

A COST-BENEFIT ANALYSIS OF LEAF HABIT AND LEAF LONGEVITY OF TREES AND THEIR GEOGRAPHICAL PATTERN

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Abstract.—To maximize net gain of a tree, leaves must be replaced when net gain of a leaf per unit time over the leaf's life span is maximum. A model in which leaf longevity is determined to maximize the net gain of a leaf per unit time is constructed. The model predicts that leaf longevity is short when initial net photosynthetic rate of the leaf is large, long when the construction cost of the leaf is large, and short when the decrease in net photosynthetic rate with time is large. The model describes leaf habit (deciduousness and evergreenness) with the length of the favorable period for photosynthesis within a year and simulates distributional pattern of leaf habit along latitudes. The percentages of evergreenness decrease with decreasing favorable-period length and reach the minimum at an intermediate length of the favorable period but increase again with a decrease in the length of the favorable period. A bimodal distributional pattern with two peaks, one at lower and the other at higher latitudes, is observed for the percentages of evergreenness. Percentages of deciduousness show a unimodal distribution pattern with a peak at midlatitude.

Leaf longevity is a property of individual leaves, while leaf habit (i.e., evergreenness and deciduousness) is a property of a population of leaves. A tree is considered evergreen if it retains leaves throughout a year, whereas a deciduous tree sheds all of its leaves and spends a portion of the year without foliage. It is generally thought that evergreen trees have leaves that live longer than those of deciduous trees, but this is not always true. An evergreen tree can replace leaves several times a year, although at any one time the tree has green leaves. In such a case, though leaf longevity is shorter than a year, the tree is still a functional evergreen. Leaf longevity and leaf habit, however, have not always been distinguished. In many cases evergreenness has been used as a surrogate for a long leaf life span (Monk 1966; Chabot and Hicks 1982).

Where environmental conditions are less variable and trees can conduct photosynthesis throughout the year as in the mesic tropics, trees are assumed to be functionally evergreen regardless of their leaf longevity. The deciduous habit is considered to be accompanied by seasonality of climatic conditions. Evergreen broad-leaved species that predominate in tropical regions usually decrease in abundance with increasing latitude, accompanied by a corresponding increase of deciduous broad-leaved species. However, at higher latitudes, evergreen conifers

predominate. Therefore, evergreen tree species show a peculiar biogeographical distributional pattern with two distributional maxima, one at lower latitudes and another at higher latitudes. This bimodal distributional pattern has been called puzzling and is not readily explained by a cost-benefit analysis alone (Chabot and Hicks 1982).

Since leaves are a resource-gaining organ, I believe to the contrary that this pattern must and can be explained on a cost-benefit basis. I develop a model in which a tree replaces its leaves to maximize its net carbon gain. The model is a simple equation consisting of a few parameters: photosynthetic rates, construction costs, and maintenance costs of a leaf. By applying the model to seasonal environments where favorable and unfavorable periods for photosynthesis alternate within a year, I explain the biogeographical pattern of leaf longevity and leaf habit.

In this article, I will (1) analyze leaf longevity from a cost-benefit point of view for resource acquisition by a tree, (2) clarify the distinction between leaf longevity and leaf habit, and (3) explain the biogeographical distributional pattern of evergreen and deciduous tree species.

THE MODEL

Let us assume that a tree can retain a definite amount of leaves at a time, for example, 10,000 leaves per tree. This is a probable assumption for a tree grown at a site where resources such as light are limited. The remaining problem for the tree is, then, when the tree should replace its leaves. As an extreme abstraction, let us consider a situation in which a tree can retain only one leaf at a time.

When should a tree replace the leaf to maximize the tree's net gain, if it can retain one leaf at a time? The answer to this question is to replace the leaf when the net gain by a leaf per unit time over the entire life span is maximum (fig. 1). That is to say, the following marginal gain (g) must be maximized:

$$g = G/t,$$

where G is the total net gain by a leaf from the time of emergence to the time of shedding and t is the leaf longevity. The total net gain by a leaf (G) is defined as total photosynthetic production by the leaf minus maintenance cost and construction cost of the leaf. Therefore, g is written as

$$g = (1/t) \left(\int_0^t p(t)dt - \int_0^t m(t)dt - C \right), \quad (1)$$

where $p(t)$ is the daily photosynthetic rate at time t , $m(t)$ is the daily maintenance cost, and C is the construction cost of the leaf. The time t maximizing g in equation (1), or t_{opt} , is considered to be the optimum longevity of the leaf for maximizing carbon gain.

