described rules, "L-systems," for defining self-referential three-dimensional branching structures that produce more realistic-appearing trees with internal detail. They were derived from the observation that, in many plant growth-processes, structures are regularly repeated. This self-similarity is exploited to produce an algorithm that replicates the structure of the plant.

The stems of all species rendered by SEALS are sized to the measured diameter at breast height and measured tree height. Stems are rendered as right cones for all monopodial species and the basal section of sympodially branching species as right frustums. Stems of monopodial species are assumed to be continuous, unbroken and parallel to the z-axis. Measured height to crown base defines the lower extent of the crown while total tree height defines its upper extent.

Rendering conifers in SEALS

The conifer species of the western United States are monopodial, having a central stem from which the primary branches protrude, and are characterized by strong apical dominance. The color and texture of the bark is determined from published species characteristics (Harlow & Harrar 1969). The allocation of primary branches along the stem in most western conifers is concentrated at whorls generally added every year from lateral buds set at the end of height growth in the previous year. The number placement, size, and angle of insertion of primary branches have been studied in detail in the western United States for young Douglas-fir (Maguire et al. 1994, Roeh 1993) and for mature Douglas-fir (Ishii et al. 2000). Whorl height was approximated with past height measurements when available or by scaling existing dominant height equations to the measured height of the tree when past measurements are not available.

Crown profile has been quantified for many species in the Pacific northwest (i.e. Hann 1997, Hann 1999). The light environment of the individual affects the crown shape in some species. The crowns become wide and compressed in an "umbrella" shape, when the individual is subjected to light stress. In addition to "umbrella" shaped crowns, these trees exhibit a smaller diameter than is expected for a tree of their species and height (Hann 1999). The presence of diameter-height ratio in the crown profile equations yields this characteristic crown shape (Hann 1999). Live whorls are rendered if they fall above the height to the base of the live crown as measured or predicted by Hanus et al. (2000).

The insertion angle for the primary branches of young Douglas-fir characterized by Roeh (1993) and Maguire et al. (1994) was used for all conifer tree species. The angle of branch insertion and the height of the branch within the crown are related to branch length by crown-profile and greatest horizontal branch extent. Branch extent in SEALS is limited by equations for the greatest horizontal extension of branches in stand grown trees (Hann 1997, Hann 1999) and by the location of its nearest neighbors. Branch taper was predicted using the equations of Ishii et al. (2000).

Although damage and recovery dominate the branch form of stressed and older trees (Ishii et al. 2000) no attempt was made to replicate this common behavior. Most of the stands for which SEALS is intended are relatively young and while there is evident branch damage a visual survey showed that the rate of occurrence was small. Stressed trees may have a significantly different foliage distribution than young unstressed trees (Ishii et al. 2000) which will affect the predicted light stream

Douglas-fir

Douglas-fir is represented by a monopodial form with branches collected in whorls that are set annually. Each whorl is placed on the stem in accordance with past height measurements or estimated by scaling the dominant height growth equations of Bruce (1981). Each branch within a whorl annually divides into three daughter segments. The middle daughter of each node grows in the same direction as the mother segment. The other daughter segments deflect by 20 degrees from the plane of their mother before correction for foliage weight. Branch droop occurs as the length of the branch increases so that long branches tend downward yielding a branch structure where branches in the upper crown point upward and branches in the lower crown point down. When the droop of the branch results in a branch angle greater than 45 degrees the direction of the central segment is displaced upward by 20 degrees. This results in a sigmoidal shape to the largest branches on the tree. Total branch extent is determined by its position in the crown and the largest crown extent equations of Hann (1999). Branches are also truncated when they meet the crowns of neighboring trees.

The leaves of Douglas-fir are arranged evenly along the daughter segments in spirals entirely around the branch in a "bottle-brush". They are represented by needle shaped polygons of 2.25 cm long and 0.25 cm wide (Harlow and Harrar 1969) of a single color and texture. The leaves persist for five to eight years so the full density of foliage is left on the last five years of growth and half of the foliage density is retained for six to eight years of growth. The bark is green on the last years growth becoming gray-brown and deeply furrowed on older stems.

Grand fir

Grand fir is also represented by a monopodial form with branches collected in annual whorls. In the same manner as Douglas-fir each branch within a whorl annually divides into three daughter segments whose middle grows in the same direction as the mother. Branch droop in grand fir also occurs as branch length increases to the point where its structure can no longer support the full weight. Grand fir branches however grow longer before bending than do those of Douglas-fir. This results in more and larger branches pointing upward in grand fir than in Douglas-fir. Total branch extent is determined by its position in the crown and the largest crown extent equations of Hann and Hanus (2001).

Grand fir leaves are represented by needle shaped polygons 3.5 cm long and 0.25 cm wide (Harlow and Harrar 1969) colored lighter on their lower surfaces. They are arranged evenly along the daughter segments in two rows on either side of the branch. The upper row of needles are 0.5 cm shorter than the lower row. The space between grand fir needles is about 1.5 times that of Douglas-fir needles. Grand fir needles are swept upward of the branch in the upper third of the crown and nearly flat in the lower two-thirds. Leaf persistence is not recorded for grand fir so it is assumed that they remain on the tree as long as the leaves of Douglas-fir. Grand fir bark is gray-brown on the segments representing the last three years of growth becoming reddish-brown and deeply furrowed on older stems.

Western hemlock

Western hemlock is represented by a monopodial form with branches collected in whorls. Each whorl is placed on the stem in accordance with past height measurements or estimated by scaling the unpublished dominant height equations of Flewelling. Branch structure of western hemlock was characterized by Kershaw and Maguire (1995) and Kershaw and Maguire (1996) was used for all conifer tree species. The angle of branch insertion and the height of the branch within the crown are related to branch length by crown-profile and greatest horizontal branch extent. In the same manner as Douglas-fir, each branch within a whorl annually divides into three daughter segments, whose middle grows in the same direction as the mother. Branch droop in western hemlock is greater than the other two conifers in SEALS. Branch tips also droop on the last years growth. A conspicuous attribute of western hemlock is a drooping terminal leader. In SEALS, the last years terminal growth is folded over to two-thirds of its length. Total branch extent is determined by its position in the crown and the largest crown extent equations of Hann (1999).

The leaves of western hemlock are arranged evenly along the daughter segments in single horizontal rows on either side of the branch. The needles are arranged flat in the horizontal plane of growth They are represented by needle shaped polygons 1.3 cm long and 0.25 cm wide (Harlow and Harrar 1969). Western hemlock leaves persist for four to seven years so the full density of foliage is left on the last four years of growth and half of the foliage density is retained for five to seven years of growth. Hemlock crowns are characteristically more open than those of Douglas-fir (Harlow and Harrar 1969). This open structure is reflected in SEALS by an increased distance between the leaves that is twice that of Douglas-fir. The bark is green on the last years growth becoming dark brown and deeply furrowed on older stems.

Rendering hardwoods in SEALS

Two species of hardwoods are rendered in SEALS, Bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*), both of which are represented by a monocaulous structure. The primary characteristic of this form is the single stem from which branches protrude at a non-zero angle. In SEALS, hardwood leaves are rendered as polygons of constant shape approximating leaf shape and size as described by Harlow and Harrar (1969). Leaves are all located above the height to the base of the live crown as measured or predicted by the equations of Hanus et al (2001).

Bigleaf maple

Bigleaf maples may exhibit multiple architectural forms through their life span. A single tree may start as a monocaulous seedling that due to damage re-sprouts with multiple trunks, one of which by chance dominates, generating a stem that sympodially branches with age. A sympodial branch structure does not maintain a central stem through its entire length. Since SEALS will be applied to stands where the location and dimension of every stem is recorded, maples are modeled as sympodial trees with long single stems. Maple branches protrude from all sides of the upper half of the central stem in a vertical direction. Sympodial branching structure results in sinuous branches when all but a single daughter segment are omitted.

Honda (1971) assumed that each tree segment is straight and has a fixed width. However each segment can be modeled as a frustum of a right cone with a set amount of taper. A mother segment produces two daughter segments through a branching process, the parameters of which are both species and position dependent. The lengths of the two daughter segments are a function of the length of the mother segment. The mother and the daughter segments have a constant branching angle.

The total area of all daughter branches at each fork is equal to the area of the mother at the fork. Daughters have non-negative diameter and a minimum of two daughters will be generated at each fork. The resulting daughter branch segments taper as a cone with a length defined by the distance from the fork to the edge of the crown. The length of the internodal segment of higher orders of branches is two-thirds of the length of the mother segment. Branching is terminated when the limit derived from crown profile equations (Hann 1999) or the crown of a neighboring tree is reached.

Bigleaf maple leaves are rounded 20 cm in diameter with three major lobes and two minor lobes. The leaves are arranged uniformly along branches opposite of one another. They are bright green on their upper surfaces and pale below. Maple is rendered with leaves of constant density on the last three segments of branches. This was done to visually replicate the leaf density found in stand grown trees. The bark is light gray-green on the last two divisions of twigs, becoming brown and deeply furrowed on older stems.

Red Alder

Red alder trees commonly exhibit a monocaulous form that may include stems clustered together. Each tree in the input data is considered to have a single stem since all trees forking below breast height are recorded as individual tree records. Branches are placed at intervals along the stem. The structure of alder branches is self-similar, each branch has the same structure as the entire tree. Each branch is consists of a central stem surrounded by sub-stems that alternate along it terminated by the crown profile or contact with neighboring crowns. The largest crown extent of red alder is determined from the equations of Hann (1997). The crown profile of alder is modeled in SEALS as a hyperbola.

Red alder leaves are ovate 11 cm long and 5.5 cm wide. They are dark on the upper surface with lighter colored ribs below. Alder is rendered with leaves on the final three segments of each branch. The bark is green on the last two divisions of twigs and light gray to whitish on older stems. Although the ribs of alder leaves are pubescent on the midrib (Harlow and Harrar 1969) this was mot modeled in SEALS.

Radiation Transport

Light consists of photons whose energy is proportionate to their frequency. The radiation field at every location in space is characterized by the number of photons passing through it and the frequency of those photons. Light intensity is characterized by the number of photons and the light spectrum is characterized by their frequency. Prediction of light intensity and spectrum through time is accomplished using radiation transport equations. The radiation transport equations describe light flow and its interactions with matter assuming that they are subject to the laws of energy, mass and momentum conservation.

Systems of radiation transport equations were developed to describe light flow in situations where scattering is isotropic (Chandrasekhar 1950). Under other conditions, such as those found in plant canopies, these systems become nonlinear, non-homogeneous and of high degree (Chandrasekhar 1950) making direct solution difficult or impossible. Heuristics have been derived to render the system of equations solvable. The most prevalent of these is the method of discrete ordinates (Chandrasekhar 1950). This method has been applied to assemblages of vegetation with agricultural and agro-forestry applications (Ross 1981, Myneni and Ross 1991).

The method of discrete ordinates simplifies the solution of the radiation transport equations by solving discrete approximations of the differential equations describing light intensity, flow and pressure at a systematic sample of points located through space at a single instant in time. The discrete ordinates solution assumes that vegetation elements are either randomly distributed and oriented in space or their distribution and orientation can be predicted.

In plant communities, foliage does not exhibit a random spatial distribution (Hallé et al. 1978), nor does it have random orientation (Oker-Blom and Kellomäki 1983). In some plant communities the distribution and orientation is statistically predictable (Ross 1981).

SEALS uses a graphic image of the forest stand to determine and store the location and orientation of all foliage and shoots. Trees are sized and located according to field measurements and their branches and leaves are represented in an approximation of their field locations. The structural arrangement of each tree is approximated from measurements and empirical relationships then "drawn" in computer memory.

The energy density, radiative flux and pressure tensor serve to fully describe the radiation field at a location in space (Carlson and Lathrop 1968). These three components represent the angular moments of the specific light intensity at every point in space. The radiation transport equations quantify these moments and can be aggregated to form a description of the light at a point in space, at a point in time.

Photons entering a plant canopy may pass between foliage elements or they may interact with canopy foliage and branches by being absorbed or scattered. The energy of absorbed photons is either used in photosynthesis, converted into heat or lost in transpiration (Kozlowski et al. 1991). Photons may be scattered from the surface of the leaf or undergo reflection and refraction within the leaf. Additional photons with frequencies in the infrared range are emitted by plant objects heated above the ambient temperature by absorption of incident photons and chemical heat emissions. Radiation transport is described by differential equations for each of these interactions which makes it the most complete description of the photon flux possible (Chandrasekhar 1950).

A further complication to the solution of the transport equations is that photon-matter interactions are dependent on the wavelength of the photon and the structure of the matter with which it is interacting. The large numbers of leaves and branches with which the photons may interact, their nonrandom spatial orientation and position, along with any changes to the numbers or position, make approximations necessary for solving the transport equations. The method of discrete ordinates approximates the light stream by solving the radiation transport equations for a finite number of locations in space at a finite number of points in time. If the space between the locations where the equations are solved is not significantly different, then the solution is representative of the actual light environment (Chandrasekhar 1950).

If each point in space is represented by a volume element (voxel) then the radiation transport equation represents the time rate of change of the number of photons due to the net streaming of photons into and out of the voxel, absorption of photons in the voxel, scattering from frequency (ν) in direction (Ω) to all other frequencies (ν') and directions (Ω'), scattering into ν and Ω from all other frequencies and directions, and emission of photons from objects contained in the voxel. A single equation combining these relationships is:

$$
\begin{aligned}
&\tfrac{1}{c}\tfrac{\partial}{\partial t}I(\vec{r},v,\underline{\Omega},t)+\underline{\Omega}\cdot\vec{\nabla}I(\vec{r},v,\underline{\Omega},t)\\
&=s(\vec{r},v,\underline{\Omega},t)-\sigma_a(\vec{r},v,\underline{\Omega},t)I(\vec{r},v,\underline{\Omega},t)\\
&+\textstyle\int_0^\infty dv'\int_{4\pi}\tfrac{v}{\upsilon'}\sigma_s(\vec{r},v\rightarrow\upsilon',\underline{\Omega}\rightarrow\underline{\Omega}',t)I(\vec{r},v\rightarrow\upsilon',\underline{\Omega}\rightarrow\underline{\Omega}',t)d\underline{\Omega}'\\
&-\sigma_s(\vec{r},v\rightarrow\upsilon',\underline{\Omega}\rightarrow\underline{\Omega}',t)I(\vec{r},v,\underline{\Omega},t)'
\end{aligned}
$$

where: c is the speed of light in a vacuum,

$I(\vec{r},v,\underline{\Omega},t)$ = the light intensity from direction $\underline{\Omega}$, with frequency v at location $\vec{r}$, at time t,

$s(\vec{r}, \nu, \underline{\Omega}, t) =$ the light emitted in direction $\underline{\Omega}$, with frequency ν at location $\vec{r}$, at time t,

$\vec{\nabla}$ is the divergence operator (equal to the sum of the partial derivatives of the vector field with respect to each coordinate),

$\sigma_a(\vec{r}, \nu, \underline{\Omega}, t) =$ the absorption of light from the direction $\underline{\Omega}$, with frequency ν at location $\vec{r}$, at time t,

$\sigma_s(\vec{r}, \nu \rightarrow \upsilon', \underline{\Omega} \rightarrow \underline{\Omega}', t)$ = the scattering of the light stream from the direction $\vec{r}$, with frequencies ν scattered to υ' in the direction $\underline{\Omega}$ scattered to direction $\underline{\Omega}'$ at time t. More complete descriptions of this relationship may be found in Ross (1981) and Myneni et al. (1986).

This equation is time consuming and complicated to estimate for all points in space at all times. It is common to simplify this equation by selecting the coordinate system such that the primary solar photon flux is parallel to one axis of the Cartesian coordinate system and solving the resultant equation for a single point in time at a subset of points in the stand. Time is fixed by selecting a solar location and orientation corresponding to a specific moment. Space is then mathematically subdivided such that the z-axis is oriented parallel to the photon stream. In addition using large initial voxels and subdividing only those containing canopy elements reduces required memory and processing time (Neyret 1998). In this situation the transport equation becomes:

$$\left[-\mu \tfrac{\partial}{\partial z} + \zeta \tfrac{\partial}{\partial y} + \xi \tfrac{\partial}{\partial x}\right] I(\vec{r}, \underline{\Omega}) + \sigma(\vec{r}, \underline{\Omega}) I(\vec{r}, \underline{\Omega}) = \int_{4\pi} \sigma_s(\vec{r}, \underline{\Omega}' \rightarrow \underline{\Omega}) I(\vec{r}, \underline{\Omega}) d\underline{\Omega}'$$

where: μ is the direction cosine in z,

ζ is the directional cosine in y,

ξ is the directional cosine in x,

σ is the interaction coefficient,

σ_s is the scattering coefficient.

Specific values for the interaction and scattering coefficients are estimated from the contents of the voxel containing r.

The interaction coefficient represents the fraction of the photon stream passing through the voxel that strikes objects contained within the voxel. The probability of interaction is a function of the optical properties, size, orientation and frequency of objects contained by the voxel. In the absence of penumbra and partial scattering, the probability of interaction is proportionate to the fraction of the side of the voxel towards which the photon is traveling that is occluded by projections of the objects contained in the voxel.

Photon interactions with the surface of an object can be calculated from the photon incidence angle, the index of refraction of the surface, and other surface characteristics. These interactions differ significantly from smooth and rough surfaces.

The scattering coefficient is estimated in a similar manner. When a photon strikes the surface of a leaf it may be absorbed or reflected from the surface the leaf. The probability of reflection and absorption depends on the frequency of the incident photon and the color and texture of the surface. Within the leaf the photon is reflected or refracted at each cell wall until it is either absorbed or transmitted through the leaf. In general, transmitted photons can emerge from the leaf in any direction with a probability given by Lambert's cosine law. Shultis and Myneni (1988) used Lambert's law to describe the distribution of reradiated photons. They found that they are reflected with a distribution of directions that is a cosine about a direction orthogonal to the leaf surface. In a similar fashion, transmitted photons exit the leaf in a cosine distribution about the surface normal on the opposite side of the leaf. Some of the heat energy absorbed by the leaf is returned to the light stream as black body radiation with no preferential direction to its intensity.

