

The basis for variation in leaf longevity of plants

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Abstract

Any theory of leaf phenology must predict leaf longevity, leaf habit, leaf expansion and its timing among other variables. These phenological traits may be important keys to understand the response of trees to climatic change. Here I concentrate on and review two of these critical phenological traits, leaf longevity and leaf habit. Theories of leaf longevity were re-evaluated and leaf longevity is concluded to be optimized to maximize plant carbon gain. From this perspective, three points are predicted. Leaf longevity is short when the photosynthetic rate of the leaf is high, when the photosynthetic rate decreases rapidly through time, or when the construction cost of the leaf is small. These predictions are well supported by empirical as well as experimental results on various plant species. The theory, which is extended to seasonal environments, is general and applicable to seasonal as well as aseasonal environments. The theory simulated the bimodal geographic distribution of evergreenness.

Introduction

The recent global climatic change chiefly caused by the increase in atmospheric carbon dioxide concentration (Bazzaz 1990; Vitousek 1992) is considered to affect various ecosystems on earth (Field *et al.* 1992; Melillo *et al.* 1993; Grabherr *et al.* 1994). Among them, forest ecosystems constitute a large part of the plant biomass in terrestrial systems (Melillo *et al.* 1993). Hence responses of trees, which are the main components of forest ecosystems, have been a central issue of physiological ecology in changing climates. Changes in the photosynthetic rates of leaves and the growth of tree seedlings in response to changes in CO₂ concentration and temperature have been measured (Bazzaz *et al.* 1990). Little attention, however, has been focused on the changes in phenology of individual trees in response to climatic changes.

Leaf phenology is assumed also to change with the climatic change. For example, the increase in mean temperature caused by the increase in atmospheric CO₂ concentration, will increase the photosynthetic rate of a leaf. The increase in photosynthetic rate may affect leaf longevity. In accordance with the rise of mean temperature, the length of favorable period for photo-

synthesis within a year, which has been known to affect some aspects of leaf phenology such as leaf longevity and leaf habit (Kikuzawa 1991), will also increase in temperate regions. How will climate change alter the length of the favorable period in monsoon Asia, and how might change of that magnitude alter foliar phenology. How climatic change will affect photosynthetic rate of a leaf, and how the change in photosynthetic rate might alter leaf longevity. Those are my primary concern in the project of Terrestrial Ecosystem of Monsoon Asia. Here, I will focus on factors affecting leaf longevity and leaf habit (evergreenness and deciduousness).

Recently Reich *et al.* (1992) reviewed leaf-longevities of various plants and obtained relationships between leaf longevity and traits such as photosynthetic rate, foliar nitrogen concentration, specific leaf area and individual plant growth. In concluding their review, Reich *et al.* proposed a web-like scheme which represents various factors affecting leaf-longevity. But from his complicated scheme, we cannot simply understand why and how factors affect leaf longevity. Though investigations to seek relationships among characteristics are a powerful tool for discovery, the relationships must remain circumstantial.

Leaf longevity is defined as the time period from emergence to fall of a leaf. Thus leaf longevity is a concept concerning an individual leaf. On the contrary, leaf habit such as evergreenness or deciduousness, indicates plant level behavior. Since most plants have more than one leaf, leaf habit is a leaf-population concept (Kikuzawa 1991).

If there is no unfavorable period for photosynthesis throughout a year, a plant will usually be evergreen. Nonetheless some plants with evergreen leaf habit may turnover their leaves by shortening leaf longevity to the point that some evergreen trees actually can have leaf-longevities shorter than one year (Kikuzawa 1991). When the length of the unfavorable period increases, the relative frequency of evergreenness decreases, but if the length of the unfavorable period increases even further, the relative frequency of evergreenness increases again, resulting in the bimodal distribution of evergreenness across latitudes (Chabot & Hicks 1982; Oohata 1990). From these facts, it often has been concluded that leaf habit is a complicated problem and cannot be explained by a single factor (Chabot & Hicks 1982; Karlsson 1992). However, I have shown previously that leaf habit can be explained as an adaptive strategy to maximize carbon gain (Kikuzawa 1991). In this article, I will review the literature on leaf-longevity and leaf habit. I will show that all the empirical and experimental results on leaf longevity and leaf habit can be understood from the viewpoint of maximizing carbon gain.

Leaf longevity

There are some plants that maintain only one leaf throughout their life, such as *Monophyllaea* which grows on the floor of equatorial rain forests (Kohyama & Hotta 1986), and others that frequently exchange their leaves and with very short leaf longevities such as floating-leaved aquatic species (Tsuchiya 1989). Leaf longevities range from as short as 15 days (Tsuchiya 1989) to more than 10 years (Reich *et al.* 1992) and reach a maximum of 45 years (Schulze *et al.* 1986). Here I define 'leaf longevity' as a leaf's life span from its emergence to fall. I exclude extremely short leaf lifespan due to accidental leaf fall caused by herbivores or other injuries.