In the next step, consider environments where favorable and unfavorable periods for photosynthesis alternate within a year. Let the length of the favorable period be f (yr; $0 < f \leq 1$) and that of the unfavorable period be $1 - f$ (yr). In

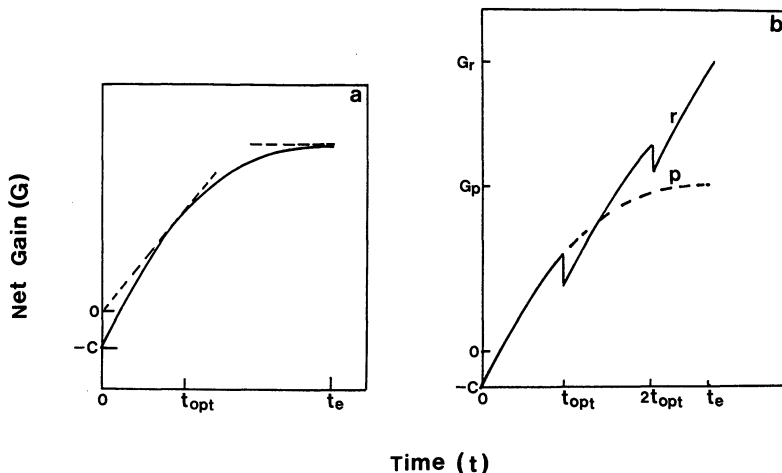


FIG. 1.—Schematic representation of net gain per leaf (G) to time (t) curve. *a*, Net gain at time zero is minus construction cost ($-C$) and increases at first rapidly and then gradually because of decrease of photosynthetic rate with time by aging. To maximize net gain by a tree the leaf must be replaced 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 tree. *b*, A comparison of net gain of a tree by replacing (r) and by persisting (p) methods of leaves. The net gain of a tree (G_r) by replacing the leaf at $t = t_{\text{opt}}$ is greater than the net gain (G_p) of a tree by retaining the leaf until $t = t_e$.

this case g is expressed as

$$g = (1/t) \left(\int_0^f p(t) dt + \int_1^{1+f} p(t) dt + \dots + \int_{[t]}^t p(t) dt - \int_0^t m(t) dt - C \right), \quad (2)$$

where the brackets are Gauss's notation.

APPLICATION OF THE MODEL

In this section, I will first analyze what factors determine leaf longevities by approximating $p(t)$ and $m(t)$ in the model with simple equations under a condition without any unfavorable period. Next I will consider circumstances in which deciduousness and evergreenness are favored under conditions in which there are favorable and unfavorable periods.

Leaf Longevity in Favorable Conditions

Photosynthetic rate after the full expansion of a leaf is considered to be a monotonic decreasing function (Sestak et al. 1985). As a most simple approximation of $p(t)$, I adopt a linear function. Maintenance cost is also assumed to decrease in proportion to the photosynthetic rate,

$$\begin{aligned} p(t) &= a(1 - t/b), \\ m(t) &= m(1 - t/b), \end{aligned} \quad (3)$$

where a , b , and m are constants.

By substituting equation (3) into equation (1) and by differentiating with respect to t , we obtain t_{opt} , which maximizes equation (1) as

$$t_{\text{opt}} = [2bC/(a - m)]^{1/2}. \quad (4)$$

From equation (4), we can deduce the following three points. (1) Leaf longevity is expected to be short when initial net photosynthetic rate (parameter $a - m$) of the leaf is large. (2) Leaf longevity is long when the construction cost of the leaf (parameter C) is large. (3) Leaf longevity is short when the decrease in net photosynthetic rate with time (parameter $(a - m)/b$) is large. These points do not conflict with the empirically obtained facts.

