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A mathematical analysis of leaf longevity of trees under seasonally varying temperatures, based on a cost–benefit model

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ABSTRACT

Questions: Under what climatic conditions is long leaf longevity, or evergreen-ness, favoured? Under what physiological conditions of leaves is long leaf longevity, or evergreen-ness, favoured? Why is evergreen-ness favoured in both tropical and frigid regions? What is the difference in biological meaning of evergreen-ness between tropical and frigid regions?

Mathematical method: Optimization with two variables, expansion and shedding times of leaves. The objective function for optimality is the amount of assimilating product per unit time of an individual leaf. We obtained the optimal expansion and shedding times of leaves by numerical calculation.

Key assumptions: (1) Air temperature varies seasonally with average temperature and the amplitude (climatic condition). (2) The key parameters of a leaf are construction cost, photosynthetic rate, and ageing rate (physiological condition). (3) A leaf adopts the optimal strategies of expansion and shedding times both under various climatic conditions and physiological conditions.

Predictions: (1) There are two climatic conditions in which evergreen-ness is optimal. The first is where average temperature is over 30°C and the amplitude is very small, as in the tropics. The other is in cold regions, such as a frigid area. (2) Low maximum photosynthetic rate and high construction cost are likely to select for evergreen leaves.

Keywords: cost–benefit model, deciduous, evergreen, leaf longevity, mathematical model, optimal strategy, temperature.

INTRODUCTION

Terrestrial plants have acquired an immense variety of leaf habits during the course of evolution over 400 million years. For example, leaf longevity of trees varies widely among

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tree species, from a few weeks in ephemerals to about 25 years or more in a tropical conifer. This is the result of adaptation to the climatic conditions under which particular tree species exist (Givnish, 1978; Chapin, 1980; Chabot and Hicks, 1982). Over the last 10 years, researchers have tried to construct a cost–benefit model of photosynthetic production to determine optimal leaf longevity and to show that leaf longevity of a particular tree species is optimal under the climatic conditions of the habitat it occupies (Harada and Takada, 1988; Kikuzawa, 1991, 1995; Kikuzawa and Ackerly, 1999).

For example, Harada and Takada (1988) constructed a mathematical model with seasonally varying temperatures and obtained the optimal times of expansion and shedding of leaves within one year (Table 1). They assumed the total amount of net photosynthetic production as the objective function for optimization, which the optimal times maximize. Therefore, they did not include the construction cost of a leaf because the quantity of the construction cost only decreases the total amount of the net photosynthetic production and does not affect the optimal times of expanding and shedding. Since they obtained the optimal times of expansion and shedding of leaves within a year, they focused only on deciduous tree species, not evergreen species, in their model.

In contrast, Kikuzawa (1991) determined the optimal leaf longevity that maximizes the net photosynthetic production *per unit time* during one or more years. In his model, the construction cost of a leaf affects optimal longevity because the longer that leaf longevity is, the less the loss per unit time by consuming the construction cost is. Using this model, he showed that evergreen-ness is likely to be favoured in areas of both low and high latitude. However, the assumption regarding temperature condition is crude. He assumed that there are two periods within a year, favourable and unfavourable for photosynthesis, and that daily photosynthetic rate during the favourable period is constant without taking seasonally varying temperatures into account (i.e. seasonally varying photosynthetic rate). Besides, he calculated only the optimal leaf longevity, rather than the optimal times of expansion and shedding. Both models have several different errors in their assumptions.

In the present paper, we propose a new cost–benefit model in which the construction cost and seasonally varying temperatures are incorporated to eradicate these errors. Both the times of expanding and shedding can be determined using this model, and the difference between them (i.e. leaf longevity) can also be calculated. We conducted several numerical calculations of this cost–benefit model and obtained the optimal solution under various

Table 1. A comparison of two previous models

	Construction cost of a leaf	Seasonality	Period	The quantity to be maximized	Outcome
Harada and Takada (1988)	Not assumed	Periodic temperature change	One year	The total amount of net photosynthetic product	The days of expansion and shedding
Kikuzawa (1991)	Assumed	Favourable or unfavourable	Multiple years	The net photosynthetic product per unit time	Leaf longevity

climatic conditions and also physiological conditions of a leaf. The questions addressed here are:

1. Under what climatic conditions is long leaf longevity, or evergreen-ness, favoured?
2. Under what physiological conditions of leaves is long leaf longevity, or evergreen-ness, favoured?
3. Why is evergreen-ness favoured in both tropical and frigid regions?
4. What is the difference in biological meaning of evergreen-ness between tropical and frigid regions?

