

# Leaf phenology as an optimal strategy for carbon gain in plants<sup>1</sup>

**K. Kikuzawa**

**Abstract:** Since leaves are essentially energy-gaining organs, the arrangement of leaves in time (leaf phenology) and in space (canopy architecture) in both seasonal and nonseasonal environments can be viewed as a central element in plant strategies for carbon gain. Interrelationships among leaf longevity, leaf habit, and leaf-emergence pattern together with shoot architecture affect plant productivity. Leaf longevity is shown to maximize carbon gain through three parameters: leaf photosynthetic rate, the decrease in photosynthetic rate with leaf age, and the initial construction costs of the leaf. This theoretical approach has been extended to seasonal environments and effectively simulated the geographical pattern of leaf habits. To avoid self-shading, plants adopt two alternative modes of leaf emergence. One is successive leaf emergence, in which plants expand one leaf at a time on a shoot; this unshaded leaf utilizes full sunlight and is only replaced by a second leaf when its photosynthetic ability declines. Plants with successive leaf emergence attain high production and have straight shoots with multilayered canopy architecture. The alternative is simultaneous leaf emergence on shoots inclined to minimize self-shading through a monolayered canopy architecture. By the inclination of the shoot, each leaf on the shoot can receive sufficient light. Plants with simultaneous leaf emergence utilize the entire growing period effectively. Taken together and in the context of shoot and canopy architecture these interrelationships among leaf longevity, habit, and emergence pattern provide the basis for a synthetic theory of leaf phenology.

*Key words:* leaf phenology, leaf longevity, leaf emergence, evergreen, deciduous habit.

**Résumé :** Puisque les feuilles constituent essentiellement des organes d'obtention d'énergie, la disposition des feuilles dans le temps (phénologie) et dans l'espace (architecture de la canopée), que ce soit dans les environnements saisonniers ou non, peut être considérée comme un élément crucial dans la stratégie des plantes pour obtenir leur carbone. Les interactions entre la longévité, le comportement et le patron d'émergence des feuilles ainsi que l'architecture des tiges affectent la productivité de la plante. On démontre que trois paramètres liés à la longévité des feuilles contribuent à maximiser le gain en carbone : le taux de photosynthèse foliaire, la diminution du taux photosynthétique avec l'âge, et le coût initial de construction de la feuille. Cette approche théorique a été étendue à des environnements saisonniers et permet de simuler le patron géographique des comportements foliaires. Pour éviter leur propre ombre, les plantes utilisent deux modes alternatifs pour l'émergence des feuilles. Un de ces modes consiste à produire les feuilles en succession, les feuilles prenant leur expansion une à une sur la tige; chaque feuille peut utiliser la totalité de la lumière sans recevoir d'ombre et n'est remplacée par une deuxième feuille que lorsque la capacité photosynthétique de la première diminue. Les plantes utilisant l'émergence successive des feuilles atteignent une forte productivité et montrent des tiges droites avec une architecture à plusieurs étages. Le mode alternatif implique une émergence simultanée des feuilles sur une tige inclinée, minimisant la projection de l'ombre sur elle même, et associée avec une architecture sur un seul étage. L'inclinaison de la tige permet à chaque feuille de recevoir suffisamment de lumière. Les plantes dont les feuilles émergent simultanément utilisent la totalité de la période de croissance. Dans leur ensemble et dans un contexte d'architecture de la tige et de la canopée, ces interrelations entre la longévité des feuilles, le port et le patron d'émergence constituent la base d'une théorie synthétique de la phénologie foliaire.

*Mots clés :* phénologie foliaire, longévité foliaire, émergence des feuilles, feuilles persistentes, port décliné.  
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**K. Kikuzawa.** Hokkaido Forestry Research Institute, Koshunai, Bibai, Hokkaido, Japan 079-01.

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## Introduction

Phenology has been defined as the timing of biological events and their relationship to seasonal climatic changes (Lieth 1974). This definition effectively characterizes the timing of seasonal events in temperate regions, where patterns of leaf emergence and leaf longevity seem to be governed mainly by seasonally changing temperatures. Various types of shoot-

elongation and leaf-emergence patterns, however, have been reported even in aseasonal tropical regions (Koriba 1948; Boojh and Ramakrishnan 1982; Lowman 1992). Thus a more general theoretical framework for phenological studies, which is applicable to nonseasonal as well as seasonal environments, is required.

