Trait Covariation and Optimality Approaches to Understand Them

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General Background

A trait is any <u>morphological</u>, <u>physiological</u> or <u>phenological</u> feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organization. (Violle et al., 2007)

Leaf: as a very important functional component of plants (wright et al. 2004)

Morphological Trait
e.g. leaf thickness, leaf size, SLA

Phenological Trait
e.g. leaf age

Physiological Trait
e.g. photosynthetic assimilation rate, and respiration rate

Chemical Trait?
e.g. leaf chlorophyll, leaf N, and leaf P

General Background

Enormous interspectic variation in plants traits has been observed (Reich et al., 1997; Wright et al., 2004)

*Table 1 from Reich et al. (1997); leaves of 111 species collected across 6 biomes worldwide

Mass-based net photosynthesis (A_{max})	nmol $g^{-1}s^{-1}$	21 $\pm$ 4	289 $\pm$ 64
Area-based net photosynthesis	μmol $m^{-2}s^{-1}$	3.7 $\pm$ 0.3	14.6 $\pm$ 1.2
Mass-based dark respiration	nmol $g^{-1}s^{-1}$	4.0 $\pm$ 0.3	35.2 $\pm$ 7.2
Leaf nitrogen concentration (leaf N)	mg/g	8.7 $\pm$ 0.6	40.9 $\pm$ 5.7
Leaf nitrogen content	g/m^2	1.2 $\pm$ 0.2	4.4 $\pm$ 1.1
SLA	cm^2/g	35 $\pm$ 6	267 $\pm$ 62
Leaf lifespan	months	2.5 $\pm$ 0.6	66.2 $\pm$ 10.6

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Such big variation is thought to represent adaptions to the range of environmental conditions spanning from tropics to tundra (Reich et al., 1997). Also, most of these traits are actually interrelated, rather than independent.

What is the pattern of trait covaraition?

Why do traits covary and even some functions appear to converge despite different trait combinations?

Papers Covered

From tropics to tundra: Global convergence in plant functioning

PETER B. REICH[*][†], MICHAEL B. WALTERS[‡], AND DAVID S. ELLSWORTH[§]

The worldwide leaf economics spectrum

Ian J. Wright[1], Peter B. Reich[2], Mark Westoby[1], David D. Ackerly[3], Zdravko Baruch[4], Frans Bongers[5], Jeannine Cavender-Bares[6], Terry Chapin[7], Johannes H. C. Cornelissen[8], Matthias Diemer[9], Jaume Flexas[10], Eric Garnier[11], Philip K. Groom[12], Javier Gulias[10], Kouki Hikosaka[13], Byron B. Lamont[12], Tali Lee[14], William Lee[15], Christopher Lusk[16], Jeremy J. Midgley[17], Marie-Laure Navas[11], Ülo Niinemets[18], Jacek Oleksyn[2,19], Noriyuki Osada[20], Hendrik Poorter[21], Pieter Poot[22], Lynda Prior[23], Vladimir I. Pyankov[24], Catherine Roumet[11], Sean C. Thomas[25], Mark G. Tjoelker[26], Erik J. Veneklaas[22] & Rafael Villar[27]

