



Leaf Photosynthesis Integrated over Time

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Summary

We review a series of papers based on Kikuzawa's (1991) cost-benefit model for leaf longevity, including its extension to whole plants and entire communities in seasonal environments. This simple model of net carbon gain over the life of a leaf can explain relationships among key foliar traits such as the positive correlation between leaf longevity (L) and leaf mass per area (LMA) and the negative correlations between photosynthetic rate (A) and both L and LMA. The extension of the model to seasonal environments can explain and reproduce various biogeographical trends including bimodality in the distribution of evergreen species across latitude, increase and decrease in L of evergreen and deciduous species with shortening of the period favorable for photosynthesis (f), modulation of L-LMA relationships with f , and decrease in functional type richness in terms of phenology patterns towards higher latitudes and altitudes. Finally, the model suggests the possibility that the lifetime carbon gain by a single leaf can be extended by analogy to predict the productivity of forest ecosystems.

I. Introduction

Leaf longevity (L) is recognized as a central element (Shipley et al. 2006) leading to general covariations among leaf mass per leaf area (LMA), photosynthetic rate (A), and foliar nitrogen content (N) in the worldwide leaf economics spectrum (LES; Reich et al. 1997; Wright et al. 2004). The tradeoffs among foliar traits comprising the LES arise in a fundamental evolutionary tradeoff between instantaneous photosynthetic rate and leaf longevity. Species fall along a functional gradient from those with high photosynthetic capacity and short-lived leaves to those with longer-lived but less productive leaves, and the distribution and abundance of species across resource regimes depends in part on their position along the LES (Reich 2014). For a given species, the inverse of L also defines the rate of leaf turnover as new leaves are produced at the periphery of a mature plant canopy and older leaves that become increasingly shaded in the canopy are shed (Kikuzawa et al. 2009). A dynamic equilibrium between leaf production and leaf shedding is widely observed in both deciduous and evergreen plant canopies, within a very short period of growing season in herbaceous and deciduous plants, and over a

number of growing seasons in evergreen plants (Kikuzawa and Lechowicz 2011).

In this chapter, we review theory that stems from Kikuzawa's (1991) model predicting leaf longevity as a function of photosynthetic rate, the construction cost of leaves, and the rate of decline in photosynthetic capacity with leaf age. The theory helps make sense of the empirical patterns in the LES and can be extended to seasonal environments to account for biogeographical trends in leaf longevity, the distribution of evergreen and deciduous species, and patterns of species richness. By rescaling the theory from single leaves to plant populations, communities, and ecosystems we show that the aggregate net productivity of a community of plants can be predicted from the life-time carbon gain of single leaves of the species comprising the community.

II. Leaf Longevity – Optimizing Model for Carbon Gain

The carbon gain (G) by a leaf is given as:

$$G = \int_0^t p_n(t) dt - C \quad (17.1)$$

where $p_n(t)$ is the net photosynthetic rate per unit leaf area at time t and C is the aggregate cost of constructing the leaf and its supporting organs including any investments in leaf defense against disease and herbivores (Kikuzawa 1991). The parameter $p_n(t)$ can be approximated by a linear decreasing function as

$$p_n(t) = a \left(1 - \frac{t}{b} \right) \quad (17.2)$$

where a is the daily photosynthetic rate per unit leaf area at the moment the developing leaf becomes functionally mature and b is the potential leaf longevity taken as the time elapsed until the photosynthetic capacity of the aging leaf declines to zero. A model suggests that the optimum timing of leaf shedding (t_{opt}) to maximize carbon gain of the plant is given by the time that maximizes the marginal carbon gain (g) at the leaf level:

$$g = \frac{1}{t} G \quad (17.3)$$

Substitution of Eqs. (17.1) and (17.2) into (17.3) gives the following analytic result:

$$t_{\text{opt}} = \left(\frac{2bC}{a} \right)^{\frac{1}{2}} \quad (17.4)$$

A. Parameter a and Mean Labor Time

The parameter a can be decomposed into the instantaneous photosynthetic rate (A_{area}) and a measure of mean labor time (m) attributable to leaf function:

$$a = mA_{\text{area}} \quad (17.5)$$

Mean labor time is defined as the ratio of the mean daily photosynthetic rate of a leaf

to the mean value of potential photosynthetic rate of the leaf assuming that the leaf could work 24 h at maximum photosynthetic rate (Kikuzawa et al. 2004). The dimension of m is seconds per day, but for convenience m is usually expressed as hours per day. The concept of mean labor time allows for the fact that various factors such as changes in photoperiod, solar angle, clouds, shading by other leaves or by other plants, water deficit, and midday depression in photosynthesis can all reduce the hypothetical maximum photosynthetic rate to a realized rate below 24 h (Kikuzawa et al. 2004). Mean labor time calculated by considering these factors for *Alnus sieboldiana* was 5.5 h per day (Kikuzawa et al. 2004). Assuming that actual leaf longevity is t_{opt} in Eq. (17.4), the mean labor time can also be estimated using Eqs. (17.4) and (17.5) as

$$m = \left(\frac{2bC}{A_{\text{area}}(0)L^2} \right). \quad (17.6)$$

Kikuzawa and Lechowicz (2006) reported mean labor times ranging from 1 to 6 h (average around 3 h day⁻¹), although Oikawa et al. (2006) reported more than 10 h day⁻¹ in an herbaceous annual plant.

B. Instantaneous Photosynthetic Rate per Unit Leaf Area, A_{area}

Kikuzawa's (1991) theory for leaf longevity, which is framed with reference to photosynthetic gains measured as A_{area} (cf. Eq. 17.1), leads to an expectation that L should be negatively correlated with A_{area} (cf. Eq. 17.4). In reality, this bivariate correlation can be modulated through the interaction between A_{area} and LMA; A_{area} can be expressed as a product of LMA and A_{mass} (photosynthetic rate per unit leaf mass), which provides a link between areal gains of photosynthate and the mass-based carbon cost (C) of constructing a leaf. In part because of this interaction with LMA, A_{area} does not differ as much among

leaves differing in longevity as does A_{mass} . For example, in a comparison among five tree species, Gower et al. (1993) found A_{mass} varied fivefold across species and was inversely correlated with L , but A_{area} varied less than twofold across species and did not correlate with L . Similarly, the A_{mass} in the LES database (Wright et al. 2004) varied 150-fold across species ($n = 770$) and A_{area} only 40-fold ($n = 825$). Wright et al. (2004) reported no correlation between A_{area} and L of well-lit leaves in the LES data while LMA and N_{area} are positively correlated (Wright et al. 2004; Onoda et al. 2017). There is essentially a tradeoff between photosynthetic capacity expressed as A_{area} which is accomplished by N_{area} , and persistence expressed as leaf longevity, but the relationship is modulated by the variation in leaf structure expressed as LMA . Onoda et al. (2017) argued that two opposing effects could largely cancel out: (1) higher LMA is correlated with higher A_{area} , because greater leaf thickness is attributable to thicker mesophyll layers and (2) leaves with higher LMA have greater cell wall density that reduces photosynthetic rates as a result of lower CO_2 diffusion. Chabot and Hicks (1982) were the first to consider that the lower photosynthetic rates in evergreen compared to deciduous species may be a consequence of dilution of photosynthetic tissue by non-photosynthetic tissue, in particular vascular tissue rich in cell-wall material. To persist longer a leaf must invest in defense against herbivory and disease as well as structural support against mechanical damage. Hence the investment in photosynthetic machinery will be diluted by allocation to these ancillary aspects of leaf function and the photosynthetic rate per unit leaf mass will be reduced. In addition to the dilution theory, the greater LMA in evergreen leaves can be attributed to other factors that reduce the photosynthetic rates of evergreens such as lower conductance of CO_2 or lower penetration of light because of the higher tissue density in evergreen leaves

(Lusk et al. 2008; Wyka and Oleksyn 2014; see also Chap. 16 of this book).

