Optimal Timing of Leaf Expansion and Shedding in a Seasonally Varying Environment¹⁾

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Abstract Optimal utilization of a seasonally varying environment by deciduous trees is studied by analyzing two mathematical models. Both models are constructed from the viewpoint of carbon economy. First, optimal times for leaf expansion and shedding in the seasonal environment that maximize the total net gain of photosynthetic products are obtained. We show that both leaf ageing and leaf mortality select for delayed leaf expansion. We suggest that the delay of leaf expansion for canopy trees is important in allowing spring ephemeral species to survive in the temperate forest floor. Second, a two-layer model, in which the lower layer of leaves is shaded by the upper, is analyzed to study the effect of self-shading on the optimal pattern of leaf expansion. We show that the succeeding expansion of leaves is more advantageous than flushing expansion, even in the situation where all leaves are constructed by the products in the previous year.

Key words: leaf phenology, optimal strategy, photosynthesis, mathematical model, community structure.

The physiological mechanism of photosynthesis has been studied extensively during the 20th century as one of the central subjects in plant biology. Since leaves are factories for photosynthetic production, the adaptive significance of leaf phenology—the birth, ageing, and death of leaves—is one of the most important problems for plant biologists.

The following three questions are posed in recent studies of the leaf phenology in temperate regions: Question 1. Individual leaf life span: "How long should a plant retain its leaves?" and "Should a plant be evergreen or deciduous?"

Question 2. Seasonal timing: "What time of the year a plant should expand or shed leaves?"

Question 3. The pattern of emergence and shedding: "Should a plant expand all its leaves simultaneously (flushing or synchronous expansion) or expand them sequentially for some length of time (succeeding or sequential expansion)?"

These three questions are not mutually exclusive. However, it is convenient to consider them separately when we try to understand the role of a particular ecological factor in molding a particular leaf habit.

Recently, the adaptive significance of leaf life span (Question 1) has been studied by many authors (Larcher, 1969,1975; Lechowicz, 1984; Harper and Bell, 1979; Chabot and Hicks, 1982; Bazzaz, 1984; Koike, 1985; Nilsen, 1986; Kikuzawa, 1982, 1983,1987). Chabot and Hicks (1982) reviewed studies on leaf life span and picked up several factors that are correlated with it: (a) leaf ageing, (b) mortality due to herbivory, (c) cost of leaf production, (d) drought stress, (e) reallocation of nutrients. In addition, some correlations between leaf life span and other characteristics of leaves have been revealed by empirical studies: (1) In deciduous plants, leaf life span is negatively correlated with photosynthetic rate (Larcher, 1969,1975). (2) Leaf life span is positively correlated with construction cost (Chabot and Hicks, 1982; Koike, 1985). (3) A leaf in a light environment has a shorter life span (Nilsen, 1986).

However, the adaptive significance of seasonal timing of emergence and shedding (Question 2) has not been considered in the literature. In this paper, we first consider this problem from the viewpoint of carbon economy by studying mathematical models. We consider the timing of leaf emergence and shed-

Presented in the 19th Symposium for the Study of Species Biology held in February, 1988.

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ding as an adaptive strategy of the plant molded in the course of evolution. We model the annual change in photosynthetic rate of leaves in a seasonally varying environment, obtain the optimal times for leaf expansion and shedding that maximize the net photosynthetic product, and analyze their dependence on parameters such as leaf ageing and leaf mortality due to herbivory or parasitism. We show that both factors select for delayed leaf expansion.

We then deal with the adaptive pattern of leaf expansion (Question 3). Kikuzawa (1982, 1983, 1987) compared the pattern of leaf expansion over six genera of northern trees and concluded that pioneer species show succeeding expansion, and that, on the other hand, species in the forest stand exhibit flushing expansion. Empirical data on the relation between expansion pattern and other factors are still insufficient for full understanding of the adaptive significance of the observed expansion patterns. Thus it is important to study theoretically factors that potentially affect the temporal pattern of leaf expansion. In the present paper, we focus on the shading by leaves of an upper layer and examine the effect of this self-shading on the leaf expansion pattern. We again construct a simple mathematical model of photosynthesis of trees with two layers of leaves and obtain the optimal time of expansion for each layer. We show that self-shading delays the optimal expansion time of the upper layer; i.e., as the self-shading becomes severer, the more successively leaves should emerge.

