A STRUCTURALLY BASED ANALYTIC MODEL OF GROWTH AND BIOMASS DYNAMICS IN SINGLE SPECIES STANDS OF CONIFERS

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ABSTRACT. A theoretically based analytic model of plant growth in single species conifer communities based on the species fully occupying a site and fully using the site resources is introduced. Model derivations result in a single equation simultaneously describes changes over both, different site conditions (or resources available), and over time for each variable for each species. Leaf area or biomass, or a related plant community measurement, such as site class, can be used as an indicator of available site resources. Relationships over time (years) are determined by the interaction between a stable foliage biomass in balance with site resources, and by the increase in the total heterotrophic biomass of the stand with increasing tree size. This structurally based, analytic model describes the relationships between plant growth and each species' functional depth for foliage, its mature crown size, and stand dynamics, including the self-thinning. Stand table data for seven conifer species are used for verification of the model. Results closely duplicate those data for each variable and species. Assumptions used provide a basis for interpreting variations within and between the species. Better understanding of the relationships between the MacArthur consumer resource model, the Chapman–Richards growth functions, the metabolic theory of ecology, and stand development resulted.

KEY WORDS: Biomass–density relationships, solar equivalent leaf area, site–vegetation relationships, plant allometry, consumer–resource model, plant geometry, self-thinning, monomolecular growth function, Chapman–Richards growth function, metabolic theory of ecology.

1. Introduction. An understanding of the energy and material fluxes in ecosystems, and the mechanistic controls of the ecological processes at the community level, has long been a goal of ecology (Yoda et al. [1963], Westoby [1984], West et al. [2009]) and is central to answering questions about the biology and ecology of global change (Enquist et al. [2003]). Understanding how biotic and abiotic factors interact to regulate community dynamics over time and across spatial and temporal scales is needed to predict climate driven variation in ecosystem processes (Enquist and Niklas [2001, 2002], Enquist et al. [2003]). West, Brown, and Enquist presented a general theoretical framework for allometric scaling laws in biology in

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a model known as WBE model (West et al. [1997,1999a,b, 2000], Enquist et al. [1998, 2000]) which provides insight into the nature of these relationships (Strub and Anateis [2008]). Central to this model is that organismal fitness occurs by maximizing the scaling of critical surface areas, while minimizing the cost of transport and support of these surface areas within existing biomechanical constraints. This model thus reduces much of the complexity of organisms and ecosystems to simple, universally applicable physical and chemical principles (Enquist et al. [2007]). The WBE model also allows the effects of growth, size, and biomass partitioning to be predicted across diverse species (Niklas et al. [2003]). Most plants perform the same basic biological tasks to grow and survive, which has resulted in evolutionary convergence in terms of size dependent efficiency (Niklas et al. [2003]).

The WBE model quantitatively describes forest structure and dynamics on the basis of a resource steady state in which the total rate of resource use is equal to the total annual rate of resource supply of the stand (West et al. [2009]). This steady state has been found to be generally maintained on monitored sites despite extensive turnover in individuals over time (Enquist et al. [2009]). The scaling of metabolism and growth in an environment of steady state resources (the law of constant yield (Niklas et al. [2003]) is largely responsible for the regular ecological patterns now prevalent (Enquist et al. [2007]), and has empirically supported WBE model predictions of growth, mortality, and successional patterns (Enquist et al. [2009]). Many of the basic premises of the WBE model are based on the central role of metabolism in governing plant form and function, and the link between form and function and resource availability described by the Metabolic Theory of Ecology (Brown et al. [2004], Price et al. [2010]). Metabolism governs the links between form and function and resource availability (Price et al. [2010]). Because the rate of resource use is proportional to metabolic rate (Enquist et al. [2007]), the individual tree-level processes of resource use, growth, and death determine the relationships between individual plants and how they influence the dynamics of populations and communities (Brown et al. [2004], West et al. [2009], Price et al. [2010]). Thus, biomass production in terrestrial plant communities, although independent of plant density (Niklas et al. [2003]), is generally proportional to rainfall in water-limited environments or to available light in light-limited environments (Grier and Running [1977], Kerkoff et al. [2005], Enquist et al [2007]).

WBE model results also indicated that interlinked allometric constraints at the individual tree level influences the allometric and metabolic attributes of populations and communities (Enquist et al. [2007]). Through metabolic demand these allometric constraints on resource use by individual plants determine overall population density, community phytomass, size structure, nutrient cycling, and productivity of whole communities and ecosystems (Brown et al. [2004], Kerkoff and Enquist [2006]). These "Ecosystem allometries" (Kerkoff and Enquist [2006], Enquist et al. [2009]), driven by the allometric patterns of the whole plant, provide a basis for understanding the structure and function of ecosystems and communities. These

structural and functional characteristics suggest that forests are organized by a set of very general scaling rules that determine "how trees use resources, fill space, and grow" (Enquist et al. [2009]).

In the derivations that follow I build on the results of Tausch [2009] to develop the model relationships between the full use of site resources (Enquist et al. [1998]) by the constant foliage or photosynthetic biomass of a species fully occupying a stand (France and Kelly [1998]) and the resulting plant growth that supports and distributes the foliage biomass. Full site occupancy is also used in determining the stand table data used to test the model. This newly developed model also reveals interrelationships between a negative exponential equation (Sever and Wild [1989]); MacArthur's [1970] consumer resource model; the monomolecular or Mitscherlich growth function (Richards [1959]), and the von Bertalanfy, Chapman–Richards, or autocatalytic growth function (Pienaar and Turnbull [1973]), with the metabolic theory of ecology (Brown et al. [2004], Price et al. [2010]) for tree growth over time.

2. Model development.

2.1. Model derivations for a single site.
The model developed in this paper builds on the single tree model of Tausch [2009], which was designed around the efficient distribution and support of the foliage in a tree, by adapting its concepts to single species stands of conifers. This model is based on the distribution and partitioning of a constant foliage biomass in a stand by the supporting structural components, both within and among its trees. As with crown growth in a single tree, tree growth and survival within the stand is also controlled from the outside in (Tausch [2009]), and the structural changes within and between the trees in a stand are emergent properties resulting from the functioning of the whole (Kerkoff and Enquist [2006]). I have assumed that just as there are universal principles underlying the organization of individual tree growth (West and Brown [2005], Tausch [2009]), similar principles underlie the changes among trees in a fully occupied single-species stand of conifers as they grow.

Just as the branching network of a single tree fills a three-dimensional volume, the crowns of a single species stand of conifers at full site occupancy fill a three-dimensional volume. This is described by the model by extending the branching structure of the individual trees to include the relationships between the trees in the stand that influence the foliar energy capture efficiency of the entire stand (Kerkoff and Enquist [2006], West et al. [2009], Price et al. [2010]). I assumed that the structural branching patterns of the individual trees controlling the foliage biomass distribution in their crowns (Tausch [2009]) can be extended to the control of the foliage biomass distribution among the trees in a stand (West et al. [2009]). I also assumed that just as the geometry of a tree's canopy influences the collective photosynthetic rate of its leaves (Horn [1971, 2000], Givnish [1988], Tausch [2009]),

so does the geometry of the combined crowns of the trees in a stand influence the collective photosynthetic rate of their leaves. The growth and survival of the trees in a stand, like the branches in the tree (Tausch [2009]) works to maintain the surface area for exchange while minimizing the sum of the support structures. These relationships determine the emergent properties of size-frequency distribution, spacing relationships, canopy configuration, mortality rates, and resource flux rates (Enquist et al. [2009]).

