

# Plant Population Growth and Competition in a Light Gradient

## A mathematical model of canopy partitioning

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### Abstract

Can a difference in the heights at which plants place their leaves, a pattern we call canopy partitioning, make it possible for two competing plant species to coexist? To find out, we examine a model of clonal plants living in a nonseasonal environment that relates the dynamical behavior and competitive abilities of plant populations to the structural and functional features of the plants that form them. This examination emphasizes whole plant performance in the vertical light gradient caused by self-shading. This first of three related papers formulates a prototype single species CANOPY STRUCTURE MODEL from biological first principles and shows how all plant properties work together to determine population persistence and equilibrium abundance. Population persistence is favored, and equilibrium abundance is increased, by high irradiance, high maximum photosynthesis rate, rapid saturation of the photosynthetic response to increased irradiance, low tissue respiration rate, small amounts of stem and root tissue necessary to support the needs of leaves, and low density of leaf, stem, and root tissue. In particular, equilibrium abundance decreases as mean leaf height increases because of the increased cost of manufacturing and maintaining stem tissue. All conclusions arise from this formulation by straightforward analysis. The argument concludes by stating this formulation's straightforward extension, called a CANOPY PARTITIONING MODEL, to two competing species.

*Keywords:* canopy partitioning model; canopy structure model; clonal growth; light competition; plant competition; plant energetics; plant shading

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## Introduction

The principal feature that distinguishes plant competition from animal competition is that most plants require exactly the same resources, namely sunlight, water, carbon dioxide, and mineral nutrients. Plant species therefore cannot avoid competition with others by partitioning resources as many animal competitors do. Yet most terrestrial communities support multiple coexisting plant species. Indeed, Wright (2002) mentions an extreme case in which a single 0.25 km<sup>2</sup> parcel of tropical rain forest in Ecuador supports 1,104 tree species (roughly equivalent to the entire native tree floras of Europe, Asia, and North America combined!), and these trees constitute only about 25% of all plant species that live there. Such observations raise the compelling question of how such plant species manage to avoid competitive exclusion (Hardin 1960).

Several mechanisms have been proposed (Barot and Gignoux 2004). Most involve environmental variation through horizontal space and/or through time. For example, similar species can coexist in some places as long as environmental conditions vary through space in such a way that each species enjoys competitive superiority somewhere (Ter Steege 1994). Often the requisite environmental variation arises through biological means. Specialized insect herbivores can decimate seeds or seedlings of one species beneath the parent tree where they occur abundantly, liberating the habitat there for occupancy by other species (Janzen 1970, Connell 1971). Sometimes plant species that compete as adults coexist because the foliage of one ameliorates otherwise harsh physical conditions beneath adult plants in a way that favors survival of another's seedlings (Callaway and Walker 1997). Nutrient uptake and release by plants can alter nutrient availability in the soil directly beneath them, promoting invasion by other species that require these nutrients in different ratios, and the resulting regional mosaic of soil nutrient concentrations can potentially support many coexisting species (Tilman 1982, 1988; Grace and Tilman 1990). Regional patchiness in environmental conditions can also be created by disturbances ranging from large scale forest fires to small scale events like the collapse of an individual tree during a storm. These disturbances create opportunities for invasion by different plant species during different stages of vegetation recovery, ultimately producing regional coexistence of many competing plant species. This process has been reproduced by Pacala *et al.* (1996) in an individual-based computer model and by a wide assortment of computer models by many others (as

reviewed by Porté and Bartelink 2002).

While acknowledging the roles of these important mechanisms, in this and two companion papers (Nevai and Vance *in review a, b*) we explore another mechanism that does not require environmental variation either through horizontal space or time. It does require a different form of biologically generated spatial environmental variation, namely the vertical gradient in light intensity created by the plant leaves that form the foliage canopy (Monsi and Saeki 1953, Idso and de Wit 1970). We consider plant species with two contrasting patterns of leaf placement. A plant that deploys its leaves high within the canopy exposes them to high irradiance that produces rapid photosynthesis. However, to secure this benefit, a tall plant must pay the considerable energetic cost of growing and then maintaining tall stems to support these leaves. In contrast, a plant that places its leaves nearer the ground will intercept less sunlight and experience slower photosynthesis, but its short stems impose a reduced energetic cost. The question we address is whether this plant height and energy budget difference can make it possible for competing plant species to coexist, particularly when their vertical leaf profiles overlap so that both plant species shade each other as well as themselves.

In nature, this potential mechanism of competitive coexistence, which we call canopy partitioning, probably does not usually operate in isolation. Rather, most plants that occupy a vertical light gradient probably also experience environmental variation through horizontal space and time. However, rather than attempting to disentangle several mechanisms of coexistence that operate simultaneously, we will study the simpler question of whether canopy partitioning by itself can produce competitive coexistence in a hypothetical setting in which the environment remains constant through both horizontal space and time. Our hope is that understanding this mechanism in isolation will help expedite future attempts to learn how it operates with others in nature.

