

The Time Value of Leaf Area

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ABSTRACT: When a plant invests in construction of a leaf, the revenue-stream that accrues is shaped by three variables: first, the light-capture area per milligram dry mass invested, analogous to a potential rate of return on investment; second, the longevity of the leaf, analogous to the expected duration of the revenue stream; and third, a time-discount rate, quantifying the fact that light-capture area deployed in the immediate future is more valuable to the plant than the same area deployed at some later time. Recent comparative data make it possible to quantify the cross-species trade-off between the first variable and the second variable. Here we develop an approach through which the consequences of the third variable, the time-discount rate, can be related to the trade-off between the first variable and the second variable. The approach involves an equal-benefit set, the cross-species equivalent of a fitness set. A wide spread of strategies is actually observed to coexist in vegetation, from low to high light capture area per gram and, correspondingly, from high to low leaf longevity. The coexistence suggests that the different observed strategies do not have a clear-cut advantage over the other. The equal-benefit set can be used to investigate what levels of time discount would make it the case that neither the highest-longevity nor the highest light-capture area per milligram strategies would have a clear advantage over the other, with regard to the time-discounted value of the revenue stream generated per milligram invested in leaf.

Keywords: specific leaf area, leaf longevity, time discounting, ecological strategies, trade-offs.

Plant growth can be understood as a process of investment leading to returns and reinvestment. Dry matter is acquired through light interception and carbon fixation and is invested in leaves, which then acquire further dry matter. (For brevity, in this article, we use “leaves” to include

phyllodes or other structures that are not morphologically leaves but that are the major green surface of the plant.)

Different species produce leaves of very different kinds. A fundamental measure is the light-capturing area per dry mass of leaf, known as specific leaf area (SLA; one-sided $\text{mm}^2 \text{mg}^{-1}$). Specific leaf area varies more than tenfold among species growing interspersed in the same habitat. Considering that SLA is analogous to a potential rate of return on investment, at first glance it might seem surprising to find a tenfold range of SLA among coexisting species. Why do species with lower SLA not evolve toward higher values? A likely answer is that low-SLA species, investing more mass per unit leaf area, build leaves with greater life span (fig. 1, from data of Reich et al. 1997, 1999; see table 1 for slopes). Hence the revenue stream from a milligram invested in low-SLA leaves lasts longer, albeit with a narrower flow.

The treatment in this article builds from the premise that the observed SLA-longevity relationships in figure 1 are constrained within outer boundaries on what is achievable. It is reasonable to expect that more flimsily constructed leaves will be more vulnerable to physical damage and more susceptible to herbivory (Coley 1987, 1988) and, consequently, will suffer a penalty in longevity. If it were possible for a species strategy to evolve higher SLA without a decline in leaf longevity or without other deleterious consequences, then they would have been expected to do so. By the same token, strategies at a distance below the outer boundary should be less competitive (other things being equal) than strategies closer to the boundary, which have an advantage in SLA without a disadvantage in leaf longevity. The fact that observed species in any given environment are arrayed along a band of negative slope can most naturally be interpreted as meaning that the zone outside (above) the band is physically unachievable and that the zone inside (below) the band is uncompetitive (Reich et al. 1999).

Some Other Influences on SLA-Longevity Relationships

As well as differing between species, SLA is also modulated during the development of individual leaves in

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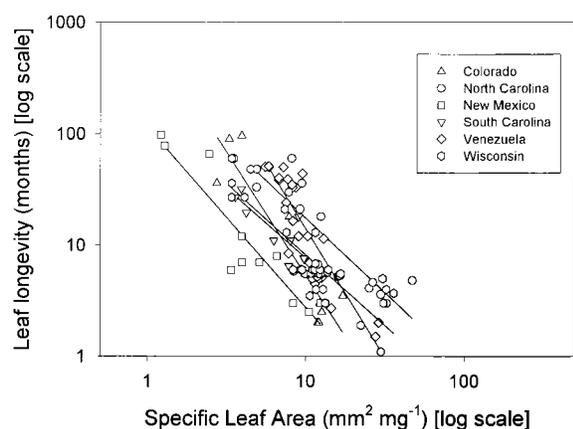