METHODS

The cost–benefit model

The model includes two additional parameters compared with Kikuzawa's (1991) model: annual average temperature (T_{av}) and amplitude of temperature (a), which represent the climatic conditions of each habitat occupied by trees. Temperature (T) at each time (t) is a cosine function, which depends on these two parameters (Fig. 1A):

$$T(t) = T_{av} - a\cos\left(2\pi \frac{t}{360}\right) \tag{1}$$

For simplicity, a year is assumed to be 360 days. The curve has a minimum ($T_{av} - a$) at the beginning of the year (day 0), increasing to a maximum ($T_{av} + a$) in the middle of the year (day 180).

The benefit ($B(e, s)$) is the total amount of net photosynthetic production during the leaf's life span, between the times of expansion, e, and of shedding, s:

$$B(e, s) = \int_{e}^{s} [L(t)G(t - e) - C_m]\mathrm{d}t \tag{2}$$

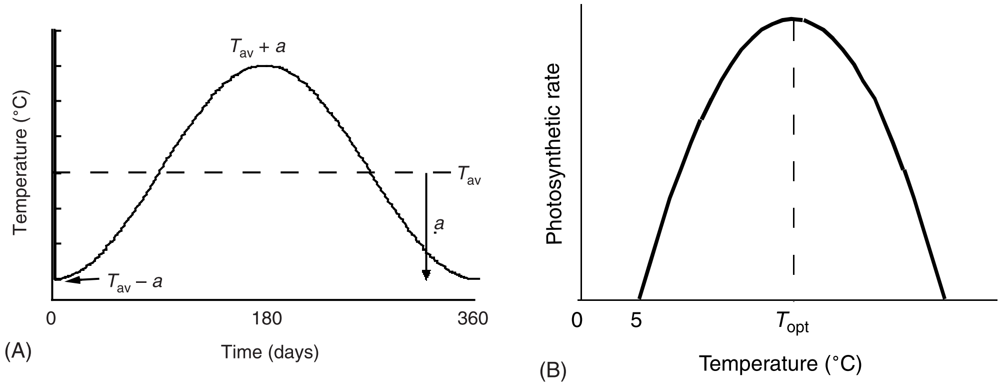


Fig. 1. Annual variation in daily temperature and photosynthetic rate. (A) The daily temperature is a cosine function with two parameters: annual average temperature (T_{av}) and amplitude of temperature (a). The maximum daily temperature is $T_{av} + a$ and the minimum is $T_{av} - a$. For simplicity, a year is assumed to be 360 days. (B) Photosynthetic rate has its maximum value at the optimal temperature (T_{opt}); the minimum temperature capable of photosynthesis is 5°C.

where

$$L(t) = L_{\max} - z(T - T_{\text{opt}})^2 \quad \text{and} \quad z = \frac{L_{\max}}{(5 - T_{\text{opt}})^2} \tag{3}$$

Photosynthetic rate at each time ($L(t)$) depends on the temperature (T) at each time (Fig. 1B). The functional form is parabolic and has a maximum value at the optimal temperature (T_{opt}) for photosynthesis, as it is known that the photosynthetic rate increases with temperature but decreases when it becomes too hot (Chabot, 1978). We set the minimum temperature capable of photosynthesis at 5°C, and thus the damping coefficient (z) is determined using the maximum photosynthetic rate ($L_{\max}$) and the optimal temperature. We also assume that a newborn leaf is affected by ageing and that the ability of photosynthesis decreases exponentially with time (Sestak *et al.*, 1985):

$$G(t) = \exp(-bt) \tag{4}$$

where b is the ageing coefficient of a leaf. Therefore, the instantaneous photosynthetic rate is $L(t)G(t-e)$ and the net photosynthetic rate is equal to $L(t)G(t-e) - C_{\text{m}}$, subtracting the maintenance cost. Integration in equation (2) is done as long as the net photosynthetic rate is positive.