This approach requires a mathematical model, or rather, because of the complexity of real-world plants, a family of related models that emphasize different aspects of real-world plant structure and function. Formulation of a particularly convenient model as a prototype for this family is the subject of this paper. We begin with general considerations. To serve our purpose best, this prototype model must incorporate four characteristics: (1) it must concern population dynamics; (2) it must include enough complexity to describe explicitly how at least the most basic structural and functional features of plants together produce population dynamics; (3) it must retain enough simplicity to

allow analytical examination of the ranges of plant attributes that produce the various outcomes of interspecies competition; and finally (4) it must have a qualitative form shared by its more inclusive and detailed relatives so that its behavior resembles theirs, at least qualitatively.

Two choices have allowed us to incorporate all four characteristics. The first was to work out the basic formulation by first constructing a model for a single plant species population living by itself. This initial focus serves two purposes. First, it facilitates discovery of a practical compromise between the realism and analytical tractability of the model's two-species extension. Second, it provides a reality check: only if the behavior of the single-species version reproduces biological intuition will emergent properties of the two-species extension have any biological credibility.

The second choice was to restrict attention to a specific group of hypothetical plants with simple, idealized properties. These plants are comprised of leaves positioned at different heights above the ground, roots in the ground, and stems that support the leaves and also transport water, nutrients, and sugar between plant parts. All essential resources except sunlight occur in excess of the plants' needs, and consequently these plants compete only for sunlight. These hypothetical plants lack all further complications of real-world plants. In particular, they experience no seasonal variation in weather, and the vertical leaf distribution of each species remains fixed through all time. These plants have a clonal growth form, which means that all stems of each species attach to a common root system that serves the whole clone. Old stems may die and new ones may grow from the ground to replace them. New stems too deeply shaded to produce much photosynthetic energy themselves may receive an energy subsidy from taller stems nearby via translocation through the root system (Gough *et al.* 2002). It is through such subsidized growth of new stems that our hypothetical clones are able to maintain a fixed vertical leaf distribution through all time.

We have adopted these rather severe restrictions because they make analysis of this important but otherwise intractable ecological problem possible. No real-world plants possess exactly these characteristics and other hypothetical features to be described shortly. However, several plant species that occupy southern California salt marshes (a community well described by Zedler 1982), such as *Salicornia virginica* and *Frankenia grandifolia*, may come close (personal observation). Although these species do reproduce via conventional seeds, by far most population changes in an established and minimally disturbed salt marsh in this region occur almost entirely through vegetative growth or loss

of established clones. These clones are capable of living for several decades at least. Except in marshes that are either newly established or recovering from a recent major physical disturbance, plant-plant interactions that occur under natural conditions during this very long period of vegetative growth seem likely (to us) to be the main causes of community structure. We hasten to acknowledge, however, that southern California salt marshes are now so thoroughly disturbed by human activities both in the marshes themselves and in their watersheds (Zedler and Onuf 1984) that how broadly this suspicion might actually apply today would be difficult to establish empirically. We suspect that it probably does apply in portions of a few marshes that experience the least anthropogenic disturbance. Concerning seasonality, southern California clonal salt marsh plants do experience some seasonal variation in growth and in height, but this seasonal variation is certainly far less extreme than occurs in almost all other temperate zone plant communities. Indeed, these plants' gross appearance and vertical foliage profile do not usually change much during the year (personal observation). The model described here and in the companion papers (Nevai and Vance *in review a, b*) is a mathematically convenient idealization of our conception of undisturbed southern California clonal salt marsh plant populations during long periods of undisturbed vegetative growth. Perhaps this idealization also resembles nature elsewhere such as, perhaps, low latitude and relatively nonseasonal grasslands or freshwater marshes dominated by clonal plant populations.

This paper deals primarily with the single-species model, which we call our CANOPY STRUCTURE MODEL. Section 1 states the assumptions of the single-species model and their immediate consequences. The derivation of the population growth equation in section 2 shows that although the model provides only a highly simplified caricature of real plants, it does explicitly connect growth of the plant population to the underlying plant structure and physiological processes that cause it. Section 3 examines how each parameter influences population persistence and equilibrium abundance. Section 4 generalizes the model in a way designed to simplify the algebra in later papers, a step that also increases realism. The desired growth equations for two competing species then emerge as a straightforward extension of this generalized version of the model. Finally, the Discussion interprets the model's principal features in biological terms, describes its limitations, and then points out how enrichments to this basic formulation can accommodate several additional features of nature.

This entire investigation was inspired by Hirose and Werger's (1995) empirical study of vegeta-

tion structure in a freshwater wetland, our own field observations of vegetation structure in southern California salt marshes, and the theoretical explorations of phytoplankton by Huisman and Weissing (1994) and Weissing and Huisman (1994) who pioneered this physiological approach to growth and competition in plant populations. By examining a fully specified dynamical system described in explicit physiological terms, our analysis enriches parts of an earlier formulation of plant population growth and competition studied by Mäkelä and Hari (1984), and it amplifies the similar and independently developed thoughts about canopy partitioning of D.E. Bunker, S.C. Stark, and W.P. Carson (in preparation).

## **1 Assumed Plant Properties and Their Consequences**

The model treats three main features of plants: their gross structure, their sunlight energy capture, and their energy use. Each subsection below describes one of these features. Its first paragraph describes assumed properties, and later paragraphs deduce consequences concerning this one plant feature.

