

Toward Synthesis of Relationships among Leaf Longevity, Instantaneous Photosynthetic Rate, Lifetime Leaf Carbon Gain, and the Gross Primary Production of Forests

Kihachiro Kikuzawa* and Martin J. Lechowicz†

1. Laboratory of Plant Ecology, Ishikawa Prefectural University, Nonoichimachi, Ishikawa 921-8836, Japan;
2. Department of Biology, McGill University, 1205 Dr. Penfield Avenue, Montreal, Quebec H3A 1B1, Canada

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ABSTRACT: The assimilation of carbon by plant communities (gross primary production [GPP]) is a central concern in plant ecology as well as for our understanding of global climate change. As an alternative to traditional methods involving destructive harvests or time-consuming measurements, we present a simple, general model for GPP as the product of the lifetime carbon gain by a single leaf, the daily leaf production rate, and the length of the favorable period for photosynthesis. To test the model, we estimated leaf lifetime carbon gain for 26 species using the concept of mean labor time for leaves (the part of each day the leaf functions to full capacity), average potential photosynthetic capacity over the leaf lifetime, and functional leaf longevity (leaf longevity discounted for periods within a year wholly unfavorable for photosynthesis). We found that the lifetime carbon gain of leaves was rather constant across species. Moreover, when foliar biomass was regressed against functional leaf longevity, aseasonal and seasonal forests fell on a single line, suggesting that the leaf production rate during favorable periods is not substantially different among forests in the world. The gross production of forest ecosystems then can be predicted to a first approximation simply by the annual duration of the period favorable for photosynthetic activity in any given region.

Keywords: leaf longevity, functional leaf longevity, mean labor time of a leaf, lifetime leaf carbon gain, gross primary production.

* Corresponding author; e-mail: kikuzawa@ishikawa-pu.ac.jp.

† E-mail: martin.lechowicz@mcgill.ca.

Rates of carbon assimilation by plant communities (gross primary production [GPP]) arise in the aggregate behavior of the leaves of many species arrayed in complex three-dimensional canopies that vary substantially from one habitat or ecosystem to another. There is no shortage of comparative data on either the functional ecology of leaves (Wright et al. 2004) or the variation in GPP (Olson et al. 2001). The challenge is to understand how variation within and among species scales up through community assembly and species interactions to affect the productivity of vegetation at a site (Ehleringer and Field 1993; Adams et al. 2004). One approach has been to opt for top-down estimates using satellite data (Running et al. 2004); this meets the needs of global systems modelers but steps aside from the questions of mechanism and functional diversity involved in scaling up productivity from leaf to canopy. Another approach is to collapse species into functional groups to simplify the scaling, but it remains unclear the degree to which interspecific variation can or should be ignored (Díaz and Cabido 2001). Others have noted the relative invariance of relationships among traits such as photosynthetic capacity, foliar nitrogen, leaf longevity, and leaf mass per unit area, suggesting the possibility of some sort of generalization across species (Reich et al. 1997; Wright et al. 2004). Building on similarly invariant relationships in metabolic scaling and ecological stoichiometry across species, Kerkhoff et al. (2005) derive general relationships between leaf- and canopy-level components of productivity. In this article, we explore the same relationships but with an emphasis on reconceptualizing foliar-level traits to facilitate a simple scaling to canopy-level productivity. We seek to provide a refined framework for the analysis of leaf-level traits by physiological ecologists that has a more direct functional connection to canopy-level traits that are relevant to global change models.

We begin by building on a consistent negative relationship between leaf longevity (L) and the instantaneous max-

imum photosynthetic rate of young but fully mature leaves ($A_{\max}(0)$) that is very well supported by broad-based comparisons among plant species (Reich et al. 1991, 1992, 1999; Wright et al. 2004). If these two variables are exactly inversely proportional across species, then the product of L and $A_{\max}(0)$ will be independent of L (Westoby et al. 2000; Mediavilla and Escudero 2003). In fact, however, the slope of this relationship on a double-logarithmic scale is significantly greater than -1 (Reich et al. 1999; Wright et al. 2004). Hence, the cumulative carbon gain of a leaf over its lifetime, which is the product of these two variables, appears to increase with L (Chabot and Hicks 1982; Gower et al. 1993; Mediavilla and Escudero 2003). To rationalize this result, Westoby et al. (2000) argued that the future persistence of leaf area should be considered less valuable than immediate production of leaf area. Alternatively, Mediavilla and Escudero (2003) argued the necessity of reparameterizing the relationship and suggested using A_{\max} averaged over the life span of a leaf (\bar{A}_{\max}) rather than the usual $A_{\max}(0)$. Taking this approach, they found that the product of \bar{A}_{\max} and L was independent of L for nine tree species in a Mediterranean climate. In this article, we take up this idea that changing the measurements we make to assess foliar function will yield deeper and more useful insights into the regulation of plant productivity. We consider two working hypotheses: first, the possibility that all leaves have a constant lifetime carbon gain, which in turn would suggest, second, that foliar function across species may be essentially constant.