Surface albedo (ω_S) for internal diffuse scattering, assuming Lambert's cosine law is:

$$\omega_S = \int_{4\pi} \gamma_S\left(\vec{r}, v, \underline{\Omega}, t\right) d\underline{\Omega} = \left[\tfrac{r_S}{\pi} \int_0^{2\pi} d\phi \int_0^1 |a| da \right] + \left[\tfrac{t_S}{\pi} \int_0^{2\pi} d\phi \int_{-1}^0 |a| da \right] = r_S + t_S$$

given that the integration is conducted in the frame of reference of the leaf (i.e. $a \equiv |\Omega \cdot \Omega_L|$). Albedo is the reflectance of the surface, thus the phase function for reflectance can be written as:

$$\gamma_R\left(\vec{r}, v, \underline{\Omega}, t\right) = K\left[\kappa, a\left(\underline{\Omega}' \cdot \underline{\Omega}\right)\right] F_r\left[\eta, a\left(\underline{\Omega}' \cdot \underline{\Omega}\right)\right] \delta_2\left(\underline{\Omega} \cdot \underline{\Omega}^*\right)$$

where: $\underline{\Omega}^*$ = the orientation vectors of the normals of the surfaces oriented such that they can scatter photons given the incident angle $\underline{\Omega}$

$a\left(\underline{\Omega}' \cdot \underline{\Omega}\right)$ = the angle between the incident photon path and the coordinate system

η = the index of refraction suggested to be 1.5 for leaves (Vanderbilt and Grant 1985)

$\delta_2\left(\underline{\Omega} \cdot \underline{\Omega}^*\right)$ = the surface delta function (to be discussed later).

$K\left[\kappa, a\left(\underline{\Omega}' \cdot \underline{\Omega}\right)\right]$ = a correction factor for surface irregularities proposed by Nilson (Myneni et al. 1991) to be: $e^{-\kappa \tan|a|}$where $\kappa \approx 0.1 \mathit{to}\ 0.3$ for leaves with diffuse pubescence or other protrusions. Since κ is the mean projection of surface structures, it is a function of the orientation of the surface and the density and size of the structures, it may be calculated for each canopy structure. The leaves of the species modeled in SEALS do not exhibit significant pubescence, therefore this term was set to 0.0.

$F_r[\eta, a(\underline{\Omega}' \cdot \underline{\Omega})]$ = the Fresnel parameter (Feynman et al. 1963)

$F_r[\eta, a(\underline{\Omega}' \cdot \underline{\Omega})] = 0.5\left[\frac{\sin^2(a-\theta)}{\sin^2(a+\theta)} + \frac{\tan^2(a-\theta)}{\tan^2(a+\theta)}\right]$ where $\theta = \sin^{-1}(\eta^{-1}\sin(a))$ from Snell's law.

Note that when the photon is on the solar path (i.e. $\alpha = 0$) and the index of refraction is 1.5 the Fresnel parameter reduces to: $F_r[\eta, a(\underline{\Omega}' \cdot \underline{\Omega})] = \left[\frac{\eta-1}{\eta+1}\right]^2 = \left[\frac{0.5}{2.5}\right]^2 = 0.2^2 = 0.04$.

The probability that a photon is scattered during its traversal of the voxel is estimated directly from its contents. It is described by the scattering phase functions for diffuse scattering from the surface of the objects within the voxel, ($P(\vec{r}, \underline{\Omega} \rightarrow \underline{\Omega})$):

$$\Gamma(\vec{r}, \underline{\Omega}' \rightarrow \underline{\Omega}) = 0.125 g(\vec{r}, \underline{\Omega}^*) K[\kappa, a(\underline{\Omega}' \cdot \underline{\Omega}^*)] F_r[\eta, a(\underline{\Omega}' \cdot \underline{\Omega}^*)]$$

The distribution of leaf surfaces oriented such that they reflect energy at specific incidence and exit directions can be calculated from their size and orientation.

Specular reflection (i.e. the portion of the incident solar stream reflected away from it) has been found to be a large component (~35%) of the scattered light energy in the understory environment (Vanderbilt & Grant 1985). The distribution of the scattering angles and frequencies of specular reflection is estimated by the scattering from adjacent voxels. The size, orientation and surface characteristics of the voxel contents determine the scattering angles and any frequency shifts that result. Size and orientation are features of the objects determined from the surfaces that make up the image. Surface characteristics are referenced from its graphics color. Leaves are given a color representing specific reflective properties, while stems have different properties.

Solutions to the transport equations are also affected by the boundaries of the image space. Information on the physical environment available to SEALS is bounded by the edges of the simulated stand drawn by VIZ4ST. Physical features such as occluding ridges were not included in the solution. This limitation is mitigated by the time discrete nature of the solution in which only ridges that selectively shade portions of the plot during the period between midmorning and mid-afternoon would alter the solution.

The intensity of light at the top of the canopy was estimated from the clear sky radiation available in the area of the subject stand. The light flux on stand edges was approximated given the estimated flux within the stand. Ground reflection was modeled as constant over the area of the plot, through time and light incidence angles. This corresponds to considering the ground as a uniformly rough surface without smooth reflecting surfaces (Beckmann & Spizzichino 1963). If a model of cloud distribution over the growing season became available it could be incorporated into SEALS.

Foliage affects the incident light stream by scattering some photons from the solar track to other angles. The location, orientation, size and optical properties of the foliage elements determine the resulting distribution of the scattered photons. The incident photon stream is reduced by the scattering of incident radiation from it and increased by the scattering of photons into it. A small contribution to diffuse radiation is made by the emission of heat from leaves. Since this radiation is outside of the PAR spectrum its magnitude is not calculated in SEALS.

Due to the size and shape of the leaves, scattering dominates the modification of the photon flux in conifer forests (Oker-Blom et al. 1991). Conifer leaves are very narrow and are arranged in groups that allow light to pass between them. This results in spaces where photon flux is dominated by the effects of scattering from the leaves. In broadleaf forests the effects of light transmission through the leaves may dominate the light environment so values of transmission would need verification.

Shoots and stems were given a rough texture of constant color. The scattering coefficient was parameterized assuming a uniformly rough texture free from reflecting surfaces or regular protuberances (Beckmann & Spizzichino 1963). The bark on all stems was assumed to be of constant texture and color which resulted in consistent scattering and absorption.

Since the instantaneous radiation intensity at each point in a plant canopy is too complex for a closed form solution, approximation techniques have been developed to calculate the flux density within small spaces (Myneni et al. 1991). The most successful of these techniques is discrete ordinates (Chandrasekhar 1950). The method of discrete ordinates divides space into small volumes on the surface of which the equations of the radiation transport equation can be solved. Only those voxels containing vegetation are subdivided, resulting in voxels of various sizes. To handle this unbalanced data structure an array of pointers containing a variable number of references was employed (Neyret 1998). The array was populated with references to the nearest occupied voxel, thus reducing the memory overhead of storing information on empty space.

Continuous solution of the transport equations requires solving the radiation transport equations for every moment in time. Incident light intensity continuously varies throughout the day due to earth rotation as well as passing clouds and other atmospheric disturbances. The locations of canopy elements are also continuously changing due to wind displacement and plant growth. Variations in local light intensity result in short duration increases in light intensity known as sun flecks, which are significant sources for light in understory environments (Holbo et al. 1985).

A sample of each week's contribution to the seasonal available light was constructed by solving the transport equations for three daily solar angles for each week of the growing season (Emmingham 1977). Solar incidence angles were calculated using the methods of Meeus (1998). The equations were solved for three daily sun positions (midmorning, noon and mid-afternoon) of the middle of each growing season week. No intensity adjustments were made for variation in atmospheric conditions.

Graphical renderings of forest stands disconnect them from information on their physical surroundings. This disconnection alters the modeled light environment by removing obscuring physical features or changing local shading due to edge correction techniques. In the subject stands used in evaluating SEALS, there have been no physical features blocking light from any tree in the stand during the mid day hours. Diffuse radiation intensity has been found to vary with depth into the canopy (Oker-Blom et al. 1991). The simulated diffuse intensity also shows a reduction in intensity with depth into the canopy so an average radiation intensity at height was used for the sides of the voxels on the edge of the plot. In addition 20 foot buffers have been used in SEALS to exclude trees that may have been under the influence of tree crowns protruding onto the plot from buffer trees. In all applications the locations of the trees have been measured and input to the program, and the plot topography has been estimated from topographic maps and local observations.

The light flux exiting each voxel enters the adjacent voxel modifying its incident light stream. This means that the transport equation solution within each voxel is not independent from the solutions of its neighbors. To account for this dependence it is necessary to add the flux from adjacent voxels to the solution and recalculate the voxel's solution. Since recalculation modifies the flux on each face, iteration of the solution is required until convergence is achieved.

The most stringent convergence criterion would be the restriction that the solution differed from the previous iteration by no more than a specified value (Myneni et al. 1991). Carlson and Lathrop (1968) propose three convergence tests of decreasing strength for approximating the empirical solution. The first Carlson-Lathrop convergence criterion requires the global rebalance factor be less than a fixed threshold, suggested by Myneni et al. (1991) to be 1.03 for forest stands. Under the second condition, convergence is still likely if the rebalance factors in 90% of the voxels are less than the threshold value. This condition results in valid convergence when there are a sufficient number of voxels and angular grids to explain the change in the flux field (Myneni et al. 1991). The third convergence criterion is applied if the second is not achieved. If the change in predicted intensity from the previous iteration in 90% of the voxels is less than a threshold of 3% (Myneni et al. 1991) then convergence is assumed, however a flag should set. The flag indicates to the user that there are volumes within the stand in which convergence may not occur given their canopy structure. Convergence within these volumes may still be achieved by subdividing their voxels, increasing the number of angular grids in the reflection model or both. Any of these alternatives will increase the processing time required for solution.

In SEALS these criterion are applied by sequentially applying the convergence criterion and iterating until convergence is met or seven iterations have been completed. In the event that the third condition is met the error flag is set and processing stops. If seven iterations have past and none of the conditions have been met then a global error flag is set and processing stops.

The global error flag indicates that a solution is not possible given the current constraints of SEALS. A long term solution to these conditions is to reduce the minimum size of the voxels and/or increase the number of angular grids within the volume where the rebalance factor is in excess of 1.03. There is no algorithm to identify the boundaries of the unstable volumes (Carlson and Lathrop 1968) so such an implementation requires applying the new solution parameters to the entire canopy volume.

The simulated available light (SAL) is the average light intensity incident on a unit of crown surface area for the tree. SAL represents the average light intensity available to the tree over the growing period. SAL is bounded by 0 and 1, where 0 represents the no light condition and 1 represents the full sun condition.

Validation of Computer Calculations

Due to the complexity of SEALS, a series of procedures were instituted to ensure that the calculation of SAL was performed in an accurate manner. The image of the individual trees were visually examined for foliage placement, consistency and size. The locations of the understory and overstory trees were plotted together and compared both with and without surface topography.

Available light values were tested by creating scenes of increasing complexity. Once the scene was created the shadow functions of OpenGL were used to project shadows at each of the growing season light angles. Scale was checked by comparing the length and width of the projected shadow to hand calculated values. Shadow interaction between multiple trees was tested using scenes of increasing complexity. In all cases the projection and rendering routines of OpenGL (Woo et al. 1997) were used.

Light intensity from three discrete ordinate solutions were compared to corresponding shadow maps produced by projecting the canopy elements onto understory crowns. The scenes were analyzed to ensure that the deepest shadows occurred where the occluding elements were close to the understory crown and they had high density if scattering did not contribute significantly to light intensity. Multiple angles of illumination were used to calibrate the shade maps to ensure that there was no explicit dependence of shade intensity on angle of illumination (Ross 1981). This might arise if the spatial distribution of the projected foliage differed from the predictions of the transport equations. Given the layered geometry of conifer crowns this type of discrepancy is most likely to occur at incident angles far from the zenith, locations where the sun shines only during the morning and evening. Restriction of the solar angles to midmorning and mid-afternoon values served to minimize this effect.

SOFTWARE PERFORMANCE

The primary limitation to direct modeling of light is the heavy demands on computer resources required to handle the large number of discrete canopy objects (Ross 1981, Oker-Blom et al. 1991, Brunner 1998) and SEALS is no exception. The processing requirements of SEALS make full use of the personal computer (PC) platform. Table 1 charts the run time of SEALS on two personal computers. From this table it can be seen that the run times are currently too long for SEALS to be used as an index of competition in operational growth models that run on a PC. It can also be seen that the decrease in elapsed time is nearly linear with processor speed. From this it may be concluded that until bus activity limits information transfer processor speed determines the run time.

Table 1. Computer specification and elapsed clock time for a single solution of the radiation transport equations.

Processor	Available RAM	Graphics RAM	Elapsed clock time
Intel Pentium II 266 MHz.	256 Mb.	4 Mb.	84 hours
Intel Pentium II 266 MHz.	256 Mb.	32 Mb.	8.5 hours
Intel Pentium III 750 MHz.	512 Mb.	4 Mb.	38 hours
Intel Pentium III 750 MHz.	512 Mb.	32 Mb.	4.8 hours
Intel Pentium III 1000 MHz.	512 Mb.	4 Mb.	27 hours
Intel Pentium III 1000 MHz.	512 Mb.	32 Mb.	3.7 hours

SEALS run times are expected to decrease as processing power increases and software improvements reduce the number of cycles per calculation. Building the graphics image contributes little to the run time. The major portion of the run time consists of the discrete ordinates solution. Reduction in run time may be achieved by implementing a parallel processing system where the solution to the next iteration is started before the end of an iteration. This would result in some wasted time if a converged solution is achieved and the next iteration is already started. Thus improvement is made only if the overlap is greater than the wasted processing time. Multithreaded processing may result in similar savings subject to the same constraints.

Discussion

SEALS is a computer program for simulating the intensity of light at all points in a sampled stand. SEALS uses data collected from a stand examination and produces two estimates of the light available to individual plants. The first, simulated available light (SAL) is an estimate of the average per unit area light intensity at the crown surface of each tree predicted from a solution of the radiation transport equations. The second pixel counted simulated hemispherical scene (PCSHS) is generated from a simulated upper hemispherical scene observed from the tip of each tree. The simulated hemispherical scene is generated from the same three-dimensional graphics image of the stand and analyzed in the manner of a hemispherical photograph (Canham 1988). Both indices produce an estimate of the light available to each tree over an entire growing season or multiseason growth interval.

Two methods have been applied to validate similar predictions. The first method is to compare the estimates to their measured analogs. The second method relates the light estimates to measured tree growth rates. Given the difficulty of collecting seasonal light values throughout the volume of a mature stand and the desire to use SEALS to describe the competitive environment of the plants in the stand, the second method was chosen.

Data from a series of managed stands was used by Hanus (2003a, 2003b) to validate the predictions of SEALS. Long term data from 12 managed stands consisting mostly of Douglas-fir was used to compare the predictions of SEALS to height growth measurements (Hanus 2003a, 2003b). It was found that SAL reduced the unexplained variation in the height growth of understory western hemlock by 48% over a nonlinear model of total tree height to a power. PCSHS explained slightly less variation, reducing it by an average of 40% (Hanus 2003a). It was also found that SAL reduced unexplained variation in height growth of overstory and understory Douglas-fir by 17.6% and PCSHS reduced it by 13.7% (Hanus 2003b). These values are similar to those achieved using direct measurements of the light environment (Comeau et al. 1993).

The difference in the explanatory power of the indices between the two studies reflects the amount of information available to SEALS to construct the estimates. The data set used by Hanus (2003a) consisted of more complete information than did the data set used by Hanus (2003b). In the data set used by Hanus (2003a), all of the understory and overstory trees were measured for diameter and height. In addition, on this plot the overstory crown extents were mapped on two occasions. In Hanus (2003b), while all species, diameters and locations were recorded only a subset of overstory tree heights were measured the rest were predicted with empirical equations. The understory on these plots was subsampled for location, height and height growth. The improved performance of both SAL and PCSHS on the plot with more complete information indicates that the indices are sensitive to the amount of information available to SEALS for constructing the graphics image of the stand.

Although SAL produces growth results as good as those derived from measurements it may be possible to improve the predictions of SEALS by increasing the precision of the locations of the canopy elements. Data are rarely collected on the degree and direction of sweep of trees in the stand. However, the location of the branches and leaves are expected to have a greater impact on the solution than the shape and sweep of the stem. Since the canopy exerts an influence over a much larger volume of space it is expected that improvements in knowledge of the location, orientation and shape of the branches and leaves will have a much larger impact on the predictions of SEALS.

Plants respond to damage dynamically so modeling damage is expected to improve the predictions of SEALS both in SAL and in PCSHS. In stands with stressed and older trees, the incidence of damage is greater. There will be a point where the incidence of damage is frequent enough that foliage distribution and hence the predicted light stream will be significantly different from the unstressed stand. Current stand examination procedures do not sample for the rates and severity of branch damage. To extend SEALS into old stands it will be necessary to improve the predictions of branch damage.

The simulation procedures used to generate both direct indices allow for the possibility of small passages through the canopy. If aligned properly these passages act as radiation conduits allowing direct beam radiation to penetrate the crown as sunflecks. Our use of discrete radiation intervals to model the light environment via SEALS may reduce the actual number of sunflecks striking understory trees but it will give more importance to those sunflecks that are predicted to fall on the understory trees. This problem can be eliminated by increasing the number of temporal radiation intervals used to model the light environment, at the expense of computer processing time.

Stand conditions can be accurately modeled only through the use of objective methods for determining stand structure. The relationships used to generate crown structure for the simulated trees in VIZ4ST were modeled as accurately as possible from past measurements and empirical relationships. Simple geometric shapes with homogeneous structure explored in the validation procedures failed to yield the same SAL values as were obtained from complex crowns. Visualization programs in which foliage components are not explicitly represented and/or simplistic crown shapes are used may not be realistic enough to calculate SAL.

Creation of the three dimensional canopy map utilized empirical relationships of stand examination measurements to describe crown structure. The height to each whorl, branch length, number of first order branches and their insertion angle come from published studies in Douglas-fir (e.g. Maguire et al. 1994, Hann 1997) and western hemlock (e.g. Kershaw and Maguire 1996). The number, length, angle and diameter of daughter segments in each higher order were based on assumptions of branch growth. At this time, it is not known how sensitive the SAL and PCSHS values are to these relationships and assumptions. Additional improvements in SEALS may be achieved by incorporating reductions in foliage longevity based upon the amount of light received by each retained leaf. Predictions of leaf mortality and growth could be fed back into the canopy reconstruction to adjust structure.