A COST-BENEFIT ANALYSIS OF LEAF HABIT AND LEAF LONGEVITY OF TREES AND THEIR GEOGRAPHICAL PATTERN
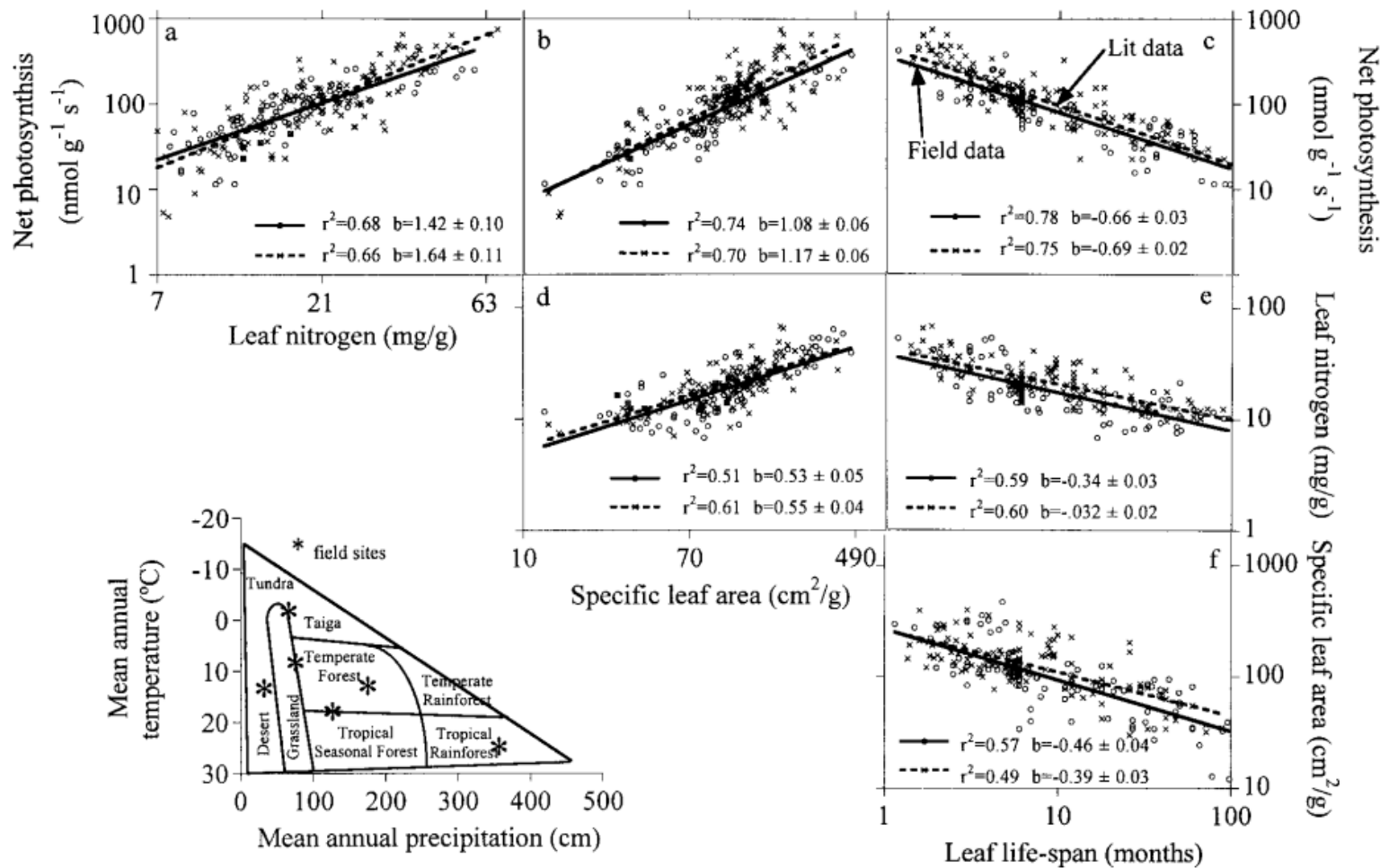
KIHACHIRO KIKUZAWA

The Time Value of Leaf Area

Mark Westoby,[1,*] David Warton,[1] and Peter B. Reich[2]

Trait Covaraition: From Tropics to Tundra

(Leaf trait data of 111 species across **6 biomes** were collected and analyzed)

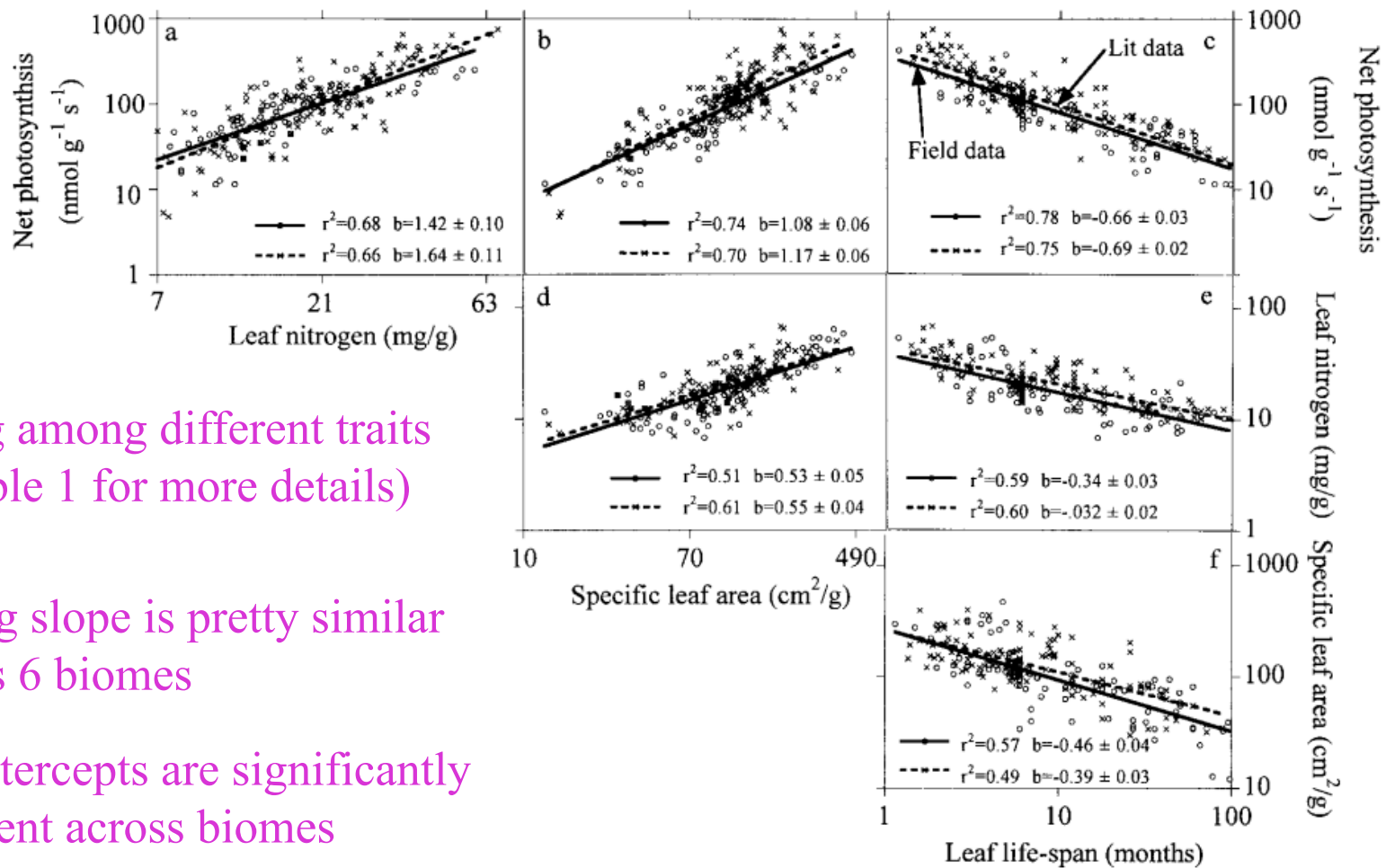*Figure 1 from Reich et al. (1997); Relations among mass-based photosynthesis, SLA, nitrogen, and LL