### **1.1 Structure**

The hypothetical plants consist of horizontally oriented leaves connected to vertically oriented stems directly beneath them which in turn connect to roots below ground. Functional tissue in stems and roots consists of all living cells associated with the vascular tubes through which occurs translocation of water, nutrients, and photosynthetically produced sugar. By definition, functional stem and root tissue includes neither the interior spaces of nonliving vascular tubes nor support structure that is no longer living. Each  $\text{m}^2$  of leaf surface is served exclusively by the vascular tubes associated with  $v \text{ m}^2$  cross-sectional area of functional tissue in stems that connect to a biomass  $r$  of functional root tissue, with biomass measured as grams of carbon (gC). All functional stem and root tissue is associated with leaves in this way. This same gross plant architecture and these same tissue ratios apply through all time. Chemical composition of all plant material is sufficiently uniform that energy content is directly proportional to carbon biomass with the same proportionality constant in all tissue types; thus tissue (or whole plant) carbon biomass constitutes a direct measure of tissue (or whole plant) energy content. Stems are uniformly distributed through horizontal space, and leaves have the same

vertical distribution above each point on the ground. Specifically, the vertical density of leaves at height  $z$  m is given by the density function  $\mathbf{s}(z)$ , so that the fraction of leaves that lie between any two heights  $a$  and  $b$  with  $a < b$  is  $\int_a^b \mathbf{s}(z) dz$ . The function  $\mathbf{s}$  is positive and continuous throughout a single height range and zero elsewhere. Leaves have vertical thickness  $\ell$  m, and functional leaf and stem tissues contain  $\lambda$  and  $\sigma$  gC per  $\text{m}^3$  of volume, respectively.

Before exploring consequences of these assumptions, we note that this postulated structure of living tissue associated with vascular tubes is consistent both with the classical pipe model of Shinozaki *et al.* (1964) and also the more recent allometric description of vascular tubes developed by West *et al.* (1999) and Enquist *et al.* (2000). We also note that our use of a density function to describe the vertical distribution of foliage follows the convention employed by Weissing and Huisman (1994) for phytoplankton in a lake and by Horn (1971), Mäkelä and Hari (1984), Osawa *et al.* (1991), and others for trees.

Let  $H$  and

$$s = \int_0^H z \mathbf{s}(z) dz \quad (1.1)$$

represent maximum and mean leaf height in m, respectively, and let

$$\mathbf{S}(z) = \int_z^H \mathbf{s}(\zeta) d\zeta \quad (1.2)$$

represent the fraction of leaf area that overlies height  $z$ . For convenience, consider a clone with  $1 \text{ m}^2$  of leaf area that occupies  $1 \text{ m}^2$  of ground area. This clone's functional leaf and stem tissues have volumes  $1 \times \ell$  and  $\int_0^H v \mathbf{S}(z) dz = v \int_0^H z \mathbf{s}(z) dz = vs \text{ m}^3$  and carbon biomasses  $\lambda \ell$  and  $\sigma vs$  gC, respectively, where the first equality arises by integration by parts and the second by eq. (1.1). Accordingly, including roots this clone has total functional biomass  $\lambda \ell + \sigma vs + r$  gC, and consequently the fractions of whole plant functional tissue carbon biomass (and energy) comprised of leaves, stems, and roots are given by, respectively,

$$\begin{aligned} f_L &= \frac{\lambda \ell}{\lambda \ell + \sigma vs + r}, \\ f_S &= \frac{\sigma vs}{\lambda \ell + \sigma vs + r}, \\ f_R &= \frac{r}{\lambda \ell + \sigma vs + r}. \end{aligned} \quad (1.3)$$

We now introduce several measures of population abundance that concern the various plant parts. Let  $L$ ,  $S$ , and  $R$  represent the functional biomasses in gC of leaves, stems, and roots associated with each  $\text{m}^2$  of ground area, and let  $x$  represent the population's leaf area index, which is the surface area of leaves in  $\text{m}^2$  that overlie each  $\text{m}^2$  of ground surface. Observe that the area of leaves at height  $z$  is  $\mathbf{s}(z)x$  and that the area of leaves that overlie height  $z$  is  $\mathbf{S}(z)x$ . Furthermore, leaf mass, functional stem mass, and functional root mass satisfy the relations

$$L = \lambda \ell x \quad S = \sigma v s x \quad R = r x. \quad (1.4)$$

Accordingly, the leaf, stem, and root fractions of eq. (1.3) hold for any leaf area  $x$ .

## 1.2 Energy capture

Sunlight above the hypothetical plant canopy has constant irradiance  $I_{\text{in}}$ , measured in  $\text{W m}^{-2}$  (Bell and Rose 1981). As this light passes vertically downward through the foliage, light absorption by leaves causes irradiance to diminish exponentially with cumulative overlying leaf area according to the Lambert-Beer Law, and consequently irradiance at height  $z$  m above the ground surface is

$$I(z, x) = I_{\text{in}} e^{-\kappa \mathbf{S}(z)x}, \quad (1.5)$$

where  $\kappa$  is the light extinction coefficient. The instantaneous rate of gross photosynthesis or energy capture by a leaf, expressed as gC produced per second per  $\text{m}^2$  of leaf surface, is a rectangular hyperbolic function of irradiance  $I$  incident upon its upper surface,

$$\varphi(I) = \phi_{\text{max}} \left[ \frac{I}{I + J} \right], \quad (1.6)$$

where  $\phi_{\text{max}}$  is the maximum photosynthesis rate and  $J$  is the half-saturation constant (Bose 1924, Rabinowitch 1951, Holling 1959).