1. Leaves invested with high concentration of nutrients, especially nitrogen, are known to have high photosynthetic ability under field conditions (Larcher 1975; Field and Mooney 1983); low nitrogen concentration is correlated with low photosynthetic rate (Chapin et al. 1980). It may be concluded that species in resource-poor sites have lower photosynthetic rates with longer leaf life span (Chapin 1980; Chabot and Hicks 1982) and species in resource-rich sites have higher photosynthetic rates with shorter leaf life span (Chapin 1980). Alders (*Alnus* spp.) are assumed to have a high photosynthetic rate because of their high growth rate in floodplains where water, nutrients, and light are abundant; alder leaf longevity is known to be short (Kikuzawa 1978, 1980, 1982, 1983; Kikuzawa et al. 1979, 1984; Tadaki et al. 1987; Kanda 1988). Woody plants in a forest understory where light is limiting are assumed to have lower photosynthetic ability and usually maintain leaves longer, in tropical rain forests (Bentley 1979) as well as in deciduous broad-leaved forests (Kikuzawa 1984). Koike (1988) showed a negative correlation between photosynthetic rates and leaf stable periods, which represent leaf longevity in several deciduous broad-leaved forests.

2. Coley (1988) found in a lowland rainforest in Panama that there are positive correlations between the leaf lifetime of 41 tree species and defense investments such as fiber and lignin.

3. The maximum leaf life span of *Abies veitchii* was longest in the forest understory (10 yr), intermediate in the understory near the forest edge (8 yr), and shortest in a clear-cut area (5 yr) (Matsumoto 1984a). The decrease in photosynthetic rate was highest in clear-cut, intermediate in forest edge, and lowest in forest understory (Matsumoto 1984b), implying an inverse correlation between leaf longevity and the slope of the photosynthetic rate/leaf age curve. An ever-green shrub, *Daphniphyllum macropodum* var. *humile*, in forest understory retains leaves for 4 yr at longest, while that in the light gap retains leaves for 2 yr (Kikuzawa 1988). The decrease in photosynthetic rates of leaves with leaf age in the light gap is larger than that in the forest understory (Kikuzawa 1989).

Leaf Longevity in Seasonal Environments

Net gain (G) and net gain per unit time (g) of a leaf are obtained using equation (2) in seasonal environments where favorable and unfavorable periods for photosynthesis alternate within a year. Net gain (G) increases throughout a favorable period and decreases during the following unfavorable period because maintenance costs during the period must be paid while there is no gain by photosynthesis. The net gain increases again in the next favorable period and decreases again

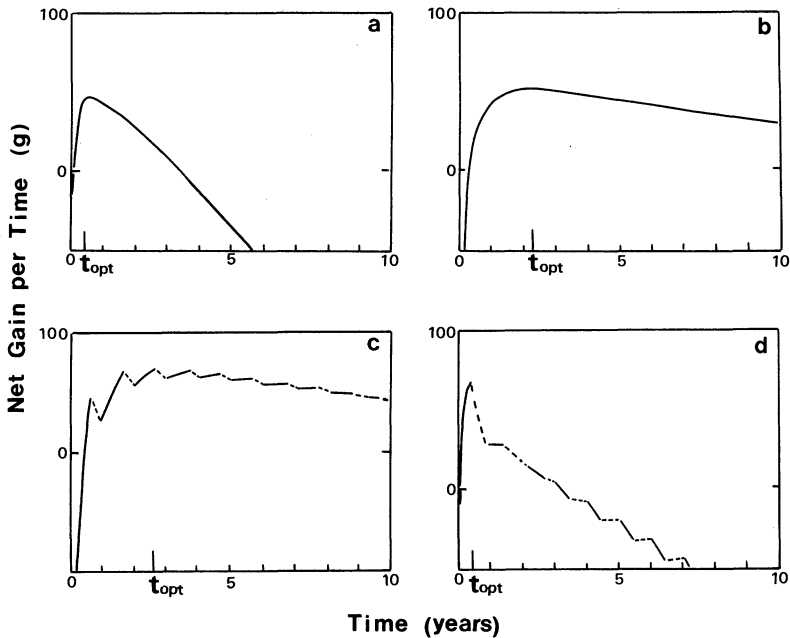


FIG. 2.—Examples of changes of net gain per unit time (g) by a leaf with time (t) with various parameter values. I calculated g using eqq. (1), (2), and (3). *Solid line* indicates net gain per unit time (g) during favorable periods, and *dashed line* is that during unfavorable periods. *a*, Leaf longevity shorter than 1 yr in a condition without any unfavorable period with the following parameters: $a = 80$, $f = 1.0$, $m = 11$, $b = 2$, and $C = 5$; t_{opt} is 0.5 yr. *b*, Leaf longevity longer than 1 yr in a condition without any unfavorable period with $a = 80$, $f = 1.0$, $m = 11$, $b = 10$, and $C = 20$; t_{opt} is 2.2 yr. *c*, Leaf longevity longer than 1 yr in a seasonal condition with $a = 50$, $f = 0.7$, $m = 6$, $b = 12$, and $C = 20$; t_{opt} is 2.7 yr. *d*, Leaf longevity shorter than 1 yr in a seasonal condition with $a = 100$, $f = 0.5$, $m = 11$, $b = 2$, and $C = 5$; t_{opt} is 0.45 yr.