Why does a plant exchange its leaves? In the simplest sense it is because exchanging leaves is more advantageous to the plant in terms of its carbon economy than not exchanging leaves. An easily understand-

able example is the phenology of deciduous trees in a temperate region. Deciduous trees shed their leaves before winter because it is advantageous for the tree to construct leaves again in spring of the next season rather than to pay the maintenance costs of keeping them throughout the winter. But in the same temperate region, some trees do retain their leaves throughout the winter. For these trees, it is advantageous to use the old leaves next year. Thus it is apparent that to shed or not to shed leaves in autumn is not solely determined by climatic factors.

Even during periods favorable for photosynthesis, such as the summer season in a mesic temperate region, or any season in a wet tropical area, some plants replace their leaves. Leaves that are to be replaced generally have a low photosynthetic rate, due to a number of factors such as decreased photosynthetic capacity caused by ageing, and/or degradation of the light environment around the leaf. Self shading by upper leaves or by competition with other plants may contribute to programmed senescence in these leaves (Mooney *et al.* 1981). Thus, rather than maintain leaves with a reduced photosynthetic capacity, the plant abscises those leaves and replaces them with new ones that have a much higher carbon gaining capacity.

Various factors have been found to correlate with leaf longevity (Chabot & Hicks 1982; Coley 1988; Reich *et al.* 1992). Reich *et al.* (1992) pointed out that leaf life-span correlates with a wide range of leaf and plant characteristics, such as leaf net photosynthetic rate, leaf conductance, leaf nitrogen concentration, specific leaf area, relative growth rate of a plant, and leaf nitrogen retranslocation. To organize and understand these complicated interrelations, a theory based on a formal mathematical model is desirable.

Chabot & Hicks (1982) presented the following equation for a leaf's photosynthetic production. Their original equation is somewhat complicated, since they considered losses due to factors such as herbivory as separate costs, but for simplicity I have combined these terms into a single construction cost (C) for a leaf. The function to be maximized is photosynthetic gain (G) of a leaf from its emergence (time 0) to time t .

$$G = \int_0^t p(t)dt - \int_0^t m(t)dt - C \quad (1)$$

where $p(t)$ is the instantaneous photosynthetic rate at time t , and $m(t)$ is the maintenance respiration rate and C is the construction cost of the leaf.

Chabot & Hicks (1982) made various arguments on leaf-longevity based on this equation. For example, in environments with high stress such as the shade in a forest understory, leaves with high photosynthetic rates have not been evolutionarily selected, mainly because even if these plants had leaves with a high photosynthetic capacity, they could not exhibit their potential in such environments (Mooney & Gulmon 1982). Thus extending leaf longevity is the only way to pay back the construction costs of the leaf and to obtain a positive carbon balance in such resource limited environments. Species with longer leaf longevities are usually found in drought-stressed environments, such as the Mediterranean region or in deserts, in shade-stressed environments such as the forest understory and in nutrient stressed environments such as bogs. To maintain leaves longer, it is necessary to invest in the protection of leaves against herbivores or pathogens. Thus to pay back the high costs with a low photosynthetic rate takes a longer period. Investment for protection may dilute photosynthetic with non-photosynthetic tissue (Chabot & Hicks 1982; Coley 1988), thus resulting in a lower photosynthetic rate, which further contributes to a prolonged leaf life span. Chabot & Hicks' important contribution is that they explicitly showed that leaf-longevity must be considered in the context of carbon economy. Their model provided plausible explanation for various aspects of leaf longevity, but it cannot explain two important phenological observations.

First, the time necessary to maximize G in Equation (1) is the time when the net photosynthetic rate of the leaf becomes 0 [$p(t) - m(t) = 0$]. The optimum strategy for a plant thus is to maintain leaves until they can no longer conduct positive photosynthesis. Therefore, under the Chabot and Hicks' model we cannot predict a situation where shortening leaf longevity is necessarily advantageous for a plant. Yet we know that the turnover of leaves frequently occurs on short time scales substantially less than the climatic period favorable for growth and photosynthesis.

The second problem in their model is that construction costs (C) in Equation (1) are independent of time (t). Thus the optimum leaf longevity to maximize G in Equation (1), or the derivative of G with t , does not have a relation to C . Although they argued the relationship between leaf construction costs and leaf longevity, their model betrayed them.