Leaf phenology, which can be redefined as the arrangements of leaves in time, could also be considered an aspect of the light-harvesting strategy of plants. Since plants harvest light by expanding leaves to gain energy and to produce organic matter, the arrangement of leaves in time and space must be a central element in any strategy of plant carbon gain. In this view, three points generally must be considered in the study of leaf phenology (Harada and Takada 1988; Kikuzawa 1989): (i) leaf longevity, (ii) leaf habit, and (iii) the timing of leaf emergence. In this paper, I will focus on leaf longevity and leaf-emergence patterns.

Two types of leaf-emergence patterns are found in temperate forests (Kikuzawa 1983, 1989): simultaneous and successive emergence. Analogous types are reported in tropical forest (Lowman 1992). Leaf longevities in temperate forests also vary. Mean leaf longevities of alder are only about 90 days (Kikuzawa 1978), while in other deciduous trees, such as maples and oaks, longevities are as long as 180 days (Kikuzawa 1983, 1988). Leaf longevities of evergreens in temperate forests are even longer, often more than 500 days (Kikuzawa 1984). Leaf longevities of tropical trees are similarly diverse. Although leaf habits of tropical trees are often evergreen, some trees have leaf longevities shorter than 1 year (Kikuzawa 1991), but many trees of tropical forest have leaf longevities longer than 1 year (Bentley 1979). These facts suggest that leaf phenology is not solely determined by climatic conditions.

Leaf phenology, or the arrangement of leaves in time, should also be considered in relation to leaf arrangement in space. For example, if a plant produces many leaves at a time, the plant could suffer from self-shading, or successive leafing could be adopted to avoid self-shading. Another alternative would be to incline shoots to expose all leaves to full sunlight to minimize the effect of self-shading. Considering the inefficiency of carbon gain when leaf phenology and canopy or shoot architecture lead to self-shading, we might expect to find an ecological linkage between leaf phenology and shoot architecture.

In this paper, I address why there are various leaf phenologies in tropical as well as in temperate regions. I show that leaf phenology is determined to maximize carbon gain under constraints of climatic conditions. My goal is to present the main elements of a synthetic theory of leaf phenology that predicts the coordinated arrangement of leaves in time (leaf longevity and leaf emergence) and space (architecture of shoots and trees).

## Leaf longevity

Chabot and Hicks (1982) first proposed that leaf longevity be considered from the viewpoint of carbon gain. They focused on several important issues concerning leaf longevity, in particular the relationships between leaf construction costs and leaf longevity and the effects of resource availability in different habitats on leaf longevity. They presented an equa-

tion to express the cumulative photosynthetic gain of a plant as the difference between photosynthetic rate during the favorable period within a year and maintenance costs during the unfavorable period, construction costs of the leaf and some costs for defense, storage of photosynthates, and transport of photosynthates. However, if the optimum longevity of the leaf is the period necessary to maximize the net photosynthetic gain by a leaf, then the apparent optimal solution is the time when the instantaneous net photosynthetic rate of the leaf drops to zero. That is to say, a plant should retain leaves until no more positive gain can be drawn from them. Although this argument is plausible, no reason to shorten leaf longevity below this physiological limit can be deduced from this analysis; yet paradoxically, leaves on some plants do senesce during the period still physiologically favorable for their activity. Moreover, the optimum leaf longevity that maximizes photosynthetic production ( $dG/dt = 0$ ) is determined independently from leaf construction costs in Chabot and Hicks' (1982) analysis. These problems indicate the need to refine and extend this initial model of leaf longevity.