Models and Results

Optimal Timing of Expansion and Shedding of Leaves

We consider Net Gain (ϕ) , which is the total net production of carbon during leaf life span; i.e., from the time of leaf expansion, e, to the time at which leaves end physiological activities, s. (Hereafter we call s the time of leaf shedding, although it is expected that the cessation of leaf activities precedes leaf shedding.) First we assume that the period needed to expand leaves is short compared to leaf longevity (flushing expansion). Thus we assume in our model that the plant expands all its leaves instantaneously at some point of time. We consider three factors which affect ϕ : (1) seasonal change in environmental conditions affecting photosynthesis, i.e., light intensity, temperature, day length, etc.; (2) change in photosynthetic ability;

and (3) change in leaf amount. We construct a model that determines ϕ as follows:

$$\phi = \int_{e}^{s} F(t-e) \{ L(t)G(t-e) - C \} dt, \tag{1}$$

where F(t-e) is the amount of leaves at time t. It will decrease with time due to mortality (e.g. herbivory or the environmental stress). Thus, $\frac{dF}{dt}$ $\leq 0 (e < t < s)$. We denote by L(t) the changes in combined effects of the environmental conditions on photosynthesis, which is expressed in terms of daily photosynthetic rate per unit amount of newly produced leaves. We assume that L(t) varies seasonally with axial symmetry with respect to t=0 and with maximum at t=0 (increasing with t in -T < t < 0and decreasing in 0 < t < T, as shown in Fig. 1). In a strong light environment, photosynthetic rate normally saturates above a certain light intensity. In this model, we assume that the photosynthetic rate is nearly saturated near the peak of L(t). G(t-e)represents the photosynthetic efficiency of leaves of age t-e, expressed as the ratio of daily photosynthetic rate by unit amount of leaves aged t-e to that by a unit amount of newly produced leaves (G(0)=1). It will also decrease with leaf age $\left(\frac{dG}{dt} \le 0\right)$ (Larcher, 1975; Harper and Bell, 1979; Field and Mooney, 1983; Bazzaz, 1984). Instantaneous net production in unit time by unit amount of leaves is expressed as L(t)G(t-e) minus C, where C is instantaneous maintenance cost of a unit amount of leaves. Thus the instantaneous net photosynthetic gain of the plant with F(t-e) is represented by a term in the integral, and integration from e to s gives ϕ as shown in eqn (1).

By differentiating ϕ by e and s, we get conditions

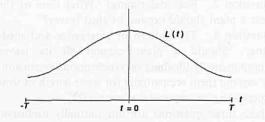


Fig. 1. Seasonal change in the environmental conditions considered in this paper. Horizontal axis, t, is time, and vertical axis, L(t), is environmental conditions expressed in terms of daily photosynthetic rate of unit amount of newly produced leaves. Axial symmetry of L(t) with respect to t=0 is assumed.

for e^* and s^* to be the optimal times that maximize ϕ as:

$$\frac{d\phi}{de}\Big|_{e=e^*} = 0$$

$$\Leftrightarrow -F(0)\{L(e^*)G(0) - C\}$$

$$+ \int_{e^*}^{s^*} \frac{d}{de} [F(t-e)\{L(t)G(t-e) - C\}] dt$$

$$\Leftrightarrow F(0)\{L(e^*)G(0) - C\}$$

$$+ \int_{e^*}^{s^*} [L(t) \frac{d}{dt} \{G(t-e^*)F(t-e^*)\}$$

$$- C \frac{d}{dt} F(t-e^*)] dt = 0, \tag{2}$$

and

$$\frac{\mathrm{d}\phi}{\mathrm{d}s}\Big|_{s=s^*} = 0$$

$$\Leftrightarrow L(s^*)G(s^* - e^*) - C = 0. \tag{3}$$

Earlier expansion of leaves (smaller e) affects ϕ in two ways. It increases ϕ by extending the length of time utilized for photosynthesis, which corresponds to the first term of eqn (2). On the other hand, it affects ϕ negatively by making leaves suffer ageing and mortality for longer periods of time, which correspond to the second terms of eqn (2). Equation (2) means that these two effects balance at the optimal time of leaf expansion e^* . Thus the earlier leaf expansion does not necessarily increase ϕ . It means also that the instantaneous net photosynthetic rate at the optimal time of leaf expansion $(L(e^*)G(0)-C)$ is positive, if leaves suffer mortality or ageing. (Note that this does not rely on the axial symmetry of L.) Equation (3) simply means that the instantaneous net photosynthetic gain should be 0 at the time of leaf shedding, s^* . Since the instantaneous gain after s* is negative, leaves only consume carbon products, and delaying the time of shedding does not give any positive benefit. We now consider e^* and s^* in three cases: Case 1 without leaf mortality or ageing, Case 2 with leaf mortality, and Case 3 with leaf ageing. We also examine the case where the maintenance cost of leaves depends on their photosynthetic ability.

Case 1 Without leaf mortality or ageing

First we consider the optimal timing in the case of no leaf mortality and no ageing, where F(t-e) = f (constant), G(t-e) = 1 (constant). In this case, the second term of eqn (2) is 0. Thus the condition for

optimality is

$$L(s_1^*)-C=L(e_1^*)-C=0,$$
 (4)

which means that the plant should expand and shed leaves when photosynthesis and maintenance cost balance. Thus $e_1^* = -s_1^*$; in other words, they are symmetric with respect to t=0 as shown in Fig. 2. (Hereafter, we refer to this as "symmetric utilization", in contrast to "asymmetric utilization" in which $e^* \neq -s^*$. Throughout this paper, we refer to symmetry with respect to t=0 as simply "symmetry".)

Case 2 With leaf mortality due to herbivory, parasitism, etc.

Next we consider the effect of leaf mortality. We can incorporate this in the model by assuming F to be a decreasing function, $\frac{dF}{dt} < 0$. For simplicity, we assume that there is no leaf ageing i.e., G=1. The second term of eqn (2) is

$$\int_{e_{2}^{*}}^{s_{2}^{*}} \{L(t) - C\} \frac{dF(t - e_{2}^{*})}{dt} dt$$

$$= [\{L(t) - C\}F(t - e_{2}^{*})]_{e_{2}^{*}}^{s_{2}^{*}}$$

$$- \int_{e_{2}^{*}}^{s_{2}^{*}} \frac{dL(t)}{dt} F(t - e_{2}^{*}) dt$$

$$= \{L(s_{2}^{*}) - C\}F(s_{2}^{*} - e_{2}^{*}) - \{L(e_{2}^{*}) - C\}F(0)$$

$$- \int_{e_{2}^{*}}^{s_{2}^{*}} \frac{dL(t)}{dt} F(t - e_{2}^{*}) dt. \tag{5}$$

The first term of eqn (5) is 0 from eqn (3). Thus eqn (2) is equivalent to

$$\int_{e_2^*}^{s_2^*} \frac{\mathrm{d}L(t)}{\mathrm{d}t} F(t - e_2^*) \mathrm{d}t = 0.$$
 (6)

Noting that

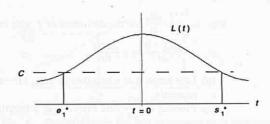


Fig. 2. Optimal times for leaf expansion (e_1^*) and shedding (s_1^*) in case 1 (no leaf mortality and no leaf ageing). $L(e_1^*)=L(s_1^*)$. Therefore, the utilization is symmetric with respect to t=0.