Kikuzawa et al. (2004) recently proposed a new concept expressed by the ratio of mean daily photosynthesis averaged over leaf lifetime and the hypothetical mean daily photosynthesis, assuming that leaves always operated at A_{\max} . This ratio, the mean labor time of a leaf (m), estimates the realized utility of a leaf—the daily time period that a leaf actually works to its full capacity (A_{\max}). Here we suggest that A_{\max} should be multiplied by this discounting factor m to obtain daily carbon gain and in turn estimate the lifetime photosynthetic gain of a leaf. Kikuzawa et al. (2004) analyzed m as the product of four interacting effects: diel change in solar angle, changes in weather conditions (clear, cloudy, and overcast days), shading (by neighbors, self-shading), and the midday and afternoon depression of photosynthesis. Unfortunately, estimating these effects directly is tedious and prone to error. In this article, we propose an alternative method to obtain m using Kikuzawa's (1991) equation for the optimum timing of leaf replacement.

Calculating lifetime carbon gain only as the product of daily photosynthetic gain and L , however, can result in an overestimation if seasonal conditions restrict photosynthetic activity to a favorable period of the year. For example, while evergreen trees in temperate and boreal

regions retain their leaves through winter, low temperatures preclude significant carbon assimilation (Schulze et al. 1977; Körner and Paulsen 2004). Even in Mediterranean climates where seasonal temperatures are mild, very little carbon assimilation was measured on sunny days in winter for evergreen oak trees (Mediavilla and Escudero 2003). Current compilations and analyses of L do not discount the length of the unfavorable period for photosynthesis for species in strongly seasonal climates (cf. Wright et al. 2004). Here we propose the concept of functional leaf longevity (L_f) that discounts the calendar life span of leaves for the times wholly unfavorable to photosynthesis.

Building on these new concepts of m and L_f , we reassess the relationships at the leaf level that underpin productivity in forest communities and ecosystems. First, we examine lifetime carbon gain by single leaves of 26 species by using data on the maximum photosynthetic rate for young leaves, $A_{\max}(0)$, the decline of photosynthetic rate with leaf age, favorable period length (f) for photosynthesis, and L . Using these data, we calculate an average A_{\max} (\bar{A}_{\max}), m , and L_f to model lifetime carbon gain for each species. Second, we apply a similar temporal discounting approach to the estimation of leaf production rates and reexamine the relationship between leaf biomass and L_p , the slope of which represents leaf production rate. We will propose a constant leaf production hypothesis that leaf production rate among different forests across the world is essentially constant during periods favorable to photosynthesis and growth. Finally, we present a simple general model for GPP in forests by using average A_{\max} , m , L_p , and f and production of leaf biomass.

Theories, Models, and Concepts

The A_{\max} -L Relationship

Our synthesis and revision of ideas about the relationships among L , instantaneous photosynthetic rate, lifetime leaf carbon gain, and the GPP of forests begins with the observation that the slope of the relationship between the potential photosynthetic rate of young leaves $A_{\max}(0)$ and L on a log-log scale is greater than -1 (Reich et al. 1991, 1992, 1999; Wright et al. 2004). The product of $A_{\max}(0)$ and L cannot be an effective index of leaf lifetime carbon gain, as is commonly assumed, for three reasons. First, as pointed out by Mediavilla and Escudero (2003), A_{\max} usually changes with time, and hence A_{\max} averaged over the leaf lifetime should be used in assessing potential carbon gains over the leaf lifetime. Second, because A_{\max} normally cannot be maintained throughout a day, m (Kikuzawa et al. 2004) should be applied to discount potential daily photosynthesis. Finally, the number of days when leaves

are actually able to photosynthesize (L_f) should be considered, not L based on a calendar period that includes unfavorable days.

Average of A_{\max}

We express A_{\max} (g carbon per unit leaf mass in carbon equivalent per unit time; ng C g C⁻¹ s⁻¹) as a decreasing function with time (t ; days):

$$A_{\max}(t) = A_{\max}(0) \left(1 - \frac{t}{b}\right). \quad (1)$$

At time t , A_{\max} can be estimated from $A_{\max}(0)$ and the constant b , which is the potential L (days) at which the photosynthetic rate becomes 0. Note that labels, units, and definitions are summarized in table 1; in this article, dry mass of leaves and photosynthetic rate are converted to carbon equivalents by using 1 mol CO₂ = 12 g C = 30 g dry mass. Substituting the actual L for t in equation (1), we obtain A_{\max} at the time of leaf fall ($A_{\max}[\text{fall}]$). In the simplest situation, we can obtain an average of A_{\max} through time as the mean of $A_{\max}(0)$ and $A_{\max}(\text{fall})$ (Ackerly 1999):