C. Potential Leaf Longevity or Parameter b

Parameter b is the potential leaf longevity, or the time required for the photosynthetic rate of the aging leaf to decline to zero. Since it is difficult to measure the rate at the instant when the rate just becomes zero, b is best estimated from the slope of repeated measurements of the same leaf over time (Koyama and Kikuzawa 2010; Kikuzawa et al. 2013a). Alternatively, the rate of decline can be estimated by the measurement of leaves at different positions on shoots or on differently-aged leaves (Kitajima et al. 1997, 2002), assuming that basal leaves are oldest and distal youngest and the ages can be estimated by the bud-scars remaining on the shoots (i.e., the chronosequence method; Osada et al. 2015). The chronosequence approach is particularly useful for species with long-lived leaves that maintain a wide range of leaf ages on individual shoots and is less laborious than repeated measurements on single leaves (Osada et al. 2015).

Kikuzawa's (1991) cost-benefit model for leaf longevity predicts that daily carbon gain should be positive at the optimum time of leaf shedding and that potential leaf longevity (b) should be longer than the optimum timing (t_{opt}) if the total number of leaves per plant is limited. But the model also predicts that the photosynthetic rate at t_{opt} should be zero with t_{opt} coinciding with b if there is no limitation to the total number of leaves per plant. In many cases, potential leaf longevity is longer than realized longevity. Kikuzawa et al. (2013a) found that potential leaf longevity (b) is around twice the realized leaf longevity. Reich et al. (2009) found that carbon balance was positive when leaves died in 10 woody Australian plant species. Ackerly (1999) also reported A_{mass} greater than zero at the time of shedding for three tropical pioneer tree species, although not so great as expected from Eq. (17.4).

By a simple simulation, Osada et al. (2015) found that, even if individual leaves are shed when daily carbon gain becomes zero, the cohort mean carbon gain for surviving leaves is positive at the mean L . The chronosequence estimate of relationship between leaf age and photosynthetic rate inevitably depends on the “surviving” leaves; hence researchers might falsely infer that all leaves are shed when their carbon balance is positive (Osada et al. 2015). Even if repeated measurements were adopted, estimated photosynthetic rate at leaf fall will be biased when average leaf longevity is used to evaluate the relationship between age and photosynthetic capacity of surviving leaves. Only repeated measurements on individual leaves can provide definitive estimates of photosynthetic rate at leaf fall.

D. Construction Costs and Parameter C

Chabot and Hicks (1982) first presented an equation for the carbon economy of a single leaf that included expenditure for defense of the leaf against herbivores and disease, defense against environmental stress, and so forth. For simplicity Kikuzawa (1991, 1995) included these terms in a single construction cost (C) for a leaf. Kikuzawa and Ackerly (1999) also suggested incorporating a cost of non-photosynthetic organs such as branch and petiole to mechanically support leaves and conducting tissues to transport water and nutrients through root, stem, and branch.

$$C = C_1 + C_s \quad (17.7)$$

Where C_1 is the costs of construction of a leaf and C_s is the costs to construct supporting organs for the leaf. The significance of costs for supporting organs is illustrated by the shorter leaf longevity of seedlings (Seiwa and Kikuzawa 1991) compared to adult trees (Kikuzawa 1983); both support and conducting systems are physically near seedling leaves, hence leaf longevity is less than in

older trees where support and transport involve greater distances (Kikuzawa and Ackerly 1999). But later, Kitajima and Poorter (2010) reported that tissue density and toughness, the two correlates of leaf longevity, increase from saplings to adults in tropical trees. However, this may be caused by the difference in light condition on saplings and adults (Russo and Kitajima 2016). Comparison of leaf longevities among plants of different life forms also suggests the importance of C_s (Kikuzawa and Ackerly 1999). Reich et al. (2009) further suggested that leaf level carbon balance should still be above zero at the leaf age of the typical leaf life span because leaves must support not only their own carbon costs but also those of other plant parts (branch, stem, or roots) that are required to sustain the canopy.

Defense necessarily has some material basis, therefore any investment into foliar defense such as a thicker cuticle, thicker epidermis, higher values of vein per unit leaf area or more concentrated chemical defenses must result in an increase in leaf mass. The aggregate investment in constituents of a leaf such as protein, chlorophyll, total nonstructural carbon (TNC), defensive chemical, and so forth (cf. Poorter et al. 2009) can be expressed simply as:

$$LMA = \sum_j M_j / A \quad (17.8)$$

where M_j is the mass of the j^{th} compound and A is leaf area (Poorter et al. 2009). This simple equation could be expanded to include all individual constituents in each tissue of a leaf as:

$$LMA = \sum_i \sum_j M_{ij} / A \quad (17.9)$$

where M_{ij} is the mass of the j^{th} compound in the i^{th} tissue in a leaf. The proportion of the total amount of the corresponding leaf attributable to the construction and defense of the

leaf is C_1 . The total investment for defense and construction then can be described as

$$C_1 = cLMA, \quad (17.10)$$

where c is a proportionality constant.

In 1980s, the construction cost or energy to convert glucose to leaf tissue was considered to vary substantially among species and hence might explain the high interspecific variation in leaf longevity. In fact, there is less than twofold variation in the construction cost among species (Williams et al. 1989; Villar and Merino 2001), although Wyka and Oleksyn (2014) reported slightly greater construction cost in evergreen (1.55 g glucose g^{-1}) compared to deciduous (1.46 g glucose g^{-1}) species. Hence, the differences in parameter C among species are attributable in large part to the differences in LMA. Since measuring defensive material is not easy, in many cases LMA is taken as a surrogate for C .