Computer generation of direct indices offers advantages over actual measurements of the light environment. Past and future light conditions for which actual light measurements are not available can be predicted, and the technique can be applied in situations where direct light measurements would be difficult to obtain. Although calculation of SAL using SEALS requires extensive processing time on a PC, this will decrease as computer processing power increases and techniques for rendering scenes improves. At that time, the characterization of competition and its dynamics will be more directly related to the physical features of the plant's light environment. Coupling SAL with explicit measures of other forms of competition should provide models of tree and stand development that are applicable to a broader range of stand conditions. SEALS could also provide a framework for explicitly linking the process of light competition to an empirical model of forest growth and yield.

The distribution of SAL at the forest floor has the potential for improving tree placement in stand reconstruction routines such as described by Hanus et al. (1998). Their routine uses a sequential inhibition routine to generate tree locations. This procedure places small trees directly under canopy gaps more frequently than under tree crowns. However, small trees often occur beyond the bounds of canopy gaps in areas where light reaches (Van Pelt and Franklin 2000). The vertical projection of overstory crowns is inadequate in fully predicting lighted areas. SEALS may provide a mechanism to identify such areas thus allowing a better indication of a stand's regeneration potential.

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CHAPTER 4

MODELING THE LIGHT ENVIRONMENT AND ITS INFLUENCE ON THE HEIGHT GROWTH OF WESTERN HEMLOCK UNDER A CANOPY OF DOUGLAS-FIR.

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February 17, 2003

For Submission to: Forest Ecology and Management
Elsevier Science Publishers, New York, NY

Abstract

Data from a plot on the George T. Gerlinger Experimental Forest in the western Willamette valley of Oregon provided an opportunity to examine the response of understory trees to changing overstory canopy structure over time. The regularly planted western hemlock trees acted as sensors of the competitive environment over the extent of the plot. This sample was used to compare examples from three classes of indirect spatially explicit indices of the light environment to each other and to two examples of direct spatially explicit light indices.

A spatially explicit available light simulator (SEALS) was used to directly model the light environment under a spatially complex canopy of Douglas-fir. Two direct methods of quantifying the light environment were generated by SEALS: the fraction of open sky above an understory tree derived from a pixel counted simulated hemispherical scene and the amount of simulated available light (SAL) incident on an understory tree. These values were derived from images of the stand generated with VIZ4ST, a visualization program for creating detailed three dimensional simulations of the structure of forest canopies.

Index comparison was based upon the reduction in mean square error over that achieved using a measure of individual tree height alone. SAL consistently explained more variation in height growth than did any other index examined. As in previous studies, there was no clearly superior performance among the indirect indices. Unlike in previous studies, the model form used for comparison was allowed to vary with the index under test.

A nonlinear model of tree height alone explained 1.9% of the variation in height growth across all growth periods. However, for each period and across all periods SAL explained the

most variation in height growth. In a model that included initial tree height, SAL explained 72.6% of the variation in height growth rate. An additional 2.3% of the variation could be explained by accounting for the geographic source of the seedlings.

Introduction

Competition occurs through spatial interaction between plants and their environment (Ford and Sorrensen 1992). Plants respond to competition by altering growth patterns to increase their acquisition of resources and to deprive their neighbors of resources (Tilman 1988). Competitive pressure and a plant's response to it is species specific (Tilman 1988). Quantifying the competitive pressure felt by an individual plant is complicated by genetic variation in the response of individual plants to that pressure. The effect of increasing competition is decreasing growth, and death results from the reduction of resources below levels necessary for respiration (Tilman 1988).

Interplant competition operates on at least three scales: (1) the stand level, (2) the micro-environment and genetic history and (3) the influence of local neighbors (Tomé and Burkhart 1989). To accurately predict reductions in plant growth a model must include descriptions of competition at all of these scales. Computer models of individual tree growth have either used basal area and/or the number of trees per unit area (Daniels and Burkhart 1988) to describe overall competition for nutrients and moisture. The micro-environment and genetic history of the plant can be described by the ratio of a measure of individual tree size, such as total height, to the stand average of that measure, if the plants share a common genetic history. The influence of local neighbors upon the light environment can be described by spatially explicit indices of competition.

Ecosystems dominated by the formation of a continuous canopy are most likely to be primarily limited by the intensity of photosynthetically active radiation (Ford and Sorrensen

1992). In these ecosystems, indices that quantify photosynthetically active radiation (PAR) should explain variation in growth better than those that quantify underground resources. Many spatially explicit measures of competition have been developed in an attempt to indirectly characterize the light environment. These have been divided into three classes by Holmes and Reed (1991): (1) size-distance (SD) relationships, (2) Competitive influence zones (CIZ), and (3) growing space (GS) measures.

SD relationships depict competition as proportionate to the size of the competing plant reduced by a function of its distance from the subject plant. CIZ measures describe competition as the proportion of the target plant's free to grow influence zone occupied by its neighbors. GS measures quantify competition as the area or volume surrounding a plant not occupied by its neighbors. The performance of these indices are expected to vary as they use different stand attributes to indirectly quantify available PAR.

The ability of members of these indirect classes of spatially explicit indices to explain variation in individual tree growth has been explored in many studies (e.g. Alamdag 1978, Daniels et al. 1986, Tomé and Burkhart 1989, Holmes and Reed 1991, Biging and Dobbertin 1992, Wimberly and Bare 1996). No single class of indirect spatially explicit index has been identified as superior to the others in explaining the variation in the growth of individual trees.

Daniels et al. (1986) found that a GS measure (area potentially available) yielded the largest partial correlation in a linear multiple regression model of loblolly pine (*Pinus teada* L.) basal area growth. A distance weighted size measure yielded the largest partial correlation in multiple regressions of diameter and basal area growth data from a spacing study of *Eucalyptus globulus* (Tomé and Burkhart 1989). Holmes and Reed (1991) reported that a CIZ index provided the largest correlation with diameter growth in red maple (*Acer rubrum* L.), while SD indices provided a higher correlation with diameter growth in paper birch (*Betula papyrifera* Marsh.) and aspen (*Populus* spp.). In the extensive analysis of Biging and Dobbertin (1992), a crown volume based SD index explained the most variation in height growth (ΔH) in Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), while a crown surface area based SD index explained the most in ΔH of white fir (*Abes concolor* [Gord. & Glend.] Lindl.) and ponderosa pine (*Pinus ponderosa* Lindl.). In Wimberly and Bare's (1996) study, a GS measure (layered area potentially available) made the largest partial contribution to a multiple regression of Douglas-fir and western hemlock (*Tsuga heterophylla* (Raf.) Sarg.) basal area growth.

The majority of comparisons have used a single model form to express the relationship between growth and each of the indices tested. However, Ledermann and Stage (2001) caution against comparing the effectiveness of competitive indices with growth model forms under the expectation that all indices will enter the model in the same way. They note that there is a close relationship between the growth model form selected and the ability of the index to explain the variation in growth. An index that may perform well in one growth model from may not perform well in another.

There have been many fewer examples of spatially explicit measures of competition that directly characterize the light environment. Accurate characterization of available light under a nonrandom, heterogeneous canopy requires a method that accounts for the three dimensional distribution of foliage. Most of these examples have used actual measurements of available light. Four techniques for measuring available light under forest canopies have been explored (Jones 1992): (1) photochemical responses, (2) thermal response, (3) optical examination and (4) photoelectric response. Two of these measurement techniques have shown promise in explaining the past growth of understory vegetation: optical examination through the use of densiometers (e.g. Vales and Bunnell 1988) or hemispherical photographic (e.g. MacDonald et al. 1990, Mailly and Kimmins 1997, Drever and Lertzman 2001) and photoelectric response through the use of electronic light meters (e.g. Comeau et al. 1993, Mailly and Kimmins 1997 and Duchesneau et al. 2001). While these techniques are based on field measurements, it is possible to reconstruct the spatial distribution of the canopy and estimate values similar to those that would have been measured during past growth periods (e.g. Silbernagel and Moeur 2001).

Two methods have been developed that show promise in replicating direct measures of understory light: (1) simulated hemispherical scenes and (2) estimated light intensity intercepted by the tree's crown. A simulated hemispherical scene at the tip of the tree (e.g. Silbernagel and Moeur 2001) can be analyzed in at least three ways; (1) sampling a subset of rays traced through the canopy (Van Pelt and North 1996, Courbaud et al. 2001, Silbernagel and Moeur 2001), (2) calculating canopy fractal dimension (MacDonald et al. 1990), or (3) by counting the proportion of pixels displaying open sky in a manner analogous to the analysis techniques of hemispherical photographs. Like Vanclay (1994) we will call these approaches open sky view techniques (OSV).

Past examples of the use of light intensity to model competition include the work of Hatch et al (1974) and Cole and Lorimer (1994) who utilized the estimated fraction of crown surface area exposed to the sun and Brunner (1998) and Brunner and Nigh (2000) who used a series of ray-traced hemispherical views to estimate crown light absorption. A more comprehensive description of light intensity is estimated through the radiation transport equations solved through the method of discrete ordinates (e.g. Ross 1981, Myneni et al. 1986). We will call these approaches light interception techniques (LI).

This study compares two examples of directly simulating the light environment to examples from each of the three classes of indirect indices. The five different approaches will be compared using long term data from a two-storied stand composed of a Douglas-fir overstory and western hemlock planted on a lattice in the understory. In the comparisons, each of the indirect indices will be related to measured height growth rate (ΔH) of the understory western hemlock using the model established by the developer of the index. The direct indices will use the model form, selected from a family of linear and nonlinear model forms that best fits the data.

Data

The data for this study came from a plot established in 1957 located on the George T. Gerlinger State Research Forest. The overstory stand of pure Douglas-fir was naturally regenerated from seed following logging of the pre-contact forest in the first decades of the 20th century. In 1957 when the stand was at a breast height age of 40 years, the overstory was uniformly spaced to 126 trees per hectare with a residual basal area of 17.2 m^2. A 0.4047 hectare plot (1.0 ac) was established and the locations of all of the residual trees were mapped. Surrounding the plot is a buffer thinned to the same levels as the plot itself.

Within the plot, a grid of western hemlock seedlings from four geographic sources were planted on 1.8 m (6 ft) centers. The regular spacing of the trees likely forced some of them into locations that they may not have inhabited in a natural stand. This broadened the range of conditions experienced by the trees making them receptors of resources beyond the normal range of conditions.

The initial planting of hemlock came from one location in Oregon and three locations in Washington state: one in Lewis county and two in Gray's Harbor County. Seedlings from the four initial sources were dispersed by planting two seed sources one after another within a row and alternating the rows with the other two seed sources planted one after the other. Thus a row of alternating seedlings from Lewis County and low elevation Gray's Harbor county were followed by a row of alternating seedlings from Oregon and high elevation Gray's Harbor county. Dead trees were replaced in 1961 with roadside seedlings from the local area.

The horizontal locations of all overstory trees on the plot were mapped to the nearest 0.3 m (1.0 ft) and a reference origin for the under-planted grid was also located to the nearest 0.3 m (1.0 ft). The elevation varied by no more than two meters across the plot. Variation in elevation was estimated from a map and the vertical location of the trees was estimated from interpolation from a triangular irregular network of elevation values. The understory and overstory trees were remeasured at various intervals during the next 35 years. Tree survival, observable physical damage and breast height diameter (D) were recorded on all trees over 1.4 m (breast height) in height. Total tree height (H) was measured on all trees shorter than breast height. A subsample of trees over breast height were measured for H and height to the base of the live crown (HCB). In addition, the extent of overstory crowns were measured and mapped twice during the observation period (1981 and 1997).

Field observations noted evidence of an unidentified rot in five of the understory trees. The infected trees were spread across the plot and the growth of the neighboring trees were not significantly different from the rest of the understory. In addition, the five trees were spread among four of the genetic sources indicating the lack of an imbalance in genetic predisposition to rot of the seedling sources. There were no other indications that disease or insect infestation occurred during the measurement sequence.

From 1959 to 1997 H was measured 17 times for the overstory trees and ten times for the understory trees, with six measurements conducted concurrently. The intervals between measurements ranged from one to six years for the overstory trees and from one to 13 years for the understory trees (with the largest interval occurring between 1973 and 1986). H of the understory trees was measured with a pole to the nearest 2.54 cm. (1.0 in) for the first seven measurements. For a subset of the overstory trees and the last measurements of the understory, H was measured to the nearest 0.3 m (1.0 ft) using the pole-tangent method (Larsen et al. 1987). H was estimated for the unmeasured overstory trees using empirical relationships developed for the northwest Oregon version of the ORGANON growth and yield simulator (Wang and Hann 1988). The values for H predicted by ORGANON were calibrated to the measured heights. Calibrated heights were constrained such that, for a tree, they never decreased during the 35 year measurement sequence. Height growth for the understory trees was calculated by subtracting the starting H from the ending H.

Since HCB was measured on a subset of the overstory trees that were measured for H, missing values for HCB were estimated from empirical relationships developed for the northwest Oregon version of ORGANON (Zumrawi and Hann 1989). HCB values were also calibrated and constrained in the same manner as were the H values.

Understory trees with observed physical damage caused by falling debris or weather were excluded from the growth analysis. Trees with multiple tops were tested for difference in expected growth response. Those that showed a response significantly different from an undamaged tree of the same position were excluded from the analysis. Trees labeled as suppressed were included in the analysis if they had no additional damage.

The measurement series was broken into five year increments that closely corresponded to the measurement interval. Tree attributes at the start and end of four periods were determined and increments were calculated for the five year growth period. Table 1 displays the mean overstory height, mean height to the base of the live overstory crown, the basal area in the overstory and understory, the crown closure from vertically projected predicted crown expanse, the number of overstory trees and the number of understory trees.

Table 1. Conditions of the stand at the start of the growth periods.

	1961	1967	1986	1992
Mean overstory H (m)	35.9	38.8	47.1	49.0
Mean overstory HCB (m)	18.4	18.8	25.7	26.5
Overstory basal area (m^2/ha)	20.3	26.7	46.6	51.9
Overstory crown closure (percent)	71.1	79.2	89.3	90.8
Number of overstory trees	53	52	51	51
Understory basal area (m^2/ha)	0	0.4	11.3	11.4
Number of understory trees	795	783	540	453

Table 2 shows the mean, range and coefficient of variation (CV) for the D, H, HCB and ΔH for the surviving understory trees at the start of the four growth periods used in the study. From this table it can be seen that mean ΔH increased in the second period, declined in the third and increased again in the final period. Seasonal ΔH is thought to be limited by the availability of moisture so the total rainfall and the average monthly temperature during each growth period was compared for differences. This examination failed to identify any deviation from the overall trend during the third period (1986 - 1992).

The average H and ΔH of the understory trees for each seedling source converged over the observation period (1961 - 1997). During the last growth period (1992) there was no significant difference in the mean group ΔH of the surviving understory trees. Mortality was not equally distributed among the seedling sources, thus, the relative proportion of individuals from the five seedling sources changed with time.

Table 2. Mean, range and CV of H, D, ΔH and HCB by seedling source for the understory western hemlock seedlings alive at the start of each growth period.

	Seedling source	1961	1967	1986	1992
H (m.)	Oregon roadside	0.2 0.1 - 0.4 42.4	1.2 0.3 - 3.8 55.8	9.1 3.2 - 16.5 28.4	11.2 3.4 - 17.4 27.4
	Gray's Harbor County WA < 150 m	0.4 0.1 - 0.9 41.0	2.6 0.5 - 5.0 36.9	10.9 6.3 - 15.0 17.3	12.5 8.7 - 17.3 16.5
	Gray's Harbor County WA > 150 m	0.4 0.1 - 0.8 33.5	2.5 0.6 - 4.9 34.4	10.7 4.8 - 16.5 18.6	12.2 5.1 - 19.0 18.6
	Lewis County WA	0.6 0.1 - 1.0 36.8	2.6 1.0 - 5.5 35.5	10.9 5.7 - 16.8 19.1	12.5 7.8 - 17.8 17.3
	Oregon	0.2 0.1 - 0.4 34.3	1.9 0.5 - 4.0 39.9	9.7 6.4 - 14.5 17.3	11.1 7.0 - 15.5 14.8
	All	0.4 0.1 - 1.0 48.9	2.3 0.3 - 5.5 44.3	10.6 3.2 - 16.8 19.7	12.2 3.4 - 19.0 18.2
DBH (cm.)	Oregon roadside	0.0 0.0 - 0.0 0	0.3 0.0 - 3.3 183.0	7.9 3.0 - 16.5 36.9	9.7 3.3 - 17.5 35.6
	Gray's Harbor County WA < 150 m	0.0 0.0 - 0.0 0.0	1.8 0.0 - 5.3 72.7	10.7 5.8 - 21.6 24.6	11.7 6.1 - 23.6 25.2
	Gray's Harbor County WA > 150 m	0.0 0.0 - 0.0 0.0	1.5 0.0 - 5.1 68.1	10.2 4.6 - 16.3 23.6	11.2 5.1 - 17.0 22.4
	Lewis County WA	0.0 0.0 - 0.0 0.0	1.8 0.0 - 6.1 71.3	10.4 4.6 - 16.3 24.7	11.9 5.8 - 17.8 22.1
	Oregon	0.0 0.0 - 0.0 0.0	0.8 0.0 - 3.8 98.4	8.6 5.1 - 16.5 26.5	9.4 6.6 - 17.8 24.0
	All	0.0 0.0 - 0.0 0.0	1.3 0.0 - 6.1 88.4	2.8 3.0 - 21.6 26.7	3.0 3.3 - 23.6 24.7
ΔH (m.)	Oregon roadside	0.1 0.1 - 2.6 65.1	1.1 0.1 - 2.9 60.3	0.6 0.1 - 1.6 70.9	0.9 0.1 - 1.7 64.8
	Gray's Harbor County WA < 150 m	1.7 0.3 - 3.3 41.0	1.9 0.1 - 3.2 31.3	1.0 0.1 - 2.5 55.7	1.0 0.1 - 2.4 55.5
	Gray's Harbor County WA > 150 m	1.6 0.2 - 3.3 39.7	1.9 0.0 - 3.2 32.0	0.9 0.1 - 2.6 65.0	1.0 0.1 - 2.2 52.4
	Lewis County Washington	1.7 0.5 - 3.7 40.1	2.0 0.2 - 3.4 28.6	0.9 0.1 - 2.5 56.1	1.0 0.2 - 2.3 47.5
	Oregon	1.2 0.4 - 2.7 43.4	5.3 0.1 - 3.2 38.2	0.7 0.2 - 1.9 67.0	0.9 0.2 - 2.1 54.6
	All	1.5 0.1 - 3.7 48.8	1.7 0.0 - 3.4 38.6	0.9 0.1 - 2.6 61.3	1.0 0.1 - 2.4 52.3

Table 2 (contd.). Mean, range and CV of H, D, ΔH and HCB by seedling source for the understory western hemlock seedlings alive at the start of each growth period.

