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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

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

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

Mathematics Subject Classification (2010): 92C80 (Plant biology); 90B35 (Scheduling 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

60 an optimal strategy at low or high latitudes than at intermediate latitudes. That prediction
61 roughly coincides with the real evergreen–deciduous tree distribution. In addition, the
62 dependence of leaf longevity on three leaf parameters (the photosynthetic rate, the
63 decrease in the photosynthetic rate with age, and the construction cost) observed in the
64 model outcomes was in line with the results of earlier empirical studies (Bentley 1979;
65 Chapin 1980; Chabot and Hicks 1982; Kikuzawa 1984; Koike 1988). Therefore, the
66 index has been viewed as appropriate in the context of optimal strategy theory.
67 Kikuzawa's index (1991) is currently repeatedly used. For example, Kikuzawa et al.
68 (2013) calculated optimal leaf longevity using the index to explain worldwide variety in
69 leaf longevity from the viewpoint of local adaptation. Advanced modelling studies also
70 used the same index (e.g. Takada et al. 2006). However, Kikuzawa's index ($G(\tau) / \tau$) only
71 represents average rate over life span of an individual leaf, not the lifelong average rate of
72 a tree. This is because the denominator (τ) only covers the time span during which a leaf
73 is retained and does not consider an interval during which a tree has no leaves. The
74 interval should be taken into account for an evaluation of the lifelong average rate, which
75 Kikuzawa (1991) intended to do. It is important to mathematically refine the well-used
76 index.
77 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

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

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

130 $$\Gamma(\tau,\sigma_i) = -C + \int_{\sigma_i}^{\sigma_i+\tau} \left(p(t_i)\theta(s) - m(t_i)\right) \mathrm{d}s = -C + \int_{\sigma_i}^{\sigma_i+\tau} \left(p(s-\sigma_i)\theta(s) - m(s-\sigma_i)\right) \mathrm{d}s \,, (1)$$

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 $(0 \le \theta(s) \le 1)$, 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, $\gamma(\varphi, \tau)$. Our goal is to identify a pair of strategies, $\{\varphi^*, \tau^*\}$, with which $\gamma(\varphi, \tau)$ 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 $\gamma(\varphi, \tau)$ if and only if we can find a positive integer $N(\varphi, \tau)$ satisfying the following conditions for any positive integer h (Fig. 2):

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

$$\sigma_{hN+1}=h\sigma_{N+1}. \tag{2b}$$

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

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

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:

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

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

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:

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

where j is any non-negative integer and f is the length of a favourable period within any year ($0 < f \le 1$). 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

$$G(\tau)=\begin{cases}-C+(a-m)\tau\left(1-\dfrac{\tau}{2b}\right)-a(1-f)\lfloor\tau\rfloor\left(1-\dfrac{\lfloor\tau\rfloor+f}{2b}\right) & \text{for} \quad j \le \tau < j+f \\ -C-m\tau\left(1-\dfrac{\tau}{2b}\right)+af\lceil\tau\rceil\left(1-\dfrac{\lfloor\tau\rfloor+f}{2b}\right) & \text{for} \quad j+f \le \tau < j+1\end{cases}. \tag{6}$$

where $\lfloor\ \rfloor$ and $\lceil\ \rceil$ 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 $\theta(s) = 1$:

$$\Gamma(\tau, \sigma_i) = -C + \int_{\sigma_i}^{\sigma_i+\tau} \big(p(s-\sigma_i) - m(s-\sigma_i)\big)\mathrm{d}\,s = -C + \int_0^{\tau} \big(p(t) - m(t)\big)\mathrm{d}\,t\,. \qquad (7)$$

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

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

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

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

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

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_I). 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 [$\gamma(\varphi_I, \tau)$, $\gamma(\varphi_S, \tau)$, and $\gamma(\varphi_C, \tau)$; respectively] either analytically or numerically and determine the leaf longevity that maximises these increase rates (τ_I, τ_S, and τ_C,

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

239 To estimate optimal leaf longevity numerically, τ_X, under a particular foliation
240 rule φ_X and particular values of the parameters $\{C, a, m, b, f\}$, we ran numerical
241 computations in the absence of rounding errors using *Mathematica 8* (Wolfram Research,
242 Inc.). Specifically, we calculated values of $\gamma(\varphi_X, \tau)$ for various values of τ, ranging from
243 $\Delta\tau$ to b and uniformly distributed at intervals of $\Delta\tau$ ($\Delta\tau$ equal to 1 / 300, thus about a day).
244 Of these τ values, that for which $\gamma(\varphi_X, \tau)$ was largest was taken to be τ_X.