Figure 1: Cross-species relationships between leaf longevity (mo) and specific leaf area ($\text{mm}^2 \text{mg}^{-1}$), from data in Reich et al. (1999).

response to the physical environment, especially in response to shading. Indeed, some capacity for species to adjust SLA tactically would be expected, given the strategic importance of the trait. In this section, we first consider whether or not the longevity-SLA relationships across species within the same flora (fig. 1) might result from different species operating in different light environments. For several reasons, we think they result from intrinsic differences in leaf strategy between species rather than from light-environment effects. First, the data for all species were obtained from leaves developed in full light, to the extent to which that was possible. Second, the high-SLA species in the data were not principally shade dwellers (Reich et al. 1999). Third, leaves developed in shaded situations typically have not only higher SLA but also greater longevity, as compared with leaves observed in the sun, both within and between species (Williams et al. 1989; P. B. Reich, unpublished manuscript). Thus the relationship produced by tactical response to shading runs crossways to the observed pattern across species in figure 1. For these reasons, we have developed our approach on the premise that the SLA-longevity relationships in figure 1 represent trade-offs, with higher SLA not achievable without sacrificing leaf longevity.

Second, consider the role of seasonality in the longevity-SLA trade-off. Where there is a clear nongrowth season (winter in cold temperate climates, dry season in some tropical climates), one would expect longevity to be discontinuously distributed in the range surrounding 1 yr. Leaf longevity should either correspond to a single growth season or less (deciduous and annual species) or to two or more growing seasons plus the intervening non-growing seasons. However, the evergreen-deciduous di-

chotomy in seasonal environments is not the main or only influence on the longevity-SLA relationships in figure 1. Longevity continues to increase with decreasing SLA in the range above 1 yr, and a similar relationship obtains for the tropical rain-forest data set from Venezuela.

In the formal treatment later in this article, potential revenue streams and discounting are treated as constant over time, this being the natural theoretical starting point. Plainly, in seasonal environments both revenue and discounting processes do vary from month to month, so the constant-rate treatment does not capture the complexities of what might happen for longevity in the range from 0.5 to 1.5 yr.

Third, the data in figure 1 suggest that longevity-SLA bands may be at different elevations for different climate zones. In New Mexico, the driest environment represented, a given SLA may achieve a shorter leaf longevity than it would in a higher-rainfall environment (fig. 1). It seems plausible that water stresses or other hazards associated with a low-rainfall environment might enforce shorter leaf longevity at a given SLA. Nevertheless, it is not among the purposes of this article to draw conclusions by comparing different vegetation types, mainly because the available vegetation types are too few. Comparisons across a range of rainfall (e.g.) have too little replication and are too confounded with other environmental variables. The purpose of this article is not to draw conclusions from data but rather to develop ideas about time discounting applied to leaves, in the form of graphs showing equal benefit sets and in the corresponding algebra.

Why Not Selection toward Greater Leaf Longevity?

Moving from higher- to lower-SLA species strategies, the gain in leaf longevity not only compensates for the loss of

Table 1: Slope of log-log relationships between leaf longevity (y) and SLA or A_{mass} (x)

Location	Log leaf longevity vs. log SLA	Log leaf longevity vs. log A_{mass}
Colorado	-2.40 (.26)	-1.53 (.11)
North Carolina	-1.54 (.20)	-1.43 (.13)
South Carolina	-1.74 (.21)	-1.16 (.11)
New Mexico	-1.45 (.40)	-.93 (.17)
Venezuela	-2.63 (.26)	-1.45 (.10)
Wisconsin	-1.19 (.14)	-1.27 (.08)

Note: Data from Reich et al. (1999). Slopes estimated as standardized major axis (Sokal and Rohlf 1995, p. 544) since we were looking for an underlying rather than a conditional relationship between variables; in other words, departures from the model in the x dimension as well as in the y dimension are to be taken into account. Standard error in parentheses.