Optimal times

The net photosynthetic production per unit time ($N(e, s)$) can be obtained from the benefit minus construction cost of the leaf (C) divided by leaf longevity, $s - e$:

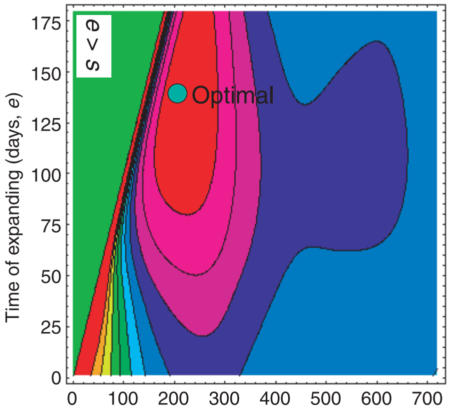
$$N(e, s) = \frac{B(e, s) - C}{s - e} \tag{5}$$

Figure 2 provides an example of the contour map of $N(e, s)$ for a given combination of other parameters. Once the times of expanding and shedding are determined, each $N(e, s)$ can be obtained using equations (1) to (4), and it has a maximum value in the (e, s) plane. There is an interior optimal point in this example, where the maximum N is realized. The combination of these two we call the optimal times.

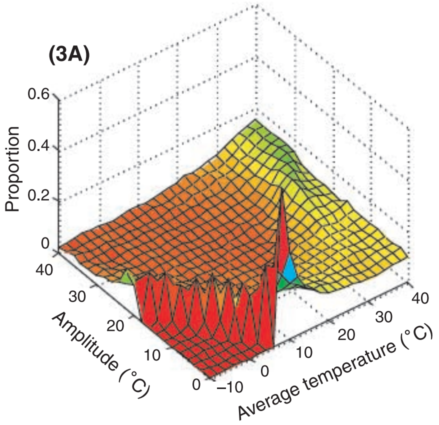
Parameter sets used

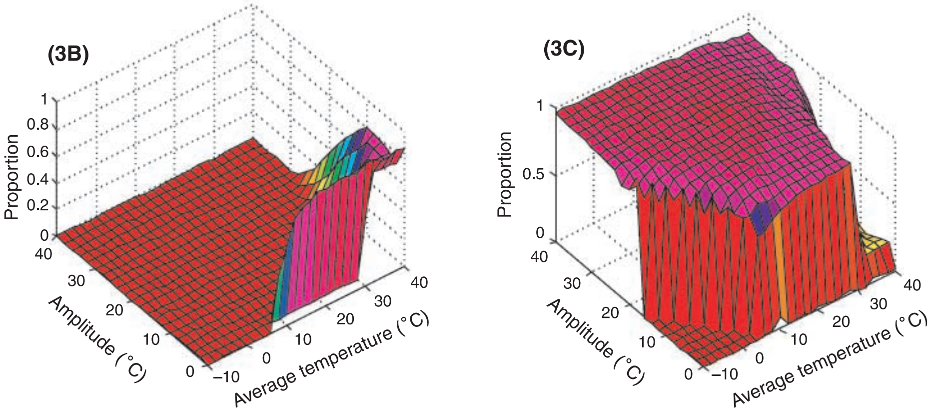
We calculate the optimal times for each combination of parameters. In this model, we use two kinds of parameter, the first of which represents the climatic conditions: average temperature and the amplitude. Average temperature ranges from −10°C to 40°C in steps of 2°C. Amplitude ranges from 0° to 40°C in steps of 2°C (from Chronological Scientific Tables, 2002). Therefore, there are 546 combinations of climatic conditions (Table 2).

The second kind of parameter represents the physiological condition of leaves; that is, maximum photosynthetic rate ($L_{\max}$), construction cost (C), ageing rate of leaves (b), optimal temperature of photosynthesis (T_{opt}), and maintenance cost (C_{m}). Each parameter has its own range (Table 2) (from Saeki and Nomoto, 1958; Larcher, 1975; Hagihara and Hodumi, 1977) and the number of combinations of physiological parameters is 880. Therefore, 500,000 cases are calculated numerically and the optimal times of expansion and shedding are obtained in each case.