Leaf longevity must be longer than the pay back time for construction costs. The pay back time is the construction cost divided by the leaf's average net daily

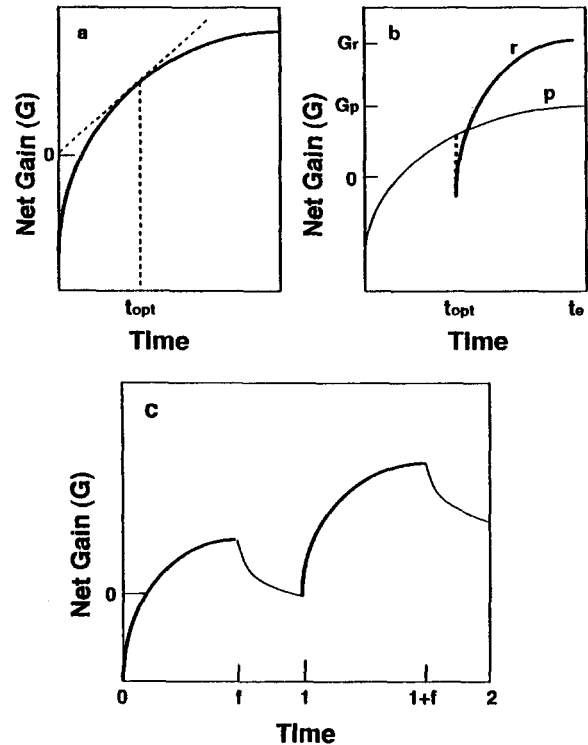


Fig. 1. Net gain of a leaf (G) to time (t) curves. a. Net gain at time zero is minus construction cost ($-C$) and increases with diminishing return because of decrease of photosynthetic rate with time by aging. To maximize net gain by a plant the leaf must be replaced when the tangent line starting from the origin touches the curve (t_{opt}). To replace the leaf when the daily net gain is zero (t_e) does not maximize net gain of the plant. b. A comparison of net gain of a plant by replacing (r) and by persisting (p) methods of leaves. The net gain of a plant (G_r) by replacing the leaf at $t = t_{opt}$ is greater than the net gain (G_p) of a plant by retaining the leaf until $t = t_e$. c. When there is an unfavorable period for photosynthesis within a year, net gain of a leaf is disrupted during the unfavorable period. The method to obtain optimal time to maximize net gain of a plant is similar to panel a. When t_{opt} is shorter than 1 (year), leaf habit is deciduous, and t_{opt} is longer than 1, the plant is evergreen. The length of favorable period within a year is f and that of unfavorable period is $1-f$.

carbon gain. Williams *et al.* (1989) concluded that leaf longevity is proportional to the ratio of cost to net photosynthetic rate. They tested this idea on seven species of *Piper* and concluded that this hypothesis was consistent with their data. Their model was also supported by research on 10 tree species in a tropical dry forest in Venezuela (Sobrado 1991).

Kikuzawa (1991) proposed a cost-benefit model of leaf longevity by assuming that there is a limit to the number of leaves that a plant can retain at a time. As an extreme case, if a plant can retain only one leaf at a time, then the problem that remains for the plant is,

when should it replace the leaf in order to maximize its carbon gain? That time is the time it takes to maximize marginal gain (or gain divided by time) of a leaf. The function g to be maximized is given by

$$g = \frac{1}{t} \left[\int_0^t p(t)dt - \int_0^t m(t)dt - C \right] \quad (2)$$

Equation (2) is simply Equation (1) divided by time (t). Equation (1) maximizes the photosynthetic gain of a leaf, while Equation (2) maximizes gain by a plant. Photosynthetic gain by two leaves which are replaced at $t = t_{opt}$ by paying construction costs, is the total gain of a plant, and is greater than the gain by a leaf which is retained until instantaneous photosynthetic rate becomes zero (Fig. 1). To examine the value of a leaf for a plant, the use of Equation (2) is appropriate.

It is usually the case that the photosynthetic rate of a leaf attains its maximum at full expansion, and then decreases with time (Jurik *et al.* 1979; Sestak 1981; Chabot & Hicks 1982; but see Jurik 1986). Maintenance respiration also decreases similarly. If photosynthetic rate does not decrease with time, there is no necessity for a plant to replace its leaves.

Let us assume linear decreases of these two variables with time. Although linear decreases may not always occur, I adopt them here as the most simple approximation. In this case, optimum leaf longevity, or the time to maximize carbon gain by a plant is given as,

$$t^* = \left\{ \frac{2bC}{a-m} \right\}^{\frac{1}{2}} \quad (3)$$

where, a is the instantaneous gross photosynthetic rate at time 0, m is the instantaneous maintenance respiration rate at time 0 and b indicates the time when the photosynthetic rate becomes 0. Equation (3) includes Williams *et al.*'s intuitive relation, and thus can be considered to be a more comprehensive equation.

From Equation (3), it is apparent that leaf longevity is determined by three parameters: net photosynthetic rate ($a-m$), construction costs (C) and the rate at which photosynthesis of a leaf decreases with time ($1/b$). Thus, the following three predictions are immediately obtained. Prediction (1): As the maximum photosynthetic rate increases, leaf longevities become shorter. Prediction (2): As the rate of which photosynthesis decreases becomes higher, leaf longevities become shorter. Prediction (3): As construction costs increase, leaf longevities become longer.

