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Article

A general method for calculating the optimal leaf longevity from the viewpoint of carbon economy

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Abstract

According to the viewpoint of the optimal strategy theory, a tree is expected to shed its leaves when they no longer contribute to maximisation of net carbon gain. Several theoretical models have been proposed in which a tree was assumed to strategically shed an old deteriorated leaf to develop a new leaf. We mathematically refined an index used in a previous theoretical model [Kikuzawa (1991) *American Naturalist* 138:1250–1263] so that the index is exactly proportional to a tree's lifelong net carbon gain. We also incorporated a tree's strategy that determines the timing of leaf expansion, and examined three kinds of strategies. Specifically, we assumed that a new leaf is expanded (i) immediately after shedding of an old leaf, (ii) only at the beginning of spring, or (iii) immediately after shedding of an old leaf if the shedding occurs during a non-winter season and at the beginning of spring otherwise. We derived a measure of optimal leaf longevity maximising the value of an appropriate index reflecting total net carbon gain and show that use of this index yielded results that are qualitatively consistent with empirical records. The model predicted that expanding a new leaf at the beginning of spring than immediately after shedding usually yields higher carbon gain, and combined strategy of the immediate replacement and the spring flushing earned the highest gain. In

18 addition, our numerical analyses suggested that multiple flushing seen in a few species of
19 subtropical zones can be explained in terms of carbon economy.

20

21 **Keywords:** leaf lifespan; optimal strategy; deciduous; evergreen; multiple flushing

22

23 **Mathematics Subject Classification (2010):** 92C80 (Plant biology); 90B35 (Scheduling
24 theory, deterministic);

1 Introduction

Leaves are organs specialised for photosynthesis, and variation in leaf traits including leaf longevity is considered to reflect adaptation to specific environmental features of the habitat (Schoettle 1990; Ackerly and Bazzaz 1995; Wright et al. 2004). A tree is expected to shed a leaf when that leaf no longer contributes to maximisation of photosynthetic output (Givnish 1978; Chapin 1980). Many studies have explored temporal variation in shedding, and have described relationships among leaf habits such as photosynthetic rate, construction cost, and decrease in photosynthetic capacity with age (Chabot and Hicks 1982; Coley 1988; Reich et al. 1992; Gower et al. 1993; Hikosaka and Hirose 2000; Hiremath 2000). For example, photosynthetic rate is negatively correlated with leaf longevity, while the construction cost and the rate of decrease in photosynthetic ability are positively correlated.

If variation in longevity is consequence of adaptation and caused by leaf habit related to photosynthesis, what common currency connects such variation with the observed variety of leaf habits? Chabot and Hicks (1982) identified that currency as carbon, and named the economy as “carbon economy”. They sought to calculate benefit and cost (including construction and maintenance cost) of fixed carbon, and to explain the

42 length of life of a leaf.

43 The concept of the carbon economy has stimulated the development of several
44 mathematical models that seek to derive optimal leaf longevity with which net carbon
45 gain is maximised (Harada and Takada 1988; Kikuzawa 1991; Takada et al. 2006).
46 Harada and Takada (1988) developed a cost–benefit model in which carbon gain and loss
47 associated with particular expansion and shedding intervals were calculated, and
48 identified durations of expansion and shedding that maximised net carbon gain. Under the
49 big-leaf assumption stating that all leaves of a tree are expanded at the same time and
50 share the same lifespan, they highlighted deciduous trees, and thus only derived total net
51 carbon gain in a year. Kikuzawa (1991) developed a new model allowing consideration of
52 the entire lifetime of a tree, so that trees with a leaf longevity of more than one year (i.e.
53 evergreen trees) could be studied. He first calculated total net gain by a single big-leaf
54 that is expanded at the beginning of a favourable period (at time zero) for photosynthetic
55 activity (i.e. spring) and shed after τ years, $G(\tau)$, where τ is a positive real number. Then
56 an index, $g(\tau) = G(\tau) / \tau$, which is average increasing rate of net carbon gain of a tree from
57 time zero to time τ , was developed as a surrogate measure of the total net gain of a tree.
58 Finally, the leaf longevity (τ) maximising that index was regarded as optimal strategy for
59 a tree. The analysis of the model indicated that evergreen life history is more likely to be

an optimal strategy at low or high latitudes than at intermediate latitudes. That prediction roughly coincides with the real evergreen–deciduous tree distribution. In addition, the dependence of leaf longevity on three leaf parameters (the photosynthetic rate, the decrease in the photosynthetic rate with age, and the construction cost) observed in the model outcomes was in line with the results of earlier empirical studies (Bentley 1979; Chapin 1980; Chabot and Hicks 1982; Kikuzawa 1984; Koike 1988). Therefore, the index has been viewed as appropriate in the context of optimal strategy theory. Kikuzawa’s index (1991) is currently repeatedly used. For example, Kikuzawa et al. (2013) calculated optimal leaf longevity using the index to explain worldwide variety in leaf longevity from the viewpoint of local adaptation. Advanced modelling studies also used the same index (e.g. Takada et al. 2006). However, Kikuzawa’s index ($G(\tau) / \tau$) only represents average rate over life span of an individual leaf, not the lifelong average rate of a tree. This is because the denominator (τ) only covers the time span during which a leaf is retained and does not consider an interval during which a tree has no leaves. The interval should be taken into account for an evaluation of the lifelong average rate, which Kikuzawa (1991) intended to do. It is important to mathematically refine the well-used index.

In the present study, we also loosen the assumption on the timing of leaf

78 expansion by considering a tree's foliation strategy that determines the interval from
79 shedding of an existing leaf to expansion of a new leaf. Deciduous trees have a distinct
80 interval after shedding leaves, which is usually the whole period unfavourable for
81 photosynthesis, namely winter season, and expand new leaves at each favourable period.
82 On the other hand, some evergreen trees almost simultaneously shed old leaves and
83 expand new ones. Moreover, some subtropical evergreen trees such as *Eurya japonica*
84 have several phenophases of leaf fall and following leaf-flushing phenophases during a
85 year (Nitta and Ohsawa 1997). The point is that, when they shed a part of existing leaves
86 in winter, they do not immediately expand new ones and wait for the next spring. To
87 describe such a variety in the leafless periods, we define the following three foliation
88 rules: (i) the immediate replacement rule states that trees should expand a new leaf
89 immediately after shedding of an existing leaf, (ii) the spring flushing rule states that trees
90 should expand a new leaf at the beginning of the next favourable season, and (iii) the
91 combined expansion rule states that trees should expand a new leaf immediately after
92 shedding of an existing leaf if the shedding occurs within a favourable season and at the
93 beginning of the next favourable season otherwise, i.e. if the shedding occurs within an
94 unfavourable season. Kikuzawa (1991) implicitly assumed the spring flushing rule
95 without examining which rule was favoured under a certain environmental setting. In the

present study, we show that the combined expansion rule provides the same or greater net carbon gain than the spring flushing rule.

We first derive a mathematically appropriate index proportional to lifelong net carbon gain of a tree, and show that Kikuzawa's index (1991) takes the same form as our new index only under the special circumstance that there is no period that is unfavourable for photosynthesis. We also consider the above three foliation rules, and derive optimal leaf longevity in the circumstances in which each rule is applied. We discuss how the duration of periods unfavourable for photosynthesis affects leaf longevity and how our model can explain multiple leaf flushing within a single year. Our new index enables evaluation of optimal leaf longevity in trees growing in complex environments that vary seasonally in terms of temperature or rainfall. Therefore, the index will be useful to estimate the influence of global climate change on leaf longevity and/or gross primary production.

2 Model

The present model is a generalised version of that of Kikuzawa (1991). For simplicity, we consider an “ideal” tree that lives forever and has at most one leaf at a time (the big-leaf

model). In addition, two intervals that form part of the life history strategy are considered. One is the interval from expansion of a leaf to the shedding thereof (leaf longevity), denoted by τ . Suppose that an ideal tree temporally having no leaves expands the i -th leaf at time σ_i . All leaves of that tree are assumed to exhibit the same longevity, regardless of the values of i or σ_i , and the i -th leaf is thus shed at time $\sigma_i + \tau$. The other relevant interval is that from shedding of an existing leaf to expansion of a new leaf, governed by the tree's foliation rule (φ). A more strict definition of φ is that the single value for σ_i is identified for any positive integer i if φ , τ , and $\theta(s)$ are known, where $\theta(s)$ is a function describing seasonal variation in environmental state. As an ideal tree is dealt, $\sigma_{i+1} \geq \sigma_i + \tau$ for any φ . A tree is regarded as deciduous if that tree experiences a leafless period at least once every year, and as evergreen otherwise (see Discussion for more detail).