$$\hat{A}_{\max} = A_{\max}(0) \left(1 - \frac{L}{2b}\right). \quad (2a)$$

Functional Leaf Longevity

We define L_f (days) as the time during the year that a leaf actually carries out photosynthesis. For evergreen leaves in seasonal environments, L_f is essentially L minus the length of unfavorable period, which may be dictated by adverse temperature or drought conditions. In the case of tree leaves in the wet tropics or deciduous leaves in seasonal climates, L is the same as L_f . Here we assume that leaves are dormant during unfavorable periods. Thus, equation (2a) is rewritten as

$$\hat{A}_{\max} = A_{\max}(0) \left(1 - \frac{L_f}{2b}\right). \quad (2b)$$

Mean Labor Time of a Leaf

Mean labor time of a leaf can be defined as a ratio of average daily carbon gain throughout the leaf life span and the hypothetical daily carbon gain, assuming that A_{\max} is maintained throughout a 24-h day (Kikuzawa et al. 2004).

Table 1: Labels and definitions

Labels	Unit	Definition
A_{\max}	ng C g C ⁻¹ s ⁻¹	Potential photosynthetic rate per unit leaf mass
$A_{\max}(0)$	ng C g C ⁻¹ s ⁻¹	A_{\max} of young fully mature leaf
$A_{\max}(t)$	ng C g C ⁻¹ s ⁻¹	A_{\max} at time t
$A_{\max}(\text{fall})$	ng C g C ⁻¹ s ⁻¹	A_{\max} at the time of leaf fall
\bar{A}_{\max}	ng C g C ⁻¹ s ⁻¹	Average A_{\max} through leaf life
A_{gmax}	ng C g C ⁻¹ s ⁻¹	Maximum gross photosynthetic rate
$a(0)$	mg C g C ⁻¹ day ⁻¹	Daily photosynthetic rate at time 0
$a(t)$	mg C g C ⁻¹ day ⁻¹	Daily photosynthetic rate at time t
B	g C m ⁻²	Leaf biomass of a forest stand
b	days	Potential leaf longevity when A_{\max} reaches 0
C	g C g C ⁻¹	Construction cost of a unit leaf per unit glucose
∂	h year ⁻¹	Duration of photosynthesis within a year
F	g C m ⁻² year ⁻¹	Annual leaf fall in a forest stand
f	days year ⁻¹	Favorable period length for photosynthesis
G	g C g C ⁻¹	Lifetime net carbon gain by a leaf
L	days	Leaf longevity in days
L_{yr}	years	Leaf longevity in year or the ratio of B and F
L_f	days	Functional leaf longevity
m	h day ⁻¹	Mean labor time of a leaf
P	g C m ⁻² year ⁻¹	GPP of a forest stand
p	g C m ⁻² day ⁻¹	Daily leaf production rate of a forest stand
r	ng C g C ⁻¹ s ⁻¹	Respiration rate per unit leaf mass
t_{opt}	days	Optimum timing of leaf replacement

Note: GPP = gross primary production.

Using the derivations that follow, we can estimate m (h day⁻¹) using optimum leaf longevity theory (Kikuzawa 1991). To maximize carbon gain by a plant, leaves should be replaced at the time when the marginal gain (gain per time) by the leaf is maximal. Daily carbon gain ($a[t]$; mg C g C⁻¹ day⁻¹) is a product of m and A_{\max} :

$$a(t) = m \times A_{\max}(t). \quad (3)$$

Because $m \neq 0$, substitution of equation (3) into equation (1) will give the following:

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

where $a(0)$ is daily carbon gain at the full expansion of a leaf.

The cumulative carbon gain from time 0 to t by a single leaf is expressed by

$$\int_0^t a(t) dt - C, \quad (5)$$

where C is construction cost of unit leaf mass in units of glucose. To maximize carbon gain per individual plant, marginal gain or the cumulative gain per time must be maximized (Bloom et al. 1985; Kikuzawa 1991). Thus, the equation

$$\frac{d}{dt} \frac{\int_0^t a(t) dt - C}{t} = 0$$

gives the optimal timing to maximize the carbon gain as the solution. If $a(t)$ is given by equation (4), the optimal timing will be given by the following (Kikuzawa 1991):

$$t_{\text{opt}} = \left[\frac{2bC}{a(0)} \right]^{0.5}. \quad (6)$$

Here we consider that actual L is optimized to realize maximum carbon gain:

$$L = t_{\text{opt}}. \quad (7)$$

We can estimate m using equations (3), (6), and (7) together:

$$m = \left[\frac{2bc}{A_{\max}(0)L^2} \right]. \quad (8)$$

In this expression, m has units of seconds per day, which are usually reexpressed as hours per day to better emphasize the part of each 24-h cycle during which a leaf functions at its full capacity.

