

Canopy ergodicity: can a single leaf represent an entire plant canopy?

Kihachiro Kikuzawa · Makoto Yagi ·
Yuji Ohto · Kiyoshi Umeki · Martin J. Lechowicz

Received: 12 February 2008 / Accepted: 4 August 2008 / Published online: 29 August 2008
© Springer Science+Business Media B.V. 2008

Abstract While leaves typically emerge near shoot apices around the outer surface of a plant canopy, their relative position “moves” deeper into the canopy as additional leaves emerge. The photosynthetic capacity (A_{\max}) of a given leaf can be expected to decline over time as its relative position (P_r) in the canopy becomes progressively deeper; this can be observed as a spatial gradient with the A_{\max} of leaves declining distally from the shoot apex. As a consequence, we propose that the photosynthetic capacity averaged over a single leaf’s lifespan is equivalent to the average photosynthetic capacity of the entire plant canopy at a given time; in other words, there is an ergodic time to space averaging in the organization and development of plant canopies. We tested this “canopy ergodic hypothesis” in two woody (*Alnus sieboldiana* and

Mallotus japonica) and two herbaceous (*Polygonum sachalinensis* and *Helianthus tuberosus*) species by following the photosynthetic capacity in 100 individual leaves from the time of their emergence until their death. We compared the average photosynthetic capacity of individual leaves through time (time-average) to the average photosynthetic capacity of all the leaves along a shoot at the time of emergence of the focal leaf (space-average). We found that A_{\max} and P_r were positively correlated and that the time-averages of three plant species (*Alnus*, *Mallotus*, and *Helianthus*) were not significantly different from the corresponding space-averages, although the averages differed among individual plants. *Polygonum*, however, did show significant differences between time and space averages. Ergodicity appears to apply to the leaf–canopy relationship, at least approximately—the average photosynthetic capacity of a single leaf through time (time-average) can represent the average photosynthetic capacity of the entire canopy.

K. Kikuzawa · M. Yagi · Y. Ohto
Center for Ecological Research, Kyoto University, Kyoto,
Japan

Present Address:
K. Kikuzawa (✉)
Department of Environmental Science, Ishikawa
Prefectural University, Ishikawa, Japan
e-mail: kikuzawa@ishikawa-pu.ac.jp

K. Umeki
Graduate School of Horticulture, Chiba University, Chiba,
Japan

M. J. Lechowicz
Department of Biology, McGill University, 1205 Avenue
Dr. Penfield, Montreal, QC, Canada H3A 1B1

Keywords Canopy photosynthesis ·
Time-average · Space-average · Canopy ergodic
hypothesis

Introduction

The canopy of plant communities has a three-dimensional structure that changes through time

(Hollinger 1989; Holbrook and Lund 1995). At any point in time, light conditions change vertically within a canopy (Monsi and Saeki 1953; Hirose and Werger 1989; Kitajima et al. 2005). Leaves at the upper or outer part of a plant canopy are usually well insolated, and leaves lower or deeper in the canopy usually shaded (Kikuzawa 2003; Hikosaka 2005). A newly emerged leaf typically is situated at the outer edge of the canopy, other leaves on the growing shoot being basipetal to this focal leaf. With the progress of time and shoot elongation, however, this focal leaf is progressively more and more shaded by newly emerging leaves above and to the side in the expanding canopy, and concomitantly, the photosynthetic capacity of the focal leaf declines with time through reallocation of limiting resources to more recently emerged leaves (Field 1983; Hirose and Werger 1987). In other words, although the actual position of a leaf is fixed on the shoot or stem, its relative position in the canopy changes from the outer edge of the canopy to its interior as the canopy expands. Progressively more and more shaded leaves below the focal leaf are shed until at last the focal leaf is among the innermost leaves deep in the canopy interior just before itself being shed (Kikuzawa 2003). The rate and temporal context of this progression from exterior to interior canopy position varies with the rates of shoot growth and leaf turnover, being generally most rapid in herbaceous or pioneer tree species with indeterminate shoot growth and slowest in woody evergreen species with slow leaf turnover. This sequence of events can be viewed as a “downward movement” of the leaf through the growing canopy. Corresponding to this “downward movement,” the focal leaf will be subjected to a predictable decline in insolation, and consequently, undergoes acclimation to lower photosynthetic capacity over time (Reich 1984; Kikuzawa 2003; Miyazawa and Kikuzawa 2004).

We believe that this “downward movement” of a single leaf through time can potentially represent the vertical structure (Hikosaka 2005; Kitajima et al. 2005) in irradiance and photosynthetic capacity from the outer edge to the deep interior of a canopy at a given time. We propose a hypothesis that the average photosynthetic capacity (and rate) through a single leaf’s life from its emergence to fall can express both the mean photosynthetic capacity and the realized mean rate of photosynthetic gain of the entire canopy

at the time of the emergence of the focal leaf. By analogy to work in statistical mechanics, we call this an “ergodic canopy hypothesis.” The ergodic hypothesis in statistical mechanics assumes that the time average for the properties of any system of interest will be equal to the averages of those same properties for all the members of the ensemble (Tolman 1979). By analogy, we predict that the average photosynthetic capacity and the realized rate of photosynthetic gain through time of a single leaf will equal the average photosynthetic capacity and the realized rate of photosynthetic gain of an ensemble of leaves in space (the plant canopy). We hypothesize, in other words, that at least at some stages in their development, plant canopies are ergodic.

Plant canopy development can be characterized in four phases: expanding, dynamically stable, statically stable, and degrading. During the expanding phase of canopy growth, new leaves develop on the shoot without loss of older leaves. However, eventually, older leaves begin to senesce and to be shed as the canopy reaches a steady state condition (dynamic stability) in which leaf fall and leaf emergence rates are in balance and leaf numbers in the canopy constant. An arrested condition (static stability) then can occur if leaf turnover stops and leaves persist, but eventually leaf senescence and loss predominate in a degrading canopy. Stages in canopy development when leaf numbers are stable, the domain of the ergodic hypothesis, occur in many plant species from diverse environments. The dynamically stable phase, for example, can easily last for more than a year in species from the aseasonal tropics. In evergreen trees, although leaf number within a year changes, the year-to-year uniformity in leaf numbers could also be considered dynamically stable. Furthermore, we will show that the domain of ergodicity can be extended by relaxing the requirement for dynamic stability of leaf number. Under relaxed conditions, approximate ergodicity can apply with the space-averaged photosynthetic capacity, a constant independent of time, and the time-averaged photosynthetic capacity only a little smaller than the space average.

To the degree that the conditions for ergodicity apply in the real world, we believe that ergodic hypothesis can yield new insights into the functional ecology of plant canopies. For example, we recently proposed a model to represent the gross primary production of plant communities as the product of the

lifetime carbon gain by a single leaf, the daily rate of leaf production, and the duration of the period favorable for photosynthetic activity within a year (Kikuzawa and Lechowicz 2006). In this framework, the total carbon gain by a plant community throughout a year (gross primary production) in principle could be obtained simply by measuring the lifetime carbon gain of a single leaf, although practically one would average a sample of leaves measured over their lifetimes. Postulating ergodicity, we argued that the lifetime carbon gain of a single leaf could be obtained by the average rate of photosynthetic capacity of a leaf through its life (Kikuzawa and Lechowicz 2006). While this possibility is appealing in principle, the operational difficulties of selecting truly “representative leaves” in an intrinsically complex and dynamic plant canopy and measuring their lifetime average photosynthetic capacity and gains are causes for some skepticism about the testability and utility of such an ergodic perspective. In this paper, we therefore make an initial test of the ergodic canopy hypothesis using two woody and two herbaceous plant species, all either planted or naturally growing in open sites. We compare (1) the canopy development of these species to assess if the dynamic stability required for canopy ergodicity exists. (2) We analyze the relationship between photosynthetic capacity and relative position to assess how the capacity is determined by leaf position. (3) We also analyze temporal trend in space averages to assess if factors other than light regime affect photosynthetic capacity. Finally, we compare (4) the average photosynthetic capacity of single leaves over their life spans with the average photosynthetic capacity of the plant canopy at a given time.