I developed this model to describe the period of growth that occurs after full use of site resources is attained (i.e., resource use is equal to the resource supply; Enquist et al. [1998], Savage et al. [2004], West et al. [2009], Price et al. [2010]), but before senescence, as described by Clark [1990], has been reached. The model assumes that the allocation of available resources among the individuals in a stand occurs throughout the growth process. It has been shown that water transpiration and net carbon gain of a desert grass (Nobel [1981]) and a desert shrub (Allen et al. [2008]) on fully occupied sites are equivalent on a per unit ground area basis regardless of the size of the plants. Other authors have reported negative correlations between net primary production and growing season water deficits (Zahner and Donnelly [1967], Gholtz [1982], Webb et al. [1983], Stephenson [1990]). Whittaker and Niering [1975] provide data on total leaf biomass, net annual production, and a moisture stress index for 10 sites that cover an elevational gradient from just above the desert to subalpine forest on the Santa Catalina Mountains, Arizona. From open canopy oak woodland to ponderosa pine forest the decrease in the moisture stress index is significantly correlated with increasing total leaf biomass.[1] Whereas in the closed canopy communities from douglas fir (*Pseudotsuga menziesii* [Mirb.] Franco.) to subalpine forest no trend of leaf biomass with the moisture stress index is observed, while total leaf biomass is about double that in the lower elevation open stands (Whittaker and Niering [1975]). However, across the full range of sites, net annual production continuously increases as the moisture stress index decreases. In a study of total leaf biomass in paired shrub- and tree-dominated plots over a range of sites, leaf biomass values of the two community types were positively correlated with each other and with a measure of site class based on the tree height over age relationships in pinyon (Tausch and Tueller [1990]). Because direct measurement of resources is difficult, a plant community measurement is often used to represent site conditions. For example, height over age site indices are extensively used in forestry (Daniel et al. [1979], Weiskittel et al. [2011]).

The model derivation starts with the assumptions that growing season conditions at all the sites are constant over time (years), that the single species tree stand on each site is fully established or fully occupies the site, that the trees present are allometrically ideal integrators of site conditions, and that the site can be modeled as a stand (Enquist et al. [2009]). The model is also confined to the period when density dependent mortality dominates (Clark [1990]). As previously reported for undisturbed forest communities (Enquist and Niklas [2001], Niklas et al. [2003],

Kerkoff and Enquist [2007]) I assume a consistent size distribution that is adequately represented by average size measurements (Li et al. [2000]).

Assign R to represent the overall resources that are annually available on a site. This level of resources (R) is assumed to be constant in the stand or site over time. Assign Z to be a total plant community vegetation measurement or dimension that is constant on an area basis once the species fully occupies the site. Assume that Z is directly related to, or is directly proportional to, the total annually available resources (R) on the site.

$$(1) \qquad\qquad\qquad\qquad Z \propto R.$$

To verify this model, a vegetation measurement for Z is needed. An example of such a measurement is equilibrium leaf area index which can be quantitatively related to climate (i.e., to available moisture) (Nemani and Running [1989], Stephenson [1990], Price et al. [2010]). At full site occupancy, a stable or constant level of foliage biomass is reached in many species and this level remains the same over a wide range of plant size and density differences (Long and Smith [1984], Franco and Kelly [1998], Enquist et al. [2007]). A stable level of total leaf area or biomass also implies a stable level of photosynthetic activity on an annual basis (ignoring year-to-year climatic fluctuations). Moreover, whole-stand transpiration (Cěrmák [1989]) is closely related to photosynthetic activity (Oren et al. [1986], Mäkellä and Hari [1986], Enquist et al. [2007]). What may be stabilizing is the total solar equivalent leaf area described by (Cěrmák [1989]). Because lower moisture stress index values are associated with higher foliage biomass levels (Whittaker and Neiring [1975]), water availability can greatly affect resource availability (Nemani and Running [1989], Stephenson [1990]). Actual evapotranspiration and measures of community production values show the same general relationship across a wide range of community types (Rosenzweig [1968], Le Houerou et al. [1988], Stephenson [1990], Wolf et al. [2011]).

The model therefore assumes that the constant level of total leaf biomass on a fully occupied site is in balance with a constant annual resource use on the site regardless of plant size (Enquist et al. [1998], Enquist et al. [2009], West et al. [2009]). I also assumed energy available at a site for plant maintenance and growth on an annual basis is proportional to solar equivalent leaf area, or alternatively, a constant total leaf biomass (i.e, $L \propto Z$ in equation (1)).

$$(2) \qquad\qquad\qquad\qquad \mathrm{Total\,Energy} \propto L,$$

where L = total solar equivalent leaf area or leaf biomass on a site. For a given value of L, there is also an annual total energy cost for the maintenance (m)of that total leaf area. There is also an energy cost for replacement of leaves (q) that die

during the year. Both costs are assumed to be proportional to the equilibrium leaf area.

(3) Net Energy From Leaves $\propto L - mL - qL \propto (1 - m - q) L \propto m'L$.

where $m' =$ combined energy to biomass conversion constant for leaf maintenance and replacement. On a total plant basis there is also an energy cost for maintenance and replacement of the living heterotrophic or nonphotosynthetic tissue in the stand. Because the heterotrophic tissue of a tree increases faster than its leaf biomass or area during individual tree growth (Ryan [1989], Tausch [2009]), the heterotrophic tissue for the total stand increases with tree growth even though total stand leaf area remains constant. After accounting for the energy used to maintain and replace both the leaves and the living heterotrophic tissue, the remaining energy is assumed to be available for growth (Kerkoff et al. [2005]). The incorporation of maintenance (h) and replacement (p) of heterotrophic tissue (B) into equation (3) gives energy remaining for growth on a site basis.

(4) Energy for Growth $\propto m'L - hB - -pB \propto m'L - (h + p) B \propto m'L - h'B,$

where $h' =$ combined energy to biomass conversion constant for maintenance and replacement, and $B =$ total heterotrophic tissue biomass of the plants on a site. Uptake of nutrients for replacement is assumed to be in balance with the annual turnover in litter fall (Clark [1990]) and luxury consumption is not incorporated.

Because total solar equivalent leaf area on a site is assumed to be constant, there is a theoretical maximum quantity of living heterotrophic plant tissue that the leaf area can support. At this maximum level, there is no energy left for growth. Let B_k be this theoretical maximum heterotrophic biomass, such that $m'L - h'B_k = 0$, or, $h'B_k = m'L$. Substituting this equation into equation (4):

(5)   Energy For Growth $\propto h'B_k - h'B \propto h' (B_k - B) \propto (B_k - B).$

Changes in nutrient storage are assumed to be proportional to changes in heterotrophic tissue biomass. Next, the rate of growth of heterotrophic tissue biomass is assumed to be directly proportional to the energy available for growth: $\frac{dB}{dT} \propto$ Energy For Growth. Substituting this equation into equation (5), $\frac{dB}{dT} \propto (B_k - B)$. Add the constant of proportionality (intrinsic growth rate (g)):

$$(6) \qquad \frac{dB}{dT} = g (B_k - B).$$

In equation (6) growth increments decrease as maximum size is approached, as demonstrated by Clark [1990]. Assume that there is a variable W on a site that is equal to the difference between B_k and B: $W = (B_k - B)$. Substituting this equation into equation (6),

$$(7) \qquad \frac{dB}{dT} = gW.$$

From the definition of W given above, the rate at, which W on a site decreases is equal to the rate at which B approaches B_k. Thus, $-\frac{dW}{dT} = \frac{dB}{dT}$. Substituting this equation into equation (7):

$$(8) \qquad \frac{dW}{dT} = -gW.$$

Equation (8) is a linear, first-order differential equation, and its solution can be determined for the time range in years $T = t - t_0$ where $t_0 =$ the beginning time, $t = $ a later point in time, and $T = $ the elapsed time for the relationship in equation (8). The value of t_0 is the point in time (age in years) at which the species attains full occupancy of the site.