Lifetime Carbon Gain

Given this reconceptualization of the variables defining leaf function, we can define the lifetime carbon gain (G ; g C g C⁻¹ leaf per leaf lifetime) by a single leaf as

$$G = m \times \hat{A}_{\max} \times L_f. \quad (9)$$

Leaf Biomass and Leaf Fall

To begin to relate leaf and canopy level, we note that after canopy closure, the leaf biomass of a forest stand typically reaches a stable condition in which annual leaf production is balanced by annual leaf fall (Waring and Running 1998). The ratio of standing leaf biomass and the biomass of annual leaf fall then gives an estimate of mean leaf longevity (L_{yr} ; years) for trees in the community:

$$L_{\text{yr}} = \frac{B}{F}, \quad (10)$$

where B is biomass of leaves (g C m⁻²) and F is annual leaf fall (g C m⁻² year⁻¹). The ratio of B and L_{yr} thus is equal to the ratio of F and f and can give an estimate for the mean (daily) production rate of leaves by a forest stand, p (g C m⁻² day⁻¹):

$$p = \frac{B}{L_f}. \quad (11)$$

GPP

GPP (g C m⁻² year⁻¹) of a plant community is the product of B , average maximum gross photosynthetic rate (\hat{A}_{gmax}), and its duration within a year:

$$\text{GPP} = B \hat{A}_{\text{gmax}} \partial,$$

where ∂ (h year⁻¹) is the duration of maximum photosynthetic rate throughout a year and \hat{A}_{gmax} is expressed by

$$\hat{A}_{\text{gmax}} = \hat{A}_{\max} + r$$

and r (ng C g C⁻¹ s⁻¹) is the average respiration rate of a leaf. For simplicity, we assume $\hat{A}_{\text{gmax}} = k \hat{A}_{\max}$, where k is

a constant of proportionality. This equation assumes that the respiration rate is proportional to the photosynthetic rate, which is reasonable. Then GPP is expressed by the following equation:

$$\text{GPP} = kB\hat{A}_{\max}\delta. \quad (12)$$

Under the assumptions that all leaves in a cohort appear and fall simultaneously and that leaf numbers are equivalent among cohorts, \hat{A}_{\max} is equal to the mean photosynthetic rate across all leaves in the canopy. The cumulative duration of photosynthetic rate δ within a year can be reduced to two components: the duration within a day (m) and the duration within a year (f):

$$\delta = mf. \quad (13)$$

Combining equations (12) and (13), we obtain

$$\text{GPP} = kBm\hat{A}_{\max}f. \quad (14)$$

To incorporate L_f into equation (14), we multiply the right-hand side of equation (14) by the identity L_f/L_f , yielding $\text{GPP} = [k(B/L_f)m\hat{A}_{\max}L_f f]$, and in turn by simplification using equations (11) and (9):

$$\text{GPP} = kpGf. \quad (15)$$

This suggests that the gross production of a plant community can be estimated as the product of p , G , and f within a year. If we take $k \times p \times G = K$, equation (15) reduces to

$$\text{GPP} = K \times f. \quad (16)$$

Methods and Data Sets

Species-Level Data for Testing the Postulated Relationships

We analyzed published data reporting $A_{\max}(0)$, b , L , and C , estimating C as 1.5 (Griffin 1994) if no value was reported. We have data from *Heliocarpus appendiculatus* (Ackerly and Bazzaz 1995), four canopy and two pioneer trees (Kitajima et al. 1997, 2002) in Panamanian seasonally dry forest, eight Mediterranean trees (Mediavilla and Escudero 2003), and five woody and two herbaceous plants in temperate Japan (Kikuzawa and Ackerly 1999; Kikuzawa 2003). We also used unpublished data on four tree species from temperate Japan: *Cleyera japonica* (K. Kikuzawa and M. Suzuki, unpublished data), *Mallotus japonicus*, *Cammellia japonica*, and *Quercus glauca* (K. Kikuzawa and Y. Miyazawa, unpublished data).

The Length of f

To estimate f , we followed Kerkhoff et al. (2005). A month was excluded from f when the difference between actual monthly precipitation and potential evapotranspiration (PET) calculated from monthly mean temperature using Thornthwaite's equation divided by PET (Kerkhoff et al. 2005) was less than -0.95 . For the months that were not too dry, the number of days with daily mean temperature exceeding 5°C (Menzel et al. 2003) was counted to give f (days year $^{-1}$). We used mean daily and monthly temperature and monthly precipitation data described in each article or data from a nearby weather station. Temperature data were corrected for elevational differences between weather stations and research site with a lapse rate of $0.0055^\circ\text{C m}^{-1}$.

Species-Specific Parameter Estimations

We obtained \hat{A}_{\max} for each of the 26 species by substituting L (days) and $A_{\max}(0)$ into equation (2a). Mean labor time was estimated using L , $A_{\max}(0)$, and parameters b and C (cf. eq. [8]). Functional leaf longevity was obtained from the actual L by multiplying $f/365$ for species L longer than 365. For species with either f equal to 365 (days) or f longer than L , $L = L_f$. For species L longer than f but shorter than 365, L_f is considered to be equal to f .