Model

Basic ergodic model

We recognize three premises a critical to the canopy ergodic hypothesis.

- (1) The photosynthetic capacity (A_{\max}) of a single leaf is highest at the time of leaf expansion and then decreases with time due to both aging and degradation of local light conditions as the canopy expands. In other words, A_{\max} is a

function of light intensity (I) and age (t) from its full expansion.

$$A_{\max} = A_{\max}(I, t) \quad (1)$$

- (2) Only the insolation regime on each leaf primarily affects A_{\max} . Other conditions such as temperature, foliar water regime, and nutrient availability can be considered more uniform within the canopy compared to insolation.
- (3) An established, non-degrading plant canopy has stable leaf numbers. When some leaves are newly added by leaf expansion at the top of a shoot, corresponding numbers of leaves will be shed at the base of the shoot and the number of leaves on a shoot therefore is constant.

Given these premises, consider a model shoot (Fig. 1) that for simplicity can retain only two leaves at a time. The shoot elongates adding a new leaf apically while shedding a leaf at the shoot base (Fig. 1a). Leaf position is recorded relative to the shoot apex (Fig. 1b). At time t_0 , a newly expanded focal leaf appears (age 0); the insolation regime at that leaf is I_0 , and A_{\max} of the leaf is $A_{\max}(I_0, 0)$. At time t_1 , one time unit after t_0 , another new leaf appears apically with age zero and insolation regime I_0 . Thus, at time t_1 , the focal leaf has “dropped” to a subapical position with insolation regime I_1 and its A_{\max} has decreased to $A_{\max}(I_1, 1)$. The A_{\max} of the new leaf at the apex is now $A_{\max}(I_0, 0)$. In this simple model, the average A_{\max} of t_0 and t_1 for the focal leaf is therefore $1/2[A_{\max}(I_0, 0) + A_{\max}(I_1, 1)]$, which is equivalent to the average A_{\max} at $t = t_1$, or at any time. From the preceding arguments, the position of a leaf, P_r , can be taken as an integrative variable representing both leaf age and relative position (light regime) within a canopy. We can expect that A_{\max} is a function of P_r .

$$A_{\max} = A_{\max}(P_r) \quad (2)$$

Here, the relative position of a leaf is defined as

$$P_r = (i - 1)/(N - 1), \quad (3)$$

where i is the positional order of a living leaf counting from one for the leaf at the base of a shoot, and N is the total number of leaves on the shoot. P_r is one for the highest leaf of a shoot, and zero for the lowest leaf.

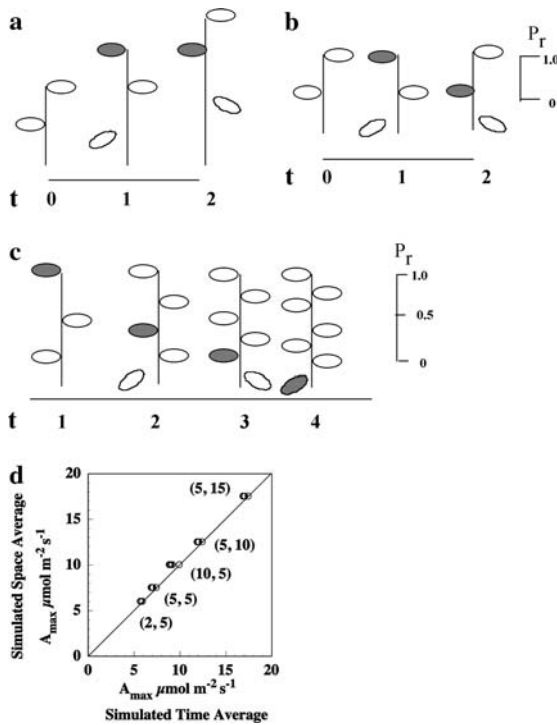


Fig. 1 Schematic representation of changes in relative leaf position (P_r), leaf age, and light condition (I) with time (t) in a model canopy. “Shaded” leaf indicates the focal leaf for which the time average photosynthetic rate was calculated. (a) leaf dynamics with shoot elongation, (b) relative representation of the canopy, leaf number was fixed with the apical leaf being $P_r = 1$. (c) An example of “extension” of the model. In this schema, two leaves appear ($m = 2$), but only one leaf drops; thus, this is an expanding phase rather than a stable phase. However, even in this case, the time average was similar but only slightly smaller than the space average. (d) Results of a simulation in which 2 new leaves appear ($m = 2$) per unit time and 1 leaf drops per unit time, and A_{max} depends on relative leaf position (P_r) as $A_{max} = pP_r + q$. We simulated 10 “time units” starting from the initial number of leaves (N) of 3. At time 1, the time average is equal to the space average, but the former slightly decreases with the progress of time. Numerals in the parentheses indicate the values of p and q used in calculations

Extended model

We can relax the conditions for ergodicity to encompass the expanding phase in canopy development. Requirements for this approximation are as follows:

- (1) The rates of emergence and shedding of leaves are constant, but not necessarily the same. We assume that the emergence rate is larger than the

shedding rate when the canopy is in the expanding phase.

- (2) A shoot allocates nitrogen to leaves so that A_{max} is a function of the relative position of a leaf. We assume that the relationship between A_{max} and P_r is linear:

$$A_{max} = pP_r + q \tag{4}$$

where p and q are positive constants.

The space-averaged A_{max} for a shoot with N leaves is given by:

$$\frac{\sum_{i=1}^N \{pP_r + q\}}{N} = \frac{\sum_{i=1}^N \{p \frac{i-1}{N-1} + q\}}{N} = \frac{p}{2} + q$$

Hence, space-averaged photosynthesis is independent of both the number of leaves and the time at which the space average is calculated.

We assume that it takes one time unit for one leaf to be shed from a shoot and m leaves emerge in the same duration. The parameter m is larger than one in the expanding phase of the leaf population. Now, consider a leaf that appears at time one at the top of the shoot with N leaves (Fig. 1c). This leaf is shed at time $N + 1$. At time t , the order of this leaf is $N - t + 1$, and the number of leaves on the shoot is $N + (m - 1)(t - 1)$. Thus, the time-averaged photosynthesis of this leaf is given as

$$\frac{\sum_{t=1}^N \{pP_r + q\}}{N} = \frac{\sum_{t=1}^N \left\{ p \frac{N-t}{N+(m-1)(t-1)-1} + q \right\}}{N}$$

This time-averaged photosynthetic capacity is only modestly less than the space-averaged photosynthetic capacity ($p/2 + q$) (Fig. 1d).

This relaxed model contains the strict conditions for ergodicity as the special case when $m = 1$; then, the time-average is equal to the space-average ($p/2 + q$) and does not depend on the number of leaves (e.g., the time when the focal leaf appears).

Materials and methods

Plant material

In order to assess the prevalence of ergodicity in nature, we collated various measurements we had made of photosynthetic capacity for leaves of different ages along growing shoots in four different

species. *Alnus sieboldiana* Winkl. (Betulaceae) is a small tree species native to southwestern Japan. The species is widely planted in central Japan to stabilize slopes and is naturalized in open spaces. We sampled the uppermost shoot on each of five 1-m tall saplings in the spring of 2000. *Mallotus japonicus* Muell. Arg. (Euphorbiaceae) is another small tree species widely distributed in Japan that commonly grows along open roadsides. We sampled the uppermost shoots on three 1-m tall saplings in 1999 and 2000. *Polygonum sachalinensis* Maxim. (Polygonaceae) is a herbaceous species usually found in sunny sites and reaching more than 1 m in height; we sampled 12 plants in an open site in 1993. *Helianthus tuberosus* L. (Asteraceae) is an herbaceous plant introduced to Japan from North America and now widely naturalized in open sites. Individual stems grow from tubers in spring, often reaching more than 1 m by autumn. At first, the phyllotaxis of the plants is opposite with two leaves at a node, but after the stems exceed 1 or 2 m, the phyllotaxis changes to alternate or to verticillate with three leaves at a node. At this stage, plants also vigorously branch and flower. We sampled three stems from each of three density plots in an experimental garden (see the next section), counted number of leaves on each stem, and measured their A_{\max} from early May to late June after which the number of sampled stems was reduced to one in each plot and measured until mid-August in 1998.

