A Canopy Photosynthesis Model for the Dynamics of Size Structure and the Competition Mode in Plant Populations

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ABSTRACT
A dynamic model for growth and mortality of individual plants in a stand is developed, based on the process of canopy photosynthesis, and assuming an allometric relationship between plant height and weight, i.e., an allocation-growth pattern of plant height and stem diameter. The following were shown by simulation: (i) competition between individuals in a crowded stand is never completely one-sided but always asymmetrically two-sided, even though competition is only for light; (ii) plants of the 'height-growth' type exhibit a greater asymmetry in competition than plants of the 'diameter-growth' type; (iii) the competition mode between plants of the 'height-growth' type becomes more asymmetric with increasing photosynthetic ability than with plants of the 'diameter-growth' type. These results can explain recent empirical results obtained from several natural plant communities.

Key words: canopy photosynthesis, competition mode, continuity equation, size distribution.

1. INTRODUCTION
Many models proposed for the study of growth dynamics in plant populations consider interactions between individuals to be based on the growth of each individual in a population. Hara (1986) proposed a canopy photosynthesis model for the growth of individual plants in a stand based on the diffusion model (Hara, 1984a, b). Assuming no a priori growth or competition functions but an allometric relationship between plant height and weight (i.e., allocation-growth pattern), this model reproduced realistic size-dependent growth of individuals as affected by competition between them. Hara's model is a non-spatial canopy photosynthesis model for one growth period. We extended Hara's canopy photosynthesis model to describe the dynamics of size structure based on the continuity equation (a simple version of the diffusion model; Yokozawa and Hara, 1992). Here, we investigate the dynamics of size structure and the mode of competition in plant populations using this dynamic model.

2. MODEL
A detailed description of the model has been given in previous papers (canopy photosynthesis model; Hara, 1986; Yokozawa and Hara, 1992). Let \( f(t,w) \) be a distribution density of individuals of plant weight \( w \) per unit area at time \( t \). We assume that the basic equation governing the dynamics of \( f(t,w) \) is given by
\[
\frac{df(t,w)}{dt} = -\frac{\partial}{\partial w} \left[ G(t,w)f(t,w) \right] - M(t,w)f(t,w),
\]
where the functional forms of \( G(t,w) \) (mean increments of plant weight \( w \) per unit time \( t \)) and \( M(t,w) \) (mortality rate of individuals of plant weight \( w \) at time \( t \)) are determined by the mode and degree of interactions between individuals. In this paper, we consider mainly competition for light. Now let \( f(t,h) \) be a distribution density of plant height \( h \) per unit area at day \( t \) in a stand. Let \( f_{LA}(x,h) \) be a density function of the vertical leaf area distribution of a plant height \( h \). Assuming the homogeneity of the stand and Beer-Lambert's law, light intensity at height \( x \) from the ground at time of day \( t_d \) at day \( t \) is given as
\[
I(t,t_d,x) = I_0 \cdot \sin \left( \frac{\pi \cdot t_d}{T_d} \right) \cdot \exp \left[ -k \cdot \int_0^{h_{max}} \int_0^{h_{max}} f_{LA}(x',h) f_{H}(t,h) dh dx' \right]
\]
where \( h_{max} \) is the maximum plant height in the stand, \( k \) is the extinction coefficient, \( I_0 \) is the maximum irradiance at midday, and \( T_d \) is the daylength. We then have the daily net photosynthetic rate per unit leaf area at \( x \) from ground for an individual of plant height \( h \) in the stand at day \( t \), as follows:
\[ p_n(t,x,h) = \int_0^{T_0} \left[ \frac{b_k}{1 + \alpha k} I(t,t_0,x) \right] \text{d}t - r_t. \]  

(3)

Here, it is assumed that the foliage layer at height \( x \) from the ground dies if \( p_n(t,x,h) \) is negative, although, of course, the height of leaf death is different in the crowded stand. Let \( f_{LA}^*(x,h) \) represent \( f_{LA}(x,h) \) in the crowded stand and let \( p_n^*(t,x,h) \), which is calculated using \( f_{LA}^*(x,h) \), represent \( p_n(t,x,h) \) in the crowded stand. We can obtain the daily net photosynthetic rate of an individual of plant height \( h \) in the stand at day \( t \) as follows:

\[ P_n^*(t,h) = \frac{u}{1 + r_t} \left( \int_0^h p_n^*(t,x,h) f_{LA}^*(x,h) \text{d}x - r_m \left( \alpha h^\beta - \frac{1}{s} \int_0^h f_{LA}^*(x,h) \text{d}x \right) \right), \]  

(4)

where \( u, r_t, r_m, s \) are conversion factor, growth respiration rate, maintenance respiration rate and specific leaf area of an isolated individual respectively. The above equation is given in terms of plant height \( h \). Therefore, we transform it into a function of plant weight, \( P_n^*(t,w) \), using the hypothetical allometric relationship between plant height, \( h \), and plant weight:

\[ w = \alpha h^\beta \]  

(5)

Finally, we have the functional form of \( G(t,w) \) in the basic equation (1), which is identical to \( P_n^*(t,w) \). Mortality function is assumed to occur only if the daily net photosynthetic rate of an individual is negative. Therefore, we assume the functional form of \( M(t,w) \) as

\[ M(t,w) = \begin{cases} 0, & (P_n^*(t,w) > 0); \\ 1, & (P_n^*(t,w) \leq 0). \end{cases} \]  

(6a) (6b)

3. RESULTS OF SIMULATION

Two sets of simulation experiments were performed as follows: (a) variation in allometric parameter \( \beta \); and (b) variation in the saturated value (\( b/a \) in eqn (3)) of light-photosynthesis curve, which was induced by varying parameter \( a \) with fixed \( b \). Parameter values used for simulations are the same as those used in Yokozawa and Hara (1992).