245 ## 4.1 The immediate replacement rule

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

and thus

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

which is the average rate of carbon gain by k leaves during j years. When a positive integer is substituted into τ (thus $j = \tau$ and $k = 1$), (12) takes exactly the same form as (9). In that case, we can derive an analytical expression by applying (6):

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

When $af - m < 0$, (13) monotonically increases with increasing τ and takes a greater value at $\tau = \lfloor b \rfloor$ than at other integer values of τ. Therefore, although $\tau = \lfloor b \rfloor$ may or may not be the τ_1 value, other integers are excluded as candidates for election as τ_1. When $af - m > 0$, (13) attains the maximum value at one or two integers satisfying

$$\sqrt{\left(t^{\ddagger}\right)^2 + \frac{1}{4}} - \frac{1}{2} \le \tau \le \sqrt{\left(t^{\ddagger}\right)^2 + \frac{1}{4}} + \frac{1}{2}, \tag{14}$$

where

$$t^{\ddagger} = \sqrt{\frac{2bC}{af - m}}. \tag{15}$$

See Appendix C for details. The τ values described above may be τ_1, and other integers are excluded as candidates for τ_1. Note that $t^{\ddagger} = t^{\dagger}$ if $f = 1$ and that the dependencies of $t^{\ddagger}$ on parameters other than f are identical to those of $t^{\dagger}$. In addition, $t^{\ddagger}$ monotonically

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

270 The results of our numerical simulations, shown in Fig. 4a, suggest that the
271 function $\gamma(\varphi_1, \tau)$ exhibits spike-like peaks when k (the denominator of the rational number
272 τ) is small. This is because trees with smaller k values more frequently synchronise
273 flushing seasons with the beginning of a favourable period (note that a leaf provides the
274 largest net carbon gain when it is expanded at the beginning of a favourable period).
275 Consequently, τ_1 has a small k value ($\tau_1 = 2$ yields $k = 1$ in the example of Fig. 4a). Our
276 comprehensive numerical simulations conducted within realistic parameter ranges (i.e.
277 $3 \le C \le 18$, $20 \le a \le 100$, $2 \le m \le 18$, $1 \le b \le 12$, and $0 < f < 1$; the same ranges as used
278 by Kikuzawa [1991]; carbon unit is arbitrary and time unit is year) revealed that an
279 integer τ ($k = 1$) was most frequently chosen as a component of numerically estimated τ_1
280 values, and no τ_1 value was associated with a k value greater than 4. In addition, τ_1
281 monotonically decreased with increasing f when parameters other than f were fixed, as
282 suggested by (14) and (15). Moreover, our numerical analysis suggests that the negative
283 dependency of τ_1 on f holds true even when the set of τ_1s contains non-integer elements
284 (e.g. τ_1 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 $j = 0, 1, 2, \ldots$. 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

303 $$\gamma(\varphi_S, j+f) = -\frac{C}{j+1} + \left(1 - \frac{j+f}{2b}\right)\left(af - \frac{j+f}{j+1}m\right). \quad (18)$$

304 Suppose, for a moment, that j is any real value between 0 and $b - f$. Then, (18) is a

305 continuous function of j. It is possible to show, by solving $d\gamma(\varphi_S, j + f) / dj = 0$, that (18) is

306 maximised at $j = j^{\dagger}$, where

307 $$j^{\dagger} = -1 + \sqrt{\frac{2bC - (1-f)(2b+1-f)m}{af - m}}, \quad (19)$$

308 given that

309 $$2bC - (1-f)(2b+1-f)m \geq af - m > 0. \quad (20)$$

310 Otherwise, $\gamma(\varphi_S, j + f)$ is maximised either at $j = 0$ or at $j = b - f$. Considering the case

311 where (20) holds, it can be seen from (19) that the locally optimal leaf longevity, τ_S,

312 which is either $\lfloor j^{\dagger} \rfloor + f$ or $\lceil j^{\dagger} \rceil + f$, increases discretely with increasing values of C and b,

313 and decreases as a increases. The effect of m on (19) depends on the values of the other

314 parameters.

315 Figs. 4b and 5b show the results of numerical computations. The figures

316 illustrate the dependencies of $\gamma(\varphi_S, \tau)$ on τ, and τ_S on f, respectively. The former

317 dependency yields the analytical result that $\gamma(\varphi_S, \tau)$ has peaks at $\tau = j + f$. The latter

318 example shows that the dependency of τ_S on f is twofold. On a local scale, τ_S continuously

319 increases with increasing f. On a global scale, however, τ_S discretely decreases with

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

4.3 The combined expansion rule

The combined expansion rule, φ_{C} (Fig. 3c), is a combination of φ_{I} and φ_{S}. The rule is identical to φ_{I} when $f = 1$. Meanwhile, if longevity satisfying $j + f \le \tau \le j + 1$ is given, trees subject to this rule exhibit exactly the same behaviour as do trees operating under rule φ_{S}. In the other cases, however, this rule leads to a unique life history. For any real positive τ, n is defined as the smallest integer satisfying

$$\lceil n\tau \rceil - n\tau \le 1 - f\,, \tag{21}$$

and we have

$$N(\varphi_{\mathrm{C}}, \tau) = n\,, \tag{22a}$$

$$\sigma_{hn+l}(\varphi_{\mathrm{C}}, \tau) = h\lceil n\tau \rceil + (l-1)\tau\,, \tag{22b}$$