E. Leaf Mass per Area (LMA)

Actual leaf longevity is positively correlated with LMA, which is consistent with the idea that leaf longevity depends in part on the defense material invested in the leaf (C_1). A positive, significant relationship was reported between leaf longevity and LMA in 19 tropical saplings (Kitajima and Poorter 2010). Similar positive trends were reported in global data sets (Reich et al. 1992; Wright et al. 2004; Donovan et al. 2011). Greater LMA is associated with thicker cuticle, thicker epidermis, and denser leaf veins, etc. (Blonder et al. 2011; Kitajima et al. 2013; Onoda et al. 2015). For example, Blonder et al. (2011) incorporated three venation parameters (distance, density, and loopiness) into a model predicting four leaf traits: A_{mass} , L , N_{mass} (nitrogen content per unit leaf mass), and LMA. Blonder et al. (2011) argued that the leaf economic spectrum relationships among the four traits were well reproduced

by their model (Blonder et al. 2011, 2013). Sack et al. (2013), however, rejected Blonder's analysis, arguing instead that vein length per leaf area contributes to the LES via leaf hydraulic conductance and thereby leaf stomatal conductance and photosynthetic rate. Venation networks augmented by investments in epidermis can also extend leaf longevity by strengthening the sandwich structure that confers a degree of structural support and mechanical defense for leaves (Onoda et al. 2015).

Leaf mass per leaf area (LMA) can be further decomposed into laminar density and laminar thickness (Castro-Diez et al. 2000; Kitajima and Poorter 2010).

$$LMA = \text{lamD} \times \text{lamT} \quad (17.11)$$

Where lamD is laminar density or leaf mass per unit leaf volume (g dry weight m^{-3}) and lamT is laminar thickness (m; Kitajima and Poorter 2010). Castro-Diez et al. (2000) compared 52 European woody plant species and found that LMA was correlated with laminar density but not with laminar thickness. A comparison of 19 tropical tree species revealed that leaf longevity did not correlate with leaf thickness, but instead with leaf density (Kitajima and Poorter 2010). Dense, thicker leaves are usually tough and long-lived but this reduces maximum photosynthetic rate due to the slow diffusion of CO_2 within the leaf as a result of thicker cell walls (Onoda et al. 2017). On the contrary, thick but low density leaves enable good CO_2 diffusion within the leaf. Investments in photosynthetic machinery can also act to increase LMA. The LMA for a given species basically reflects a balance struck between making tough leaves that confer greater L versus leaves better suited to photosynthesis that have lower L (Lusk et al. 2008; Reich 2014).

There are both plastic and evolutionary responses of quantitative traits to environmental gradients. For example, L is usually longer in shaded individuals than in those

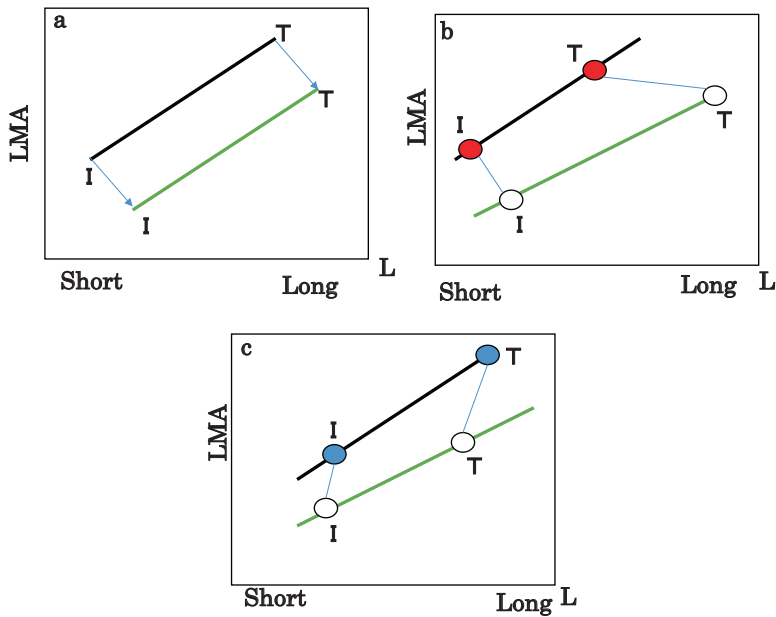


Fig. 17.1. Schematic representation of counter gradient (**a**, **b**) and co-gradient (**c**) variation of LMA with L. **Panel a:** The effect of changes in habitat light condition on the LMA-L relationship (plastic response having negative gradient) which differs from the LMA-L relationship among species (evolved relationship with positive gradient). The thick black line represents the LMA-L relationship in a sunny environment and the thick green line in a shady environment; thin arrows indicate the plastic changes in shade tolerant (T) and intolerant (I) species. (Redrawn from Lusk et al. 2008). **Panel b:** Red circles and thick black lines represent the L-LMA relationship in a sunny environment and white circles and thick green lines in a shady environment; thin lines represent plastic responses. Response in L is greater in the species with longer L, while response in LMA is relatively greater in the species with shorter L. **Panel c:** Co-gradient variation in the LMA-L relationship in the case of soil fertility. Closed blue circle represents less fertile soil and white circle fertile soil. Responses in LMA are greater than L in all species. (Panels **b** and **c** are redrawn after Russo and Kitajima (2016)) (Colour figure online)

grown in brighter sites (plastic response) and also longer in shade tolerant species adapted to late-successional habitats than in light demanding species (evolutional response). Lusk et al. (2008) distinguish co-gradient variation in leaf traits (i.e. similar directions of plastic response and evolutionary trends) and counter-gradient variation (i.e. the direction of plastic response differs from the evolutionary response). For example, there is indeed a marked divergence between the plastic and evolutionary responses of LMA to shade. Within species, individuals grown in shaded habitats have lower LMA than those grown in sunnier habitats. But in interspecific comparisons, shade tolerant species tend to have higher LMA than light demanding species (Lusk et al. 2008; Fig. 17.1a).

Russo and Kitajima (2016) proposed a similar conceptual model to that by Lusk et al. (2008) that more explicitly predicts the degree of plastic responses of L and LMA to experimentally standardized light conditions in different species adapted to sun and shade conditions (Fig. 17.1b, c). They predicted that species having longer L will show greater plasticity to changing light in L than in LMA because of the existence of an upper limit in LMA, but species having shorter L will show less plasticity in L because of the existence of a lower limitation in L. Their prediction was supported by an experiment on 41 Panamanian tree species. In the case of responses of L and LMA to soil nutrient conditions, directions of responses among species and among leaves within species are

predicted to be similar (i.e., co-gradient variation Fig. 17.1c; Russo and Kitajima 2016).

F. Leaf Economic Spectrum (LES)

As shown in the previous chapter of this book, the pattern of correlations among leaf traits referred to as the leaf economic spectrum (Wright et al. 2004) reflects contrasting strategies for productivity (Reich 2014) that are strikingly consistent among biomes (Reich 2014; Reich et al. 1997, 1999). One end of the spectrum represents slow-growing species that produce long-lived, structurally expensive leaves with low photosynthetic rate. The other end represents fast-growing species that produce short-lived leaves with low LMA and high photosynthetic rate. Of the various leaf traits, three (A_{mass} , L, and LMA) or four (A_{mass} , L, LMA, and Nitrogen content) can explain a large part of the variation observed among plant species (Shipley et al. 2006; Donovan et al. 2011). Important correlations among traits include the negative correlations between A_{mass} and L, which is largely determined by A_{mass} and LMA (Osnas et al. 2013), the positive correlation between L and LMA, and the positive correlation between A_{mass} and N_{mass} .