Reich et al. 1997. PNAS

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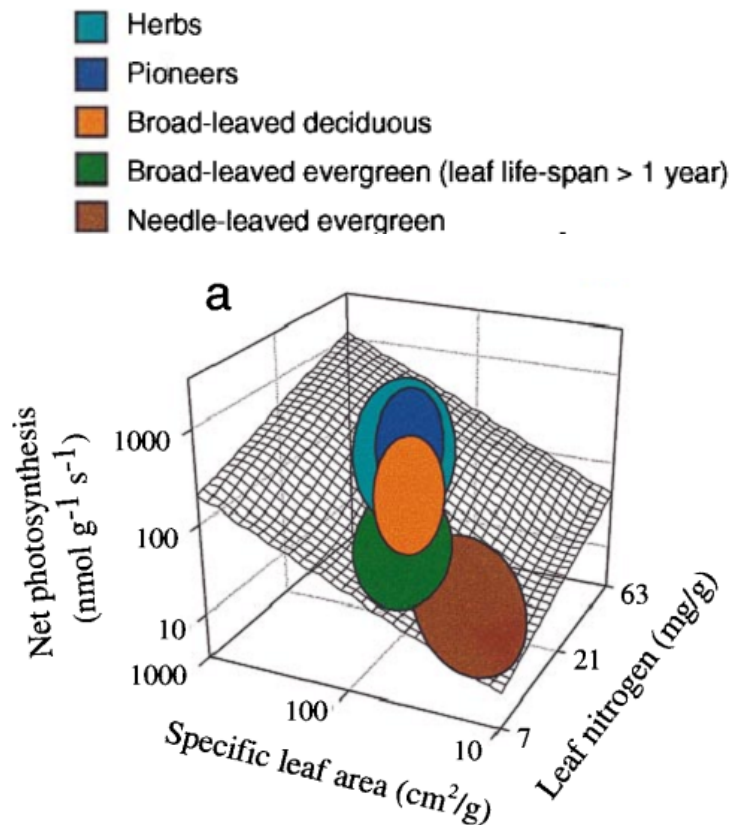

* Scaling among different traits (see table 1 for more details)