Archer & Tieszen (1980) reported that maximum photosynthetic rates of tundra plants are inversely related to leaf longevity. Mooney & Gulmon (1982) also found this inverse relation. Reich *et al.* (1991, 1992) compared photosynthetic rates of various species and obtained negative relationships between photosynthetic rate and leaf longevity. It is well known that there is a positive correlation between leaf photosynthetic rate and nitrogen content of the leaf (Mooney *et al.* 1981; Field & Mooney 1983; Lajtha & Whitford 1989). Thus leaf longevity is negatively correlated also with leaf N content (Del Arco *et al.* 1991; Reich *et al.* 1991, 1992; Diemer *et al.* 1992; Thomas 1992). Experimental addition of nitrogen shortens leaf longevity (Shaver 1981; Koike & Sanada 1989; Tsuchiya 1989; Lajtha & Whitford 1989). Short longevity of leaves with high photosynthetic rate and with high nitrogen contents may be attributable either to the fact that there should be a trade off between to maintain high photosynthetic rate and to maintain it long, or to the fact that the degree of shading of old leaves at the lower position of a shoot by younger leaves at higher positions is great due to vigorous shoot growth. Redistribution of nitrogen from lower, shaded leaves to higher, sun lit leaves are well documented (Hirose & Werger 1987; Hirose *et al.* 1988). Plants in resource rich sites where light, water and nutrient are available are known to have shorter leaf longevities, since photosynthetic rates can be high in such sites. For example, in the temperate region, pioneer species such as alders or birches which invade open sites where light is usually abundant have shorter leaf longevities (Kikuzawa 1978, 1980, 1982, 1983; Kikuzawa *et al.* 1984; Tadaki *et al.* 1987; Kanda 1988). In contrast, plants that live in sites where resource availability is low usually have longer leaf longevities than the plants in resource rich sites. For example, in the forest understory where light is limited, many plant species have longer leaf lifespan (Bentley 1979; Kawano 1983; Kikuzawa 1984, 1988; Coley 1988). But in the understory of temperate deciduous-forests, many plant species with short leaf-longevity are also well known (Kawano *et al.* 1982; DePamphilis & Neufeld 1989). These vernal species utilize light conditions during snow melt and leaf-expansion of canopy trees (Kawano 1970). Plants on mountain ridges where water is limited have leaves with longer lifespan than those in valleys (Goldberg 1982). Plants in bogs where nutrients are limited are also known to have longer leaf longevities (Small 1972; Moore 1980).

Plastic extension of leaf longevity of same species in accordance with resource limitation has also been reported. For example, negative correlations have been found between leaf longevity and light intensity in forest understories (Nilsen 1986; Kikuzawa 1988; Kai *et al.* 1991). In addition, artificial shading prolongs leaf longevity (Kikuzawa 1988; Seiwa & Kikuzawa 1991; Kai *et al.* 1991). Artificial flooding also prolongs leaf-longevity of flood-tolerant species, but shortens that of flood-intolerant species (Terazawa & Kikuzawa 1994).

Prediction (2) states that if the rate at which photosynthesis decreases is high, leaf longevity becomes short, which implies that if the rate of ageing is rapid, the leaf will die soon. That is somewhat tautological and thus may be acceptable as a matter of course. A shrub species in the understory of deciduous broad-leaved forest, *Daphniphyllum macropodum* var. *humile*, retains leaves as long as 4 years, while under canopy gaps leaves are retained 2 years at the longest. Photosynthetic rates of current leaves in canopy gaps is high, but that of 1 year old leaves is low; consequently the decrease in photosynthetic rate with time is rapid. For plants in the understory, the rate of decrease in photosynthesis is low (Kikuzawa 1989). Similar trends have been found for *Abies veitchii* (Matsumoto 1984a, b). Dwarf pine (*Pinus pumila*) in the Japanese alpine region, retains leaves for ca. 5 years. Leaves mature slowly, and the photosynthetic rate reaches its peak only in September of the year of the leaf's appearance, or even in June of the next year. From then on the photosynthetic rate decreases slowly until the fifth year (Kajimoto 1990). Similar slow decreases in photosynthetic rates have also been reported for long-lived foliage in *Picea mariana* by Greenway *et al.* (1992). Photosynthetic rates of pioneer species such as alders and birches in temperate forests are high initially, but decrease rapidly with time, while rates of late successional species, such as maples, are low but decrease slowly with time (Koike 1987, 1990).