For $T = t - t_0$, the solution to equation (8) is:

$$(9) \qquad W = W_0 \exp\left(-gT\right).$$

Substituting $W = (B_k - B)$ and $W_0 = B_k - B_0$ into equation (9), $(B_k - B) = (B_k - B_0) \exp\left(-gT\right)$, or, $-B = -B_k + (B_k - B_0) \exp(-gT)$. Thus

$$(10) \qquad B = B_k - (B_k - B_0) \exp\left(-gT\right).$$

Equation (10) is also known as the monomolecular or Mitscherlich growth function (Richards [1959], Seber and Wild [1989]).

A plant community measurement to represent the total living, heterotrophic tissue in a stand is needed for testing equation (10), but such a variable has almost never been directly measured. Ryan [1989, 1990] found stem maintenance respiration to be linearly correlated with live cell volume in the trunks of two tree species. Moore [1989] modified the JABOWA forest gap simulator (Botkin et al. [1972]) by including a variable describing the decreased growth of tree volume with increasing tree size, which simplified the maximum growth equation and improved the fit of the JABOWA model to empirical data. Above- and below-ground growth are also closely allometrically related (Shipley [1989], Omdal and Jacobi [2001], Xiao and

Ceulemans [2004]). The total wood volume of a stand is potentially as close as any existing measurement to an estimate for B.

Assume that another plant variable X, representing either the stand total wood volume or the average value of the trees present, has a standard allometric (or power) relationship with B (total of living heterotrophic tissue biomass) with the allometric constant a and allometric exponent j.

$$(11) \qquad\qquad\qquad\qquad B = aX^j .$$

Substituting equation (11) into equation (10) on a site where at its maximum carrying capacity, (k), that is $B = B_K$, then $X = X_K$ and $aX^{\mathrm{j}} = aX_k^j - (aX_k^j - aX_o^j)\exp(-gT)$, or $X^j = X_k^j - (X_k^j - X_o^j)\exp(-gT)$. Take both sides to the $(1/j)$th power.

$$(12) \qquad\qquad X = [X_k^j \left(X_k^j - X_0^j \right)\exp(-gT)]^{(1/j)},$$

where X is the variable changing over time (years), and the parameter g can be interpreted as the intrinsic growth rate, or abiotic resource assimilation rate (Moore [1989]) of the species. Equation (12) is dependent on j independent of a in equation (11).

Equation (12) is one form of the solution to the von Bertalanfy, Chapman–Richards, or autocatalytic growth function (Richards [1959], Pienaar and Turnbull [1973], Seber and Wild [1989]). It is also a solution to the volume growth function derived using dimensional analysis by Khil'mi [1962], the basic form of which is:

$$(13) \qquad\qquad \frac{dX}{dT} = fX^h + pX.$$

The solution to equation (13) can be shown to be of the same form as equation (12).[2]

2.2. Model derivation for multiple sites. Over multiple sites (n) the value of $X_{k,n}$ will thus be a function of Z_n, the index of available resources or site potential (Niklas et al. [2003], Kerkoff and Enquist [2006]). In a study of the relationships between site index (SI) and estimates of gross primary productivity (GPP) from remote sensing (Weiskittel et al. [2011]) showed that the relationship between SI and GPP was allometric with the exponent on SI variable, but consistently less than 1.00. Thus, because ecosystem allometries generally hold across a wide array

of relationships and communities (Kerkoff and Enquist [2006]), I assume that the relationship between $X_{k,n}$ and Z_n is also represented by an allometric function.

$$(14) \qquad\qquad\qquad\qquad X_{k,n} = cZ_n^d,$$

where C = the allometric constant and d = the allometric exponent.

Equation (12) can be combined with equation (14) and then modified for use in testing the model with stand table data. Stand tables are organized with rows as site classes and columns as age classes. Site classes (n) represent the average height of a tree of a set age, usually 100 years, and are usually presented in 10 foot (3.04 m) increments. Age classes (i) are usually in increments of 10 years. Modified for this purpose the combination of equations (12) and (14) becomes:

$$(15) \qquad\qquad X_{i,n} = \left\{ \left(cZ_n^d\right) - \left[\left(cZ_n^d\right)^j - X_{0,n}^j \right] \exp(-gT_i) \right\}^{I/j},$$

where $X_{i,n}$ = the value of the variable for age class i, and site class n ($i = 0$ is the age class at full site occupancy), n = the number of the site class used in the analysis (Z_n), $X_{0,n}$ = the initial conditions at each of the n site classes (i.e., at full site occupancy), and T_i = the value of T in years at each age class i (T_0 = stand age in years for the age class representing full site occupancy).

Equation (15) is the core equation of this structurally based analytic model of growth and biomass dynamics. It describes the changes in the values of stand variable $X_{i,n}$ at time class (i) and site class n based on the maximum value of $X_{i,n}$ at carrying capacity $(cZ_n^d)^j$ and the difference between that maximum value and the value of $X_{i,n}$ when full site occupancy was first reached ($X_{0,n}^j$), times a negative exponential based on intrinsic growth rate of the species involved g times the age at time class (i) $(\exp(-gT_i)''^{I/j})$. In the analyses of the stand table data based on equation (15) the model is based on the values of c, d, g, and j for each variable (stand table) of each species that provides the best overall fit to the data combining all site and age classes.

2.3. Relationships between Z and other stand variables. Equation (15) assumes a constant energy level Z that is proportional to a constant level of foliage biomass, which provides a constant annual level of energy from photosynthesis at each site. Density reductions at a site from tree growth (self-thinning) lead to the division of the constant foliage biomass of the stand among fewer individuals as the average plant size increases (Long and Smith [1984], Givnish [1986], Enquist [2007]). Similarly density reductions lead to increases in shoot height (Gorham [1979]) and DBH (Long and Smith [1984], Zeide [1987]) of individual trees.

Although directly related to Z, total foliage biomass is not available in stand table data. The basal area is constant over all site classes in a fully occupied ponderosa pine stand older than about 60 years (Meyer [1938]), and in a short leaf pine stand older than about 40 years of age (USDA Forest Service [1976]) which indirectly indicates a constant level of foliage biomass. After full site occupancy is reached in balsam fir (*Abies balsamea*, Sprugel [1984]), basal area, foliage biomass, aboveground net primary production, and aboveground respiration all become approximately constant. Barreto [1989] also noted that basal area and the leaf area index are constant during a stand's life. If a direct relationship between total basal area and total foliage biomass (Long and Smith [1984], Tausch and Tueller [1989], Tausch [2009]) is assumed, than total basal area can be used for Z in equation (1), along with the index of height at a stand's given age to determine the site conditions widely used in commercial forestry.

