

**A Model of Competition Incorporating Plasticity through Modular Foliage and Crown Development**



Kristin A. Sorrensen-Cothorn; E. David Ford; Douglas G. Sprugel

*Ecological Monographs*, Vol. 63, No. 3 (Aug., 1993), 277-304.

Stable URL:

<http://links.jstor.org/sici?sici=0012-9615%28199308%2963%3A3%3C277%3AAMOCIP%3E2.0.CO%3B2-Z>

*Ecological Monographs* is currently published by The Ecological Society of America.

---

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/esa.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

---

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact [support@jstor.org](mailto:support@jstor.org).

# A MODEL OF COMPETITION INCORPORATING PLASTICITY THROUGH MODULAR FOLIAGE AND CROWN DEVELOPMENT<sup>1</sup>

KRISTIN A. SORRENSEN-COTHERN

*Center for Quantitative Science in Forestry, Fisheries and Wildlife, HR-20,  
University of Washington, Seattle, Washington 98195 USA*

E. DAVID FORD<sup>2</sup>

*Center for Quantitative Science in Forestry, Fisheries and Wildlife, HR-20, and  
College of Forest Resources, AR-10, University of Washington, Seattle, Washington 98195 USA*

DOUGLAS G. SPRUGEL

*College of Forest Resources, AR-10, University of Washington, Seattle, Washington 98195 USA*

**Abstract.** The model of competition for light presented here uses modular autonomy to incorporate plasticity in plant growth under competition. Once plants are characterized as composed of modules, then model structure for competition changes in a fundamental way. Interactions between the plant module and its local resource environment must be modeled rather than the traditionally viewed interactions between whole plants and their neighbors. We assume that a plant module interacts with its local resource environment regardless of whether this environment was altered by a neighbor or by the same plant.

Two spatial processes are considered: resource acquisition and growth. The spatial pattern of resource acquisition by a module determines a growth and allocation pattern, e.g., the elongation of branches into a gap. The spatial structure of a module and its connection to the whole tree then determines the pattern of resource distribution and resource acquisition of the next time step. Plasticity of plant growth is incorporated by variation in both the efficiency of resource capture of modules and patterns of resource allocation for individuals of different canopy positions and results in individuals in the community having different spatial structures.

The model simulates the three-dimensional development of tree crown structure over time. It is applied to the 30-yr development of a dense, spatially aggregated stand of *Abies amabilis* beginning with an initial pattern of seedlings. The importance of incorporation of plasticity is apparent when the model output is compared to observed height distribution and crown structure data. Simulations indicate that asymmetrical crown development, one form of plasticity, is advantageous to stand productivity and becomes more advantageous as the degree of spatial aggregation in the initial spacing of trees increases.

*Key words:* *Abies amabilis*; modular growth; plant plasticity; stand spatial structure; tree competition.

## INTRODUCTION

Competition arises when individuals in a community obtain an inadequate supply of a resource necessary for growth because of the use of the resource by other plants. This defines competition as a process that changes over time, and points toward two processes interacting over three dimensional space: (1) resource distribution and acquisition and (2) growth and resource allocation. Modeling may best capture the dynamics of the growth process where these two processes interact. To describe this interaction, models must define the structural and physiological properties of plants in relation to the environmental factors over which

they competed. A definition of plant structure must allow the description of the competition process as it changes over time, for different species, and under different spatial or environmental conditions. This may need to include plant plasticity. In this work, we focus on the process of competition for light in a dense and variable stand of trees.

Competition models have focused on the outcome of competition rather than the process (Ford and Sorrensen 1992). Competition determines size hierarchies of plants (Harper 1967, Ford 1975, Mohler et al. 1978, Weiner 1985, Schmitt et al. 1986, Weiner and Thomas 1986), and results in the spatial evenness of large plants (Ford 1975) and survivors (Kenkle 1988). The focus of modeling at the individual plant level has been to produce these observed patterns, an end which can be accomplished using general hypotheses about competition for space (e.g., Bella 1971, Gates et al. 1979,

<sup>1</sup> Manuscript received 21 March 1991; revised 2 November 1992; accepted 4 November 1992.

<sup>2</sup> Address reprint requests to this author.

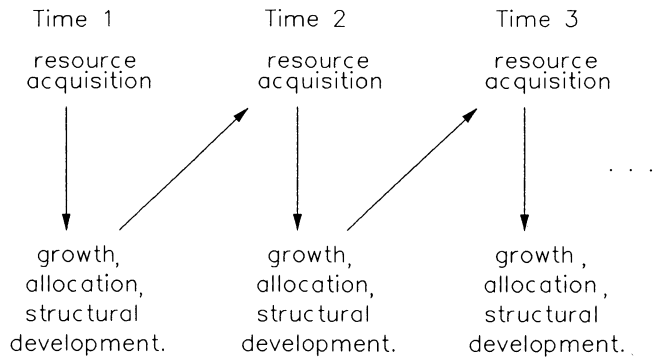


FIG. 1. The logical sequence of calculation used in the WHORL model. This structure enables the development of plant plasticity by individual plants to be calculated over time as the environment experiences changes.

Ford and Diggle 1981, Bonan 1988, Nance et al. 1988). However, the interaction between resource acquisition and growth/allocation is not addressed. Without consideration of this interaction the questions commonly posed by these models of whether competition is one sided (i.e., larger plants influence smaller ones but not vice versa), symmetric or asymmetric (i.e., linear or nonlinear interaction), or a first- or second-order interaction (i.e., nearest neighbor or more distant neighbors influence a subject), give answers which are artifacts of the spatial pattern and growth phase under study (Ford and Sorrensen 1992).

The realization that there are marked differences between species in their patterns of self-thinning (Weller 1987*a, b*, Zeide 1987) focuses attention on defining the process of crown growth and canopy gap formation. The thinning slope  $\beta$  in the equation  $B = \beta \log N + \log K$  (where  $B$  is stand biomass density,  $N$  is individuals per square metre, and  $K$  is a constant) differs significantly between species grown in single species stands (Weller 1987*a*). Consistency of thinning exponents between species has been hypothesized based on the geometry of two-dimensional space filling, where the assumption is made that complete canopy closure is maintained through the combined action of crown growth and self-thinning. However, empirical evidence shows that crown growth and canopy gap formation due to self-thinning are not balanced in general for different time stages, site quality (Zeide 1987), or species tolerance (Weller 1987*b*, Zeide 1987).

It is the exact pattern of gaps and plant overlap that is needed to predict the outcome of competition under plastic growth. Harper (1967) noted that plants change form as competition acts over time, a plastic response, and plasticity is an inherited characteristic that may influence and be influenced by competition (Khan et al. 1976*a, b*, Sultan 1987). In trees, plasticity is observed within as well as between individuals with different canopy positions. Differences occur between upper and lower canopy foliage in physiological characteristics (Leverenz and Jarvis 1980), stem height-diameter allometry (Cannell et al. 1984), bud produc-

tion and bud survival (Jones 1985), and shoot extension (Jones 1985, Franco 1986).

These differences lend support to the modular theory of growth (Harper 1967, Jones 1985, Lovell and Lovell 1985, Franco 1986) that describes plants as having components able to sense and respond differentially to environmental stimuli such as resources or contact. Under this theory a plant does not compete with its neighbors but rather components of a plant compete with, and respond to, components of its neighbors or of itself. This then necessitates the consideration of multiway interaction of neighbors, and multiway interactions imply that the effect of one neighbor on a subject may depend on other neighbors of either or both trees.

#### *Statement of the problem*

Underlying species differences in thinning, crown growth, plasticity, and modularity, are the processes of (1) resource acquisition from the environment and (2) growth, allocation, and structural development by plants and the interdependency of these processes over time. In a competition-dominated environment, the spatial pattern of resource acquisition determines a growth and allocation pattern, for example the elongation of branches into a gap. The spatial pattern of growth then determines subsequent patterns of resource distribution and resource acquisition in the sequence illustrated in Fig. 1. The response process includes survival and can be generalized to include fecundity and other responses of interest.

The linking of these two processes in sequence in a model is essential when competition may span several phases of community or stand development. This is because crown plasticity implies that the growth process affects the acquisition process dynamically. Models based on competition for space ignore this second link in the above process. They repeat the first link over time: resource acquisition =  $\text{fn}(\text{height, neighbors})$  implies height growth; resource acquisition =  $\text{fn}(\text{height, neighbors})$  implies height growth. Furthermore, plastic growth cannot be described by a simple measure such

as height or stem diameter increment, but must result from plant modularity.

Incorporation of plasticity therefore dramatically influences the necessary model form and the assumptions which define this form. In the next section we discuss some critical assumptions implied by the forms of recent competition models and how these require changes in order to incorporate plasticity.

#### INDIVIDUAL PLANT COMPETITION MODELS: REVIEW OF ASSUMPTIONS MADE AND QUESTIONS ASKED

Most competition models define a general space for each individual and characterize it in one of four forms. The most reduced spatial characterization of competing plants is via neighborhood models (Mack and Harper 1977, Pacala and Silander 1985, Ford and Sorensen 1992). A neighborhood is defined by a radius around a subject plant. The number of plants that occurs within a neighborhood of a subject plant is used to calculate a competition index.

A second model form makes a two-dimensional projection of space potentially occupied by a plant onto the  $x$ - $y$  plane (Bella 1971, Ek and Monserud 1974, Gates et al. 1979, Bonan 1988). Often this is assumed to be the space that would be occupied by an open grown tree of the same trunk diameter (e.g., Ek and Monserud 1974). Plant form is assumed not to change. In the largest group of this model type, each individual is assigned a disk-shaped zone representing its assumed crown projection. Typically, the disk radius is proportional to height or stem diameter, and neighbors are defined as two trees having overlapping disks, with the overlapped portion divided according to their relative sizes.

The third model form, the area potentially available to a plant (Moore et al. 1973, Nance et al. 1988), acknowledges that space utilized may not correspond to crown projection. Non-overlapping polygons are constructed around each individual by drawing perpendicular tessellations between a subject and each of its near neighbors. An individual is assumed to utilize the area within its polygon. The tessellation may be located between the subject and neighbor according to their relative sizes, allowing more space for larger trees (Moore et al. 1973, Daniels et al. 1986). Location may be further constrained in proportion to the expected crown radius of open grown trees having the same basal diameters as the subject and neighbor (Nance et al. 1988).

The fourth model form considers three-dimensional plant structure (Hatch et al. 1975, Ford and Diggle 1981). The status of a plant is assumed to decrease according to the degree to which the "cones of influence" of larger plants overtop it. The angle of these cones of influence may be a function of time stage of competition (Ford and Diggle 1981), sun angle (Hatch et al. 1975), or the species (Cannell et al. 1984). These

models recognize the three-dimensional nature of crown competition; however, they assume uniform crown geometry with size as the only variable.

#### *Assumptions commonly made by competition models*

Some common critical assumptions regarding plant structure and resource acquisition are implied in these types of models. The first four assumptions focus on the abstraction of plant interaction and response, while the last two are concerned with plant structure implied by the attributes of space occupied or potentially utilized by the individual.

*i. Response is on the whole plant level (symmetry).*—The response to competition, death or growth, is defined with regard to integrated (whole) individuals, and not their components. This implies that (a) growth is symmetric and (b) symmetric growth depends only on the sum and not the spatial pattern of interaction intensities. Whole plant response is assumed by all competition models mentioned above.

*ii. Response is defined on one variable (nonplasticity).*—Growth is defined by a single size measure, e.g., height increment, and any two- and three-dimensional attributes are derived allometrically from this measure. All information about past effects of neighbors is contained in the single response measure. This assumption, used by all models mentioned, precludes consideration of plasticity, which requires more than one measure of size or condition. A model may assume *i* and not *ii* by defining response based on several attributes which are of a whole tree scale, for example crown angle.

*iii. Interaction is on the whole plant level.*—Competitive interaction occurs between whole individuals (subjects and neighbors), rather than between components of individuals. Whole plant interaction is assumed by neighborhood models (Pacala and Silander 1985, 1990). Most overlap or space partitioning models (Bella 1971, Moore et al. 1973, Ek and Monserud 1974, Gates et al. 1979, Bonan 1988, Nance et al. 1988), as well as the models of Ford and Diggle (1981) and Hatch et al. (1975), retain information about the horizontal location of the interaction. However, vertical location of the interaction is not considered.

*iv. Interaction is pairwise (Gates et al. 1979).*—First, the definition of a neighbor is based only on information about the subject and the neighbor. Second, the competition effect on a subject is the accumulation of a series of pairwise interactions with each of its neighbors. Between a competing pair, the space is then either partitioned (Moore et al. 1973, Gates et al. 1979, Nance et al. 1988) or weighted (Bella 1971, Ek and Monserud 1974, Bonan 1988). The definition of neighbors in a pairwise manner implies that, given the current sizes of two plants, the effect of plant B on plant A is not mediated by the effect of a third plant C on B.

The potential space is implicitly defined by most models as the region within which resource acquisition is possible in the current growth interval. Assumptions *i* and *ii* imply that its structure is a symmetric function of a single response variable. Because all past neighbor influences are contained in the size of this space, it can be considered as the space existing prior to the consideration of current competition. Assumptions *v* and *vi* further specify the potential space and therefore plant structure and resource uniformity.

*v. The potential space that may be influenced by a plant is equal to the space where its resource acquisition may be influenced by others.*—Division of potential space is two-sided but may be weighted symmetrically or asymmetrically, possibly determined by crown angle and shape (Gates et al. 1979). This assumption is dropped in the following cases: sun angle extends the shadows of plants (e.g., Hatch et al. 1975), crown shape is approximately flat topped (e.g., Ford and Diggle 1981, special case of Gates et al. 1979), or different species compete (e.g., Pacala and Silander 1990).

*vi. Potential space is uniform in its potential contribution to growth.*—All points within the projection of the individual's space may contribute equally to a plant's growth. The use or omission of this assumption has implications as to the effect of self-shading. If a crown is considered as a cone, with internal foliage rendered insignificant by self-shading, then its projection is a uniformly weighted disk (Gates et al. 1979). Mitchell (1975) also uses this reasoning to project crown surfaces onto the plane.

#### *Ecological questions investigated by competition models*

The general foundation of models on whole plant, one-dimensional response (*i* and *ii*) is reflected in the approaches taken to investigate the following questions.

*How important is competition relative to genetic and environmental influences on relative growth rates?*—Bonan (1988) applied an overlapping disk competition measure in a growth simulation where neighborhood effects, symmetric vs. asymmetric allocation, and genetic effects were varied in a factorial design. In the absence of competition, the growth equation represented a negative relationship between relative growth rate and size. Positively correlated growth rates were required for size hierarchies to form. Both neighborhood effects and genetic variation in growth rate were important in inducing this positive relationship. However, when both factors were in effect, the role of neighborhood competition, in increasing relative growth rate variation and the development of size hierarchy, was still apparent. Partial confounding by random variation in intrinsic growth rate is also observed by Ford and Diggle (1981) in their simulations of lattice spacings.

Bonan also admits that the balance between com-

petition and other sources of growth variation obtained in his simulations is a mathematical artifact. His mathematical formulation indicated that pattern-induced (competitive) variation in growth was somewhat confounded by random (genetic) variation in growth, depending on the respective ranges of these variations. However, the ranges of variation depended on the specification of arbitrary constants and so no biological theories were investigated. Indeed, the potential for confounding of random variation over pattern-induced variation is quite obvious without using a mathematical model; this notion is fundamental to statistics. What is of interest is the prediction of the degree of confounding based on biological mechanisms. To examine this, the mechanisms of the competitive process must be addressed. Crown shape, shade tolerance, a particular limiting resource, degree of aggregation, and growth phase involved may all be factors interacting with genetic, environmental, and neighborhood variation. For example, Schmitt et al. (1986) found that size hierarchy development in laboratory experiments was related to spatial density only at low irradiation levels.

*Is competition symmetric or asymmetric?*—The degree of asymmetric allocation is generally defined as the extent that a jointly used space or resource quantity is allocated disproportionately to the larger plant of a pair. Thus, asymmetric allocation is defined only for a pair of plants (assumption *iv*) each having a single whole plant response variable (*i*, *ii*). Furthermore, the common approach is to apply an asymmetry coefficient to allocate a uniformly important potential space (assumption *vi*) rather than modeling the implications that a non-uniformly important space has upon asymmetry. The latter is the process-oriented approach; asymmetry is a quantifiable outcome of the process rather than a driving variable.