$$\frac{\mathrm{d}L(-t)}{\mathrm{d}t} = -\frac{\mathrm{d}L(t)}{\mathrm{d}t} \tag{7}$$

due to the symmetry of L and that

$$F(-t-e_2^*) > F(t-e_2^*)$$
 (8)

due to our assumption of leaf mortality, we have

$$\left|\frac{\mathrm{d}L(t)}{\mathrm{d}t}F(-t-e_2^*)\right| > \left|\frac{\mathrm{d}L(t)}{\mathrm{d}t}F(t-e_2^*)\right| \quad (9)$$

for positive t (Fig. 3). As a result,

$$|e_2^*| < |s_2^*|$$
 (10)

is necessary for eqn (6) to hold. In other words,

 $L(e_2^*)>L(s_2^*)$ and utilization is asymmetric (Fig. 4). Thus a plant should expand leaves later than in case 1, and the environmental conditions at the time of leaf expansion are expected to be better than those that give zero net photosynthetic rate. Moreover, $F(-t-e_2^*)/F(t-e_2^*)$ becomes smaller as mortality becomes greater so that smaller $|e_2^*|/|s_2^*|$ is needed for eqn (6) to hold. Thus higher leaf mortality selects for delayed leaf expansion and short leaf life span. This accords well with empirical observations (Chabot and Hicks, 1982; Kikuzawa, 1986).

Case 3 With ageing

Now we consider ageing of leaves, which is ex-

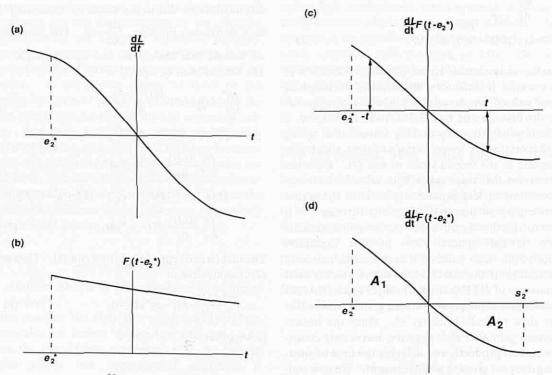


Fig. 3. (a) $\frac{dL}{dt}$, or the derivative of L with respect to t. Reflecting the symmetry of L, $\frac{dL(-t)}{dt} = -\frac{dL(t)}{dt}$.

- (b) Leaf amount as a function of time, $F(t-e_2^*)$. Due to mortality, leaf amount decreases as time proceeds.
- (c) Product of $\frac{dL}{dt}$ and $F(t-e_2^*)$ as a function of time. Note that

$$\left|\frac{\mathrm{d}L(-t)}{\mathrm{d}t}F(-t-e_2^*)\right| > \left|\frac{\mathrm{d}L(t)}{\mathrm{d}t}F(t-e_2^*)\right|.$$

(d) Equation (6) is satisfied if the area to the left of t=0 axis, A_1 , is equal to the area to the right, A_2 . Thus s_2^* must be larger than $|e_2^*|$.

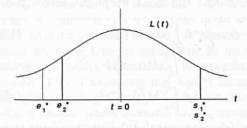


Fig. 4. Optimal times for leaf expansion (e_2^*) and shedding (s_2^*) in case 2 (with leaf mortality). $L(e_2^*) > L(s_2^*)$ $(=L(e_1^*)=L(s_1^*))$. Therefore the optimal time for expansion is later than in case 1.

pressed as a decrease of photosynthetic ability of leaves as they age. It can be incorporated in the model by assuming G to be a decreasing function, $\frac{dG}{dt} < 0$. For simplicity, we assume that there is no leaf mortality i.e., F(t-e)=f. The second term of eqn (2) is

$$f \int_{e_{3}^{*}}^{s_{3}^{*}} L(t) \frac{\mathrm{d}G(t - e_{3}^{*})}{\mathrm{d}e_{3}^{*}} \, \mathrm{d}t$$

$$= -f \int_{e_{3}^{*}}^{s_{3}^{*}} L(t) \frac{\mathrm{d}G(t - e_{3}^{*})}{\mathrm{d}t} \, \mathrm{d}t$$

$$= -f \left[L(t)G(t - e_{3}^{*}) \right]_{e_{3}^{*}}^{s_{3}^{*}} + f \int_{e_{3}^{*}}^{s_{3}^{*}} \frac{\mathrm{d}L(t)}{\mathrm{d}t} G(t - e_{3}^{*}) \mathrm{d}t$$

$$= -f L(s_{3}^{*})G(s_{3}^{*} - e_{3}^{*}) + f L(e_{3}^{*})G(0)$$

$$-f \int_{e_{3}^{*}}^{s_{3}^{*}} \frac{\mathrm{d}L(t)}{\mathrm{d}t} G(t - e_{3}^{*}) \mathrm{d}t. \tag{11}$$