As the allometric parameter, \( \beta \), in eqn (5) decreases, there is more allocation to height growth giving plants that may be termed as 'height-growth' type, because for the same value of \( w \), plants with smaller \( \beta \) have greater height \( h \). Similarly, plants with large values of \( \beta \) are defined as 'diameter-growth' type. On the other hand, \( \alpha \) in eqn (5) is a scaling factor: dimensionless statistics such as CV (coefficient of variation) and skewness are independent of \( \alpha \). Direct comparison of the absolute value of mean plant weight for different values of \( \alpha \) is meaningless, because the mean of \( w \) is proportional to \( \alpha \).

The growth rate of an individual plant surrounded by larger neighbours is reduced because of the shading effect from them, which is generally regarded as asymmetric one-sided competition for light (e.g. Kuroiwa, 1960; Weiner, 1990). Therefore, we investigated relationships between the RGR (relative growth rate) of an individual plant and the accumulated leaf area of other neighbouring plants. We define ARGR as a difference between RGR in an isolated condition and RGR in a crowded condition for an individual of plant weight \( w \). Accumulated leaf area can be used as a competition function, \( C(t,w) \), which is a monotonically decreasing function of \( w \) and expresses the effect of other individuals on the growth of the one subject of size \( w \) at time \( t \). Therefore, \( C(t,w) \) can be given as the total leaf area of individuals larger than \( w \) at time \( t \)

\[ C(t,w) = \int_{w_0}^{w_{\text{max}}} \left( \int_0^{w'} \left( f_{LA}(x,h') \text{d}x \right) \cdot f_{HL}(h') \text{d}h'. \right) \]  

(7)

We see that \( C(t,w_0) = \text{LAI} \) (leaf area index) and \( C(t,w_{\text{max}}) = 0 \), where \( w_0 \) and \( w_{\text{max}} \) represent the minimum and maximum plant weights in the stand, respectively. Under completely one-sided competition, the relationship between ARGR and \( C(t,w) \) at a given time \( t \) is given as a monotonically increasing function passing through the origin, whereas under completely symmetric two-sided competition ARGR is a constant irrespective of \( C(t,w) \). Our model shows that the mode of competition is between these two extremes, two-sided but asymmetric, even though competition was assumed to be only for light. Therefore we approximate the relationship between ARGR
and $C(t, w)$ as follows:

$$\Delta RGR = c_1 C(t, w) + c_2 C(t, w_0),$$

(8)

over a wide range of stand development except for the early growing stage, where $c_1$ and $c_2$ are constants, $c_1$ represents a slope of the linear $\Delta RGR - C(t, w)$ relationship, and $c_2 C(t, w_0)$ ($= c_2 \text{LAI}$) is the intercept on the ordinate. $c_1 = 0$ and $c_2 = 0$ represent the extremes of symmetrically two-sided and completely one-sided competition, respectively.

The slope of the $\Delta RGR - C(t, w)$ relationship, $c_1$, becomes gentler and $c_2$ increases as the value of $\beta$ increases (Fig. 1), indicating that the asymmetry in competition decreases as the allocation-growth pattern becomes 'diameter-growth' type from 'height-growth' type. This is regarded as a characteristic of symmetric two-sided competition (e.g. Hara, 1986; Weiner, 1990). Figures 2A and B show the relationships between the mode of competition and the saturated value of the light-photosynthesis curve ($b/a$ in eqn (3)) for $\beta = 2.0$ and $\beta = 3.0$ respectively. In both cases, the asymmetrical mode increases as the value $b/a$ increases, while the symmetric two-sided mode for $\beta = 2.0$ decreases or keeps constant, indicating that the one-sidedness mode of plants of 'height-growth' type is more intensified by the photosynthetic ability increase than that of plants of 'diameter-growth' type.

4. DISCUSSION

Our model has revealed the relationships between the mode of competition and allocation-growth and between the mode of competition and the photosynthetic ability: (i) competition between individuals in a crowded stand is always between one-sided and symmetric two-sided, and completely one-sided competition is never realised, even though competition is only for light; (ii) as the allocation-growth pattern changes from 'height-growth' type to 'diameter-growth' type, the mode of competition changes from highly asymmetrical to more symmetrical. Therefore, it should be noted that plants of the 'diameter-growth' type tend to exhibit a two-sided competition effect which is close to symmetrical, even though competition is only for light, suggesting that competition for light is not always one-sided as has been hypothesized (e.g. review by Weiner, 1990); (iii) as the photosynthetic ability, which is expressed in terms of the saturated value of the light-photosynthesis curve, increases, the relative one-sided competition mode of plants of the 'height-growth' type is more intensified than that of plants of the 'diameter-growth' type.

Plants of the 'height-growth' type are regarded as early-successional shade-intolerant species, whilst plants of the 'diameter-growth' type are regarded as late-successional shade-tolerant species (Hara, Kimura and Kikuzawa, 1991). Our theoretical result (ii) conforms to the
findings by Hara et al. (1991; "two-sided competition" according to them means a completely symmetric two-sided competition in this paper) that diameter growth of Abies veitchii and A. mariesii (species of 'diameter-growth' type) is less affected by one-sided competition than is diameter growth of Betula ermanii (a species of 'height-growth' type); dynamics of diameter growth are parallel to those of weight growth rather than to those of height growth (e.g. Hara, 1984a, b). Moreover, result (iii) suggests that competition between individuals of plants of the 'diameter-growth' type is less affected by the changes of physiological parameters such as the photosynthetic ability, which can be induced by environmental change, than with plants of the 'height-growth' type, although, of course, we have not taken account of the dynamics of the physiological response to environmental variation.

REFERENCES