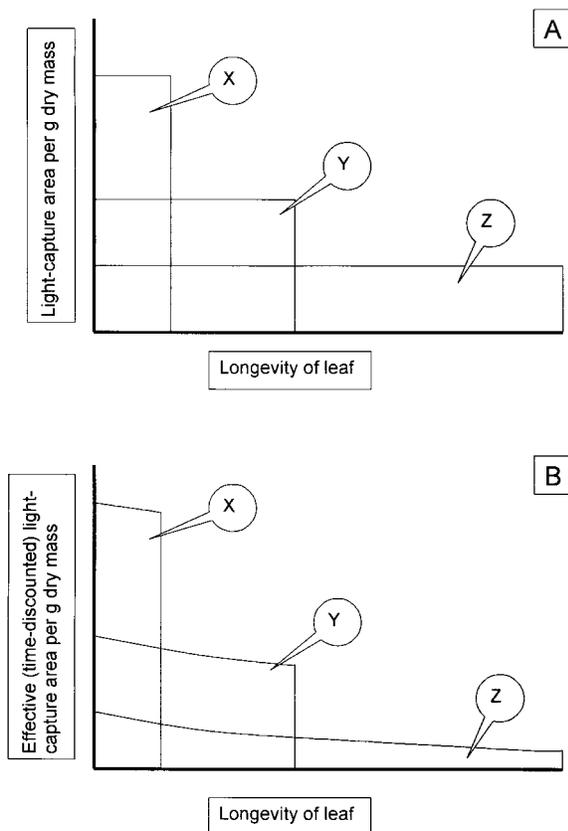


Figure 2: Schematic illustration of the effect of time discounting on the benefit returned per milligram dry mass deployed. *A*, Benefit construed as the simple rectangle representing leaf area per milligram dry mass multiplied by the longevity of the leaf. Because longevity increases across strategies $X \rightarrow Y \rightarrow Z$ faster than area per milligram decreases, strategy Z returns the greatest benefit. *B*, Benefit returned from a given leaf area is construed as depreciating over time. Depending on the time-discount rate, the three strategies can return the same lifetime benefit per milligram invested.

area deployed per gram but actually outweighs it (fig. 1 and table 1, slopes steeper than -1 for all vegetation regions). A species with half the SLA will (on average) have more than twice the leaf life span. Consequently, the area deployed multiplied by the time over which it is deployed tends to be greater for low-SLA leaves (fig. 2A). The generality of this fact has only recently become apparent from the compilation of comparative information (fig. 1; Reich et al. 1997, 1999). This raises the opposite question to the one discussed previously. Why do species with higher SLA not tend to evolve toward lower values? Why does selection to increase leaf longevity not outweigh selection to increase light-capture area per milligram?

The suggested answer to this question is that light captured (and carbon fixed and dry matter acquired) in the

distant future is less valuable to the plant than light captured in the near future (fig. 2B). This time-discounting effect is familiar in investment economics and is known as the "time value of money" (Levy and Sarnat 1994). By analogy, the topic of this article is the time value of leaf area. Using a discount rate, future benefits can be converted back to their present value for comparison with current benefits.

In the context of plant growth, future persistence of leaf area should be less valuable than immediate production of leaf area for several reasons: First, there is reduced revenue from older leaves, the result of overshading as the surrounding vegetation and the plant itself continue to grow. Second, there is reduced revenue from older leaves, due to accumulation of algae, fungi, debris, and so forth on the leaf surface and as a result of damage from herbivores. (Note that the risk that the whole leaf will be lost to herbivory or to physical damage is not a cause of time discounting because the effect of this risk is already included within leaf longevity as measured.) Third, there is the risk that the plant will no longer be alive to benefit. And finally, there is the compound-interest effect: earlier dry matter acquisition can itself be reinvested, and the resulting compound-interest effect can generate more growth than the simple interest from an individual leaf producing revenue over a longer life span. This compound-interest effect can also be called a "reinvestment" or an "opportunity-cost effect." It can apply to population growth as well as to individual growth components of fitness. For example, if some of the dry matter acquired is devoted to seed production, then population growth may be accelerated by seeds produced sooner rather than later.