Many equations have been used to produce a term that asymmetrically weights or divides the common resource space between two overlapping individuals as a function of their relative sizes (Bella 1971, Moore et al. 1973, Gates et al. 1979, Bonan 1988, Nance et al. 1988). Bimodality and skewness in size distributions has been simulated assuming asymmetric allocation on regular spacings (Diggle 1976, Gates 1978) and by assuming symmetric allocation on irregular spacings (Miller and Weiner 1989). The investigation of asymmetric allocation should focus attention on the exact mechanisms involved and their dependence on spacing. However, the commonly used asymmetry coefficients rarely reflect the biological mechanism determining asymmetry.

Gates et al. (1979) provide an important exception where asymmetry is the result of a mechanism modeled directly rather than a driving coefficient. The model is constructed via an axiomatic approach. Gates et al. start with the two-dimensional disk model, implicitly using assumptions *i*, *v*, and *vi*. They then formally state

a complete set of assumptions about competing plants, including pairwise interactions (*iv*), which are required so that the overlapped area of two projected plant spaces is partitioned by drawing a boundary curve. The partition can represent symmetric or asymmetric partitioning of space. With additional assumptions about the crown structure similarity (nonplasticity), the location of this partition is related to the crown shape of the tree. So under nonplasticity the asymmetry of the space partitioning increases as the species crown shape varies from conical to round-topped to flat-topped.

The definition of asymmetry is more complex when multiway interaction and plasticity is considered. As plasticity necessitates, the consideration of the dual process of acquisition and growth asymmetry in each of these processes can be defined.

*What are the bounds of influence of one plant upon another?*—The focus on the radius of interaction as it relates to size and conspecific or interspecific competition provides useful information when interaction mechanisms are not well understood, and perhaps in particular when interactions occur outside the physical boundaries of plants. The radius may be constant or a function of a simple measure of plant size (assumptions *i* and *ii*) and interaction inside the radius is whole plant (*iii*) and pair-wise (*iv*). Intensity of interaction may be constant (assumption *vi*) within the prescribed radius (Pacala and Silander 1985, 1990) or may be assumed to increase along smaller radii, e.g., the “soft boundary” described in Diggle (1983).

Neighborhood models specifically investigate both the radius of interactions and the constant intensity of influence within this radius. The simple form of neighborhood models has been used to estimate interaction parameters using statistical optimization. These models provide informative summaries and comparisons between data sets can be made. For example, Pacala and Silander (1990) make conclusions about the maximum range for interaction and the asymmetry of interspecific competition based on the estimated 95% confidence intervals for the radius of interaction of various data sets. Ford and Diggle (1981) also estimate the radius of interaction for the data set. They model the vertically varying radius of interaction imposed by the “cone of influence” of an individual. The angle of the cone  $\theta$  is constant over the population and reflects the overall intensity of competition for a given time stage (Ford and Diggle 1981) and species (Cannell et al. 1984).

Pacala and Silander (1990) point out that the radius of interaction is a phenomenological rather than mechanistic parameter and therefore its behavior in response to changes in the physical environment cannot be determined. The fit of the radius of interaction to a data set depends, in completely unknown and unspecified ways, on the particular time phase and spatial pattern of the data. However, phenomenological-based models are useful as a summary of a data set.

*What is the importance of spatial pattern of neighbors?*—Given the same locality mean density of neighbors, are plants affected differently for different directional distributions of the neighbors? This question addresses the transition from whole plant interaction (*iii*) to location-specific interaction. Regression analysis of variance has been used to test the significance of contribution from indices of spatial pattern over that of mean density which describes the whole plant interaction. Pacala and Silander (1985, 1990) found that given the number of neighbors, their actual distances to the subject did not add significant information about fecundity in two annual species. However, in their 1990 paper, they describe the spatial patterns as only weakly aggregated, and under this condition, spatial pattern would tend not to be important, so their conclusion cannot be taken as strong. As aggregation increases or dispersed and aggregated spacings are considered together, then variation in pattern (e.g., a plant surrounded vs. located on the edge of a clump) may become more important. It should be noted that summaries of spatial pattern such as angular dispersion (Pacala and Silander 1985, Pukkala and Kolström 1987) provide limited description of spatial pattern because different patterns may give the same summary value.

## MODEL DESCRIPTION

### Overview

The objective is to incorporate plasticity into a three-dimensional conspecific model of competition for light, called WHORL. Modeling plasticity requires that we incorporate modular autonomy, which in turn requires distinction of the dual processes of resource acquisition and growth. The reasoning is as follows: plastic growth implies plant modules grow somewhat independently. Once plants are characterized as being composed of modules, the modeling algorithm for competition changes from subject-neighbor interactions to module-local environment interactions, although the status of the individual within the community does influence the nature of these interactions. We assume that a module of a plant interacts with its local resource environment regardless of whether this environment was altered by a neighbor or by the same plant. From this assumption the question arises and is addressed here: Can rules for tree growth under a spatially varied resource also fully describe competition between trees? We define resource acquisition and growth rules for a tree with only one minor rule, operating under infrequent conditions, which specifically addresses the interaction of more than one tree.

The incorporation of plasticity requires consideration of plant modularity. In contrast to the assumptions of most competition models, our model assumes: (*i'*) response is both modular and whole plant; (*ii'*) response is multidimensional with horizontal (branch) and vertical (height) dimensions at least partially in-

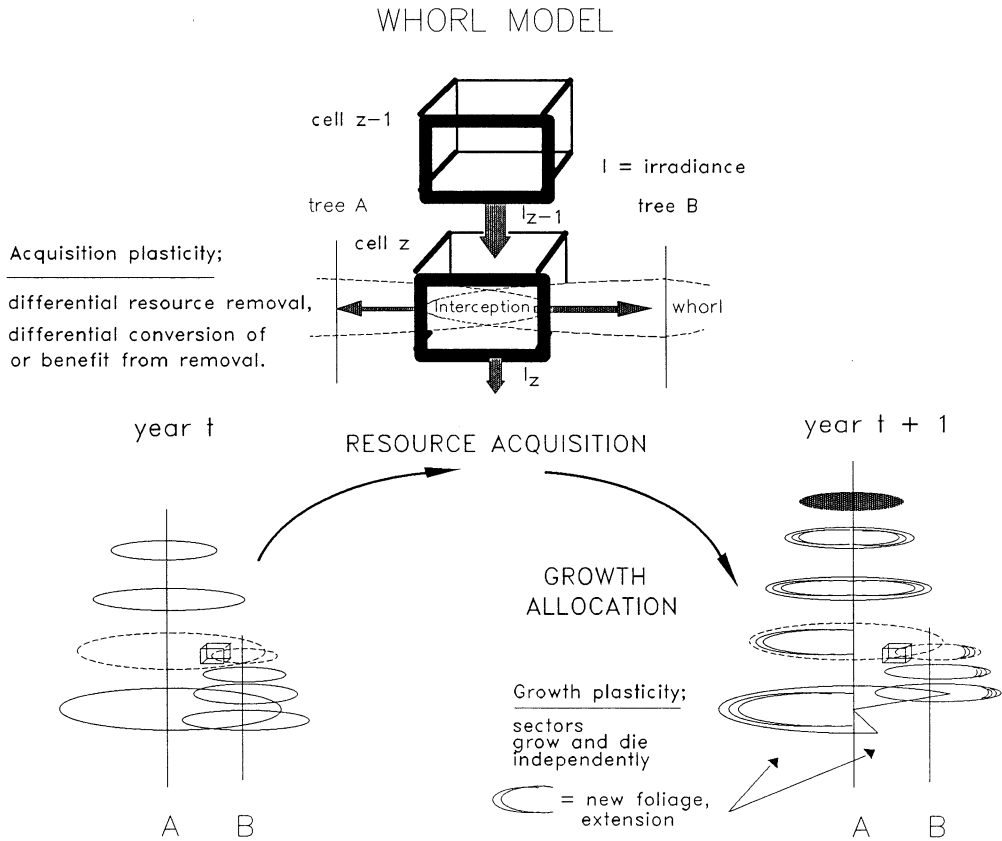


FIG. 2. Diagrammatic representation of WHORL model algorithm. Each tree is represented as a series of whorls stacked along a center axis. Incoming irradiance is considered vertically in columns. Interaction between individual trees is described by interaction between whorls that overlap in a vertical projection. Interaction results in reduction in foliage density and in radiation flux in the area of overlap. Foliage density and available radiation at a given point determine resources acquired and this pattern of acquisition determines growth, which can occur independently between whorls and between sectors of whorls that represent branches. The calculation of multiway resource acquisition between many trees is simplified by division of the plot into a grid of three-dimensional cells within which there is no resolution. Calculation proceeds cell by cell, and the model determines which tree elements overlap this cell and then assigns acquisition of available resources within that cell to those trees.

dependent; and (iii') interaction is modular. Assumptions (*iv-vi*) of the previous section are not directly in conflict with plasticity. However, acquisition of an irradiation resource implies (*iv'*) multiway consideration of neighbors. Furthermore, a single generalization of the potential space of a plant, be it an herb or tree, ignores many highly varied plant processes at work. Instead we use a more detailed three-dimensional characterization of the plant which incorporates mechanisms which result in self-shading and asymmetric allocation: (*v'*) potential space is three-dimensional and therefore competition between plant components is determined by their relative vertical position (e.g., a plant component affects but is not affected by a component directly below it); (*vi'*) potential space is not uniform in its potential contribution due to the effects of past competition and also to current self-shading.

Tree growth follows the dual process as depicted in Fig. 2. Crown components grow in response to the detailed pattern of resource acquisition, and then create

the new pattern of resource distribution for the following year. We investigate plasticity in both the resource acquisition and growth processes. The model is derived from process-based assumptions (Tables 1 and 2) which arise from considering the dual processes of resource acquisition and growth. The model input and output parameters are summarized in Table 3.

Several of the model assumptions represent notable simplifications while others represent an increase in detail over the assumptions implicit in other models. The assumption of vertical rather than angular irradiation (resource acquisition assumption 1) is a simplification for the study plots during the growing season and perhaps for most other forest systems of interest. Because only vertical irradiation is assumed, the model will not be able to account for some aspects of stand and crown structure including: (1) a possible height growth advantage for individuals on the southmost edge of a clump over those on the opposite edge, (2) asymmetry in branch growth due to shading from fo-

TABLE 1. Resource acquisition assumptions.

| Assumptions  | Explanation   |
|--|---|
| 1. Competition for irradiation.  | Competition for irradiation dominates competition for other resources. No distinction is made between direct beam and diffuse radiation. Incoming irradiation enters from the vertical only.  |
| 2. Modular and multiway interaction. Competition occurs between foliage elements.  | Competition for radiation occurs when foliage elements obtain a reduced amount of irradiation because of interception by other foliage elements. Competing elements can occur on the same tree or between different trees and must be vertically aligned because of assumption 1.   |
| 3. Fractional interception.  | Each unit volume of a foliage element acquires, and removes from the resource pool, a fraction of the radiation present at its particular location. This fraction is the interception rate of the foliage.  |
| 4. Foliage is represented by only two attributes: interception rate ( $r$ ) and photosynthate conversion efficiency ( $E$ ). |   |
| 4.1. Interception rate (foliage density) depends on irradiation.   | With increasing depth in a canopy, self-shading and competition create an irradiation-poor environment that contributes to needle loss. Transmittance of light through a cell is calculated based on its leaf area index using Beer's Law, $P = \exp(-f \cdot \text{LAD} \cdot d)$ , where $P$ is the probability or rate of transmittance, LAD ( $\text{m}^2/\text{m}^3$ ) is leaf area density, $d$ (m) is the path distance through the foliage of the cell in the direction of the light beam, and $f$ (unitless) is the fraction of leaf area projected on a plane normal to the beam (Norman and Welles 1983). If $d$ is defined to be the cell height and $f$ is assumed constant, there is a one-to-one correspondence between interception rate $r$ and leaf area density LAD,<br>$r = 1 - P = 1 - \exp(-f \cdot \text{LAD} \cdot d)$ In fact, interception rate is the driving variable of the model and leaf area index is calculated from $r$ rather than the other way around. |
| 4.2. Efficiency of conversion to photosynthate is independent of irradiation.  | The second attribute of foliage, conversion efficiency ( $E$ ), is represented as a multiplier that transforms irradiation intercepted into photosynthetic production.  |
| 4.3. Acquisition plasticity. Interception rate (foliage density) and efficiency depend upon the tree's height class.         | Height status, relative to the height of the dominant trees, is used to classify whether the foliage of a tree has sun, shade, or intermediate characteristics. The relationships of 4.1 and 4.2 may be specified to depend on this status so that suppressed trees maintain and produce foliage at lower irradiation (higher $r$ ) and are more efficient at conversion (higher $E$ ) to photosynthate.  |
| 5. Joint utilization of the same small volume of resource space assumes equal sharing.                                       | We assume that if foliage from many whorls overlap within the same cell, the total irradiation intercepted is the same as if the foliage occupied vertically aligned cells, i.e., there is no difference in any penumbra effect acting on distant or close foliage. And we assume total interception within a cell is allocated according to the foliage densities of each tree, which may vary because of sun/shade status.  |

liage elements not vertically aligned and (3) and asymmetry in branch growth that is due only to self-shading. However, the assumption of vertical irradiation greatly simplified the mathematics and algorithms necessary to meet acquisition assumption 2, modular interaction. The simplification made possible, in terms of computer time, the exploration of other assumptions. Further development of the model will incorporate angular irradiation.

Acquisition assumption 4 delineates between the two fundamental properties of acquisition, resource removal and resource delineation. The assumption 4.1, that interception rate decreases with decreasing irradiation, differs from that of current canopy radiation models (Norman and Jarvis 1975, Norman and Welles 1983, Oker-Blom and Kellomäki 1983, Oker-Blom 1986, Wang and Jarvis 1990) in that here foliage density is determined by the local irradiation environment rather than assumed in the form of a stochastic dis-

tribution or a function of canopy depth. The assumption 4.2, that efficiency of conversion to photosynthate is independent of irradiation, neglects saturation phenomena. The dependency of both interception and efficiency on tree status rather than on a more localized measure of status is another simplification. In the data discussed below (see *Plasticity in the observed data: Sun/shade foliage morphology*), the ratio of silhouette area to leaf area is seen to vary continuously with local light level for a range of tree heights. However, height status is related to the length of time which a tree has been overtopped and is indicative of its relative amount of sun vs. shade types of foliage. Although silhouette area to leaf area ratio ( $f$ ) does change, we calculate leaf area index, LAI, as though a change in interception rate,  $r$ , is due only to a change in leaf area, not a change in  $f$ .

The treatment of crown structure as a series of whorls (growth assumption 6) differs from the solid cone rep-



TABLE 2. Growth assumptions.

| Assumptions   | Explanation   |
|---|---|
| 6. Crown structure.   |   |
| 6.1 A tree crown is represented as a series of two-dimensional whorls.  | Whorls are represented as discs located at discrete points along a vertical axis (tree stem).   |
| 6.2 Whorls are divided into sectors to represent branches.  | Generally, we have used four sectors. To mimic branch distribution, the sectors of a tree are oriented randomly relative to other trees and are shifted by $\pi/4$ for alternating whorls within a tree. Note that foliage density, as stated above, is dependent only on irradiation level and is not spatially clustered about a branch. That is, each sector would be uniformly covered with foliage if no irradiation variation existed.  |
| 7. Modular response, branch growth plasticity. Whorl sectors, each representing a branch, grow annually or die dependent on their own relative production and independent of the whorl and tree status. | Relative production is defined as production per unit foliage, and is thus an index of the excess of production over maintenance respiration of leaves. It does not, however, include the maintenance respiration of branches. An entire sector increments radially outward from the tree axis as a function of its relative production and dies if this drops below a specified level. This level may be constant or varied according to relative height class as in assumption 4.3 (Kellomäki 1980). Sector growth is independent of height growth with the exception that new whorls added have a radius proportional to the height growth above them. |
| 8. Annual height extension is dependent on relative production of the whole tree.   | Height extension is assumed to be a whole tree response, a function of the total amount of production per unit foliage (relative production). Net production, i.e., production – maintenance, might be a better determinant of growth but involves more complexity in modeling.   |
| 9. Tree mortality.  | A tree dies when all its whorls have died.  |

representations in several important ways. First, a solid cone representation gives greatest weighting to foliage on the cone surface because this continuous surface blocks radiation from internal foliage. (This becomes more important when irradiation at an angle is considered.) Second, the whorls correspond to a history of height growth that can vary markedly as stand structure changes and the competition process develops (Cochrane and Ford 1978). This structure then facilitates the incorporation of dynamic allocation to height growth and differential branch extension. Third, different mean inter-whorl increments assign different individual crown densities in a natural manner. Kellomäki (1986) found branch densities (number of branches/decimetre of bole length) of suppressed *Pinus sylvestris* to be significantly higher than those of dominant trees. Finally, the location of whorls represents the foliage overlap between trees in detail: one part of a whorl extending directly above another whorl part will have a vertical advantage. In the examples presented, we take the vertical location of whorls to the finite resolution of 10 cm. If two or more whorls overlap within this distance, no particular whorl is given vertical advantage.