in the succeeding unfavorable period. The net gain per unit time (g) is also an oscillating curve as shown in figure 2. The time t that gives the maximum g is considered to be t_{opt} .

When t_{opt} is shorter than or equal to the length of the favorable period (fig. 2*d*), the tree is assumed to shed the leaf by the end of the favorable period and to become leafless during the succeeding unfavorable period. Thus the tree is considered to be deciduous. When t_{opt} is longer than 1 yr (fig. 2*c*), the tree is assumed to retain leaves during the unfavorable period; thus the tree is assumed to be evergreen.

Leaf Longevity and Leaf Habit

When the optimum leaf longevity (t_{opt}) is shorter than the length of the favorable period, the tree will replace its leaf at t_{opt} with a new leaf (fig. 3*c*). This is an example of a deciduous tree, the leaf longevity of which is shorter than the favorable period. Leaf longevity and the favorable period will be of similar length

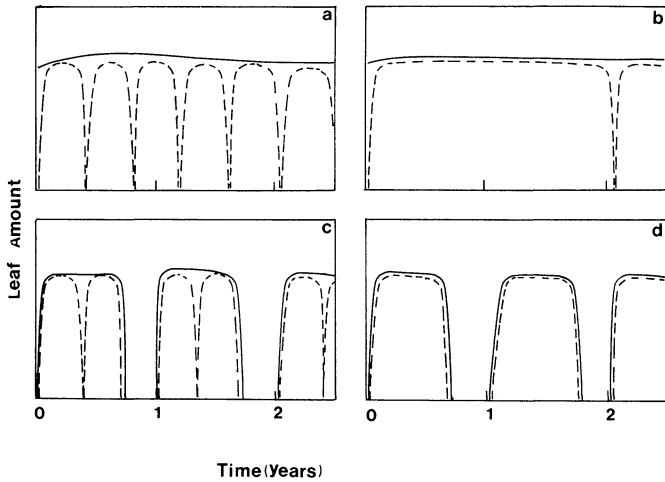


FIG. 3.—Comprehension of leaf habit and leaf longevity. *Dashed line* indicates leaf area of a leaf, and *solid line* indicates that of a tree. *a*, Evergreenness with shorter leaf longevity; *b*, evergreenness with longer leaf longevity; *c*, deciduousness with shorter leaf longevity; *d*, deciduousness with longer leaf longevity.

(fig. 3*d*) when (1) calculated optimum leaf longevity (t_{opt}) is equal to the length of the favorable period (f), (2) t_{opt} is slightly shorter than f , but the remaining period ($f - t_{\text{opt}}$) is too short for the tree to replace the leaf, and (3) t_{opt} is slightly longer than f , but the difference ($t_{\text{opt}} - f$) is too short to pay back the maintenance costs during the following unfavorable period. When there is no unfavorable period during the year, trees can usually perform photosynthesis throughout the year by a leaf that is replaced at t_{opt} , and thus the leaf habit is assumed to be evergreen. Even in such a stable condition, leaf longevity varies depending on the parameters in equation (3) (fig. 2*a*, 2*b*). There are evergreen trees, the leaf longevity of which are shorter (fig. 3*a*) and longer (fig. 3*b*) than 1 yr.

BIOGEOGRAPHICAL PATTERN

I assume that, in a mesic tropical region, there is no unfavorable period ($f = 1.0$) and that leaf habit is evergreen. But leaf longevity is either shorter or longer than 1 yr depending on parameter values in equation (1).

The length of the favorable period decreases with increasing latitude. In temperate regions where f is less than 1.0, evergreen and deciduous habits coexist. Which of the two habits is selected depends again on the parameter values in equation (2). I conduct a simulation by changing parameter values to determine leaf habit in each set of parameters (see the following section).