(2)


(3A)


(3B)

(3C)

Fig. 2. A contour map of the net photosynthetic rate per unit time (N). There is an interior optimal point (green dot) where the maximum N is realized. Parameter values used in this example are: $T_{\rm av} = 15$, $a = 15$, $L_{\max} = 5$, $T_{\rm opt} = 30$, $C_{\rm m} = 0.05$, $b = 0.002$, $C = 50$. The optimal time for expanding is day 136 and that of shedding day 225; the left-upper green region in the figure shows where shedding occurs earlier than expansion.

Fig. 3. The proportions of three solutions among ~900 combinations of physiological parameters in each climatic condition. The flat region around 0°C is where trees cannot undertake photosynthesis because of the very low temperature. (A) *Evergreen*: the proportion of evergreen leaves is high in two regions. (B) *Beginner*: the proportion of beginners is high, sometimes as high as 0.9, where the amplitude is small and/or the average temperature is high. (C) *Deciduous*: these values represent the remaining proportion after the other two leaf patterns have been accounted for.

RESULTS

The optimal times of expanding and shedding depend on both climatic and physiological parameters. However, three patterns are apparent as optimal solutions. One is a deciduous pattern, where the longevity is less than one year and the expansion of leaves begins in the middle of that year. The second is an evergreen pattern, where the leaves expand from the

Table 2. Parameters used in the model

Parameters	Symbol	Range	Interval	Unit
Climatic conditions				
Average temperature	T_{av}	−10 to 40	2	°C
Amplitude	a	0 to 40	2	°C
Physiological conditions				
Maximum photosynthetic rate	L_{max}	0.1 to 5	0.7	$g\,C \cdot day^{-1} \cdot m^{-2}$
Construction cost	C	10 to 100	10	$g\,C \cdot m^{-2}$
Ageing rate of leaves	b	0.001 to 0.005	0.0005	day^{-1}
Optimal temperature for photosynthesis	T_{opt}	30	—	°C
Maintenance cost	C_m	0.05	—	$g\,C \cdot day^{-1} \cdot m^{-2}$

middle of the year and the longevity exceeds one year. The third is where the leaf expands from the beginning of a year. We call this pattern the 'beginner'. The 'beginner' pattern includes the two cases where the leaf life span is either less than or more than one year. The beginner solution means that a leaf should be expanded from the coldest day of a year to obtain the maximum N. This is because it is warm enough to construct a leaf even on the coolest day. Therefore, it is better to expand the second leaf just after shedding the first leaf. This also implies that trees with beginner leaves are evergreen even if the longevity of the beginner leaves is less than one year. We present our results based on these three patterns of the optimal solution.

Dependence on climatic conditions

Under what climatic conditions is long leaf longevity, or evergreen-ness, favoured? Figure 3A shows the proportions of evergreen leaves in ~900 combinations of physiological parameters for each climatic condition. The proportion of evergreen leaves is high in two climatic conditions. The first is where the average temperature is over 30°C. The other is the neighbourhood of the severely cold region – that is, the frigid area. Here the proportion of evergreen leaves reaches 0.6.

Figure 3B shows the proportions of beginner leaves. The proportion is high, sometimes reaching 0.9, where the amplitude is very small or the average temperature is high. Therefore, in the tropical region where the amplitude is small and the average temperature is high, beginner leaves are likely to be favoured. Figure 3C shows the proportions of deciduous leaves.

Comparison with Kikuzawa's results

We compare the results reported by Kikuzawa (1991) with those of the present study. Kikuzawa examined the relationship between the proportion of the favourable period for photosynthesis and the proportion of evergreen leaves. He obtained a bimodal distribution pattern with two peaks of evergreen-ness, one at low (i.e. large f) and the other at high latitude (i.e. small f).