	Seedling Source	1961	1967	1986	1992
HCB (m.)	Oregon roadside	0.1 0.0 - 0.2 42.4	0.6 0.1 - 2.2 70.2	4.3 1.8 - 6.1 23.8	4.8 1.5 - 8.5 43.2
	Gray's Harbor County WA < 150 m	0.2 0.1 - 0.5 38.3	1.5 0.2 - 3.0 42.3	4.6 2.9 - 6.5 17.9	5.6 2.0 - 10.6 33.4
	Gray's Harbor County WA > 150 m	0.2 0.1 - 0.5 33.5	1.4 0.2 - 3.0 39.6	4.5 1.7 - 6.2 21.4	5.5 2.1 - 12.9 34.6
	Lewis County Washington	0.3 0.1 - 0.6 36.8	1.5 0.4 - 3.3 41.0	4.5 2.5 - 7.4 20.9	5.7 0.7 - 10.2 34.4
	Oregon	0.1 0.0 - 0.2 34.3	1.0 0.2 - 2.4 48.2	5.1 3.9 - 6.2 12.4	4.0 1.0 - 7.4 36.0
	All	0.2 0.0 - 0.6 48.9	1.2 0.1 - 3.3 51.3	4.5 1.7 - 7.4 20.1	5.5 0.7 - 12.9 35.7

Table 3 shows the counts and percentages for the seedlings that died during the first year and over the 35 year observation period. The highest mortality is in seedlings from the Oregon sources. This might be due to the difference in average initial H, as the trees from Oregon were shorter than the trees from Washington. The high mortality in the replacement seedlings (Oregon roadside) may also be due in part to inferior planting locations.

Table 3. Counts and percentages of the mortality of the understory western hemlock seedlings.

Seedling Source	Number planted	Number Dead after 1 year (1959)	Percent dead after 1 year (1959)	Number Dead in all periods	Percent dead in all periods
Lewis County WA	277	70	25	125	45
Gray's Harbor County WA < 150 m	281	77	27	138	49
Gray's Harbor County WA > 150 m	294	75	26	139	47
Oregon	296	187	63	252	85
Oregon roadside	409[1]	N/A[1]	N/A[1]	378	92
Total	1,148	409	36	1,032	66

There were no indications of linear spatial trends in ΔH or mortality thus it is assumed that the availability of substrate nutrients and water are constant across the plot and vary only due to inter-tree competition. There is no evidence that *Phellinus weirii*, which is present in adjacent stands, exerted an effect on specific locations within the plot. It is further assumed that the measurable differences in growth and survival, of an individual tree are based on genetic ancestry and competitive stress.

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[1] Not included in the total number of seedlings planted.

INDIRECT INDICES OF THE LIGHT ENVIRONMENT

Light competition is expected to be the dominant spatial interaction between trees in this stand. Therefore a set of spatially explicit measures suitable for characterizing light competition, one from each of the indirect classes (SD, CIZ and GS) were selected for evaluation. The indirect indices chosen were restricted to those based upon H since in the initial measurements, some of the understory trees were shorter than breast height.

Size-Distance

The majority of SD indices use a ratio of D to quantify relative tree size. Since some of the seedlings had not reached breast height, a measure was selected that used a function of H as the measure of tree size. Of the SD indices described by Ford and Diggle (1981), Pretzsch (1995), and Biging and Dobbertin (1992), the index from Biging and Dobbertin (1992) using the fraction of competitor's crown volume within a critical height angle of 50° with the apex at crown base (CVHCBU-H1) was chosen as the SD measure of light competition:

$$CVHCBU-H1_j = \Sigma_{i=0}^{n} \varepsilon_{ij}\left(\frac{CVa_i}{CV_j}\right)$$

where

CVa_i = the crown volume of the ith competitor of the jth subject tree above the critical height angle (50°) from the height of the crown base of the jth subject tree,

CV_j = the crown volume of the jth subject tree ,

ε_{ij} = the linear expansion factor of the ith competitor of the jth subject tree used to correct for finite plot size (Martin et al. 1977).

This choice was based upon the evaluations presented in Biging and Dobbertin (1992) and upon our own unreported evaluations with the data used in this study. CVHCBU-H1 takes on a value of zero with no competition and gets increasingly larger with increasing competition.

Competitive Influence Zones

The CIZ measures of Arney (1972), Bella (1971) and Ek and Monserud (1974) were examined, and the index of Bella (1971) using a ratio of tree height was selected as the CIZ measure:

$$CIO_j = \Sigma_{i=1}^{n}\left[\frac{IZO_{ij}}{IZA_j} \times \left(\frac{H_i}{H_j}\right)\right]$$

where

H_i is the height of the ith competitor,

H_j is the height of the jth subject tree,

IZO_{ij} is the area of overlap between the influence zones of the ith competitor and the jth subject tree

IZA_j is the area of the influence zone of the jth subject tree.

This index was corrected for edge effects by dropping understory trees with influence zones extending beyond the plot boundaries. The area of the zone of influence was defined to be the predicted maximum crown width (MCW) of a tree of the same size and species as the subject tree as predicted by the equations of Hann (1997). CIO was chosen as the CIZ index, based upon published comparative evaluations in which it was included (e.g. Alemdag 1978, Daniels at al. 1986, Biging and Dobbertin 1992) and upon our own unreported evaluations with the data used in this study. CIO takes on a value of zero with no competition and gets increasingly larger as competition increases.

Growing Space

The GS index selected for this study was calculated as the area of the polygons produced from a weighted area potentially available (APA) tessellation (Pelz 1977). The bisectors of the line segments joining the subject tree with each of its nearest neighbors was weighted by a ratio of tree height as described by Pelz (1977). The computer program of Fortune (1987) was used to locate the vertices of APA polygons. Edge correction was accomplished by eliminating all understory trees with APA polygons in contact with the plot edge (Okabe et al. 2000). Small values of APA indicate high levels of competition while large values indicate low levels of competition. APA can not have a value of zero.

DIRECT INDICES OF THE LIGHT ENVIRONMENT

Direct computer simulation of the distribution of light intensity beneath a canopy requires an accurate description of canopy structure. A computer program that estimates canopy structure from tree measurements and empirical relationships of tree foliage is available in SEALS (Hanus 2003). SEALS uses published empirical relationships to reconstruct the three dimensional distribution of crown components from stand survey measurements of Pacific Northwest tree species. There were five species on the plots used for this study; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), grand fir (Abies grandis (Dougl. Ex D. Don) Lindl.), bigleaf maple (*Acer macrophyllum* Pursh) and red alder (*Alnus rubra* Bong.). SEALS replicates an approximation of the canopy structure from available measurements collected in past stand examinations for these species.

The physical locations of the trees, their D, H and HCB were passed to SEALS which rendered a three dimensional image of canopy foliage distribution at the start of the five-year growth period. The horizontal displacement from the corner of the plot was recorded at establishment for each overstory tree. Ground topography was approximated from observations collected with the understory measurements coupled with topographic maps. Elevation values for each plot were represented as an irregular triangular network from which individual tree elevation was estimated using interpolation based on non-uniform rational B-splines (Woo et al. 1997).

Two direct methods of characterizing the light environment were simulated from the three dimensional image rendered by SEALS: an open sky view index and a light interception index.

Open Sky View

The OSV index used in this study was pixel-counted, simulated hemispherical scene (PCSHS), the fraction of open sky pixels in a simulated hemispherical scene weighted by their location with respect to the seasonal solar track. Tree measurements were passed into a special OpenGL (Woo et al. 1997) version of VIZ4ST (Hanus and Hann 1997) and a simulated hemispherical scene was generated as viewed from the location of the tip of each tree. The simulated hemispherical scenes were analyzed in the manner of a hemispherical photograph using methods described by Campbell and Norman (1989).

Inter-tree gaps in the canopy contribute significantly to the ability of plants to grow beneath otherwise full canopies (e.g. Hutchinson and Matt 1976, Canham et al. 1990). Holbo et al. (1985) found that sunflecks also contribute significant amounts to canopy light and average sunfleck percentages could be estimated from hemispherical photographs without considering the solar declination at the time the photograph was taken. This allowed predictions of seasonal light intensity to be made from a single hemispherical photograph, an assumption which carries over to PCSHS. A single simulated view was used to characterize the light environment for the growing period.

Silbernagel and Moeur (2001) found that computer simulation can be used to replicate the images generated with hemispherical photographs. They concluded that canopy gap fraction was well replicated by a simulated canopy consisting of appropriately sized geometric solids. They identified the lack of finer resolution crown structure as contributing to an underestimation of within crown canopy openness. In their study this was somewhat mitigated by the overestimation of between tree gaps due to underestimation of crown width. The combination of these details brought their estimates of canopy openness very close to those reported for similar stands (Silbernagel and Moeur 2001).

In hemispherical photographs, diffuse radiation is characterized by weighting the exposed sky visible in areas not along the solar track less than those areas on the solar track (Canham et al. 1990). Radiation components potentially useful for photosynthesis are reflected onto plants from leaves and other overstory canopy elements (Hutchison and Matt 1976). This radiation component is not quantified by hemispherical photographs. PCSHS takes on a value of zero when there is extreme competition and a value of one in the absence of competition.

Light Interception

Two attributes of PAR have been identified as potentially important to tree growth: intensity and spectrum (Oliver and Larson 1990). This study will treat both the spectrum and intensity of PAR as light. No attempt will be made to discern which particular attributes of the ambient light environment are important to tree growth.

In addition to the intensity and spectrum of PAR, photosynthesis and thus plant growth is also limited by temperature. Photosynthesis does not occur below the freezing point of water and growth ceases due to cell death near 130° F. Between these extremes photosynthesis increases rapidly to a plateau and then declines again as temperature continues to increase (Oliver and Larson 1990). Within a stand, temperature is highly correlated with direct radiation (Myneni et al. 1986). We will therefore, make no attempt to discern between the effects of light and temperature.

Brunner (1998) describes a method for calculating a simulated LI index, absorbed percentage of the above canopy light (APACL). To calculate APACL, measurements of the location and size of each tree is passed to a program (tRAYci) that constructs from them a three dimensional model of the stand. In this model, trees are represented by cylindrical stems, topped by crown envelopes consisting of simple geometric shapes (i.e. cones or ellipses). Foliage density is assumed constant within the crown envelope. To meet the assumptions of the Beer-Lambert law it was further assumed that, within each crown, there is no significant light scattering, the crown elements are small in size, numerous and they have a random orientation and distribution (Larsen and Kershaw 1996).

The percentage of above canopy light (PACL) is calculated on the intersection of a 0.2 m. three dimensional regular lattice throughout the volume of the stand. At each lattice point on a tree's crown envelope, a systematic series of rays are projected out of the stand. These rays are restricted to the upper half of a sphere centered on the point. The total distance of foliage through which each ray passes is then summed for the point. Light intensity along the jth ray is reduced using Beer-Lambert law:

$$PACL_j = ACL \times e^{-0.5 \times DOST \times \sum_{s=0}^{ns}(LAD_s \times PL_s)}$$

where

ACL = the above canopy light intensity,

LAD_s = the leaf area density for species s (constant for all trees),

PL_s = each ray's foliage path length through species s

DOST = the number of days of the growing season that the ray path terminates in the solar track. The foliage density is constant within and between all of the trees on the plot. Thus extinction depends only on the total path length and not on the path's orientation. APACL is calculated by summing each ray's PACL value weighted by its path length through the subject canopy, for all of the sample points within the canopy envelope of the subject tree.

Brunner and Nigh (2000) used a simplified version of tRAYci (Brunner 1998) to estimate PACL, APACL and weighted leaf area (WLA) for Douglas-fir trees from a 50 year old even aged stand in British Columbia, Canada. WLA was calculated by integrating APACL over each tree's distribution of leaf area. In their simplification, APACL is calculated from PACL using just the vertical path length through the foliage envelope of the subject tree. They then related ΔH to PACL, APACL and WLA and found that ΔH was best predicted using a nonlinear hyperbolic model of WLA which explained 64.5% of its variation. Mean APACL alone for the tree was not a satisfactory predictor of ΔH. They also reported a strong linear relationship between WLA and the tree's leaf area (LA) for trees from all crown classes except the suppressed class. It is recognized that current tree size is a good predictor of growth (Tome and Burkhart 1989) and since WLA is so closely related to a measure of tree size (i.e., LA), the predictive ability of WLA for non suppressed trees is likely related as much to the size of the tree as the predicted amount of light it received.

The inability of APACL to explain ΔH may be due to: (1) violations of the assumptions of the Beer-Lambert law in conifer crowns (2) the use of oversimplified crown forms (3) a violation of the assumption of constant leaf area distribution within the crown (4) and/or the lack of a method to account for absorption and transmission variation due to penumbral effects.

Many studies (e.g. Ross 1981, Myneni and Impens 1985, Oker-Blom and Kellomaki 1983, Larsen and Kershaw 1996) have shown that foliage clumping affects both the absorption and transmission of light through canopy space. The difference in the amount of light passed through a clumped crown and the amount of light passed through an unclumped crown is dependent on the path angle traced through the foliage and the degree and type of clumping (Oker-Blom and Kellomaki 1983). Since Douglas-fir foliage is clumped into shoots and branches which are non-randomly arranged into whorls (Norman and Jarvis 1975) it does not fit the assumptions of the Beer-Lambert law and the light absorption and scattering will vary with light path angle. This difference in absorption will increase as the path angle gets further from the zenith (Ross 1981). The assumption of a uniform distribution of foliage within crowns results in an underestimation of transmitted light (Larsen and Kershaw 1996).

Brunner and Nigh (2000) assumed a conic crown shape for all trees regardless of their crown class however, Hann (1999) showed that the crown form of Douglas-fir trees was not conic and that it changed with the position of a tree in the stand. As a result the crowns of suppressed trees are shaped more like an umbrella than a cone (Hann 1999). Since the calculation of APACL is sensitive to crown shape (Brunner 1998), Brunner and Nigh's (2000) conclusion that WLA was superior to LA for predicting ΔH in suppressed trees may be caused by their choice of a constant crown shape for suppressed trees.

The technique employed by Brunner and Nigh (2000) for distributing leaf area within a tree crown assumes that the foliage weight monotonically increases with depth into the crown. However, Schmid and Morton (1981) and Kershaw and Maguire (1995) found that distribution of foliage biomass in Douglas-fir peaks at approximately 60% of crown length and then declines. Since the calculation of APACL is sensitive to changes in crown architecture (Brunner and Nigh 2000) a more accurate model of foliage distribution will affect the predictions.

Since the sun is not a point light source, rays from one side of its disk partially illuminate areas shaded by rays from the other side of the disk. This partial illumination is known as penumbra. Penumbra has been found to make a significant contribution to the available light both within and below the crown (Denholm 1981, Oker-Blom 1985). Currently indirect indices have no mechanism for including the effects of penumbra in their estimates.

In an effort to address these shortcomings, we developed a program called SEALS (Spatially Explicit Light Simulator) that does not depend upon the Beer-Lambert law and that uses a more complete description of the crown structure for each tree (Hanus 2003). The resulting LI index from SEALS is the simulated ambient light (SAL) incident on a tree for each of the growing seasons in the five-year growth period. It is calculated from an approximate solution of the radiation transport equations using the method of discrete ordinates (Chandrasekhar 1950). SAL is the average incident light per square foot of crown surface area.

Computer calculation of light interception has proven to be a daunting task because it requires the modeling of shadows from many arbitrarily sized small bodies arranged non-randomly in space. Techniques for shadow modeling developed in the field of computer graphics rely exclusively on the intersection of projected shapes with volume shapes (Woo et al. 1997). In computer generated scenes, the areas of intersection are colored in a complementary or grayed tone. This is very fast but assumes constant shade intensity within the projected shape and thus is not suitable for directly modeling the light environment. The method of discrete ordinates (Chandrasekhar 1950) is a more refined method of directly estimating ambient light.

Given D, H and HCB at the start and end of the five-year growth period, annual values were computed using linear interpolation of the three attributes. A special OpenGL (Woo et al. 1997) version of VIZ4ST (Hanus and Hann 1997) was used by SEALS to create a three dimensional image of the stand at the start of each annual growth interval during the five-year growth period. This image was used to calculate SAL for each of the trees.

In the method of discrete ordinates, space is divided into volume cubes of arbitrary size on the sides of which the differential equations describing the light environment can be solved. Four light attributes must be quantified for each volume element: emission, absorption, reflection and transmission (Chandrasekhar 1950). A solution to the radiation transport equations consists of jointly solving these four differential equations for the six faces of each cubic volume element for every moment in time.

A full solution of the radiation transport equations requires a time continuous estimation of light flux at every point in the stand. This was beyond available computational processing power so the ambient light incident on each tree was calculated by approximating the solution to the radiation transport equations with a time discrete estimate. Since the apparent angle of the sun changes with the seasons, variation in solar exposure was simulated by altering solar incidence angles for weekly sun positions for each week during the growing season using the methods and computer functions of Meeus (1998). The equations were solved for three daily sun positions midmorning, noon and mid afternoon of Wednesday of each growing week. At each of these solar positions, the shade intensity was calculated for the crown surface of each tree. No adjustments to light intensity were made for changes in atmospheric conditions. The average light intensity per square foot of crown surface area was used as the LI index for each tree.