Leaf construction cost, the amount of resource invested in constructing the leaf, may be evaluated in terms of carbon or nutrients (Bloom *et al.* 1985; Chapin 1989; Williams *et al.* 1989). Construction cost per unit of leaf area is composed of two components; leaf mass per unit leaf area (SLW) and cost synthesizing the mass. If cost of unit mass varies less than SLW, SLW may be used as a rough estimates of cost per leaf area. Cost of unit mass evaluated by carbon (g glucose/g mass) varied 39% in seven *Piper* species in a tropical forest (Williams *et al.* 1989). In temperate

regions, sclerophyllous leaves with high SLW (g m^{-2}) are usually evergreen with a longer life span whereas thin leaves with a low SLW have shorter longevity. There is a positive correlation between mean SLW of leaves and mean life span of leaves estimated by leaf biomass to mean leaf fall ratio in various forests. Subarctic or temperate evergreen conifers have the highest SLW values of around 200 g m^{-2} (Tadaki *et al.* 1967a, b; Saito 1982; Saito *et al.* 1979; Mizui *et al.* 1987). Mean leaf longevity are also long, ranging from 3 to 6 years. Evergreen broad-leaved trees of warm-temperate forests (Tadaki 1968; Kira & Yabuki 1978), and tropical rainforests (Edwards 1977; Edwards & Grubb 1977; Kira 1978; Tanner 1980a, b) exhibit an SLW of around 100 g m^{-2} and have mean leaf longevity ranging from 1 to 2 years. Pioneer evergreen trees in tropical regions (Kawahara *et al.* 1981; Kanazawa & Sato 1986) or deciduous broad-leaved trees in temperate regions (Kikuzawa & Asai 1978; Kikuzawa *et al.* 1984) have SLW of less than 100 g m^{-2} and leaf lifespan of less than one year. In open lowlands in Austria, leaf longevity of herbaceous plants were 40–95 days and SLW values were $30\text{--}60 \text{ g m}^{-2}$ (Diemer *et al.* 1992).

Prediction (3) suggests either that to pay back higher construction costs a leaf needs a longer period of time to assimilate the necessary carbon or that long-lived leaves should invest more in protective structures or compounds (Chabot & Hicks 1982; Williams *et al.* 1989). Payback times of temperate evergreen leaves are about double those of deciduous leaves (Saeki & Nomoto 1958). The cuticle layer on the leaf surface is considered to be a protective tissue and the ratio of cuticle to whole leaf thickness may be considered a part of leaf's construction cost (Koike 1988). A positive correlation was found between the cuticle ratio and leaf longevity of deciduous broad-leaved trees in Hokkaido, northern Japan (Koike 1988). Similarly, positive correlations have been reported between the concentrations of defensive chemicals, fiber and lignin in leaves and leaf life spans for 41 tree species in a Panamanian tropical forest (Coley 1988). If these protective compounds are not so expensive relative to other compounds in the leaf, these compounds are not directly related to leaf longevity. In some cases (Merino *et al.* 1982; Chapin 1989; Williams 1989), construction cost is not directly related to leaf longevity. But protective compounds affect leaf longevity indirectly through reducing photosynthetic rate by diluting photosynthetic tissues with non-photosynthetic tissues (Williams *et al.* 1989).

Plants retranslocate nutrients from leaves back to the plant body before leaf-fall (Goodman & Perkins 1959; Chapin 1980; Chapin & Kedrowski 1983; Cote & Dowson 1986; Jonasson 1989; Chapin & Moilanen 1991). If the retranslocation rate is high, it may roughly be considered to be equivalent to the initial construction of low-cost leaves, from the view point of nutrient economy. Thus a corollary of Prediction (3) is that leaf longevity will be long for plants with low nutrient-retranslocation rates. However, Small (1972) reported that evergreen species re-absorbed a higher percentage of leaf nutrients than deciduous species. This resulted in a greater 'nutrient-use efficiency', which has been considered an important adaptation of evergreen species in infertile environments (Small 1972; Moore 1980; Chapin 1980). But recently, Jonasson (1989) pointed out that estimates of re-absorption by Small (1972) were based not on pool sizes but on concentration and thus were overestimations. Jonasson suggested that re-absorption in evergreens is generally comparable to, or even lower than, other life forms. Del Arco *et al.* (1991) reported that mean nitrogen retranslocation of deciduous trees is higher than that of evergreen trees. However, even though the highest retranslocation rate was exhibited by a deciduous species (*Betula*), the lowest was also by a deciduous species (*Prunus*). A negative correlation was found between nitrogen retranslocation and leaf life span (Reich *et al.* 1992).

The preceding three predictions are derived from the three parameters in Equation (3). In these arguments, I examined these parameters independently, changing only one parameter while the other two are held constant. However, if a parameter covaries with another parameter, and the direction of effect for the two parameters are opposite, the effects may be canceled out and the individual effects will be masked. For example, construction cost of photosynthetic tissue is expensive and thus leads to prolong leaf longevity, but the increase in photosynthetic tissue will increase the photosynthetic rate of the leaf and entails shorter leaf longevity. As the result of the compensation, only the ratio of photosynthetic rate to cost may be proportional to leaf-longevity (Williams *et al.* 1989). In many cases in the real world, these three parameters all affect leaf longevity in the same direction. For example, it was suggested that attainment of higher photosynthetic rates conflicts with maintaining leaves longer (Chabot & Hicks 1982), since it is necessary to invest in protection of leaves against herbivores, pathogens and environmental vicissitudes to maintain the leaves.