Branch and height growth depend on relative production (growth assumptions 7 and 8) rather than net production, i.e., production – maintenance. The latter may be a better determinant of growth but involves more complexity in modeling.

#### Calculation

Model calculation proceeds by three algorithms. First is the initialization of crowns given their heights and possibly past competition effects. Second, resource ac-

quisition is calculated. A light beam is followed down each individual column of cells on the plot, and its interception by foliage is calculated. Third, annual growth is calculated for each tree in the plot. Growth of each sector of each whorl and height extension for the whole tree are calculated from the photosynthetic production of each sector, and of the whole tree, respectively. Algorithms 2 and 3 are repeated each year. The model parameters are introduced in this section and discussed in detail in *Sensitivity to parameters*, below.

1. *Initialization of tree crowns.*—Initial crown structures must be estimated by assessing the effects of past competition. The following crown shape parameters, together with tree height, specify the radius and position of each whorl assigned to a tree: mean inter-whorl distance, crown apex angle (determines whorl radius at a given height), and crown length ratio (crown length : tree height). When simulating growth from an initial seedling phase, as is done in the work reported here, these parameters are assumed constant. However, if the model is initiated at a stage beyond seedlings (Sorensen 1989), then each parameter can be calculated for each tree as a function of its current height, where the functions are estimated from data collected on independent stands.

2. *Resource acquisition within each cell.*—The radiation flux through a vertical column of cells is fractionally attenuated whenever one or more whorls intercept a cell. Unintercepted irradiation passes to the next cell down:

$$I_z = I_{z-1}(1 - r_{z-1}),$$

TABLE 3. Model parameters used in WHORL, and their abbreviations, units and types.

| Parameter             | Name  | Explanation  | Units  | Type               |
|-----------------------|---|--|--|--------------------|
| $I$                   | Irradiation flux  | May be absolute or relative (percentage of above canopy irradiation).    | $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ or unitless. | Input.             |
| $r$                   | Interception rate   | Fraction of irradiation intercepted by foliage.                          | Unitless.  | Output.            |
| LAD                   | Leaf area density   | Foliage density associated with $r$ .                                    | $\text{m}^2/\text{m}^3$  | Output.            |
| $R$                   | Maximum interception rate                                 | Interception rate of unshaded foliage.                                   | Unitless.  | Input, nonplastic. |
| $D$                   | Maximum required relative irradiation                     | Relative irradiation below which there is no living foliage.             | Units of irradiation.  | Input, plastic.    |
| $k$                   | Coefficient of decline                                    | Controls convexity of foliage response to irradiation decay.             | Unitless.  | Input, plastic.    |
| $E$                   | Conversion efficiency of radiation absorbed to production | Rate of conversion of irradiation flux to production.                    | $\frac{\text{units of production}}{\text{irradiation flux}}$         | Input, plastic.    |
| INT                   | Interception  | Irradiation intercepted by a shaded cell of foliage.                     | Units of irradiation.  | Output.            |
| TINT                  | Total interception  | Total interception by multiple whorls occupying a given cell.            | Units of irradiation.  | Output.            |
| relative.production.S |   | Relative production contributed to a sector by all of its foliage cells. |  | Output.            |
| relative.production.T |   | Relative production contributed to a tree by all of its sectors.         | Units of production.   | Output.            |
| SINC                  | Sector increment rate                                     | Controls rate of sector growth.  | Length increment (m) per unit relative production of the sector.     | Input, nonplastic. |
| HINC                  | Tree height increment rate                                | Controls rate of height increment.                                       | Height increment (m) per unit of tree relative production.           | Input, nonplastic. |
| SDEATH                | Minimum production required to sustain a sector.          | relative.production.S at which a sector will die.                        | Units of production.   | Input, plastic.    |

where  $I_z$  is the irradiation entering cell  $z$ ,  $I_{z-1}$  is the irradiation entering the cell above  $z$ , and  $r_{z-1}$  is the interception rate implied by the foliage density of the cell above  $z$ .  $I_z$  may be described in units of millimoles per square metre per second or in terms of relative irradiation (e.g., percent of above canopy irradiation) without affecting the model results. In this paper relative irradiation is used to facilitate interpretation of irradiation attenuation.

If only one whorl overlaps a cell, then the interception rate,  $r_z$ , is modeled by a simple equation which produces an asymptotic relationship between irradiation flux and interception rate (i.e., foliage density):

$$r_z = R \left( \frac{I_z - D}{I_0} \right)^K,$$

where  $R$  (unitless) is the maximum interception rate corresponding to foliage that is unshaded and therefore at full density ( $0 < R < 1$ ),  $K$  (unitless) is the coefficient of decline ( $0 < K < 1$ ), and  $D$  (units of  $I_z$ ) is the flux at and below which there is no living foliage. (The

parameters  $R$ ,  $K$ , and  $D$  are estimated in the model calibration.) Irradiation intercepted by a shaded cell (INT) of a given whorl equals the irradiation available multiplied by the interception rate ( $\text{INT} = r_z I_z$ ). Interception is then translated to production according to an estimated conversion efficiency  $E$  (units of production/irradiation flux),

$$\text{production} = E (\text{INT}),$$

and is assigned to each sector which overlaps the cell. When multiple whorls overlap the cell, the  $N$  whorls collectively intercept the same amount of irradiation as if they occupied successive cells. Total interception, TINT, from the  $N$  whorls is calculated ( $\text{TINT} = I(1 - (1 - r)^N)$ ). This amount is then allocated to cell interception for each individual, according to relative foliage densities which may vary due to sun/shade status.

Leaf area density  $\text{LAD}_z$  ( $\text{m}^2/\text{m}^3$ ) for each cell is determined from  $r_z$  using Beer's Law,

$$\text{LAD}_z = \frac{-\ln(1 - r_z)}{f.d}.$$

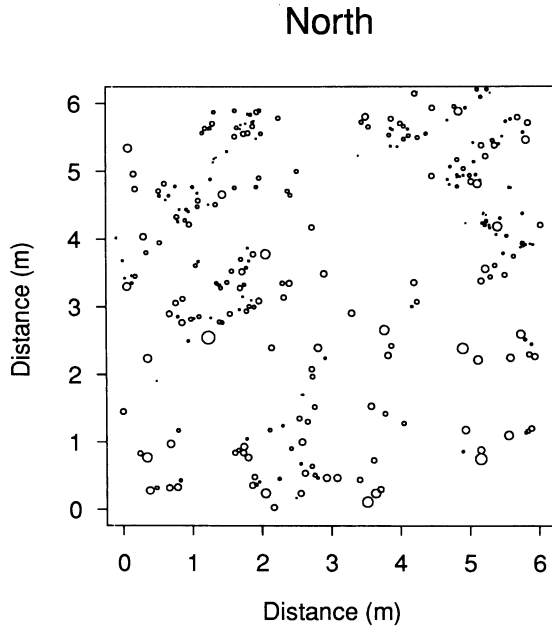


FIG. 3. Stem map of naturally regenerated *Abies amabilis* on a permanent plot, with stem diameters shown at twice natural size.

3. *Annual growth.*—The model represents the translation of interception to production to annual growth using only a few simple steps, but the parameters controlling these steps have units that are not easily interpreted. Production, calculated for each cell in the resource acquisition phase of the model, is summed for each sector to obtain total production. This quantity is divided by total foliage density ( $r_z$ ) of the sector to get relative production for the sector  $\text{relative.prod.S}$  (production/interception rate), and then summed over all sectors of a tree to get relative production for the tree,  $\text{relative.prod.T}$ . Sector and height increment for the tree are then calculated respectively as  $\text{SINC} \times \text{relative.prod.S}$  and  $\text{HINC} \times \text{relative.prod.T}$ , where  $\text{SINC}$  and  $\text{HINC}$  (growth in metres  $\div$  relative production) are constant parameters fitted in the model calibration. If  $\text{relative.prod.S}$  is less than  $\text{SDEATH}$  (fitted parameter), the sector dies. Finally, a new whorl is created at the top of the tree, with a radius proportional to height increment of the tree. Effects of nonlinear height growth formulation are investigated by simulation.

Cell  $x$ ,  $y$ ,  $z$  dimensions were chosen to balance speed of calculation with accuracy in assigning areas to whorls. For the plots simulated here, which were  $6 \text{ m} \times 6 \text{ m}$  and had up to 300 trees, cells of height 0.1 m and widths 0.1 or 0.2 m were satisfactory for both criteria. We used cells of  $0.1 \text{ m} \times 0.1 \text{ m}$ , resulting in a computation time on a SUN Sparcstation 1Plus (32 megabytes of memory) of  $\approx 30$  min to simulate 30 yr of plot development.

#### PLASTICITY IN THE OBSERVED DATA

The model was parameterized for a dense stand of *Abies amabilis* that regenerated under an old overstory and then grew following a clear-cut removal ca. 1957. Site conditions are described in Grier et al. (1981). All trees were mapped some 20 yr after the overstory clear-cut, and were apparently present as seedlings before the clear-cut. There appears to have been no reproduction in the stand since then. The pattern and size of the seedlings prior to the clear-cut are not known. However, observations in a 200-yr-old stand nearby indicate the seedlings probably originally occurred in large dense patches and were between 0.1 and 0.7 m height and of different ages. The current large-scale variation in spatial pattern of stems is probably due to the large stumps of the overstory remaining and incidental destruction during the clear-cut process. Typically, intense growth and competition starts immediately after overstory clear-cutting and after 30 yr has resulted in extremely varied tree sizes and wood volumes per unit area. It is postulated that three factors contribute to this variation: the ability of *Abies amabilis* to survive and to grow vigorously after release from a long period of suppression, the high density of stems and the competition that this generates within some patches, and the heterogeneous spatial pattern of the patches themselves, which vary in size and initial density of stems.

Two data sets were used in the model calibration. The first (Grier et al. 1981; D. G. Sprugel, *unpublished data*) consists of the location and basal diameter (15 cm above the soil) in 1978, 1985, and 1987 (Fig. 3); and the height in 1985 and 1987 (all trees on a  $6 \text{ m} \times 6 \text{ m}$  plot, plot C). Heights in 1987 ranged from  $< 1 \text{ m}$  to  $> 6 \text{ m}$ . The density and variation in size provide an extreme situation in which to model competition.

The second data set (Brooks 1987; D. G. Sprugel, *unpublished data*) gives quantitative information on crown structure (Fig. 4). Thirty-eight trees near plot C were destructively sampled, and branch length and height for all living branches were recorded. The 24 trees shown in Fig. 4 were sampled randomly within a portion of the site. The remaining 14 trees were taken within a  $3 \text{ m} \times 3 \text{ m}$  clump, plot R, where all trees were mapped and measured for height and basal diameter. Irradiation attenuation was also measured in this plot prior to sampling.

#### *Branch extension vs. height increment: crown apex angle*

The relationship between height growth and branch extension was visibly altered by competition (Fig. 4) so that suppressed trees generally had wider crown angles. Crown angle coefficient, CAC, was quantified as follows. From the top of the tree down to the widest branch on the tree, the longest branches of each whorl were identified. CAC was calculated as the slope of the

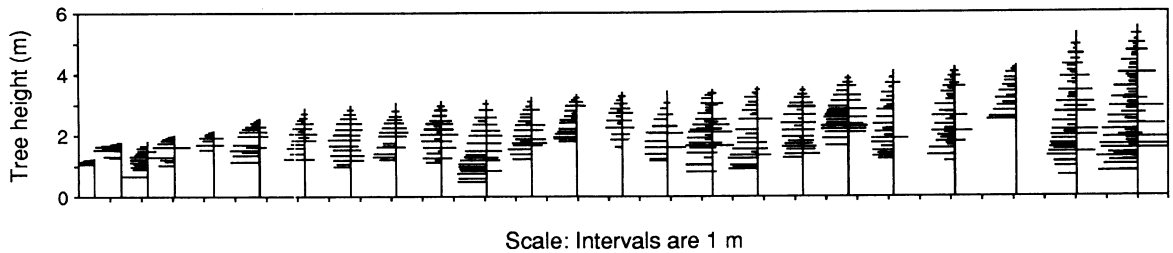


FIG. 4. Measured crown structures of *Abies amabilis* represented by maximum branch length at each whorl position drawn on the left and minimum branch length on the right. No branch on the right indicates the occurrence of two or less living branches at that whorl position. Trees are ordered by height and positioned so that no overlap appears between crowns.

regression of these branch lengths,  $l$ , and the square root of branch depth,  $\rho$ , from the tree top,  $l = CAC\sqrt{\rho}$ . CAC was calculated for each of the 38 trees.

CAC was negatively correlated with height (Sorrensen 1989), but the relationship is very nonlinear, with a nonconstant variance (decreasing with an increase in height). Many small and medium trees had very large CACs, while for trees taller than 3 m, CAC is smaller and unrelated to height. Crown samples from plot R had substantially higher CACs, as well as a less varied relationship to height, than those of the random sample. These two observations suggest that if competition effect is estimated by height or an indicator well correlated to size, for example space available, then individuals within a clump cannot be considered as a random and independent sample of the population. The  $R^2$  values of regression-based competition predictors on one plot are likely to be higher than would be obtained for a random and independent sample of the population.

#### *Asymmetry and crown length*

Crown structures were quite variable. Branches within the same whorl grew and died at different rates and crown asymmetry had developed. Some suppressed trees as tall as 2 or 3 m had whorls consisting of only one or two branches directed toward an "edge" of the clump or where there was more light. This is a frequent but informal observation in this stand. It was also observed that crown die-off occurred between two or more large trees very close together. Considering crown length to the lowest living branch, crown length ratio (crown length : height, CLR) was not constant and only weakly correlated with height (Sorrensen 1989). Two trees may grow to approximately the same height in the same amount of time and yet have very different crown lengths. It is reasonable that this variation indicates the importance of subtle differences in spatial pattern and the multiway interactions arising from a given pattern, as well as genetic differences.

Trees sampled on Plot R (the clump) were again noticeably different from the random sample; they had lower CLR and much lower variance of CLR given height. The spatial point pattern on Plot R at the time of sampling was relatively regular, and this may have

influenced the observed consistency in CLR given height.

#### *Sun/shade foliage morphology*

It is well known that foliage morphology in conifers differs for foliage produced in shaded vs. sun environments and that the change in morphology is accompanied by differences in photosynthetic efficiency (Levrenz and Jarvis 1980). However, a quantitative relationship between irradiation quantity and the degree of morphological adaptation has not been established for a particular system to our knowledge. We explored the relationship between one shade adaptation indicator, the ratio of silhouette foliage area of the intact twig to total foliage area on the twig (SLAR), and irradiation quantity for trees of different competitive status. Current foliage was sampled from six trees, ranging from 0.87 to 4.00 m, within one clump near the study plots. The shoot clippings were taken at 3–10 heights along each tree, from the apical tip of the branch or from a side shoot near the tip if the tip was damaged. The last  $\approx 2$  cm of the shoot tip was analyzed for silhouette area and flat leaf area, using a LI-COR leaf area meter. Before clipping, irradiation quantity was measured at each foliage sample, using a LI-COR quantum sensor. Irradiation at the top of the canopy was measured just before sampling each tree so that percent irradiation could be compared. Sampling was conducted during an overcast day in late May.

Rather than a categorized response, SLAR varied continuously with percent irradiation transmittance (Fig. 5). The same relationship fit all trees regardless of height. Only the three small trees, heights 0.87 to 1.50 m, had current foliage below an irradiation level of 17% above the canopy value. The three largest trees, with heights 2.9–4.0 m, had current foliage produced down to 17–20% irradiation levels and not below, an unexpectedly consistent response. Large trees did not appear to produce new foliage at irradiation levels as low as suppressed trees.