All four of these sources of time discounting operate together and add up to give an overall rate of time discounting. Their relative importance in any given field situation remains a matter of judgement, since no attempt has yet been made to estimate them relative to each other. Previous discussions of time discounting in leaves have emphasized the compound-interest effect. Harper (1989) observed that the compound-interest or opportunity-cost effect applies while exported assimilates are translocated for use in the growth of new leaves but not while assimilates are translocated to storage instead of being reinvested. This point was developed in relation to the optimal distribution of mineral resources and defenses during the life of leaves. Poorter (1994) discussed differences in relative growth rates between species from the perspective of the payback time for investment in leaves. These authors were mainly concerned with the compound-interest effect and its relationship to growth rates, but it seems likely that the pace of overshading by competing vegetation will

be an important source of time discounting in many situations.

Equal-Benefit-Set Formulation

Here we develop an equal-benefit-set framework for considering the effects of time discounting on alternative leaf strategies for SLA and longevity. Our purpose is to address two issues. First, approximately what level of time discounting would have the effect of setting the expected level of SLA at some intermediate level (as plants are actually observed to have), instead of selection driving longevity toward ever-higher values and SLA toward ever-lower values (as implied by the observation that gains in longevity outweigh losses in SLA; fig. 1)? Second, when time discounting is taken into account, is SLA predicted to have a narrow and clear-cut optimum, or are a wide range of SLA strategies predicted to generate similar time-discounted returns? This second question is of interest because species strategies coexisting in vegetation are actually observed to span quite a wide range of SLA and leaf longevity (fig. 1).

Let the revenue stream to a plant from a leaf after leaf expansion but near the outset its life be expressed as $SLA \times E$, where SLA is leaf area (mm_2) per milligram dry mass of leaf, and E is the rate at which a square millimeter exports photosynthate to the remainder of the plant. The variable E is expressed in milligrams of dry mass that could be constructed from the photosynthate, for comparability with the denominator of SLA. It is different from a maximum potential photosynthetic rate A_{area} , as might be measured via gas exchange. It reflects actual rather than potential photosynthesis and includes effects such as stomatal closure resulting from restricted water supply. Further, E is a rate of export to the remainder of the plant, rather than a rate of acquisition by the leaf. In addition, E is what the rate of export would be if there were no increase in shading, no deterioration of the leaf surface, no risk of plant death, and no cost of compound-interest effects. These time-discounting factors are to be expressed through a different parameter, the discount rate k , introduced below. It would be mathematically possible to partition k into some components that would be detectable in the actual export stream from the leaf (shading and deterioration of the leaf's surface) and other components that would not be detectable (risk of the plant no longer being alive and compound-interest effects). This partitioning could be valuable if data were available on actual exports through the course of a leaf's life but is not undertaken here.

Now suppose the value of $SLA \times E$ were to deteriorate by a constant proportion k per month. The return to the plant from a milligram dry mass invested in a leaf would

then be $SLA \times E$, integrated over the lifetime of the leaf (longev) but time discounted back to its present value. The present value of lifetime return ("return" for short, R) would have units of the present value of milligrams dry mass revenue over the leaf's lifetime per milligrams invested and would be (for nonnegative discount rates, $k \geq 0$)

$$R = \int_0^{\text{longev}} (E \times SLA \times e^{-kt}) dt,$$

$$R = \frac{E \times SLA}{k} [1 - e^{(-k)\text{longev}}].$$

To characterize the set of leaf longevity-SLA combinations that confer equal R , rearrange this equation to express longevity as a function of SLA while treating R , E , and k as parameters:

$$\text{longev} = \left(-\frac{1}{k} \right) \ln \left(1 - \frac{Rk}{E \times SLA} \right).$$

"Equal-benefit" contours can then be constructed on the log longevity–log SLA plane for any given time-discount rate k , and the effect of k on the contour shapes can be investigated (fig. 3). Contours further from the origin represent higher values of R/E , the present value of return over a leaf's lifetime (mg mg^{-1}) expressed as a multiple of the exported revenue ($\text{mg mm}^{-2} \text{mo}^{-1}$) near the outset of the leaf's life. Each contour represents equal lifetime return on investment in leaves in this sense, across a range of SLA-longevity strategies. The possible role of variation across species in E will be addressed later.