Stand-Level Data for Testing the Postulated Relationships

We selected forest stands with fairly closed canopies for which both B and F were reported by Cannell (1982) and added some Japanese data. If f was 365 days, we considered the site aseasonal or wet tropical forest. If f was less than 365, we considered the site seasonal temperate, boreal, or dry tropical forest. We analyzed data for B and F from 49 aseasonal and 97 seasonal sites. Finally, we used GPP and f data for 24 forest stands in Kira (1969).

Results

Leaf longevity, $A_{\max}(0)$, and leaf parameter values together with calculated m and lifetime net carbon gain for 26 species are summarized in table 2.

The $A_{\max}(0)$ -L Relationship

$A_{\max}(0)$ scaled to L on a log-log scale with slope -0.705 (not illustrated), significantly more shallow than -1 ($r^2 = 0.865$; $P = .001$).

Table 2: Measured or estimated leaf parameters

Species	L (days)	$A_{\max}(0)$ ($\text{ng g}^{-1} \text{s}^{-1}$)	b (days)	C (g g^{-1})	m (h day^{-1})	f (days year^{-1})	L_f (days)	G (g g^{-1})	Source
<i>Acer mono</i>	149	2,345	235	1.5	1.5	193	149	3.22	Kikuzawa and Ackerly 1999
<i>Alnus hirsuta</i>	112	1,670	185	1.5	2.9	201	112	3.46	Kikuzawa and Ackerly 1999
<i>Alnus sieboldiana</i>	91	1,662	144	1.5	3.5	282	91	3.25	Kikuzawa et al. 2004
<i>Anacardium excelsum</i>	315	690	985	1.4	4.5	306	306	7.15	Kitajima et al. 1997
<i>Annona spraguei</i>	221	1,857	482	1.6	1.9	306	221	5.28	Kitajima et al. 1997
<i>Antirrhoea trichantha</i>	174	1,637	550	1.4	3.5	306	174	7.45	Kitajima et al. 1997
<i>Betula platyphylla</i>	109	1,358	238	1.5	4.9	202	109	5.05	Kikuzawa and Ackerly 1999
<i>Camellia japonica</i>	902	512	1,488	1.5	1.2	323	798	3.05	K. Kikuzawa and Y. Miyazawa, unpublished data
<i>Castilla elastica</i>	206	2,006	365	1.6	1.5	306	206	4.02	Kitajima et al. 1997
<i>Cecropia longipes</i>	76	4,777	109	1.2	1.0	306	76	2.15	Kitajima et al. 2002
<i>Cleyera japonica</i>	1,850	444	4,509	1.5	1.0	323	1,637	5.14	K. Kikuzawa and Y. Miyazawa, unpublished data
<i>Fagus crenata</i>	154	1,118	227	1.5	2.9	282	154	2.92	Kikuzawa 2003
<i>Heliocarpus appendiculatus</i>	29	5,630	36	1.6	2.6	365	29	2.30	Ackerly and Bazzaz 1995
<i>Ilex aquifolium</i>	750	478	1,939	1.5	2.4	283	582	4.85	Mediavilla and Escudero 2003
<i>Mallotus japonicus</i>	111	3,602	210	1.5	1.6	282	111	4.18	K. Kikuzawa, unpublished data
<i>Pinus halpensis</i>	1,083	195	2,524	1.5	3.7	283	840	4.26	Mediavilla and Escudero 2003
<i>Pinus pinaster</i>	1,536	300	3,764	1.5	1.8	283	1,191	4.54	Mediavilla and Escudero 2003
<i>Pinus pinea</i>	1,065	470	2,285	1.5	1.4	283	826	3.83	Mediavilla and Escudero 2003
<i>Pinus sylvestris</i>	1,464	365	2,399	1.5	1.0	283	1,135	2.65	Mediavilla and Escudero 2003
<i>Polygonatum odoratum</i>	86	2,637	154	1.5	2.6	201	86	3.86	Kikuzawa 2003
<i>Polygonum sachalinensis</i>	63	2,585	96	1.5	3.1	201	63	3.04	Kikuzawa 2003
<i>Quercus glauca</i>	1,163	598	1,375	1.5	.6	323	1,029	1.81	K. Kikuzawa and Y. Miyazawa, unpublished data
<i>Quercus rotundifolia</i>	711	641	1,607	1.5	1.7	283	551	4.09	Mediavilla and Escudero 2003
<i>Quercus suber</i>	450	908	1,821	1.5	3.3	283	349	8.25	Mediavilla and Escudero 2003
<i>Taxus baccata</i>	1,863	203	2,945	1.5	1.4	283	1,444	2.51	Mediavilla and Escudero 2003
<i>Urera caracasana</i>	93	1,693	111	1.5	2.5	306	93	2.08	Kitajima et al. 2002

Note: L = leaf longevity; A_{\max} = potential instantaneous photosynthetic rate; b = potential leaf longevity; C = leaf construction cost; m = mean labor time of leaves; f = favorable period length; L_f = functional leaf longevity; G = lifetime net carbon gain by a leaf, expressed as g carbon per g carbon of leaf per whole lifetime of the leaf.