#### SENSITIVITY TO PARAMETERS

Negative feedbacks to the growth of individual trees are present in a competition-dominated environment: increased growth rate leads to increased competitive

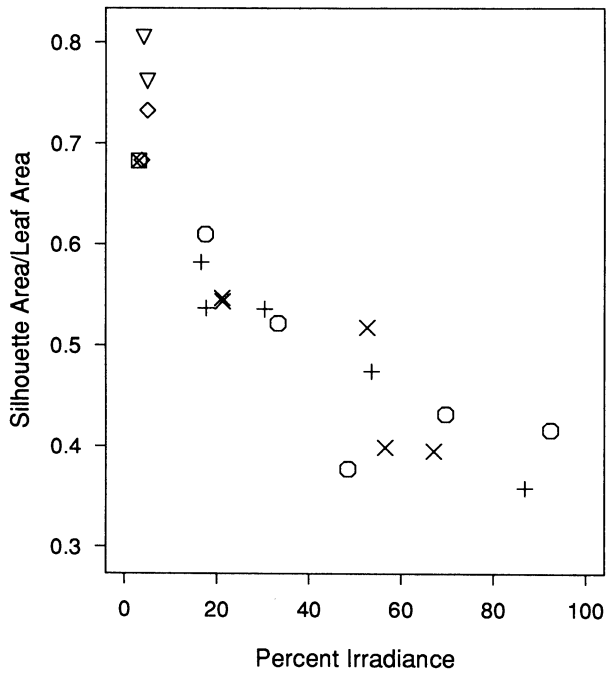


FIG. 5. Silhouette area : total foliage area ratio for *Abies amabilis* in relation to percent of incident irradiance measured at the sample point within the canopy relative to the top of the canopy. Samples shown are from a single tree at heights:  $\circ$  4.0 m;  $+$  3.3 m;  $\times$  3.0 m;  $\triangle$  1.6 m;  $\nabla$  1.3 m;  $\diamond$  0.9 m.

overlap, increased maximum foliage densities (at high irradiance levels) lead to decreased irradiation and foliage densities below. We now compare the simulated responses of a group of trees in competition to those of an open grown tree, noting the balance of such feedbacks and the sensitivities of model outputs to the parameters. We also discuss the effect of foliage regime on the shade tolerance of a species in a pure stand.

Structure of simulated communities is influenced by parameter variation and plasticity in the acquisition and growth processes. Community structure can be described by four variables: plot leaf area index (LAI), survival of individuals, total height attained by the trees on the plot, and the mean height of living trees. These measures are partly interdependent; given all else equal, a decrease in tree survival causes a decrease in total height attained and an increase in mean height of surviving trees. However, an important feature of the model is that these output measures vary separately as parameters are adjusted due to the differing feedback compensation mechanisms controlled by the parameters.

Competitive outcome varies with initial spatial pattern, as well as model parameterization. The effect of model parameters is compared to the range of response due only to varying initial spacing. The different initial spatial patterns are generated from a Poisson distribution with a constant mean stem initial density, 4 trees per  $m^2$ , on a  $6\text{ m} \times 6\text{ m}$  plot with boundaries

wrapped in a torus. The wrapped boundaries were constructed by allowing trees at one edge of the plot to compete with trees on the opposite edge, so that the opposing edges were figuratively connected.

#### Baseline conditions

The baseline parameterization uses informal estimates of the model parameters obtained prior to model calibration (Table 4). Acquisition plasticity is not included here, so the same foliage-irradiation relationships hold for all trees. Realistic values were estimated for the unitless parameters,  $R$  and  $K$ , based on calibration to plot-specific irradiation attenuation data (described in *Calibration and prediction of observed patterns*). Realistic values for the remaining parameters ( $D$ , HINC, SINC, and SDEATH) were not investigated because these parameters govern a highly simplified series of steps translating irradiation intercepted to annual growth. The values of these parameters reflect the values assigned to maximum irradiation flux ( $I_0 = 100$ ), and conversion factor ( $E = 1.0$ ), and do not have meaning in the absolute, only in relation to each other (e.g., in this section SINC is 10 times larger than HINC). The investigation of realistic parameter values will become worthwhile as the model's representation of physiological processes is improved.

The emphasis in this section of the work is to investigate the many model outputs and their sensitivity to parameters. To increase speed of simulation, growth parameters represent a faster growing tree than occurs for the species and site conditions in the study area, but is realistic for other species. A baseline simulation envelope was created from running the baseline parameterization of the model on ten spatial patterns. One of these patterns is then used for the remaining runs where parameters are changed one at a time from their baseline values (Table 4).

#### Resource acquisition parameters

Changes in resource acquisition parameters alter, in opposite directions, the irradiation levels and foliage densities through the canopy. Because relative production equals irradiation intercepted divided by foliage density, a change in resource acquisition parameters implies a relatively strong change in relative production (e.g., an increased irradiation interception divided by a decreased foliage density). Relative production, and therefore growth, is high when parameters are set so that foliage density is low and irradiation levels are therefore high.

The parameter  $R$  is the fraction of light intercepted by an unshaded whorl.  $R$  represents the maximum foliage density for the species. In this paper, the unshaded whorls of *Abies amabilis* were assumed to have a leaf area density (LAD) that resulted in 20% ( $R = 0.2$ ) of the incoming vertical irradiation being intercepted. Changes in  $R$  have the largest effect on the relationship between irradiation and LAD at high ir-

TABLE 4. Sensitivity to change in each parameter. Values given in leftmost column are baseline value and (range tested).

| Parameters   | Summary of directional response of output variables |                           |                        |                              |                    |
|--|---|---------------------------|------------------------|------------------------------|--------------------|
|  | Direction of adjustment                             | Leaf area index over time | Total height (year 20) | Mean living height (year 20) | Survival over time |
| Resource acquisition parameters  |   |                           |                        |                              |                    |
| <i>R</i> : fraction of irradiation intercepted by whorl at top of canopy<br>0.2<br>(0.1–0.3) | <i>R</i> ↓  | ↓                         | ↑                      | ↑                            | ↑                  |
| <i>K</i> : power coefficient of foliage density attenuation<br>0.2<br>(0.05–0.5)             | <i>K</i> ↑  | ↓                         | ↑                      | (↑)*                         | ↑                  |
| <i>D</i> : relative irradiation level at which all foliage dies (%)<br>4<br>(0–20)           | <i>D</i> ↑  | ↓                         | (↑)                    | (↑)                          | (↓)                |
| Growth parameters  |   |                           |                        |                              |                    |
| HINC: height increment per unit production<br>0.0002<br>(0.0001–0.0003)                      | HINC ↑  | (no change)               | ↑                      | ↑                            | ↓                  |
| SINC: sector increment per unit production<br>0.002<br>(0.001–0.003)                         | SINC ↓  | ↓                         | ↑                      | ↑                            | ↑                  |
| SDEATH: relative production at which sectors die<br>40<br>(20–40)                            | SDEATH ↑  | ↓                         | ↓                      | ↓                            | (↓)                |

\* Arrows in ( ) indicate a slight change.

radiation levels (Fig. 6) and thus affect foliage densities in the entire canopy. A reduced value of *R* decreases foliage throughout the canopy (Fig. 7) so that light penetrates deeper into the canopy and the resulting plot leaf area index (LAI) is lower (Fig. 8a, *R* decreased). However, with increased irradiation available, acquisition is increased relative to foliage density and therefore relative production and growth increase. Individual tree survival (Fig. 8b, *R* decreased) and total height (Fig. 8c, *R* decreased) are enhanced. The height dis-

tribution is shifted by ≈ 1 m but remains similar in shape (Fig. 8d, *R* decreased). In summary, even though LAI is reduced, both dominant and suppressed trees benefit from the increased availability of resources deeper into the canopy. A similar result occurs in an open grown tree.

*K* is the power coefficient controlling the convexity of foliage response to irradiation decay with increasing depth in the canopy. Although the biological interpretation of *K* is not precise, *K* relates to the contrast

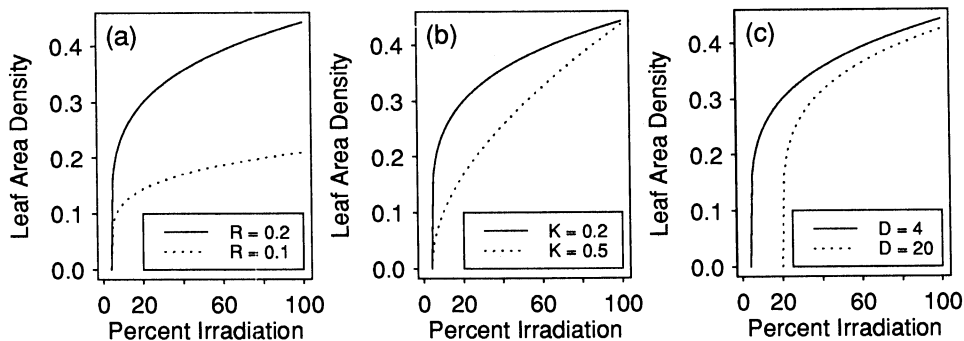


FIG. 6. Examples of the different form of the relationship between leaf area density (LAD) and percent irradiation, as resource acquisition parameters (·····) are changed from the baseline parameter values (—). (a) A reduction in maximum interception rate, *R*; (b) an increase in attenuation power coefficient, *K*; (c) an increase in the minimum irradiation level at which foliage survives, *D*.

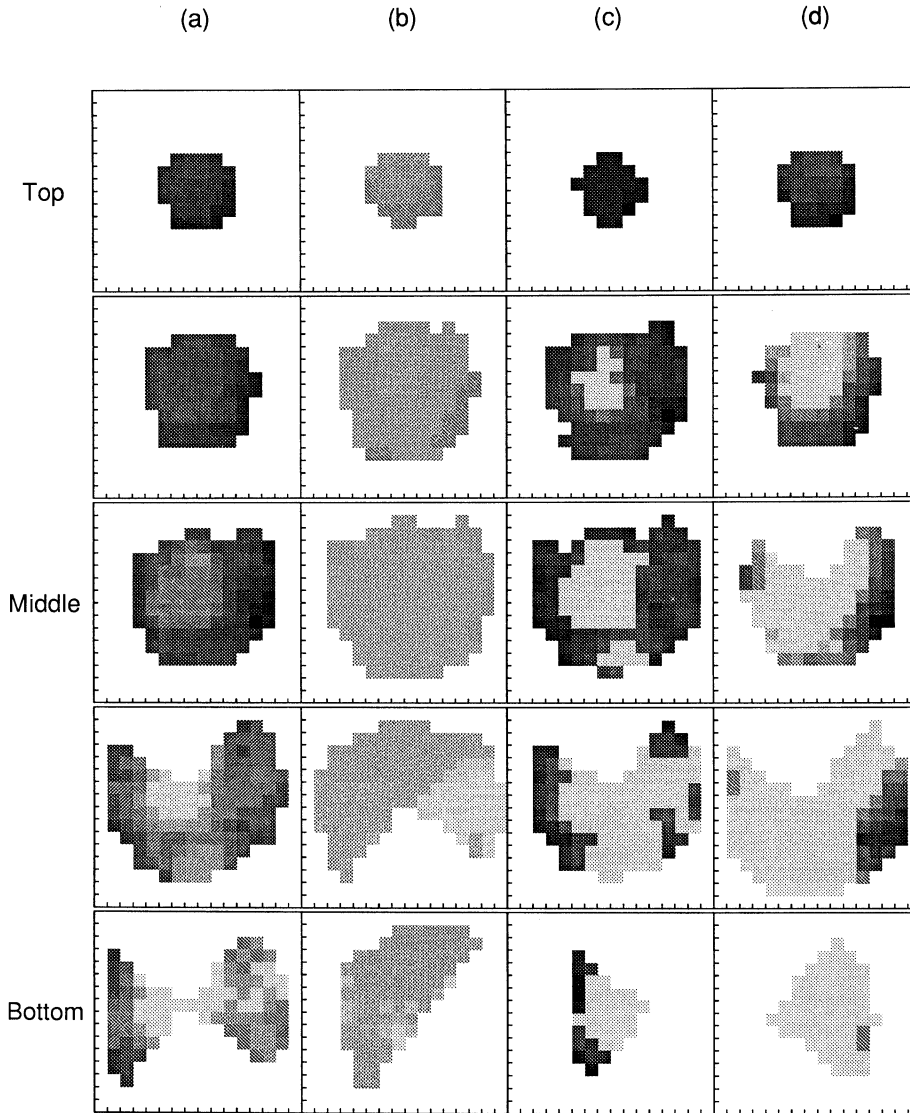


FIG. 7. Foliage distributions on whorls at a series of positions from the top to the bottom of a crown simulated with different parameter values. The same initial conditions and spatial arrangement of trees were used for each simulation. The whorls shown are from the same tree at the same spatial location in each simulation. Each whorl is centered in a block of  $1.6 \text{ m} \times 1.6 \text{ m}$  and each foliage cell is  $0.1 \text{ m} \times 0.1 \text{ m}$ . (a) Baseline parameter values (symbols defined in Fig. 5 legend);  $R = 0.2$ ,  $K = 0.2$ ,  $D = 4$ ; (b)  $R$  decreased ( $R = 0.1$ ); (c)  $K$  decreased ( $K = 0.1$ ); (d)  $D$  increased ( $D = 20$ ).

between high and low foliage densities in open grown and competing trees.  $K$  is presumably dependent on the foliage characteristics of the species, for example, leaf angle, efficiency of photosynthate production, and maintenance requirements.  $K$  may also exhibit plasticity and therefore vary within an individual; we used this in calibrating the model. Changes in  $K$  affect the middle of the LAD–irradiation curve (Fig. 6b) and therefore foliage densities in the middle and lower canopy. In baseline simulations,  $K$  was set so that foliage response at high to medium light was fairly flat and response at low light levels was steep. A low value of  $K$  ( $<0.2$ ) produces a highly contrasted foliage distribution where foliage is either dense or nonexistent (Fig.

7c). When  $K$  is increased to create a steeper upper canopy foliage attenuation, foliage distribution is less contrasted and LAI decreases (Fig. 8a,  $K$  increased). However, as with a decrease in  $R$ , more acquisition relative to foliage density occurs, and survival (Fig. 8b) and total height (Fig. 8c) increase. Most classes in the height distribution have increased frequencies due to the extra surviving trees (Fig. 8d). Height growth of an open grown tree also increases.

$D$  is the irradiation level at which all needles of a shoot die and changes mainly affect the lower part of the canopy (Fig. 6c). As with  $K$ ,  $D$  is likely to vary depending on the foliage characteristics of the species and also due to plasticity exhibited between individuals

and within an individual. For a high value of  $D$ , foliage die-off occurred at a higher irradiation level and total foliage was greatly reduced (Fig. 8a,  $D$  increased). However, in contrast to the results for decreased  $R$  and increase  $K$ , foliage reduction occurred mainly in the middle and especially lower canopy (Fig. 7d). Therefore, large trees were positively affected while small trees experienced both reduced irradiation and reduced foliage were negatively affected. Survival decreased (Fig. 8b) and total height attained increased very slightly (Fig. 8c). The height distribution shifted slightly in the positive direction (Fig. 8d). For an open grown tree, height increases slightly due to the reduction of foliage and increase in irradiation in the lower crown.

$E$  is the relative efficiency of conversion to photosynthate. In this section  $E$  was fixed at 1.0, reflecting an assumption that all foliage is equally efficient, but in calibrating the model it was essential to use plasticity in  $E$ .

#### *Resource utilization/growth parameters*

Height increment is controlled by the slope HINC which represents increment per unit relative production, i.e., growth efficiency. When the efficiency of height growth was increased, total foliage was nearly unchanged over time (Fig. 8a, HINC increased), while survival decreased (Fig. 8b). Total height attained over time increased (Fig. 8c) as did the range of heights at year 30 (Fig. 8d). In the model, HINC is assumed to be a nonplastic, species dependent parameter.