Thus eqn (2) reduces to

$$\int_{e_3^*}^{s_3^*} \frac{\mathrm{d}L(t)}{\mathrm{d}t} G(t - e_3^*) \mathrm{d}t$$

$$= L(s_3^*) G(s_3^* - e_3^*) - C. \tag{12}$$

The righthand side of eqn (12) is zero from eqn (3). Noting that L is symmetric and that G is a decreasing function of t, we can again show that $|e_3^*| < |s_3^*|$ by the same argument as in case 2. Thus leaf ageing also selects for delayed leaf expansion (Fig. 5). A plant should expand leaves later and shed leaves earlier than in case 1. As a result, leaf life span will become shorter.

Case 4 Dependence of maintenance cost on photosynthetic production

So far, we assumed that maintenance cost of leaves, C, is constant. However, it is often the case that maintenance cost is positively correlated with

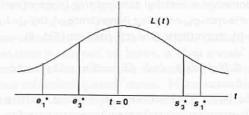


Fig. 5. Optimal times for leaf expansion (e_3^*) and shedding (s_3^*) in case 3 (with leaf ageing). $L(e_3^*) > L(s_3^*)$ $(> L(e_1^*) = L(s_1^*))$. Therefore the optimal time for expansion is later than in case 1.

photosynthetic rate: Highly productive leaves need much energy to maintain themselves (for example, McCree, 1970; Yokoi et al., 1978; Kimura et al., 1978; Penning de Vries et al. 1974). Therefore, cost, C, can be written approximately as

$$C = C_0 + aL(t)G(t - e) \tag{13}$$

where C_0 and a(0 < a < 1) are positive constants. Then

$$\phi = \int_{e_4}^{s_4} F(t - e_4)$$

$$\{ L(t)G(t - e_4) - C_0 - aL(t)G(t - e_4) \} dt$$

$$= (1 - a) \int_{e_4}^{s_4} F(t - e_4)$$

$$\{ L(t)G(t - e_4) - \frac{C_0}{1 - a} \} dt.$$
(14)

This means that replacement of C in the preceding analysis by $\frac{C_0}{1-a}$ gives the optimal timing. Thus the results of the previous models change not qualitatively, but quantitatively. If other parameters are fixed, the optimal time for expansion

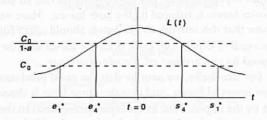


Fig. 6. Optimal times for leaf expansion (e₄*) and shedding (s₄*) in case 4 (maintenance cost depends on photosynthetic rate). For fixed value of C₀ and g, strong dependence of the maintenance cost on photosynthetic rate, large a, makes the optimal leaf life span shorter.

becomes later and that for shedding becomes earlier as a increases, or as the dependence of the cost on the photosynthetic rate gets stronger (Fig. 6).

Self-shading and Succeeding Expansion of Leaves

So far, we have assumed a "flushing" pattern of leaf expansion, namely simultaneous expansion of all the leaves that are produced in a year. Another expansion" expansion pattern, "succeeding (Kikuzawa, 1982, 1983, 1986), is known, in which trees expand their leaves sequentially during some length of time. If annual net photosynthetic rate of a leaf is determined solely by the times of expansion and shedding, and all the leaves are produced by the product of the previous year, then the optimal times should be the same for all the leaves produced. Thus the flushing type of leaf expansion is expected in the optimal leaf phenology.