At $k = 0$, the equal-benefit contours are straight lines with slope = -1 (fig. 3A). Since the observed longevity-SLA bands have steeper slopes than -1 (fig. 1; table 1), species at the high-longevity, low-SLA end of the observed relationships would lie on higher contours, if there were no time discounting ($k = 0$). This is a graphical restatement of the point made earlier, that in the absence of time discounting, selection would be expected to drive longevity indefinitely upward and SLA indefinitely downward because species gain more in leaf longevity than they lose in area deployed per dry mass.

With time discounting (nonzero k), the equal-benefit relationship between log leaf longevity and log SLA becomes nonlinear. In particular, the R/E contours toward the higher longevities are pushed outward with increasing k (fig. 3B compared with fig. 3A). This is because time discounting means that there are diminishing returns, moving toward ever-higher leaf longevity and ever-lower

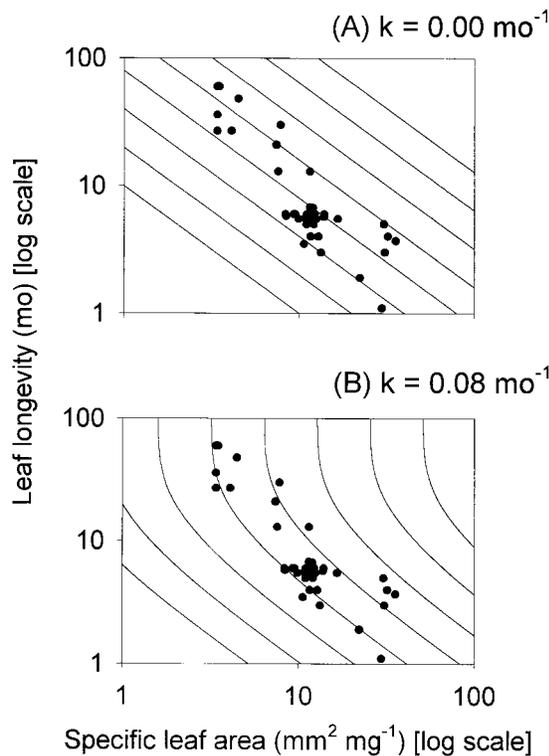


Figure 3: Contours of equal benefit R/E (present value of time-discounted returns from a mg dry mass invested over the lifetime of the leaf, mg mg^{-1} , expressed as multiples of the revenue export rate from a unit of leaf area at the outset of its mature life, $\text{mg mo}^{-1} \text{mm}^{-2}$). A, In the absence of discounting ($k = 0$) the contours are straight lines with slope = -1.0 . B, Discounting at $8\% \text{ mo}^{-1}$ ($k = 0.08$). Data given are for Wisconsin species (see fig. 1).

SLA. These diminishing returns should shape one edge of the observed spread of longevity-SLA combinations. Biologically, the log-scaled, equal-benefit contours curve upward because discounting has a greater effect going from 50 to 100 mo of leaf longevity than from 5 to 10 mo of longevity. Because of the curvature produced by time discounting, species at the low end of the SLA spectrum need not lie at higher R/E than species at higher SLA. At shorter longevity, the contours remain almost linear because time discounting has less effect. The equal-benefit contours do not appear to set any clear upper limit to SLA. The observed upper boundary of SLA coincides with a lower boundary to leaf longevity on the order of 1–3 mo (fig. 1). We suggest that other factors not considered in this article's treatment shape the high-SLA, short-longevity edge of the observed spread of species strategies. Costs of reextracting nitrogen to redistribute it to newer leaves must militate against too-short leaf longevity, and leaves with SLA above some level may be too flimsy to survive even moderate winds.