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

Substituting (22) into (3), we obtain

$$\gamma(\varphi_{\mathrm{C}}, \tau) = \frac{\sum_{i=1}^{n} \Gamma(\tau, (i-1)\tau)}{\lceil n\tau \rceil}\,. \tag{23}$$

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

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

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_I 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:

$$\gamma(\varphi_I, j+1) = \gamma(\varphi_S, j+1) = \gamma(\varphi_C, j+1) < \gamma(\varphi_S, j+f) = \gamma(\varphi_C, j+f). \quad (25)$$

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

In light of the above results, the followings hold:

i) Neither τ_S nor τ_C can be an integer;

ii) When τ_I takes an integer value, (φ_I, τ_I) is not the optimal strategy because it is always inferior (in terms of carbon economy) to (φ_S, τ_S) and (φ_C, τ_C),

iii) When τ_S takes the form $j + f$, (φ_C, τ_C) is not inferior to (φ_S, τ_S), and,

iv) When $\tau_S = b$, (φ_S, τ_S) may or may not be superior to (φ_C, τ_C).

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

5 Discussions

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

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

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

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

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

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

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

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

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

455 A clear shortage of the present model is that effect of competition among trees
456 has not been incorporated into it. The theory of an evolutionarily stable strategy (ESS;
457 Maynard Smith and Price 1973) considers that natural selection does not always
458 maximise individual fitness and that an evolutionarily converged strategy depends on the
459 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

$$G(\tau) = -C + \int_0^{\tau} \left(p(s)\theta(s) - m(s) \right) \mathrm{d}s \,. \tag{A1}$$

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

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

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 $j \le \tau < j + f$, 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 $0 \le \tau < f$ and thus $j = 0$, the loss term is calculated as

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

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

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

If $j + f \le \tau < j + 1$, 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

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

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

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

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 $\tau = t^*$ ($j \le t^* < j + f$), 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 $\mathrm{d}g(\tau)/\mathrm{d}t = 0$. 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 $\mathrm{d}\gamma(\varphi_1, \tau) / \mathrm{d}\tau = 0$ 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 $\gamma(\varphi_1, \lfloor t^{\ddagger} \rfloor) \geq \gamma(\varphi_1, \lceil t^{\ddagger} \rceil)$ as

$$\gamma(\varphi_1, \lfloor t^{\ddagger} \rfloor) \geq \gamma(\varphi_1, \lceil t^{\ddagger} \rceil) \Leftrightarrow -\frac{C}{\lfloor t^{\ddagger} \rfloor} + \frac{(af - m)\lfloor t^{\ddagger} \rfloor}{2b} \geq -\frac{C}{\lceil t^{\ddagger} \rceil} + \frac{(af - m)\lceil t^{\ddagger} \rceil}{2b} \Leftrightarrow t^{\ddagger} \leq \sqrt{\lfloor t^{\ddagger} \rfloor \lceil t^{\ddagger} \rceil}, \tag{C1}$$

and vice versa.

In conclusion, the optimal integer leaf longevity for trees subject to the immediate replacement rule (φ_{I}) is $\lfloor t^{\ddagger} \rfloor$ if (C1) holds and $\lceil t^{\ddagger} \rceil$ otherwise, which can be also expressed as (14).

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

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

$$\frac{f}{Q} \le \tau < \min\left\{\frac{f}{Q-1}, \frac{1}{Q}\right\}. \tag{D1}$$

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

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

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

544 the range (D1) is calculated as

545 $$\gamma(\varphi_C, \tau) = -QC + (Q-1)\int_0^{\tau}(a-m)\left(1-\frac{t}{b}\right)\mathrm{d}t + \int_0^{f-(Q-1)\tau} a\left(1-\frac{t}{b}\right)\mathrm{d}t - \int_0^{\tau} m\left(1-\frac{t}{b}\right)\mathrm{d}t .$$

546 (D2)

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

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

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

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

551 yields

552 $$\frac{\mathrm{d}}{\mathrm{d}\tau}\gamma(\varphi_C, \tau) = -(Q-1)(Q\tau - f)\frac{a}{b} - Qm\left(1-\frac{\tau}{b}\right). \quad \text{(D3)}$$

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

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

555 $$\gamma(\varphi_C, \frac{f}{Q}) = -QC + (a-m)f\left(1-\frac{f}{2bQ}\right). \quad \text{(D4)}$$

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

557 respect to q:

558 $$\frac{\mathrm{d}}{\mathrm{d}q}\left[-qC + (a-m)f\left(1-\frac{f}{2bq}\right)\right] = -C + \frac{(a-m)f^2}{2bq^2} = -\frac{C}{q^2}(q+q^{\dagger})(q-q^{\dagger}), \quad \text{(D5)}$$

559 where $q^{\dagger}$ is defined as

560 $$t^\dagger = \frac{f}{q^\dagger} \Leftrightarrow q^\dagger = \frac{f}{t^\dagger} = f\sqrt{\frac{a-m}{2bC}}\,. \qquad \text{(D6)}$$

561 Therefore, the continuous function of q attains a maximum value at $q = q^\dagger$. It follows that

562 the original discrete function (D4) takes a maximum value either at $Q = \lfloor q^\dagger \rfloor$ or at

563 $Q = \lceil q^\dagger \rceil$. 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

564 $$q^\dagger \leq \sqrt{\lfloor q^\dagger \rfloor \lceil q^\dagger \rceil}\,, \qquad \text{(D7)}$$

565 and vice versa.

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

567 $f / Q^\dagger$, 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_I), no leafless period exists. In total, 3 (k) leaves

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

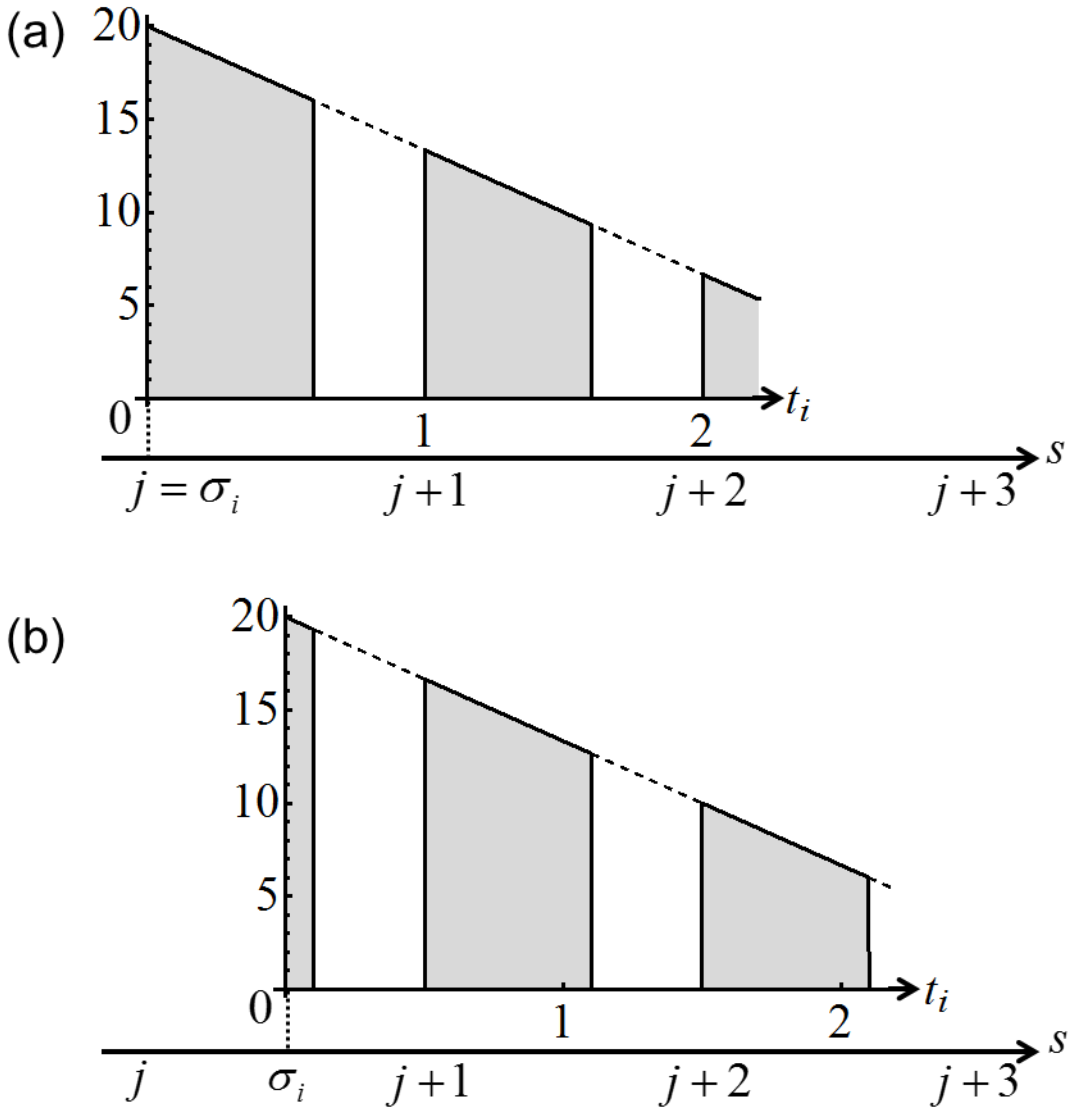
651 **Fig. 4** Examples of the dependencies of long-term rates of increase in net carbon gain of
652 trees subject to (a) the immediate replacement rule, (b) the spring flushing rule,
653 and, (c) the combined expansion rule on τ. Discrete points were obtained at
654 intervals of $\Delta\tau = 1 / 300$ and joined. Dotted lines in (c) are duplications of (a) and
655 (b). The values of the other relevant parameters were $C = 10.5$, $a = 60$, $m = 10$,
656 $b = 6.5$, and $f = 0.7$