Ranges of Parameters

Here I examine the effect of parameter values and length of favorable periods on leaf longevity and leaf habit. Before carrying out the simulation, I will

approximate ranges of parameter values. First, I will set the ratio of parameters a and m .

According to Larcher (1975), maximum net photosynthetic rates and respiration rates for deciduous broad-leaved trees are 15–25 mg CO₂ g⁻¹ h⁻¹ and 3–4 mg CO₂ g⁻¹ h⁻¹, respectively; for evergreen broad-leaved trees, 10–25 and 0.7; and for evergreen conifers, 3–18 and 1, respectively. From these values I calculated relative values of parameter a to m as 6–9 (deciduous broad-leaved trees), 10–37 (evergreen broad-leaved trees), and 4–19 (evergreen conifers). In the present simulation I adopt ranges of a/m as 1–50, which covers the above ranges. Because photosynthesis is less than maximum photosynthetic values during much of the 24-h day, the lower end of the range contains more realistic values.

Next, I will discuss the ratio of parameters a and C . Saeki and Nomoto (1958) calculated the payback time for the construction cost by the net photosynthesis of a deciduous broad-leaved tree (DBL) to be 15 d and that of an evergreen broad-leaved tree (EBL) to be 30 d. For evergreen conifers (EC) I estimated it to be 50–80 d, from the photosynthesis data and specific leaf mass values given by Hagihara and Hozumi (1977). Converting these values to annual-net-photosynthesis-to-construction-cost ratios in a nonseasonal environment, we get 24 (DBL), 12 (EBL), and 4–7 (EC). Setting respiration ratio to total photosynthesis equal to 10%, we can convert the above values to the annual-gross-photosynthesis-to-construction-cost ratios, which are 27 (DBL), 13 (EBL), and 4–8 (EC). On the other hand, from equations (1) and (3), the annual photosynthesis in a nonseasonal environment is obtained from $\int_0^1 p(t)dt = a[1 - 1/(2b)]$. Setting b equal to 6.5, or the intermediate value of the range of parameter b (see below), this corresponds to $0.92a$. Therefore, a/C ratios are assumed to be approximately 30 (DBL), 18 (EBL), and 5–9 (EC). In the present simulation I use an a/C ratio of 1 to 33, which covers the above range.

Parameter b indicates the time (yr) when the photosynthetic rate and maintenance respiration rate become zero. In this model I adopt the range of 1 to 12 as the values of parameter b , which roughly covers ranges of leaf life span of trees. Even if b is greater than 1 (yr), t_{opt} could be less than 1 with changes in other parameters. Therefore, I did not adopt b less than 1 in this model.

Effect of the Length of Favorable Period on Leaf Habit

Here I show that the leaf habit will change only with the length of favorable period (f) even if a leaf has the same parameter values of a , b , m , and C . Equation (2), or net gain by a leaf per unit time, is divided into two parts, or