Parameters in Eq. (17.4) can be interpreted to be leaf traits in LES and many correlations among leaf traits can be reproduced by Eq. (17.4). Although there is a report that real values of L for three pioneer tree species were from 24 to 60% greater than model predictions (Ackerly 1999), we can predict L from the calculated t_{opt} values. The daily photosynthetic rate (parameter a) can be interpreted as an instantaneous rate (A_{mass}) mediated by mean labor time m . The effects of construction cost C in Eq. (17.4) can be referenced against LMA by Eq. (17.9). Hence, many relationships between leaf traits in the LES can be linked to leaf parameters in Eq. (17.4). For example, L and A_{mass} are negatively correlated. L and LMA are positively correlated, although the correlation between N and A_{mass} is not explicitly shown in Eq. (17.4). In conclusion, many

leaf traits and correlations between traits are expressed in the single Eq. (17.4).

III. Extension of the Model to Seasonal Environments

A. Favorable Period (f)

Equation (17.1) is a model of leaf carbon gain in an ideal stable environment where plants can perform photosynthesis every day throughout a year. For example, one may consider the conditions in the equatorial wet tropics where temperature and water supply do not limit plant growth. In regions outside the equatorial tropics, however, photoperiod, solar angle, air temperature, precipitation amounts, and other environmental factors that influence photosynthetic activity all change seasonally. In general, when air temperature falls below about 5 °C photosynthesis diminishes rapidly (Luo et al. 2002). Many plants shed leaves during the winter season when air temperature drops below freezing (deciduous habit), although some retain leaves during winter (evergreen habit). In warm temperate regions, some plants perform photosynthesis in winter on warmer days. Since insolation is better on the forest floor of deciduous forests in winter, evergreen plants in the understory can be more productive during winter (Miyazawa and Kikuzawa 2006). But in cool temperate and boreal regions low winter temperatures and heavy snow depth preclude photosynthetic activity. Even in tropical regions where temperature is usually high throughout a year, a dry season with monthly rainfall less than about 25 mm can limit photosynthetic activity (Eamus and Prior 2001). Similarly, a dry summer in temperate regions is not suitable for photosynthesis (Manzoni et al. 2015). In these sorts of unfavorable periods for photosynthesis, some plants shed all their leaves (drought deciduous) and some retain dormant leaves (summer evergreen), with many intermediate types (Eamus and Prior 2001; Manzoni et al. 2015).

Kikuzawa (1991) allowed for these effects by adapting his basic model to seasonal environments where favorable and unfavorable periods alternate within a year. In favorable periods, all plants photosynthesize but in

unfavorable periods some plants shed leaves and show a deciduous habit, while other plants retain leaves in a dormant state (evergreen). The consequent carbon gains per unit time can be written as,

$$g = \frac{1}{t} \left(\int_0^f p_g(t) dt + \int_1^{1+f} p_g(t) dt + \dots + \int_{[t]} p_g(t) dt - \int_0^t r(t) dt - C \right) \quad (17.12)$$

where $p_g(t)$ is gross photosynthetic rate, $r(t)$ is the respiration rate of a unit leaf area ($p_n = p_g - r$) and $[]$ indicates Gaussian notation. Note that photosynthesis is carried out only during f in each year but maintenance respiration persists throughout all seasons.

Kikuzawa's (1991) model implicitly assumed that leaves appeared at the start of the favorable period, but Seki et al. (2015) explicitly showed there are, in fact, three alternative strategies for seasonal timing of leaf expansion: (1) immediately after shedding of an old leaf, (2) only at the beginning of favorable season, and (3) a combination of (1) and (2): immediately after shedding of an old leaf if the shedding occurs during f or otherwise at the beginning of favorable season. Their new model clarified that the combined strategy will usually yield the highest carbon gain.

B. Functional Leaf Longevity (L_f)

From the functional point of view, leaf longevity must be changed by considering periods within the year when that function is precluded. For example, for photosynthesis, functional leaf longevity is defined as the time during the year that a leaf actually carries out photosynthesis (Kikuzawa and Lechowicz 2006). For evergreen leaves in seasonal environments, we can assume that leaves are dormant during an unfavorable period and thus L_f is essentially L minus the unfavorable period. In the case of plants in the wet tropics or deciduous

plants in temperate regions, L_f is essentially the same as L .

We can extend the concept of functional leaf longevity to a consideration of forest productivity. The ratio of total leaf biomass in the canopy and leaf longevity, which suggests the leaf production rate, is greater in aseasonal forests (wet tropics) than in seasonal forests (seasonal tropics, temperate, boreal, and subarctic regions; Fig. 17.2a). If we use functional leaf longevity instead of leaf longevity, however, this apparent difference between seasonal and aseasonal forests disappears. Both types of forests can be regressed by a common single line (Fig. 17.2b), suggesting similar leaf production rates prevail in the favorable periods across latitudes (Kikuzawa and Lechowicz 2006). The main difference between tropical and non-tropical forests is not the mean annual temperature itself, but the temperature-mediated variation in favorable period length.

C. Leaf Lifetime Performance

We can define lifetime carbon gain (P_L ; g dry weight g^{-1} dry weight) as the product of average daily carbon gain and functional leaf longevity (Kikuzawa and Lechowicz 2006). The former in turn is defined as the product of mean labor time ($s \text{ day}^{-1}$) and average instantaneous photosynthetic rate (\bar{A}_{mass} , as g dry weight g^{-1} dry weight s^{-1}). Finally, P_L is given as,

$$P_L = mL_f \bar{A}_{\text{mass}} \quad (17.13)$$

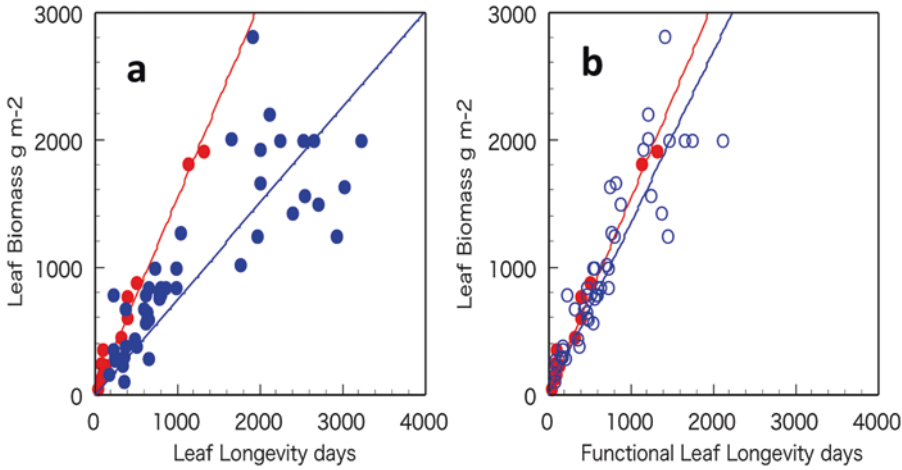


Fig. 17.2. The relationships between leaf biomass and both (a) leaf longevity and (b) functional leaf longevity. (Redrawn after Kikuzawa and Lechowicz 2006). Blue closed circles in (a) and open circles in (b) indicate forests in seasonal environments and red closed circles those in non-seasonal environments. The slope of lines in (a) indicates average daily leaf production rate, which in non-seasonal forests (red line, $\sim 1.5 \text{ g dry weight m}^{-2} \text{ day}^{-1}$) is around twice that of seasonal forests (blue line, $\sim 0.75 \text{ g dry weight m}^{-2} \text{ day}^{-1}$). (b) Blue open circles indicate leaf production in seasonal forests, which is not much different from non-seasonal forests (red closed circle) (Colour figure online)