We assumed the minimum temperature capable of photosynthesis to be 5°C. Therefore, the favourable period is the interval where the temperature exceeds 5°C. From equation (1), the proportion of the favourable period (f) is defined as:

$$f = 1 - \frac{1}{\pi}\cos^{-1}\left(\frac{T_{\mathrm{av}} - 5}{a}\right) \tag{6}$$

We conducted a numerical calculation of the optimal times of expansion and shedding from $f = 0.05$ to 1.0 in steps of 0.05.

The habitat of the plant becomes more severe as the value of f is decreased. When f is less than 0.15, there is no tree that expands its leaf (Fig. 4). The percentage of evergreen and beginner leaves has two peaks. One peak is around $f = 0.25$ and the other is at $f = 1$. The difference between these two peaks is that the second peak includes a high proportion of beginner leaves. This result is similar to that of Kikuzawa, although the proportion of evergreen leaves was lower in the present study.

Dependence on physiological conditions

Figure 3 shows only the proportions of evergreen or beginner leaves. However, evergreen leaves might not be uniformly favoured in physiological condition space. The second question of interest is under what physiological conditions is evergreen-ness, or beginner leaves, favoured? For the climatic condition of two cities in Russia, we calculated optimal leaf longevity, as well as expanding and shedding dates.

Figure 5A shows the results for Habarovsk, which is located at 48°25′N, 135°08′E in a frigid area. The average temperature and the amplitude for Habarovsk are 2°C and 20°, respectively. Figure 5B shows the results for Yakutuk, which is located at 62°02′N, 129°43′E, again in a frigid area. The average temperature and the amplitude for Yakutuk are −10°C and 30°C, respectively. These climatic conditions correspond to one of the two areas where the proportion of evergreen leaves is relatively high in Fig. 3; that is, the neighbourhood of

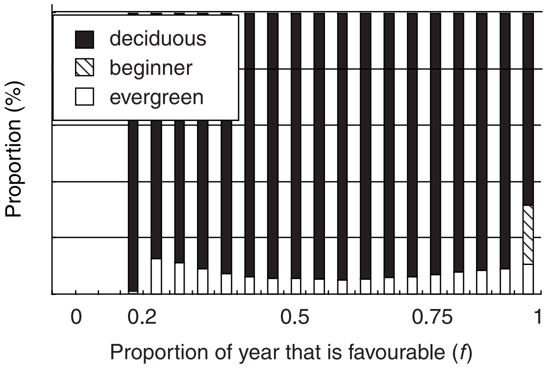


Fig. 4. The proportion of the year that is favourable for photosynthesis and the proportion of evergreen leaves. When f is less than 0.15, no tree expands its leaf. The proportion of evergreen and beginner leaves has two peaks, around $f = 0.25$ and at $f = 1$.