Study sites

Alnus and *Mallotus* were grown naturally in a 0.1 ha open site on the campus of the Center for Ecological Research of Kyoto University in Ohtsu, central Japan (Kikuzawa 2003). Mean annual temperature in Ohtsu was 14.8°C, highest in August (27°C) and lowest in January (4°C). Mean daily and maximum temperatures on days when measurements were made in 2000 were 18.9°C and 24.3°C in May, increased to 28.5°C and 34.1°C in August, and declined to 6.0°C and 12.3°C in December. A *Helianthus* planting in the nursery of the Botanical Garden of Kyoto University, Kyoto, central Japan consisted of six 1-m² plots situated in a 5 × 10 m area with the plots separated by at least a meter from one another. Either 5, 25, or 100 tubers were planted in each plot, replicated 3, 2, or 1 time(s), respectively. We refer to these hereafter as 5-, 25-, or 100-stem plots. Climate conditions in

Ohtsu and Kyoto are very similar; the difference in the annual mean temperature is less than 1°C. Finally, the *Polygonum* study was made in Bibai, Hokkaido, in northern Japan, where mean annual temperature was 7°C, highest in August (21°C) and lowest in January (−6.7°C). Mean daily and maximum temperatures of days in 1993 when plants were sampled were 15.1°C and 20.0°C in June and 19.9°C and 25.0°C in August. The sampled *Polygonum* plants were grown naturally in an open site of 1500 m²; the 12 sampled shoots were situated about 1 m apart and the effect of mutual shading was small.

Measurements

For each species, we selected one shoot per individual plant and counted the number of leaves on the shoot at one- or two-week intervals, recording newly emerged and newly fallen leaves. Fallen leaves and their positions were clear from leaf scars compared against the previous observation.

Photosynthesis

The photosynthetic capacity of each leaf in situ was measured at 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and CO₂ concentration at 350 ppmV using a Licor 6400 (Lincoln, Nebraska). Measurements were carried out from 8 to 11 local time and occurred on the same or the nearest day as the recording of leaf emergence and abscission. The same leaves were assayed at each measurement time. Measurements were carried out five to eleven times at one- or two-week intervals from May through August, or as late as December if healthy leaves persisted.

Leaf selection for average in time

We selected focal leaves for analysis near the upper part of a canopy ($P_r > 0.8$, soon after emergence) and followed them throughout most of their lifespan as their P_r progressively declined with growth of the stem ($P_r < 0.2$, soon before abscission). Leaves that appeared very early in the season usually had an initial P_r lower than 0.8 and were excluded from the analysis; leaves that appeared late in the season did not move to a deeper position as they aged (their P_r is usually greater than 0.2), and were also excluded. Fourteen focal leaves were selected from *Alnus*, 26

from *Polygonum*, 39 from *Mallotus*, and 21 from *Helianthus*. Photosynthetic capacities measured several times for each of the focal leaves gave 100 “time-averaged” photosynthetic capacities that could be compared against the “space-averaged” capacities on a total of 27 stems.

Leaf selection for average in space

Corresponding to the 100 time-averaged photosynthetic rates, we obtained 100 average photosynthetic rates for shoots (space-average). If the focal leaf was situated at the top of the stem at the initial stage, the average photosynthetic rate of leaves at all nodes of the stem at that time yielded the space average corresponding to the time average. If the focal leaf was not situated at the top of the stem at the initial stage, the photosynthetic rates of all leaves below the focal leaf (including the focal leaf) of the stem at that time yielded the space average. In this way, we obtained 100 space-averaged photosynthetic rates, each corresponding to the time average required to test the ergodic hypothesis.

Statistical analysis

Factors affecting A_{\max}

In order to examine the factors affecting A_{\max} , we regressed A_{\max} on P_r and leaf age separately, and compare the results using the Akaike Information Criterion (AIC).

Temporal trend in space-average photosynthesis rates

In order to examine whether a temporal trend in space-averaged photosynthetic capacity existed, we applied the following statistical model to the data:

$$A_{i,j} = b_0 + b_1D + I_j + \varepsilon_{i,j}$$

where $A_{i,j}$ is the space-average photosynthetic capacity of the j -th individual in the time i , D is a duration in days from a certain date to a measurement date, I_j is a random effect with variance σ_1^2 that is associated with the j -th individual, and $\varepsilon_{i,j}$ is a random error

having a variance σ^2 . For *Mallotus*, we used only data obtained in 2000 for this analysis.

Comparison between time-averaged and space-averaged photosynthetic capacity

In order to test whether the method of averaging (time-average vs. space-average) influences the estimate of average photosynthetic capacity, we fitted the following mixed-effects models. For *Alnus* and *Polygonum*, we fitted a mixed model:

$$A_{i,j,k} = b_0 + b_1M + I_i + L_{i,j} + \varepsilon_{i,j,k}$$

where $A_{i,j,k}$ is the average of the j -th leaf on the i -th individual, M is a bivariate variable representing the method of averaging ($M = 1$ for time-average and $M = 0$ for space-average), I_i and $L_{i,j}$ are random effects for individual stem and leaf within individual stem with variances σ_1^2 and σ_L^2 , respectively, and $\varepsilon_{i,j,k}$ is a random error with variance σ^2 . For *Mallotus*, we fitted the mixed model:

$$A_{i,j,k} = b_0 + b_1M + b_2Y + I_i + L_{i,j} + \varepsilon_{i,j,k}$$

where Y is a bivariate variable representing the measurement year ($Y = 0$ for 1999 and $Y = 1$ for 2000). For *Helianthus*, we fitted the the mixed model:

$$A_{i,j,k} = b_0 + b_1M + b_3D + I_i + L_{i,j} + \varepsilon_{i,j,k}$$

where D is planting density.

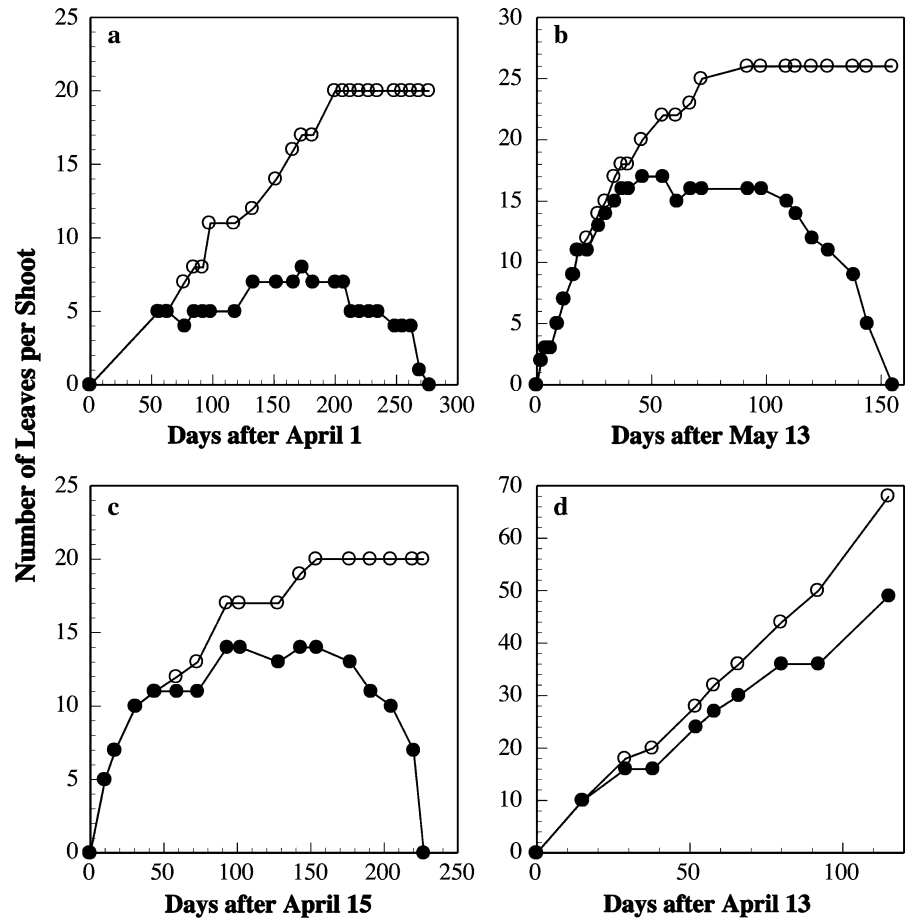
In order to fit these models, we used the function `lme()` in R (R Development Core Team, 2006) with the maximum likelihood method option (method = “ML”). We selected the “best” model using the Akaike Information Criterion (AIC) by comparing candidate models whose variables were a subset of the variables in the full model.