$$g = g_1 + g_2,$$

where

$$g_1 = (1/t) \left(\int_0^f p(t)dt + \dots + \int_{[t]}^t p(t)dt \right)$$

and

$$g_2 = (1/t) \left(- \int_0^t m(t)dt - C \right).$$

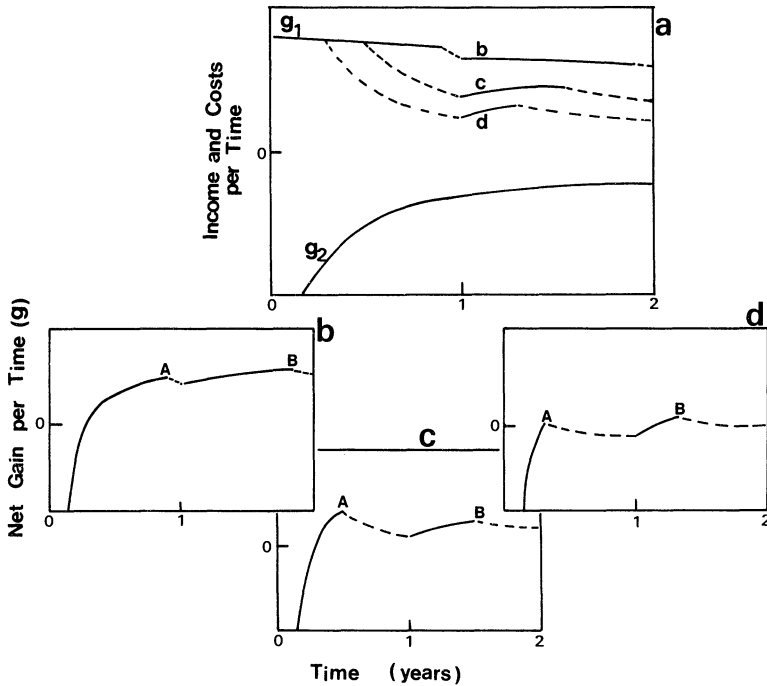


FIG. 4.—An example of leaf-habit shift from long through intermediate to short favorable period (f), while other parameters are fixed ($a = 80$, $b = 5$, $C = 18$, $m = 14$). *a*, Net gain per time (g) is divided into two parts: income per time (g_1) and costs per time (g_2). Whereas g_2 is expressed as a common increasing curve, g_1 is expressed by three different curves (*b*, *c*, and *d*) according to the length of favorable period (f). Thus the difference between the two curves results in various g curves as shown in panels *b*, *c*, and *d*. *b*, Evergreenness ($B > A$) with a long favorable period ($f = 0.9$). *c*, Deciduousness ($A > B$) with an intermediate favorable period ($f = 0.5$). *d*, Evergreenness ($B > A$) with a short favorable period ($f = 0.3$).

Since parameters other than f are constant, g_2 is expressed as a common increasing curve with time irrespective of the shape of g_1 (fig. 4*a*), whereas g_1 exhibits various curves according to the values of f . Thus the differences between the two curves show various consequences of net gain per unit time (g) with time as shown in panels *b*, *c*, and *d* of figure 4, although maintenance and construction costs are the same in the three cases. When $f = 0.3$, for example, g_1 decreases rapidly at $t = 0.3$. However, the rapid decreasing rate of g_1 is compensated by the rapid increasing rate of g_2 at $t = 0.3$, resulting in the rather slow decreasing rate of g at $t = 0.3$ in figure 4, panel *d*.

Furthermore, the increasing rate of g_1 in the second year becomes greater with shorter f (fig. 4*a*). During the favorable period in the second year, g_1 is subdivided into gains in the first and second year and is expressed as

$$g_1 = (1/t)(P(f) + P(2)),$$

where $P(f) = \int_0^f p(t)dt$ and $P(2) = \int_1^{1+f} p(t)dt$. The more rapid second-year

increase in g_1 in simulations with a short favorable period was not due to differences in rates of second-year carbon gain. All simulations used the same decreasing function with time to describe carbon gain during favorable periods. Differences in the slope of g_1 with time during the second year result from different rates of decline in the contribution of carbon gained the first year ($P(f)$) to g_1 . As t increases, $P(f)/t$ decreases with a rate proportional to $P(f)$. Thus, the rate of increase of g_1 at the beginning of the second year is more rapid when the favorable period is shorter and $P(f)$ is lower. The opposing influences of length of favorable period on the amount of carbon gained the first year and of the amount of carbon gained the first year on the rate of decline of g_1 with time result in a complex effect of length of favorable period on predicted leaf longevity as predicted from the relative values of g at the end of the first favorable period (fig. 4, point A) and at the end of the second favorable period (fig. 4, point B).

When f is long ($1 - f$ is short), the decrease in net gain during the unfavorable period is small and thus the tree can attain higher net gain in the second year. Therefore, evergreenness will be favored in areas with a longer favorable period (fig. 4b). When the length becomes shorter, the decrease in net gain during the unfavorable period becomes larger, and therefore the net gain per unit time in the second year becomes smaller than that in the first year. Thus deciduousness will be favored (fig. 4c). When the favorable period becomes still shorter, it is difficult for the tree's net gain to be sufficient during the first year because of the short favorable period. The tree will need two or more seasons for its net gain to be sufficient. Thus evergreenness will again be favored (fig. 4d).

Simulation

To obtain changes in leaf habit with the changes in the length of the favorable period with various sets of parameter values, a simulation was carried out by substituting equation (3) into equation (2) and by changing parameters a , b , C , and m (see legend of fig. 5) for each f value from 0.2 to 1.0. The optimum time (t_{opt}) to maximize net gain per unit time (g) was obtained in the range of time t from 0 to 10 yr. Examples of calculation are shown in figure 2. When the value of g was not positive at any t values, the parameter set was discarded.