Sector increment is controlled by the slope SINC representing increment per unit relative production, and this influences crown shape. When sector growth was decreased and narrow crowns were produced, growth of LAI had a substantially reduced initial slope but exceeded baseline levels after year 20 (Fig. 8a, SINC decreased). Wide crowns utilized plot space more rapidly, but the gains in LAI were short-lived; for narrower crowns, survival was increased (Fig. 8b, SINC decreased). An interesting result of decreased sector growth was that total height increased (Fig. 8c, SINC decreased). Although narrow crowns received a slight loss in relative production of whorls through increased within-tree vertical overlap of whorls, this was more than offset by an increased relative production due to the reduced whorl overlap between trees. In contrast, for an open grown tree, a reduction of sector growth resulted in more self-shading and therefore a reduction in relative production and height growth.

Sector death is determined by a critical value, SDEATH, of relative production. When SDEATH was increased, reducing the number of living branches, total foliage was greatly decreased after the first few years (Fig. 8a, SDEATH). Survival and total height decreased (Fig. 8b, c, SDEATH decreased), indicating a foliage-survival relationship opposite to that produced by changes in all other parameters except  $D$  and HINC. Increases in SDEATH and  $D$  imply that densities at

high irradiation levels are not substantially reduced and therefore a reduction in foliage low in the canopy is not mitigated by increased irradiation.

#### *Discussion of shade tolerance in a pure stand*

Tree growth is simulated as a complex product of relative production, the amount of irradiation intercepted divided by a cost of maintaining foliage. For a sector, relative production equals  $\Sigma Ir/\Sigma r$ . If  $I$  and  $r$  are constant for all of the  $c$  cells in a sector, then sector relative production equals  $I$ . As the variation in  $I$  and  $r$  across the sector increases, relative production becomes somewhat greater than  $I$ , representing a higher productivity for the sector if foliage is concentrated in a few cells. This definition of relative production is somewhat arbitrary but was chosen because it resulted in a realistic crown structure for an open grown tree.

An implication of this cost function is that higher densities (e.g., high  $R$  or low  $K$ ) always resulted in lower irradiation levels throughout the canopy and therefore lower relative production. Rather than indicating a peak in relative production at some level of foliage-irradiation regime, this cost function maximizes relative production at  $R$  near 0, which is clearly unreasonable, and  $K$  values  $>1$ , which we also consider unreasonable. Although lacking appropriate limiters at extreme parameter values, this function provides a reasonable approximation of the growth process for the parameterizations used here.

The results indicate that shade tolerance of a species (i.e., decreased mortality and increased growth) is related to the foliage-irradiation regime. If foliage maintenance is a significant cost then a given amount of irradiation interception is most optimally attained at high irradiation levels and low foliage density rather than the opposite. Therefore, shade tolerance in a pure stand is not enhanced, and may be reduced, by better foliage survival. Zeide (1985) notes that species considered to be tolerant in mixed stands are able to sustain higher foliage densities than neighbor species under competition for irradiation. However, increased foliage survival does not enhance shade tolerance in a pure stand. "[In pure stands] the ability of tolerant species to utilize more light is counterbalanced by their denser canopies, just as higher light requirements of intolerant species are offset by their sparser canopies" (Zeide 1985). An exception to this is that enhanced foliage survival in the lower canopy only (via the parameter  $D$ ) increases shade tolerance in a pure stand. In the next section, we also show that if the increase in foliage density is differentially incurred by the suppressed branches and trees via acquisition plasticity, then shade tolerance in a pure stand is enhanced.

#### SENSITIVITY TO INITIAL SPATIAL PATTERN AND PLASTICITY

It was hypothesized that competitive outcome would depend on the degree of aggregation in the initial spatial



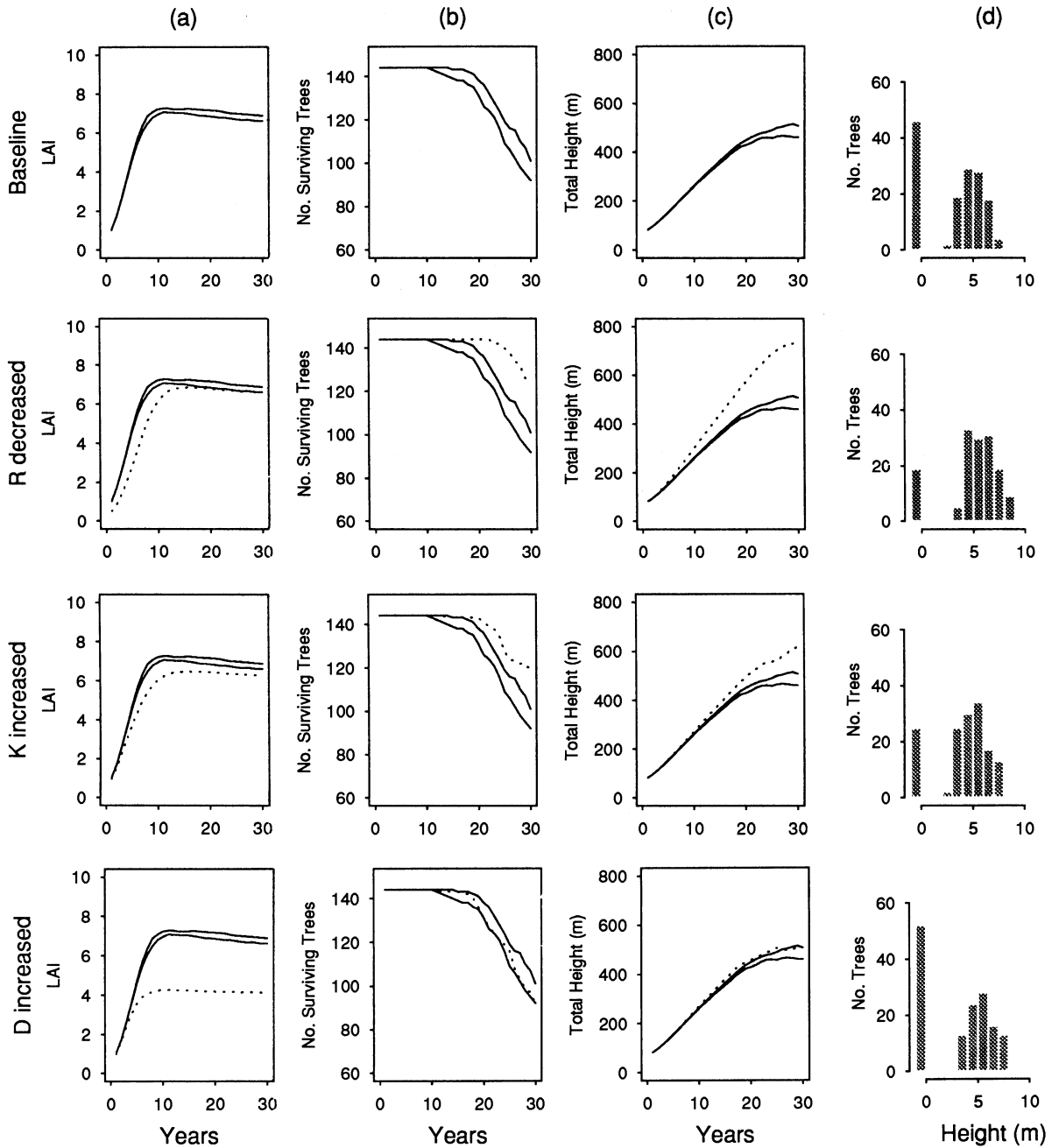


FIG. 8. Sensitivity to parameter variation of WHORL model outputs (a) leaf area index, (b) surviving trees, (c) total height of trees on simulated plot, and (d) frequency distribution of tree heights at year 30 where the leftmost column represents dead trees. Baseline parameters are defined in Table 4. The baseline simulation envelope, —s, indicates the minimum and maximum values at each year, from simulations on 10 random spacings with a mean density of 4 trees/m<sup>2</sup>. The baseline simulation envelope is repeated on each sensitivity test, where ···· shows the effect of a change in one parameter: *R* decreased, *R* = 0.1; *K* increased, *K* = 0.5; *D* increased, *D* = 20; HINC decreased, HINC = 0.0003; SINC decreased, SINC = 0.003; SDEATH decreased, SDEATH = 20.

pattern and that this effect might depend on whether different types of plasticity were incorporated into the model. Acquisition plasticity is represented in the model as differential foliage survival among height classes. Growth plasticity is represented in two ways: sectors

grow and die independently, and sectors die differentially dependent on tree height class. Independence in sector growth/death implies an asymmetrical plastic response. The corresponding nonplastic assumption is simulated by having all sectors in a whorl grow sym-

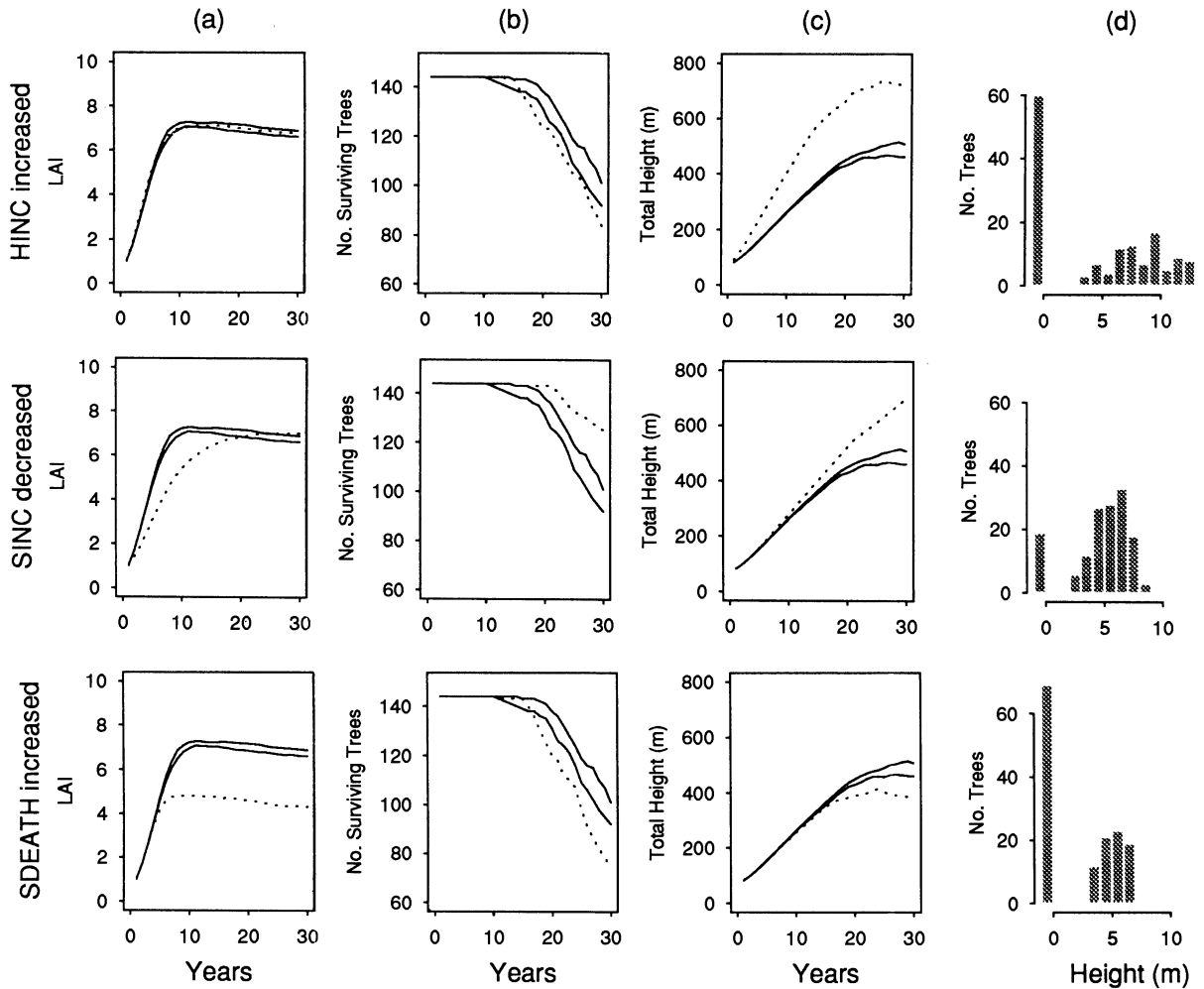


FIG. 8. Continued.

metrically in accordance with relative production summed over the whorl. In contrast, differential foliage survival and sector death rate are whole tree attributes and do not in themselves produce crown asymmetry. As modeled here, decreasing branch die-off is effectively equal to increasing the effective conversion efficiency gained by small size classes via acquisition plasticity. Therefore, in this section, we group these effects together as whole tree plasticity, and isolate the effect of the asymmetric plasticity due to sector independence.

We investigated two levels of whole tree plasticity (constant vs. size-class dependent  $R$ ,  $K$ ,  $D$ , and  $SDEATH$ ), two levels of asymmetric plasticity (dependent vs. independent sector growth), and four levels of spatial aggregation (Table 5) in a factorial design and calculated the impact on LAI, total height, tree survival, and crown structure. Each condition in the factorial design was replicated on four realizations of the aggregation level to provide a range of response due to difference between patterns.

### Results

The interactions between the effects of spatial pattern, asymmetric plasticity, and whole tree plasticity can be viewed by comparing the development of simulated communities over 30 yr (Fig. 9). An interaction between the effects of spacing and asymmetric growth is apparent: At the lowest aggregation level, asymmetric growth has little effect on stand production because all trees are surrounded relatively evenly. However, at high aggregation levels, asymmetric growth markedly increases production. At year 30, the ranges of LAI, total height, and survival under asymmetry were increasingly separated from those under symmetry as initial aggregation was increased. LAI decreased with aggregation for the symmetric case but remained the same or increased with aggregation for the asymmetric case.

Whole tree plasticity greatly increased productivity as measured by the three indicators. In addition, it appeared to increase the advantage of asymmetry over

TABLE 5. Factors in the three-way factorial design to investigate interactions.

| Factor                       | Levels   | Calculations   |
|------------------------------|--|--|
| Asymmetric growth plasticity | 1. Nonplastic:<br>Symmetric whorl growth and death                                 | Sector Increment =<br>$\text{SINC} \left( \frac{\sum_i^N \text{relative.production}.S_i}{N} \right)$<br>where;<br>SINC = growth slope<br>N = number of sectors/whorl |
|                              | 2. Plastic:<br>Asymmetric sector growth and death                                  | SINC(relative.production.S)  |
| Whole tree plasticity        | 1. Nonplastic:<br>K = 0.2<br>D = 4<br>E = 1<br>SDEATH = 40                         |  |
|                              | 2. Plastic:<br>K = 0.2<br>D = (0, 2, 2)<br>E = (3, 1.5, 1)<br>SDEATH = (1, 20, 40) |  |
| Aggregation                  | (1) Random*<br>(2) Double Poisson†<br>(3) Double Poisson†<br>(4) Double Poisson†   | Specification of distribution:<br>N = 144<br>N = 144, n = 6, r = 0.5<br>N = 144, n = 12, r = 0.5<br>N = 144, n = 20, r = 0.9   |

\* Total of  $N$  points, randomly distributed.

† Randomly pick a coordinate, assign between 1 and  $n$  points within a radius  $r$ , and then repeat until  $N$  total points have been assigned.

symmetry for aggregated patterns. Whole tree plasticity increased the survival of trees <3 m in height, which is also the group with the most asymmetric crowns and therefore benefits most from asymmetry.

An increase in initial spatial aggregation resulted in reductions in the three response variables. However, an exception occurs when both types of plasticity are in effect: then LAI and survival increased as aggregation increased.

Several trends are apparent in the development of LAI, survival, and total height. Under nonplastic acquisition and branch death, LAI leveled off by year 10. However, under plasticity, LAI continued to increase through year 30 (Fig. 9a). The effect on total height was similar (Fig. 9c). Whole tree plasticity did not delay the onset of mortality but slowed the rate dramatically during the remaining years (Fig. 9b). The advantage of asymmetry at aggregated spacings arose early for LAI and was strongest around year 10–15. The advantage of asymmetry for total height also began early on, especially for aggregated spacings, and increased over time so that the largest differentiation from the responses under symmetry was at year 30. The same was true for survival over time.

Crown structures of 10 randomly chosen trees over a range of heights were sampled for each simulation condition. The crown structures for small and medium (<4 m tall) trees were quite variable in terms of apex

angle and number of living whorls. Crown angles were wider for smaller trees only when whole tree plasticity was in effect. These results were also observed during the model calibration.