Mean Labor Time of a Leaf

Mean labor time of a single leaf calculated using equation (8) varied greatly, ranging from 0.6 h day^{-1} for *Quercus glauca* to values as high as 4.9 h day^{-1} for *Betula platyphylla*. No significant correlation was found between $A_{\max}(0)$ and m ($r^2 = 0.000$; $P = .996$; not illustrated), an indication that $A_{\max}(0)$ does not dominate in determining m but rather shares influence with the other parameters in a coordinated way that allows selection to work on the complex of traits in achieving a given value of m .

Lifetime Carbon Gain

Leaf lifetime net carbon gain is independent of L (fig. 1; $r^2 = 0.004$; $P = .761$). The maximum value for the 26 species was 8.25 g C g C^{-1} in *Quercus suber*, and the minimum value was 1.81 g C g C^{-1} in *Q. glauca*. The ratio

of maximum to minimum value was 4.55, rather small in comparison with the variation in L (more than 60 times).

The B-L Relationship

Leaf biomass is significantly correlated with L in both aseasonal and seasonal forests (fig. 2a). These regressions on L suggest that F (i.e., annual leaf production) is greater in aseasonal forests than in seasonal forests, but when we regressed B against L_f , aseasonal and seasonal forests fell on a single regression (fig. 2b). This suggests that p within f does not differ appreciably between forests in different climatic regimes.

Discussion

We have shown that species from diverse ecosystems converge to common values for certain variables integral to

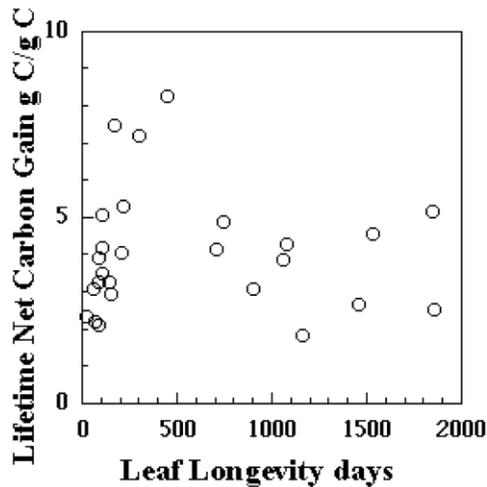


Figure 1: Leaf lifetime net carbon gain (g carbon per g carbon of leaf) plotted against leaf longevity for 26 plant species ($r^2 = 0.004$; $P = .761$).

plant productivity. We identify two hypotheses that summarize the outcome of this initial inquiry, the constant leaf lifetime carbon gain hypothesis and the constant leaf production hypothesis. Recognizing the approximate constancy of leaf production rates and lifetime carbon gain rates requires adjustments to the frames of reference presently used to quantify foliar function. Foremost among these are the new concepts of L_f defined in this article and the mean labor time of leaves recently identified by Kikuzawa et al. (2004).

Mean Labor Time

Initially mean labor time (MLT) was defined as the product of four terms: diel change in solar angle, changes in weather conditions, shading, and the midday and afternoon depression of photosynthesis. In this sense, the concept of MLT is close to that of light use efficiency (Monteith 1972; Rosati and Dejong 2003; Rosati et al. 2004), although the latter does not consider midday depression. Rather than laboriously measure the four factors separately, we now have shown it is possible to deduce m from L . This deduction assumes that actual L is optimal, which can be questioned, but this method based on the integrated effect of the four factors should be more robust than the errors inherent in the product of the four factors measured separately (Lo 2005).

The optimum theory of carbon gain is implicitly based on the assumption that trees are carbon limited or at least that foliar function is organized primarily by carbon economy. If there were no limitation on the number of leaves

maintained simultaneously by a plant, then leaves should be retained until their photosynthetic rate becomes 0, which clearly is not the case. Particularly in closed canopies, leaf function becomes limited by shading, so theories of leaf function based on carbon limitation are relevant. Investments of other resources such as nitrogen and phosphorus can play some role in L through competing demands for resources in developing fruits (Fernandez-Escobar et al. 2004), but modulation of nutrient uptake and growth at the whole-tree level (Silla and Escudero 2003) as well as storage reserves (Chapin et al. 1990; Fernandez-Escobar et al. 2004) can reduce direct competition for nutrient resources between foliage and competing sinks. Furthermore, there is good coordination between foliar investments of nitrogen and carbon in relation to leaf turnover (Hikosaka 2005), so it is reasonable to follow the costs and benefits of carbon investments as determinants of L .

Because microenvironmental conditions around a single leaf change with time, some may argue that to represent the entire canopy by a single leaf is problematic. But because MLT includes the effect of shading, the actual photosynthetic rate will be given, at least on an average, by the product of m and A_{\max} , so long as fully sunlit leaves are sampled to estimate A_{\max} .