However, we can think of at least two situations, not mutually exclusive, in which succeeding emergence is more beneficial than the flush type. First, plants may use the photosynthetic product gained in a particular year to produce leaves in the same year. Iwasa and Cohen (1989) considered plants which suffer mortality or loss of stored product during the winter. They showed that those plants should not store much of their product to the next year but should use up most of it for reproduction in autumn, because they may lose it in winter. Thus only a small number of leaves could be expanded in spring if they use the stored product only, and they should produce leaves by using the photosynthetic product gained after spring. As a result, these plants should expand leaves succeedingly.

Second, annual net photosynthetic rate of a leaf may be affected by the times of expansion and shedding of other leaves on the same plant. For example, if leaves which expanded earlier are shaded by those expanded later, net photosynthetic rate of the earlier leaves is reduced by the later leaves. Here we show that this self-shading of leaves should select for succeeding expansion, even if all the leaves are produced by the product of the previous year.

For simplicity, we assume that the plant produces two layers of leaves, and that the lower layer is shaded by the upper. The lower layer corresponds to the leaves at the basal part of a newly produced shoot; the upper layer corresponds to those at the upper part. We assume that all the leaves are constructed by the material produced in the previous year. Further, we assume that leaves suffer neither mortality nor ageing. The annual net photosynthetic gain is

$$\phi_{\text{UPPER}} = f_{\text{U}} \int_{e_{\text{U}}}^{s_{\text{U}}} (L(t) - C) dt, \qquad (15)$$

$$\phi_{\text{LOWER}} = f_{\text{L}} \int_{e_{\text{L}}}^{e_{\text{U}}} (L(t) - C) dt + f_{\text{L}} \int_{e_{\text{U}}}^{s_{\text{L}}} (hL(t) - C) dt, \qquad (16)$$

in which we assume that the photosynthetic rate of shaded leaves is lowered by a factor h(<1), due to deterioration of light conditions. f_U and f_L are leaf amounts of the lower and the upper layer, respectively. The optimal times are e's and s's that maximize total net gain, $\phi(=\phi_{\text{UPPER}}+\phi_{\text{LOWER}})$. Thus the conditions are

$$\frac{d\phi}{de_{L}}\Big|_{e_{L}=e_{L}} = 0 \iff L(e_{L}^{*}) - C = 0$$

$$\Leftrightarrow L(e_{L}^{*}) = C, \qquad (17)$$

$$\frac{d\phi}{ds_{L}}\Big|_{s_{L}=s_{L}^{*}} = 0 \iff hL(s_{L}^{*}) - C = 0$$

$$\Leftrightarrow L(s_{L}^{*}) = \frac{C}{h}, (18)$$

$$\frac{d\phi}{de_{U}}\Big|_{e_{U}=e_{U}^{*}} = 0 \iff (f_{L}-f_{U})\{L(e_{U}^{*}) - C\}$$

$$-f_{L}\{hL(e_{U}^{*}) - C\} = 0$$

$$\Leftrightarrow L(e_{U}^{*}) = \frac{f_{U}C}{f_{U}-(1-h)f_{L}} > L(e_{L}^{*}), \qquad (19)$$

$$\frac{d\phi}{ds_{U}}\Big|_{s_{U}=s_{U}^{*}} = 0 \iff L(s_{U}^{*}) - C = 0$$

$$\Leftrightarrow L(s_{U}^{*}) = C, \qquad (20)$$

for

$$\frac{f_{\mathrm{U}}C}{f_{\mathrm{U}} - (1 - h)f_{\mathrm{L}}} < L(0) \left(\Leftrightarrow h > \frac{f_{\mathrm{U}}C - L(0)\{f_{\mathrm{U}} - f_{\mathrm{L}}\}}{f_{\mathrm{L}}} \right)$$
(21)

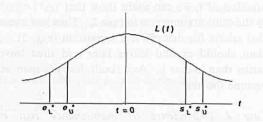


Fig. 7. Optimal times for the lower layer of leaves (e_L^*) and s_L^*) and for the upper layer of leaves (e_U^*) and s_U^*). If h < 1, e_U^* is larger than e_L^* or the succeeding expansion is selected.