Results

Canopy development

Leaf emergence of *Alnus* occurred in early to mid-April, and the number of leaves increased until mid-May (for about 50 days) without leaf fall, stabilizing at about 5 leaves per shoot after which nearly constant new leaf emergence and abscission continued until late October (around 180 days from leafing out). Hence the period of dynamic stability when

Fig. 2 Changes in the cumulative number of leaves emerged (*open circle*) and the standing number of leaves actually attached (*closed circle*) on representative shoots of (a) *Alnus sieboldiana*, (b) *Polygonum sachalinensis*, (c) *Mallotus japonicus*, (d) *Helianthus tuberosus*



ergodicity might occur is about 130 days from late May to late October (Fig. 2a). As new leaf emergence ceased, leaf number was rather stable until the end of November because of less leaf-fall; this can be considered a statically stable phase, which is followed by canopy degradation after December to January in the next year.

Canopy expansion in *Polygonum* occurs in the first 30–40 days of the growing season, and the dynamically stable phase is from about 40 to 100 days (Fig. 2b), with no static stability phase and canopy degradation from about 100 to 150 days. In *Mallotus*, no leaf fall occurs within 50 days after leaf emergence (canopy expansion phase) and dynamic stability occurs from 50 days to 150 days (Fig. 2c); after 150 days, leaf number was statically stable for around 30 days and then degraded. Leaf fall started around 30 days in *Helianthus*, and the period from 30 to 120 days approached but never fully reached dynamic stability; new leaf emergence exceeded leaf

fall so leaf number was increasing (Fig. 2d). Because of the acropetal appearance of new leaves along the stem and the basipetal shedding of old leaves in the dynamic phase, the P_r of the focal leaf decreased with time in all four species (Fig. 3), but once new leaf emergence stopped, P_r changed little until canopy degradation began (Fig. 3a–c).

Photosynthetic capacity

The photosynthetic capacity was usually higher in younger leaves, and the photosynthetic capacity of a given leaf decreased over time (Fig. 4). Since the decrease in P_r (Fig. 3) corresponded to the decrease in A_{\max} (Fig. 4) with time, A_{\max} can be expressed as the function of P_r (Eq. 2), as shown in Fig. 5, as positive, significant linear correlations. The dependency of A_{\max} on P_r differs among species (Fig. 5), reflecting the degree of self and mutual shading. In *Helianthus*, coefficients of determination (r^2) and

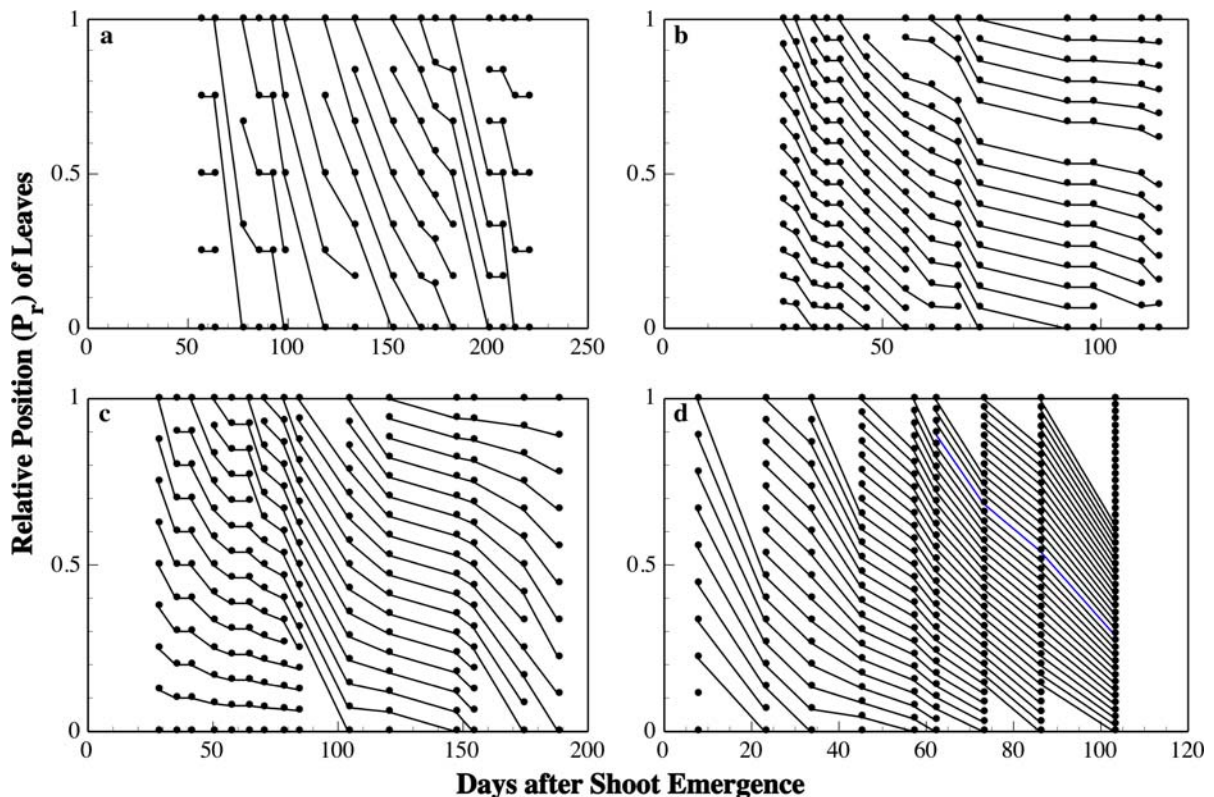


Fig. 3 Changes in the relative position (P_r) of leaves on a shoot with time since shoot emergence. (a) *Alnus sieboldiana*, (b) *Polygonum sachalinensis*, (c) *Mallotus japonicus*, and (d) *Helianthus tuberosus*. A representative shoot of each species is

shown. Shoot position was calculated as $P_r = (i-1)/(N-1)$, where N is the total number of leaves on a shoot, and i is the order from the shoot base of leaves attaching the shoot

gradients (b) of regression of photosynthetic capacity (A_{\max}) against relative position (P_r) were greater in denser plots (0.486, 14.1 for 5-stems/m², 0.732, 17.6 for 25-stems/m², and 0.763, 21.4 for 100 stems/m²). For *Alnus*, *Mallotus*, and *Helianthus*, the model with the relative position of leaf used as an explanatory variable had a smaller AIC than the model with the leaf age as an explanatory variable (Table 1), indicating that the A_{\max} had a closer relationship with the relative position than with leaf age. For *Polygonum*, the model with the relative position of leaf used as an explanatory variable had a larger AIC than the model with the leaf age as an explanatory variable.