Under the assumptions for Z in a stand the average resources used by each individual tree is Z (equation (1)) divided by the stand density N.

$$(16) \qquad \bar{Z} = Z_n N^{-1}, \text{ or } Z_n{}^{-1} = N,$$

where $\bar{Z}$ = the average of Z. Equation (16) represents plant growth within a constant Z with density declining as $\bar{Z}$ increases with plant growth. For the average value of each tree, the variable $\bar{X}$ is substituted for X in equation (12) under the assumption that each $\bar{X}$ has an allometric relationship with $\bar{Z}$:

$$(17) \qquad \bar{Z} = a\bar{a}^j,$$

again a = the allometric constant and j = the allometric exponent. The constant a and the exponent j are assumed to remain unchanged as Z varies across the individual sites. Equations (16) and (17) were then combined and simplified, $a\bar{X}^j = Z\,N^{-1}$, or, $\bar{X}^j = a^{-1}\,Z\,N^{-1}$

Take both sides to the $1/j$ power:

$$(18) \qquad \bar{X} = a^{-1\backslash j} Z^{(1\backslash j)} N^{-(1\backslash j)} \text{ and } \bar{X} = c'Z^{d'}\,N^{-d'}$$

where: $c' = a^{-(1/j)}$, and $d' = 1/j$. Thus, $\bar{X}$ has a positive allometric relationship with $\bar{Z}$ and an inverse allometric relationship with density. Solved for density, equation (18) is the same as Woodward's [1987] equation (9) in his Chapter 5.

Assume X is the total community dimension from which $\bar{X}$ has been computed. Multiplying both sides of equation (18) by N gives an equation that relates to X and N.

$$(19) \qquad\qquad X = c' Z_n^{1/j} N^{1-d'}, \text{ or } X = c' Z^{d'} N^{1-d'},$$

where c' and d' are the same as in equation (18). As with $\bar{X}$, its total X has a negative allometric relationship with density and a positive allometric relationship with site conditions as represented by Z.

2.4. Interpretation of the allometric exponent j.   Allometry is commonly used to examine relationships between plant form, function and growth (Enquist et al. [1999], West et al. [1999a], Enquist and Niklas [2002], Niklas [2009]) and to show a common, robust, and mechanistic basis for multiple levels of biological organization (Enquist [2002]) that provide insight into the nature of these relationships (Strub and Anateis [2008]). Allometric relationships describe a constant specific or relative growth rate between measurements of organism size and shape that are commonly observed (Tausch [1980], West et al. [2000], Niklas [2004]). Although the relationships between the dimensions of an individual tree and its foliage biomass are not truly allometric (Tausch [2009]) they can be closely approximated by allometric analyses. Thus, to simplify the development of the model presented here, I have assumed the allometric description of these relationships to be adequate.

I used the concepts of monolayer and multilayer tree crowns from Horn [1971] to derive 'theoretical end points' for the values of j in equations (11), (12), (15) and (17) which are used in interpreting the values of j resulting from calibrating the model with stand table data. One end point is the expected values of j assuming a perfect multilayer crown. In a perfect multilayered crown the foliage bulk density (Tausch [2009]) is constant regardless of crown size (i.e., a defoliated portion of the crown (Tausch [2009]) never develops). Site resources are insufficient for a closed crown to develop, and resource control of foliage quantity in tree crowns appears to be below ground.

The other end point is a perfect monolayer tree crown. In this crown, a single layer of foliage completely covers the surface of the crown with no gaps (i.e., the functional depth (Tausch [2009]) consists of a single layer of foliage). In a single-species stand with a closed canopy the distribution and quantity of foliage in the individual trees are controlled by available light (Tausch [2009], West et al. [2009]).

I made additional assumptions for the derivation of additional values of j. First, average crown diameter ($\bar{C}$) is directly or isometrically proportional to average crown height $\bar{H}$, ($\bar{C} \propto \bar{H}$). In accordance with the crown volume formula of Tausch [2009], average foliage biomass $\bar{L}$ is proportional to $\bar{H}^3$ in a multilayer crown

($\bar{L} \propto \bar{H}^3$) and proportional to $\bar{H}^2$ in a monolayer crown ($\bar{L} \propto \bar{H}^2$). Average trunk diameter ($\bar{D}$) is proportional to $\bar{H}^{1/3}$ ($\bar{D} \propto \bar{H}^{2/3}$), and average total weight $\bar{W}$ (or total trunk plus branch volume, Tausch [2009]) is proportional to average basal area times average height ($\bar{W} \propto \bar{D}^2 \bar{H}$). At full site occupancy a constant L is in balance with R over a growing season (year), and fully uses available R without crown closure in a multilayered stand, whereas crown closure is always present in the light-limited monolayered stand. Average foliage biomass $\bar{L}$ is inversely proportional to density ($\bar{L} \propto N^{-1}$) at both end points (West et al. [1997], Enquist et al [1998]). Under these assumptions it is straight forward to derive the full table of values of j between pairs of both average tree and site variables; total wood volume (W), an estimate of total trunk and branch weight in the stand, average wood volume ($\bar{W}$), total basal area ($\bar{D}^2 N$), average basal area ($\bar{D}^2$), average branch diameter ($\bar{D}$), average tree height ($\bar{H}$), average foliage biomass ($\bar{L}$), and density (N) (multilayer, Table 1; monolayer, Table 2).

Under the assumptions of this model there is a third theoretically possible condition for a fully occupied stand, namely a multilayered stand that reaches the light limitation of full crown closure before the foliage biomass has reached a balance with the total soil-based resources on the site ($L < L_k$) available to the species over the growing season. Under these conditions tree growth is constrained by the crown area, but it is possible for the total foliage biomass to continue to increase as the trees grow and density declines. This situation assumes that $\bar{L} \propto \bar{H}^3$ and that $\bar{H}^2 \propto N^{-1}$, which changes the allometric relationships between $\bar{L}$ and some of the other variables (Table 3). Relationships not included in Table 3 are the same as those in Table 2. Once L stabilizes at L_k and is in balance with the soil-based resources, the relationships of the perfect multilayer stand in Table 1 are followed with any further growth that may occur. This third scenario is discussed further in Section 2.5

Because a tree has both a functional depth and a defoliated volume (Tausch [2009]) the value of the exponent of $\bar{H}$ in an allometric relationship with $\bar{L}$ can theoretically be anywhere between 2.0 and 3.0 depending on the relationship between the species' functional depth and its mature size ($2 \leq j \leq 3$). The larger the functional depth is, relative to the mature tree size, the closer to the multilayer end point that species is. Conversely, the smaller the functional depth is relative to the mature tree size the closer the species is to the monolayer end point the species is. Again assuming a constant L for the stand and $H^{(2<j<3)}$, the values of j for the rest of the variable pairs will covary, and will also be in between those in Tables 1 and 2.

2.5. Site resource availability.   Trees in a stand utilize two types of resources over the growing season. The first is the light energy from the sun that is available over the growing season for the species to use (a percentage of total insolation). The second is the soil-based resources of water and nutrients. Where the soil-based

TABLE 1. Allometric exponents between pairs of nine tree and site variables for a perfect multilayered tree growing in an open canopy situation with full site occupancy.

Variables	Total wood volume	Average wood volume	Total basal area	Average basal area	Average trunk diameter	Average tree height	Average foliage biomass	Density
TWdVol	——	0.250	////	0.333	0.667	1.000	0.333	-0.333
AWdVol	4.000	——	////	1.333	2.667	4.000	1.333	-1.333
T Bas	0.0	0.0	——	0.0	0.0	0.0	0.0	0.0
ABas	3.000	0.750	////	——	.000	3.000	1.000	-1.000
ADia	0.667	0.375	////	0.500	——	1.500	0.500	-0.500
AHgt	1.000	0.250	////	0.333	0.667	——	0.333	-0.333
AFlgBio	3.000	0.750	////	1.000	2.000	3.000	——	-1.000
Density	-3.000	-0.750	////	-1.000	-2.000	-3.000	-1.000	——

////not defined.