Surplus production (gross primary production minus leaf respiration; Monsi 1960) of a forest stand can be defined by the following.

$$P = B\partial\bar{A}_{\text{mass}} \tag{17.14}$$

where B is leaf biomass of the stand, ∂ is the cumulative duration of favorable time for photosynthesis, the product of daily (m) and seasonal (f) favorable period ($\partial = mf$). Equation (17.14) can be extended by incorporating $L_f/L_f = 1$.

$$P = \frac{B}{L_f} fmL_f \bar{A}_{\text{mass}} \tag{17.15}$$

where B/L_f represents daily leaf production (see Fig. 17.2) and thus $(B/L_f)f$ represents annual leaf production. The product of the last three terms in Eq. (17.15) is life time gain (P_L) of a leaf. Surplus production then should be easily obtained as the product of annual leaf production, which can be esti-

mated by annual leaf fall using litter-traps, and the life-time gain of a single leaf (Kikuzawa and Lechowicz 2006).

To demonstrate this possibility, 55 leaves were selected in an artificial beech stand and their photosynthetic rate was periodically measured. Parameter b was estimated from the linear decline of A_{mass} (Fig. 17.3a), and parameter m using Eq. (17.5). Finally, P_L was estimated to range from 1.5 to 6 g dry weight g^{-1} dry weight, an average of 3.0 g dry weight g^{-1} dry weight (Fig. 17.3b). In short, 1 g dry weight of beech leaf produced on average 3 g dry weight of biomass, which can be used for the production of leaves, and production and maintenance of stems, roots and so forth.

The concept of lifetime performance can be extended to other aspects of leaf performance such as lifetime respiration or lifetime transpiration. For example, Suzuki et al. (2013) applied the concept to herbivore damage to leaves in forests on Mt. Kinabalu, Malaysia. Fallen leaves were collected by litter traps set on the forest floor, and the leaf area lost to herbivorous insect larvae (i.e. the

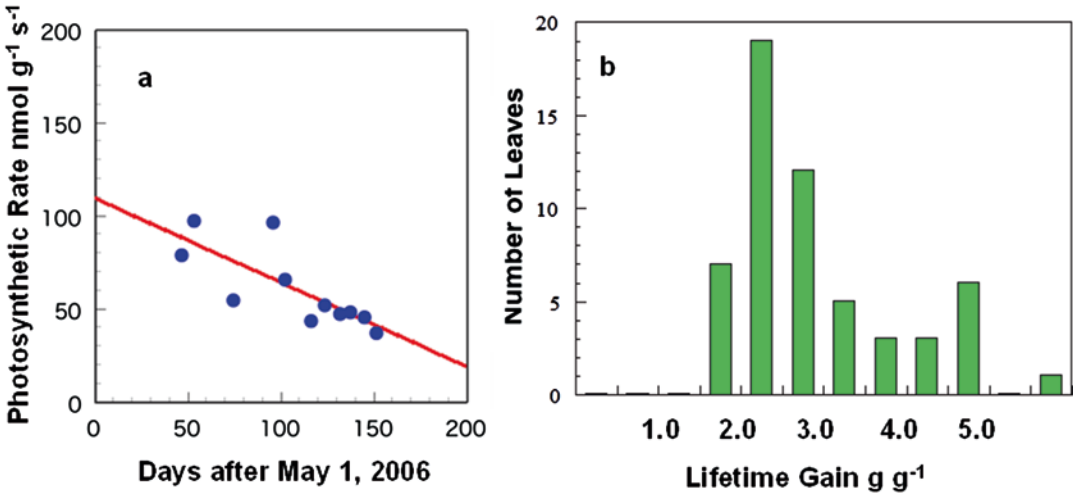


Fig. 17.3. Lifetime photosynthetic gain by beech (*Fagus crenata*) leaves. (a) Decline of photosynthetic rate with time for a beech leaf. ($A_{mass} = -0.45 \text{ day} + 110$.) (b) Histogram of lifetime photosynthetic biomass gain (g dry weight biomass gain/g dry weight leaf) by single leaves. Average was 3.0 g dry weight g⁻¹ dry weight

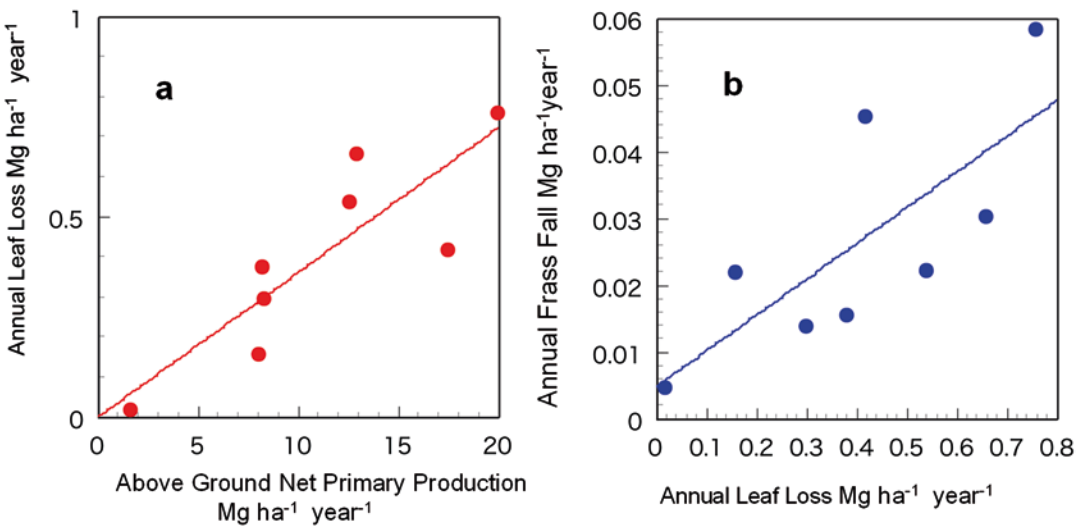


Fig. 17.4. (a) Annual leaf loss estimated from lifetime leaf loss against aboveground net primary production in tropical montane forests at different altitudes (700 m~3100 m above sea level) on Mt. Kinabalu. (Redrawn after Suzuki et al. 2013). Annual leaf losses were around 5% of aboveground net primary production (ANPP; Leaf Loss = 0.036 ANPP+0.0017; $r^2 = 0.73$). (b) Annual frass fall against annual leaf loss. Frass fall is less than 10% of leaf loss. (Frass Fall = 0.054 Leaf Loss+0.0049; $r^2 = 0.57$)

lifetime leaf loss) estimated to be 0.02~0.76 mg dry weight ha⁻¹ year⁻¹. This estimate correlated well to the above ground net production (Fig. 17.4a) of forests at dif-

ferent altitudes on Mt. Kinabalu, and was also positively correlated with frass fall collected in the litter traps (Fig. 17.4b; Kikuzawa et al. 2002).