The age of the i -th leaf at time s is $t_i = s - \sigma_i$ (Fig. 1). Each leaf is expanded at time σ_i at a cost of construction and photosynthesises until shed, incurring a maintenance cost during this interval. The photosynthetic rate depends on the continuous age of the leaf and the environmental state representing how much the weather is favourable for photosynthesis. Therefore, the net gain earned by the i -th leaf, $\Gamma(\tau, \sigma_i)$, is given by the following equation:

$$\Gamma(\tau, \sigma_i) = -C + \int_{\sigma_i}^{\sigma_i + \tau} (p(t_i)\theta(s) - m(t_i))ds = -C + \int_{\sigma_i}^{\sigma_i + \tau} (p(s - \sigma_i)\theta(s) - m(s - \sigma_i))ds, (1)$$

where C is the construction cost of a new leaf, $p(t)$ is the potential photosynthetic rate of a leaf of age t , and $m(t)$ is the daily maintenance cost for that leaf. We assume that $\theta(s)$ represents the seasonal state at time s ($0 \leq \theta(s) \leq 1$), and that the actual gross photosynthetic rate is decreased to $p(t)\theta(s)$ (the solid line in Fig. 1). We also assume that $\theta(s)$ is a one-year periodic function, rendering it necessary to consider within-year variation only, thus neglecting between-year variation or secular changes in environmental factors. Following Kikuzawa (1991), we set $\sigma_1 = 0$ and define $G(\tau)$ as the net gain of the first leaf [i.e. $G(\tau) = \Gamma(\tau, 0)$].

The objective function requiring maximisation is the net carbon gain of a tree after a sufficiently long time. It is mathematically more convenient to analyse the time-averaged index of this function, a long-term (i.e. over many leaf turnovers) net carbon assimilation rate of a tree, $\chi(\varphi, \tau)$. Our goal is to identify a pair of strategies, $\{\varphi^*, \tau^*\}$, with which $\chi(\varphi, \tau)$ is maximised for a given set of parameters. It is possible to clearly define the long-term rate mentioned above if and only if it is possible to evenly divide a sequential set of leaves into subsets, each of which provides the same subtotal net gain to the tree. In other words, we can formally obtain $\chi(\varphi, \tau)$ if and only if we can find a positive integer $N(\varphi, \tau)$ satisfying the following conditions for any positive integer h (Fig. 2):

$$\sum_{i=(h-1)N+1}^{hN} \Gamma(\tau, \sigma_i) = \sum_{i=1}^N \Gamma(\tau, \sigma_i), \quad (2a)$$

$$\sigma_{hN+1} = h\sigma_{N+1}. \quad (2b)$$

The criterion $\gamma(\varphi, \tau)$ is then given by

$$\gamma(\varphi, \tau) = \frac{\sum_{i=(h-1)N+1}^{hN} \Gamma(\tau, \sigma_i)}{\sigma_{hN+1} - \sigma_{(h-1)N+1}} \equiv \frac{\sum_{i=1}^N \Gamma(\tau, \sigma_i)}{\sigma_{N+1}}. \quad (3)$$

Note that it is usually possible to define σ_{N+1} as the minimum σ_i value that is a positive integer, because the period length of seasonal change is unity and, thus, the $(N + i)$ -th leaf is expected to provide the same net gain as the i -th leaf.

The above method can be used for any forms of the functions $p(t)$, $m(t)$, and $\theta(s)$. In this paper, we hereafter apply the same simple functional forms as what were used in Kikuzawa (1991) in order to examine the pure effect of renewed methodology on the model predictions. Referring to the empirical record indicating that net photosynthetic rate of a leaf is a monotonic decreasing function of age of the leaf (Šesták et al. 1985), Kikuzawa (1991) assumed the simplest linear functions:

$$p(t) = \max\left\{0, a\left(1 - \frac{t}{b}\right)\right\}, \quad (4a)$$

$$m(t) = \max\left\{0, m\left(1 - \frac{t}{b}\right)\right\}, \quad (4b)$$

where $a = p(0)$, $m = m(0)$ ($a > m > 0$), and $b > 0$. The parameter b can be viewed as the potential maximum leaf longevity, and optimal leaf longevity should not be greater than b .

Kikuzawa (1991) also assumed a dichotomous variable reflecting favourable and unfavourable situations for photosynthesis:

$$\theta(s) = \begin{cases} 1 & \text{for } j \leq s < j + f \\ 0 & \text{for } j + f \leq s < j + 1 \end{cases}, \quad (5)$$

where j is any non-negative integer and f is the length of a favourable period within any year ($0 < f \leq 1$). Note that when seasonal state is described in this manner, an individual leaf exhibits the greatest net gain when that leaf is expanded at an integer time point, thus at the beginning of a favourable period. Note also that non-seasonal environments can be analysed by setting $f = 1$. Definitions of parameters are summarised in Table 1.

Before we proceed, we can calculate $G(\tau)$ as

$$G(\tau) = \begin{cases} -C + (a - m)\tau \left(1 - \frac{\tau}{2b}\right) - a(1 - f) \lfloor \tau \rfloor \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right) & \text{for } j \leq \tau < j + f \\ -C - m\tau \left(1 - \frac{\tau}{2b}\right) + af \lceil \tau \rceil \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right) & \text{for } j + f \leq \tau < j + 1 \end{cases}.$$

where $\lfloor \cdot \rfloor$ and $\lceil \cdot \rceil$ denote rounding down and up to the nearest integer, respectively (see Appendix A for the derivation). Use of this equation often helps to reduce the computational effort required to obtain the value of τ by which the value of (3) is maximised (see below).

We formulate the three basic foliation rules defined in a natural manner:

φ_I : The *immediate replacement rule*, under which a tree expands a new leaf immediately after shedding of an existing leaf;

φ_S : The *spring flushing rule*, under which a tree expands a new leaf at the beginning of the favourable period that follows the shedding of an existing leaf;

φ_C : The *combined expansion rule*, under which a tree expands a new leaf immediately after shedding of an existing leaf if the period is favourable, and at the beginning of the next favourable period otherwise.

Fig. 3 contains graphical representations of these rules.

3 Non-seasonal environments

In a non-seasonal environment, i.e. when $f = 1$, we can simplify (1) by substituting

$$\theta(s) = 1:$$

$$\Gamma(\tau, \sigma_i) = -C + \int_{\sigma_i}^{\sigma_i + \tau} (p(s - \sigma_i) - m(s - \sigma_i)) ds = -C + \int_0^{\tau} (p(t) - m(t)) dt. \quad (7)$$

Note that we have replaced s with $\sigma_i + t$. Now, $\Gamma(\tau, \sigma_i)$ does not depend on σ_i or s , that is, the timing of expansion does not affect the carbon gain and every leaf yields the same net gain in non-seasonal environments. It is obvious that trees that do not exhibit any interval between shedding and expansion have the highest net gain. The immediate replacement

199 rule, φ_1 , yields

$$200 \quad \sigma_i(\varphi_1, \tau) = (i-1)\tau \quad (8)$$

201 for any positive integer i . It is easy to show that $N(\varphi_1, \tau) = 1$ fulfils condition (2) when

202 $f = 1$, and thus we obtain

$$203 \quad \gamma(\varphi_1, \tau) = \frac{\Gamma(\tau, \sigma_1)}{\sigma_2} = \frac{G(\tau)}{\tau}. \quad (9)$$

204 The term on the extreme right of (9) is exactly what was defined as $g(\tau)$ by Kikuzawa
205 (1991) and has been used to estimate optimal leaf longevity in all environments in terms
206 of photosynthetic efficiency.

207 Obviously, $\gamma(\varphi_1, \tau) \geq \gamma(\varphi, \tau)$ for any τ and φ , (i.e. $\varphi^* = \varphi_1$), and all that is
208 necessary is to calculate optimal leaf longevity, τ^* . Substituting $f = 1$ into (6) yields

$$209 \quad G(\tau) = -C + (a - m)\tau \left(1 - \frac{\tau}{2b}\right). \quad (10)$$

210 By solving $d\gamma/d\tau = 0$ for τ , we formally obtain $\tau^* = t^\dagger$, where

$$211 \quad t^\dagger = \sqrt{\frac{2bC}{a-m}}. \quad (11)$$

212 This result is again the same as that derived by Kikuzawa (1991). The implication that
213 leaf longevity would be extended when b or C is larger and $a - m$ smaller is qualitatively
214 consistent with empirical records not only from non-seasonal or tropical environments
215 but also from various ecosystems worldwide (reviewed in Kikuzawa et al. 2013).

216 In addition, it is possible to show that $t^\dagger < b$ is equivalent to $G(b) > 0$. The latter

inequality is a necessary condition for each leaf to contribute a positive net gain of a tree. This means that, in non-seasonal environments, trees must shed their leaves before those leaves lose all photosynthetic capacity.