Let  $\Phi(x)$  represent the canopy photosynthesis rate per unit ground area in a plant population with leaf area index  $x$ . From the energy-capture properties, it follows that  $\Phi(x)$  is just the rate  $\varphi(I(z, x))$  of photosynthesis per unit leaf area by leaves at height  $z$  multiplied by the area  $\mathbf{s}(z)x$  of leaves at

height  $z$  per unit ground area and then integrated over the vertical extent of the canopy,

$$\begin{aligned}\Phi(x) &= \int_0^H \varphi(I(z, x)) \mathbf{s}(z) x \, dz \\ &= \int_0^H \phi_{\max} \left[ \frac{I_{\text{in}} e^{-\kappa \mathbf{S}(z)x}}{I_{\text{in}} e^{-\kappa \mathbf{S}(z)x} + J} \right] \mathbf{s}(z) x \, dz,\end{aligned}$$

(Thornley and Johnson 1990). Employing the change of variable  $\alpha = \mathbf{S}(z)$  and rearranging simplifies this expression to

$$\Phi(x) = x \int_0^1 \phi_{\max} \left[ \frac{I_{\text{in}}}{I_{\text{in}} + J e^{\kappa \alpha x}} \right] d\alpha. \quad (1.7)$$

We choose not to reduce this integral to a closed form expression because doing so would obscure the general form of the population growth equation we will emphasize shortly. Observe that canopy height  $H$  and the vertical leaf density function  $\mathbf{s}(z)$  do not appear in eq. (1.7).

### 1.3 Energy use

In the hypothetical plants, leaves, stems, and roots instantaneously receive the fractions  $f_L$ ,  $f_S$  and  $f_R$  of the photosynthetic energy produced by leaves, and each expends energy at rate  $m$  gC per second per gC of functional tissue on maintenance respiration. When its energy gain rate exceeds its maintenance respiration rate, each tissue type experiences positive somatic growth at a rate proportional to its net rate of energy gain, with proportionality constant  $g_P \in (0, 1)$ , and the remaining energy is lost as additional respiration associated with somatic growth (McCree 1970, Thornley 1970, Penning de Vries *et al.* 1974, Mäkelä 1986; see Amthor 2000 or Thornley and Cannell 2000). Each plant tissue type experiences death, or in stems and roots conversion from functional tissue into nonmetabolizing support structure, at basal rate  $\delta$  gC per second per gC of functional tissue. When its maintenance respiration rate equals or exceeds its energy gain rate, each tissue type experiences added death (or negative somatic “growth”) at a rate proportional to its net rate of energy loss, with proportionality constant  $g_N$ . Neither somatic growth nor tissue death alters the vertical leaf density function  $\mathbf{s}(z)$ .

These energy use properties imply that the plant population’s leaf carbon biomass  $L$  obeys the differential equation

$$\frac{dL}{dt} = g \left[ f_L \Phi(x) - mL \right] - \delta L, \quad (1.8)$$

where

$$g = \begin{cases} g_P, & \text{if } [f_L\Phi(x) - mL] > 0 \\ g_N, & \text{if } [f_L\Phi(x) - mL] \leq 0, \end{cases}$$

and that stem carbon biomass  $S$  and root carbon biomass  $R$  each obey a differential equation of this same form but with  $f_S$  and  $f_R$  in place of  $f_L$ .

## 2 The Population Growth Equation

A complete description of plant population growth arises from these three sets of assumptions. This description employs leaf area index  $x$  as the measure of population abundance. Inserting expressions for  $f_L$ ,  $L$ , and  $\Phi(x)$  from eqs. (1.3), (1.4), and (1.7), respectively, into eq. (1.8) yields, after some rearrangement, the population growth equation

$$\begin{aligned} \frac{dx}{dt} &= xf(x), \\ f(x) &= g \left( \frac{\phi_{\max}}{\lambda\ell + \sigma vs + r} \int_0^1 \left[ \frac{I_{\text{in}}}{I_{\text{in}} + Je^{\kappa\alpha x}} \right] d\alpha - m \right) - \delta, \end{aligned} \tag{2.1}$$

where  $g = g_P$  when the population's net energy gain per gC that appears as the parenthetical quantity is positive and  $g = g_N$  when it is nonpositive, and  $s$  is the (constant) mean leaf height parameter introduced in eq. (1.1). We call eq. (2.1) our CANOPY STRUCTURE MODEL. This equation clearly reveals the well known fact that canopy height  $H$  and the vertical leaf density function  $\mathbf{s}(z)$  exert their influence solely through their effect on mean leaf height  $s$ , because neither  $H$  nor  $\mathbf{s}(z)$  appears explicitly in the population growth equation.

Table 1 summarizes this section and the preceding one by displaying all assumed plant properties and their immediate consequences upon which all equations so far depend.