#### CALIBRATION AND PREDICTION OF OBSERVED PATTERNS

The model produces multiple outputs which inform about its effectiveness. The comparison of multiple outputs to data produces multiple assessment criteria. Because the choice of which of many criteria to include or emphasize in calibration is subjective, the definition of what is optimal is subjective also. For example, height distribution may be predicted well according to some measure and yet the predicted crown structures may be unreasonable. No matter how close the fit to height distribution, model parameters could not be said to be “statistically significant”; to exalt such a fit implies that a biased choice was made, that crown structure was not important. Furthermore, the model may produce outputs that are important but for which we lack appropriate data. When criteria can be defined with flexibility, it is not possible to obtain a completely objective statement (e.g., statistical significance) about the model’s prediction of the data.

It is reasonable to optimize some weighted combination of output criteria, thus reducing the multivariate criteria to a univariate one. The selection of outputs

to be included, and their weighting, must be done prior to the calibration based on modeling goals and available data. The outputs are likely to require different measures of fit such as  $R^2$  for the prediction of individuals points and a Kolmogorov–Smirnov criteria for comparing frequency distributions. In addition, the outputs themselves may vary in their sensitivity to parameterization. The weighting of measures of fit must consider their different scales and the sensitivities of the outputs to parameter changes. A related problem is that some measures of fit will involve complex pattern recognition and thus create a smaller scale version of the same multivariate criteria problem we are faced with overall. If an objective prioritizing system is applied, we may have a calibration that is best, by our definition. However, we have not produced a simple measure that is comparable to a distribution, as is a Student's  $t$  value, or even to the values produced by other models, as in some cases is an  $R^2$  value.

Even if some single criteria combining several outputs is produced, there may be many parameterizations which optimize this criteria. This is because the numerous and varied parameters of complex models may impart a high degree of flexibility in the control of model outcome. In this case, it is reasonable to categorize parameterizations (e.g., good, medium, and bad). Then the calibration objective is to uncover implications of the models assumptions through analyzing all parameterizations which are “good,” all which are “bad,” etc. Thus, sensitivity analysis becomes an integral component of the calibration.

Another problem in calibration is that it is often impossible to measure some attributes of each individual or even of a sample without disturbing permanent plots. In our case, the detailed measurement of crown structure had to be sampled on a separate plot from that being modeled, introducing uncertainty in the representativeness of this sample.

All of the above problems, multiple outputs with varied measures of fit, flexibility of parameterization, and measurements that must be performed outside the plot in question, occur in the following calibration. We assume that because of multiple outputs, what is optimal is not precisely defined. In addition, the flexibility induced by the many parameters, and the uncertainty in data comparison induced by out-of-plot disruptive field measurements, further negates the meaning of “optimal parameterization” in the sense in which Ford and Diggle (1981) were able to use optimization procedures in fitting a four-parameter competition model. Our objective is therefore to qualitatively evaluate the model's predictions and at the same time assess the importance of the assumptions of plasticity in resource acquisition and linear vs. nonlinear height growth.

#### *Methods*

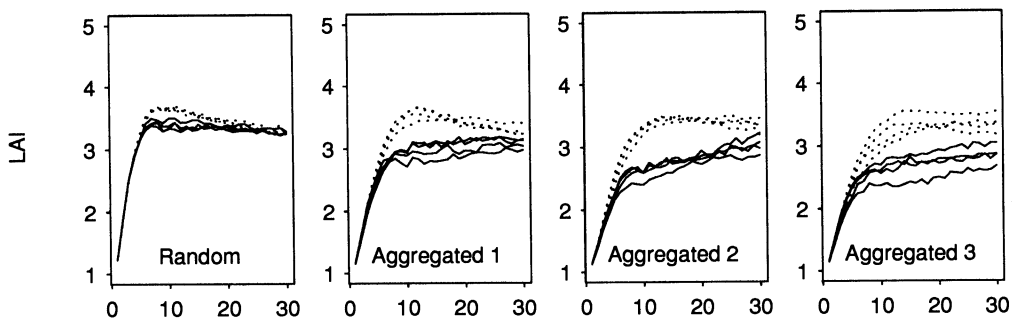
We simulated the 30-yr growth of trees initialized in the estimated spatial pattern of study plot C just

after the clear-cut in 1957. Outputs generated under different parameterizations were evaluated by comparison to measurements made on plot C 30 yr after the clear-cut. The first measurements on the plot were taken in 1978, 21 yr after the cut. So to simulate the entire development of the plot some assumptions must also be made about initial spatial pattern and initial heights. Average annual mortality between 1978 and 1985 was  $\approx 5$  trees per year. Mortality rate for the first 5–10 yr after release is assumed to be lower than this average because irradiation conditions were improved for all trees. We therefore assumed that 10 yr of mortality at the average rate occurred before 1978. To incorporate this, 50 extra trees were added to the plot's 1978 spatial pattern. These 50 points were added using a double Poisson process (aggregation) atop the original points. A point previously existing was drawn randomly and then a randomly drawn number  $n$  of points were assigned random locations within a predefined radius around the existing point. In mature stands near the study site, understory heights are commonly in the range from  $\approx 0.3$  to 0.7 m. From this we assumed that heights just after the clear-cut were distributed as a truncated normal random variable with mean 0.5, standard deviation 0.5, and limits of 0.35 and 0.65.

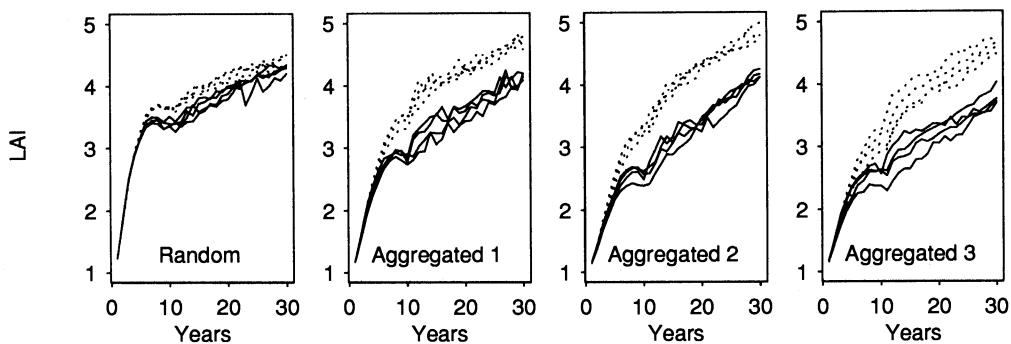
Neighborhoods outside plot boundaries are not known. Even if boundary neighbors were known, we would also need to know their neighbors, and so on, to mimic the plot conditions precisely. Boundaries of the plot are wrapped in a torus; therefore, we simulate a plot with similar but not identical density and clumping pattern.

In calibrating the parameters, we distinguish between parameters that represent characteristics measurable in the field and are constrained to a measured or estimated range, and parameters that are fit freely based on model outcome. Resource acquisition parameters describe the instantaneous process of irradiation attenuating through the canopy and can be estimated directly from field measurements and independent of the model. Calibration of the model is only meaningful if we constrain these parameters to vary within the range of uncertainty observed in the measurements. Although no direct measurements were available, ranges for  $R$  and  $K$  were estimated using irradiation attenuation output of the 1-yr model, which only predicts the foliage-irradiation regime and not new growth (Sorensen 1989). When the model was initialized with the measured current conditions on plot R, it predicted measured irradiation attenuation well when  $R$  was in the range 0.15–0.25 and  $K$  was 0–0.3.  $D$  and  $E$  values were constrained to an informally estimated range. In contrast, no constraint was placed on possible values for the growth parameters. Growth parameters describe seasonal increment as a function of resource acquisition at a single time point assumed to represent an average for the season. The growth parameters are therefore derived from the model form; they are com-

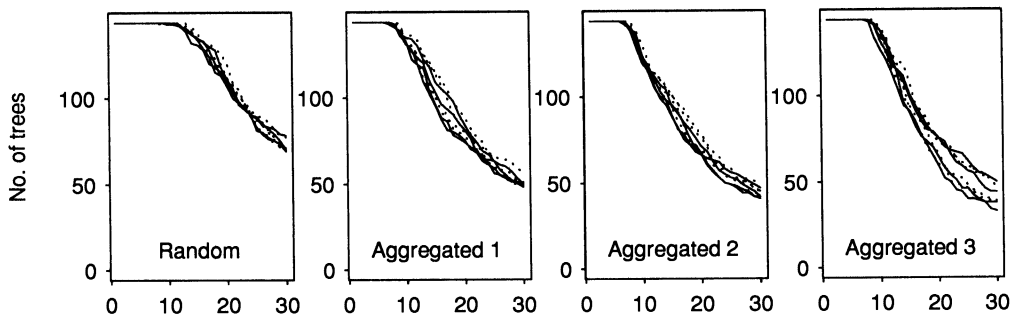
(a) Non-plastic acquisition



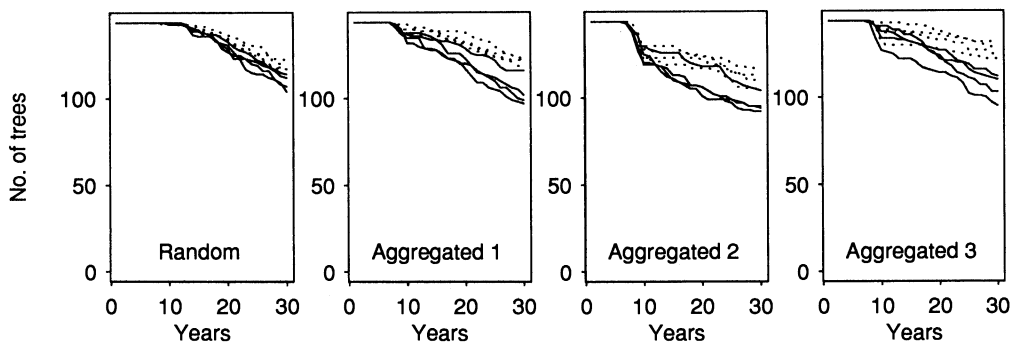
Plastic acquisition



(b) Non-plastic acquisition



Plastic acquisition



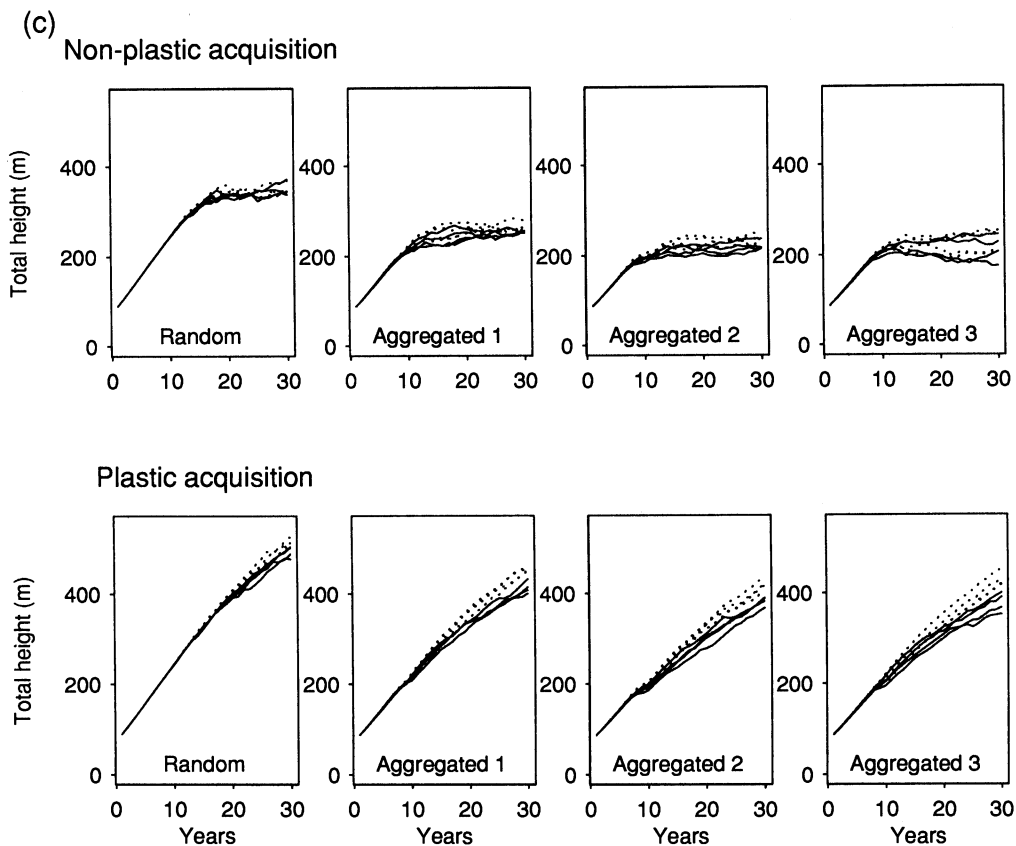


FIG. 9. The effects of initial aggregation and plasticity on (a) leaf area index, (b) number of surviving trees, and (c) total height of trees. Simulations are identified by initial aggregation levels (random to aggregated 3), nonplastic vs. plastic resource acquisition (upper and lower), asymmetric vs. symmetric branch growth and death (— vs. ·····), and random realizations of a given aggregation level (multiple lines of the same type). See Table 5 for parameter values.

pletely dependent on the acquisition parameters and must be fit based on model outcome.

Four assessment outputs were chosen: the histogram of observed heights at year 30, the relationship between height at year 30 and the previous 2-yr height increment, and crown structure of both plot-grown and open-grown trees. These criteria were chosen to coincide with data collected and to examine key aspects of the model structure: the prediction of the relative competition status of interdependent individuals, and the prediction of growth form as it develops over time. The prediction of foliage distribution cannot be used as a criterion because we lack appropriate data. Height distribution can be manipulated via growth equations without regard to realistic crown structure and foliage distribution. Crown structure, which reflects both height increment and foliage distribution, affords an integrated look at the assumptions involved in both the growth and acquisition processes.

Evaluation of the fit of each output to corresponding data involved only qualitative comparisons, in part because of the uncertainties about the true initial and boundary conditions of the plot. Our assessment involved considering the above outputs in a prioritized

order. The first step was to select branch and height growth parameters that resulted in a crown angle and inter-whorl increments realistic for a tree grown without neighbors (Fig. 10). That is, we assume here that a tree had the same growth efficiency whether under competition or not. The second step involved running the model under many parameterizations and ranking these by the height distribution and, independently, by the crown structure. Height distribution fit was judged by comparing the cumulative distribution of a given run to that expected under the observed height distribution (Fig. 11). Crown structure was judged informally by using two-sided crown drawings where the largest branch of a whorl is drawn to one side and the smallest branch to the other side (data in Fig. 3, simulations in Fig. 12). Twenty-eight trees ranging in height were sampled at year 30 for each simulation. Because crowns varied considerably, it is important to display all the trees from this sample rather than selecting a few. With only a subset of the great number of possible parameterizations tested and no formal definition of an optimal parameterization, a simulation must rank high in both height distribution and crown structure criteria. The definition of "best" runs presented here

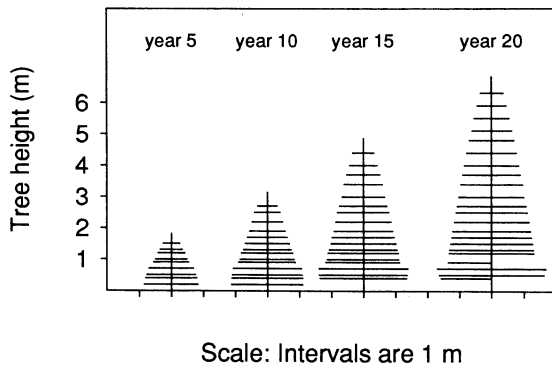


FIG. 10. Tree grown without competition from neighbors.

is considered only approximate: top ranking and other parameterizations are considered “best” runs while others are classified as “good” or “bad.” The third output, growth rate prior to year 30, was of lesser importance in distinguishing parameterizations because it was less sensitive than the other two.

### Results

Two parameterizations, I and II (Table 6) were considered to be best (Fig. 12 a, b); however, other close parameterizations might have made some small improvement in the three criteria. Both runs incorporated plasticity in acquisition, allowing foliage survival and conversion efficiency to be higher for smaller trees. Branch growth plasticity was also incorporated by allowing sectors to grow independently and reducing the minimum relative production required to sustain a branch for small trees. In addition, both these runs specified a foliage regime that produced relatively low foliage densities and high irradiation levels (Table 6). Implications of low and high foliage regimes were discussed in *Sensitivity to parameters*.