Such non-photosynthetic investments will dilute photosynthetic tissue and thus lower the assimilation rate (Chabot & Hicks 1982). There is a tradeoff between higher photosynthetic rate and its longer maintenance. For example, leaves of *Fragaria virginiana* senesced more quickly in high light than in darker conditions (Jurik *et al.* 1979). Another line of evidence that supports this trade-off hypothesis comes from chloroplast ultrastructure changes in leaves of *Rhododendron maximum* (Nilsen *et al.* 1988). High irradiance induces rapid development of chloroplast plastoglobuli which in turn reduce photosynthetic capacity. The parameter $a-m$ would appear to be inversely correlated with b in Equation (3).

Similar considerations are applicable to the rate of which ambient light conditions around a leaf degrade. If the degradation rate is rapid, leaf longevity is shortened. Leaves of *Fragaria virginiana* produced under high light conditions are generally discarded when shaded whereas low-light leaves live longer and retain photosynthetic capacity for longer periods (Jurik *et al.* 1979). These may be summarized that leaf longevity is prolonged when the whole plants are shaded, while when some leaves of plants are shaded the longevity of shaded leaves are shortened. The leaves of desert annuals which develop in relatively light-unlimited environments, change little in photosynthetic capacity with age. In contrast, photosynthetic capacity decreases with increasing leaf age in annuals of closed canopy communities because older leaves are heavily shaded (Mooney *et al.* 1981). In a same habitat, self-shading of lower leaves by upper leaves may be more severe in rapidly growing plants which produce many leaves than in slowly growing plants which produce fewer leaves. Thus it may be assumed that rapidly growing plants with high photosynthetic rates will have leaves with shorter lifespan than slowly growing plants. Coley (1988) and Reich *et al.* (1992) each observed a negative correlation between height growth or relative growth rate (RGR) of plants and leaf life span.

Thus the characteristics common to plants with short leaf-longevity may be summarized as 'short leaf-longevity syndromes'. Plants in resource rich sites exhibit high RGR, with high leaf photosynthetic rates, and low construction costs, but the photosynthetic rates decrease rapidly through time. On the other hand, plants in resource poor environments have 'long leaf-longevity syndromes' with low RGR, low photosynthetic rates and high construction costs, and their photosynthetic rate decreases slowly with time.

Leaf habit

If a tree retains leaves throughout a year, that tree is designated evergreen. If a tree sheds all of its leaves at some time during a year, then that tree is classified as deciduous. Leaf habit, or evergreenness and deciduousness, is a tree level concept, while leaf longevity is an individual leaf concept. Even if a tree usually retains leaves all year, it is possible that individual leaf longevities are shorter than 1 year. That leaf longevities of evergreens are longer than those of deciduous trees is a concept peculiar to the temperate region. In tropical regions, there are several examples of evergreen trees with leaf longevities shorter than 1 year (Gill & Tomlinson 1971; Kawahara *et al.* 1981; Shukla & Ramakrishnan 1984; Kanazawa & Sato 1986; Coley 1988; Nunez-Farfan & Dirzo 1989; Reich *et al.* 1991, 1992).

If the favorable period for photosynthesis lasts throughout a year, plants must fully utilize this period in order to remain competitive with other plants. Thus they must show an evergreen leaf-habit, irrespective of leaf longevity patterns. Deciduousness first appears in environments where favorable and unfavorable periods for photosynthesis alternate within a year. In temperate regions, where there can be an unfavorable period for photosynthesis, species which shed leaves before the onset of this period are dominant. However, there are many evergreen species in these regions which retain leaves throughout this period. Moreover, the relative frequency of evergreenness increases in subarctic regions. Thus the relative frequency of evergreenness across latitudes shows a peculiar bimodal distribution (Chabot & Hicks 1982; Oohata 1990).

Here I will apply the model introduced in the previous section to seasonal environments. A newly introduced parameter is the length of the favorable period within a year f ($0 < f < 1$). Thus the length of the unfavorable period is $1-f$. Substituting this parameter into Equation (2), we obtain,

$$g = \frac{1}{t} \left\{ \int_0^f p(t)dt + \int_1^{1+f} p(t)dt + \dots + \int_{[t]}^t p(t)dt - \int_0^t m(t)dt - C \right\} \quad (4)$$

where [] is Gausse notation. The optimum time (t) which maximizes g is the optimum leaf longevity. When $f = 1$, then Equation (4) reduces to Equation (2), thus is the more comprehensive, general equation.

When $f = 1$, leaf habits of all the plants are evergreen. When f is less than 1, and optimum leaf longevity is shorter than 1, then the plants are assumed to be deciduous (Fig. 1c). If optimum leaf longevity is longer than 1, the leaf habit of the plant is evergreen.

Conditions which select for evergreenness and deciduousness in seasonal environments are summarized as corollaries of predictions in the previous section. Corollary (1) Photosynthetic rates of deciduous leaves are higher than those of evergreen leaves. Corollary (2) Rates of which photosynthesis decreases through time are higher in deciduous than evergreen habits. Corollary (3) Leaf construction costs are larger in evergreen than deciduous habits.