## 3 Population Persistence and Equilibrium Abundance

The specific growth rate function  $f$  in eq. (2.1) has three convenient qualitative properties:

- f<sub>1</sub>.  $f$  is continuous and piecewise differentiable for  $x \geq 0$ ;
- f<sub>2</sub>.  $f$  is a decreasing function of  $x \geq 0$ ;

f<sub>3</sub>.  $f < 0$  for large values of  $x$ .

The function  $f$  is in fact differentiable for all  $x \geq 0$  except (possibly) at the unique value of  $x$  at which the parenthetical quantity in eq. (2.1) is zero.

Before discussing population persistence and equilibrium abundance, we note that the general population growth equation  $dx/dt = xf(x)$ , with the form and biological interpretation of  $f$  left unspecified, is sometimes loosely referred to as the Kolmogorov model in tribute to Kolmogorov's (1936) classical study of a predator-prey model whose two coupled differential equations have the form  $dx_i/dt = x_i f_i(x_1, x_2)$  for  $i = 1, 2$ . Since Kolmogorov never actually studied the single-species case to our knowledge, when  $f$  satisfies properties f<sub>1</sub>, f<sub>2</sub>, and f<sub>3</sub>, we call this model THE FUNDAMENTAL GROWTH EQUATION OF POPULATION ECOLOGY because of its great versatility in approximating population growth in many different settings. The foregoing derivation provides one example in which this general equation, with a suitably defined growth rate function, describes the growth of a population in terms of explicitly described features of the organisms involved. The uses of this fundamental growth equation, however, extend far beyond this particular example. Indeed, this equation's qualitative form is precisely the feature shared by a very diverse collection of enrichments to the prototype model discussed here, a point anticipated by Mäkelä and Hari's (1984) use of Lotka-Volterra equations to study plant competition for sunlight.

Concrete applications of the fundamental growth equation, of course, virtually always rest on simplifying assumptions and/or apply only in special cases. For example, this particular application requires, among other things, that all three tissue types share the same values of  $m$  and  $\delta$ , a point to which we will return in the Discussion.

### 3.1 Persistence

Whether the hypothetical plant population persists or experiences extinction in this model depends on the sign of  $f(0)$ . If  $f(0) \leq 0$ , then 0 is the unique globally attracting equilibrium point, and the population eventually becomes extinct. If  $f(0) > 0$ , then there is a unique positive equilibrium population abundance  $x^*$ , which is globally attracting, and the population persists. This  $x^*$  is defined implicitly by the relation  $f(x^*) = 0$ .

For the specific growth rate function  $f$  of eq. (2.1), the persistence condition is

$$g_P \left( \frac{\phi_{\max}}{\lambda\ell + \sigma vs + r} \left[ \frac{I_{\text{in}}}{I_{\text{in}} + J} \right] - m \right) - \delta > 0, \quad (3.1)$$

which can be satisfied only if

$$\phi_{\max} \left[ \frac{I_{\text{in}}}{I_{\text{in}} + J} \right] > m(\lambda\ell + \sigma vs + r). \quad (3.2)$$

The qualitative influences of all model parameters on population persistence are evident by inspection of conditions (3.1) and (3.2). Condition (3.2) states simply that in the limit as population abundance tends to 0, gross canopy photosynthesis must exceed maintenance respiration. Gross canopy photosynthesis is relatively large whenever the maximum photosynthesis rate  $\phi_{\max}$  and the canopy surface irradiance  $I_{\text{in}}$  are relatively large and the photosynthesis half-saturation constant  $J$  is relatively small. Whole plant maintenance respiration is relatively small when the per unit biomass maintenance respiration rate  $m$  and all parameters that contribute to whole plant biomass  $\lambda\ell + \sigma vs + r$  associated with each  $\text{m}^2$  of leaf area are relatively small.

If condition (3.2) is satisfied, then the persistence condition (3.1) is satisfied too if the growth rate of new plant tissues exceeds the loss rate of existing plant tissues through death or conversion into nonconducting support structure. This condition holds if plant growth efficiency  $g_P$  is relatively large and tissue death rate  $\delta$  is relatively small. Observe that the light extinction coefficient  $\kappa$  does not influence persistence, as all leaves in an infinitesimal population intercept essentially full sunlight. All of these qualitative influences of model parameters on population persistence corroborate biological intuition. As noted earlier,  $H$  and  $\mathbf{s}(z)$  exert their influence on persistence only through mean leaf height  $s$ . Table 1 summarizes these results.

### 3.2 Equilibrium abundance

When the persistence condition (3.1) holds, equilibrium population abundance, as measured by equilibrium leaf area index  $x^*$ , satisfies

$$f(x^*) = g_P \left( \frac{\phi_{\max}}{\lambda\ell + \sigma vs + r} \int_0^1 \left[ \frac{I_{\text{in}}}{I_{\text{in}} + J e^{\kappa\alpha x^*}} \right] d\alpha - m \right) - \delta = 0, \quad (3.3)$$

where again  $g = g_P$  because the parenthetical quantity is positive. Although this equation defines  $x^*$  in terms of model parameters only implicitly, the qualitative effect on  $x^*$  of increasing any parameter can be determined by inspection. Indeed, any parameter change that causes  $f$  to increase also causes  $x^*$  to increase, because  $f$  evaluated at  $x^*$  must always equal zero. Thus, equilibrium population abundance  $x^*$  increases with increases in the growth efficiency  $g_P$ , the maximum photosynthesis rate  $\phi_{\max}$ , and the canopy surface irradiance  $I_{\text{in}}$  but decreases with increases in the photosynthesis half-saturation constant  $J$ , the light extinction coefficient  $\kappa$ , the maintenance respiration rate  $m$ , the tissue death rate  $\delta$ , and all structural parameters in the quantity  $\lambda\ell + \sigma vs + r$ . These qualitative influences too corroborate biological intuition. As with persistence,  $H$  and  $\mathfrak{s}(z)$  influence equilibrium abundance only through mean leaf height  $s$ . Table 1 summarizes these effects.