To summarize the argument thus far, the equal-benefit contours produced by time discounting have properties capable of accounting for the two problems posed at the outset. First, why is there not a clear advantage for greater longevity even at the expense of lower SLA? And second, how can it be that species coexist with a wide range of SLA-longevity strategies?

Influence of Different Factors on Time-Discounted Lifetime Benefit and Fitting Equal Benefit Sets to Observed Data

The congruence of an R/E contour with longevity-SLA data can be affected by all three of the elements of a given longevity-SLA relationship (fig. 3), that is, by the slope of the relationship, by its elevation, and by the range of SLAs spanned. If the observed SLA-longevity relationship is more steeply negative, faster discount will be needed for an R/E contour to be congruent with the data. Biologically, this is because a steeper line represents a greater longevity benefit for a given SLA decrease, and this shifts the balance toward selection for greater longevity, unless the effect is counteracted by faster discounting. If the observed longevity-SLA relationship has the same slope but is at lower elevation, that is, less longevity at a given SLA, then effects depend on whether the relationship lies in a higher or lower range of SLA. At higher SLA, the R/E -balancing discount rate is little affected, though the congruence is at a lower R/E contour. Toward the left, in the lower range of SLA, lowering the level of the SLA-longevity relationship makes for congruence at a slower discount rate.

By fitting the equal-benefit equation $\text{longev} = -(1/k) \times \ln(1 - [R \times k]/[E \times \text{SLA}])$ to observed SLA-longevity data, we have estimated what value of k is closest to having the effect of equalizing benefit across the observed range of SLA, within each vegetation type (fig. 4). The fitting was a nonlinear equivalent of a major-axis fit; sums of squares were minimized in a direction perpendicular to the contour described by the equation, rather than minimized in the same direction for each data point as in a linear model. The mechanics of fitting are described in the appendix.

For the four temperate-vegetation floras (Wisconsin, North and South Carolina, and New Mexico) best-fit k values were similar at $0.05\text{--}0.08 \text{ mo}^{-1}$. These discount rates of $5\%\text{--}8\% \text{ mo}^{-1}$ that would best equalize benefit across the set of coexisting species correspond to per-year discount rates of approximately $45\%\text{--}65\%$. The Colorado alpine-vegetation and the Venezuelan tropical-forest data sets were best fitted by somewhat higher k values. However, the differences were marginally significant at best (see appendix for discussion of attaching confidence intervals to k values).