Functional Leaf Longevity and Its Implications

The concept of L_f builds on the older concept of unfavorable periods in the annual cycle that preclude any significant photosynthetic activity for most species, such as winter in high latitudes or the dry season in seasonal tropics (Chabot and Hicks 1982; Kikuzawa 1991). Leaf longevity is typically recorded as the time elapsed from emergence of a leaf to the fall of a leaf without discounting unfavorable periods (cf. Wright et al. 2004). This datum quantifies temporal duration but without allowance for the periods when leaves cannot actually fulfill their photosynthetic function. To consider the functional ecology of total carbon gain over the lifetime of a leaf, we should discount nonfunctional days from the leaf lifetime when longevity spans one or more annual cycles. By using this measure of L_f , we can refine our understanding of variation in foliar design and move toward a more effective scaling from leaf- to canopy-level productivity.

Favorable Period Length

Estimating f is not straightforward. In this article, we followed the method of Kerkhoff et al. (2005), which assumes that thresholds for moisture and temperature define favorability and then ignores any influence of temperature or moisture variation above the thresholds for activity. In

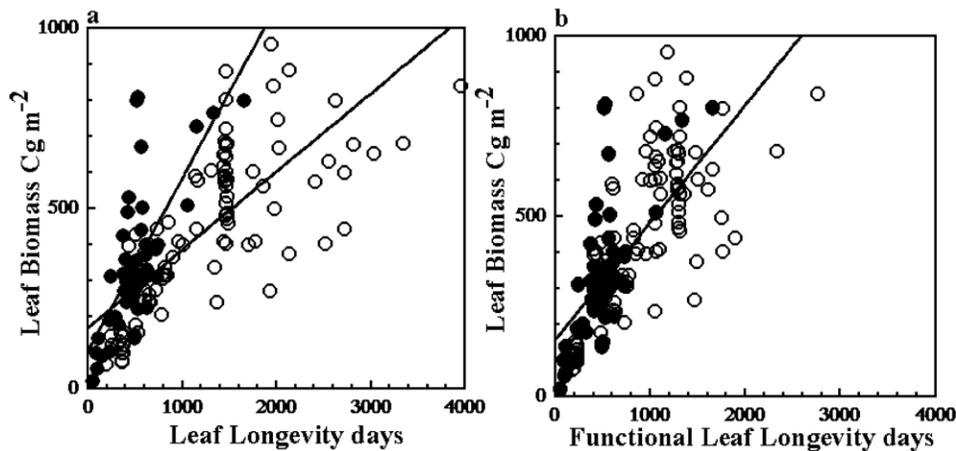


Figure 2: Leaf biomass of aseasonal (filled circle) and seasonal (open circle) forests against leaf longevity (a) and functional leaf longevity (b). a, Leaf biomass (g m^{-2}) and leaf longevity (days). The slopes of the aseasonal and seasonal forests differ significantly ($P = .01$). Aseasonal forests: $B = 0.479L + 102$; $r^2 = 0.519$; $P < .001$. Seasonal forests: $B = 0.217L + 167$; $r^2 = 0.550$; $P < .001$. b, Leaf biomass and functional leaf longevity. The slopes of the two types of forests converge and are essentially equal ($P = .155$). All forests: $B = 0.326L_f + 156$, $r^2 = 0.537$; $P < .001$.

reality, mean daily temperature, for example, fluctuates from 5° to 30°C or more in f in temperate regions with effects on photosynthetic rate. Alternative methods have been devised to incorporate these effects for the calculation of f . For example, Luo et al. (2002) proposed an equation to express f based on the difference of actual daily (or monthly) temperature and optimum temperature for photosynthesis. We calculated f using Luo et al.'s equation, but this did not change our results. Given the importance of f in our model, it would be good to develop a robust, practical estimate of f based on the seasonality of both temperature and rainfall.

Lifetime Net Carbon Gain by Single Leaves

Researchers have long recognized the negative correlation between photosynthetic rate and L (Larcher 1975) and have accumulated considerable data in support of this generalization (Wright et al. 2004). A comparable relationship also exists at the ecosystem level; for example, Tadaki (1986) showed that net production rate per unit B (production efficiency) of deciduous stands is greater than that of evergreen stands. Chabot and Hicks (1982) offered a functional rationale for these negative relationships in a cost-benefit analysis. They argued that to promote high photosynthetic rates, substantial nitrogen must be invested in photosynthetic enzymes, but high foliar nitrogen attracts herbivores and shortens L . Long-lived leaves therefore require greater investments in defenses. These investments conflict with investments in photosynthetic machinery, making well-defended, tough, and long-lived

leaves with high photosynthetic rates unlikely (Reich 2001). On the contrary, there are no comparable constraints on making short-lived leaves with low photosynthetic rates. Even if such leaves were constructed, however, they should not be favored by natural selection because productivity is critical to survival and reproduction. Thus, the negative correlation of A_{max} and L has been viewed as an outcome of natural selection acting jointly on these two functionally correlated traits (Reich et al. 1991, 1992; Westoby et al. 2000; Mediavilla and Escudero 2003). This view leads to the expectation that the product of A_{max} and L should be independent of L , but in fact this is not the case in the large data set compiled by Reich et al. (1991, 1992, 1997, 1999; Reich 2001). Westoby et al. (2000) rationalized this outcome by considering the time value of a leaf—early returns on foliar investment can offset later losses.