657 **Fig. 5** Examples of the dependencies of locally optimal leaf longevities of trees subject to
658 (a) the immediate replacement rule, (b) the spring flushing rule, and, (c) the
659 combined expansion rule on f. Discrete points were obtained from numerical
660 computations conducted at an accuracy of $\Delta\tau = 1 / 300$ and joined. The dotted
661 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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$j+3$

Fig. 2

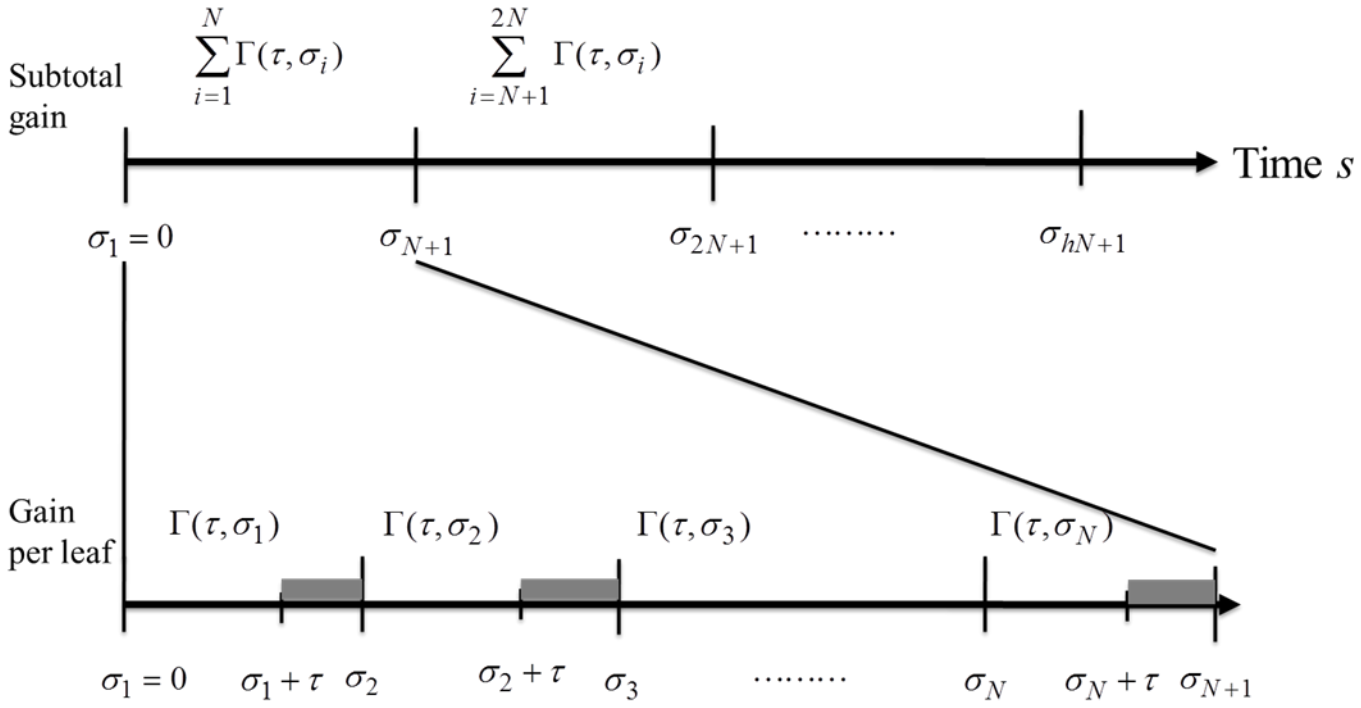

Subtotal gain
$\sum_{i=1}^{N}\Gamma(\tau,\sigma_i)$
$\sum_{i=N+1}^{2N}\Gamma(\tau,\sigma_i)$
Time s
$\sigma_1=0$
σ_{N+1}
σ_{2N+1}
σ_{hN+1}
Gain per leaf
$\Gamma(\tau,\sigma_1)$
$\Gamma(\tau,\sigma_2)$
$\Gamma(\tau,\sigma_3)$
$\Gamma(\tau,\sigma_N)$
$\sigma_1=0$
$\sigma_1+\tau$
σ_2
$\sigma_2+\tau$
σ_3
σ_N
$\sigma_N+\tau$
σ_{N+1}