Building on the earlier analysis of Chabot and Hicks (1982), Kikuzawa (1991) considered that the photosynthetic rate of the whole plant should be maximized rather than that of a single leaf. Under this alternative analysis, he obtained the following formula:

$$[1] \quad F = G/t \\ = \left(\frac{1}{t}\right) \left\{ \int_0^t p(t)dt - \int_0^t m(t)dt - C \right\}$$

where  $G$  is the carbon gain by a leaf that results from subtracting construction ( $C$ ) and maintenance costs ( $m(t)$ ) from the photosynthetic gain ( $p(t)$ ). The function ( $F$ ) that must be maximized is ( $G$ ) divided by time ( $t$ ). The time ( $t^*$ ) that maximizes the function is the optimum leaf longevity. If both  $p(t)$  and  $m(t)$  are simple linear decreasing functions, optimum leaf longevity is given as

$$[2] \quad t^* = \left(\frac{2bC}{a-m}\right)^{1/2}$$

where  $b$  is the time when the photosynthetic rate of the leaf becomes zero. Equation 2 includes the equation obtained by Williams et al. (1989) in an analysis that considered leaf longevity to be related not simply to the leaf's construction costs but to the ratio of photosynthetic rate to construction costs of a leaf.

It is apparent from eq. 2 that leaf longevity is determined by three parameters: (i) net photosynthetic rate ( $a - m$ ), (ii) construction costs ( $C$ ), and (iii) the time when the photosynthetic rate becomes zero ( $b$ ) or the rate ( $1/b$ ) at which photosynthesis of a leaf decreases. This analysis yields three predictions: (1) as the maximum photosynthetic rate increases, leaf longevities become shorter; (2) as the rate of decrease in photosynthesis becomes higher, leaf longevities become shorter; and (3) as construction costs increase, leaf longevities become longer. While these predictions are not novel or unexpected, they follow from a relatively simple analysis that provides a unified, mechanistic basis for variation in leaf longevity (Kikuzawa 1991).

Reich et al. (1991, 1992) compared photosynthetic rates

of many diverse tree species and obtained negative relationships between photosynthetic rate and leaf longevity (prediction 1). Since there is a positive correlation between leaf photosynthetic rate and nitrogen content (Mooney et al. 1981; Field and Mooney 1983; Lajtha and Whitford 1989), leaf longevity is also negatively correlated with leaf N content (Reich et al. 1992). Artificial addition of nitrogen shortens leaf longevity (Shaver 1981; Koike and Sanada 1989).

A shrub species in forest understory, *Daphniphyllum macro-podium humile*, usually retains leaves for 4 years but in canopy gaps retains them for only 2 years. Photosynthetic rates of leaves less than 1 year in age in the canopy gaps are high, but those of 1-year leaves are low, suggesting that leaf photosynthetic capacity decreases rapidly under high light conditions (Kikuzawa 1989). For plants in the understory, the rate of decrease is slower (prediction 2).

Payback times of temperate evergreen leaves are about double those of deciduous leaves (Saeki and Nomoto 1958). In temperate regions, sclerophyllous leaves with high specific leaf weight (SLW) are usually evergreen, with a longer life span, whereas leaves with a low SLW have shorter longevities (prediction 3).

### Leaf habit

When we apply eq. 1 to seasonal environments in which favorable ( $f$ ) and unfavorable ( $1 - f$ ) periods alternate within 1 year, we obtain the following equation:

$$[3] \quad F = G/t \\ = \left( \frac{1}{t} \right) \left\{ \int_0^f p(t) dt + \int_1^{1+f} p(t) dt + \dots + \int_{|t|}^t p(t) dt - \int_0^t m(t) dt - C \right\}$$

As in eq. 1, the time ( $t^*$ ) that maximizes  $F$  is the optimum leaf longevity of the plant. In seasonal environments, if  $t^*$  is shorter than 1 year, the plant is deciduous, and if  $t^*$  is longer, the plant is evergreen. When  $f = 1$ , eq. 3 reduces to eq. (1). In nonseasonal environments where  $f = 1$ , leaf habit is usually evergreen irrespective of leaf longevity.