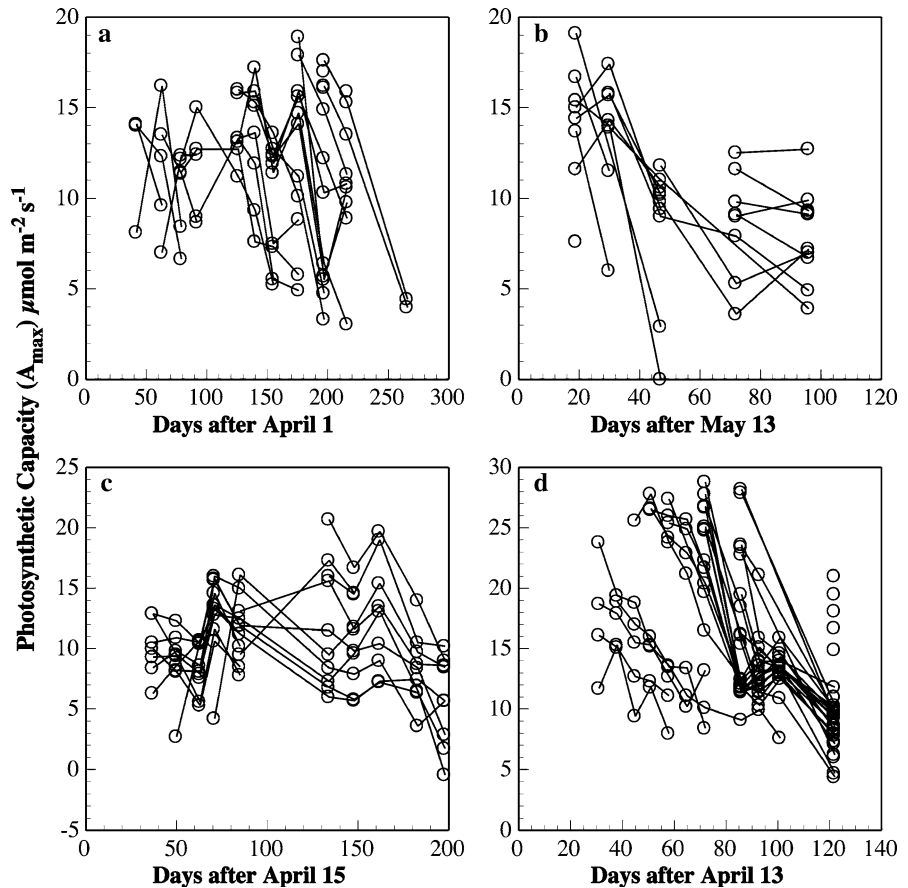
During the dynamic stability phase, a shoot has leaves of different ages (Fig. 3) and thus different photosynthetic capacities (Fig. 4). Hence, the average photosynthetic capacity per shoot (space average) did not vary greatly different with time in the dynamic stability phase (Fig. 6). The space-averaged photosynthetic capacity decreased in the degrading phase

(Fig. 6a, d), and tended to be higher in the expansion phase (Fig. 6b). If some measurements at the expanding or the degrading phases are excluded from the analysis, no temporal trend in space-averaged photosynthetic capacity was found; this is the case when omitting the last measurement for *Alnus*, the first two measurements for *Polygonum*, and the first and the last four measurements for *Helianthus* (Table 2).

Comparison between time-averaged and space-averaged photosynthesis

For *Alnus*, *Mallotus*, and *Helianthus*, the “best” model explaining average photosynthetic capacity did not contain the method of averaging (time-average vs. space-average), indicating that the time average and space average did not differ significantly. The “best” model, however, did include the method of averaging for *Polygonum* (Table 3); the space

Fig. 4 Changes in the maximum photosynthetic rate of each leaf on a shoot with time. Photosynthetic rates of the same leaf are connected by lines. (a) *Alnus sieboldiana*, (b) *Polygonum sachalinensis*, (c) *Mallotus japonicus*, and (d) *Helianthus tuberosus*. The photosynthetic rate of a representative shoot of each species is shown



average was greater than the time average for *Polygonum*. In scatter plots of the time average for photosynthetic capacity and the corresponding space average, the data points fell along a line of equality ($Y = X$) for *Alnus*, *Mallotus*, and *Helianthus* (Fig. 7a, c, d), but tended to be above the line for *Polygonum* (Fig. 7b).

Discussion

An essential premise of the canopy ergodic hypothesis is that a single leaf typically exists in a series of light conditions over its lifespan, a long-recognized fact (Kira 1975) affirmed in this study. In all the four species we studied, the relative position of a focal leaf on a shoot during the expanding and dynamic stability phases in the canopy decreased with time as the leaf “moved” from the outer edge of the growing canopy “down” to its deep interior. In response to this change in ambient light, a focal leaf can be

expected to adjust its photosynthetic ability by reallocating limiting resources as its potential for photosynthetic gains declines (Field 1983; Hikosaka and Terashima 1995). This dependency of photosynthetic capacity (A_{\max}) on the leaf position (P_r) differs among our study species, probably reflecting the degree of self-shading imposed by canopy architecture, and in the case of high-density plantings of *Helianthus*, a degree of shading by neighbors as well.

There was variation in canopy architecture among the species where only self-shading prevailed: shoots of *Alnus* grew more vertically and shoots of *Mallotus* and *Polygonum* grew more horizontally. Self-shading should therefore be greater in *Alnus* (Kikuzawa et al. 1996), and may contribute to the observed differences in the dependency of A_{\max} on P_r . Despite quantitative differences in A_{\max} on P_r relationship among species, all the study species qualitatively satisfy the requirement for a change in foliar photosynthetic capacity as a leaf ages and changes position in an expanding canopy.

Fig. 5 Relationships between maximum photosynthetic rate (A_{\max}) and relative position of leaves (P_r). **(a)** *Alnus sieboldiana*, $A_{\max} = 8.63P_r + 6.46$ ($\mu\text{mol m}^{-2} \text{s}^{-1}$), $r^2 = 0.359$ ($P < 0.0001$), **(b)** *Polygonum sachalinensis*, $A_{\max} = 4.28P_r + 7.79$, $r^2 = 0.128$ ($P < 0.0001$), **(c)** *Mallotus japonicus*, $A_{\max} = 4.48P_r + 8.83$, $r^2 = 0.153$ ($P < 0.0001$), and **(d)** *Helianthus tuberosus*, $A_{\max} = 11.75P_r + 6.19$, $r^2 = 0.596$ ($P < 0.0001$)

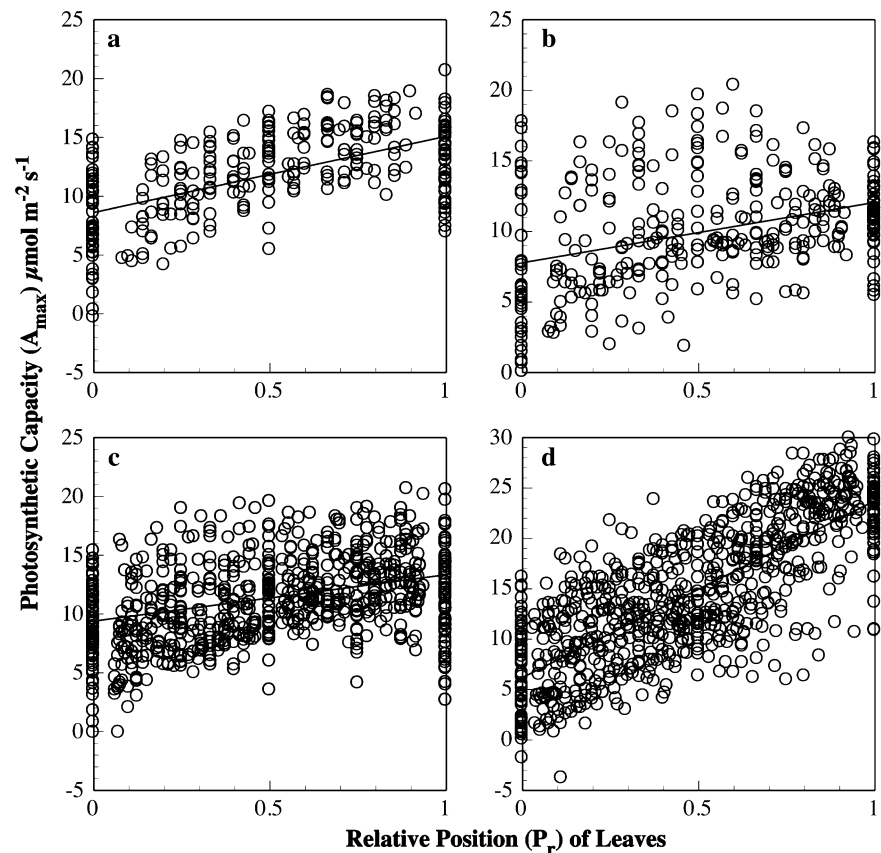


Table 1 Coefficients of regression* of the light-saturated photosynthetic rates on the relative position of the leaf and leaf age