SEALS processing time was further reduced by building the scene in graphics memory and implementing a hierarchical data structure to hold the results of the radiation transport equations. An array of pointers to adjacent occupied voxels was used to hold the attribute values for the hierarchically subdivided stand space (Neyret 1998). The total volume occupied by the trees, 0.4047 ha (1 ac) in area and 58.5 m (192 ft) in height, was divided into cubes 2.4 m (8 ft) on a side, each of which was subdivided into eight cubes only if they contained vegetation. If the smaller cubes contained vegetation they were in turn subdivided by eight until each cube containing vegetation was 0.15 m (6 in) on a side. For the smallest cube the transport equations were applied to the vegetation elements within and its solution aggregated up the hierarchy until the entire stand was covered. Cubes free from vegetation passed the light stream without alteration while cubes inside of tree boles blocked all light transport.

Modeling of light in natural scenes is further complicated by penumbral effects due to the size of the sun's disk and the structural complexity of objects in the canopy. The clumped distribution of leaves and branches result in small passages through the canopy. The location of these passages varies with time and can be deterministically predicted only with an exhaustive survey of the canopy foliage (Tilman 1988). However, a model such as VIZ4ST (Hanus and Hann 1997) can predict the between-tree spaces defined by the crown shape of the trees and it can estimate the spaces within the crown from the spatial arrangement of branches and leaves.

When viewed from the earth the sun subtends an angle of a little over 0.25° (15’59”.63) which is large enough to generate regions of partial shade (Meeus 1998). If atmospheric effects are discounted, then the size, shape and distance from the observation point are the factors affecting the intensity of the incoming light stream. Since the sun is not a point light source, rays from one side of its disk partially illuminate areas shaded by rays from the other side of the disk. The effects of penumbra were introduced within each occupied cube and aggregated to the surrounding cubes by SEALS.

Index Values

The mean and range for the spatial indices by growth period are displayed in Table 4. It can be seen that, for the SD and CIZ indices, the mean index value declines and the mean value of GS increases during the observation period. The average value of OSV remains nearly constant while the average value of LI is the smallest during the third period.

Table 4. Mean and range for the spatially explicit indices at the start of each growth period.

Class (index)	1961	1967	1986	1992
SD (CVHCBU-H1)	289.97 (209.75 - 321.07)	89.36 (2.73 - 449.77)	1.70 (0.27 - 15.34)	1.33 (0.39 - 11.74)
CIZ (CIO)	62.89 (0.0 - 209.58)	25.43 (0.0 - 135.08)	9.79 (1.20 - 25.22)	9.42 (1.61 - 26.32)
GS (APA)	0.724 (0.100 - 10.868)	7.648 (0.134 - 35.799)	46.529 (8.541 - 126.406)	54.778 (9.275 - 164.825)
OSV (PCSHS)	0.0559 (0.0494 - 0.0891)	0.0535 (0.0449 - 0.0888)	0.0585 (0.0445 - 0.0878)	0.0558 (0.0446 - 0.0897)
LI (SAL)	0.4162 (0.3894 - 0.9351)	0.3490 (0.3075 - 0.6233)	0.2453 (0.2067 - 0.8257)	0.2511 (0.1920 - 0.7206)

Analysis Methods

Growth differences between trees in the same stand are the result of variation in environmental conditions (Harper 1977) as well as differences in their personal history (Horn 1971) and genetic backgrounds (Tilman 1988). These differences result from local environmental conditions favoring certain genetic types due to variations in soil composition, light availability and temperature regimes as well as chance historic events, such as falling branches, that impede growth.

In regression analysis it is assumed that the model form is correctly specified and the expected value of the error term is zero (Kmenta 1971). If this is not the case, then the residual error is likely to be overstated and significant relationships may not be identified (Kmenta 1971). It is likely that the way in which each of the indices quantify competitive pressure is different (Ledermann and Stage 2001). If this is the case, then no single model form for the relationship of growth rate to competition index will be optimal for all indices. Since an explicit theory of competition providing guidance in model form selection is yet to be specified (Ford 1999), the model form developed by the index originator was used in creating the specific model forms for this study. Many of the original model forms predicted either change in D or change in basal area and used D as the measure of size. In general our modifications substituted ΔH for the dependent variable and used H as the measure of size.

Height growth has been characterized as a nonlinear function of H, productivity and competition (e.g. Wensel et al. 1987, Hann and Scrivani 1987). For a single plot this relationship reduces to a nonlinear function of H and competition. As our basic model we chose to characterize this relationship for the ith tree as a power function of H:

$$\Delta H_i = b_0 H_i^{b_1}$$

where b_0 and b_1 are parameters to be estimated from the data. To maintain a constant relationship between H and ΔH across growth periods, b_1 was fixed to values from 0.1 to 1.0, in unit's of 0.1, and the equation was fit to data from each of the four growth periods. The fixed value of k_1 which yielded the lowest average MSE across the four growth periods was selected and replaced b_1 in the model form:

$$\Delta H_i = b_0 H_i^{k_1} \qquad [1]$$

The SD measure of Biging and Dobbertin (1992) used an exponential function of CVHCBU-H1 to reduce potential height growth. Substituting equation [1] for potential ΔH in their equations yields the following nonlinear relationship:

$$\Delta H = b_0 H^{k_1} e^{b_1 (CVHCBU\text{–}H1)^{k_2}} \qquad [2]$$

As with k_1, k_2 was fixed to values from 1 to 4, in whole units, and the equation was fit to data from each of the growth periods. The fixed value of k_2 which yielded the lowest average MSE across the four growth periods was selected as the best.

The CIZ measure of Bella (1971) used a quadratic function of D and a third order polynomial model of CIO to characterize ΔD in their multiple linear regression. Substituting equation [1] for the quadratic function of D into this model form yields the following relationship for ΔH:

$$\Delta H = b_0 + b_1 H^{k_1} + b_2 CIO + b_3 CIO^2 + b_4 CIO^3 \qquad [3]$$

The GS measure of Pelz (1977) was applied by Moore et al. (1973) to predict 10-year basal area growth. They used D, H, age and crown surface area as their measures of size and a quadratic polynomial model form of height-weighted APA as independent variables in their multiple linear regression. Substituting equation [1] for the measures of size into their model form yields the following relationship for ΔH:

$$\Delta H = b_0 + b_1 H^{k_1} + b_2 APA + b_3 APA^2 \qquad [4]$$

The relationship between the gap light index (Canham 1988) derived from hemispherical photographs and ΔH has been examined by Coates and Burton (1999) and Drever and Lertzman (2001) using a nonlinear hyperbolic model form:

$$\Delta H = \frac{a_0 X}{a_1 + X}$$

where X equals gap light index. The hyperbola can also be expressed in the following manner:

$$Y = \frac{a_0}{1+a_1X^{-1}}$$

Substituting $PCSHS^{k_2}$ for X and multiplying by equation [1] yields:

$$\Delta H = \frac{b_0H^{k_1}}{1+b_1PCSHS^{k_2}} \qquad [5]$$

where $k_2 = 1, 2, 3$ or 4, selected in the manner described previously. Since both X^{-1} and e^{-X} exhibit "reverse-J" curve shapes, the nonlinear logistic function was examined as an alternative model form:

$$Y = \frac{a_0}{1+\exp(-a_1X)}$$

Again multiplying the logistic function by equation [1] and substituting $PCSHS^{k_2}$ for X yields:

$$\Delta H = \frac{c_0H^{k_1}}{1+\exp(c_1PCSHS^{k_2})} \qquad [6]$$

where $k_2 = 1, 2, 3$ or 4, selected in the manner described previously.

The relationship between a simulated LI index, weighted leaf area, and ΔH was examined by Brunner and Nigh (2000) who also used a nonlinear hyperbolic model form to explain ΔH. Substituting SAL^{k_2} into equation [5] yields the following model form:

$$\Delta H = \frac{b_0H^{k_1}}{1+b_1SAL^{k_2}} \qquad [7]$$

where k_2 = 1, 2, 3 or 4 selected in the manner described previously. The logistic function can also be used in the same manner as was done for PCSHS to yield the following logistic function of SAL^{k}_{2}:

$$\Delta H = \frac{b_0 H^{k_1}}{1+\exp(b_1 SAL^{k_2})} \qquad [8]$$

where k_2 = 1, 2, 3 or 4 selected in the manner described previously.

The b parameters in the equations were estimated from fits to data from each of the four growth periods using procedure "REG" for linear models or procedure "NLIN" for nonlinear models (SAS Institute 1999). An R-student test for outliers was applied to the data (Myers 1990) and residuals were examined for homogeneity of variance by plotting them against predicted values and by application of Levene's (1960) test. The comparison between model forms was based upon the amount of variation in ΔH explained by them and their associated indices of competition for each of the four growth periods. In the same manner as Bravo et al. (2001), comparisons were based upon the percentage reduction in mean square error (MSE) over a basic model form that is a function of size alone.

The equation judged to be best was then fit to the combined data using appropriate growth period indicator variables on the b parameters. The indicator variables whose parameters were not significantly different from zero ($\alpha = 0.05$) were eliminated from the equation.

Results

Most past comparative studies have used even-aged stands for evaluating the performance of the various indices. This study used a two-storied stand, with a height difference of over 116 feet between the stories (Tables 1 and 2). The two-storied structure, coupled with the regular lattice under-planting, placed trees in areas of the stand they would be unlikely to occupy naturally. This increased the range of the light environments that western hemlock trees experienced on the plot and it probably contributed to the large amount of early mortality (Table 3). The large range was further enhanced by the loss of an overstory tree between the first and second growth periods and another between the second and third growth periods. Furthermore, the vigorous growing overstory produced a changing light environment over time as crown closure increased (Table 1). Under these conditions the overstory will make a major contribution to shading of understory trees. As a result, we believe this plot represents an extreme challenge for characterizing light competition.

These observations of the dynamic light environment existing in this stand are mimicked by the predicted values of SAL and, to a lesser extent, PCSHS. For a given growth period, both PCSHS and SAL predict large ranges in their values (Table 4). However, SAL shows a decline across the observation period as expected and PCSHS remains mostly unchanged (Table 4).

A fit of equation [1] to the data from the four growth periods yielded a k_1 value of 0.6. This was then used for all other equations. It was found that a k_2 value of one was best for equations [2] and [5] and a k_2 value of two was best for equations [6], [7] and [8]. The

R-student test found no outliers in the data, and the examination of the residuals indicated that their variance was homogeneous for all of the equations.

Table 5 displays the MSE of fits of equation [1] to data from each growth period, and the relative MSE, expressed as a percentage of equation [1], for fits of the remaining equations containing the competition indices. The largest percentage improvement in relative MSE over the fit of equation [1] is shown in bold type. SAL values from SEALS produced the greatest average reduction in relative MSE (48.5%) for the indices tested and provided a consistently superior prediction of ΔH than any other index in each period. The worst performance for SAL occurred in the first growth period which started three years after planting and one year after replanting. The size and distribution of post logging residue is unknown therefore its shade was not included in calculations of SAL for the first growth period.

PCSHS was consistently the second best index. The reduction in residual error due to PCSHS is consistent with the reductions due to SAL. The performance of the indirect indices is not consistent. Each indirect index reduced MSE more than the others during one of the periods. The SD index reduced relative MSE less (24.7%) than was observed by Biging and Dobbertin (1992) for white fir (35.3%) but more than they observed for Douglas-fir (14.1%). The average percent reduction in relative MSE due to the CIZ index (24.7%) was less than that reported by Alemdag (1978) for white spruce (33.1%). The average reduction in relative MSE for the GS index (24.2%) was much larger than the average reported for three hardwood species (6.2%) by Moore et al. (1973).

Table 5. The MSE of equation [1] and relative MSE for equations including the competition index expressed as a percentage of equation [1], by growth period. Bolded values represent the largest reduction in relative MSE over equation [1] in each period.

Class (index)	Equation	Period 1	Period 2	Period 3	Period 4
	[1]	2.8760	1.3194	2.8164	2.2834
SD (CVHCBU-H1)	[2]	99.95	45.60	89.39	68.21
CIZ (CIO)	[3]	96.75	42.46	91.66	70.43
GS (APA)	[4]	97.34	42.12	92.46	71.45
OSV (PCSHS)	[5]	83.17	41.60	67.65	49.43
LI (SAL)	[8]	**76.63**	**40.71**	**59.50**	**30.22**

With the exception of the second growth period, equation [1] yielded approximately the same MSE across the observation period (Table 5). The second growth period's smaller MSE is explained by the strong correlation between the first and second periods' ΔHs (r = 0.7938) and the fact that the size of H at the start of the second growth period is dominated by the ΔH of the first growth period.

SD and CIZ indices produced very similar average results, with the CIZ index performing slightly better in the first two periods and the SD index performing slightly better in the last two periods. To explore performance differences among the indirect indices, the number of overstory and understory competitors as well as their contribution to index values were computed (Table 6). The values of the SD and CIZ indices were dominated by overstory competition in the early growth periods, with the average number of overstory trees contributing to the indices increasing over time. For the SD index this was due to increases in the distance from the crown base of the understory trees to the tops of the overstory trees (Table 1 and 2) and for the CIZ index this was due to increases in MCW. However, the number of overstory competitors declined from all to about half the total number of competitors for both indices, though the contribution of overstory competitors to them remained dominated by the overstory for the entire observation period (i.e. the understory contributed little to the values of the indices). The average SD index value included many more of the overstory trees than did the average CIZ index value. However, the results of this study indicate that the contribution of distant overstory competitors may be very small for the SD index. This was verified by the discovery that the strength of the relationship between the SD index to ΔH was insensitive to changes in the critical height angle used to select competitors. The average CIZ index included only the trees near to each subject tree.

The value of the GS index was based almost entirely on understory trees for all periods and the contribution of the overstory to the average GS value was negligible (Table 6). The average number of competitors changed little during the observation period. This is because, in the GS index, only the immediately adjacent trees are defined as competitors and they are used as competitors until they die. Even though the GS index is composed mostly of understory trees and the CIZ index mostly of overstory trees, both performed in a very similar manner, with their respective reductions in relative MSE differing by less than 2% in any period. This similarity in performance reflects a similarity in defining the region of competition. In a regular lattice, the amount of overlap in neighboring circles is closely aligned with the amount of space between immediate neighbors. The difference in the two measures increased as the occupied positions in the understory lattice declined and the spatial distribution of the seedlings departed from a regular spacing.

Table 6. Description of competitors for the indirect indices of the light environment.

Class (index)	Growth period	Average number of overstory competitors	Average number of understory competitors	Percent of overstory competitors	Percent contribution of overstory to index value
SD (CVHCBU-H1)	1	26.8	0.0	100.00	100.00
	2	29.4	0.0	93.30	99.99
	3	36.7	33.0	52.50	98.84
	4	38.3	34.8	52.30	98.58
CIZ (CIO)	1	1.2	0.0	100.00	100.00
	2	1.7	0.6	81.40	80.21
	3	2.9	3.5	46.70	92.10
	4	3.1	3.1	51.60	92.42
GS (APA)	1	0.023	4.0	9.46	2.84
	2	0.004	4.1	9.40	2.98
	3	0.009	4.4	13.78	1.77
	4	0.014	4.7	16.61	1.84

Equation [8] was expanded to include indicators for the growth periods and fit to the combined data set:

$$\Delta H = \frac{\left(c_0+I_{gp2}c_{0gp2}+I_{gp3}c_{0gp3}+I_{gp4}c_{0gp4}\right)H^{0.6}}{1+\exp\left[\left(c_1+I_{gp2}c_{1gp2}+I_{gp3}c_{1gp3}+I_{gp4}c_{1gp4}\right)SAL^2\right]} \qquad [9]$$

where: I_{GP2} is the indicator of period two, I_{GP3} is the indicator of period three and I_{GP4} is the indicator of period four. Results from fitting this equation to the combined data set indicated that there were significant differences in the c_0 parameters by period, but not in the c_1 parameters.

The average H and ΔH differed not only by growth period but also by seedling source within growth period (Table 3), and the proportion of surviving understory trees in each seedling source changed during the observation period (Table 7). The impact of the H differences upon ΔH attributed to seedling source should be accounted for in equation [9]. However, each seedling source may also react differently to a particular light environment due to genetic differences in foliage efficiency or in crown structure (St. Clair 1994). To examine this further, equation [10] was formed to include not only growth period indicators, but also indicators for seedling source:

$$\Delta H = \frac{\left(c_0+I_{gp2}c_{0gp2}+I_{gp3}c_{0gp3}+I_{gp4}c_{0gp4}+I_{ss2}c_{0ss2}+I_{ss3}c_{0ss3}+I_{ss4}c_{0ss4}+I_{ss5}c_{0ss5}\right)H^{0.6}}{1+\exp(c_1 SAL^2)} \quad [10]$$

where: I_{ss1} is an indicator that the seedling was from Lewis County WA,

I_{ss2} is an indicator that the seedling was from the low elevation site in Gray's Harbor County WA,

I_{ss3} is an indicator that the seedling was from the high elevation site in Gray's Harbor County WA,

I_{ss4} is an indicator that the seedling was from the Oregon site.

Equation [10] was fit to the combined data from all periods and the regression parameters for all of the indicators were tested for significance from zero ($\alpha = 0.05$). It was found that the ΔH response of the seedlings fell into two groups that were significantly different from one another: (1) both Oregon groups and the high elevation sites in Gray's Harbor County and (2) the Lewis County and the low elevation sites in Gray's Harbor County. After accounting for the groupings of seedling sources, the period differences were no longer significant indicating that the model form and its parameters were applicable across all growth periods for a given seedling source:

$$\Delta H = \frac{[c_0 + c_{0ss}(I_{ss1} + I_{ss2})]H^{0.6}}{1 + \exp(c_1 SAL^2)} \qquad [11]$$

Equation [11] fit to the combined data set had an adjusted coefficient of variation (R_a^2) of 0.7262, while the same equation without H (i.e., the power on H was set to 0.0) produced an R_a^2 of 0.4873.

Table 7. Proportion of the living understory trees by seed source for each growth period.