4 Two-seasonal environments

In two-seasonal environments, trees exhibiting appropriate intervals between shedding and flushing may attain a larger net carbon gain than do trees without such intervals (φ_1). Here, we define a deciduous tree as a tree that has leafless periods at least once a year, whereas all other trees are defined as evergreens (this concept is expanded in Fig. 3 and the caption thereof). Thus, a tree with $\tau \geq 1$ is also evergreen regardless of its foliation rule. On the other hand, a tree with $\tau < 1$ is not always deciduous, in which case interaction of the foliation rule and environmental parameter determines whether that tree is deciduous or evergreen. For example, a tree with φ_C and $\tau = 1 / 2$ is deciduous if $f < 1 / 2$ and evergreen otherwise.

For each of the three examined foliation rules, we derive the long-term increase rates [$\chi(\varphi_1, \tau)$, $\chi(\varphi_S, \tau)$, and $\chi(\varphi_C, \tau)$; respectively] either analytically or numerically and determine the leaf longevity that maximises these increase rates (τ_1 , τ_S , and τ_C ,

respectively). Next we compare the values of $\chi(\varphi_1, \tau_1)$, $\chi(\varphi_S, \tau_S)$, and $\chi(\varphi_C, \tau_C)$. Note that, in two-seasonal environments, it is not generally the case that $\chi(\varphi_1, \tau)$ takes the same form as derived by Kikuzawa (1991); thus, $g(\tau)$ is not always in play. In Appendix B, we describe the mathematical consequences of direct application of $g(\tau)$ in two-seasonal environments.

To estimate optimal leaf longevity numerically, τ_X , under a particular foliation rule φ_X and particular values of the parameters $\{C, a, m, b, f\}$, we ran numerical computations in the absence of rounding errors using *Mathematica 8* (Wolfram Research, Inc.). Specifically, we calculated values of $\chi(\varphi_X, \tau)$ for various values of τ , ranging from $\Delta\tau$ to b and uniformly distributed at intervals of $\Delta\tau$ ($\Delta\tau$ equal to $1 / 300$, thus about a day). Of these τ values, that for which $\chi(\varphi_X, \tau)$ was largest was taken to be τ_X .

4.1 The immediate replacement rule

Trees following the immediate replacement rule, φ_1 (Fig. 3a), are always evergreen. Although (8) holds for any f , (9) is not usually derived when $f < 1$ because different leaves expanding in different seasons afford different net gains. Moreover, it is only when $f = 1$ that we can define $\chi(\varphi_1, \tau)$ for irrational values of τ . On the other hand, for any rational number $\tau = j / k$, where j and k are positive integers, we have $N(\varphi_1, \tau) = k$ and $\sigma_{N+1} = j$,

251 and thus

$$252 \quad \gamma(\varphi_1, \tau) = \frac{\sum_{i=1}^k \Gamma(\tau, (i-1)\tau)}{j}, \quad (12)$$

253 which is the average rate of carbon gain by k leaves during j years. When a positive

254 integer is substituted into τ (thus $j = \tau$ and $k = 1$), (12) takes exactly the same form as (9).

255 In that case, we can derive an analytical expression by applying (6):

$$256 \quad \gamma(\varphi_1, \tau \in \mathbf{N}) = -\frac{C}{\tau} + (af - m) \left(1 - \frac{\tau}{2b} \right) + \frac{af(1-f)}{2b}. \quad (13)$$

257 When $af - m < 0$, (13) monotonically increases with increasing τ and takes a greater

258 value at $\tau = \lfloor b \rfloor$ than at other integer values of τ . Therefore, although $\tau = \lfloor b \rfloor$ may or may

259 not be the τ_1 value, other integers are excluded as candidates for election as τ_1 . When

260 $af - m > 0$, (13) attains the maximum value at one or two integers satisfying

$$261 \quad \sqrt{(t^\ddagger)^2 + \frac{1}{4}} - \frac{1}{2} \leq \tau \leq \sqrt{(t^\ddagger)^2 + \frac{1}{4}} + \frac{1}{2}, \quad (14)$$

262 where

$$263 \quad t^\ddagger = \sqrt{\frac{2bC}{af - m}}. \quad (15)$$

264 See Appendix C for details. The τ values described above may be τ_1 , and other integers

265 are excluded as candidates for τ_1 . Note that $t^\ddagger = t^\dagger$ if $f = 1$ and that the dependencies of $t^\ddagger$

266 on parameters other than f are identical to those of $t^\dagger$. In addition, $t^\ddagger$ monotonically

increases with a decrease in f . This reveals a monotonic trend to the effect that the leaf longevity of evergreen trees is longer in colder zones (i.e. those with smaller f values) than in warmer or more humid zones (i.e. with larger f values).

The results of our numerical simulations, shown in Fig. 4a, suggest that the function $\lambda(\phi, \tau)$ exhibits spike-like peaks when k (the denominator of the rational number τ) is small. This is because trees with smaller k values more frequently synchronise flushing seasons with the beginning of a favourable period (note that a leaf provides the largest net carbon gain when it is expanded at the beginning of a favourable period). Consequently, τ has a small k value ($\tau = 2$ yields $k = 1$ in the example of Fig. 4a). Our comprehensive numerical simulations conducted within realistic parameter ranges (i.e. $3 \leq C \leq 18$, $20 \leq a \leq 100$, $2 \leq m \leq 18$, $1 \leq b \leq 12$, and $0 < f < 1$; the same ranges as used by Kikuzawa [1991]; carbon unit is arbitrary and time unit is year) revealed that an integer τ ($k = 1$) was most frequently chosen as a component of numerically estimated τ values, and no τ value was associated with a k value greater than 4. In addition, τ monotonically decreased with increasing f when parameters other than f were fixed, as suggested by (14) and (15). Moreover, our numerical analysis suggests that the negative dependency of τ on f holds true even when the set of τ s contains non-integer elements (e.g. τ shown in Fig. 5a is decreased from 2 to $5/3$ as f is increased).

4.2 The spring flushing rule

Trees subject to the spring flushing rule, φ_s (Fig. 3b), are regarded as deciduous if $\tau < 1$ and evergreen otherwise. When this rule applies, the following holds for any τ :

$$\sigma_i(\varphi_s, \tau) = (i-1) \lceil \tau \rceil. \quad (16)$$

This rule seems to be what Kikuzawa (1991) had in mind. However, the value of locally optimal leaf longevity, τ_s , appropriately derived using $\gamma(\varphi_s, \tau)$, is sometimes one-year longer than that derived using Kikuzawa's (1991) index, $g(\tau)$.

The criterion $\gamma(\varphi_s, \tau)$ can be defined for any real number τ , where $N(\varphi_s, \tau) = 1$ and $\sigma_2 = \lceil \tau \rceil$:

$$\gamma(\varphi_s, \tau) = \frac{G(\tau)}{\lceil \tau \rceil}. \quad (17)$$

Because the denominator of the right-hand side of (17) does not change within the range $j < \tau < j+1$, we can easily show that, with increasing τ , $\gamma(\varphi_s, \tau)$ increases within the ranges $j < \tau < j+f$ (during which interval a leaf produces more carbon than that leaf consumes) and decreases within the ranges $j+f < \tau < j+1$ (during which interval a leaf produces no carbon). Hence, $\gamma(\varphi_s, \tau)$ has a local maximum at $\tau = j+f$ for each $j = 0, 1, 2, \dots$. All that is required is to choose τ_s from the candidates thus defined (and $\tau = b$ in the case of $j < b < j+f$).

Substituting $\tau = j+f (\leq b)$ into (6) and (17) yields

$$\gamma(\varphi_s, j + f) = -\frac{C}{j+1} + \left(1 - \frac{j+f}{2b}\right) \left(af - \frac{j+f}{j+1}m\right). \quad (18)$$

Suppose, for a moment, that j is any real value between 0 and $b - f$. Then, (18) is a continuous function of j . It is possible to show, by solving $d\gamma(\varphi_s, j + f) / dj = 0$, that (18) is maximised at $j = j^\dagger$, where

$$j^\dagger = -1 + \sqrt{\frac{2bC - (1-f)(2b+1-f)m}{af - m}}, \quad (19)$$

given that

$$2bC - (1-f)(2b+1-f)m \geq af - m > 0. \quad (20)$$

Otherwise, $\gamma(\varphi_s, j + f)$ is maximised either at $j = 0$ or at $j = b - f$. Considering the case where (20) holds, it can be seen from (19) that the locally optimal leaf longevity, τ_s , which is either $\lfloor j^\dagger \rfloor + f$ or $\lceil j^\dagger \rceil + f$, increases discretely with increasing values of C and b , and decreases as a increases. The effect of m on (19) depends on the values of the other parameters.

Figs. 4b and 5b show the results of numerical computations. The figures illustrate the dependencies of $\gamma(\varphi_s, \tau)$ on τ , and τ_s on f , respectively. The former dependency yields the analytical result that $\gamma(\varphi_s, \tau)$ has peaks at $\tau = j + f$. The latter example shows that the dependency of τ_s on f is twofold. On a local scale, τ_s continuously increases with increasing f . On a global scale, however, τ_s discretely decreases with

320 increasing f because of a decrease in $j^\dagger$.