TABLE 2.   Allometric exponents between pairs of nine tree and site variables for a perfect monolayered tree growing in a closed canopy situation with full site occupancy.

Variables	Total wood volume	Average wood volume	Total basal area	Average basal area	Average trunk diameter	Average tree height	Average foliage biomass	Density
TWdVol	——	0.500	2.000	0.667	1.333	2.000	1.000	–1.000
AWdVol	2.000	——	4.000	1.333	2.667	4.000	2.000	–2.000
TBas	0.500	0.250	——	0.333	0.667	1.000	0.500	–0.500
ABa	1.500	0.750	3.000	——	2.000	3.000	1.500	–1.500
ADia	0.750	0.375	1.500	0.500	——	1.500	0.750	–0.750
AHgt	0.500	0.250	1.000	0.333	0.667	——	0.500	–0.500
AFlgBio	1.000	0.500	2.000	0.667	1.333	2.000	——	–1.000
Density	–1.000	–0.500	–2.000	–0.667	–1.333	–2.000	01.000	——

TABLE 3. Allometric exponents between the average foliage biomass and each of the other eight tree and site variables for the perfect multilayered tree growing in a closed canopy situation with full site occupancy.

Variables	Total wood volume	Average wood volume	Total basal area	Average basal area	Average trunk diameter	Average tree height	Average foliage biomass	Density
AFlgBio	1.500	0.750	4.500	1.000	2.000	3.000	——	−1.500

TABLE 4. Parameter values, conditional R^2, and SEE% from calibrating equation (15) for predicting average height using the full stand table data for seven conifer species, using site class as an index of site resources.

Species	j	g	c	d	R^2	SEE%
Ponderosa pine	1.2998	0.005547	0.5050	1.0326	0.99	1.49
Western hemlock	0.9003	0.01882	0.3151	1.0277	0.99	0.43
Douglas fir	1.0119	0.01897	0.3601	1.0024	0.99	0.31
Red fir	0.9084	0.005745	0.9366	1.1761	0.99	2.68
Loblolly pine	0.9027	0.04190	0.3277	1.0190	0.99	0.38
Long Leaf pine	0.9002	0.02414	0.2628	1.1066	0.99	0.59
Short leaf pine	0.8998	0.02485	0.3196	1.0741	0.99	0.59

TABLE 5. Parameter values, conditional R^2, and SEE% from calibrating equation (15) for predicting average diameter (DBH) using the full stand table data for seven conifer species, using site class as an index of site resources.

Species	j	g	c	d	R^2	SEE%
Ponderosa pine	0.8001	0.004382	4.0438	0.7216	0.99	1.12
Western hemlock	0.8633	0.009200	5.3844	0.5610	0.99	1.07
Douglas fir	0.6991	0.009352	0.2193	1.1986	0.99	1.85
Red fir	1.2930	0.003219	3.5426	0.9667	0.99	2.77
Loblolly pine	0.8002	0.01948	0.8727	0.9055	0.99	0.68
Long leaf pine	0.8004	0.01314	1.2561	0.8163	0.99	0.66
Short leaf pine	0.8030	0.009638	0.4166	1.1573	0.99	2.90

resources, particularly water, are sufficiently limiting there is complete root utilization of soil resources and foliage biomass becomes stable before crown closure. Once crown closure occurs in a monolayered species the total foliage biomass is assumed to be constant, and the available the solar energy becomes limiting factor. In a closed canopy, however, the availability of soil-based resources can still apparently influence the efficiency of photosynthesis, and the productivity of the site.

For model derivation and testing I assume two types of resources; energy resources from the sun, and soil-based (edaphic) resources of water and nutrients. I also assume that the amounts of solar energy, r_s and of edaphic resources r_e, utilized

TABLE 6. Parameter values, conditional R^2, and SEE% from calibrating equation (15) for predicting density using the full stand table data for seven conifer species, using site class as an index of site resources.

Species	j	g	c	d	R^2	SEE%
Ponderosa pine	−0.2563	0.009075	6964.6	−0.8891	0.99	1.86
Western hemlock	−0.6182	0.008283	20994	−0.9952	0.99	1.51
Douglas fir	−0.9496	0.003861	179760	−1.4926	0.99	3.43
Red fir	−0.3526	8.167×10^{-6}	0.002023	−1.6447	0.99	6.04
Loblolly pine	−0.7695	0.01336	2.6864	−1.6228	0.99	1.74
Long leaf pine	−1.002	0.0003841	0.01760	−0.7460	0.99	2.44
Short leaf pine	−0.3997	0.01924	3.792×10^5	−1.6759	0.99	3.17

TABLE 7. Parameter values, conditional R^2, and SEE% from calibrating equation (15) for predicting total wood volume using the full stand table data for seven conifer species, using site class as an index of site resources.

Species	j	g	c	d	R^2	SEE%
Ponderosa pine	1.0392	0.008738	0.08277	2.3603	0.99	3.18
Western hemlock	0.8998	0.01219	11.803	1.0045	0.99	0.92
Douglas fir	0.9520	0.01441	2.0477	1.3005	0.99	3.25
Red fir	1.0090	0.0007142	483.99	0.9961	0.99	4.55.
Loblolly pine	0.9002	0.0464	1.3410	1.3710	0.99	0.99
Long leaf pine	0.9006	0.01154	0.7038	1.6524	0.99	4.38
Short leaf pine	0.9042	0.02835	2.4323	1.3143	0.99	0.88

per square meter of the site over the growing season (year), are also constant across the site. Of the two edaphic resources, water often is a limiting factor.

Over the growing season the trees in a stand use total resources R, which is a function of both the total solar, R_s, and total edaphic, R_e, resources used over the growing season (year). From this the average resource use per tree in a fully occupied stand can be computed.

$$\text{(20)} \qquad \text{Solar} : \bar{R}_s = R_s N^{-1},$$

(21) $\qquad$ Edaphic $: \bar{R}_e = R_e N^{-1}.$

Under full resource use there is an average occupied functional area of the site that should have an isometric relationship with the average functional crown volume and average foliage biomass of the individual trees. Dividing the average resource use by each tree in the stand by the respective resources available per square meter gives the average occupied Functional Area for the respective resource.

(22) $\qquad$ For solar $: \bar{A}_s =_s /r_s,$

(23) $\qquad$ For edaphic $: \bar{A}_e =_e /r_e.$

From each of these average occupied Functional Areas $(\bar{A})$ an average Functional Diameter $(\bar{P})$ of that area can be computed for a circular area of equal size.

(24) $\qquad$ For solar $: \bar{P}_s = 2(\mathrm{sqrt}(_s/),$

(25) $\qquad$ Foredaphic $: \bar{P}_e = 2(\mathrm{sqrt}(_e/).$

When a site is fully occupied by an open stand of a multilayered tree species that is fully utilizing the edaphic resources available to it, then $\bar{A}_e N$ is equal to the total area occupied by the stand. When a site is fully occupied by a stand of a monolayered tree species that is fully utilizing the solar resources available to it, then $\bar{A}_s N$ is equal to the total area occupied by the stand. Thus, the average occupied area $\bar{A}$ can be estimated by dividing the area of the stand by its density.