Species	Explanatory variable	p	q	r^2	AIC
<i>Alnus</i>	Relative position	9.1317 (0.6233)	7.9233 (0.3044)	0.4742	1172.655
	Leaf age	-0.100770 (0.008035)	16.682839 (0.452412)	0.3979	1205.160
<i>Polygonum</i>	Relative position	4.2760 (0.6179)	7.7904 (0.3722)	0.1277	1802.051
	Leaf age	-0.114056 (0.008554)	14.067798 (0.357117)	0.3529	1699.334
<i>Mallotus</i>	Relative position	5.7209 (0.4144)	7.5232 (0.2449)	0.2952	2238.970
	Leaf age	-0.037361 (0.004751)	13.115107 (0.376718)	0.1196	2340.599
<i>Helianthus</i>	Relative position	19.9689 (0.9774)	5.8522 (0.3647)	0.5786	1745.630
	Leaf age	-0.23348 (0.01469)	19.04030 (0.54668)	0.4538	1825.014

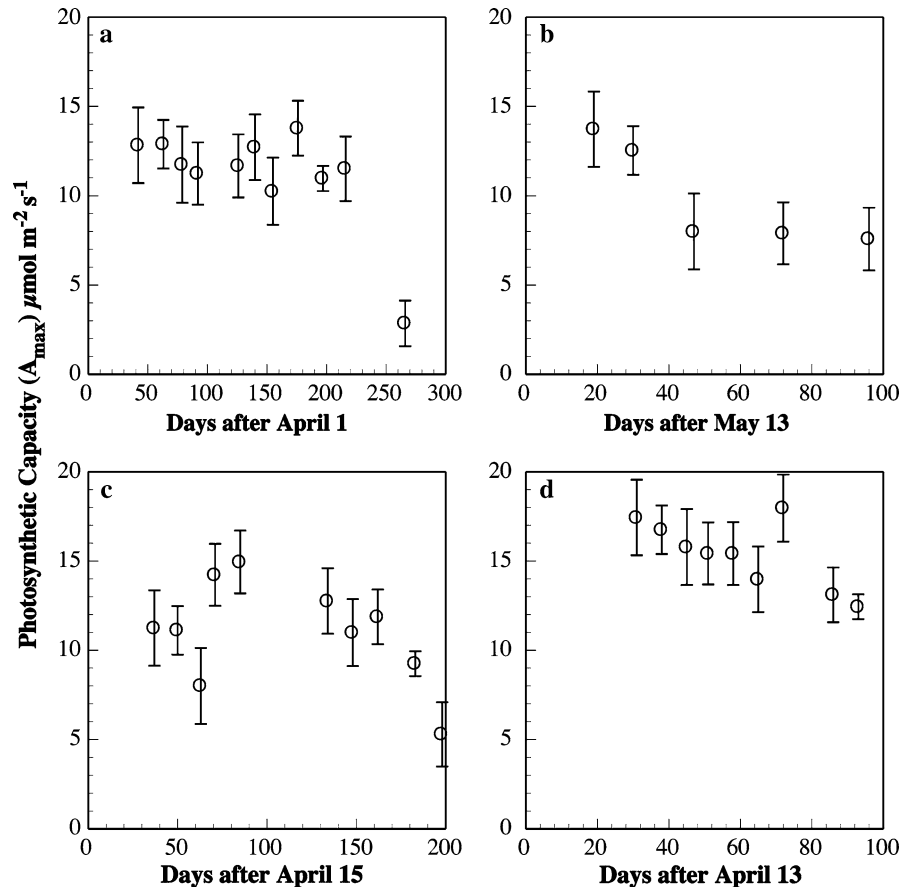
* Regression models are $A_{\max} = p P_r + q$ or $A_{\max} = p L + q$, where A_{\max} is the light-saturated photosynthetic rate, P_r is relative position of a leaf within a shoot, L is leaf age in days, and p and q are regression coefficients

Numbers in parenthesis are the standard errors of the corresponding estimates

There is an inherent space–time correspondence in the biology of canopy expansion: the more basipetal leaves on a growing shoot are older than the more apical. The decline of photosynthetic capacity of a single leaf with time is a universal trend (Sestak 1981; Kitajima et al. 1997, 2002; Mediavilla and

Escudero 2003; Koike 1990) found in both herbaceous (Thomas and Stoddart 1980; Hodanova 1981) and woody plants (Koike 1990; Kikuzawa 2003). This decline has usually been attributed to the degradation of leaf function with age, and it can also be explained by acclimation to microenvironmental

Fig. 6 Changes in the average maximum photosynthetic rate (space-average) with time. Average values with s.d. are shown. Except for the latest (or earliest) measurements, there were no significant differences among space averages with time in each species. **(a)** *Alnus sieboldiana*, **(b)** *Polygonum sachalinensis*, **(c)** *Mallotus japonicus*, and **(d)** *Helianthus tuberosus*



change around a leaf in the canopy, especially insolation (Hodanova 1981; Hikosaka et al 1994; Kikuzawa 2003). The decline in photosynthetic capacity with time may reflect an age-dependent decline in investments for maintaining leaf function that is optimized at the whole-canopy level (Hikosaka et al. 1994; Hikosaka 2005), a possibility providing a functional rationale for ergodicity. Mooney and Gulmon (1979) suggested that the photosynthetic capacity is saturated at lower nitrogen content at lower light condition than at higher light condition and hence that greater investment of nitrogen for photosynthetic machinery in darker condition is not advantageous for plants. Field (1983) proposed a model predicting the optimal daily photosynthetic gain by investing nitrogen for each leaf in accordance with the light capture by each leaf. Furthermore, Hirose and Werger (1987) proposed an optimum nitrogen allocation model that maximized carbon gain and tested the model for some herbaceous communities. It is advantageous for plants to

reallocate nitrogen from lower leaves in darker conditions and to transport it to upper leaves in brighter conditions (Hirose 2005; Hikosaka 2005), although real nitrogen allocation does not always follow predicted optimal allocations (Hollinger 1996; Hikosaka 2005). We conclude that the decline of maximum photosynthetic capacity with time is due to these sort of adjustments of resource allocation to each leaf to maximize carbon gain at the whole-canopy level. This is concordant with both the decline of maximum photosynthetic capacity with leaf position for leaves in our study species and with the premises of the canopy ergodicity hypothesis.

Do our data then support the ergodic hypothesis?