321 **4.3 The combined expansion rule**

322 The combined expansion rule, φ_C (Fig. 3c), is a combination of φ_1 and φ_S . The rule is
 323 identical to φ_1 when $f = 1$. Meanwhile, if longevity satisfying $j + f \leq \tau \leq j + 1$ is given,
 324 trees subject to this rule exhibit exactly the same behaviour as do trees operating under
 325 rule φ_S . In the other cases, however, this rule leads to a unique life history. For any real
 326 positive τ , n is defined as the smallest integer satisfying

$$327 \quad \lceil n\tau \rceil - n\tau \leq 1 - f, \quad (21)$$

328 and we have

$$329 \quad N(\varphi_C, \tau) = n, \quad (22a)$$

$$330 \quad \sigma_{hn+l}(\varphi_C, \tau) = h\lceil n\tau \rceil + (l-1)\tau, \quad (22b)$$

331 for any non-negative integers h and l . Trees subject to this rule are regarded as deciduous
 332 if $n\tau < 1$ and evergreen otherwise.

333 Substituting (22) into (3), we obtain

$$334 \quad \gamma(\varphi_C, \tau) = \frac{\sum_{i=1}^n \Gamma(\tau, (i-1)\tau)}{\lceil n\tau \rceil}. \quad (23)$$

335 For deciduous trees subject to φ_C (i.e. $n\tau < 1$), the analytical results described in

Appendix D can be derived. In short, the only candidate for τ_c among the possible τ values is $\tau = f / Q^\dagger$, where $Q^\dagger$ is an integer satisfying

$$\sqrt{\left(\frac{f}{t^\dagger}\right)^2 + \frac{1}{4}} - \frac{1}{2} \leq Q^\dagger \leq \sqrt{\left(\frac{f}{t^\dagger}\right)^2 + \frac{1}{4}} + \frac{1}{2}. \quad (24)$$

In other words, a deciduous tree subject to this foliation rule maximises its long-term carbon gain when it uses up $Q^\dagger$ leaves during each favourable season. Using (24), we can show that the dependencies of the candidate for τ_c , $f / Q^\dagger$, on parameters other than f are the same as those of $t^\dagger$.

Figs. 4c and 5c show the dependency of $\gamma(\varphi_c, \tau)$ on τ and the dependency of τ_c on f , respectively, obtained by numerical simulations. In our comprehensive numerical analyses, τ_c always took the form $\tau_c = (j + f) / k$, where j was a non-negative integer and k a positive integer not larger than 3. Instances where $k = 1$ were most frequently observed. The outcome of the above analytical work, $\tau = f / Q^\dagger$, is a special form of $(j + f) / k$. Indeed, when $j = 0$ was selected in our numerical analysis, k was always equal to $Q^\dagger$.

See also the dotted lines in Figs. 4c and 5c, which are copies of the outcomes when the φ_l or φ_s rules are applied, as plotted in Figs. 4a, 4b, 5a, and 5b. The figures show that, when $f < 1$, the following relationships hold for any non-negative integer j :

$$\gamma(\varphi_l, j + 1) = \gamma(\varphi_s, j + 1) = \gamma(\varphi_c, j + 1) < \gamma(\varphi_s, j + f) = \gamma(\varphi_c, j + f). \quad (25)$$

353 These relationships can be easily derived analytically upon consideration of the
 354 definitions of the foliation rules. Specifically, it is obvious that trees operating under φ_i ,
 355 φ_S , and φ_C constraints exhibit exactly the same behaviour for any integer τ . In other words,
 356 such trees shed an existing leaf and expand a new leaf at the beginning of a favourable
 357 season when the leaf longevity value is an integer. In addition, trees operating under φ_S
 358 and φ_C rules exhibit exactly the same behaviour for $\tau = j + f$, waiting for the beginning of
 359 a favourable season to expand a new leaf after shedding an existing leaf at the end of the
 360 previous favourable season.

361 In light of the above results, the followings hold:

- 362 i) Neither τ_S nor τ_C can be an integer;
- 363 ii) When τ_i takes an integer value, (φ_i, τ_i) is not the optimal strategy because it is always
 364 inferior (in terms of carbon economy) to (φ_S, τ_S) and (φ_C, τ_C) ,
- 365 iii) When τ_S takes the form $j + f$, (φ_C, τ_C) is not inferior to (φ_S, τ_S) , and,
- 366 iv) When $\tau_S = b$, (φ_S, τ_S) may or may not be superior to (φ_C, τ_C) .

367 Furthermore, the numerical results that we obtained indicate that τ_i is very likely to be an
 368 integer value (Fig. 5a) and τ_S is rarely equal to b because it occurs only when
 369 $\chi(\varphi_S, \lfloor b \rfloor - 1 + f) < \chi(\varphi_S, b)$. Summarising the above results, we can usually expect
 370 (φ_C, τ_C) to be the optimal strategy.

371

372 **5 Discussions**

373 In this paper, we show that use of the index proposed by Kikuzawa (1991) does not
374 provide the maximum achievable lifelong net carbon gain when the period unfavourable
375 for photosynthesis is encountered by a tree during a year. We have derived a
376 mathematically rigorous and more general method that allows calculation of optimal leaf
377 longevity for an ideal tree, and next applied simple linear and step functions to calculate
378 leaf productivity and seasonal state, respectively, following Kikuzawa (1991). The model
379 outcomes are in good agreement with the results of empirical studies. For example, the
380 model predicted that each leaf lives longer if leaf construction cost is high and shorter if
381 the initial photosynthetic rate is high, which is indeed observed empirically. In addition,
382 our new methodology allowed comparison among life history strategies for foliation
383 timing, which Kikuzawa (1991) did not considered. Results of our analyses suggested
384 that life history of expanding new leaves at the beginning of spring yields higher carbon
385 gain than life history of replacing discarded leaves by new leaves immediately.

386 The most contentious feature of the present study may be the use of an ideal tree,
387 which is assumed to retain at most one leaf at a time. This one leaf is the so-called big-leaf

and may be interpreted as an aggregate of all leaves on the tree. Then, one may be of the view that the big-leaf assumption is an acceptable simplification of a deciduous tree showing flush-type leaf-emergence but not an evergreen tree because the latter tree has leaves of different ages present at any one time. In some cases, however, we may regard a real individual tree as an aggregate of multiple shoot groups in each of which only the uppermost shoot has leaves of the same age and lower shoots have no leaves. A newly-emerged shoot can join the group as the new uppermost shoot, in which case the previous uppermost shoot will sooner shed its leaves due to avoidance of self-shading and may transport its resources to the uppermost shoot of the same or another group. An ideal tree and the big-leaf in the present model then correspond to each one of the shoot groups and an aggregate of leaves of the single leafy shoot of each group, respectively. It follows that an evergreen tree consisting of x shoot groups can retain up to x leafy shoot of different age classes (Figs. 3 and 6).

The effect of the length of a favourable period, during which leaves are assumed to photosynthesise, on optimal leaf longevity depends on the foliation strategy of the tree. When discarded leaves are replaced immediately by new leaves, the results of analytical and numerical computations suggest that the optimal leaf longevity is shorter when the period favourable for photosynthesis is longer. When new leaves are expanded only at the

beginning of a favourable period, optimal leaf longevity also becomes shorter if the favourable period lengthens greatly (as in a comparison of subtropical and subarctic species). However, it becomes longer when the favourable period lengthens slightly (as in a comparison of species of the same climatic zone) because a tree benefits from retention of existing leaves at the end of the current favourable season. It follows that the leaf longevity of deciduous trees following the spring flushing rule increases with increasing length of the favourable period. The result agrees with those of Kikuzawa et al. (2013), who showed, by reference to empirical records, that the leaf longevities of deciduous and evergreen trees become longer and shorter, respectively, as the favourable period becomes longer (see also Xiao 2003 and Reich 2014).

We also tested a more sophisticated yet surely possible foliation rule: new leaves are expanded immediately after existing leaves are shed if shedding occurs within a favourable period and at the beginning of the next favourable season otherwise. Under this rule, trees may expand their leaves more than once a year (Fig. 3c), which is more likely to be possible when the favourable period is longer (Fig. 5c). That may explain the multiple (three times a year) flushing of evergreen *Eurya japonica* trees found in subtropical zones (Nitta and Ohsawa 1997). Such a life history is shown in Fig. 6, within the framework of the present model. Numerical analysis revealed that application of this

combined expansion rule usually yielded the highest net carbon gain of a tree's lifetime. However, when f was not very large, the combined expansion rule yielded exactly the same life history as what the spring-flushing rule yielded (Fig. 5). Therefore, the model predicts that multiple flushing occurs only in the restricted regions in subtropical zones. This may be the cause of non-prevalence of multiple-flushing life history. Use of the original model of Kikuzawa (1991) never yielded this type of optimal solution under seasonal environments. This is because Kikuzawa's (1991) optimisation method itself implicitly assumes that trees operate under the spring flushing rule in two-seasonal environments. The present study clarifies the importance of considering leaf longevity as part of the complex lifetime of a plant, thus also emphasising the necessity of choosing an appropriate foliation rule.