Fig. 3

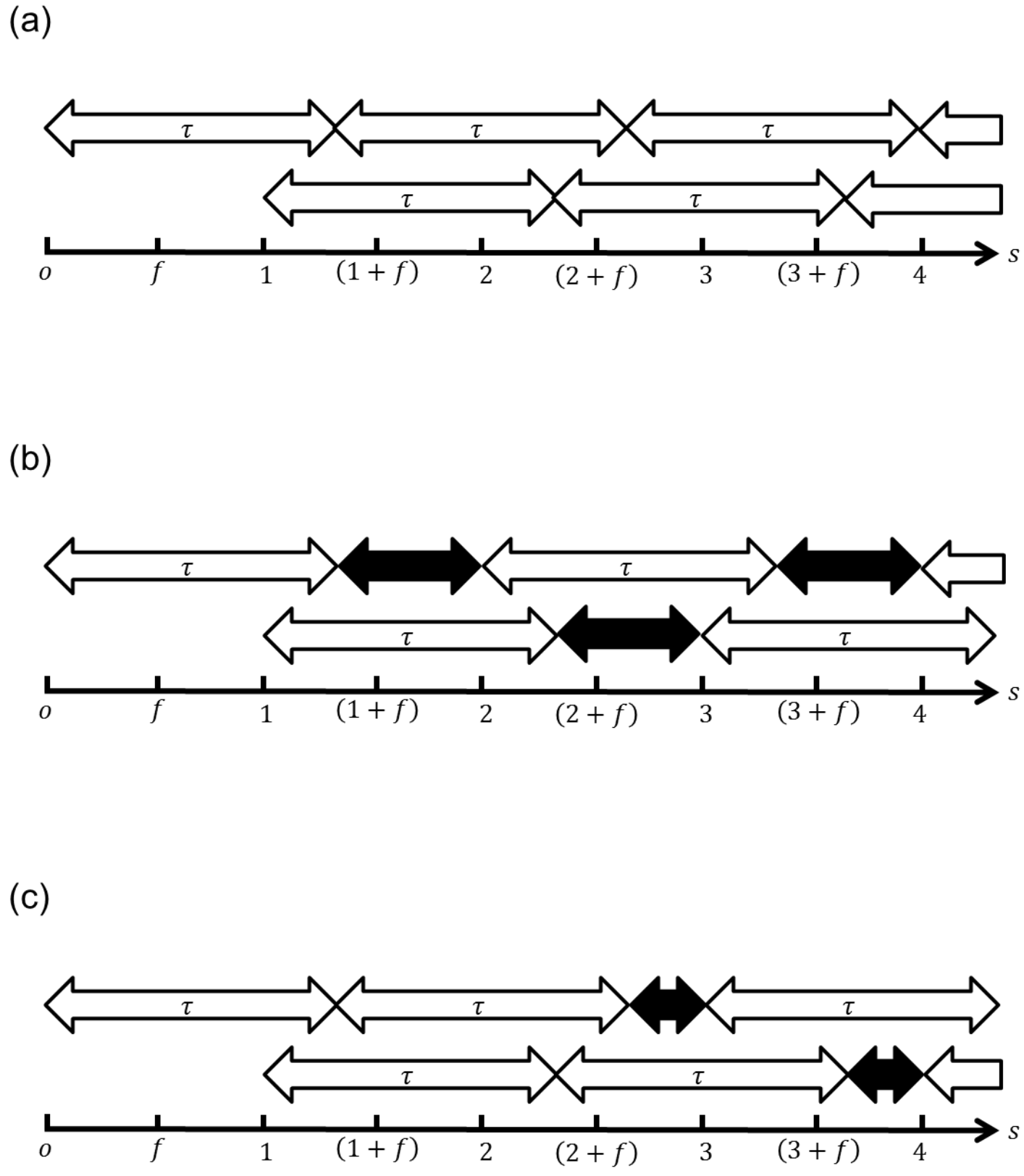

(a)
τ
τ
τ
τ
τ
o
f
1
(1 + f)
2
(2 + f)
3
(3 + f)
4
s
(b)
τ
τ
τ
τ
τ
o
f
1
(1 + f)
2
(2 + f)
3
(3 + f)
4
s
(c)
τ
τ
τ
τ
τ
o
f
1
(1 + f)
2
(2 + f)
3
(3 + f)
4
s