IV. Plant Size, Plant Performance and L

Leaf longevity is related to a broad array of traits associated with variation in plant life history (Reich 2014). The shorter L the more rapid is the acquisition of resources, juvenile growth, reproductive maturation, and the shorter the plant lifespan. For example, Reich et al. (1992) reported a negative relationship between the relative growth rate (RGR) of individual plants and L. Similarly, Seiwa and Kikuzawa (2011) showed a negative trend between RGR of seedlings and L.

A. Normalization Constant of Allometry

West et al. (1997) proposed a general metabolic scaling equation to show the relationship between plant performance (Q) and plant mass (M).

$$Q = Q_0 M^\theta \quad (17.16)$$

where Q is any value relating to some aspect of metabolism such as leaf mass, photosynthesis, or respiration, θ is a scaling exponent which takes a value usually less than unity, and M is plant mass. Q_0 is a normalization constant that adjusts the general relationship (M^θ) across environments and species.

Although Eqs. (17.14) and (17.15) are for production of forest stands, they are equally applicable to the production of individual plants if we consider parameter B as the leaf biomass of an individual plant. Instantaneous photosynthetic rate declines with time as daily rate does in Eq. (17.2).

$$A_{\text{mass}} = A_{\text{mass}}(0) \left(1 - \frac{L}{b}\right) \quad (17.17)$$

Average photosynthetic rate, \bar{A}_{mass} is given as

$$\bar{A}_{\text{mass}} = A_{\text{mass}}(0) \left(1 - \frac{L}{2b}\right) \quad (17.18)$$

On the other hand, applying Eq. (17.16) to the leaf biomass-plant biomass allometry, we obtain the following:

$$B = \beta M^\theta \quad (17.19)$$

where β is a normalization constant. Substitution of Eq. (17.6), which is written using A_{mass} as

$$m = \left(\frac{2bC}{A_{\text{mass}}(0)LMA L^2} \right). \quad (17.20)$$

Substitution of this equation and Eqs. (17.18) and (17.19) into (17.15) gives an individual plant's surplus production as

$$P = \frac{fC}{LMA L} \left(\frac{2b}{L} - 1 \right) \beta M^\theta \quad (17.21)$$

It is noteworthy that productivity is independent of photosynthetic rate (A_{mass}) but is affected by leaf longevity (L). In the bracket of Eq. (17.21), b/L represents the ratio of potential to actual leaf longevity. Usually, potential leaf longevity is longer than realized L and thus this equation expresses surplus production. Kikuzawa et al. (2013a) examined the ratio of potential to realized L for 34 species-year-site combinations and found the ratio to be approximately 2.0.

B. Relative Growth Rate

If we assume that a fixed ratio (γ) of production is allocated to an increment of plant mass then $dM/dt = \gamma P$. Relative growth rate (RGR) is $(1/M)dM/dt$. If we set $b/L = 2$, then the following is easily derived from Eq. (17.21).

$$\text{RGR} = 3\gamma \frac{fC}{\text{LMA}L} \beta M^{\theta-1} \quad (17.22)$$

If first-year seedlings are compared, γ will be invariant among individual plants of the same species, since plant size at the end of the first growing season is determined by seed reserves and current year production and seed size is relatively invariant within the same species (Westoby and Rice 1982; Westoby et al. 1992). The effect of θ will also disappear in the case of seedlings, since θ takes a value near unity for small plants (Reich 2001). Considering these simplifications, Eq. (17.21) can explain the negative relationship between RGR and L (Reich et al. 1992; Seiwa and Kikuzawa 2011; Kikuzawa et al. 2013a). This relationship can be extended to the comparison of RGR across species when the seedling size is far greater than the supply from seed reserve, or where differences in seed size among species are not so great.

The negative relationship between RGR and L as indicated in Eq. (17.22) could also be derived from traditional growth analysis (Poorter et al. 2009)

$$\text{RGR} = \frac{1}{w} \frac{dw}{dt} = \frac{1}{A} \frac{dw}{dt} \frac{A}{w} = \frac{1}{A} \frac{dw}{dt} \frac{w_L}{w} \frac{w}{A} \quad (17.23)$$

Where $1/w(dw/dt)$ is RGR, $1/A(dw/dt)$ is net assimilation rate (NAR), A/w is leaf area ratio and w_L is leaf weight. w_L/A in the denominator of the fourth term is nothing but the LMA and is positively correlated with L. Thus, RGR is predicted to be negatively correlated with L from the growth analysis.

V. Ecosystems

A. Productivity of a Stand

Resource acquisition is asymptotic with the investment for resource capture. For example, total photosynthesis by an individual plant is best expressed as a quadratic equation against total leaf mass, not by a straight line (Koyama and Kikuzawa 2009). Similarly, the growth equation for an individual plant is expressed by a logistic equation (Shinozaki and Kira 1956), which allows for the relationship between total plant biomass per unit land area (y) against plant number per unit land area (n) as

$$y = n / (dn + e) \quad (17.24)$$

where d and e are parameters of the equation (Kikuzawa and Lechowicz 2016). Under completely one-sided competition, this inevitably leads to the cumulative mass versus cumulative number relationship:

$$Y = N / (DN + E) \quad (17.25)$$

where Y is cumulative mass from the largest tree in a stand, N is cumulative number of trees in the stand also from the largest tree, and D and E are parameters that ultimately correspond to d and e , respectively (Kikuzawa 1999; Kobayashi and Kikuzawa 2000; Kikuzawa and Lechowicz 2016). Eq. (17.24) in turn leads to the distribution density function ($\phi(M)$) for tree mass (M) (Hozumi et al. 1968) as

$$\phi(M) = \frac{\sqrt{E}}{2D} M^{-3/2} \quad (17.26)$$

Multiplying Eqs. (17.26) and (17.21) and integration of the individual plant production in relation to plant mass from the largest to smallest individuals gives the production of a stand:

$$P_T = \frac{3\sqrt{E}}{D(2\theta-1)} \frac{fC}{LMA L} \beta M_{\max}^{\theta-\frac{1}{2}} \quad (17.27)$$

where P_T is the stand production of a pure stand which is composed of a single species; the term M_{\min} (the smallest plant mass in the stand) is omitted as it is too small to matter compared to M_{\max} (mass of the largest individual). In case of the total production in a mixed species stand, which is composed of multiple species, P_T will be given by the summation of production P_i of each species present, which can be a daunting task.