In our hypothetical plants with their vertical stems, mean stem length is of course equal to mean leaf height. With all primary parameters held constant, inspection of eq. (3.3) reveals that  $x^*$  decreases as mean stem length  $s$  increases toward its supremum  $s_{\max}$ , defined as the value of  $s$  at which  $x^*$  vanishes. This pattern too concurs with biological intuition: with all else equal, as stems become longer, plants must devote more energy to stem growth and maintenance, and this increased energy demand necessarily reduces the amount of energy available for the manufacture and maintenance of leaves. Thus, tall stems are always an energy drain for plants, and they can potentially confer a net benefit only to plants engaged in competition.

## 4 Generalization and Extension to Two Competing Species

### 4.1 Generalized canopy structure model

Rewriting our canopy structure model (2.1) in more compact notation simplifies subsequent algebra and inspires a generalization. Define the function

$$\phi(x) = \phi_{\max} \left[ \frac{I_{\text{in}}}{I_{\text{in}} + J e^{\kappa x}} \right] \quad (4.1)$$

and the composite constants

$$\gamma = \frac{g}{\lambda\ell + \sigma vs + r} \quad \text{and} \quad C = \left( m + \frac{\delta}{g} \right) (\lambda\ell + \sigma vs + r). \quad (4.2)$$

It is obvious by inspection that the function  $\phi(x)$  has four qualitative properties:

P<sub>1</sub>.  $\phi$  is defined and continuously differentiable for  $x \geq 0$ ;

P<sub>2</sub>.  $\phi > 0$  for  $x \geq 0$ ;

P<sub>3</sub>.  $\phi' < 0$  for  $x \geq 0$ ;

P<sub>4</sub>.  $\phi \rightarrow 0$  as  $x \rightarrow \infty$ ,

and that the positive constants  $\gamma$  and  $C$  are actually two-valued because  $g$  is two-valued. In terms of  $\phi(x)$ ,  $\gamma$ , and  $C$ , our canopy structure model (2.1) can be written as

$$\begin{aligned} \frac{dx}{dt} &= xf(x), \\ f(x) &= \gamma \left[ \int_0^1 \phi(\alpha x) d\alpha - C \right]. \end{aligned} \tag{4.3}$$

The qualitative parameter influences on equilibrium population abundance listed in Table 1 depend not on the explicit algebraic form of the function  $\phi(x)$  but rather on its qualitative shape as described by properties P<sub>1</sub>–P<sub>4</sub>. Indeed, let us now abandon the algebraic form of eqs. (4.1) and (4.2) altogether and suppose instead that just properties P<sub>1</sub>–P<sub>4</sub> hold. In this more general model, when  $f(0) = \gamma[\phi(0) - C] > 0$ , or equivalently when

$$\phi(0) > C$$

so that leaf photosynthesis rate in an infinitesimal population that casts no shade exceeds a composite plant growth and maintenance cost parameter, the population persists. When it persists, there is a unique positive equilibrium abundance  $x^*$  that satisfies  $f(x^*) = 0$ , or equivalently

$$\int_0^1 \phi(\alpha x^*) d\alpha = C.$$

We now let  $x^* = x^*(C)$  and differentiate this equation with respect to  $C$  to get

$$\frac{dx^*}{dC} \int_0^1 \phi'(\alpha x^*) \alpha d\alpha = 1.$$

Property P<sub>3</sub> guarantees that

$$\frac{dx^*}{dC} < 0.$$

Therefore, equilibrium abundance  $x^*$  decreases as the cost parameter  $C$  increases.

The practical value of this generalization is that it accommodates increased realism. For example, replacing the standard rectangular hyperbolic function  $\varphi(I)$  of section 1.2 with the more realistic nonrectangular hyperbolic function (Johnson and Thornley 1984) would produce a composite photosynthesis function  $\phi(x)$  that still satisfies properties P<sub>1</sub>–P<sub>4</sub>.