Fig. 4

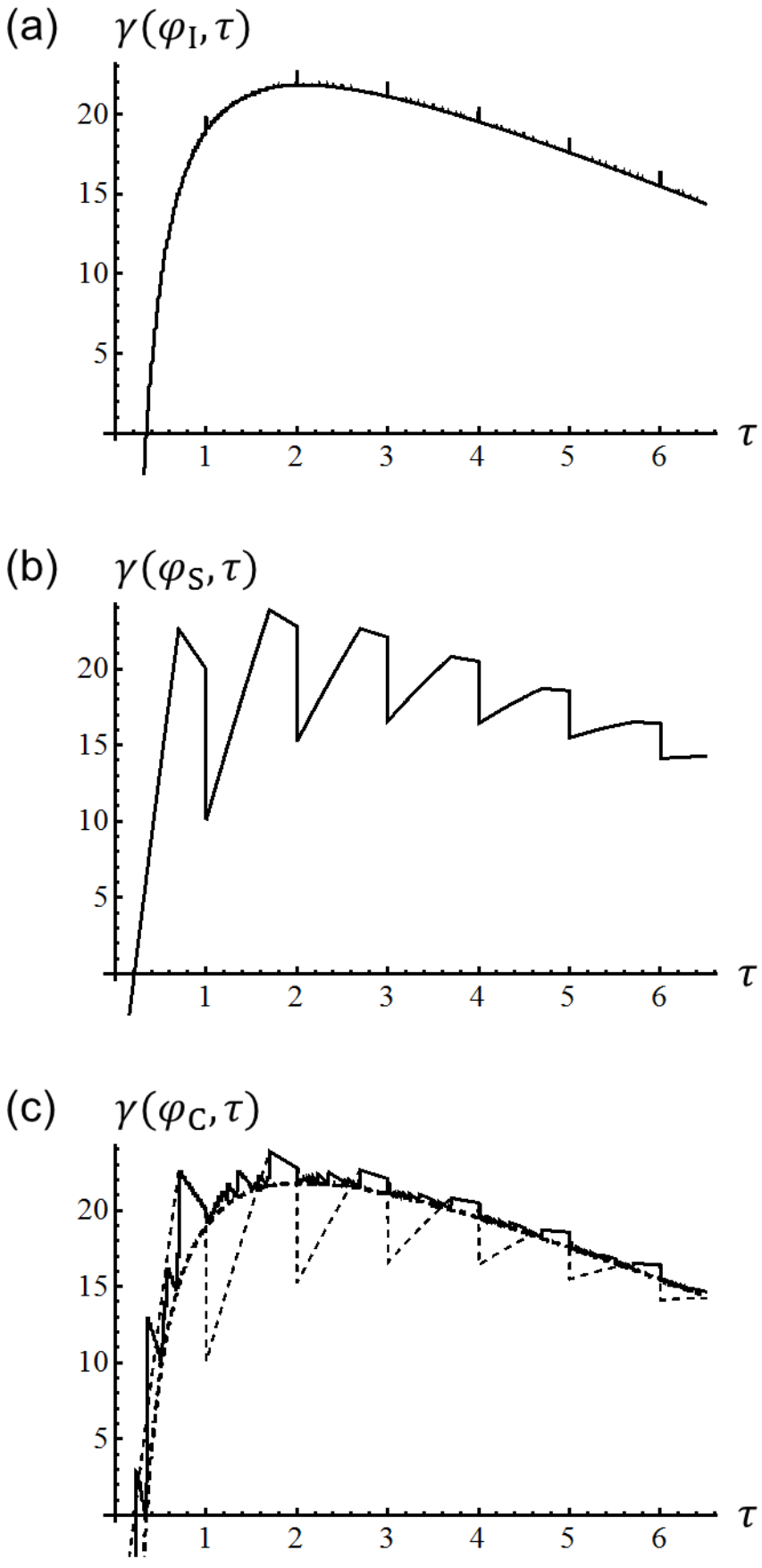
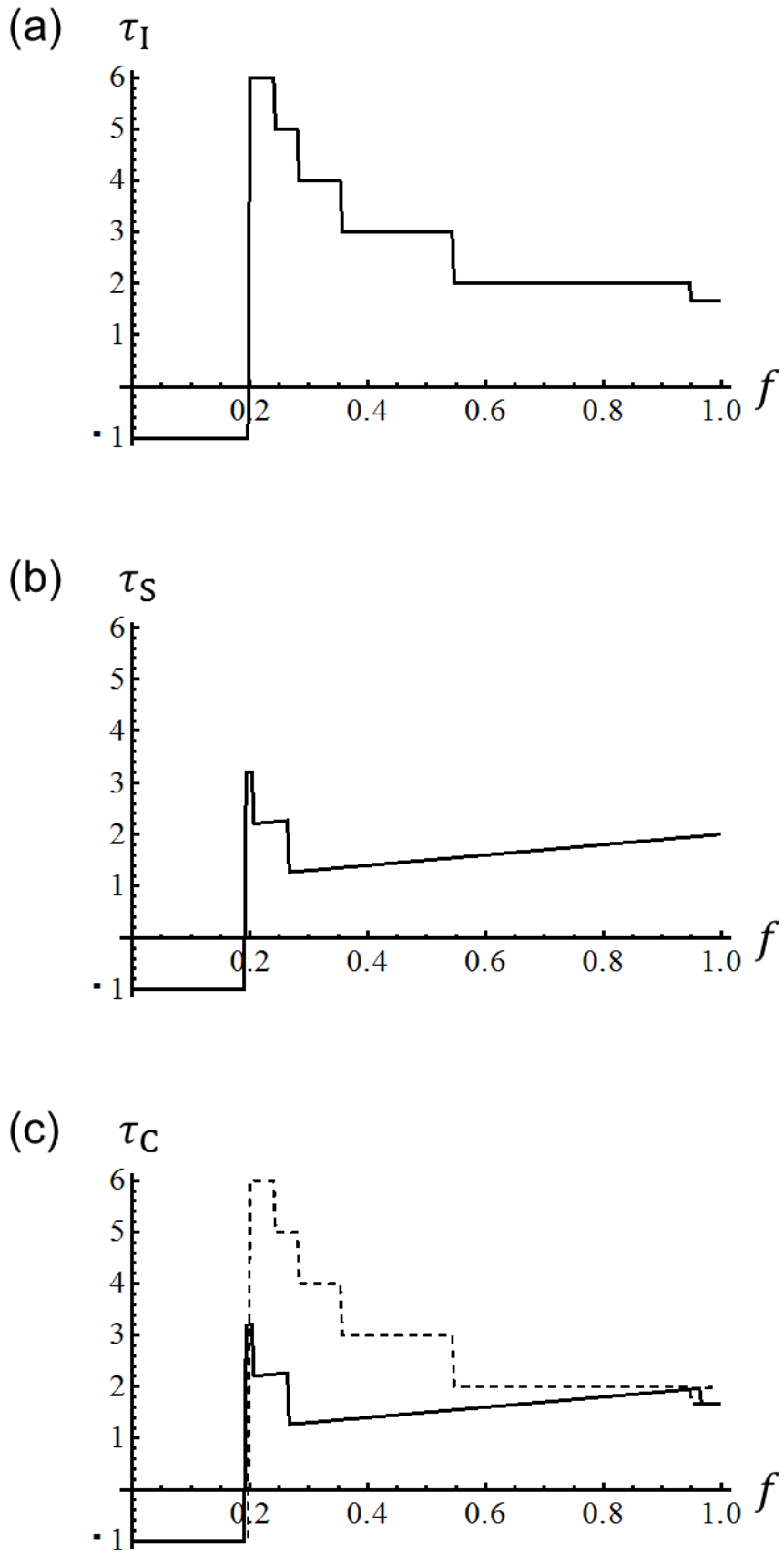