When a multilayer stand reaches light limiting crown closure before $L = L_k$, and when total use of edaphic resources (R_e) has not yet been achieved, L can continue to increase until it stabilizes with R_e as L_k. Under these conditions, the assumptions about $(B_k – B)$ in equation (5) need additional interpretation. First, there is still a theoretical B_k associated with L_k that is in balance with R_e. The response in tree growth to changes in $(B_k – B)$ is still determined by increases in B, which now includes increases in L as the average crown area increases. Because the increases in both L and B are constrained by the same rate of increase in average crown area, I assumed that equation (6) still closely approximates the pattern of growth responses required by the model. Once L_k is reached, the assumptions supporting equation (6) are again those associated with the theoretical multilayer crown.

This transition can potentially be detected in the data. From Table 1, $\bar{H} \propto N^{-0.333}$. Squaring both sides average crown area, $= \bar{H}^2 = N^{-0.667}$. Multiplying both sides by N shows that the total crown area is proportional to $N^{0.333}$. The positive relationship of crown area with density indicates that once L_k is reached, and the annual availability of R_e is fully utilized, further tree growth will result in a reduction in the total crown cover of the stand as density declines. As a result, the relationship between $\bar{P}$ and $\bar{H}$ differs between stands older and younger than the age at which L_k is reached.

3. Methods.

3.1. Stand table data. Stand table data are averages obtained by a combination of mathematical and manual curve fitting of lines to raw field data from a large number of sampled sites representing full stand occupancy. The results are represented by a smoothed set of curves (Meyer [1938]). Stand table curves are also developed by assuming a constant site growth potential. As in the model presented here, stand tables both summarize and simplify the processes involved, and the stand table data are used here as a form of metadata. The stand tables used were developed over a span of 50 years, with computers used only with those most recently developed.

Stand table data for seven conifer species were used to test equation (15); ponderosa pine (Meyer [1938]), western hemlock (Banner [1962]), Douglas fir (McArdle [1930]), red fir (Schumacher [1928]), and loblolly pine, long leaf pine, and short leaf pine (USDA Forest Service [1976]). In stands of ponderosa pine older than about age 60 and in short leaf pine stands older than about 40 years the total basal area is constant across all site classes which allows stand age on sites fully occupied by one of these two species to be estimated. Although in stands of the other five species total basal area does not reach a constant value, its rate of increase slows substantially in the same age range of 40–60 years. For use in the model, average tree height, average trunk diameter (DBH), stand density, and total wood volume from the stand table data were converted to metric units. The functional area and diameter were determined for each species as described in model derivations. Other derived variables are discussed in the Supplementary Information. For each species all site classes with data covering the maximum age in the tables were used for model testing. The data were organized in two ways for analysis. First, for each species separate data sets were prepared for each site class. Second, for each species the data for all site classes were combined into a single data set.

3.2. Data analysis. Plant shape is assumed to remain constant with growth, and all plant dimensions are assumed to be known without error. All allometric

relationships between plant measurements are assumed to be linearly allometric in a log-log plot (Causton and Venus [1981]). All analyses used nonlinear, iterative, least-squares analysis procedures that did not require data transformation (Packard and Birchard [2008], Packard [2009]).

To test equation (15), I began by assuming that the total wood volume of each species could be used as the initial estimate, or index of its total biomass of living, heterotrophic tissue. By using total volume for B in equation (11) and predicting it by using the other variables, initial estimates for the values of j for each species could be obtained. The average value of j obtained with equation (11) from the analyses for each species was used with data for each individual site class for the analyses with equation (12) to determine initial estimates of X_k and g. The individual site values of X_k used in equation (11) were predicted from both site class and total basal area to obtain initial estimates of c and d for use in equation (15). An iterative, nonlinear, least-squares analysis procedure was used with the combined data sets for each species, and estimates of j, g, c, and d from previous analyses as starting conditions, to determine their final parameter values with equation (15). For all species, the site index (class) was used to represent Z in equation (15). Total basal area, which is constant at a site once full site occupancy occurs, was also used for ponderosa pine and short leaf pine (Supplementary Information).

Previous studies that examined density changes through time (i.e., self-thinning) used analysis methods that compare variables individually with density through logarithmic data transformation, an approach that has a potential for introducing bias (Baskerville [1972], Lee [1982], Sprugel [1983], Tausch and Tueller [1988]). This model used a whole-stand table approach for analysis of changes in density over time, so that the results would be more directly related to whole-stand dynamics.

Conditional R^2, also called modeling efficiency (Huang et al. [2009] or fit index; Brand and Smith [1985]), and the standard error of the estimate (SEE) for the fit between model results and stand table data, were also computed for all analyses. The latter is expressed as a percentage of the difference between the means of the predicted and stand table values (SEE%) divided by stand table values. Computation of these values permitted direct comparisons of the results across variables and species.

4. Results.   Site class was found to be usable for the estimation of the K values for each variable analyzed for all seven species. The model results in ponderosa pine for average height, average diameter (DBH), density and total wood volume are plotted in Figure 1 to show the agreement between the model results and stand table data (Figure 1). Among these variables, the results for total wood volume were a bit less precise than those for the other three variables. The analysis results for the same four variables in western hemlock (Figure 2) were equivalent to each other and to those for the first three variables in ponderosa pine. In the analysis results,
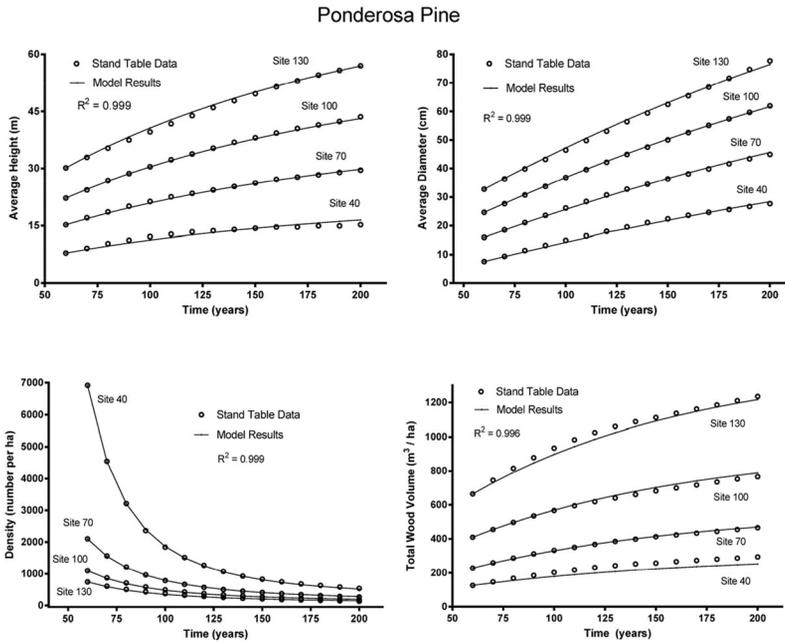
FIGURE 1. Results of the calibration of equation (15) against the full stand table data for ponderosa pine for the variables average height, average diameter (DBH), density, and total wood volume. Conditional R^2 values for each variable were computed from the simultaneous fit to all site classes and ages in each respective stand table. Parameter values used in equation (15) for each analysis are listed in Tables 4–7.

the values of all four parameters; j, g, c, and d are generally as expected from model assumptions (Tables 4–7). They, along with the values for the conditional R^2 and SEE%, across all seven species, indicate that the model results closely matched the data from the individual stand tables used. Results for the other derived variables for each species are in the Supplementary Information.