(Fig. 7). Inequality (21) means that L(0) is large enough to compensate for the decrease in the lower layer's products caused by shading. A plant should expand the lower layer of leaves later as shading becomes more severe, because $L(e_U^*)$ is a decreasing function of h. Considering that $L(e_U^*)$ increases with e_U^* before the peak of L(t), we see that shading makes h smaller, which increases $L(e_U^*)$, which in turn increases e_U* (delay of leaf expansion of the upper layer). Since the expansion time of the lower layer is independent of h, the time interval between the first expansion and the second increases; in other words, the succeeding pattern is favored as shading deepens. When h=1 (no shading), $L(e_L^*)=L(e_U^*)$ =C from eqns (17) and (19); thus the flushing pattern is favored. However, when h is less than 1, the total photosynthetic gain, ϕ , obtained by the optimal succeeding expansion is larger than that obtained by flushing expansion.

If inequality (21) is not satisfied—in other words, if deterioration of the environments by shading is extremely severe—then the plant should not expand the upper layer of leaves even if the plant has enough material to produce them.

Here we have assumed that there are only two layers. In the appendix, we analyze a multi-layer model and show that severer shading selects for longer time intervals between expansion of layers in the *n*-layer model. Thus we conclude that self-shading makes the pattern of succeeding expansion optimal.

Discussion

Plants, due to lack of migratory ability, have developed diverse life history strategies to utilize the environment allotted to them effectively. The strategy of "timing" studied in the present paper is important in temporally varying environments. In order to understand the adaptive significance of diverse leaf phenology observed in the temperate regions where the environments are seasonally varying, timing of leaf expansion and shedding is one of the most important factors to be considered. We suggest that the seasonal pattern of changes in net photosynthetic rate plays an important role in determining the optimal timing and that we need data on it to reach a full understanding of leaf phenology of temperate deciduous trees.

We examined the effects of leaf mortality and leaf ageing on the optimal timing of leaf expansion and shedding. As a result, we showed that both factors select for delayed expansion of leaves and shorter leaf life span. These results are intuitively understandable: if the high mortality caused by predation is imposed on leaves, a plant should expand leaves late to face the peak rate of photosynthesis before losing many leaves. If leaves lose their photosynthetic ability faster, the plant should expand its leaves later in order to face the favorable season with fresh leaves.

It is particularly important that the instantaneous net photosynthetic rate at the optimal time of expansion is not equal to zero, if there exists either leaf ageing or leaf mortality after expansion. This will promote coexistence of plant species in different layers. If canopy trees delay leaf expansion until environmental conditions get better than those that give positive net production, then environmental conditions for plants living under these trees change as shown in Fig. 8. Thus plants on the forest floor can show positive gain in the early spring before canopy trees expand their leaves. There are many species called "spring ephemeral", which emerge early in spring and become dormant soon after the forest canopy closes. The delayed leaf expansion by canopy trees will be a key factor that enables survival of these plants.

According to our models, greater photosynthetic

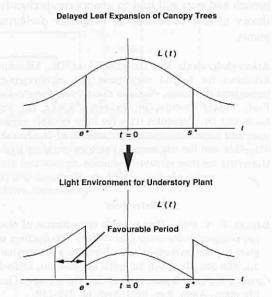


Fig. 8. Effect of delayed leaf expansion of canopy trees on the environmental conditions for the plants in the forest floor. Due to the delayed leaf expansion of the canopy trees, there exists a favorable period for plants under it before they expand leaves.

rate, which is equivalent to larger L(t), selects for longer leaf life span. This contradicts Larcher's result (Larcher, 1975) that there is a negative correlation between leaf life span and photosynthetic rate. This contradiction may disappear if there are positive correlations between photosynthetic rate and parameters such as maintenance cost, ageing rate, predation rate, etc., whose increase selects for shorter leaf life span. In order to test this hypothesis, detailed information on physiological and ecological parameters of leaves is needed for a variety of species.