Seedling source	1961	1967	1986	1992
Lewis County WA	0.2589	0.2705	0.3108	0.3225
Gray's Harbor County WA < 500 ft.	0.2268	0.2332	0.2595	0.2606
Gray's Harbor County WA >500 ft.	0.2321	0.2407	0.2622	0.2769
Oregon	0.1036	0.1082	0.0838	0.0814
Oregon roadside	0.1786	0.1736	0.0838	0.0586

The values of R_a^2 for the fits to the combined data using SAL and H are better than those found in past empirical studies of height growth for loblolly pine (Table 8)

Table 8. R_a^2 from previous studies that developed spatially explicit empirical models of ΔH.

Source	Species	R_a^2
Daniels and Burkhart (1975)	Loblolly pine	0.34
Burkhart et al. (1987)	Loblolly pine	0.46
MacFarlane et al. (2002)	Loblolly pine	0.15

Discussion

As in the previous comparative studies of Alemdag (1978), Noone and Bell (1980), Lorimer (1983), Martin and Ek (1984), Daniels et al. (1986), Tome and Burkhart (1989), MacDonald et al. (1990), Holmes and Reed (1991), Biging and Dobbertin (1992), and Wimberly and Bare (1996), this study failed to identify a clearly superior class of indirect spatially explicit indices. This indicates to us that the indirect spatially explicit indices are not providing a consistent and accurate characterization of the light environment. Perhaps the fact that all three indirect indices include both competitors that do not cast shade on the subject tree, as well as those that do, limits their utility in describing the light environment.

This apparent inability to describe the light environment may help to explain why these indirect spatially explicit indices have not performed as well as indirect spatially implicit measures of competition (Alamdag 1978, Martin and Ek 1984, Lorimer 1985, Daniels et al 1986, Biging and Dobbertin 1995, Wimberly and Bare 1996). Our results, however, indicate that a direct spatially explicit index, SAL, can perform as well as spatially implicit indices of competition currently used in empirical models. Since SAL is a measure of the current outcome of competition for light, its ability to well characterize ΔH gives hope that the difference between the predictive ability of empirical models and the poorer predictive ability of process models (e.g. Mohren and Burkhart 1994, Korzukhin et al. 1996, Mäkelä et al. 2000, Yaussy 2000) may soon cease to exist.

SAL consistently explained more variation than did the OSV index. Like all OSV indices, PCSHS explicitly characterizes direct beam radiation and estimates diffuse radiation.

While some LI indices indirectly estimate diffuse radiation (Brunner 1998), the LI index used in this study (SAL) explicitly quantifies both direct and diffuse radiation. OSV indices constructed from actual hemispherical photographs have been successful at explaining a significant fraction of ΔH (e.g. Coates and Burton 1999, Drever and Lertzman 2001). It has been noted that penumbra is important to the amount of light received by an understory tree (Oker-Blom 1985). At a fixed level of contrast in actual hemispherical photographs, solar penumbra reduces the impact of distant vegetation on the OSV index, thus increasing the amount of open sky recorded in a hemispherical photograph (Chan et al. 1986). The effects of penumbra were not included in the computer simulated scenes used to calculate PCSHS, but was included in the calculation of SAL.

An unresolved issue with the utility of OSV indices is their applicability to a broad range of stand structures. Current applications using actual hemispherical photographs have been limited to understory trees (e.g. Coates and Burton 1999, Drever and Lertzman 2001). Since they were designed to characterize over-topping vegetation, they may not adequately characterize the light environment of overstory trees. Since PCSHS simulates hemispherical photographs it may also exhibit this weakness.

Because of the uniformly spaced overstory and the regular lattice under-planting, this evaluation of the indirect and direct indices represents a challenging test for characterizing the light environment. While the direct indices have performed well in this evaluation, their usefulness needs to be tested in other light environments, such as exist in the overstory, and on species other than the very tolerant western hemlock examined in this study.

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CHAPTER 5

MODELING THE LIGHT ENVIRONMENT AND ITS INFLUENCE ON THE HEIGHT GROWTH OF DOUGLAS-FIR GROWING ON MANAGED PLOTS.

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February 17, 2003

For submission to : Forest Science
Society of American Foresters, Bathesda, MD

Abstract

Data from plots on the George T. Gerlinger Experimental Forest in the western Willamette valley of Oregon were used to model the relationship of height growth in Douglas-fir to two direct and three indirect spatially explicit indices of light. The two direct spatially explicit measures of the light environment were based upon a simulated hemispherical scene and upon a solution of the radiation transport equations. The three indirect spatially explicit measures of the light environment were based upon size distance relations, the overlap of crown areas or the area potentially available.

A spatially explicit available light simulator (SEALS) was used to directly model the light environment under spatially complex canopies of Douglas-fir. Two direct methods of quantifying the light environment were generated by SEALS: the fraction of open sky above an understory tree derived from a pixel counted simulated hemispherical scene (PCSHS) and the amount of simulated available light (SAL) incident on an understory tree. These values were applied to images of the stand generated with VIZ4ST, a visualization program for creating detailed three dimensional simulations of the structure of forest canopies.

Index comparison was based upon the reduction in mean square error over that achieved using a measure of individual tree height alone. SAL consistently explained more variation in height growth than did any other index examined. As in previous studies, there was no clearly superior performance among the indirect indices. Unlike in previous studies, the model form used for comparison was allowed to vary with the index under test.

Nonlinear models of Douglas-fir height growth including SAL reduced unexplained variation by an average of 46.6% in the overstory and 17.6% in the understory over a model including height alone. On average, SAL reduced the unexplained variation by 34.8%. PCSHS reduced unexplained variation in Douglas-fir height growth by an average of 20.8% in the overstory and 13.7% in the understory over a model including height alone. On average PCSHS reduced the unexplained variation in height growth by 27.6%.

Introduction

Competition is the mechanism by which plants influence the growth of their neighbors (Tilman 1988). Light competition provides the prevailing limitation to growth in plant communities that form continuous canopies (Ford and Sorrensen 1992). Spatially explicit indices that were developed to quantify the general competitive environment among trees growing in forest stands have been applied to environments limited by light. These indices use an indirect approach to quantifying the light environment usually employing a measure of crowding. They have been divided into three classes by Holmes and Reed (1991): (1) size-distance (SD) relationships, (2) competitive influence zones (CIZ), and (3) growing space (GS) measures.

SD indices use a function of subject and competitor size and a function of the distance between the subject tree and its competitors to quantify competition. The size function is usually a ratio of competitor to subject size while the inverse of distance between the trees is used as the function of distance. CIZ indices use the overlap of the areas occupied by a free to grow tree of the same size as the subject tree. These influence zones are typically set to the size of the predicted maximum crown extent of the tree. GS indices use the area potentially available to the subject tree as a measure of competitive environment. The area potentially available to each tree is computed from a Voronoi tessellation of the forest stand. The Voronoi polygons are usually calculated using a weighting scheme with bisectors weighted by the ratio of the competitor to subject tree size.

Direct characterization of the light environment has been attempted with two techniques. This is because accurate characterization of available light under a nonrandom, heterogeneous canopy requires a method that accounts for the three dimensional distribution of foliage in the stand. These examples most commonly use actual measurements of available light. Measurements of available light under forest canopies have used four techniques (Jones 1992): (1) photochemical responses, (2) thermal response, (3) optical examination and (4) photoelectric response. Two of these measurement techniques have lent themselves to explaining past understory vegetation growth: optical examination of the overstory density through the use of densiometers (e.g. Vales and Bunnell 1988) or hemispherical photographs (e.g. MacDonald et al. 1990, Mailly and Kimmins 1997, Drever and Lertzman 2001) and photoelectric response through the use of electronic light meters (e.g. Comeau et al. 1993, Mailly and Kimmins 1997 and Duchesneau et al. 2001). These techniques may be replicated through the use of the reconstructed spatial distribution of the canopy. From this reconstruction values similar to those that would have been measured during past growth periods may be estimated (e.g., Silbernagel and Moeur 2001).

The ability of members of the indirect classes of spatially explicit indices to explain variation in individual tree growth has been explored in many studies (e.g. Alamdag 1978, Daniels et al. 1986, Tomé and Burkhart 1989, Holmes and Reed 1991, Biging and Dobbertin 1992, Wimberly and Bare 1996, Hanus 2003b). No single class of indirect spatially explicit index has been identified as superior to the others in explaining the variation in the growth of individual trees.

Hanus (2003b) compared three indirect indices of light competition to two direct indices of light competition in understory western hemlock (*Tsuga heterophylla* (Raf.) Sarg.). It was found that the direct indices of competition explained more of the variation in height growth (ΔH) than did any of the indirect methods. This study extends the comparison of Hanus

(2003b) to Douglas-fir growing in both the overstory and the understory of predominantly managed plots.

Data

The data for this study came from plots established on the George T. Gerlinger State Research Forest in the late 1950's. The overstory was nearly pure Douglas-fir that naturally regenerated from seed following logging of the pre-contact forest in the first decades of the 20th century. In a constant levels of growing stock study four replications of four 0.4047 ha (1 acre) plots were established using a complete block sampling design. Each of the 0.4047 ha plots was constructed from four square 0.1012 ha subplots. The subplots were contiguous although not all of the replicates were arranged in a square pattern. All of the plots, including the "controls", were subjected to a conditioning thinning that reduced the trees to an approximately even spatial distribution of well formed trees. In addition another square 0.4047 ha plot (31) was thinned to 51 well spaced Douglas-fir trees and under-planted with a dense (1.83 by 1.83 m) understory of western hemlock. At plot establishment each tree was tagged with a unique number and its species and diameter at breast height (D) was recorded. In addition each tree's location was measured to the nearest 1 foot (0.3048 m.) from the southwest corner of the subplot on which it was growing.

Each of the blocks in the constant levels of growing stock study contained a control plot and three treatment plots. The treatment plots were maintained at fixed levels of basal area in crop trees with D greater than 19.3 cm. The lightest thinning (plots 29, 34 and 40) maintained the basal area between 36.7 and 43.6 m^2/ha. The moderate thinning (plots 24, 28, 35 and 38) maintained basal area between 29.8 and 36.7 m^2/ha while the heaviest thinning (plots 22, 30 and 36) basal area was held between 23.0 and 29.8 m^2/ha. The better formed more vigorous trees were retained in each thinning. Each plot was thinned to its assigned levels in 1960, 1965 and 1972. A surrounding buffer strip was thinned to the same levels as the plot. Since the buffer trees were not mapped they could not be used to calculate spatially explicit indices. However, they did serve to ensure that conditions at the edge of the plot were similar to those near the center. To reduce the impact of the effects of off plot trees on the values of the spatially explicit indices only square plots were used for this study

A systematic series of 2 m. radius fixed area subplots were located on some of the treatment plots in 1995 (Beer 1999). On each of these subplots the species, total height (H) and the distance between branch internodes for the past 5 years, of the largest and a randomly selected seedling was recorded. The amount of herbaceous vegetation within the subplot was estimated by quadrant. Plots dominated by herbaceous vegetation were dropped from this analysis. It was also noted if the subplot was dominated by an understory hardwood. Since no details of the structure or size of the hardwoods dominating the subplot were recorded, trees from subplots so designated were dropped from this analysis.

For this study, plot elevation and topography was estimated from topographic maps and transferred to the tree locations via interpolation from an irregular triangular network. Trees were remeasured at intervals from 1 to 6 years over the next 35 years. Tree survival, crown class, observable physical damage and D were recorded on all trees over 1.37 m. (breast height) in height. A subsample of trees were measured for H and height to crown base (HCB).

Measurements in 1991 or 1992 and in 1995 were used to construct a 5-year ΔH estimate for the same 1991 to 1995 growth interval used by Beer (1999). There were 13 years between the final treatment and the start of the growth interval.

All trees were measured for D while a subset were measured for H and HCB to the nearest foot (0.3048 m.) using the pole-tangent method (Larsen et al. 1987). H was estimated for the unmeasured overstory trees using empirical relationships developed for the northwest Oregon version of the ORGANON growth and yield simulator (Wang and Hann 1988). The values for H predicted by ORGANON were calibrated to the measured heights.

HCB was measured on a subset of the overstory trees that were measured for H, missing values for HCB were estimated from empirical relationships developed for the northwest Oregon version of ORGANON (Zumrawi and Hann 1989). HCB values were also calibrated in the same manner as were the H values. ΔH was calculated by subtracting the starting H from the ending H for those trees with actual measurements of H and HCB near 1991 and 1995.

Table 1 shows the age, 50 year base age site index (SI), basal area (BA), number of trees per hectare (TPH), crown closure (CC), proportion of the basal area in Douglas-fir of the overstory trees, and the maximum slope in degrees, mean tree elevation for the plots used in this study. It can be seen that there is a narrow range of overstory age of only 13 years and an 11.4 m range in Bruce's (1981) site index. Maximum slope was determined by the extremes of tree elevation. CC was determined by projecting the estimated crown extents onto the plot area and calculating the fraction of the plot covered by crown which ranged from 81% to 94%. The overstory basal area ranged from 34.5 to 59.4 m^2/ha and the number of overstory trees per hectare ranged from 123.5 to 444.8 trees.

Table 1. Summary of overstory conditions and plot conditions at the start of the five year growth period.

Plot	Age	SI	BA	TPH	CC	Proportion of Douglas-fir	Slope	Elevation
22	70	33.4	39.1	257.0	84	0.99	12.5	359.8
24	70	39.7	43.0	242.2	82	0.97	13.6	328.0
27	74	29.3	58.9	444.8	84	0.99	12.0	331.5
28	74	35.2	37.6	274.3	84	0.99	34.2	315.7
29	75	36.1	55.5	286.6	90	0.99	5.5	321.2
30	74	32.1	34.5	237.2	81	0.99	10.5	334.5
31	75	34.1	50.9	123.5	82	1.00	1.0	323.1
34	65	28.5	57.8	276.7	94	1.00	19.1	464.0
35	63	39.9	59.4	227.3	94	0.97	15.1	474.5
36	65	31.5	43.9	229.8	83	0.98	9.5	501.6
38	65	33.8	50.4	385.5	92	0.99	11.4	496.7
40	62	35.8	52.3	395.4	87	1.00	35.0	505.2

Table 2 shows the mean and range for D, H, HCB, ΔH and the number of sampled trees (N) for the overstory trees and Table 3 shows the same values for the sampled understory trees for plots with such trees. It can be seen that the plots with the lowest basal area did not necessarily have the largest average understory ΔH. Plot 30 had the lowest basal area however plot 36 had the largest ΔH. The relationship between the number of overstory trees and the average understory ΔH is much stronger. The plots with the most overstory trees had the lowest understory ΔH while the plots with the least trees had the largest understory ΔH.

Table 2. Summary of overstory trees by plot, mean and range in parentheses.

Plot	D (cm)	H (m)	HCB (m)	ΔH (m)	N
22	52.5 (20.8 - 77.5)	38.8 (21.0 - 49.1)	25.6 (15.2 - 37.1)	1.5 (0.3 - 2.1)	18
24	47.8 (20.6 - 78.5)	40.7 (29.5 - 50.6)	25.7 (22.3 - 29.3)	1.1 (0.3 - 1.9)	17
27	43.9 (29.2 - 59.4)	39.7 (35.1 - 46.0)	31.2 (28.0 - 36.9)	0.5 (0.3 - 0.9)	8
28	45.5 (19.8 - 71.4)	37.3 (25.1 - 50.8)	27.1 (21.1 - 32.7)	0.8 (0.1 - 1.9)	11
29	48.4 (16.0 - 78.5)	40.8 (19.1 - 51.5)	29.6 (15.4 - 34.9)	0.6 (0.1 - 1.3)	17
30	48.0 (19.6 - 78.7)	35.5 (20.8 - 45.9)	22.0 (15.2 - 27.2)	0.9 (0.3 - 1.6)	17
31	73.0 (47.0 - 109.2)	49.4 (40.8 - 53.1)	26.9 (20.7 - 37.1)	0.9 (0.5 - 1.4)	38
34	56.0 (43.2 - 79.2)	42.2 (37.5 - 48.1)	29.8 (21.5 - 33.6)	0.8 (0.4 - 1.3)	15
35	56.2 (37.8 - 81.0)	42.9 (36.5 - 49.0)	28.7 (27.0 - 30.0)	1.0 (0.5 - 1.4)	15
36	51.5 (33.0 - 72.4)	36.6 (30.7 - 41.5)	22.7 (19.8 - 28.0)	1.7 (1.1 - 2.3)	16
38	41.7 (20.6 - 69.1)	32.7 (21.6 - 39.9)	20.6 (18.0 - 22.6)	0.9 (0.2 - 2.3)	15
40	46.3 (27.7 - 69.1)	35.6 (28.7 - 43.6)	23.7 (18.3 - 28.3)	1.2 (0.3 - 2.2)	15

In can also be seen that plot 35 is counter to the trend in understory ΔH relative to its crown closure and basal area. Plot 35 has a high average understory ΔH despite a large basal area and crown closure. It also has the greatest number of understory seedlings with the largest average H.

Table 3. The number of observations, the mean and range (in parentheses) of H and ΔH for the understory Douglas-fir trees by plot.

Plot	N	H (m)	ΔH (m)
22	15	0.9 (0.3 - 1.6)	0.5 (0.2 - 0.7)
24	7	0.9 (0.2 - 1.6)	0.5 (0.4 - 0.8)
28	8	0.3 (0.1 - 1.6)	0.4 (0.0 - 0.8)
30	32	1.8 (0.1 - 3.8)	0.9 (0.0 - 2.5)
34	34	0.8 (0.2 - 1.7)	0.4 (0.0 - 0.8)
35	39	2.3 (0.2 - 3.9)	0.9 (0.0 - 1.6)
36	40	2.3 (0.2- 4.5)	1.2 (0.0 - 2.6)
38	21	0.5 (0.2 - 0.9)	0.3 (0.1 - 0.5)
40	4	0.3 (0.1 - 0.4)	0.2 (0.1 - 0.2)

Indirect indices of the light environment

The overstory trees on the plots used in this study arose at nearly the same time and exhibit continuous canopies, thus it is expected that light competition is the dominant inter-tree spatial interaction. Based upon this assumption a set of spatially explicit measures suitable for characterizing light competition, one from each of the indirect classes (SD, CIZ and GS) were selected for evaluation and comparison to the direct indices. Because not all of the understory trees had attained breast height, only indirect indices using a function of H were selected. A more detailed description of the rationale used in selection can be found in Hanus (2003b).