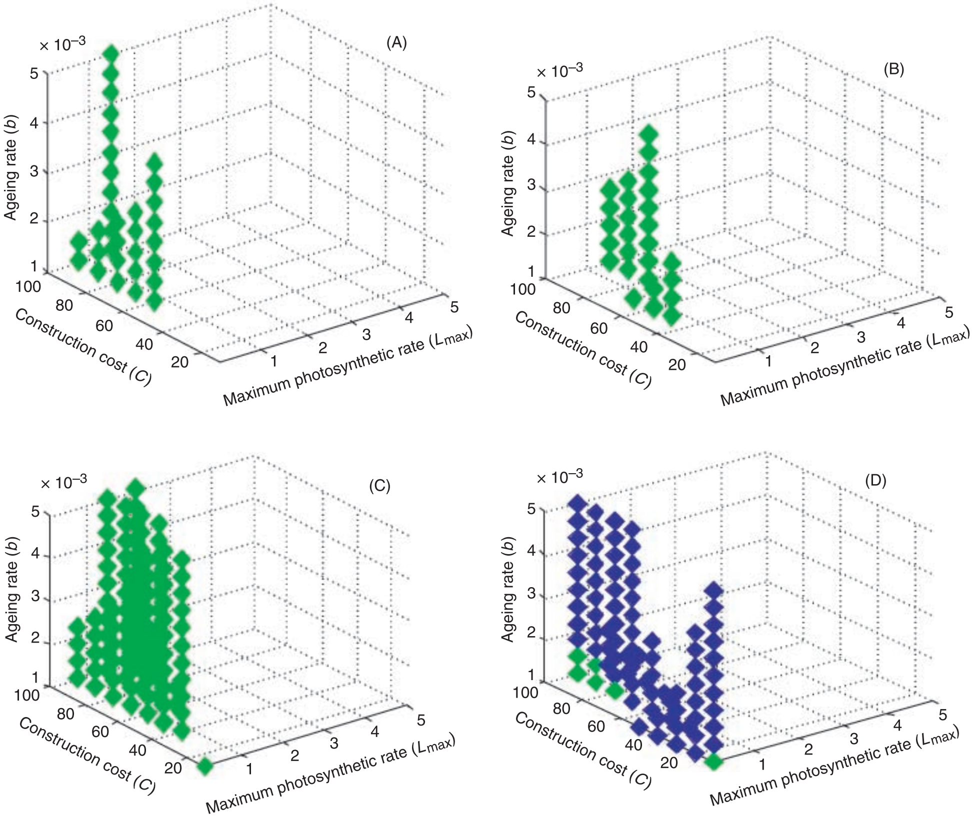


Fig. 5. The result of four examples. The first two examples are for cities in Russia and the latter two are virtual examples. The average temperature and the amplitude are: (A) 2°C, 20°C in Habarovsk; (B) −10°C, 30°C in Yakutuk; (c) 40°C, 36°C where the proportion of evergreen leaves is relatively high in Fig. 3A; (d) 40°C, 2°C where the proportion of beginner leaves is relatively high in Fig. 3B. Green diamonds represent the physiological condition for which evergreen leaves are favoured, blue diamonds the physiological condition for which beginner leaves are favoured

the severely cold region. Diamonds in these figures show the physiological conditions under which evergreen-ness is favoured (i.e. leaf longevity exceeds one year). Evergreen leaves are favoured where the maximum photosynthetic rate is low and the construction cost is high.

We also selected two climatic conditions with combinations of average temperature and amplitude as follows: 40°C, 36°C and 40°C, 2°C (Fig. 5C). The optimal leaf longevity, expanding and shedding dates are calculated under these conditions. These two climatic conditions correspond to one of the two areas where the proportion of evergreen and beginner leaves is relatively high in Fig. 3. Figure 5D also shows the physiological conditions under which evergreen-ness or beginner is favoured – that is, low maximum photosynthetic rate and high construction cost. The conclusion from Figs. 5C and 5D is that the conditions for evergreen-ness and beginner are: (1) low maximum photosynthetic rate and (2) high construction cost.

DISCUSSION

We propose a new cost–benefit model where the construction cost and seasonally varying temperatures are incorporated. We conducted several numerical calculations of this cost–benefit model and obtained the leaf longevity under various climatic conditions and physiological conditions. The important parameters in the present paper are average temperature and the amplitude. Kikuzawa (1991) constructed a similar mathematical model, and obtained a bimodal distribution pattern with two peaks of evergreen-ness, one at a low (i.e. large f) and the other at a high latitude (i.e. small f). He found that this represents the biogeographical distribution pattern of deciduous and evergreen habitats (Kikuzawa, 1995; Kikuzawa and Ackerly, 1999). He assumed there are two periods within a year, favourable and unfavourable for photosynthesis, and considered only that proportion of the year that was favourable. However, a variety of the combinations of average temperature and amplitude are realized with the same f-values (Fig. 6). These combinations also showed different results for evergreen-ness (Fig. 3), although the summarized results (Fig. 4) show the same trend as those of Kikuzawa. Thus, average temperature and amplitude are more plausible factors than latitude or the proportion of the favourable period to determine the leaf longevity or whether evergreen-ness or deciduousness is optimal.