Late frost is usually regarded as an important factor that determines the times of leaf expansion in a temperate climate. Lockhart (1983) proposed a model that predicts the optimal growth initiation time that maximizes average annual net photosynthetic production for shoot buds of deciduous plants. In contrast to our model, his model assumed taxonomically determined fixed date of leaf shedding and no seasonal change in environmental conditions and leaf ability. His main conclusion is that not only the mean but also the variance in the last frost date plays a crucial role in determining optimal time of leaf expansion. We do not deny the importance of late frost in determining the time of leaf expansion. However, we disregarded this factor in our analysis for simplicity. Combining his approach and ours will lead to a more comprehensive theory of leaf phenology of temperate deciduous plants.

Acknowledgements We are grateful to Dr. Kihachiro Kikuzawa for helpful suggestions and encouragement throughout this study. We also thank Prof. Yota Yokoi, Prof. Shoichi Kawano, Dr. Takayoshi Koike, Dr. Yoh Iwasa and Dr. Toshihiko Hara for their valuable suggestions and introduction to the literature, and Dr. Nanako Shigesada and the mathematical biology group of Kyoto University for their valuable discussion.

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Appendix

Multi-layer model with self-shading

Suppose that there are n layers with the same amount, f, of leaves. Each layer is numbered as shown in Fig. 9. For simplicity, we assume neither leaf mortality nor ageing. The top layer can utilize full sunlight and has photosynthetic rate L(t). Photosynthetic rate is decreased by a factor h(<1) when sunlight passes a layer of leaves. Thus the layer shaded by m layers has the photosynthetic rate only $h^mL(t)$. Therefore, annual net photosynthetic gain of the i-th layer, ϕ_i , is

$$\begin{aligned} \phi_i &= \sum_{k=1}^{i-1} \int_{e_{k+1}}^{e_k} f\{h^{i-1-k}L(t) - C\} \, \mathrm{d}t \\ &+ \int_{e_i}^{s_i} f\{h^{i-1}L(t) - C\} \, \mathrm{d}t, \end{aligned}$$

where e_i and s_i represent the times of expansion and shedding of the *i*-th layer, respectively. Thus total net gain of a plant, $\phi = \sum_{i=1}^{n} \phi_i$, is written as

$$\phi = \sum_{i=1}^{n} \sum_{k=1}^{i-1} \int_{e_{k+1}}^{e_k} f\{h^{i-1-k}L(t) - C\} dt + \sum_{i=1}^{n} \int_{e_i}^{s_i} f\{h^{i-1}L(t) - C\} dt.$$

The optimal times are e's and s's that maximize ϕ . Thus the conditions are

$$\frac{d\phi}{de_i}\Big|_{e_i=e_i^*} = 0 \iff h^{n-i}L(e_i^*) - C = 0$$

$$\Leftrightarrow L(e_i^*) = \frac{C}{h^{n-i}},$$

$$\frac{d\phi}{ds_i}\Big|_{s_i=s_i^*} = 0 \iff h^{i-1}L(s_i^*) - C = 0$$

$$\Leftrightarrow L(s_i^*) = \frac{C}{h^{i-1}},$$

Thus the plant should expand the *i*-th layer of leaves later as shading becomes more severe since $L(e_i^*)$ is a decreasing function of h. Duration of leaf expansion, $e_1^* - e_n^*$, increases as shading deepens because $L(e_n^*) - L(e_1^*)$ is an increasing function of h.

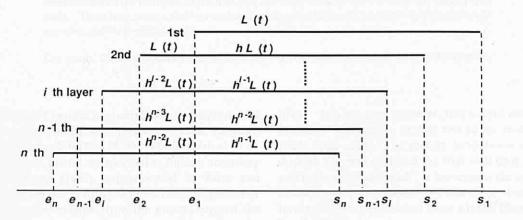


Fig. 9. An *n*-layer model with self-shading: there are *n* layers with the same amount, f, of leaves. Each layer is numbered from the top to the bottom. The top layer can utilize full sunlight and has photosynthetic rate L(t). Shading by a layer of leaves decreases photosynthetic rate by a factor h(<1). Thus a layer of leaves shaded by m layers has photosynthetic rate $h^mL(t)$. e_i and s_i represent the times of expansion and shedding of the i-th layer, respectively.

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