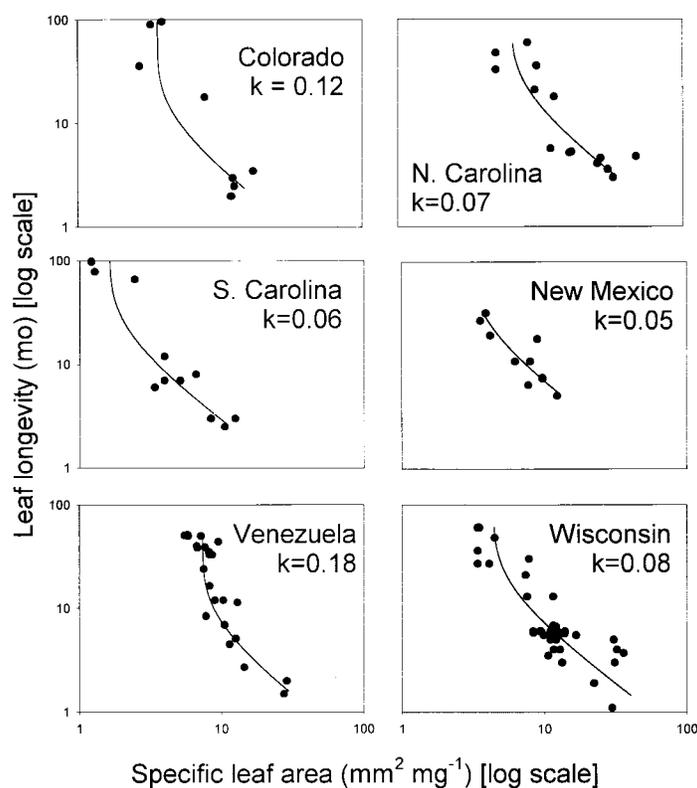


Figure 4: Contours of equal benefit R/E fitted (see text) to the available cross-species SLA–leaf-longevity data for six vegetation regions (see fig. 1). The k value associated with each R/E contour represents the time-discount rate per month that best has the effect of balancing benefit across the observed range of SLA values for different species.

Potential Role of Differences in Export from the Leaf

Up to this stage, we have treated E , the export from the leaf per month and per unit area before taking account of time-discounting effects, as a quantity not correlated with SLA. When variation in E is uncorrelated with SLA, the contours describing equal R/E across the SLA-longevity space are also contours that equalize benefit R across the range of SLA-longevity strategies. The previous section shows that moderate levels of time-discounting k are needed to make these contours reasonably congruent with observed SLA-longevity data for sets of coexisting species. How might this conclusion be affected if E varied systematically with SLA?

If E tended to be lower for low-SLA species, then R/E would tend to be higher for species toward the upper left, even before time discounting. The maximum photosynthetic rate A_{area} does in fact tend to be lower for low-SLA species (Reich et al. 1997, 1999). This is reflected in longevity- A_{mass} relationships, which are somewhat shallower than longevity-SLA relationships (table 1). Indeed, it might

be argued that the leaf's potential return on investment could be better characterized by the photosynthetic potential deployed per gram (A_{mass}) than by the light-capture area deployed per gram (SLA). The question is whether $SLA \times E$ would be better aligned with SLA or with A_{mass} , that is, whether E is unpatterned with respect to SLA or whether it varies across the range of SLA in a similar pattern to A_{area} . The decline in A_{area} at lower SLA and greater longevity may arise because the diffusion path for CO_2 in the leaf becomes longer as lamina depth or tissue density increases (Parkhurst 1994; Smith et al. 1997) or because species with greater leaf longevity are selected to allocate less nitrogen in the form of photosynthetic machinery per unit leaf area (e.g., Kitajima et al. 1997). It might be argued that this pattern in A_{area} would also be reflected in export from the leaf considered over a month. It might equally be argued that stronger reinforcement of the leaf permits carbon uptake to continue at lower water potentials, that lower nitrogen reduces respiration costs, and, generally, that actual export of photosynthate integrated over a month need not be closely aligned with the

maximum potential photosynthetic rate. Since it is unclear whether A_{mass} is superior to SLA as an indicator of actual export from the leaf and since SLA is more readily measured, we have elected to develop theory and data fitting in terms of $\text{SLA} \times E$ while treating E as uncorrelated with SLA. However, theory with the same structure could easily be developed in terms of $A_{\text{mass}} \times E'$, where E' would be a parameter relating A_{mass} to actual export from the leaf.

In any event, the longevity- A_{mass} relationships generally also have slopes steeper than -1 (table 1). That is, nonzero time-discount rates would still be needed to produce equal-benefit contours most congruent with observed longevity- A_{mass} relationships, though at slower discount rates than for observed longevity-SLA relationships.

Discussion

Although a leaf may be produced in the best possible position initially, it cannot subsequently be repositioned on the stem structure. Consequently, leaves may progressively be overtopped and shaded during their lifetime by the leaves of competitors. This basic fact of life for plants restricts the value of ever-increasing leaf longevity. Further, it rewards plants for producing leaves above their already-existing leaves, even at the expense of self-shading. Consequently, the relative position of leaves deteriorates in part as a result of the plant's own growth and in part as a result of the growth of competitors.