We addressed four questions using our cost–benefit model. The first is under what kind of climatic conditions is evergreen-ness favoured? For beginner and evergreen leaves, there are two conditions. The first is when average temperature is over 30°C and the amplitude is very small, as in the tropics. We believe this type of greenness represents evergreen, broad-leaved tree species. The other is in the neighbourhood of a severely cold region, such as a frigid area. We believe this type of evergreen-ness represents conifer tree species. We found that evergreen leaves in the tropical region were composed mostly of beginner leaves and are qualitatively different from evergreen leaves in the frigid region. We found another region where evergreen-ness is favoured in Fig. 3A. Both average temperature and amplitude are

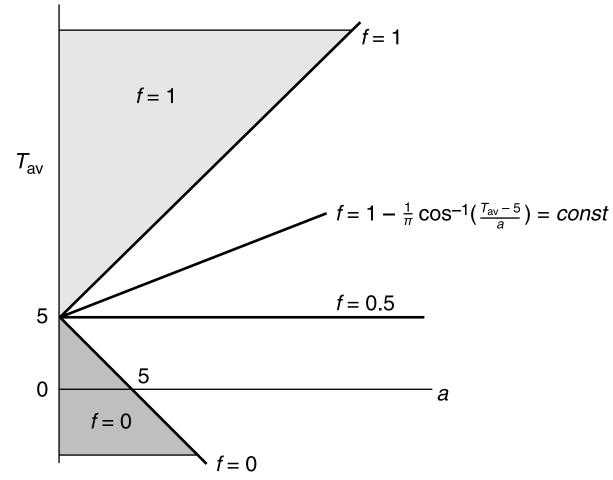


Fig. 6. The combination of average temperature and amplitude along the constant f line. The same favourable period (f) has a variety of combinations of average temperature (T_{av}) and amplitude (a). The $f = 0.5$ line is parallel to the amplitude axis. The dotted and hatched areas represent $f = 1$ and $f = 0$, respectively.

high there, but it has not been realized at present because there is no place on Earth where the yearly maximum temperature is over 70°C, although it might be realized if global warming proceeds at the present rate.

The second question is under what physiological conditions of leaves is evergreen-ness favoured. Our results show that evergreen leaves are not favoured uniformly in physiological condition space (Fig. 5C). A low maximum photosynthetic rate and high construction cost are likely to select for evergreen and beginner leaves (Figs. 5C and 5D). The reason for this is as follows: a low maximum photosynthetic rate necessarily means a long time to recover the construction cost. If ageing rate is high, long leaf longevity does not always provide the highest net photosynthetic rate per unit time (*N*). However, if ageing rate is low, long leaf longevity could provide the highest *N* when the construction cost is high and maximum photosynthetic rate is low. The situation might be the same as in the case of beginner leaves with more than one year's longevity. Taking account of the need for ageing more or less, long leaf longevity, or evergreen-ness, is not always superior to short leaf longevity. If a sudden drought or extreme drop in temperature occurs, it could make the large construction cost of evergreen species wasteful. The risk would be higher in the case of long leaf longevity.

The third and forth questions addressed are to do with why evergreen-ness is favoured both in tropical and frigid areas. As shown here, there is a large discrepancy in the biological meaning between them. In the tropical region, most evergreen-ness in this model is realized by beginner leaves whether longevity exceeds one year or not. The region where the proportion of beginner leaves is positive in Fig. 3B corresponds to the dotted area in Fig. 6 – that is, the proportion of the favourable period equals 1. Therefore, evergreen-ness occurs in the tropical region because of the favourable climatic conditions. On the other hand, evergreen-ness in the frigid region is always realized by leaves with more than one year of longevity. The photosynthetic rate would be very low due to low temperatures and, as a result, the net photosynthetic production per unit time would increase gradually with longevity when ageing rate is sufficiently low. The balance between ageing rate and the gradual increase in speed makes the optimal shedding day more than one year. If the construction cost of a leaf is high in the frigid region, it would take a long time to recover the construction cost and to achieve a peak value of *N*. Therefore, a high construction cost and low maximum photosynthetic rate are the necessary conditions for evergreen-ness.

In the present study, we used average temperature and amplitude as an index of climatic conditions. The strength of these parameters is that they are measured in meteorological observatories in every country, and that future temperature distribution is predicted by a global circulation model. If global warming were to change the temperature distribution on Earth, we could also predict changes in leaf longevity and in the biogeographical pattern of deciduous and evergreen species, using the cost–benefit model.

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