## 4.2 Canopy partitioning model

Extending our generalized canopy structure model (4.3), which can also be written as

$$\begin{aligned} \frac{dx}{dt} &= x f(x), \\ f(x) &= \gamma \left[ \int_0^\infty \phi(\mathbf{S}(z)x) \mathbf{s}(z) dz - C \right], \end{aligned}$$

to two-species competition is now straightforward. These species are assumed to compete only for sunlight, and the irradiance at any height  $z$  within the canopy now depends on the area of leaves of both species that lie above that height. Thus, if species  $i$ , whose abundance we represent by its leaf area index  $x_i$ , has its own vertical leaf density function  $\mathbf{s}_i(z)$  and related leaf distribution function  $\mathbf{S}_i(z)$ , growth parameter  $\gamma_i$ , cost parameter  $C_i$ , and composite leaf photosynthesis function  $\phi_i$ , then the two competing species abundances now obey the dynamical system

$$\begin{aligned} \frac{dx_i}{dt} &= x_i f_i(x_1, x_2), \quad \text{for } i = 1, 2, \\ f_i(x_1, x_2) &= \gamma_i \left[ \int_0^\infty \phi_i(\mathbf{S}_1(z)x_1, \mathbf{S}_2(z)x_2) \mathbf{s}_i(z) dz - C_i \right]. \end{aligned} \tag{4.4}$$

We call this two-species extension our CANOPY PARTITIONING MODEL. Here the dependence of each photosynthesis function  $\phi_i$  on each individual argument satisfies properties very similar to P<sub>1</sub>–P<sub>4</sub> but slightly more inclusive to accommodate the possibility that one species' leaves may lie partially or entirely above the other's. We do not know whether eq. (4.4) in its full generality will yield to analysis. Our analysis (Nevai and Vance *in review a, b*) concerns the case in which both species have rectangular

vertical leaf density functions and share the same light extinction coefficient.

## Discussion

Our canopy structure model possesses three attributes essential for constructing an analytical theory that explores whether canopy partitioning, *i.e.*, placement of leaves at different heights above the ground, can make possible the coexistence of two competing plant species. These features are: (i) it explicitly describes how the basic structural and functional features of (hypothetical) plants together give rise to population growth, (ii) it is simple enough mathematically that straightforward analysis reveals how each plant feature influences population persistence and equilibrium abundance, and (iii) it's straightforward extension describes the growth dynamics of two competing populations. The fact that this model specifies equilibrium population abundance only as an implicit function of plant properties guarantees that corresponding analysis of two-species competition will be much harder, but the transparency of the single-species version inspires confidence that the two-species analysis will succeed.

Developing our single-species canopy structure model in such a way that its extension to two species would remain amenable to classical analysis required two major concessions. The first is restricting attention to hypothetical plants whose vertical leaf distribution remains constant through all time. We chose not to incorporate assumptions resembling those of Mäkelä and Hari (1984), Valentine (1985), Mäkelä (1986), and Osawa et al. (1991) to introduce height growth, because this feature would very likely have made global analysis of the full two-species model impossible, at least without prior understanding of the “simple” case (Nevai and Vance *in review a, b*) lacking vertical growth. Our constant vertical leaf distribution assumption requires not just a nonseasonal environment but also a mechanism that allows upward growth of initially deeply shaded young stems into the better illuminated foliage canopy. Such a mechanism exists only in clonal plants whose structure allows translocation of sugar from mature stems through the root system to newly developing stems elsewhere in the clone. Thus, the constant vertical leaf distribution assumption restricts our model to clonal plants that occupy a nonseasonal and undisturbed environment, plants that constitute only a tiny fraction of the biosphere.

The second major concession is that our other assumptions radically simplify both plant structure

and plant energy metabolism by ignoring a suite of phenomena known to be important in nature. An abbreviated list of these simplifications follows: (1) The hypothetical plant population is limited solely by sunlight. (2) The importance of each tissue type in the clone lies solely in its role in energy acquisition and use. (3) Leaves at all heights in the canopy have identical physiological properties. (4) The clone's vertical leaf distribution is perfectly homogeneous through horizontal space, an impossible pattern in plants whose individual stems have different lengths and whose leaves have finite size. (5) Leaf, stem, and root tissue all have equal metabolic rates and equal death rates, and newly photosynthesized energy is allocated to each tissue type in proportion to its fractional representation in the clone.

Fortunately, our explorations currently underway reveal that replacing these (and other) simplistic assumptions with carefully formulated more realistic alternatives does not cause the model to deviate from the qualitative form of the fundamental growth equation of population ecology. This observation leads us to suspect that most such enrichments will share most qualitative features of the simple prototype model formulated here, though finding out for sure may in some cases prove challenging.

Detailed descriptions of some such enrichments will appear elsewhere. Here we comment briefly (and without proof) on the simplifications listed above: (1) Our generalization to photosynthesis functions of nonrectangular form allows inclusion of parameters that concern other potentially co-limiting resources. Converting these parameters to functions allows plant water relations (Thornley and Johnson 1990, Niklas 1992, Thornley 1996, Nobel 1999) and nutrient status (Kull and Jarvis 1995, Thornley 1998, Anten and Hirose 2001) to influence the photosynthesis rate dynamically as the plant population grows. (2) Explicit consideration of subjects like stem strength and root uptake of water and nutrients requires additional consideration of allometry and scaling (West *et al.* 1999, Enquist *et al.* 2000), enrichments that will change the magnitude but we suspect not the qualitative mathematical form of population growth. (3) Allowing photosynthesis parameters to depend on the irradiance at which leaves mature, which of course varies with leaf height, does change population dynamics, but in a manner still accommodated by the fundamental growth equation. (4) Wind that causes leaf movement and the multidirectionality of light that strikes leaf surfaces both somewhat mitigate effects of horizontal heterogeneity in a plant canopy inevitably caused by finite leaf size. The sun's daily movement across the sky, which mitigates these effects further, and its absence at night certainly affect

whole clone photosynthesis, but in a way fully accommodated by the fundamental growth equation. This claim holds whether leaves track the sun's movement or not. Similarly, provided that the vertical leaf distribution of the whole clone remains fixed, the horizontal locations of individual stems of varying height affect the magnitude but not the gross qualitative form of population growth. (5) We purposely banished inequality of different plant tissue metabolic and death rates from the prototype model discussed here because they substantially complicate mathematical analysis. Generalizing to accommodate these inequalities requires a complicated scheme of dividing photosynthesized energy between plant tissue types. These inequalities and this scheme do not cause population growth to deviate from the form of the fundamental growth equation.