Saeki & Nomoto (1958) measured photosynthetic rates of deciduous and evergreen species and found the former are higher than the latter. Larcher (1975) summarized photosynthetic rates of various species and documented that photosynthetic rates of deciduous species are higher than those of evergreen species. Schulze *et al.* (1977) compared photosynthetic rates of an evergreen coniferous species (*Picea abies*) with those of a deciduous broad-leaved species (*Fagus sylvatica*) and reported that the latter is two to three times greater than the former. More recent work reviewed by Ceulemans & Saugier (1991) also revealed the same trend. Evergreen species are usually found in environments where it is difficult to acquire resources (Monk 1966). For example, from alpine or arctic environments, dominance by evergreen species was reported (Bell & Bliss 1977; Kudo 1991). In temperate species, photosynthetic rates of deciduous species decrease more rapidly with time than those of evergreen species. Temperate evergreen species usually have thicker leaves than deciduous species.

Now let us examine whether Equation (4) can simulate the peculiar bimodality in relative frequencies of evergreenness across latitudes. Interestingly, changing only parameter f , with the other parameters remaining constant, brings about evergreenness and deciduousness (Kikuzawa 1991). In areas where the favorable period (f) is long and the unfavorable period ($1 - f$) is short, it is advantageous for many plants to retain leaves during the short unfavorable period, since the costs of retaining leaves through unfavorable period is not large. When the length of the unfavorable period becomes longer, however, the maintenance costs of leaves during this period increases and thus leaf shedding before the onset of the unfavorable period (deciduousness) is selected. When the length of the unfavorable period become even longer, it becomes

difficult for a leaf to payback its construction costs by photosynthetic gain during a single season because the favorable period is too short. These plants are obliged to retain leaves for more than one year to pay back those costs and evergreenness is again favored. Archer & Tieszen (1980) presumed that evergreen leaves of Alaskan tundra plants must be retained for more than one growing season in order to provide a positive carbon contribution to the plant.

Simulations with varying f with various parameter sets successfully showed the bimodal distributions of relative frequency of evergreenness through the length of favorable period (Kikuzawa 1991). Since the change in f is considered to be mostly a latitudinal change in the length of the favorable period, this relation is interpreted to be the bimodal distribution of evergreenness across latitudes.

Some temperate deciduous tree species have evergreen congeners at lower latitudes, such as trees belonging to the genera *Magnolia*, *Quercus*, *Symplocos* and others. For example, *Quercus gilva*, *Q. glauca* in southwest Japan are evergreen while *Q. mongolica* and *Q. serrata* in northern Japan are deciduous. Also some temperate deciduous species have evergreen congeners at higher latitudes. For example *Rhododendron dilatatum* is a deciduous shrub species in the temperate region, while *R. aureum* is an evergreen dwarf shrub in the alpine region. Even the same species may alter its leaf-habit across latitudes. *Trema orientalis*, *Ficus elastica* and *Duabanga sonneratioides* exhibit the evergreen habit in Singapore but show the deciduous habit in northern Malaysia and other regions (Koriba 1948). Of the 18 'wintergreen' species or evergreens whose leaf longevity is less than 2 yrs on King Christian Island (77° 50' N), ten species are deciduous in Greenland (72° 50' N). The six evergreen species whose leaf longevity is longer than 2 year in King Christian Island, are 'wintergreen' in Greenland (Bell & Bliss 1977).

In alpine regions, snow depth varies considerably, being affected by the prevailing winds during winter or by small changes in topography within a narrow area. At the same altitudes (1700 m) in Hokkaido, northern Japan, snow cover disappears in June on some sites while in other sites snow cover lasts until September (Kudo 1991, 1992). Consequently, the favorable period changes drastically within a small area. Leaf longevity of alpine shrubs in the area have changed in response to the length of the favorable period such that leaf life spans were longer with the shorter favorable period (Kudo 1992). The relation between leaf longevity and the length of favorable period is well

simulated by Equation (4) (Kikuzawa & Kudo unpublished).

Recently Karlsson (1992) carried out similar investigations to Kudo (1992), and he investigated leaf life spans of several evergreen shrubs at different latitudes. He also found that leaf life spans were longer at higher latitudes (shorter f). But since his data were taken at different altitudes as well as latitudes, he could not establish a general trend and concluded that evergreenness can not be understood by a single hypothesis. However, introduction of the concept of the length of the favorable period (f) would help explain his data.

The above arguments on the latitudinal distribution of evergreen and deciduous habits are also applicable to altitudinal distributions. In tropical regions, day-length hardly changes throughout a year. Although mean temperature may decrease, the length of favorable period (f) is not altered by altitudes; for trees, f is usually 1 across altitudes unless it crosses timber lines beyond where $f = 0$. Below timber lines, tropical mountains are covered with evergreen species. While in temperate regions, f decreases with altitudes. Thus the distributional change of leaf-habit with latitude is telescoped over the mountain slopes across altitudes in temperate regions. Evergreen species on tropical high mountains which are adapted lower mean temperature throughout a year, can not be distributed in temperate low land where alternate a favorable and an unfavorable periods within a year. These arguments are consistent with findings by Ohsawa (1990) in monsoon Asia.