Parameterizations I and II gave the best fit of all parameterizations tested for height distribution and crown structure respectively and a good fit with respect to both criteria. The height histogram produced by parameterization I predicts class frequencies very similar to observed frequencies for mortality and the 0.5–<3.5 m size classes. However, this and all simulations underestimated the number of trees that stayed alive but remained <1 m tall. It is theoretically possible to adjust to parameters such that the smallest trees neither die nor grow out of this size class; however, many attempts to do this while maintaining other parts of the height histogram failed. In addition, the model overestimated the number of trees which grow out of the 3.5–<5.5 m classes and into higher size classes.

Simulated trees <1.5 m were always asymmetrical and had somewhat flattened crowns, although top branches were not as long as those observed. The model predicted that suppression of height increment preceded the suppression of sector (branch) increment. Trees

from 1.5 to 3 m had an intermediate crown apex angle, and were quite variable in crown length and asymmetry. Some had a rounded form where growth of lower branches had slowed or stopped, while others had lower branches that continued to extend. This variation was also present in the observed data. Trees >3 m tended to have a wider apex angle and a shorter crown than measured, although this was variable in both the simulated and observed crowns.

Among the medium to large trees, simulated inter-whorl increment was shorter than measured, and crowns appeared more dense than was observed. As judged by the inter-whorl increments of the observed crowns, the actual growth history indicated that height increments were smaller than predicted in the first 20 yr after release and greater in the last 10 yr. However, these trees were destructively sampled outside the plot being simulated and therefore may not be representative of crowns grown in the simulated plot. Only the last 2-yr increment is known for plot C. The predicted 2-yr growth increments on plot C appear to be unbiased and to have a similar shape as that observed. However, the predicted increments are much less varied for trees in the 3–6 m classes.

*Plasticity.*—Two types of plasticity were tested: differential acquisition for a given irradiance and differential sector death for a given acquisition level. We tested the effects by comparing the fully plastic model to a model with nonplasticity in one or the other effects. For both effects, nonplasticity was simulated by using constant instead of size class varying parameters. Sector independence, the third type of plasticity, was assumed for all simulations. When sector death was

TABLE 6. Best parameterizations of plasticity and range tested.\*

| Parameterization I       | Most extreme values tested |
|--------------------------|----------------------------|
| Acquisition              |                            |
| $R = 0.15$               | $R = 0.15$                 |
| $K = \{0.05, 0.2, 0.3\}$ | $K = \{0.05, 0.2, 0.3\}$   |
| $D = \{0.0, 2.0, 4.0\}$  | $D = \{0.0, 2.0, 9.0\}$    |
| $E = \{3.0, 1.5, 1.0\}$  | $E = \{3.0, 1.5, 1.0\}$    |
| Sector growth            |                            |
| $SDEATH = \{1, 5, 10\}$  | $SDEATH = \{1, 20, 40\}$   |
| Parameterization II      | Most extreme values tested |
| Acquisition              |                            |
| $R = 0.15$               | $R = 0.15$                 |
| $K = \{0.05, 0.2, 0.3\}$ | $K = \{0, 0, 0.2\}$        |
| $D = \{0.0, 2.0, 4.0\}$  | $D = \{0, 0, 2.0\}$        |
| $E = \{3.0, 1.5, 1.0\}$  | $E = \{0, 0, 1.0\}$        |
| Sector growth            |                            |
| $SDEATH = \{1, 10, 20\}$ | $SDEATH = \{0, 0, 10\}$    |

\* Plasticity was assigned according to relative tree height in the stand. Once the height of the fifth largest tree (dominant height) was >2.0 m, three classes were constructed at each annual cycle, and different values for  $K$ ,  $D$ , and  $E$  were assigned. The left, middle, and right values within each pair of {} brackets are for trees  $\leq 0.5$ ,  $>0.5$  to  $\leq 0.75$ , and  $>0.75$  times the dominant height, respectively.

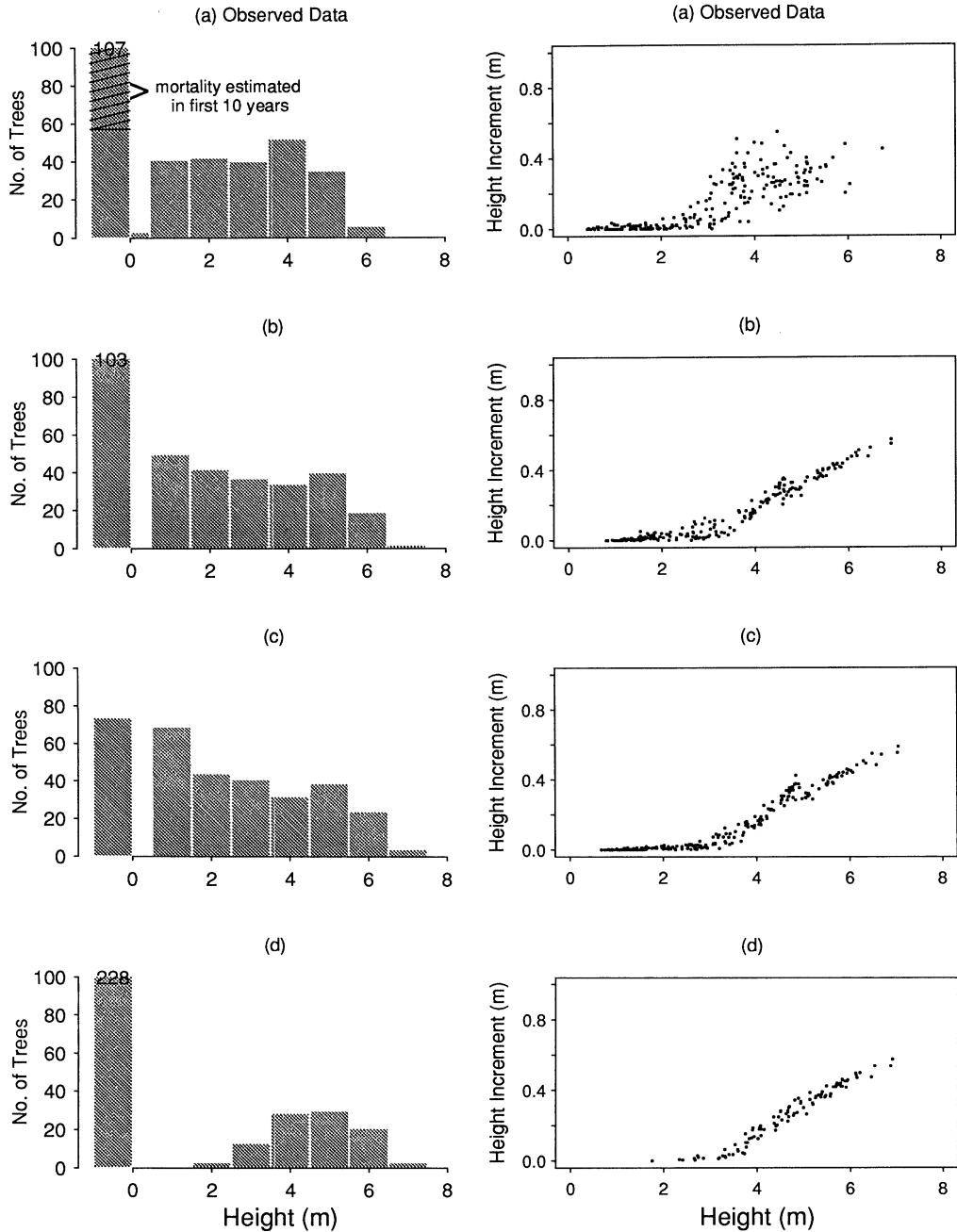


FIG. 11. Frequency distribution of tree heights at year 30, and relationship between last 2-yr height increment and height at year 30. The leftmost column of each histogram represents dead trees. (a) Observed data. (b) Parameterization I. (c) Parameterization II. Both parameterizations I and II incorporate plasticity. See Table 6 for parameter values. (d) Parameterization III, not incorporating plasticity. See Table 5.

changed from constant to plastic, survival and growth were greatly increased, so that all size classes <6 m had increased numbers. When acquisition was changed from nonplastic to plastic, survival and growth were also increased (Figs. 11 and 12). Acquisition plasticity was important to reproduce the large variation in crown length and number of living branches observed among small and medium trees in the field (Figs. 3 and 12).

In addition, acquisition plasticity also slightly increased variation in the relationship between 2-yr height increment and height at year 30 for 2–3 m tall trees. However, the simulated variation was much less than that observed.

*Height growth formulation.*—Simulations with height growth specified as a linear function of acquisition were compared to simulations with nonlinear height growth.



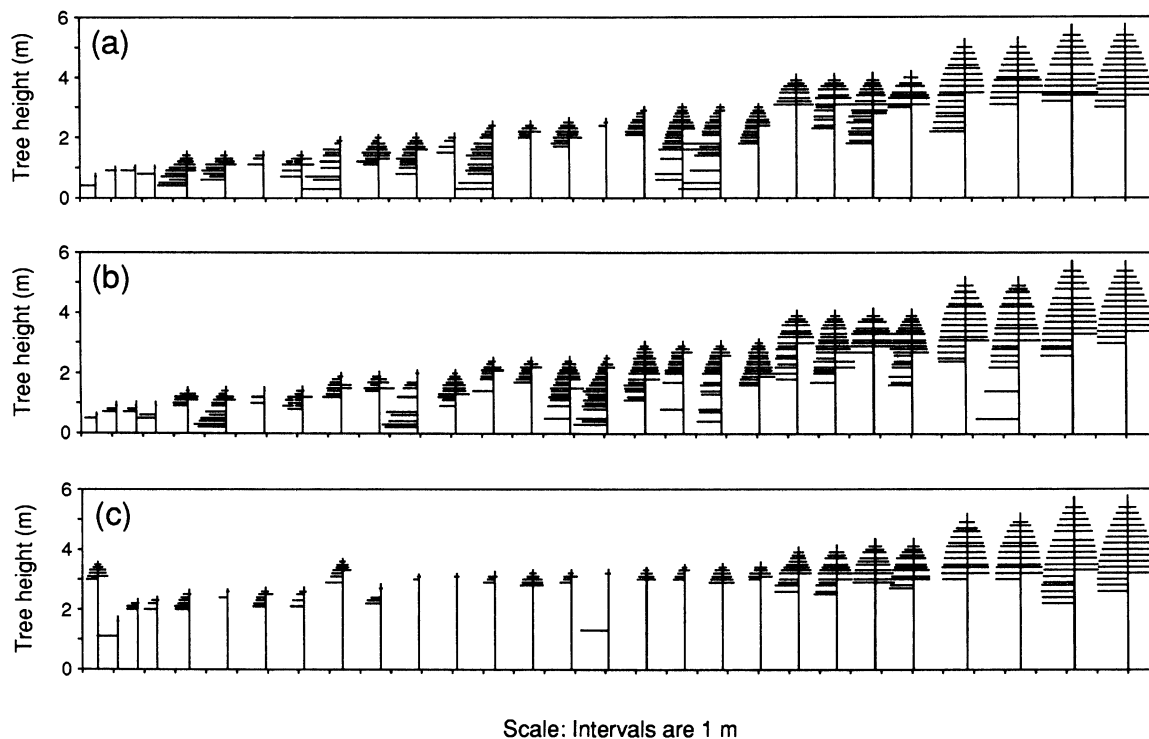


FIG. 12. Simulated crown structures, randomly chosen from increasing height classes. Crown structure is represented by maximum branch length at each whorl position drawn on the left and minimum branch length on the left. No branch on the right indicates the occurrence of three or less living branches at the whorl position. (a) Parameterization I and (b) parameterization II incorporating acquisition plasticity, (c) parameterization III not incorporating plasticity.

Nonlinearity in this function, with a decrease in the rate of height growth increment per unit of acquisition, did not enhance or substantially detract from the fit. The parameterizations discussed here assumed a linear height growth function.

#### *Discussion of calibration and predictions*

Plasticity in resource interception and conversion was required to simulate the occurrence of suppressed trees <1.5 m alongside 6 m tall trees within a plot. Acquisition plasticity was also required to simulate the overall variation in crown length observed within a plot. This was because acquisition plasticity increases the growth and survival of suppressed branches on suppressed trees.

The parameterization resulting in an appropriate enhancement of suppressed branches and trees implied a large differential in the acquisition parameters between suppressed, intermediate, and dominant trees. Efficiency of conversion ( $E$ ) for foliage was three times higher for suppressed than for dominant trees. For suppressed and dominant trees respectively,  $K$  was set at 5 and 30% of its allowed range (0–1), SDEATH was set at 1 and 20% of its allowed range ( $\approx 0$ –100), and  $D$  was set at 0 and 4% of its allowed range (0–100). The differential implied by these parameters does not seem unreasonable considering the large difference in light environments encountered by suppressed vs. dominant trees.

Crown angles were wider than observed for large trees and were reasonable or possibly too narrow for small and medium trees. This implies that sector growth rates used in the simulations were too high for tall trees only. We assumed that SINC was constant under competition and the same for an open grown tree. To improve prediction of crown angle variation, SINC would be reduced, affecting all trees. Widening of crown angles under suppression could be increased via the acquisition or growth processes. If acquisition can be enhanced for small and medium trees via acquisition plasticity, then height growth will also be enhanced and crown angle widening will not occur. The crown widening must be achieved through the alteration of the relationship between height and sector growth, i.e., through the alteration of cost functions in the growth process. Cost functions incorporate maintenance requirements and the availability of photosynthate for transport to the trunk. In the model the cost of maintaining foliage is incorporated into branch relative production; however, in reality, other physiological and structural factors enter in. Export to the trunk is then assumed to be equal to or a constant proportion of the relative production of a branch. However, simulations of branch growth show this to be a much more complex relationship (Ford and Ford 1990, Ford et al. 1990). The underestimation of crown angle variation by the model may indicate that the assumption of export as a constant proportion of branch productivity is invalid,

that export to the trunk for height growth is reduced further than is proportional for very suppressed branches or for suppressed trees.

The model does not simulate existence without growth. Yet this occurs in the study plot. The observed frequency of trees between 0.35 and 1 m tall on the plot was not predicted by the model although many parameterizations were devised for this purpose. It was impossible to tune the model such that some trees would grow very slowly, or not at all, in height but remain alive. This indicates, again, the inadequacy of branch and height cost functions. The export from branch to trunk may be proportionally lower for suppressed branches or trees than for well-lit branches or trees. This would allow height growth to be slowed without reducing sector growth. A more effective change in the cost functions may be required to mimic observations. Cost functions may need to incorporate the possibility of growth stopping for some amount of time before the branch and tree death.

#### GENERAL DISCUSSION

It is challenging to elucidate general theories of competition in light of the broad system variation found in resource requirements, species traits, spatial pattern, plasticity, and distinctive time phases in plant and system development. In attempting to be general, competition models have used assumptions about the abstract plant form and the interaction between and response of subjects and neighbors. These assumptions, common to most models, are phenomena based rather than process based. For example, the phenomenon of asymmetric allocation of overlapped area is assumed to be a driving variable rather than an outcome of plant processes. These assumptions also prohibit plasticity. A focus on the processes of resource acquisition and utilization rather than neighbor-subject interactions results in more specialized models. However, it is our opinion that such models will enable more informative comparisons between systems and further the development of general ecological theories.

#### *Crown structure*

The effects of competition on crown structure can be modeled by considering the interaction between the two spatial processes of resource acquisition and growth over time. This model predicts realistic crown asymmetry, crown length, crown apex angle, and large variation in these parameters among and between height classes. Incorporation of plasticity in both these processes was found to be crucial in simulating a crown structure resembling those measured. To predict the observed crown asymmetry, sector growth independence is, of course, essential. To predict the observed widening of crown angles of suppressed trees, differential foliage survival and efficiency (acquisition plasticity) is important, while the ability to grow asymmetrically (growth plasticity) is less important.

Discrepancies between the measured and predicted

crowns reveal potential improvements to the model. The difficulties in predicting slow or nongrowing trees which remain alive and in generating the full range of crown apex angles seen between suppressed and large trees indicate the need for the inclusion of more physiological and structural factors into the cost functions for branch and tree growth. In addition, more complex cost and growth rules are needed to describe transitions in the relationship between height growth and acquisition accurately. For example, what is the change, if any, in height growth per amount of acquisition as a tree experiencing "normal growth" suddenly becomes suppressed in height growth? The processes of acquisition and of maintenance and growth costs are important in understanding when and why such transitions occur.