Recall that even with enrichments like these, the model will still apply only to clonal plants that live in a nonseasonal environment. Expanding our model to confront a larger portion of the biosphere will require considerable further extension. We suspect that greatest progress might arise by proceeding in two stages. First, seasonally varying increase and decrease in plant height should be introduced into the prototype model, employing time-dependent height growth assumptions similar to those of Mäkelä and Hari (1984), Valentine (1985), Mäkelä (1986), and Osawa *et al.* (1991). This first step seems likely to produce a nonautonomous population growth model of the form  $dx/dt = x\tilde{f}(t, x)$ , in which the specific growth rate function  $\tilde{f}$  depends upon population abundance  $x$  as specified in properties f<sub>1</sub>-f<sub>3</sub> and upon time  $t$  in a periodic or perhaps more complex manner. Analysis of this enrichment can employ the well-known relation between this nonautonomous model and its autonomous relative  $dx/dt = xf(x)$ , where  $f(x)$  is the time average of  $\tilde{f}(t, x)$  (Vance and Coddington 1989, Vance 1990, Redheffer and Vance 2003). Extending this analysis to two species, however, will be difficult.

The second step is to extend the model further to nonclonal, sexually reproducing plants. Making this generalization requires dropping the assumption of horizontal homogeneity in the population's vertical leaf distribution and making each plant's light environment depend only on the near neighbors that actually shade it. Up to now, this subject has required elaborate individual based computer population models (*e.g.*, Pacala *et al.* 1996), but the explorations of Bolker and Pacala (1999), Dieckmann and Law (2000), and Bolker *et al.* (2000) provide some hope that analysis may be possible using moment closure methods.

While application to nature of our prototype model itself is extremely limited, its simplicity en-

courages exploration of its many possible elaborations. The compelling fact that species diversity in most real-world terrestrial plant communities remains largely unexplained to date makes this further exploration desirable.

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Table 1. Hypothetical plant properties and their effects on  $f(0)$  and  $x^*$ 

quantity	leaves	stems	roots	eq. no.	effect on $f(0)$	effect on $x^*$	units
<b>structure</b>							
vertical leaf density at height $z$ m	$s(z)$				—	—	$m^{-1}$
canopy height	$H$				—	—	m
fraction of leaves overlying height $z$	$S(z)$			(1.2)	↓	↓	$m^2 m^{-2}$
cross sectional area / unit leaf area	$\ell$	$v$		(1.1)	↓	↓	m
thickness or mean length	$\lambda$	$s$			↓	↓	$gC m^{-3}$
bulk density	$f_L$	$f_S$	$f_R$	(1.3)	↓	↓	$gC m^{-2}$
fraction of population biomass	$\lambda\ell$	$\sigma vs$	$r$		↓	↓	$gC m^{-2}$
biomass / unit leaf area	$L$	$S$	$R$	(1.4)	↓	↓	$m^2 m^{-2}$
biomass / unit ground area	$x$						
<b>energy capture</b>							
irradiance at height $H$ m	$I_{in}$				↑	↑	$W m^{-2}$
light extinction coefficient	$\kappa$				—	↓	$m^2 m^{-2}$
irradiance at height $z$ m	$I(z, x)$			(1.5)	↑	↓	$W m^{-2}$
maximum photosynthesis rate / unit leaf area	$\phi_{max}$				↑	↑	$gC m^{-2} s^{-1}$
half-saturation irradiance	$J$				↓	↓	$W m^{-2}$
photosynthesis rate / unit leaf area	$\varphi(I)$			(1.6)	↓	↓	$gC m^{-2} s^{-1}$
canopy photosynthesis rate / unit ground area	$\Phi(x)$			(1.7)	↓	↓	$gC m^{-2} s^{-1}$
<b>energy use</b>							
maintenance metabolic rate / unit biomass	$m$	$m$	$m$		↓	↓	$gC gC^{-1} s^{-1}$
growth efficiency	$g_P$	$g_P$	$g_P$		↑	↑	$gC gC^{-1}$
fraction of biomass growth	$f_L$	$f_S$	$f_R$		↓	↓	—
basal death or conversion rate	$\delta$	$\delta$	$\delta$		↓	↓	$gC gC^{-1} s^{-1}$
malnourishment death rate coefficient	$g_N$	$g_N$	$g_N$		—	—	$gC gC^{-1}$
<b>growth rate</b>							
surface area / unit ground area	$dx/dt$			(2.1)	↓	↓	$m^2 m^{-2} s^{-1}$