Discussion

The temperate evergreen-deciduous paradigm can not be a general theory, since it can not be applied all over the world. From this view, recent investigations on leaf longevity in tropical regions are important. From the work by Coley (1988), Reich *et al.* (1991, 1992) and Lowman (1992), leaf life-spans in non-seasonal environments have been clarified. Reich *et al.* (1992) in particular, examined extensive data-sets and presented several correlations between leaf life-span and other leaf's traits.

However, the studies of correlations will never explicitly show how the one affects the other. Mathematical models may yield insights into causality. From this stand point the seminal achievements by Chabot & Hicks (1982) must be emphasized. They defined a leaf as a carbon-gaining organ, and considered maximization of carbon gain by a leaf. My refinement of their

model, dividing their equation by time t , successfully predicts leaf longevity in conjunction with other leaf traits. These predictions are supported by empirical as well as experimental data.

The equations in my previous paper (Kikuzawa 1991) have wide applicability to non-seasonal as well as seasonal environments. Equation (2) is the function in non-seasonal environments. While Equation (4) is that in seasonal environments. By putting $f = 1$, Equation (4) reduces to Equation (2), thus Equation (4) is the general theory of leaf-longevity and leaf-habit.

From the above analysis, it is expected that global increase in mean temperature will affect the photosynthetic rate and thus will result in the changes in leaf longevity. However, the increase in mean temperature also alter the length of favorable period (f) in temperate regions, which will also affect the leaf-longevity and leaf habit. Thus the prediction of phenological change in accordance with climatic change is complicated. In order to separately examine the effects of temperature and favorable length on leaf longevity, it will be necessary to investigate leaf phenology of plants in areas with different mean temperature but similar favorable period as well as in areas with similar temperature but with different length of favorable period. Research in leaf phenology along altitude of tropical mountain is desired.

Experimental studies would be desirable to test and refine the model predictions by measuring the necessary parameters directly. As model systems, I would suggest investigating plants in extreme environments. At one extreme are plants with the shortest leaf longevity, for example, aquatic floating plants. Model parameters may be easily determined, because of the short experimental period, there is little self shading and probably no limits by other factors such as water or nutrient deficiencies. At the other extreme are plants with the longest leaf longevity, such as *Monophyllaea* in forest understories (Kohyama & Hotta 1986). To examine the effects of self shading on leaf phenology, some prostrate plants of forest floors or sand dunes might also be studied. Some lianas having both crawling and climbing types may prove useful for studying the effects of shading. Hikosaka *et al.* (1994) tried to separate the effects of leaf aging and self-shading on some leaf traits of a vine by growing plants horizontally.

Harada & Takada (1988) have pointed out three aspects in the study of leaf phenology. The first is leaf longevity and leaf habit. The second is the timing of leaf appearance and the third is leaf emergence pat-

tern. Only the first problem has been considered in this review.

The second aspect, leaf appearance timing, has been considered to be determined only by temperature conditions (Anderson 1974; Lechowicz 1984; Wang *et al.* 1992) in temperate regions as a proximate cause. But Harada & Takada (1988) considered an ultimate cause of each plant's seasonal timing and presented that various patterns are probable by combinations of a leaf's trait and seasonal changes in environmental conditions. Sakai (1992) further developed their model using game theory and pointed out the combination of various patterns were evolutionary stable strategy. The second problem thus has been considered in seasonal environments. A remaining issue is the timing of leaf emergence in non-seasonal environments. Are there any problems concerning the timing of leaf appearance and what governs the timing in non-seasonal environments? From this view point, studies by Aide (1988, 1992, 1993) who pointed out the importance of herbivory as a selective agent on the timing of leaf production in tropical region are suggestive.

Two types of leaf emergence of trees were found in temperate trees (Kikuzawa 1983). Flush type, or leaves which appear simultaneously in a short period, and successive type, or leaves which appear one by one over a longer period. The analogues of these two types are also found in tropical forests (Lowman 1992). Iwasa & Cohen (1989) constructed a mathematical model concerning leaf emergence patterns in seasonal environments. Whether it could be applicable to non-seasonal environments is a problem remaining in this field.

As already mentioned, leaf phenology is a field concerning the arrangement of carbon-gaining organs through time. The complementary field is the arrangement of leaves in space, but no studies have been found concerning relations of arrangements of leaves in time and in space. The field is open for us is to study relationships between leaf longevity, leaf appearance timing and leaf emergence patterns, and to construct a synthetic theory for the comprehension of leaf arrangement in time and in space. This theory must have generality applicable to seasonal as well as non-seasonal environments.

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