The deciding test for ergodicity is whether or not the average photosynthetic capacity of a single leaf throughout its life is equivalent to the average photosynthetic capacity of a canopy at a given time. During the large part of the growing season when leaf

Table 2 Results of the analysis to detect temporal trend in time-averaged photosynthetic rate

Species	Parameter	Estimate	Standard error	P-value
<i>Alnus</i>	b_0	12.125409	0.6503501	0.0000
	b_1	-0.000761	0.0045357	0.8676
	σ_1	0.3015614		
	σ	1.749651		
<i>Polygonum</i>	b_0	8.945152	0.8396431	0.0000
	b_1	-0.014988	0.0114287	0.2143
	σ_1	0.5084955		
	σ	0.9774309		
<i>Mallotus</i>	b_0	10.625986	0.5460790	0.0000
	b_1	-0.001931	0.0051355	0.7094
	σ_1	5.287708e-05		
	σ	1.408011		
<i>Helianthus</i>	b_0	16.310498	1.955776	0.0000
	b_1	-0.023424	0.023258	0.3225
	σ_1	4.067514		
	σ	1.486436		

numbers in the canopy are at or near stability, this is the case for both woody species that we studied, *Alnus* and *Mallotus*. In herbaceous species, the situation is less certain. The dynamically stable phase in canopy development in *Polygonum* was brief, only about 60 days; the space-averaged and time-averaged

photosynthetic capacities in *Polygonum* correlated consistently, but space-averaged values were significantly greater than the time-averaged ones. This deviation from expectation may arise in the greater insolation of all leaves in the canopies of the spatially isolated *Polygonum* plants that we studied. That possibility is consistent with our results in the *Helianthus* plants that we studied, which grew in crowded populations. The space and time averages for photosynthetic capacity in *Helianthus* were not significantly different, despite the fact that leaf numbers never entirely stabilized in the steadily expanding canopy. On balance, we believe that acclimation of leaf function and canopy development may generally be coordinated under a principle of ergodicity, but that possibility requires testing across a wider range of species and environments.

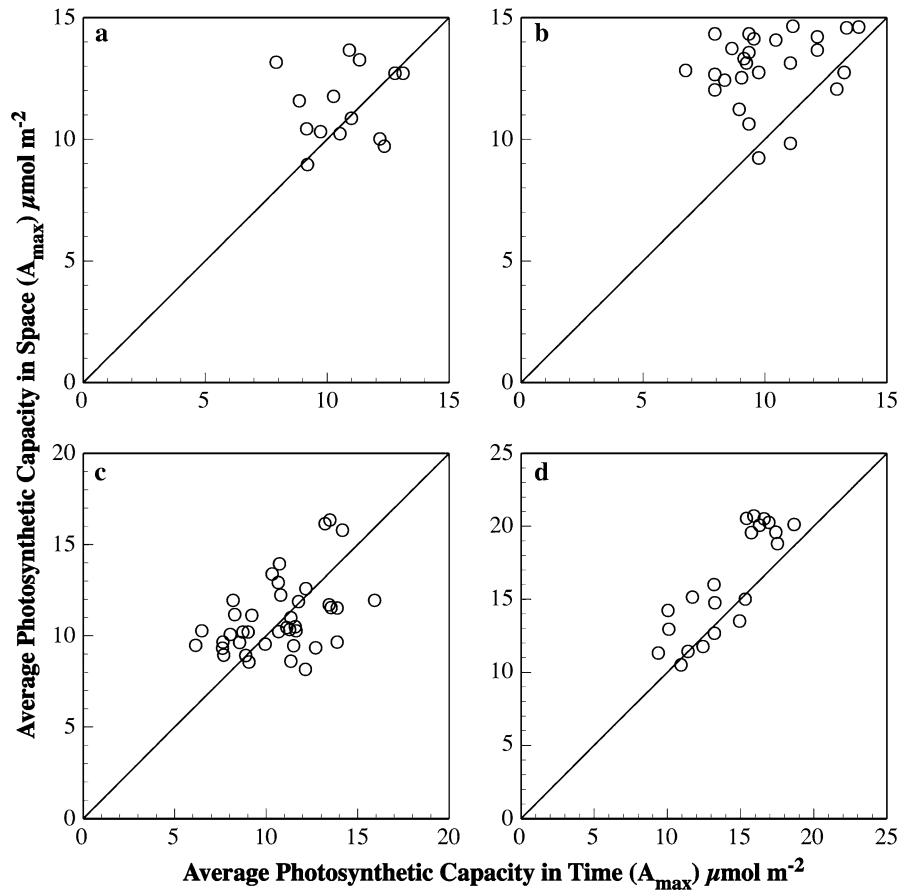
Our initial tests of the canopy ergodicity hypothesis have focused on woody and herbaceous species with successive leafing during development of their canopies. There are many species in which the canopy in a given year develops as a simultaneous flush of new leaves so that there is no change in the relative position of each leaf through a growing season (Kikuzawa 1983, 2003). Within a single year, this would seem to undercut the functional rationale proffered for the ergodic effect, but in these instances, ergodicity might still apply to the acclimation of the leaf function across years in the

Table 3 Maximum likelihood estimate of the parameters in the “best” model*

Species	Parameter	Estimate	Standard error	t-value (d.f.)	P-value
<i>Alnus</i>	b_0	11.125	0.426	26.123 (24)	<0.0001
	σ_1	0.628			
	σ	1.417			
<i>Polygonum</i>	b_0	12.996	0.447	29.062 (44)	<0.0001
	b_1	-2.759	0.394	-7.004 (44)	<0.0001
	σ_1	0.894			
	σ	1.392			
<i>Mallotus</i>	b_0	11.794	0.446	26.461 (39)	<0.0001
	b_2	-1.687	0.594	-2.838 (6)	0.0296
	σ_1	0.389			
	σ_L	1.104			
<i>Helianthus</i>	σ	1.616			
	b_0	18.108	1.107	16.364 (39)	<0.0001
	b_3	-0.062	0.019	-3.311 (1)	0.1867
	σ_1	1.241			
	σ	1.278			

* b_0 is the intercept; b_1 is the coefficient for the averaging method; b_2 is the coefficient for the measurement year; b_3 is the coefficient for planting density; σ_1^2 is a variances of a random effect for individual; σ_L^2 is a variances of a random effect for leaf within individual; σ^2 is a variance of random error

Fig. 7 Comparison of average photosynthetic capacity of a single leaf through time (time average) and average photosynthetic capacity of a shoot based on all its leaves at a given time (space average). **(a)** *Alnus sieboldiana*, **(b)** *Polygonum sachalinensis*, **(c)** *Mallotus japonicus*, and **(d)** *Helianthus tuberosus*



annually expanded canopy of woody species. Graminoids are another example of a growth form in which the canopy ergodicity hypothesis might be expected to fail, because the fundamentally different organization of canopy growth in graminoids violates the assumptions of the hypothesis. The space–time equivalence inherent to the hypothesis assumes that leaves appear successively from apical meristems situated at the top of growing shoots that progressively shade leaves below them as the canopy expands. With the exception of the bamboos, graminoid leaves appear from a basal meristem and the plant canopy has a vertically organized structure that minimizes self-shading (Hirose et al. 1989). In this case, it will be hard to apply the rationale developed in this paper.

For woody plants, and particularly for large trees, the influence of canopy structure on ergodicity is also more complicated than in herbaceous forbs. The ergodic effect may or may not apply for leaves displayed on branch systems that develop and persist

over long time spans. Shoot emergence does not start from the soil surface as in a stem of herbaceous plants, but rather from meristems situated throughout the persistent, woody canopy structure (Ishihara and Kikuzawa 2004). Within a single growing shoot, new leaves are situated acropetally to older leaves (Miyazawa and Kikuzawa 2004), but individual shoots are situated at various depths in the woody canopy. Hence, the tree canopy as a whole is a mosaic of new and old leaves. Although new leaves are not always found only at the top of the canopy (Kitajima et al. 2005), new shoots represent only a very small part of the total tree canopy (Maillette 1982a, b); therefore, in a single year, a tree canopy is akin to an herb with flushing growth habit. We might assume that over time periods that exceed a single growing season, it is the branches in a woody canopy that are the unit of ergodicity rather than the leaves. Shoots and branches are known to be shed within a year and recruited (Ishii and Ford 2001; Seiwa et al. 2006). Fujiki and Kikuzawa (2006) proposed a model

of stem replacement that would maximize the reproductive success of an individual plant. Testing this possibility experimentally will require many measurements over many years, but in principle, the test is possible. It would be immediately more useful first to test the ergodicity of photosynthetic capacity in additional annual and perennial herbs.