An interesting result is that varying only the length of the favorable period ( $f$ ), while holding the other parameters constant, can change the prediction of leaf habit from evergreenness to deciduousness and vice versa. When  $f = 1$ , plants can conduct photosynthesis throughout a year and they are evergreen. In areas where  $f$  is long and  $1 - f$  is short, it is advantageous for many plants to retain leaves during the short unfavorable period, since the costs of retaining leaves through the unfavorable period are not large. When the length of the unfavorable period becomes longer, the maintenance costs of leaves during this period increase, and thus leaf shedding before the unfavorable period (deciduousness) is favored. When the length of the unfavorable period becomes even longer, it is difficult for a leaf to pay back its construction costs by photosynthetic gain during a single season because the favorable period is too short. Then plants are obliged to retain leaves for more than 1 year to pay back construction costs, and the evergreen habit is again favored. A simulation

using eq. 3 with various combinations of parameters results in a bimodal distribution of evergreenness across the length of favorable periods. This simulation nicely explains the bimodal distribution of evergreenness across latitudes (Kikuzawa 1991). Although these observations are not new, only the present model can account for the puzzling bimodal pattern of evergreenness with reference to a single factor, carbon gain.

### Leaf emergence

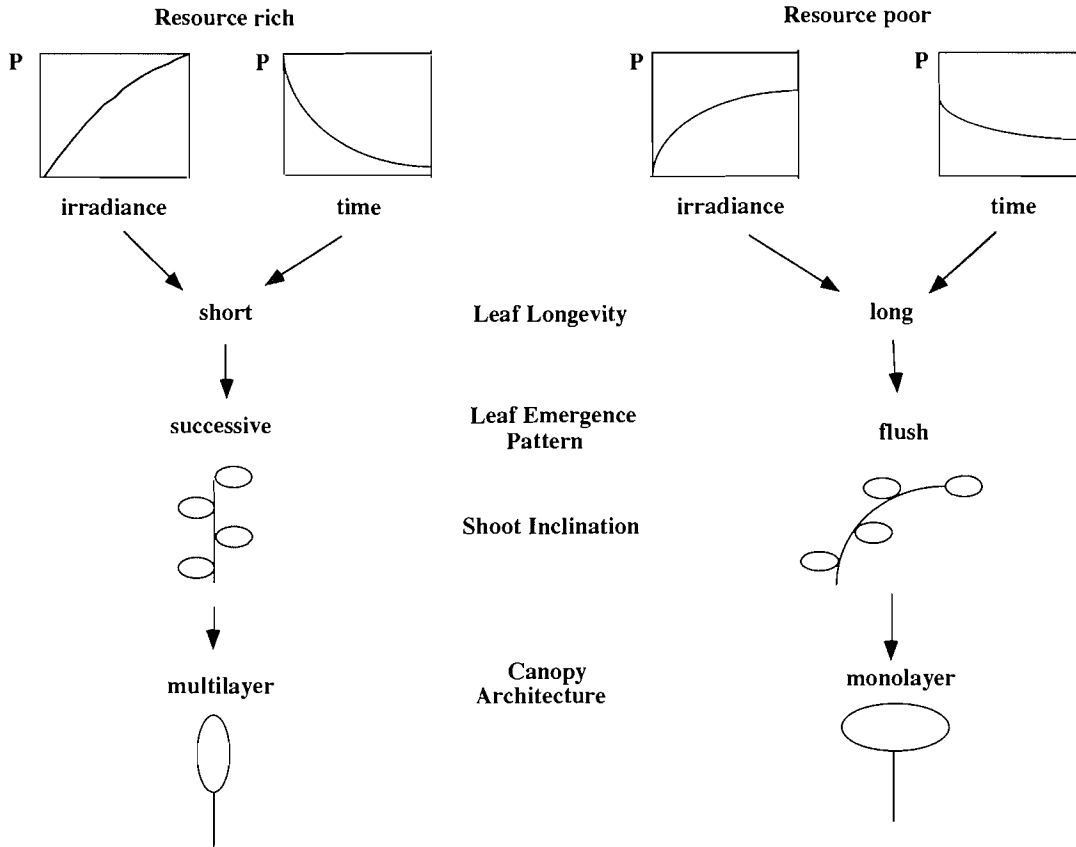
Two types of leaf-emergence patterns have been recognized in temperate deciduous broad-leaved forests (Kikuzawa 1983). One is flushing or synchronous leafing in which all the leaves appear within a short period, and the other is successive leafing in which leaves appear one by one over a longer period. Tree species that are members of mature forests usually show flushing patterns of leaf emergence, while trees that invade early successional environments, such as flood plains, usually exhibit successive leafing (Kikuzawa 1982, 1983).