Here, we will propose an alternative, more feasible method to estimate productivity in a mixed species stand. From Eq. (17.15), surplus production of species i (P_i) is expressed as

$$P_i = \frac{B_i}{L_{fi}} f_i m_i L_{fi} \bar{A}_{massi} \quad (17.28)$$

where the suffix i expresses each species. This equation can be simplified as,

$$P_i = F_i P_{Li} \quad (17.29)$$

The leaf production per species i (F_i) can be obtained using litter traps set on the forest floor. Repeated measurements of photosynthesis (cf. Fig. 17.3a) and monitoring of leaf numbers will give the average lifetime gain by a leaf (P_{Li}). The total surplus production of the forest ecosystem is then given by

$$P_T = \sum_i F_i P_{Li} \quad (17.30)$$

B. Longevity of Fallen Leaves in Ecosystems

Since leaf fall is an important path connecting the production processes in an ecosystem to the decomposition processes, the characteristics of fallen leaves can influence ecosystem function (Kikuzawa 2004). Various traits affecting decomposition processes vary with leaf longevity, which differs substantially among herbaceous and woody plant life forms (Kikuzawa and Ackerly 1999). Other leaf traits such as LMA, nitrogen content, and photosynthesis also vary among life forms, for example among annual and perennial forbs, grasses, deciduous trees, evergreen trees, and needle-leaf conifers (Niinemets et al. 2015). Some chemical defense materials can remain in fallen leaves, which together with mechanical traits such as high LMA act against consumption and decomposition by soil animals and microorganisms on the forest floor (Cornelissen and Thompson 1997; Cornelissen et al. 1999; Thomas and Sadras 2001). Santiago (2007) showed that the decomposability of leaf tissue for 35 plant species in a tropical forest was related to LES characteristics. Thin or less dense leaves with high nutrient concentrations from fast-growing species were easily decomposable whereas thick and tougher leaves from slow-growing species were not readily decomposable. These differences in decomposability in fallen leaves affect the nature of soils, micro- and meso-organisms in forest soils, and thereby ultimately affect the nutrient circulation in forest ecosystems.

Similarly, tree leaves occasionally fall in streams where differences in the decomposition rate are observed among species. For example, the rate of leaf-area loss in the stream was greater in alder (*Alnus glutinosa*) than in oak (*Quercus petraea*) leaves. Aquatic insect larvae (shredders) are responsible to the leaf area-loss, which in turn was affected by the presence of predacious insect-larvae such as dragonflies (Jabiol et al. 2014).

C. Comparison of Ecosystems

In the leaf economics spectrum (LES), Reich (2014) recognized two extreme strategies of plants: slow and fast. The slow strategy is characterized by a low rate of photosynthesis but longer leaf longevity and high LMA, the fast strategy by high but rapidly declining A_{mass} , short L, and low LMA. Analogous to slow and fast leaf traits, ecosystems can be similarly classified as slow and fast.

Terrestrial forest ecosystems are typically slow ecosystems where forests are characterized by high levels of plant mass stored in the woody biomass of trees with long lifespans. Among forest ecosystems, some are relatively fast and some are relatively slow. Fast forest ecosystems at high latitudes in the northern hemisphere, for example, are dominated by early successional species such as *Alnus*, *Betula*, *Populus*, and *Mallotus* with short L (Kikuzawa 1983). Slow forest ecosystems in these regions are dominated by tree species such as *Fagus* and *Quercus* with leaves of longer L that are not easily decomposable and therefore accumulate as litter layers in the soil and with higher biomass. In contrast, aquatic ecosystems can be characterized as very fast with primary producers such as phytoplankton, aquatic algae, and aquatic herbaceous plants that have short longevity and much lower biomass than the trees that dominate forest terrestrial ecosystems.

By analogy to trade-offs among leaf-traits, we can expect some relationships among ecosystem-traits. Keystone traits characterizing ecosystems are the longevity of photosynthetic organs and their supporting systems. In forest ecosystems, leaves are supported by woody roots, stems, and branches. A major portion of the carbon that the plants in these ecosystems accumulate is invested in these woody organs. This results in great C_s in Eq. (17.7) and thus great C in Eq. (17.4) and finally entails long L. On the other hand, in aquatic ecosystems, photosynthetic organs can float in water by buoyancy

and thus minimize C_s (Kikuzawa and Ackerly 1999). Differences in the arrangement of leaves in different environments entails different turnover of leaves. Additionally, energy flow through herbivores in terrestrial ecosystems is smaller (Fig. 17.4) than in aquatic ecosystems (Cyr and Pace 1993). Terrestrial plants are hard, tough, and not readily digestible, and herbivores are more limited by predators (Polis 1999; Jabiol et al. 2014).

VI. Biogeographical Patterns

Several biogeographical patterns that map onto LES traits have been recognized such as latitudinal trends in LMA, leaf longevity, and the relative proportion of species with evergreen versus deciduous habits. The functional basis of such patterns arises in adaptations to the onset of an unfavorable season for productivity. In broad terms, plants follow one of two alternative strategies that comprise the contrasting foliar habits. Deciduous trees shed all their leaves and resume photosynthesis at the next favorable period. Evergreen species retain leaves through the unfavorable period, paying a maintenance cost but with the advantage that photosynthesis resumes quickly at the start of the next favorable period using leaves that were retained during the winter and/or during a period of low water availability. In evolutionary terms, the relative advantages of the two foliar habits is decided by a combination of environmental factors and foliar traits that together define alternative adaptations to maximize carbon gain. We illustrate the nature of these complex interactions in a series of examples.

- (a) Broadleaf evergreen trees dominate in tropical, subtropical, and warm temperate forests, deciduous trees in temperate forests, and needle-leaf or small-leaved evergreen trees in boreal and subarctic forests at high latitudes. Chabot and Hicks (1982) found this to