Acknowledgements We thank Iwao Kojima for preparing the site and helping the experiments. The work was partly supported by a Grant in Aid from the Japanese Ministry of Education, Culture, Sports, Science and Technology to K.K. (#09304073 and #11213202) and by funds from the Natural Sciences and Engineering Council of Canada to MJL.

References

- Field C (1983) Allocating leaf nitrogen for the maximization of carbon gain: leaf age as a control on the allocation program. *Oecologia* 56:341–347. doi:[10.1007/BF00379710](https://doi.org/10.1007/BF00379710)
- Fujiki D, Kikuzawa K (2006) Stem turnover strategy of multiple-stemmed woody plants. *Ecol Res* 21:380–386. doi:[10.1007/s11284-006-0169-7](https://doi.org/10.1007/s11284-006-0169-7)
- Hikosaka K (2005) Leaf canopy as a dynamic system: Eco-physiology and optimality in leaf turnover. *Ann Bot (Lond)* 95:521–533. doi:[10.1093/aob/mci050](https://doi.org/10.1093/aob/mci050)
- Hikosaka K, Terashima I (1995) A model of acclimation of photosynthesis in the leaves of C₃ plants to sun and shade with respects to nitrogen use. *Plant, Cell Environ* 18:605–618
- Hikosaka K, Terashima I, Katoh S (1994) Effects of leaf age, nitrogen nutrition and photon flux density on the distribution of nitrogen among leaves of a vine (*Ipomoea tricolor* Cav.) grown horizontally to avoid mutual shading of leaves. *Oecologia* 97:451–457. doi:[10.1007/BF00325881](https://doi.org/10.1007/BF00325881)
- Hirose T (2005) Development of the Monsi-Saeki theory on canopy structure and function. *Ann Bot (Lond)* 95:483–494. doi:[10.1093/aob/mci047](https://doi.org/10.1093/aob/mci047)
- Hirose T, Werger MJA (1987) Maximizing daily canopy photosynthesis with respect to the leaf nitrogen allocation pattern in the canopy. *Oecologia* 72:520–526. doi:[10.1007/BF00378977](https://doi.org/10.1007/BF00378977)
- Hirose T, Werger MJA, Van Rheenen WA (1989) Canopy development and leaf nitrogen distribution in a stand of *Carex acutiformis*. *Ecology* 70:1610–1618. doi:[10.2307/1938094](https://doi.org/10.2307/1938094)
- Hodanova D (1981) Photosynthetic capacity, irradiance and sequential senescence of sugar beet leaves. *Biol Plant* 23:58–67. doi:[10.1007/BF02909212](https://doi.org/10.1007/BF02909212) Praha
- Holbrook NM, Lund CP (1995) Photosynthesis in forest canopies. In: Lowman MD, Nadkarni NM (eds) *Forest canopies*. Academic Press, London, pp 411–430
- Hollinger DY (1989) Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. *Funct Ecol* 3:53–62. doi:[10.2307/2389675](https://doi.org/10.2307/2389675)
- Hollinger DY (1996) Optimality and nitrogen allocation in a tree canopy. *Tree Physiol* 16:627–634
- Ishihara M, Kikuzawa K (2004) Species-specific variation in shoot production patterns of five birch species with respect to vegetative and reproductive shoots. *Can J Bot* 82:1393–1401. doi:[10.1139/b04-099](https://doi.org/10.1139/b04-099)
- Ishii H, Ford ED (2001) The role of epicormic shoot production in maintaining foliage in old *Pseudotsuga menziesii* (douglas-fir) trees. *Can J Bot* 79:251–264. doi:[10.1139/cjb-79-3-251](https://doi.org/10.1139/cjb-79-3-251)
- Kikuzawa K (1983) Leaf survival of woody plants in deciduous broad-leaved forests. 1. Tall trees. *Can J Bot* 61:2133–2139
- Kikuzawa K (2003) Phenological and morphological adaptations to the light environment in two woody and two herbaceous plant species. *Funct Ecol* 17:29–38. doi:[10.1046/j.1365-2435.2003.00707.x](https://doi.org/10.1046/j.1365-2435.2003.00707.x)
- Kikuzawa K, Koyama H, Umeki K, Lechowicz MJ (1996) Some evidence for an adaptive linkage between leaf phenology and shoot architecture in sapling trees. *Funct Ecol* 10:252–257
- Kikuzawa K, Lechowicz MJ (2006) Towards a synthesis of relationships among leaf longevity, instantaneous photosynthetic rate, lifetime leaf carbon gain and the gross primary production of forests. *Am Nat* 168:373–383. doi:[10.1086/506954](https://doi.org/10.1086/506954)
- Kira T (1975) Primary production of forests. In: Cooper JP (ed) *Photosynthesis and productivity in different environments*. Cambridge University Press, Cambridge, pp 5–40
- Kitajima K, Mulkey SS, Wright SJ (1997) Decline of photosynthetic capacity with leaf age in relation to leaf longevities for five tropical canopy tree species. *Am J Bot* 84:702–708. doi:[10.2307/2445906](https://doi.org/10.2307/2445906)
- Kitajima K, Mulkey SS, Samaniego M, Wright SJ (2002) Decline of photosynthetic capacity with leaf age and position in two tropical pioneer tree species. *Am J Bot* 89:1925–1932. doi:[10.3732/ajb.89.12.1925](https://doi.org/10.3732/ajb.89.12.1925)
- Kitajima K, Mulkey SS, Wright SJ (2005) Variation in crown light utilization characteristics among tropical canopy trees. *Ann Bot (Lond)* 95:535–547. doi:[10.1093/aob/mci051](https://doi.org/10.1093/aob/mci051)
- Koike T (1990) Autumn coloring, photosynthetic performance and leaf development of deciduous broad-leaved trees in relation to forest succession. *Tree Physiol* 7:21–32
- Maillette L (1982a) Structural dynamics of silver birch 1. The fates of buds. *J Appl Ecol* 19:203–218. doi:[10.2307/2403005](https://doi.org/10.2307/2403005)
- Maillette L (1982b) Structural dynamics of silver birch 2. A matrix model of the bud population. *J Appl Ecol* 19:219–238. doi:[10.2307/2403006](https://doi.org/10.2307/2403006)
- Mediavilla S, Escudero A (2003) Photosynthetic capacity, integrated over the lifetime of a leaf, is predicted to be independent of leaf longevity in some tree species. *New Phytol* 159:203–211. doi:[10.1046/j.1469-8137.2003.00798.x](https://doi.org/10.1046/j.1469-8137.2003.00798.x)
- Miyazawa Y, Kikuzawa K (2004) Phenology and photosynthetic traits of short shoots and long shoots in *Betula grossa*. *Tree Physiol* 24:631–637
- Monsi M, Saeki T (1953) Über den Lichtfaktor in den Pflanzengesellschaften und seine Bedeutung für die Stoffproduktion. *Jpn J Bot* 14:22–52
- Mooney HA, Gulmon SL (1979) Environmental and evolutionary constraints on the photosynthetic characteristics of

- higher plants. In: Solbrig OT, Jain S, Johnson GB, Raven PH (eds) Topics in plant population biology. Columbia University Press, NY, USA, pp 316–337
- Reich PB (1984) Relationships between leaf age, irradiance, leaf conductance, CO₂ exchange, and water-use efficiency in hybrid poplar. *Photosynthetica* 18:445–453
- Seiwa K, Kikuzawa K, Kadowaki T, Akasaka S, Ueno N (2006) Shoot life span in relation to successional status in deciduous broad-leaved tree species in a temperate forest. *New Phytol* 169:537–548
- Sestak Z (1981) Leaf ontogeny and photosynthesis. In: Johnson CB (ed) Physiological processes limiting plant growth. Butterworths Co., London, pp 147–158, 395 pp
- Thomas H, Stoddart JL (1980) Leaf senescence. *Annu Rev Plant Physiol* 31:83–111. doi:[10.1146/annurev.pp31.060180.000503](https://doi.org/10.1146/annurev.pp31.060180.000503)
- Tolman RC (1979) The principle of statistical mechanics. Dover Publications, NY, 358 pp