Iwasa and Cohen (1989) constructed a model in which plants unfold their leaves at the beginning of the growing season in temperate regions and then produce additional leaves by utilizing photosynthates from the first leaves. The plants continue this process until they cease new leaf production and start storing photosynthates for the next growing season. Their model predicts that in stable environments, the flushing habit, which stops leaf production early in the season and immediately begins to store photosynthates for the next year, will be selected. Conversely, in unstable environments, successive leafing, which continues leaf production until late in the growing season, will be favored. Although comparable type of leaf emergence also are reported in tropical regions (Lowman 1992), it remains unclear whether Iwasa and Cohen's model for trees in temperate regions can also explain such patterns from aseasonal environments.

In an alternative to Iwasa and Cohen's (1989) analysis, I consider self-shading an important factor affecting the patterns of leaf emergence. If a plant has ample resources at the beginning of a season to produce the current season's leaves, how should the plant unfold them, simultaneously or sequentially? If there is little effect of shading by upper leaves on lower leaves, all the leaves can utilize the full season. The plant then will unfold all leaves at the start of the growing season to maximize seasonal carbon gain by a shoot. On the contrary, if the upper leaves heavily shade the lower leaves, the effect of self-shading on leaf-emergence pattern cannot be ignored. If the photosynthetic capacity of a leaf is initially high but decreases rapidly with leaf age, it is advantageous for a plant to unfold only one leaf that can photosynthesize in full light. When the photosynthetic rate of this leaf decreases and thus the effect of shading by a second, distal leaf on the first leaf can be minimized, only then should the second leaf be expanded. The plant will expand the third, fourth, and subsequent leaves in a similar sequential manner through the season. Hence, in this case, plants with successive leafing can attain higher photosynthetic production during one season than those with flush leafing. No matter how high the effect of self-shading may be, if lower leaves can utilize low light effectively, simultaneous leafing is not disadvantageous. In this case, therefore, flush leafing will again be favored.

The above arguments can be illustrated and formalized in

**Fig. 1.** Elements in a synthetic theory of leaf phenology based on maximizing plant carbon gain. Phenological patterns in two extreme environments are illustrated. In resource-rich (light) environments, plants produce leaves that can utilize full light, but this capacity declines quickly with leaf age. Shoots elongate vertically with sequential leaf emergence. Crown architecture is slender and multilayered. In resource-poor environments, leaves can utilize poor light effectively and are retained longer. Leaves appear simultaneously as a flush. Shoots are inclined to avoid self-shading, and crown architecture is monolayered.



a simple model where only two leaves appear on a shoot in a single season. While the first leaf appears at the start of the season, the optimum timing ( $t_s^*$ ) of the second leaf's appearance to maximize photosynthetic production of the shoot throughout a season ( $T$ ) is given as:

$$[4] \quad t_s^* = \frac{1}{2b} \log \left\{ 1 - \frac{h(1+AI_0)}{1+AhI_0} \right\} + \frac{T}{2}$$

where  $A$  is the inverse of the light intensity at which the leaf attains half maximal rates of photosynthesis. When  $A$  is large, leaves can utilize weak light efficiently, Parameter  $b$  is the rate of decrease in photosynthesis with leaf age and  $h$  is a coefficient characterizing the transmission of light through a leaf. The smaller  $h$  is, the more shade the leaf casts. Parameter  $I_0$  in equation 4 is the ambient light intensity. Here I will examine the effect of plant traits such as  $h$ ,  $A$ , and  $b$  on the timing of the appearance of a second leaf under constant ambient light conditions.