Size-Distance

While the majority of SD indices use a ratio of breast height diameter to quantify relative tree size not all of the understory trees had attained breast height. The index from Biging and Dobbertin (1992) that used the fraction of the competitor's crown volume within a critical height angle of 50° with apex at crown base (CVHCBU-H1) was chosen as the best SD measure of light competition:

$$CVHCBU-H1_j = \Sigma_{i=0}^{n} \varepsilon_{ij}\left(\frac{CVa_i}{CV_j}\right)$$

where:

CVa_i = the crown volume of the i^{th} competitor of the j^{th} subject tree above the critical height angle (50°) from the height of the base of the live crown,

CV_j = the crown volume of the j^{th} subject tree

ε_{ij} = the linear expansion factor of the i^{th} competitor of the j^{th} subject tree used to correct for finite plot size (Martin et al. 1977).

CVHCBU-H1 takes on a value of zero with no competition and gets increasingly larger with increasing competition.

Competitive Influence Zones

The index of Bella (1971) using a ratio of tree height was selected as the CIZ measure:

$$CIO_j = \Sigma_{i=1}^{n}\left[\frac{IZO_{ij}}{IZA_j} \times \left(\frac{H_i}{H_j}\right)\right]$$

where:

H_i = the height of the i^th^ competitor,

H_j = the height of the j^th^ subject tree,

IZO_{ij} = the area of overlap between the influence zones of the i^th^ competitor and the j^th^ subject tree,

IZA_j = the area of the influence zone of the j^th^ subject tree.

This index was corrected for edge effects by dropping trees with influence zones extending beyond the plot boundaries. The area of the zone of influence was defined to be the predicted maximum crown width (MCW) of a tree of the same size and species as the subject tree as predicted by the equations of Hann (1997). CIO takes on a value of zero with no competition and gets increasingly larger with increasing competition.

Growing Space

The GS index selected for this study was calculated as the area of the polygons produced from a weighted area potentially available (APA) tessellation (Pelz 1977). The bisectors of the line segments joining the subject tree with each of its nearest neighbors was weighted by a ratio of tree height as described by Pelz (1977). The computer program of Fortune (1987) was used to locate the vertices of the APA polygons. Edge correction was accomplished by eliminating all trees with APA polygons in contact with the plot edge (Okabe et al. 2000). Small values of APA indicate high levels of competition while large values indicate low levels of competition. The values of APA are always greater than zero.

Direct indices of the light environment

Direct computer simulation of the distribution of light intensity beneath a canopy requires an accurate description of canopy structure. A computer program that estimates canopy structure from tree measurements and empirical relationships of tree foliage is available in SEALS (Hanus 2003a). SEALS uses published empirical relationships to reconstruct the three dimensional distribution of crown vegetation from stand survey measurements of Pacific northwest tree species. There were five species on the plots used for this study; Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), western hemlock (*Tsuga heterophylla* (Raf.) Sarg.), grand fir (Abies grandis (Dougl. Ex D. Don) Lindl.), bigleaf maple (*Acer macrophyllum* Pursh) and red alder (*Alnus rubra* Bong.). SEALS replicates an approximation of the canopy structure from available measurements collected in past stand examinations for these species.

The physical locations of the trees and their D, H and HCB were passed to SEALS which rendered a three dimensional image of canopy foliage distribution at the start of the five-year growth period. The horizontal displacement from one of the corners of the plot was recorded at establishment for each overstory tree. Ground topography was approximated from observations collected with the understory measurements coupled with topographic maps. Elevation values for each plot were represented as an irregular triangular network from which individual tree elevation was estimated using interpolation based on non-uniform rational B-splines (Woo et al. 1997).

Two direct methods of characterizing the light environment were simulated from the three dimensional image rendered by SEALS: an open sky view index and a light interception index.

Open Sky View

The OSV index used in this study was pixel-counted, simulated hemispherical scene (PCSHS), the fraction of open sky pixels in a simulated hemispherical scene weighted by their location with respect to the seasonal solar track. Tree measurements were passed into a special OpenGL (Woo et al. 1997) version of VIZ4ST (Hanus and Hann 1997) and a simulated hemispherical scene was generated as viewed from the location of the tip of each tree. The simulated hemispherical scenes were analyzed in the manner of a hemispherical photograph using methods described by Campbell and Norman (1989).

Inter-tree gaps in the canopy contribute significantly to the ability of plants to grow beneath otherwise full canopies (e.g. Hutchinson and Matt 1976, Canham et al. 1990). Holbo et al. (1985) found that sunflecks also contribute significant amounts to canopy light and average sunfleck percentages could be estimated from hemispherical photographs without considering the solar declination at the time the photograph was taken. This allowed predictions of seasonal light intensity to be made from a single hemispherical photograph, an assumption which carries over to PCSHS. A single simulated view was used to characterize the light environment for the growing period.

Silbernagel and Moeur (2001) found that computer simulation can be used to replicate the images generated with hemispherical photographs. They concluded that canopy gap fraction was well replicated by a simulated canopy consisting of appropriately sized geometric solids. They identified the lack of finer resolution crown structure as contributing to an underestimation of within crown canopy openness. In their study this was somewhat mitigated by the overestimation of between tree gaps due to underestimation of crown width. The combination of these details brought their estimates of canopy openness very close to those reported for similar stands (Silbernagel and Moeur 2001).

In hemispherical photographs, diffuse radiation is characterized by weighting the exposed sky visible in areas not along the solar track less than those areas on the solar track (Canham et al. 1990). Radiation components potentially useful for photosynthesis are reflected onto plants from leaves and other overstory canopy elements (Hutchison and Matt 1976). This radiation component is not quantified by hemispherical photographs. PCSHS takes on a value of zero when there is extreme competition and a value of one in the absence of competition.

Light Interception

Two attributes of PAR have been identified as potentially important to tree growth: intensity and spectrum (Oliver and Larson 1990). This study will treat both the spectrum and intensity of PAR as light. No attempt will be made to discern which particular attributes of the ambient light environment are important to tree growth.

In addition to the intensity and spectrum of PAR, photosynthesis and thus plant growth is also limited by temperature. Photosynthesis does not occur below the freezing point of water and growth ceases due to cell death near 130° F. Between these extremes photosynthesis increases rapidly to a plateau and then declines again as temperature continues to increase (Oliver and Larson 1990). Within a stand, temperature is highly correlated with direct radiation (Myneni et al. 1986). We will therefore, make no attempt to discern between the effects of light and temperature.

The LI index calculated in SEALS is the simulated ambient light (SAL) incident on a tree for each of the growing seasons in the five-year growth period. It is calculated from an approximate solution of the radiation transport equations using the method of discrete ordinates (Chandrasekhar 1950). SAL is the average incident light per square foot of crown surface area.

Computer calculation of light interception has proven to be a daunting task because it requires the modeling of shadows from many arbitrarily sized small bodies arranged non-randomly in space. Techniques for shadow modeling developed in the field of computer graphics rely exclusively on the intersection of projected shapes with volume shapes (Woo et al. 1997). In computer generated scenes, the areas of intersection are colored in a complimentary or grayed tone. This is very fast but assumes constant shade intensity within the projected shape and thus is not suitable for directly modeling the light environment. The method of discrete ordinates (Chandrasekhar 1950) is a more refined method of directly estimating ambient light.

Given D, H and HCB at the start and end of the five-year growth period, annual values were computed using linear interpolation of the three attributes. A special OpenGL (Woo et al. 1997) version of VIZ4ST (Hanus and Hann 1997) was used by SEALS to create a three dimensional image of the stand at the start of each annual growth interval during the five-year growth period. This image was used to calculate SAL for each of the trees.

In the method of discrete ordinates, space is divided into volume cubes of arbitrary size on the sides of which the differential equations describing the light environment can be solved. Four light attributes must be quantified for each volume element: emission, absorption, reflection and transmission (Chandrasekhar 1950). A solution to the radiation transport equations consists of jointly solving these four differential equations for the six faces of each cubic volume element for every moment in time.

A full solution of the radiation transport equations requires a time continuous estimation of light flux at every point in the stand. This was beyond available computational processing power so the ambient light incident on each tree was calculated by approximating the solution to the radiation transport equations with a time discrete estimate. Since the apparent angle of the sun changes with the seasons, variation in solar exposure was simulated by altering solar incidence angles for weekly sun positions for each week during the growing season using the methods and computer functions of Meeus (1998). The equations were solved for three daily sun positions midmorning, noon and mid afternoon of Wednesday of each growing week. At each of these solar positions, the shade intensity was calculated for the crown surface of each tree. No adjustments to light intensity were made for changes in atmospheric conditions. The average light intensity per square foot of crown surface area was used as the LI index for each tree.

SEALS processing time was further reduced by building the scene in graphics memory and implementing a hierarchical data structure to hold the results of the radiation transport equations. An array of pointers to the nearest occupied voxel was used to hold the attribute values for the hierarchically subdivided stand space (Neyret 1998). The total volume occupied by the trees, 0.4047 ha (1 ac) in area and 58.5 m (192 ft) in height, was divided into cubes 2.4 m (8 ft) on a side, each of which was subdivided into eight cubes only if they contained vegetation. If the smaller cubes contained vegetation they were in turn subdivided by eight until each cube containing vegetation was 0.15 m (6 in) on a side. For the smallest cube the transport equations were applied to the vegetation elements within and its solution aggregated up the hierarchy until the entire stand was covered. Cubes free from vegetation passed the light stream without alteration while cubes inside of tree boles blocked all light transport.

Modeling of light in natural scenes is further complicated by penumbral effects due to the size of the sun's disk and the structural complexity of objects in the canopy. The clumped distribution of leaves and branches result in small passages through the canopy. The location of these passages varies with time and can be deterministically predicted only with an exhaustive survey of the canopy foliage (Tilman 1988). However, a model such as VIZ4ST (Hanus and Hann 1997) can predict the between tree spaces defined by the crown shape of the trees and it can estimate the spaces within the crown from the spatial arrangement of branches and leaves.

When viewed from the earth the sun subtends an angle of a little over 0.25° (15'59".63) which is large enough to generate regions of partial shade (Meeus 1998). If atmospheric effects are discounted, then the size, shape and distance from the observation point are the factors affecting the intensity of the incoming light stream. Since the sun is not a point light source, rays from one side of its disk partially illuminate areas shaded by rays from the other side of the disk. The effects of penumbra were introduced within each occupied cube and aggregated to the surrounding cubes by SEALS.

Index Values

The mean and range for the spatial indices of the overstory and understory trees by plot are displayed in tables 4 and 5, respectively. It can be seen that the mean values of LI have the smallest variation among the plots for the overstory trees. This is probably due to the small range of crown closure and the common aspect of the plots. Probably due to the multiple levels of thinning among the treatment plots, the mean value of CVHCBU-H1 exhibited the most variation among the plots for the overstory trees. For the understory trees, PCSHS had the smallest between plot variation and APA had the largest.

Table 4. Mean and range for the spatially explicit indices for the overstory trees.

Plot	SD (CVHCBU-H1)	CIZ (CIO)	GS (APA)	OSV (PCSHS)	LI (SAL)
22	0.0483 (0.0141 - 0.2686)	0.87 (0.34 - 1.27)	577.2 (281.6 - 903.4)	0.75 (0.19 - 1.0)	0.68 (0.46 - 0.77)
24	0.1189 (0.0210 - 0.4697)	1.33 (0.60 - 1.83)	418.8 (202.6 - 702.3)	0.47 (0.16 - 1.0)	0.71 (0.58 - 0.81)
27	0.1538 (0.0474 - 0.4136)	1.86 (1.14 - 3.25)	319.2 (183.4 - 480.6)	0.88 (0.15 - 1.0)	0.71 (0.65 - 0.79)
28	0.2162 (0.0323 - 0.9332)	1.17 (0.36 - 1.67)	531.0 (194.7 - 1407.1)	0.41 (0.14 - 1.0)	0.60 (0.35 - 0.69)
29	0.2784 (0.0359 - 1.4630)	1.65 (0.71 - 3.59)	413.2 (162.5 - 912.4)	0.41 (0.16 - 1.0)	0.80 (0.73 - 0.87)
30	0.0840 (0.0173 - 0.3038)	1.01 (0.25 - 2.45)	545.2 (159.3 - 955.3)	0.64 (0.16- 1.0)	0.69 (0.60 - 0.76)
31	0.0336 (0.0134 - 0.0834)	0.91 (0.08 - 1.41)	973.4 (517.2 - 1711.5)	0.91 (0.20 - 1.0)	0.67 (0.39 - 0.76)
34	0.0551 (0.0174 - 0.1461)	1.32 (0.67 - 1.80)	437.5 (231.5 - 735.9)	1.0 (1.0 - 1.0)	0.77 (0.45 - 0.88)
35	0.1162 (0.0485 - 0.2265)	1.57 (0.74 - 2.87)	470.0 (254.8 - 745.1)	0.54 (0.18 - 1.0)	0.81 (0.75 - 0.88)
36	0.0363 (0.0168 - 0.0855)	0.85 (0.31 - 1.57)	584.1 (284.1 - 797.6)	0.77 (0.13 - 1.0)	0.67 (0.56 - 0.77)
38	0.1317 (0.0209 - 0.6621)	1.68 (1.17 - 2.94)	292.7 (130.6 - 478.4)	0.54 (0.19 - 1.0)	0.78 (0.44 - 0.90)
40	0.1009 (0.0300 - 0.3049)	1.87 (1.09 - 2.60)	290.9 (170.9 - 457.8)	0.45 (0.19 - 1.0)	0.79 (0.45 - 0.95)

Plot 27 was conditioned at plot establishment but not subjected to additional overstory density reduction. No conifer trees regenerated on this plot. Table 5 contains no entry for plot 29 since it was not sampled for regeneration. Plot 31 is also absent from Table 5 since the planted understory is exclusively western hemlock.

Table 5. Mean and range for the spatially explicit indices for the understory trees.

Plot	SD (CVHCBU-H1)	CIZ (CIO)	GS (APA)	OSV (PCSHS)	LI (SAL)
22	359.1 (10.9 - 495.2)	49.9 (2.6 - 100.4)	0.99 (0.08 - 2.73)	0.07 (0.06 - 0.08)	0.28 (0.19 - 0.34)
24	745.3 (21.7 - 904.3)	68.1 (27.8 - 111.0)	0.81 (0.05 - 2.63)	0.07 (0.06 - 0.08)	0.26 (0.17 - 0.39)
28	550.7 (19.1 - 712.4)	107.9 (28.8 - 211.4)	0.42 (0.05 - 2.88)	0.07 (0.06 - 0.08)	0.37 (0.28 - 0.45)
30	229.5 (3.6 - 525.2)	42.7 (0.0 - 277.1)	4.00 (0.05 - 13.83)	0.07 (0.06 - 0.09)	0.31 (0.21 - 0.61)
34	463.6 (11.7 - 598.8)	84.6 (33.1 - 271.3)	0.64 (0.05 - 2.14)	0.07 (0.06 - 0.09)	0.17 (0.08 - 0.26)
35	300.9 (10.2 - 1300.8)	51.9 (11.4 - 235.4)	3.31 (0.05 - 11.11)	0.05 (0.04- 0.06)	0.19 (0.07 - 0.38)
36	49.0 (2.2 - 392.7)	29.6 (5.0 - 82.1)	6.97 (0.05 - 30.08)	0.10 (0.07 - 0.14)	0.30 (0.19 - 0.50)
38	493.7 (459.2 - 532.7)	120.2 (37.6 - 226.0)	0.23 (0.05 - 0.77)	0.08 (0.06 - 0.10)	0.18 (0.06 - 0.31)
40	675.5 (653.9 - 692.5)	161.5 (137.1 - 173.3)	0.08 (0.05 - 0.12)	0.06 (0.06 - 0.07)	0.21 (0.02 - 0.27)

Analysis Methods

Growth differences between trees in the same stand are the result of variation in environmental conditions (Harper 1977) as well as differences in their personal history (Horn 1971) and genetic backgrounds (Tilman 1988). These differences result from local environmental conditions that favor certain genetic types due to variations in soil composition, light availability and temperature regimes as well as chance historic events, such as falling branches, that impede growth.

In regression analysis it is assumed that the model form is correctly specified and the expected value of the error term is zero (Kmenta 1971). If this is not the case, then the residual error is likely to be overstated and significant relationships may not be identified (Kmenta 1971). It is likely that the way in which each of the indices quantify competitive pressure is different (Ledermann and Stage 2001). If this is the case, then no single model form for the relationship of growth rate to competition index will be optimal for all of the indices. Since an explicit theory of competition providing guidance in model form selection is yet to be specified (Ford 1999), the model form developed by the index originator was used in creating the specific model forms for this study. Many of the original model forms predicted either change in D or change in basal area and used D as the measure of size. In general our modifications substituted ΔH for the dependent variable and used H as the measure of size.

ΔH has been characterized as a nonlinear function of H, productivity and competition (e.g. Wensel et al. 1987, Hann and Scrivani 1987). For a single plot this relationship reduces to a nonlinear function of H and competition. As our basic model we chose to characterize this relationship for the ith tree as a power function of H:

$$\Delta H_i = b_0 H_i^{b_1}$$

where: b_0 and b_1 are parameters to be estimated from the data. To maintain a constant relationship between H and ΔH across growth periods, b_1 was fixed to values from 0.1 to 1.0, in unit's of 0.1, and the equation was fit to data from each plot. The fixed value of k_1 which yielded the lowest average MSE across the plots was selected and replaced b_1 in the model form:

$$\Delta H_i = b_0 H_i^{k_1} \qquad [1]$$

The SD measure of Biging and Dobbertin (1992) used an exponential function of CVHCBU-H1 to reduce potential ΔH. Substituting equation [1] for potential ΔH in their equations yields the following nonlinear relationship:

$$\Delta H = b_0 H^{k_1} e^{b_1 (CVHCBU\text{–}H1)^{k_2}} \qquad [2]$$

As with k_1, k_2 was fixed to values from 1 to 4, in whole units, and the equation was fit to data from each plot. The fixed value of k_2 which yielded the lowest average MSE across the plots was selected as the best.