#### *Foliage and irradiation attenuation*

In the model, a given flux of irradiation is used more efficiently when the amount of foliage is reduced and irradiation levels are maintained deeper into the canopy. Thus, in a pure stand, a species with high foliage survival in poor light is predicted to have reduced productivity. However, if higher foliage density is maintained differentially by individuals in the lower canopy then productivity as measured by total height and LAI increases. In effect, the stand is now mixed with increased shade tolerance for one group of individuals, enhancing their productivity. This focuses attention on the need to define their foliage response curves more precisely and for different species.

#### *Plasticity and the importance of spatial pattern*

Without plasticity, an increase in initial spatial aggregation results in a decrease in plot productivity as measured by decreases in LAI, survival, and total height. When plasticity is incorporated, the range of LAI among different realizations of aggregated patterns increases, but the mean LAI does not decrease and may even increase with initial aggregation.

An increase in initial tree aggregation also enhances the advantage of asymmetric growth over symmetric growth with respect to all productivity measures. Asymmetric growth of a plant occurs when its components grow independently and when the pattern of competition varies around it, therefore no advantage is gained when pattern is completely uniform. On aggregated patterns, the LAI gains of asymmetric growth over symmetric growth are highest during the first 15 yr, after which time the rates of LAI increase over time are either equal (the time traces are parallel) or the rates under asymmetric growth drop with respect to the rates under symmetric growth. However, LAI may in some cases be negatively correlated to growth and survival. For aggregated patterns the advantage of asymmetry with respect to survival and total height increases with time. We did not test longer simulations to determine whether advantages due to asymmetric

growth decrease as self-thinning causes spatial pattern to become more uniform.

Plasticity in acquisition, while clearly advantageous, is equally advantageous on random and aggregated patterns. It seems reasonable that acquisition plasticity becomes more important as density, and hence overlap, increases, although this was not investigated.

#### *Improvements*

Both the sensitivity analysis and calibration of the model for a specific plot indicate a need to improve the cost functions which describe the maintenance and growth potential of a branch. For example, the proportion of branch wood to foliage, the requirement of branch thickening along with lengthening, hydraulic priority, and export to the trunk may vary with branch irradiation environment and vertical location within a tree. These factors also may vary in relation to the overall status of the tree. The model's ability to predict the existence of very slow-growing or nongrowing trees may be enhanced by altering the cost functions such that at some level of acquisition, branch or trunk maintenance is met but no growth is possible. A memory component may be necessary; for example, branch mortality may be related to the number of years spent in a suppressed state.

Other branch shapes can be represented almost as simply as the pie-shaped sector used here. For example each sector could have the shape of a diamond where the inner sides of the diamonds join together in a smaller circle, and the outer portions create a star-shaped whorl. This branch shape would result in an increased clustering in the foliage distribution in a whorl and throughout the canopy. In canopy irradiation models, total photosynthesis differs greatly between a uniform and clustered foliage distribution.

#### *Problems in model evaluation*

If the objectives of a modeling exercise are to understand or test assumptions about a process, the output of multiple measures has many advantages. For example, in this model, assumptions regarding the growth process cannot be tested by only assessing prediction of height. Similarly, the assumptions regarding resource acquisition cannot be tested only by assessing the prediction of foliage distributions. Growth assumptions are involved in predicting foliage distributions and vice versa. However, multiple outputs create problems in the objective calibration and evaluation of a model. In particular multiple outputs must be weighted in importance (e.g., Gentil and Blake 1981) and, as in this work, may have varied measures of fit. Multiple outputs may generally arise from complex models, with many parameters imparting such flexibility that uniquely optimal parameterizations may not exist.

However, the evaluation of single output competi-

tion models has also presented fundamental problems. These arise from the empirical, data-dependent form of the models and the spatial correlation of underlying error. When tested against data, indices of competition status are generally used to predict growth over a relatively small time increment, where new size (height or stem diameter) is well correlated to original size. While the space available for individuals is a predictor of size and growth, self-thinning and size hierarchy cause size to be a predictor of space available: there is no clear independent variable. With original size well-correlated to space available the achievement of the model can only be assessed as the information provided by the index beyond that contained in original size, i.e., after size is already in the regression equation. Competition indices have added varying amounts of explanation of diameter growth beyond that explained by original size (0–50 percent increase in variation accounted for, Beck 1974, Hatch et al. 1975, Daniels et al. 1986, Pukkala and Kolström 1987). These studies pertain to plantation situations or nonaggregated spacings, conditions where growth is generally more predictable.

The discrepancies between observations and predictions may be due to many different factors, such as measurement error, estimation error, and oversimplification in the model. A good biologically based model should predict the actual outcomes of the system so well that the only error left is measurement error (Guttorp and Walden 1987). In addition, we accept error from intentional oversimplifications of certain hopefully random effects (e.g., genetic variation, soil variation). However, it is usually the case that unintentional oversimplification in the model influences the spatial structure of the error resulting in neither independent nor identically distributed error (Guttorp and Walden 1987). It is likely that a less than perfect model will be biased, overestimating growth in some conditions and parts of the plot and underestimating growth on other parts. And it is likely that error within a spatially related plot is an underestimate of error sampled randomly from the population.

The problem of spatial correlation of error arises in the evaluation of any spatial model. When the model outcome is compared to the observed outcome for each individual, the spatial depiction of the individual errors may indicate particular shortcomings of the model and suggest improvements (Sorrensen 1989). In this paper individual trees were not compared to their corresponding field measurements primarily because of the difference between the assumed plot boundary conditions (wrapped) and the actual boundary conditions which were not measured. However, spatial correlation also is inherent in output that is not individual specific, such as height histograms and the crown structure of a random sample, as were compared in this work. One method to avoid spatial correlation of error is to model large areas and use only a randomly dispersed subsam-

ple of individuals for the assessment of the model's predictions.

#### ACKNOWLEDGMENTS

The authors are grateful to J. Renée Brooks for helpful discussions and for providing the data used for crown structure analysis. The authors also thank Peter Westhagen for substantial programming contributions. E. David Ford's and part of Kristin A. Sorrensen-Cothorn's contributions were sponsored by the Synthesis and Integration Project of the Joint U.S. Environmental Protection Agency-U.S.D.A. Forest Service Forest Response Program, a part of the National Acid Precipitation Assessment Program. Although the research reported in this article has been partly funded by the U.S. Environmental Protection Agency under the cooperative agreement CR814640 with the University of Washington, it has not been subject to Agency review and therefore does not necessarily reflect the views of the Agency, and no official endorsement should be inferred. The establishment of the forest plots were made through NSF Grant NSF DEB 77-15317. Douglas G. Sprugel and part of Kristin A. Sorrensen-Cothorn's contributions were supported through NSF Grant NSF BSR 84-15590 and USDA 86-FTY-0-0220. Computer code is available from Center for Quantitative Science, HR-20, University of Washington, Seattle, WA 98195 USA.

#### LITERATURE CITED

- Beck, D. E. 1974. Predicting growth of individual trees in thinned stands of yellow poplar. Pages 47-51 in J. Fries, editor. Growth models for tree and stand simulation. Research Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, Sweden.
- Bella, I. E. 1971. A new competition model for individual trees. *Forest Science* 17:364-372.
- Bonan, G. B. 1988. The size structure of theoretical plant populations: spatial patterns and neighborhood effects. *Ecology* 69:1721-1730.
- Brooks, J. R. 1987. Foliage respiration of *Abies amabilis*. Thesis. University of Washington, Seattle, Washington, USA.
- Cannell, M. G. R., P. Rothery, and E. D. Ford. 1984. Competition within stands of *Picea sitchensis* and *Pinus contorta*. *Annals of Botany* 53:349-362.
- Cochrane, L. A., and E. D. Ford. 1978. Growth of Sitka spruce plantation: analysis and stochastic description of the development of the branching structure. *Journal of Applied Ecology* 15:227-244.
- Daniels, R. F., H. E. Burkhart, and T. R. Clason. 1986. A comparison of competition measures for predicting growth of loblolly pine trees. *Canadian Journal of Forest Research* 16:1230-1237.
- Diggle, P. J. 1976. A spatial stochastic model of inter-plant competition. *Journal of Applied Probability* 13:662-671.
- . 1983. Statistical analysis of spatial point patterns. Academic Press, London, England.
- Ek, A. R., and R. A. Monserud. 1974. Trials with program FOREST: growth and reproduction simulation for mixed species even- or uneven-aged forest stands. Pages 56-73 in J. Fries, editor. Growth models for tree and stand simulation. Research Note 30, Department of Forest Yield Research, Royal College of Forestry, Stockholm, Sweden.
- Ford, E. D. 1975. Competition and stand structure in some even-aged plant monocultures. *Journal of Ecology* 63:311-333.
- Ford, E. D., A. Avery, and R. Ford. 1990. Simulation of branch growth in the *Pinacea*: interactions of morphology, phenology, foliage productivity and the requirement for structural support on the export of carbon. *Journal of Theoretical Biology* 146:15-36.
- Ford, E. D., and P. J. Diggle. 1981. Competition for light in a plant monoculture modelled as a spatial stochastic process. *Annals of Botany* 48:481-500.
- Ford, E. D., and K. A. Sorrensen. 1992. Theory and models of inter-plant competition as a spatial process. Pages 363-407 in D. DeAngelis and L. Gross, editors. Individual-based models and approaches in ecology. Chapman and Hall, New York, New York, USA.
- Ford, R., and E. D. Ford. 1990. Structure and basic equations of a simulator for branch growth in the *Pinacea*. *Journal of Theoretical Biology* 146:1-13.
- Franco, M. 1986. The influence of neighbors on the growth of modular organisms with an example from trees. *Philosophical Transactions of the Royal Society, London*. B 313:209-225.
- Gates, D. J. 1978. Biomodality in even-aged plant monocultures. *Journal of Theoretical Biology* 71:525-540.
- Gates, D. J., A. J. O'Connor, and M. Westcott. 1979. Partitioning the union of disks in plant competition models. *Proceedings of the Royal Society, London*. A 367:59-79.
- Gentil, S., and Blake, G. 1981. Validation of complex ecosystem models. *Ecological Modelling* 14:21-38.
- Grier, C. C., K. A. Vogt, M. R. Keyes, and R. L. Edmonds. 1981. Biomass distribution and above- and below-ground production in young mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* 11:155-167.
- Guttorp, P., and A. Walden. 1987. On the evaluation of geophysical models. *Geophysical Journal of the Royal Astronomical Society* 91:201-210.
- Harper, J. L. 1967. A Darwinian approach to plant ecology. *Journal of Ecology* 55:247-270.
- Hatch, C. R., D. J. Gerrard, and J. C. Tappeiner. 1975. Exposed crown surface area: a mathematical index of individual tree growth potential. *Canadian Journal of Forest Research* 5:224-228.
- Jones, M. 1985. Modular demography and form in silver birch. Pages 223-237 in J. White, editor. Studies on plant demography: a Festschrift for John Harper. Academic Press, New York, New York, USA.
- Kellomäki, S. 1980. Growth dynamics of young Scots pine. *Communications Instituti Forestalis Fenniae* 98:1-50.
- . 1986. A model for the relationship between branch number and biomass in *Pinus sylvestris* crowns and the effect of crown shape and stand density on branch and stem biomass. *Scandinavian Journal of Forest Research* 1:455-472.
- Kenkle, N. C. 1988. Pattern of self-thinning in Jack pine: testing the random mortality hypothesis. *Ecology* 69:1017-1024.
- Khan, M. A., J. Antonovics, and A. D. Bradshaw. 1976a. Adaptation to heterogeneous environments. II. Phenotypic plasticity in response to spacing in *Linum*. *Australian Journal of Agricultural Research* 27:519-531.
- Khan, M. A., J. Antonovics, and A. D. Bradshaw. 1976b. Adaptation to heterogeneous environments. III. The inheritance of response to spacing in flax and linseed (*Linum usitatissimum*). *Australian Journal of Agricultural Research* 27:649-659.
- Leverenz, J. W., and P. G. Jarvis. 1980. Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.). X. Acclimation to quantum flux density within and between trees. *Journal of Applied Ecology* 17:697-708.
- Lovell, P. H., and P. J. Lovell. 1985. The importance of plant form as a determining factor in competition and habitat exploitation. Pages 209-221 in J. White, editor. Studies on plant demography: a Festschrift for John Harper. Academic Press, New York, New York, USA.
- Mack, R. N., and J. L. Harper. 1977. Interference in dune annuals: spatial pattern and neighborhood effects. *Journal of Ecology* 65:345-363.
- Miller, T. E., and J. Weiner. 1989. Local density variation

- may mimic effects of asymmetric competition on plant size variability. *Ecology* **70**:1188–1191.
- Mitchell, K. J. 1975. Dynamics and simulated yield of Douglas-fir. *Forest Science Monographs* **17**:1–39.
- Mohler, C. L., P. L. Marks, and D. G. Sprugel. 1978. Stand structure and allometry of trees during self-thinning of pure stands. *Journal of Ecology* **66**:599–614.
- Moore, J. A., C. A. Budelsky, and R. C. Schlesinger. 1973. A new index representing individual tree competitive status. *Canadian Journal of Forest Research* **3**:495–500.
- Nance, W. L., J. E. Grissom, and W. R. Smith. 1988. A new competition index based on weighted and constrained area potentially available. Pages 134–142 in A. R. Ek, Stephen R. Shifley, and Thomas E. Burk, editors. *Forest growth modelling and prediction*. United States Department of Agriculture-Forest Service, General Technical Report NC-120.
- Norman, J. M., and P. G. Jarvis. 1975. Photosynthesis in sitka spruce (*Picea sitchensis* (Bong.) Carr.). V. Radiation penetration theory and a test case. *Journal of Applied Ecology* **12**:839–878.
- Norman, J. M., and J. M. Welles. 1983. Radiative transfer in an array of canopies. *Agronomy Journal* **75**:481–488.
- Oker-Blom, P. 1986. Photosynthetic radiation regime and canopy structure in modeled forest stands. *Acta Forestalia Fennica* **197**:1–4.
- Oker-Blom, P., and S. Kellomäki. 1983. Effect of grouping of foliage on the within-stand and within-crown light regime: comparison of random and grouping canopy models. *Agricultural Meteorology* **28**:143–155.
- Pacala, S. W., and J. A. Silander, Jr. 1985. Neighborhood models of plant population dynamics. I. Single-species models of annuals. *American Naturalist* **125**:385–411.
- Pacala, S. W., and J. A. Silander, Jr. 1990. Field tests of neighborhood population dynamic models of two annual weed species. *Ecological Monographs* **60**:113–134.
- Pukkala, T., and T. Kolström. 1987. Competition indices and the prediction of annual radial growth in Scots pine. *Silva Fennica* **21**:55–67.
- Schmitt, J., D. W. Ehrhardt, and M. Cheo. 1986. Light-dependent dominance and suppression in experimental radish populations. *Ecology* **67**:1502–1507.
- Sorensen, K. A. 1989. A three dimensional model of above ground competition incorporating crown plasticity and multiway interaction. Thesis. University of Washington, Seattle, Washington, USA.
- Sultan, S. E. 1987. Evolutionary implication of phenotypic plasticity in plants. *Evolutionary Biology* **21**:127–178.
- Wang, Y. P., and P. G. Jarvis. 1990. Description and validation of an array model—MAESTRO. *Agricultural and Forest Meteorology* **51**:257–280.
- Weiner, J. 1985. Size hierarchies in experimental populations of annual plants. *Ecology* **66**:743–752.
- Weiner, J., and S. C. Thomas. 1986. Size variability and competition in plant monocultures. *Oikos* **47**:211–222.
- Weller, D. E. 1987a. A reevaluation of the  $-3/2$  power rule of plant self-thinning. *Ecological Monographs* **57**:23–42.
- . 1987b. Self-thinning exponent correlated with allometric measures of plant geometry. *Ecology* **68**:813–821.
- Zeide, B. 1985. Tolerance and self-tolerance of trees. *Forest Ecology and Management* **13**:146–166.
- . 1987. Analysis of the  $3/2$  power of self-thinning. *Forest Science* **33**:517–537.