We have developed, in the first part of the present analyses, the general method for obtaining optimal leaf longevity. Using the same method, we can further analyse new problems detected in the latter part of our analyses because most of those problems are attributed to application of the simplest linear and binary functions proposed by Kikuzawa (1991) to physiological and environmental, respectively, states (eqs. (4) and (5), respectively; but see also Kitajima et al. 1997). One of the problems is that we have not found the parameter range within which a tree subject to the immediate replacement

rule earns a larger carbon gain than does a tree subject to the spring flushing rule. It follows that, from the viewpoint of the carbon economy, no species should adopt the immediate replacement rule, but the rule is in fact adopted by many non-tropical broadleaf evergreen species. Obviously, this situation arises because we used a binary function to represent seasonal state, assuming that trees do not photosynthesise at all during an unfavourable season. If we alternatively assume a slowly varying periodic function to represent the seasonal state, the immediate replacement rule may be the best strategy to be employed under certain circumstances. For example, Takada et al. (2006) applied a temperature-dependent periodic function to explore how leaf longevity is affected by average air temperature and annual amplitude of temperature. Reanalysing Takada et al. (2006) by the present general method allows us to obtain optimal leaf longevity in more realistic environments, with consideration of climatic features such as temperature or rainfall.

A clear shortage of the present model is that effect of competition among trees has not been incorporated into it. The theory of an evolutionarily stable strategy (ESS; Maynard Smith and Price 1973) considers that natural selection does not always maximise individual fitness and that an evolutionarily converged strategy depends on the individual strategies of mutants that may possibly invade populations (Anten 2002). In

terms of the carbon economy, trees are thought to compete for sunlight. Evolutionarily stable leaf longevity would be affected by shading effect of neighbouring trees (Sakai 1992; see also Givnish 2002). Further works considering the effect of the competition are required.

In short, we extended the mathematical model derived by Kikuzawa (1991) and developed a new approach using both the timing of leaf expansion and shedding to derive an appropriate measure of optimal leaf longevity. The outcomes of our model are more in line with empirical records than outcomes derived using Kikuzawa's model (1991).

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Appendix A: Derivation of net gain afforded by the first leaf

The gain afforded by the first leaf, the continuous age of which is equal to the absolute

time, is

$$G(\tau) = -C + \int_0^\tau (p(s)\theta(s) - m(s))ds. \quad (A1)$$

Substituting (4) into (A1) and applying (5), we obtain

$$G(\tau) = -C + (a - m)\tau \left(1 - \frac{\tau}{2b}\right) - a \int_0^\tau (1 - \theta(s)) \left(1 - \frac{s}{b}\right) ds. \quad (A2)$$

Note that the third (negative) term on the right-hand side of (A2), which we henceforth describe as the loss term, represents the carbon gain that the first leaf would have earned if no unfavourable period existed.

If $j \leq \tau < j + f$, where j is any non-negative integer and thus $j = \lfloor \tau \rfloor$, the first leaf experiences a total of $\lfloor \tau \rfloor$ unfavourable intervals. Except the case of $0 \leq \tau < f$ and thus $j = 0$, the loss term is calculated as

$$a \sum_{i=1}^{\lfloor \tau \rfloor} \left[\int_{i-1+f}^i \left(1 - \frac{s}{b}\right) ds \right] = a(1-f) \sum_{i=1}^{\lfloor \tau \rfloor} \left(1 + \frac{1-f}{2b} - \frac{i}{b}\right) = a(1-f) \lfloor \tau \rfloor \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right). \quad (A3)$$

If $0 \leq \tau < f$, the loss term is obviously zero, and thus the term on the extreme right of (A3) holds for this case. Consequently, we have

$$G(\tau) = -C + (a - m)\tau \left(1 - \frac{\tau}{2b}\right) - a(1-f) \lfloor \tau \rfloor \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right). \quad (A4)$$

If $j + f \leq \tau < j + 1$, where j is any non-negative integer, the first leaf further experiences a part of an unfavourable period at the end of its life (i.e. from $j + f$ to τ). The carbon gain that the first leaf earns during this period is

$$a \int_{\lfloor \tau \rfloor + f}^{\tau} \left(1 - \frac{s}{b}\right) ds = a \left[\tau \left(1 - \frac{\tau}{2b}\right) - (\lfloor \tau \rfloor + f) \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right) \right]. \quad (\text{A5})$$

As the loss term can be calculated as the sum of (A3) and (A5), we may show (A4) minus (A5) as

$$\begin{aligned} G(\tau) &= -C - m\tau \left(1 - \frac{\tau}{2b}\right) + af(\lfloor \tau \rfloor + 1) \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right) \\ &= -C - m\tau \left(1 - \frac{\tau}{2b}\right) + af \lceil \tau \rceil \left(1 - \frac{\lfloor \tau \rfloor + f}{2b}\right). \end{aligned} \quad (\text{A6})$$

Appendix B: Analytical Results for Kikuzawa's Criterion

It can be shown, by substituting (6) into $g(\tau)$, that if $g(\tau)$ has at least one positive part, the parameter attains a maximum value at either one of the following two forms of τ : $\tau = j + f$ and $\tau = t^*$ ($j \leq t^* < j + f$), where j represents a non-negative integer and

$$t^* = \sqrt{\frac{2b}{a-m} \left[C + a(1-f)j \left(1 - \frac{j+f}{2b}\right) \right]}. \quad (\text{B1})$$

To obtain (B1), we use $\lfloor \tau \rfloor = j$ and $dg(\tau)/d\tau = 0$. Note that $1 - (j+f)/(2b)$ in (B1) is always positive because $2b > j+f$. Kikuzawa (1991) argued that, when $g(\tau)$ is maximised at a point other than $\tau = j + f$, which we have shown is definitely $\tau = t^*$, the truly optimal leaf longevity would be located near that point. For example, if t^* is close to $j + f$, the

ultimate leaf longevity would be $j + f$ and the tree should expand the second leaf at the beginning of the next favourable season (i.e. at $s = j + 1$). In other words, Kikuzawa (1991) indeed noted that it was not always possible to measure the optimal leaf longevity in a two-seasonal environment by simply maximising the criterion $g(\tau)$. We have shown that this statement holds true even when $g(\tau)$ is maximised at $\tau = j + f$.

Appendix C: Locally optimal leaf longevity of trees that replace leaves at the beginning of a favourable season

In this appendix, we obtain an integer by use of which the discrete function (13) is maximised when $af - m > 0$. Let us first consider (13) to be a continuous function of the real number τ . By solving $d\chi(\varphi, \tau) / d\tau = 0$ for τ , we can show that the continuous function attains a maximum point at $\tau = t^\ddagger$, where $t^\ddagger$ is defined as (15). It follows that the original discrete function (13) assumes a maximum value at either $\tau = \lfloor t^\ddagger \rfloor$ or $\tau = \lceil t^\ddagger \rceil$.

When $t^\ddagger \geq 1$, we can simplify the condition $\chi(\varphi, \lfloor t^\ddagger \rfloor) \geq \chi(\varphi, \lceil t^\ddagger \rceil)$ as

$$\chi(\varphi, \lfloor t^\ddagger \rfloor) \geq \chi(\varphi, \lceil t^\ddagger \rceil) \Leftrightarrow -\frac{C}{\lfloor t^\ddagger \rfloor} + \frac{(af - m)\lfloor t^\ddagger \rfloor}{2b} \geq -\frac{C}{\lceil t^\ddagger \rceil} + \frac{(af - m)\lceil t^\ddagger \rceil}{2b} \Leftrightarrow t^\ddagger \leq \sqrt{\lfloor t^\ddagger \rfloor \lceil t^\ddagger \rceil},$$

(C1)

and vice versa.

526 In conclusion, the optimal integer leaf longevity for trees subject to the
 527 immediate replacement rule (φ_I) is $\lfloor t^* \rfloor$ if (C1) holds and $\lceil t^* \rceil$ otherwise, which can be also
 528 expressed as (14).