If an isometric relationship between foliage biomass and $\bar{A}$ is assumed then the allometric exponent for $\bar{H}$ when used in predicting $\bar{A}$ should approximate the relationship between average crown volume and average foliage biomass. This exponent varies from 2.00 for a theoretical monolayer to 3.00 for a theoretical multilayer species (Tables 1 and 2). The average of these exponents from model results for each of the seven species analyzed in ascending order were: red fir (2.013), long leaf pine (2.292), western hemlock (2.330), douglas fir (2.578), short leaf pine (2.821), loblolly pine (2.938), and ponderosa pine (3.250). The seven species thus essentially cover the theoretical range of possible values. According to these data the red fir's crown structure in a stand appears to function close to that of a theoretical monolayer. In fact, in my experience old, red fir dominated stands at high elevation sites
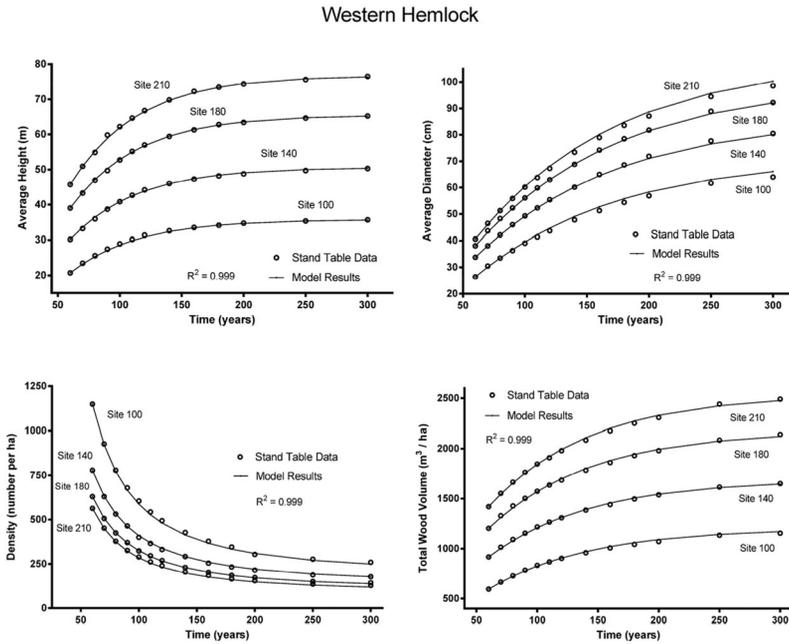
Western Hemlock

FIGURE 2. Results of the calibration of equation (15) against the full stand table data for western hemlock for the variables average height, average diameter (DBH), density, and total wood volume. Conditional R^2 values for each variable were computed from the simultaneous fit to all site classes in each respective stand table. Parameter values used in equation (15) for each analysis are listed in Tables 4–7.

generally have no understory vegetation, indicating a near total utilization of the available light by the trees.

For ponderosa pine the lowest five site classes all had exponents that were greater than 3.00, and for the highest five exponents were all less than 3.00. In stands of this open crown species, competition with plant species in the understory always occurs. As average tree size increases and the energy remaining for growth decreases (equation (5)), it appears that the energy available for competition also decreases. Apparently the total foliage biomass of stands of the lower site classes decreases as average tree size increases, and the understory becomes more competitive. These changes in ponderosa pine can be visualized by examining the relationship between $\bar{H}$ and $\bar{P}$ (Figure 3). In general the slope can be seen to be the steepest for site class 50 and then to gradually decrease to site class 130.

In similar analyses in western hemlock (Figure 3) the results appear to reflect the scenario described in model development where crown closure occurs before $L = L_k$. In all site classes in the age range from 60 to about 140 years an
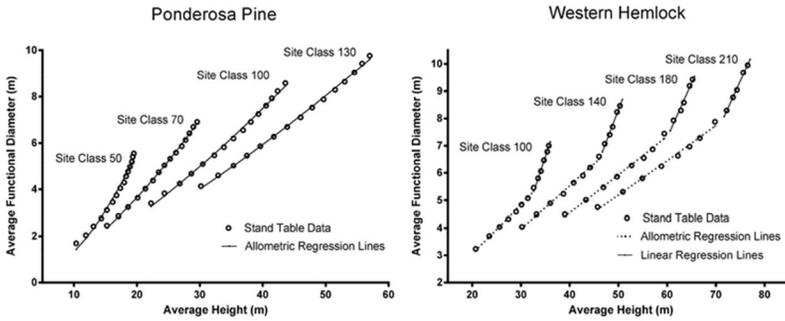
FIGURE 3. Relationships between average tree height ($\bar{H}$) and average functional diameter ($\bar{P}$) for four site classes of ponderosa pine and four of western hemlock. The nine site classes of ponderosa pine and eight of western hemlock that have been omitted for clarity have equivalent patterns. The two fitted lines for each site class of western hemlock represent the results of nonlinear allometric regression analysis for stands 60–140 years old and of linear regression analysis results for stands 160–300 years of age.

allometric relationship exists between $\bar{H}$ and $\bar{P}$. In each site class the slope between $\bar{P}$ and $\bar{H}$ abruptly becomes steeper beyond 140 years of age. Apparently, when this species reaches around 140 years of age L reaches L_k and the crown cover of the stand begins to open up as the stand dynamics become more those of a multilayer species. The same relationship can be seen in douglas fir (Figure S3). This sharp change in slope as the total crown cover opens up may indicate the beginning of a process that results in the more complex stand structure described as old-growth. The more structurally complex canopies resulting from gaps in old-growth stands (Gray et al. [2012]) also results in higher nitrogen use efficiency and higher annual net primary productivity, although total leaf area index remains relatively stable (Hardiman et al. [2013]). The other species analyzed do not show this clear shift in slope (Supplementary Information).

Other published exponent values from studies of multiple species are often close to the exponent value predicted by the often reported self-thinning law for total biomass of –0.50 (Westoby [1984], Zeide [1987], Weller [1989]). If it is assumed that total wood volume is close to total biomass then this self-thinning value falls between the theoretical multilayered (–0.33) and monolayered (–1.00) exponent values (Tables 1 and 2). The self-thinning slopes for B, the estimate of the total stand heterotrophic biomass for each species, are the values of j in Table 6. Except for ponderosa pine at -0.2563 all of the values are dispersed across the range between the theoretical value of –0.33 for a multilayered species and that of –1.00 for a monolayered species. The ponderosa pine value is consistent with the value of the allometric exponent of $\bar{H}$ used to predict $\bar{A}$ discussed previously.

The allometric exponents associated with self-thinning are not the only ones that vary between Tables 1 and 2. Variation in allometric exponents has long been observed (Price et al. [2007]). They compared the allometric exponents for height versus stem radius, height versus plant mass, and radius versus plant mass for a range of plant species including Sonoran Desert species, trees from the Cannell Forestry data base, and angiosperm leaves. Price et al. [2007] observed that over the range of data used, increases and decreases in the allometric exponents were correlated, a covariation of traits that occurs across many plant functional types.