When f is less than 1.0, the leaf habit (deciduousness or evergreenness) for each set of parameter values was determined on the basis of whether t_{opt} is longer or shorter than 1 yr. When f is 1.0, all leaf habit is considered to be evergreen; only whether leaf longevity is shorter or longer than 1 yr was recorded. For each of the total combinations of parameter values at each f level, the percentages of deciduousness and evergreenness are calculated and shown in figure 5.

When we consider the changes in parameter f as the decrease in length of favorable period only with increasing latitude, we can regard figure 5 as a biogeographical distributional pattern of deciduous and evergreen habits. All the leaf habits in the area with $f = 1.0$ are considered to be evergreen. However, there are percentages of evergreenness with leaf longevity shorter than 1 yr (fig. 3). The percentages of evergreenness decrease with decreasing f and reach the minimum at $f = 0.5$; thereafter they increase again with a decrease in f . A bimodal distributional pattern with two peaks, one at lower and the other at higher lati-

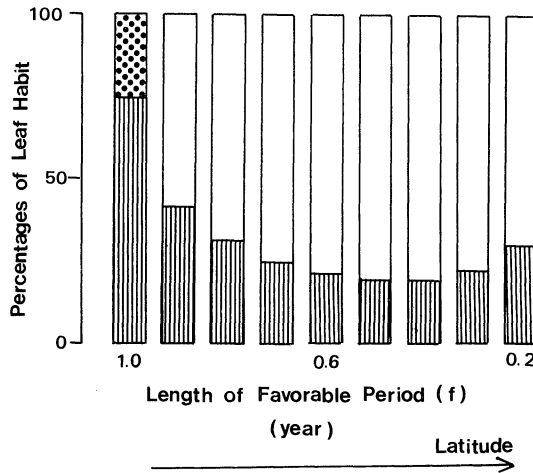


FIG. 5.—Percentages of deciduous and evergreen habits with various lengths of favorable period ($f = 0.2$ – 1.0). Percentages were simulated by varying parameters a from 20 to 100, C from 3 to 18, b from 1 to 12, and m from 2 to 18 in eq. (4) when $f = 1.0$ and eq. (2) when $f < 1.0$. Maximum g in eq. (2) on each parameter value was obtained and leaf habit was determined using t_{opt} value that gives the maximum g . *Striped area* in the histogram represents percentage of evergreenness, and *open area* represents percentage of deciduousness. *Dotted area* when $f = 1.0$ represents evergreenness with leaf longevity shorter than 1 yr.

tudes, was observed for the percentages of evergreenness. Percentages of deciduousness show a unimodal distribution pattern with a peak at midlatitude (fig. 5).

DISCUSSION

The most important assumption adopted in this article is that a tree can retain only one leaf at a time. This implies that there is a constraint that limits the number (or mass) of leaves that a tree can retain at a time. The constraint may be limited resources such as water, nutrients, or light or some kind of limitation resulting from the tree's architecture. If there is no constraint on the leaf number at a time, it will be obvious that the tree retains as many leaves as possible up to the time when the daily net gain of a leaf ($p(t) - m(t)$) becomes zero (Y. Harada, personal communication). Actual situations in nature may fall between these two extremes.

In the model, I assumed that the construction cost is paid at the initial phase of the leaf's life span. But in reality construction costs are spent over days or weeks during leaf expansion (Jurik and Chabot 1986). Therefore the model is abstraction. However, this abstraction will bring no change for the calculation of t_{opt} , unless the construction costs are spent beyond t_{opt} .

The model indicates that to shed leaves early is advantageous without any mutual shading. Although severe mutual shading may reduce photosynthesis and may entail early leaf fall, there is evidence that leaves are shed early in the season without mutual shading. The first leaf of *Alnus hirsuta* expands early in May in

Hokkaido and is usually shed in late May or early June when the inside of the tree crown remains in light. Even isolated trees that receive abundant solar light shed their leaves early in the season (Kikuzawa 1978). Thus shading is not considered to be a main factor in the early leaf fall in *A. hirsuta*. An artificial shading on alder branches does not shorten leaf life span (K. Kikuzawa, unpublished manuscript). In some reports, especially in species of forest understory, shading prolonged leaf life span (Nilsen 1986; Kikuzawa 1988).