529

530 **Appendix D: Locally optimal leaf longevity of deciduous trees** 531 **subject to the combined expansion rule**

532 This appendix focuses on deciduous trees subject to the combined expansion rule (φ_C),
 533 and our argument has two parts. First, we show that leaf longevity written as $\tau = f / Q$
 534 yields the largest total net gain within the range of

$$535 \quad \frac{f}{Q} \leq \tau < \min \left\{ \frac{f}{Q-1}, \frac{1}{Q} \right\}. \quad (\text{D1})$$

536 for any positive integer Q . In the second part, we identify the value of Q by which the total
 537 net gain is maximised. In this two-step manner, we obtain a locally optimal leaf longevity
 538 for a deciduous tree subject to the φ_C rule. We exclude other values of τ associated with a
 539 deciduous character from consideration as the chosen value of τ_C .

540 Consider a tree expanding Q leaves during a favourable period and shedding the
 541 Q -th leaf at a certain time during the following unfavourable period. In other words,
 542 consider a τ value satisfying $(Q-1)\tau < f \leq Q\tau < 1$, which is identical to (D1). By

definition, the tree is deciduous, and $N(\varphi_C, \tau) = Q$ holds true. Using (23), $\gamma(\varphi_C, \tau)$ within

the range (D1) is calculated as

$$\gamma(\varphi_C, \tau) = -QC + (Q-1) \int_0^\tau (a-m) \left(1 - \frac{t}{b}\right) dt + \int_0^{f-(Q-1)\tau} a \left(1 - \frac{t}{b}\right) dt - \int_0^\tau m \left(1 - \frac{t}{b}\right) dt.$$

(D2)

The first term on the right-hand side of (D2) represents construction cost of Q leaves. The

second term represents the net gain earned by the first $Q - 1$ leaves. The third and fourth

terms represent the gain by the Q -th leaf during the remaining favourable period and the

maintenance cost of the Q -th leaf, respectively. Differentiating (D2) with respect to τ

yields

$$\frac{d}{d\tau} \gamma(\varphi_C, \tau) = -(Q-1) \left(Q\tau - f \right) \frac{a}{b} - Qm \left(1 - \frac{\tau}{b} \right).$$

(D3)

As (D3) is always non-positive, (D2) is maximised at $\tau = f / Q$.

Substituting $\tau = f / Q$ into (D2) yields

$$\gamma(\varphi_C, \frac{f}{Q}) = -QC + (a-m)f \left(1 - \frac{f}{2bQ} \right).$$

(D4)

Next, let us replace Q of (D4) with a continuous variable, q , and differentiate it with

respect to q :

$$\frac{d}{dq} \left[-qC + (a-m)f \left(1 - \frac{f}{2bq} \right) \right] = -C + \frac{(a-m)f^2}{2bq^2} = -\frac{C}{q^2} (q + q^\dagger) (q - q^\dagger),$$

(D5)

where $q^\dagger$ is defined as

$$t^\dagger = \frac{f}{q^\dagger} \Leftrightarrow q^\dagger = \frac{f}{t^\dagger} = f \sqrt{\frac{a-m}{2bC}}. \quad (\text{D6})$$

Therefore, the continuous function of q attains a maximum value at $q = q^\dagger$. It follows that the original discrete function (D4) takes a maximum value either at $Q = \lfloor q^\dagger \rfloor$ or at $Q = \lceil q^\dagger \rceil$. When $q^\dagger \geq 1$, we can simplify the condition $\chi(\varphi_C, f / \lfloor q^\dagger \rfloor) \geq \chi(\varphi_C, f / \lceil q^\dagger \rceil)$ to

$$q^\dagger \leq \sqrt{\lfloor q^\dagger \rfloor \lceil q^\dagger \rceil}, \quad (\text{D7})$$

and vice versa.

In conclusion, the optimal leaf longevity for deciduous trees subject to φ_C is

$f / Q^\dagger$, where $Q^\dagger = \lfloor q^\dagger \rfloor$ if (D7) holds and $Q^\dagger = \lceil q^\dagger \rceil$ otherwise, as shown in (24).

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Figure captions

Fig. 1 Reduction in photosynthetic rate caused by ageing and variation in the seasonal environment. The age of the i -th leaf at time s is $t_i = s - \sigma_i$. The potential photosynthetic rate decreases with age (broken line). In this example, $a = 20$, $b = 3$, and $\theta(s) = 1$ for $j < s < j + f$ and $\theta(s) = 0$ otherwise, where $f = 0.6$. The actual photosynthetic rate is decreased to $p(t)\theta(s)$ (solid line). (a) $\sigma_i = j$ and (b) $\sigma_i = j + 0.5$. When $\tau = 2.2$, the gain (shaded area) is 18.8 for (a), and 15.6 for (b)

Fig. 2 Sequential leaf expansion and shedding. The grey zone near the bottom line represents the leafless period, determined by the foliation rule (φ). The period between 0 and σ_{hN+1} is divided into h subsets so that the subtotal net gain within any subset is the same

Fig. 3 Graphical representation of the three foliation rules derived in the present study. We set $f = 1/2$ and $\tau = 4/3$. The filled arrows indicate the leafless periods of each ideal tree, determined by the foliation rule (φ). For each of the three rules, we show two ideal trees, which correspond to different parts of an actual tree. One ideal tree expands its first leaf at time $s = 0$ and the other at time $s = 1$. (a) Under the immediate replacement rule (φ), no leafless period exists. In total, 3 (k) leaves

grow over 4 (j) years. (b) Under the spring flushing rule (φ_s), $4/3$ years of leafiness alternate with $2/3$ years of leaflessness. When an actual tree consists of the two ideal trees plotted above, no overall leafless period is evident. (c) Under the combined expansion rule (φ_c), $8/3$ years of leafiness alternate with $1/3$ years of leaflessness. Two leaves are present during a leafy period. When an actual tree consists of the two shoot groups each of which corresponds to an ideal tree plotted above, no overall leafless period is evident

Fig. 4 Examples of the dependencies of long-term rates of increase in net carbon gain of trees subject to (a) the immediate replacement rule, (b) the spring flushing rule, and, (c) the combined expansion rule on τ . Discrete points were obtained at intervals of $\Delta\tau = 1/300$ and joined. Dotted lines in (c) are duplications of (a) and (b). The values of the other relevant parameters were $C = 10.5$, $a = 60$, $m = 10$, $b = 6.5$, and $f = 0.7$

Fig. 5 Examples of the dependencies of locally optimal leaf longevities of trees subject to (a) the immediate replacement rule, (b) the spring flushing rule, and, (c) the combined expansion rule on f . Discrete points were obtained from numerical computations conducted at an accuracy of $\Delta\tau = 1/300$ and joined. The dotted lines in (c) are duplications of (a) and (b). A large part of the dotted line from (b) is

hidden behind the solid line, meaning that the spring flushing rule and the combined expansion rule yield the same locally optimal leaf longevity within that range of f . The values of the other relevant parameters were $C = 10.5$, $a = 60$, $m = 10$, and $b = 6.5$

Fig. 6 Illustration of multiple flushing in *Eurya japonica*. We chose an f value of 0.78, estimated from the data of Nitta and Ohsawa (1997), and set $\tau = (7 + f)/3 = 2.59$. Under the combined expansion rule (φ_c), and given that an actual tree consists of three shoot groups each of which corresponds to an ideal tree that expand their first leaves at $s = 0, 2$, and 5 , an actual tree expands three leaves at different times during the 10th year