The pace of this deterioration of relative position—driven ultimately by the pace at which new leaves are produced upward among all competitors in a given stratum and environment—should be among the most important forces shaping the longevity-SLA strategy of a species. In order to estimate it directly, one would need to measure the actual deterioration of carbon budget over a leaf's life. (Measuring A_{mass} under conditions not limited by light or water would not be adequate.)

Pending a direct approach to this matter, we have addressed a related question: what time-discount rate, applied to known SLA and leaf-longevity values, removes the apparent advantage of high-longevity, low-SLA species relative to others coexisting in the same vegetation? Equal-benefit contours for plausible rates of time discounting (fig. 4) appear capable of accounting for the observed coexistence of species spanning a wide range of SLA and capable also of setting a lower boundary to the range of SLA and an upper boundary to the range of leaf longevity that one would expect to observe.

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ogy Group, Macquarie University. Funding for collaboration came from the Australian Research Council, Macquarie University, and the U.S. National Science Foundation. This is contribution 309 from the Research Unit for Biodiversity and Bioresources, Macquarie University.

APPENDIX

Fitting Nonlinear E -Contours to SLA-Longevity Data

Nonlinear lines-of-best-fit were estimated from \log_{10} transformed data. Thus the data were actually fitted to

$$y = a + \log_{10}[x - \log_{10}(10^x - b)]. \quad (\text{A1})$$

For each population, the line was estimated by minimizing the sum of squared euclidean distances of the points from the line. This can be considered a nonlinear equivalent of a major-axis fit (Rayner 1985). To calculate the distance of a point from the line, it was necessary to find the closest point on the line to each observed data point x_i, y_i . The closest point is referred to here as the "expected" point, $e x_i, e y_i$, and is where the normal from the line to the observed data point cuts the line. The solution for the expected x -ordinate for each point was found as the largest solution to the following equation, evaluated with an iterative procedure (Newton's method):

$$0 = 1/\log_{10}(e \times b) \times (10^{e x_i} - b) \\ \times [x_{oi} - \log_{10}(10^{x_{oi}} - b)] \times (x_{oi} - x_i) + y_i - y_{oi}, \quad (\text{A2})$$

where (x_{oi}, y_{oi}) satisfies equation (A1) for all i .

The minimization procedure was relatively straightforward once the expected point was located. The derivative of the residual sum of squares, the sum of squared euclidean distances, with respect to each parameter, is as follows: with respect to a ,

$$2 \sum_{i=1}^n (y_i - e y_i),$$

with respect to b ,

$$\left(\frac{2 \log_{10} e}{b}\right) \sum_{i=1}^n (x_i - e x_i).$$

Equating these derivatives to 0, the minimization procedure then reduces to the problem of finding (a, b) such that the sum of residuals in both x and y directions is 0.

Table A1: Best-fit k values, with upper and lower k values that double the residual sum of squares

Location	Best-fit k value	Lower RSS- doubling k value	Upper RSS- doubling k value
Colorado	.12	.04	.31
North Carolina	.06	.01	.18
South Carolina	.06	.00	.12
New Mexico	.05	.00	.15
Venezuela	.18	.09	.40
Wisconsin	.08	.00	.48

Note: Time-discount rate per month, from fitting nonlinear R/E contours as described in the appendix to leaf longevity-SLA data as in figure 4.

We have not been able to devise a method for attributing confidence limits with a known P value to the best-fit k values. A conservative approximation is to estimate the k values that have the effect of doubling the residual sum of squares (RSS), relative to the RSS associated with the best-fit k values (table A1). Using these RSS-doubling values as if they were confidence limits, the five locations (Colorado, North Carolina, South Carolina, New Mexico, and Wisconsin) are clearly not different from each other. The lower RSS-doubling k value for Venezuela is above the best-fit k value for four of those five, but in the other direction, the upper RSS-doubling k values for Colorado, North Carolina, and Wisconsin overlap the best-fit k value for Venezuela. In summary, although there is a suggestion that Venezuela has a higher k value than at least some of the temperate-zone locations, the evidence is not consistent enough to draw a firm conclusion.

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