Leaf life span is believed to be determined by the balance of costs and benefits to the leaf (Chabot and Hicks 1982). In this article, I consider that leaf longevity is determined to optimize a leaf's net gain per time. This optimum time corresponds to the time to maximize the net gain of a hypothetical tree with a tightly constrained amount of leaf biomass (fig. 1). In the present model, net gain per unit time is positively affected by the parameter $(a - m)$ and negatively affected by b and C . Thus leaf life span is long when b and/or C are large and short when $(a - m)$ is large (eq. [4]). In the real world, net gain is affected by environmental conditions such as resource availability in the habitat and seasonal resource variability. High photosynthetic rates, if any, cannot be attained at a resource-limited site (Chabot and Hicks 1982). Parameter a is considered to be low at such a site. Positive net gain with lower photosynthetic rates necessitates longer leaf life span. Extended leaf longevities in resource-poor environments are considered to be a means by which resources are used more efficiently (Monk 1966; Small 1972a, 1972b; Thomas and Grigal 1976; Moore 1980). Long leaf life spans were observed in forest understory in both tropical (Bentley 1979) and temperate regions (Kikuzawa 1988), in peat bogs (Small 1972a), and in a Mediterranean climate (Moore 1980; Field and Mooney 1983). To carry out photosynthesis for a longer period, higher values of parameter b will be necessary. To retain leaves for a longer period, investments for defense against environmental stresses such as herbivory are necessary. Such investments enlarge construction cost (C) of the leaf. To invest large costs for the defense will dilute photosynthetic material and will thus lower the photosynthetic ability of the leaf. In addition, a longer period will be necessary to pay back large costs. Thus leaf parameters and leaf longevity affect each other. Recently, Williams et al. (1989) argued that not the construction cost of leaves but the ratio of construction cost to daily carbon gain correlates with leaf life span. According to equation (3), as Williams et al.'s ratio $C/(a - m)$ increases, t_{opt} increases.

As for the seasonal variability in environmental conditions, I adopt only the length of the favorable period. This is designated as parameter f . Even if a leaf has similar parameter values, evergreenness and deciduousness alternate with changes in the f value (fig. 4). As a consequence, biogeographical pattern of evergreenness becomes bimodal (fig. 5). Assuming similar suites of environments at each latitude, there are evergreen as well as deciduous habits depending on other parameters. Figure 5 is a potential distribution, based only on length of favorable season. In the real world, variation in environment and resource availability with latitude may put additional constraints on leaf habit and leaf longevity.

In regions where trees can conduct photosynthesis throughout the year ($f = 1.0$), it is apparent that trees retain leaves all year (evergreenness). However, in

such regions, there are a variety of leaf longevities depending on the resource availability of habitats. Recent studies reveal that there are many evergreen species with leaf longevities shorter than 1 yr in tropical regions (Gill and Tomlinson 1971; Kawahara et al. 1981; Shukla and Ramakrishnan 1984; Kanazawa and Sato 1986; Coley 1988).

Evergreenness shows a peculiar biogeographical distribution pattern: a bimodal distribution with one peak at lower latitudes and another peak at higher latitudes (fig. 5). In tropical, subtropical, and warm-temperate regions, evergreen broad-leaved species predominate while in temperate regions, there are many deciduous broad-leaved species. And, in subarctic regions, evergreen conifers predominate. Chabot and Hicks (1982) call this a puzzling pattern that apparently could not be solved by a cost-benefit analysis of leaves. In fact, the present model simulates the bimodal distributional pattern of evergreenness over latitude, indicating that a cost-benefit analysis alone can explain this biogeographical pattern.

In the present model, I adopt a simple linear-decrease equation to approximate the time trend of photosynthetic rate. It is not reasonable that such a simple approximation can be applicable to various tree species, but the arguments remain valid as long as the photosynthetic rate is some decreasing function with time (Y. Harada, personal communication). Photosynthetic rates of leaves are age-dependent (Chabot and Hicks 1982) and usually are decreasing functions with time after full expansion of leaves (Chabot and Hicks 1982; Sestak et al. 1985). When I adopt other decreasing functions such as exponential and quadratic ones, distributional trends of leaf habits similar to those in figure 5 are obtained (K. Kikuzawa, personal observation). Hence, I think that the trends shown in this article have wide applicability. Extensive information on the time trend of photosynthetic rates together with leaf habit and longevity of various species in various regions would strengthen the test of the model.

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