Fig. 1

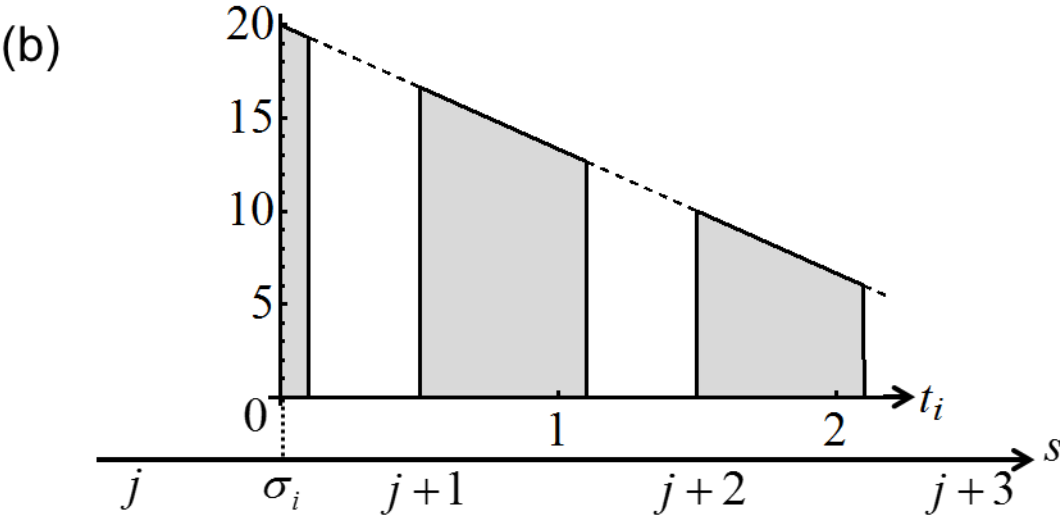
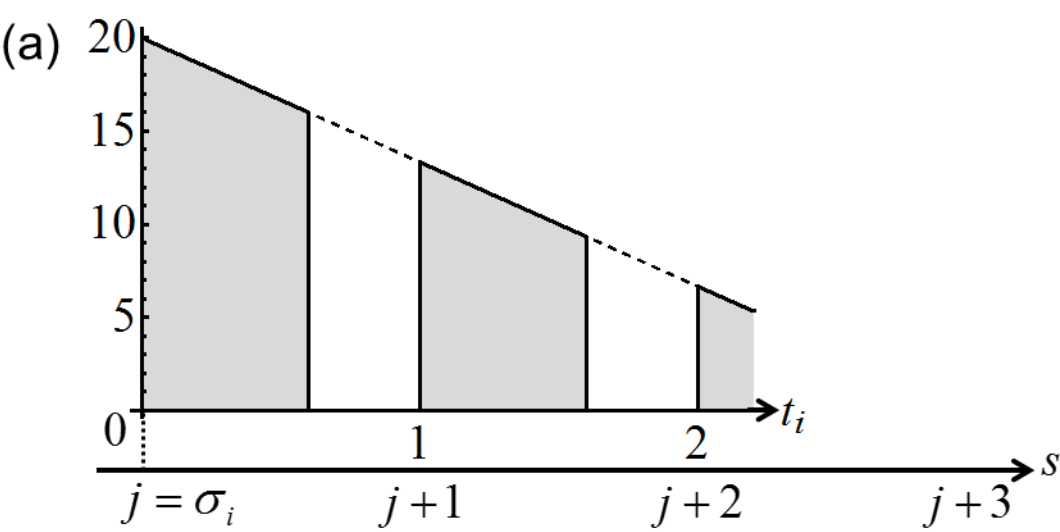


Fig. 2

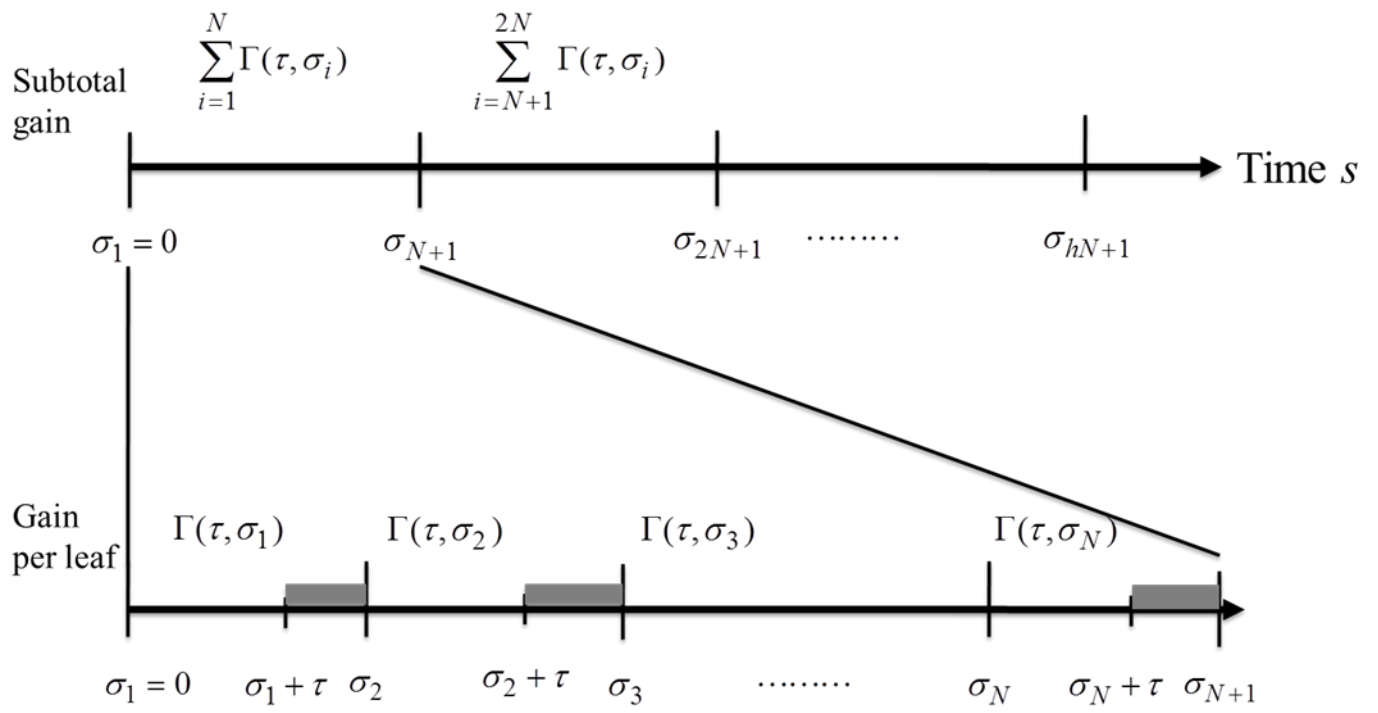
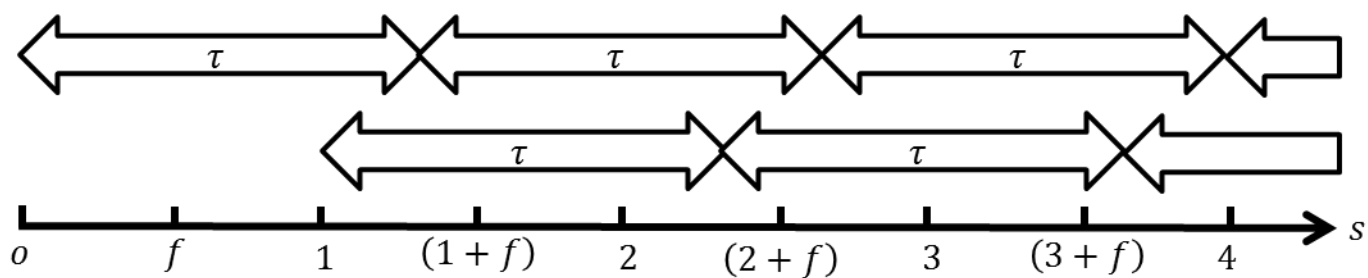
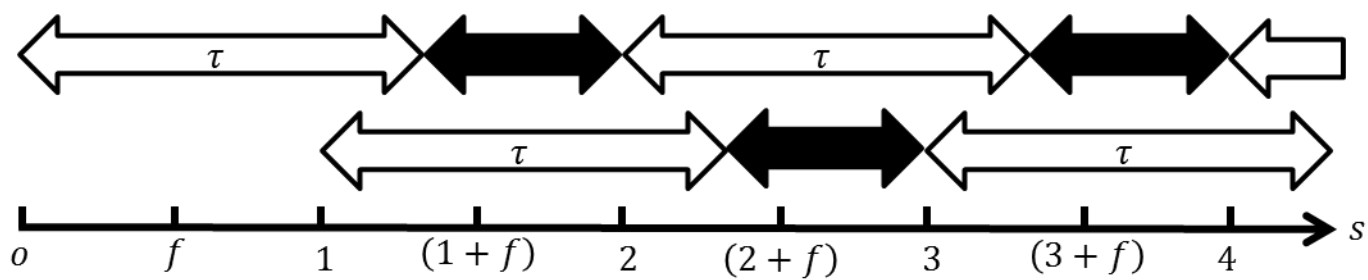


Fig. 3

(a)



(b)



(c)