The CIZ measure of Bella (1971) used a quadratic function of D and a third order polynomial model of CIO to characterize ΔD in their multiple linear regression. Substituting equation [1] for the quadratic function of D into this model form yields the following relationship for ΔH:

$$\Delta H = b_0 + b_1 H^{k_1} + b_2 CIO + b_3 CIO^2 + b_4 CIO^3 \qquad [3]$$

The GS measure of Pelz (1977) was applied by Moore et al. (1973) to predict 10-year basal area growth. They used D, H, age and crown surface area as their measures of size and a quadratic polynomial model form of height-weighted APA as independent variables in their multiple linear regression. Substituting equation [1] for the measures of size into their model form yields the following relationship for ΔH:

$$\Delta H = b_0 + b_1 H^{k_1} + b_2 APA + b_3 APA^2 \qquad [4]$$

The relationship between $PCSHS^{k}{}_{2}$ and ΔH has been examined by Hanus (2003b) using the following expression of the hyperbolic model form:

$$\Delta H = \frac{b_0 H^{k_1}}{1 + b_1 PCSHS^{k_2}} \qquad [5]$$

where $k_2 = 1, 2, 3$ or 4, selected in the manner described previously.

The relationship between a $SAL^{k}{}_{2}$ and ΔH was also examined by Hanus (2003b) using the following logistic function:

$$\Delta H = \frac{b_0 H^{k_1}}{1+\exp(b_1 SAL^{k_2})} \qquad [6]$$

where $k_2 = 1, 2, 3$ or 4 selected in the manner described previously.

The b parameters in the equations were estimated from fits to data from each plot using procedure "REG" for linear models or procedure "NLIN" for nonlinear models (SAS Institute 1999). An R-student test for outliers was applied to the data (Myers 1990) and residuals were examined for homogeneity of variance by plotting them against predicted values and by application of Levene's (1960) test. The comparison between model forms was based upon the amount of variation in ΔH explained by them and their associated indices of competition for each plot. In a manner analogous to that used by Biging and Dobbertin (1992, 1995) and Bravo et al. (2001), comparisons were based upon the percentage reduction in mean square error (MSE) over a basic model form that is a function of size alone.

Equation [6] was fit to the combined overstory and understory data from all plots. To examine the effects of productivity variation between plots site index was substituted for $H^{k}{}_{1}$ and the equation refit to the combined overstory and understory data from all plots.

Results

In common with the majority of past comparative studies, trees growing in even-aged stands were used for evaluating the performance of the various indices. Unlike the majority of past comparative studies, this study included treated plots in the analysis. In the treated plots the residual overstory trees were very homogeneous in both size and growth (Table 1).

A fit of equation [1] to the data from all of the plots combined yielded a k_1 value of 1.2. This was then used for all the equation fits. It was found that a k_2 value of 0.7 was best for equations [2] and [5] and a k_2 value of 1.5 was best for equation [6]. The R-student test found no outliers in the data, and the examination of the residuals indicated that their variance was homogeneous for all of the equations.

Table 6 displays the MSE of fits of equation [1] to the combined overstory and understory Douglas-fir data from each plot, and the relative MSE, expressed as a percentage of equation [1], for fits of the remaining equations containing the competition indices. The largest percentage improvement in relative MSE over the fit of equation [1] is shown in bold type. SAL values from SEALS produced the greatest average reduction in relative MSE (34.8%) for the indices tested and PCSHS had the second largest average reduction (27.6%). The worst performance for SAL was on plot 31 while the best performance occurred on plot 29.

The indirect indices performed consistently worse than the direct indices. Table 6 shows that there was no consistently best indirect index. APA performed best among the indirect indices on seven plots, CVHCBU-H1 best on four plots and CIO performed best on a single plot. There was no relationship between the performance of the indices and past silvicultural treatments received by the plots. CVHCBU-H1 reduced relative MSE slightly better (15.5%) than was observed by Biging and Dobbertin (1992) for Douglas-fir (14.1%). The average percent reduction in relative MSE due to CIO (16.8%) was less than that reported by Alemdag (1978) for white spruce (33.1%). The average reduction in relative MSE for APA (20.3%) was more than the average reported by Moore et al. (1973) for three hardwood species (6.2%).

Table 6. The MSE of equation [1], relative MSE for equations including the competition index expressed as a percentage of equation [1] the mean relative MSE, standard deviation (SD) or the relative MSE and the coefficient of variation for the relative MSE, for both overstory and understory Douglas-fir trees by plot. Bolded values represent the largest reduction in relative MSE over equation [1] for each plot.

Plot	MSE	SD (CVHCBU-H1)	CIZ (CIO)	GS (APA)	OSV (PCSHS)	LI (SAL)
	[1]	[2]	[3]	[4]	[5]	[8]
22	1.2272	100.0	85.0	68.8	100.0	**66.1**
24	1.3501	100.0	75.5	74.3	56.0	**55.9**
27	0.4998	85.5	95.4	92.2	63.3	**61.9**
28	2.2195	100.0	100.0	92.6	94.4	**83.6**
29	1.5472	25.5	17.0	37.3	25.1	**15.9**
30	3.3458	100.0	89.8	82.5	98.7	**82.3**
31	0.3613	95.4	100.0	100.0	100.0	**92.9**
34	0.3398	100.0	100.0	93.1	92.0	**91.3**
35	1.4580	100.0	100.0	67.1	67.6	**66.2**
36	2.4042	100.0	89.4	88.8	69.8	**65.5**
38	1.4634	61.9	95.2	68.3	55.8	**55.5**
40	2.1446	46.1	51.0	91.0	46.3	**45.6**
mean		84.5	83.2	79.7	72.4	65.2
SD		25.704	25.200	17.496	14.496	21.506
CV		30.4	30.3	22.0	22.0	33.0

Table 7 shows the reduction in MSE of ΔH of overstory trees by plot. Since plots 27, 29 and 31 had only observations from overstory trees the results from these fits are recorded in Table 6. It can be seen that in the overstory SAL consistently reduces unexplained variation better than the other measures. SAL explained more of the variation in overstory ΔH than did any of the other measures on all but a single plot. On six plots PCSHS failed to explain any additional variation in overstory ΔH. As with the combined data there was no consistent best indirect index. Of the indirect indices each was best on four of the plots.

Table 7. The MSE of equation [1], relative MSE for equations including the competition index expressed as a percentage of equation [1] the mean relative MSE, standard deviation (SD) or the relative MSE and the coefficient of variation for the relative MSE, for overstory Douglas-fir trees by plot. Bolded values represent the largest reduction in relative MSE over equation [1] for each plot.

Plot	MSE	SD (CVHCBU-H1)	CIZ (CIO)	GS (APA)	OSV (PCSHS)	LI (SAL)
	[1]	[2]	[3]	[4]	[5]	[8]
22	1.5070	82.2	93.6	95.1	100.0	**62.9**
24	1.4689	97.8	69.3	68.3	51.5	**51.4**
28	2.6895	91.2	89.2	76.4	77.9	**39.3**
30	0.9261	78.9	75.1	**74.7**	100.0	79.2
34	0.5076	79.5	62.1	100.0	100.0	**30.6**
35	0.6004	82.7	100.0	95.4	100.0	**77.0**
36	1.6500	100.0	100.0	93.8	100.0	**52.4**
38	2.8372	70.1	64.9	74.1	58.0	**44.2**
40	2.0904	54.0	41.3	51.0	75.2	**33.2**
mean		81.8	77.3	81.0	84.7	52.2
SD		14.142	19.961	16.205	19.755	17.738
CV		17.3	25.8	20.0	23.3	34.0

Table 8 shows the reduction in MSE of ΔH of understory trees by plot. It can be seen that in the understory SAL is consistently better than the other measures. SAL explained more of the variation in understory ΔH on five of the nine plots. On the four plots where it did not explain the most variation it was nearly as good as the best index, never worse by more than 3.8 percent. Unlike the results for the overstory, PCSHS explained some additional variation in ΔH of understory trees on all of the plots. PCSHS explained the most variation on three of the plots where SAL was not best. On only one plot was an indirect index, APA, better than the direct indices.

In the understory PCSHS was consistently the second best index. On five of the plots where it was not best, it explained the second largest amount of variation. The indirect indices performed poorly in the understory. On only five occasions did an indirect index explain any additional variation in ΔH beyond H.

In general, the reduction in residual variation for all of the indices was not as great in the understory as in the overstory. The indirect indices reduced unexplained variation by 1.8 percent in the understory while unexplained variation was reduced by indirect indices an average of 22 percent in the overstory. SAL reduced unexplained variation by an average of 47 percent in the overstory and 18 percent in the understory. PCSHS reduced unexplained variation by 21 percent in the overstory and 14 percent in the understory. The poor performance of all of the indices may indicate that understory trees could be responding to additional factors not accounted for by the available sample. Unsampled competing shrubs or trees may be impacting the sampled understory tree. In the overstory, all obstructions in the light path were sampled and the performance of the direct indices was better.

Table 8. The MSE of equation [1], relative MSE for equations including the competition index expressed as a percentage of equation [1] the mean relative MSE, standard deviation (SD) or the relative MSE and the coefficient of variation for the relative MSE, for understory Douglas-fir trees by plot. Bolded values represent the largest reduction in relative MSE over equation [1] for each plot.

Plot	MSE	SD (CVHCBU-H1)	CIZ (CIO)	GS (APA)	OSV (PCSHS)	LI (SAL)
	[1]	[2]	[3]	[4]	[5]	[8]
22	2.3489	100.0	100.0	100.0	98.7	**96.2**
24	2.7657	97.7	100.0	100.0	61.3	**60.6**
28	2.4643	100.0	100.0	100.0	96.1	**95.5**
30	3.9135	100.0	100.0	**67.5**	67.6	68.2
34	1.7032	95.1	100.0	100.0	**94.0**	97.8
35	4.2564	100.0	100.0	94.8	**92.5**	92.7
36	6.8498	100.0	100.0	100.0	96.4	**62.6**
38	2.3071	100.0	96.4	100.0	98.0	**95.7**
40	1.8091	100.0	100.0	100.0	**71.9**	72.2
mean		99.2	99.6	95.8	86.3	82.4
SD		1.715	1.200	10.755	14.868	16.028
CV		1.7	1.2	11.2	17.2	19.5

Discussion

The direct indices of the light environment examined in this study performed better than did the indirect indices in explaining variation in ΔH of Douglas-fir. As was found by Hanus (2003b) in understory western hemlock, SAL explained more variation in both overstory and understory trees than did any of the other indices examined. PCSHS explained more variation than did the indirect indices, but its performance was better in the understory than in the overstory. Since the view of the open sky was taken from the tip of the tree and the majority of the overstory trees were nearly the same H, little of the sky was obscured on most of the trees. Current applications using actual hemispherical photographs have been limited to understory trees (e.g. Coates and Burton 1999, Drever and Lertzman 2001). Since they were designed to describe over-topping vegetation, they may not adequately characterize the light environment of overstory trees. The performance of PCSHS on only the understory trees was better than on the overstory trees (Tables 7 and 8) however on average it did not explain as much variation in ΔH as SAL.

The results of this study further confirm the findings of previous comparative studies (Alemdag 1978, Noone and Bell 1980, Lorimer 1983, Martin and Ek 1984, Daniels et al. 1986, Tome and Burkhart 1989, MacDonald et al. 1990, Holmes and Reed 1991, Biging and Dobbertin 1992, Wimberly and Bare 1996 and Hanus 2003b) that also failed to identify a clearly superior class of indirect spatially explicit index. Hanus (2003b) concluded that the indirect spatially explicit indices were not providing a consistent and accurate characterization of the light environment, which may help explain why these indirect spatially explicit indices have not performed as well as indirect spatially implicit measures of competition (Alamdag 1978, Martin and Ek 1984, Lorimer 1985, Daniels et al 1986, Biging and Dobbertin 1995, Wimberly and Bare 1996).

The performance of SAL in the understory was not as good as it was in the overstory. This is probably due to the lack of complete data on understory vegetation that may affect the light environment but was not sampled on the small plots used to characterize the understory. Since all overstory trees on the plot were sampled for species and D, the overstory was better represented than was the understory. Hanus (2003b) found that SAL explained a significant portion of the variation in the ΔH of the understory western hemlock on plot 31 when the overstory and understory are well characterized. On plot 31, each tree in the understory was measured in great detail over a 35 year period. We conclude that it is important to characterize the vegetation of the understory and overstory to generate accurate and precise values of SAL and PCSHS for all applications.

The simulation procedures used to generate both direct indices allow for the possibility of small passages through the canopy. If aligned properly these passages act as radiation conduits permitting direct beam radiation to penetrate the crown as sunflecks. The use of discrete radiation intervals to model the light environment via SEALS may reduce the actual number of sunflecks striking the trees but it will give more importance to those sunflecks that are predicted to fall on the trees. If it is determined that performance of the indices is degraded by the specific time interval used it can be altered by changing the number of radiation intervals used to model the light environment. Increasing the time intervals will results in additional computer processing time.

It is not known how sensitive SAL and PCSHS are to changes in the empirical relationship used in SEALS. It is known that the location of the canopy elements affects the ability of SAL to explain variation in ΔH. For example, it was found that ignoring local plot topography degraded the overall explanatory power of SAL by about ten percent.

The adjusted coefficient of determination (R_a^2) for the fit of equation [6] to the combined data using SAL and H was 0.71, which is better than those found in past empirical studies of ΔH for loblloly pine (Table 9).

Table 9. R_a^2 from previous studies that developed spatially explicit empirical models of ΔH.

Source	Species	R_a^2
Daniels and Burkhart (1975)	Loblolly pine	0.34
Burkhart et al. (1987)	Loblolly pine	0.46
MacFarlane et al. (2002)	Loblolly pine	0.15

Equation [6] with H^k_1 replaced by site index was fit to the combined overstory and understory data for all plots but failed to explain as much variation as did equation [6] with H^k_1. Given the small range in overstory tree age, this result may be due to H integrating both productivity and the tree's vertical position in the stand. If SAL is to be applied across more general conditions, an alternative model form that includes productivity will be needed. It must be generated from a data set with a broader range in age and site index than was available for this study.

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CHAPTER 6

GENERAL CONCLUSION

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February 17, 2003

For submission to: Not for submission

GENERAL CONCLUSION

The work presented in this dissertation examines spatially explicit measures of the light environment of trees growing in managed stands of the coastal Pacific Northwest. In these stands the predominant limitation to individual tree growth is light. The accurate characterization of tree growth in these conditions requires predicting the intensity of light received by each tree. This characterization is more than an estimate of tree crowding, represented by the location of its nearest neighbors. It includes the locations of competitors but also includes the structure of competitors canopies and their effect on the light stream.

Canopy structure can be represented in graphics memory using empirical relationships for the size and distribution of foliage, shoots and stems. Once the graphics image is constructed it may be processed to estimate the intensity of light at every point within the forest volume. This processing is conducted in two ways: using the fraction of open sky visible from the point and by solving the radiation transport equations for the intensity of light at the point.

Chapter 2 examined how studies of spatially explicit indices of competition have been compared. The compilation of these studies exposed some potential weakness of previous analyses. Most of the studies used a single model of competitive pressure on individual tree growth and even though they were conducted in stands where competition for light was the major spatial interaction, they included only indirect models of light competition.

Chapter 3 described SEALS a computer program for describing forest canopy structure. It examined the application of the radiation transport equations to forest stands and described SAL, a new direct spatially explicit index of the light environment. SAL was derived by solving the transport equations at the surface of each tree's crown and accumulating light for the entire growth interval. Chapter 3 also described approximations used in computing SAL that might be modified by the summarization of data on tree structure.

Chapter 4 described the application of two direct spatially explicit indices, SAL and PCSHS as descriptors of the light intensity available to understory western hemlock trees. PCSHS is an OSV index derived from the graphics image produced by SEALS. It was found that models including the two direct indices of the light environment better predicted understory height growth than did models including indirect spatially explicit indices. SAL reduced unexplained variation in height growth rate by 48% over a nonlinear model of total tree height to a power. PCSHS explained slightly less, reducing residual variation an average of 40%. Both direct indices performed better than the indirect indices of spatial competition. SAL was consistently the best index of competition in understory western hemlock.

Chapter 5 extended the comparison of Chapter 4 into a new species and into overstory trees. It was found that SAL was still consistently better at describing height growth than the other indices examined. SAL reduced unexplained variation in height growth by 17.6%, PCSHS reduced unexplained variation in height growth by 13.7%. Due to its method of calculation PCSHS failed to explain any of the variation in overstory height growth on five of the 12 plots. This was not surprising since the heights of the trees on these plots was very similar and the southern aspect minimized the contributions of slope to shifting the tree tops. This does indicate that the application of PCSHS should be restricted to understory trees where the light at the tip of the tree is being obstructed by overstory conditions. SAL did not suffer from these problems making it a better choice for characterizing light competition in overstory trees.

SAL was consistently the best performing index of those selected for this study. It performed better than all the other indices in both species and in both the understory and the overstory. Many approximations were used to construct the model of the overstory vegetation used in this study. It is likely that some of them are degrading the performance of SAL. In time it may be possible to incorporate new information into SEALS reflecting better knowledge of the spatial relationships of the canopy elements.

It has been found that on average only about 4% of the light intensity at points within in a conifer canopy is the result of diffuse radiation. If this result proves more general then the calculation of SAL can be greatly simplified by only accounting for the direct beam radiation incident on the subject tree's crown. Such a calculation can be achieved by projecting the canopy elements onto the subject tree's crown surface and subtracting from the amount of incident light the tree would have received in the absence of shade. This is an efficient calculation that can be accomplished with much less computational overhead.

The goal of this study was to reduce the gulf between empirical models of tree growth and process based models of tree growth. The method for doing this was to relate empirical relationships describing foliage spatial distribution to the process of light competition. If growth reductions can be related to physical processes then they can be used to guide future investigations and to develop new relationships. I believe that I have shown that in one small part of the world light competition can be explained using physical models of the light environment. I now leave it to other scientists to either confirm my findings in other areas and species or to refute and refine these models.

SAL is very computationally expensive to calculate thus rendering its use impractical for an operational growth model. In the future, computer processing power and improved algorithms will render its calculation nearly instantaneous. At that time it will be practical to consider incorporating a direct index of available light into a simulator of forest growth. Until that time, SAL can serve as an inspiration for further examinations of individual tree growth.

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