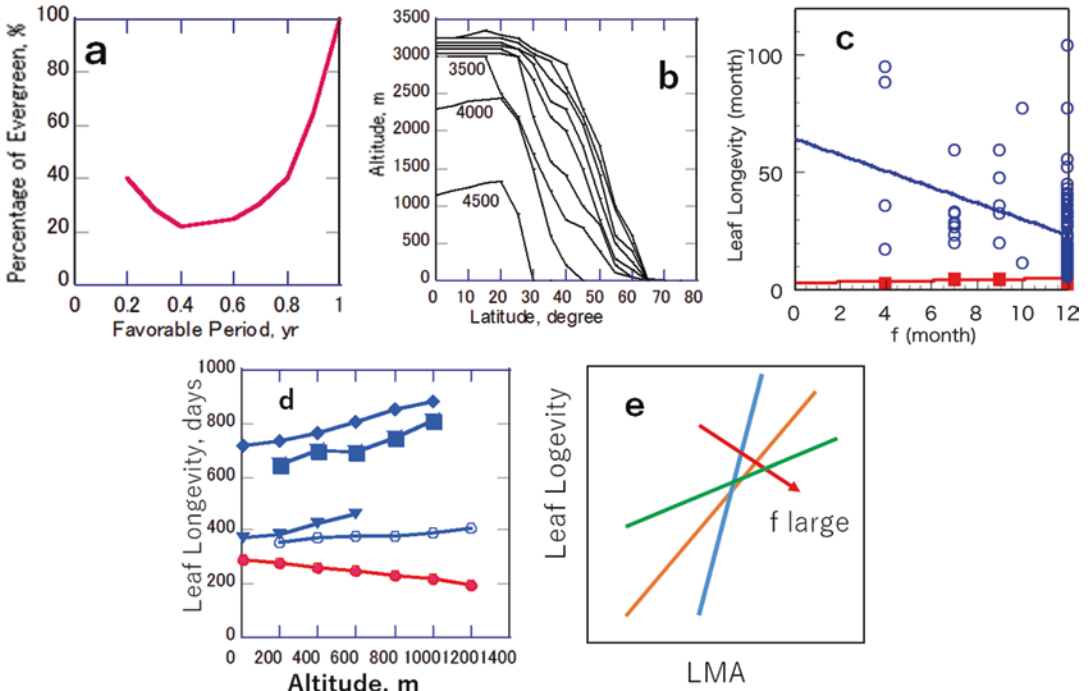


Fig. 17.5. Biogeographical patterns at both global and local scales reproduced by Eq. (17.12). (a) A schematic representation of global pattern of percentage of evergreen species. Two peaks were observed at lower and higher f . Redrawn after Kikuzawa (1991). (b) A schematic representation of plant species richness in monsoon Asia. The number of species is highest at low latitude and altitude and decreases toward higher latitude and altitude. Numerals affixed to the curves are number of species. (Redrawn after Kikuzawa (1996)). (c) Different global patterns of leaf longevity against f . L of deciduous species increases while that of evergreen species decreases with increasing f . (Redrawn after Kikuzawa et al. (2013b)). (d) Different altitudinal patterns of evergreen (green symbol) and deciduous (red symbol) species on Yakushima Island. *Sm* *Stewartia monadelpha*, *Qs* *Quercus salicina*, *Cc* *Castanopsis cuspidata*, *La* *Litsea acuminata*, *Dr* *Distylium racemosum*. (Redrawn after Fujita et al. (2012)). (e) L-LMA relationships modulated by f . In short f , the gradient of the L-LMA relationship is steep, but it becomes gentle with greater f . (Redrawn after Kikuzawa et al. (2013b))

be a puzzling bimodal pattern for evergreen species, but Kikuzawa (1991) was able to explain the bimodal pattern by extending Eq. (17.12) (cf. Fig. 17.5a).

- (b) The number of tree species is richest in tropical rain forest and decreases towards higher latitudes and higher altitudes. Several models have been proposed to explain this pattern but none reproduce the pattern successfully (Pianka 1966; Iwasa et al. 1993). Kikuzawa (1996) was able to reproduce the pattern by considering different parameter values of a , b , C , and r in simulations under given f values in Eq. (17.12). Each combination of parameter values a , b , C , and r was considered to represent one species, and the parameter

space was explored to count the number of species that achieved positive carbon balance under a given f . The number of evergreen species with positive carbon balance was highest at low latitude and low altitude and decreased toward higher altitudes and latitudes (Fig. 17.5b).

- (c) Kudo (1991, 1992) tried to clarify the effect of the length of the snow-free period (f) on the phenology of alpine plants in a limited geographical area in northern Japan where the timing of snow disappearance differs from site to site providing different f with other factors being equal (Kudo 1992; Kikuzawa and Kudo 1995). Leaf longevity (L) of two evergreen plants decreased with

increasing f , while L of a deciduous plant increased with f . Wright et al. (2005) reported a similar contrast in the relationship between L and mean annual temperature (MAT) for evergreen and deciduous species. Leaf longevity of evergreen trees decreased with increasing MAT but L of deciduous species increased. Decreases in L with increasing MAT have also been reported at a global scale for evergreen conifers (Reich et al. 2014) and at a local scale in China (Zhang et al. 2010). These contrasting trends for L against MAT can be interpreted as a corollary of the relationship between L and favorable period length (f ; Kikuzawa et al. 2013b) (Fig. 17.5c). Mean annual temperature is correlated with f (Enquist 2011; Kikuzawa et al. 2013b), especially when data for tropical mountains are excluded. Equation (17.11) suggests that the divergent trends in evergreen and deciduous plants can be interpreted as the outcome of adaptive behavior of plants to maximize carbon gain. With decreasing f , the model predict that evergreen species need to prolong their leaf longevity to compensate for the shorter photosynthetic period within a year. Thus, in evergreen species L is negatively correlated with f . Deciduous species could behave similarly, but in doing so, by definition, they would no longer be deciduous (Kikuzawa et al. 2013b).

- (d) On temperate mountains, MAT and f decrease with altitude; changes in temperature and f are a simple analog of latitudinal change. Hence it is not surprising that the L for deciduous *Stewartia monadelphica* (Theaceae) on a temperate mountain in Japan decreased with elevation, while that of four evergreen species increased (Fig. 17.5d; Fujita et al. 2012). Similar altitudinal trends were also found on a mountain slope in central Japan (Takahashi and Miyajima 2008). However, although MAT decreases with altitude on tropical mountains, f is unchanged (Kikuzawa 1996). In this case, only MAT affects L in the condition of $f = 1.0$, and Eq. (17.3) can predict the altitudinal change in L . Parameter a will
- decrease with altitude in eq. (17.3) and thus L is predicted to increase with altitude.
- (e) As shown in Sect. 2.5 (Fig. 17.1), there are positive correlations between L and LMA. In a global analysis, Wright et al. (2005) found that the slope of L -LMA changed systematically with MAT. Similar changes were also found when Kikuzawa et al. (2013b) examined the L -LMA relationships with respect to f . The actual L -LMA relationship was steeper in shorter f than that in longer f . (Fig. 17.5d). These changes in the slope of the L -LMA relationships are simulated using Eq. (17.12), indicating that the change in the slope of the L -LMA relationship is caused by adaptation to different f . Evergreen leaves in shorter f need a longer L for a given LMA to pay back their construction cost, while deciduous leaves in a short f have shorter L for a given LMA due to the limited length of the growing season, which results in a steeper slope in shorter f .

VII. Conclusions

Plant productivity is often viewed simply through the lens of net photosynthetic activity, whether assessed by gas exchange measurements at the level of single leaves or eddy covariance measurements at the level of entire plant canopies. In this review of work derived from Kikuzawa's (1991) theory for leaf longevity, we have tried to make the case for the value and utility of an alternative perspective that gives a certain primacy to leaf longevity. On the one hand, leaf longevity can be considered simply as a part of the leaf economic spectrum (Wright et al. 2004; Shipley et al. 2006), a complex of foliar traits that also includes the leaf's net photosynthetic rate, its dark respiration rate, its nitrogen and phosphorus concentrations, and the ratio of its mass and areal surface. On the other hand, leaf longevity stands apart as the only one of the LES traits that integrates the influence of all the others over the leaf lifespan – in other words, leaf longevity has the character of an emergent foliar trait. In this

sense, leaf longevity is perhaps the LES trait that best links function at the level of single leaves to function at the level of the plant canopy, and even perhaps to the production of plant communities (Kikuzawa and Lechowicz 2016).

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