A large  $t_s^*$  in eq. 4 implies successive leaf emergence, and a small  $t_s^*$  a flushing type of leaf emergence. From eq. 4 it is apparent that  $t_s^*$  becomes small when  $A$  is large and  $b$  is small. That is, if a plant can utilize weak light effectively, or if the rate of decrease in photosynthesis with leaf age is slow, then flushing leaves simultaneously at the start of the

season uses the season to full advantage. In contrast, if a plant can utilize strong light effectively, and the photosynthetic rate decreases rapidly, successive leafing will be selected to allow high photosynthetic production by utilizing full sunlight until the first leaf's ability declines, and only then opening a second leaf.

When leaf transmissivity (parameter  $h$  in equation 4) increases,  $t_s^*$  will decrease. Thus it is expected that in flushing species  $h$  will be large and in successive-leaving species it will be small. We (K. Kikuzawa, H. Koyama, K. Umeki, and M.J. Lechowicz, unpublished data) found that in two flushing species (*Quercus* and *Tilia*), the angle from the vertical line to an apical shoot is large, that is, the shoot inclines greatly (see Shoot inclination in Fig. 1). This architecture decreases self-shading. In the two successive leafing species (*Alnus* and *Betula*), apical shoots elongate vertically (Fig. 1), resulting in more shading of lower leaves by upper leaves. The less vertical architecture avoids self-shading, which is the potential disadvantage of flush emergence, and by inclining the shoot ensures ample light reaches the lower leaves. Species with more vertical stem architecture can attain greater tree height by elongating the apical shoot and thus can avoid shading by surrounding trees. These species minimize the effect of self-shading by successive leaf emergence. In turn, the inclination of the apical shoot should affect the inclination

of lower shoots and consequently the shape of the crown of the tree. Vertical elongation of the apical shoot leads to a relatively slender crown, while the inclination of the apical shoot results in a wider, spreading crown.

### Toward a synthetic theory of leaf phenology

Since leaves are essentially light-harvesting organs, I have focused on insolation to rationalize and summarize the contrasting arrangements of leaves in time and space (Fig. 1). I have shown that the leaf longevity is short when the photosynthetic capacity of the leaf is high, when the rate of decrease in photosynthesis is great, and when construction costs of the leaf are small. These arguments on leaf longevity imply that in sites with high resource availability, plants produce leaves with the ability to rapidly acquire resources, thereby sacrificing leaf longevity (Chabot and Hicks 1982). In resource-poor sites, on the contrary, plants construct leaves that can utilize lower resources and retain them longer (Chapin 1980). When the rate of photosynthesis decreases rapidly with leaf age, leaves appear successively on a shoot, and the shoot elongates vertically. If the rate of decrease in photosynthesis is low and leaf longevity long, flush leafing on a shoot will be advantageous, and shoots will incline to avoid self-shading.

In early successional conditions where resources are usually available, plants promote their photosynthetic production by replacing leaves with higher photosynthetic ability within a short period. Leaves that can utilize high irradiance and attain high photosynthetic rates cannot utilize low light efficiently, and their photosynthetic rates decline rapidly with time. Since it is not advantageous for the plants to expand such leaves simultaneously because of self-shading, they expand leaves one by one successively over a longer period. Self-shading is not a serious problem for plants with successive leaf emergence. These plants elongate their apical shoot vertically and can thus attain greater plant height to avoid shading by surrounding individuals. In this case, the tree crown becomes slender, like that defined as multilayered and considered the architecture best suited to utilizing high light (Horn 1971; Boojh and Ramakrishnan 1982).

In shaded environments, plants produce leaves that can utilize low light effectively but not high light. It is beneficial for such plants to extend leaf longevity. These plants can attain higher production by simultaneous leaf emergence. Plants with the flushing type of leaf emergence frequently incline their apical shoot to avoid self-shading. The inclination of the apical shoot in turn leads to monolayered canopy architecture, which is typical of late successional species.

In this working synthesis (Fig. 1), seasonal changes in environmental conditions are not considered directly. The two extreme conditions compared in the scheme, however, also exist in seasonal environments. Thus these considerations may also apply to seasonal environments. The real difference between seasonal and nonseasonal environments is not the availability of resources but seasonality in resource availability. The only difference in seasonal environments is that species with leaf longevity shorter than 1 year become deciduous, and those with longer than 1 year become evergreen. This working synthesis thus offers a bridge between resource-based and climate-based models of leaf phenology.

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