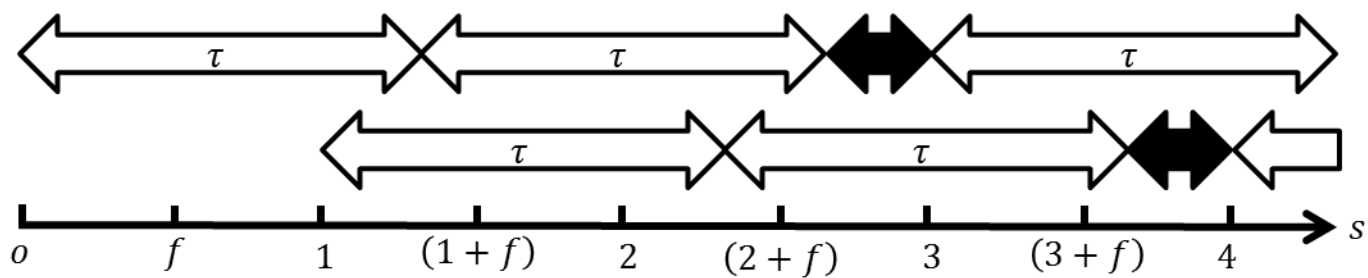


Fig. 4

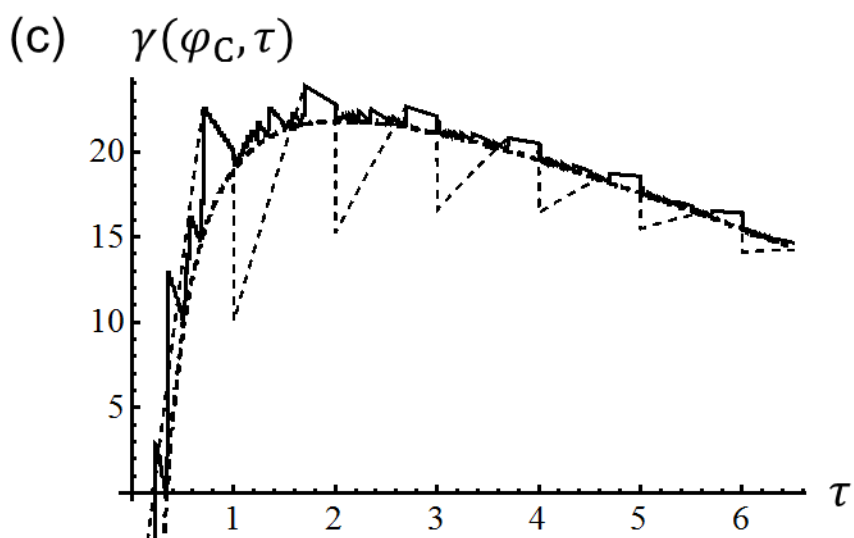
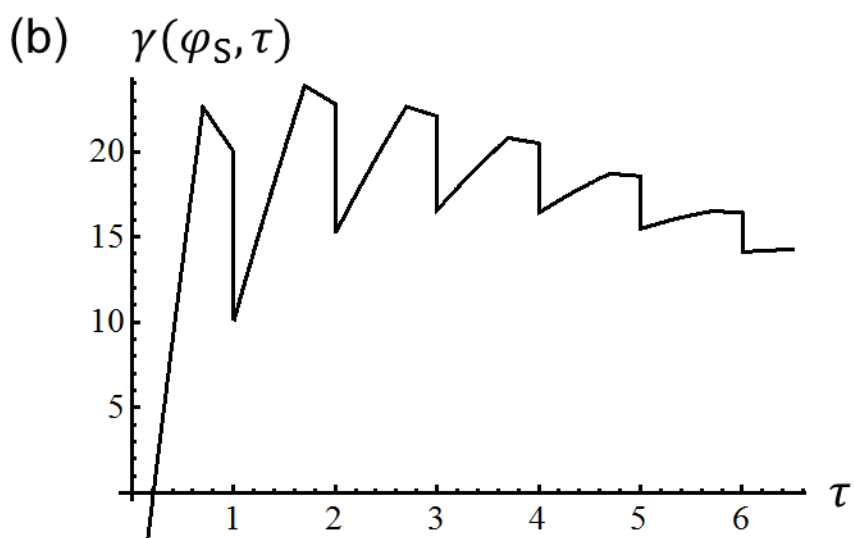
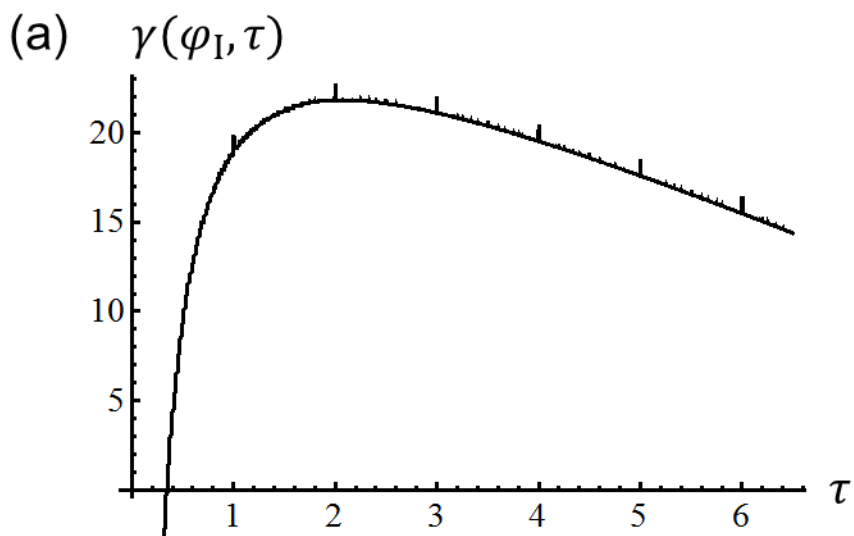


Fig. 5

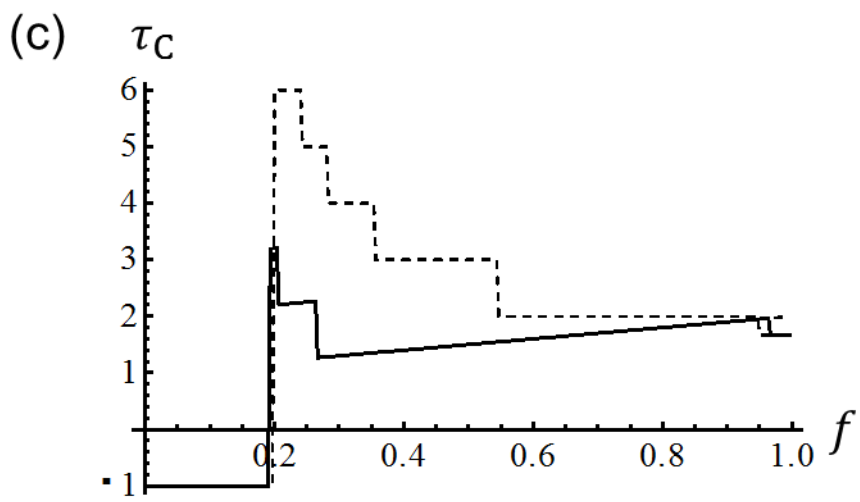
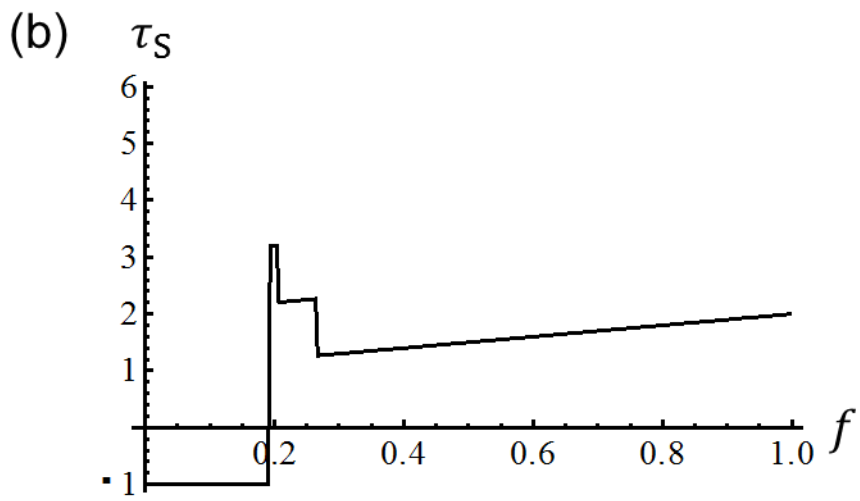
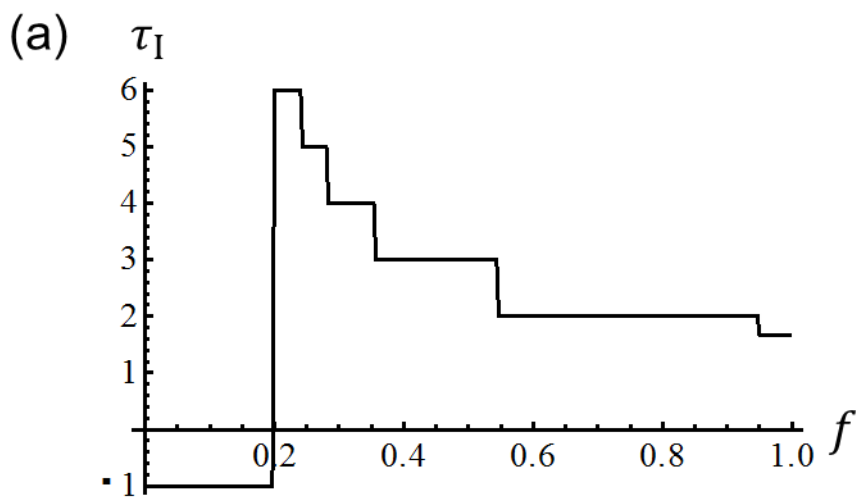


Fig. 6