There is, however, an alternative rationale for the observed relationships. It is possible that natural selection does not act on the $A_{\text{max}}-L$ surface but rather on a tripartite relationship in foliar design: $m \times \hat{A}_{\text{max}} \times L_f$. We already have laid out the basis of this view, which rests on adjustments in the traits quantifying foliar function. First, to obtain carbon gain throughout a leaf's life span, A_{max} should be averaged through time as \hat{A}_{max} (Mediavilla and Escudero 2003). To assess the realized productivity linked to \hat{A}_{max} , the time during the year when the leaf actually could work to capacity should be considered—MLT within a day and f within a year. Using this approach to assessing foliar design, we obtained nearly constant lifetime gain across species (fig. 1), although this initial analysis draws on far fewer than the thousands of species reported by

Reich and his colleagues (1997, 1999, 2001). We call this the constant lifetime carbon gain hypothesis.

Leaf Production Rate of Forests

In this study, we found that the leaf fall and thus leaf production rates differ significantly between aseasonal and seasonal forests (fig. 2a). This confirms earlier reports (Bray and Gorham 1964; Vogt et al. 1986) that annual leaf litter production decreases with latitudes, tropical rain forests being greatest. These trends have been attributed to latitudinal differences in mean temperature, growing period length, solar angle, and similar factors. The analysis shown in figure 2b using L_r suggests that the main cause of the differences between aseasonal (wet tropical) and seasonal (dry tropical, temperate, or boreal) forests could be simply geographic changes in the favorable period for photosynthesis. We therefore suggest a constant leaf production hypothesis: p within f is not so greatly different between regions.

GPP

GPP of a closed forest can be expressed as the product of p , G , and f , as expressed by equation (15). We have proposed here that p and G are essentially constant elements in foliar design for all species; if one accepts p and G as constants, then GPP is determined only by f and could be constant among forests within a single region so long as their canopy is closed (eq. [16]). We call this the constant gross production hypothesis, which has some support in the available data. For example, Kira and Shidei (1967) and Kira (1969, 1975) summarized gross production data of forests in the West Pacific region and concluded that gross production could be explained by leaf area duration (Kira 1975), which is the product of leaf area index and the length of growing period. The latter term is equivalent to f . We examined GPP data used by Kira (1975) in relation to f . As suggested by our analysis in the present study, f alone can explain much, although not all, of the variation in GPP ($r^2 = 0.567$; $P < .001$). The relationship is sufficiently robust to provide at least a first approximation to global patterns of variation in GPP across latitudes; patterns in residual variation can help identify site-specific secondary factors such as edaphic conditions or successional stage that modify GPP from regional norms. In addition, we expect that the power of f in predicting regional levels of GPP will increase as more refined estimators for this key variable are developed.

Conclusion

We have offered evidence in support of two working hypotheses, a constant lifetime carbon gain hypothesis and a constant leaf production hypothesis. Lifetime carbon gain by a single leaf can be expressed as the product of m , average maximum photosynthetic rate, and L_r . This lifetime carbon gain is independent of L and can be considered constant across a wide range of species. We refer to this as the constant lifetime carbon gain hypothesis, which organizes a great deal of information about trade-offs in foliar design. We in turn recognize a parallel constant leaf production hypothesis, which scales the constancy at the single leaf level up to the level of the forest canopy. At first this constancy does not appear to hold because the regression between total B in forest canopies and L is significantly steeper in tropical rain forests than in other forests. But if L_r and total B are considered instead, then tropical rain forests (aseasonal) and other (seasonal) forests fall on the same regression. That is, leaf production expressed per day of favorable period is not significantly different across different regions in the world. Individual species differ greatly in the aspects of leaf function, array, and turnover, but in the end all species appear to approach the same lifetime carbon gain by single leaves and the same rate of leaf production.

We have shown that gross production of a forest could be expressed by the product of leaf production rate, lifetime carbon gain, and favorable period duration. The constancy of leaf production rates and lifetime carbon gains has implications for estimating the gross production of world ecosystems. Because the former two of the three terms can be considered constant, to a first approximation gross production can be predicted simply by the duration of the period favorable for photosynthetic activity in any given region. Much of the apparent diversity in foliar traits appears to simply reflect different ways to achieve a constant lifetime carbon gain for individual leaves in a given environmental regime. This is an example of a many-to-one mapping relationship in functional design whereby diverse interacting traits can be combined in different ways to achieve the same net functional effect (Alfaro et al. 2005; Kerkhoff et al. 2005; Marks and Lechowicz 2006).

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