(a) $\gamma(\varphi_I, \tau)$
20
15
10
5
1
2
3
4
5
6
τ
(b) $\gamma(\varphi_S, \tau)$
20
15
10
5
1
2
3
4
5
6
τ
(c) $\gamma(\varphi_C, \tau)$
20
15
10
5
1
2
3
4
5
6
τ

Fig. 5


(a)
τ_I
6
5
4
3
2
1
-1
0.2
0.4
0.6
0.8
1.0
f
(b)
τ_S
6
5
4
3
2
1
-1
0.2
0.4
0.6
0.8
1.0
f
(c)
τ_C
6
5
4
3
2
1
-1
0.2
0.4
0.6
0.8
1.0
f

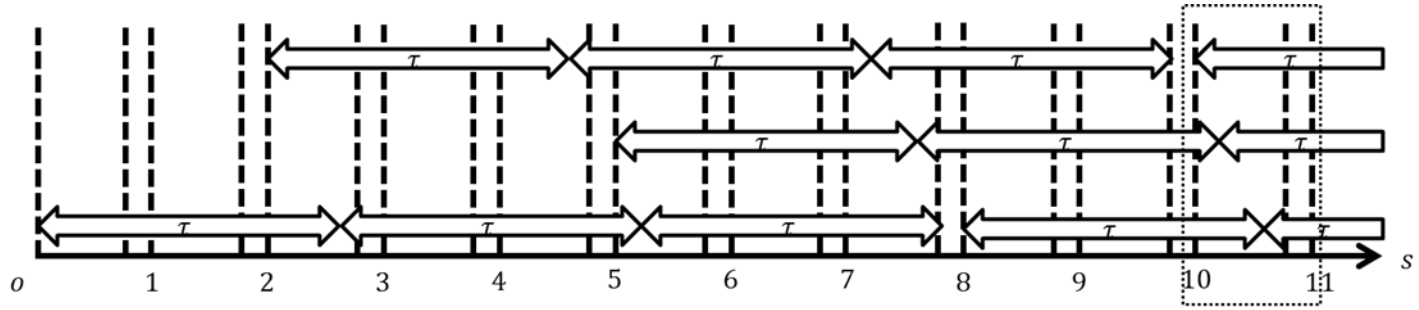



Fig. 6