In a study of the energetic equivalence rule Deng et al. [2008] evaluated the relationships between average plant mass and both average leaf biomass and plant density using 21 taxa representing trees, shrubs, and herbaceous plants from the literature. The ratio of the allometric exponents on plant mass versus both average leaf area and density were used to compute an exponent ratio for each taxum. The average of those ratios across taxa, –0.99, did not significantly differ from –1.00. In Table 1 the allometric exponent on average wood volume (closely related to average plant mass) versus average foliage biomass is 0.750, versus density it is –0.750, giving a ratio of –1.00. In Table 2, the same exponents are 0.500 and –0.500, again giving a ratio of –1.00. The results indicate that the 21 taxa populations (Deng et al. [2008]) used were approaching, or had reached, full resource use, and a constant foliage biomass, on their respective sites. There are other similar-stand based allometric exponents that differ between Tables 1 and 2, that also have identical ratios. However, these values for j cannot be fully interpreted because of the analysis procedures used, the uncertain relationships between B and total biomass across species, and the possible effects of variation in stand table construction methods. Additional analyses using equation (15) with derived variables and summary tables by species are provided in the supplemental material.

5. Discussion.   This model was used to analyze each variable of each species across multiple sites and stand ages with a single equation (15). Variables are linked through their relationships with Z, as represented by the site index, and the relationship between a stable stand foliage biomass and an increasing total stand heterotrophic nonphotosynthetic biomass with tree growth. While equation (15) is a simplification used to examine how a fully occupied system might function, such simplifications make exploration of the ecological processes involved possible (Clark [1990]). "The art of modeling is in summarizing and selecting the detail necessary to gain insight into a complex process of interest" (Reynolds and Ford [2005]). Because this model is theoretically based it is possible to develop specific hypotheses regarding the biological, ecological processes behind the results obtained, and how those processes may deviate from the assumptions of the model.

Equations (12), (15), and the equation for anamorphic site index curves (Aquirre-Bravo and Smith [1986]) are all derived from the same basic differential equation (equation (13)). Also, the assumptions used for model development here expand on

the underlying assumptions of the methods used to develop anamorphic site index curves.

Identification of a dimension of the total plant community that is directly related to site condition has had limited investigation. The plant community variable total solar equivalent leaf area appears to be a theoretically reasonable candidate for this purpose. A closely related variable, total leaf biomass or area was proposed by Long and Smith [1984], who reviewed several studies that suggested that total leaf biomass or area stabilizes at full site occupancy. Total leaf biomass provides the photosynthesis for community production as a function of resource availability (Whittaker and Niering [1975], Grier and Running [1977], Waring et al. [1978], Nemani and Running [1989]).

The model developed here uses several assumptions based on biological processes, but these processes may or may not function as hypothesized, particularly at individual sites or in other species. Additional validation analyses with actual field data are needed to sort out whether these possible effects exist and the nature of their influence. Other indices of total community resource availability or use can be substituted for leaf area. However, a dimension usable as a substitute for leaf area in one community may not be usable in another. Full testing of the model will require independent estimation of the total living heterotrophic tissue for each species.

This model also provides biological interpretation of the parameters in the Chapman-Richards equation (equation (12)). The area of application is more restricted and more closely defined by the model developed here than in past uses of this equation, which have generally considered time zero (t_0) to be arbitrary and of limited biological meaning (Richards [1959]). Here time zero is the time point at which full site occupancy, or annual full site resource use, is reached by the species. The values of j in equations (12) and (15) have previously been empirically determined, and not functionally defined (Pienaar and Turnbull [1973]). In this model, j is the exponent of a power relationship between the variable of interest and the total heterotrophic living tissue of the community. The parameter g is the intrinsic growth rate, or assimilation rate (Moore [1989]), of the species. Past models of stand dynamics have not fully explained the source of the variation in both the allometric exponent (j in equation (11)), or the species specific allometric constant (a in equation (11)), or how the vertical and horizontal stratification of the canopy changes through time (Reynolds and Ford [2005]). The same occurs with the model developed here. It does, however, provide a baseline for exploring these sources of variation.

6. Conclusions. The pattern of stand growth dynamics in single species stands of conifers is dependent on a constant foliage biomass utilizing the annually available resources on the site. With the ratio of heterotrophic to photosynthetic tissue

increasing with tree size, resources available for growth and competition decrease as a function of tree size. These processes are modeled using a single equation (15), that is based on a maximum (carrying capacity) value for each variable, and the difference between than maximum value and the value at some elapsed time T, times a negative exponential based on the product of the intrinsic species growth g and T.

These patterns of stand dynamics in single species stands appear to be emergent properties of a self-organized system (Camazine et al. [2001], Sole' and Bascompte [2006]) functioning within a constant level of annually available resources, which is reflected in a stable total stand foliage biomass. This system appears to have three primary components that determine the distribution of the total foliage biomass among the trees in the stand as they grow. The first is the annual growth of foliage by the terminal buds. Second, is the interaction of this foliage growth to change the structure of the individual branches. Third is the interactions of the individual branches changing structure of the entire tree crown (Tausch [2009]). In stands with closed crowns this includes interactions with branches in adjacent crown as well. Simultaneously the changing structure of the individual trees changes the crown structure of the entire stand through a self-organization processes. All of these stand level changes are centered around the efficient distribution of foliage biomass of the entire stand for intercepting solar radiation, while minimizing the energetic expense of the heterotrophic tissue supporting that foliage (Tausch [2009]). Even on sites where the environmental conditions are too limiting for crown closure to occur, there is a simultaneous minimizing of the energetic expense of the heterotrophic root system for the efficient retrieval of soil resources to maintain the total foliage biomass of the stand.

These observations suggest that self-thinning is one emergent property of the self-organization process in single species stands that results from growth and development over time within a constant level of resources. The slope of the resulting self-thinning line for each species is determined by the relationship between its functional depth for foliage (Tausch 2009) and the average mature size of the species. The smaller the ratio between functional depth and mature size, the closer the species is to a theoretical monolayer, and the larger the closer to a theoretical multilayer (Tables 1 and 2). Thus, the other stand based allometric relationships within the stands for each species covary across species as a function of the distribution of foliage within their crowns. The consistency of these relationships across multiple species appears to indicate rules of local interactions for self-organization within stands of each species are functionally equivalent regardless of the species.

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Supporting Information. Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Table S1. Ponderosa pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions.

Table S2. Western hemlock parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions

Table S3. Douglas fir parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions.

Table S4. Red fir parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions

Table S5. Loblolly pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions.

Table S6. Long Leaf pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions.

Table S7. Short Leaf pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using site class as an index of site conditions

Table S8. Ponderosa pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using total basal area as an index of site conditions

Table S9. Short Leaf pine parameter values, conditional R^2, and SEE% for equation (15) calibrated for 10 variables from the full stand table data, using total basal area as an index of site conditions

Table S10. List of principle assumptions used in model derivation.

Figure S1. Relationships between (1) foliage biomass and the weighted moisture index and (2) annual productivity and the weighted moisture index from Whittaker and Niering [1975] for sites along an elevation gradient from open oak woodland to subalpine fir. (1) Lines for foliage biomass in the open and closed canopy communities were calculated by separate regression analyses. (2) Linear regression analysis was used across all sites to analyze annual productivity.

Figure S2. Relationships between average height and average functional diameter in loblolly pine and long leaf pine. Allometric regression lines were computed by site class. The other site classes, omitted for clarity, show relationships similar to those presented.

Figure S3. Relationships between average height and average functional diameter in douglas fir, red fir and short-leaf pine. Allometric regression lines were calculated for all species, and linear regression lines were calculated for the douglas fir data after the abrupt change in slope. The other site classes, omitted for clarity, show relationships similar to those presented.