* Scaling slope is pretty similar across 6 biomes

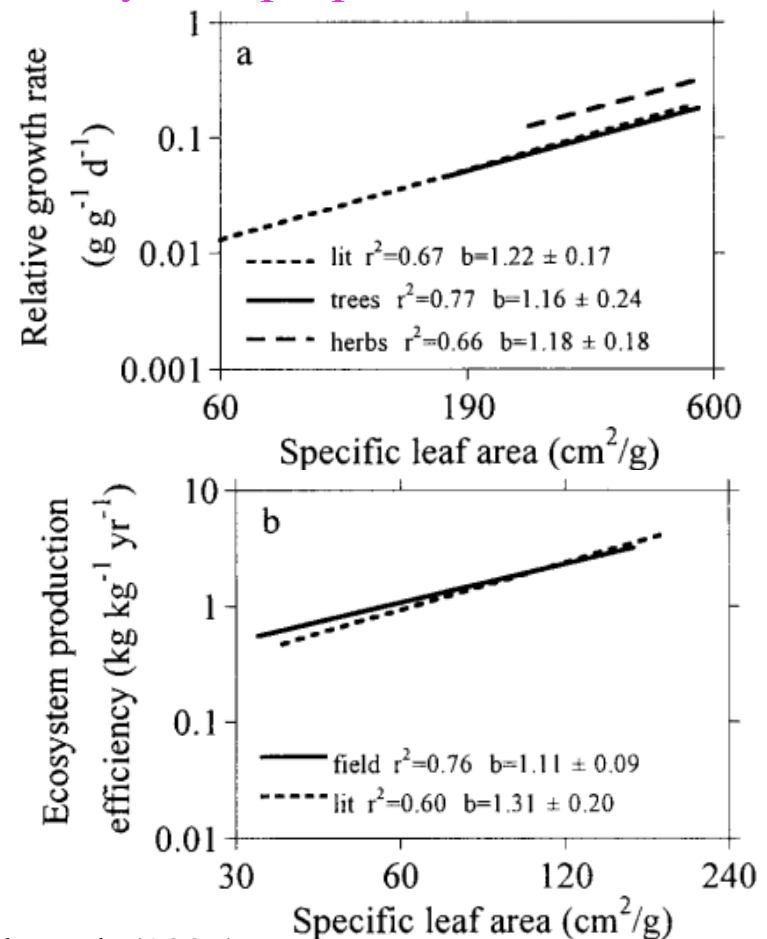* The intercepts are significantly different across biomes

Reich et al. 1997. PNAS

Trait Covaraition: From Tropics to Tundra

* Multiple leaf trait relationships
are similar regardless of biome or
climate regime

* Variation in leaf traits among species
also was related strongly to whole plant
and ecosystem properties

*left panel: Figure 3, and right panel: Figure 4 from Reich et al. (1997)

Reich et al. 1997. PNAS

Summary of Reich et al. (1997)'s Paper

a "pattern" : Scaling relationship of leaf traits was found and demonstrated convergent evolution and global generality in plant functioning

a "hypothesis" : interrelated constraints that involve compromises in leaf structure and function, because of limits on the multiple services that carbon and N can perform in a leaf

e.g. No combination of thin, short-lived leaves and low Amax
e.g. No combination of thick, dense, and/or long lived leaves with high mass-based leaf N, Amax and Dark respiration rate

(1) In thick/dense leaves, within-leaf shading can limit the amount of light reaching chloroplasts
(2) Leaves of high N are attractive nutritionally, and thus subject to higher rates of herbivory
(3) Species that grow fast and have high Amax would be at a disadvantage in maintaining long-lived foliage and impose a less than optimal allocation of resources at different positions

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     maintaining long-lived foliage and impose a less than optimal allocation
     of resources at different positions (not efficient)

Summary of Reich et al. (1997)'s Paper

Some points mentioned but still quite unknown :

(1) Why area based Amax don't hold the same relationship as mass based Amax, with SLA, Leaf life span, and Leaf nitrogen

(2) What actually controls the scaling intercept among these relationships

(3) Still lack of strong tools to explain the pattern found in this paper
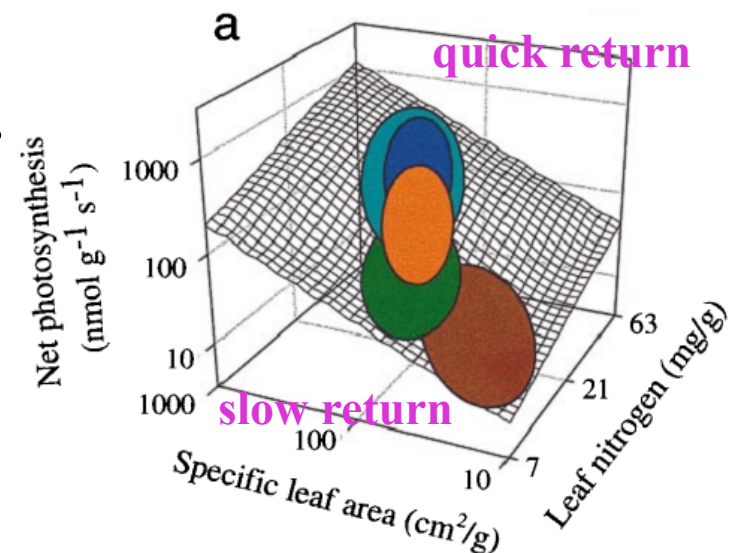
Leaf Economics Spectrum

(Global plant trait network (Glopnet) spanning 2548 species from 219 families at 175 sites worldwide)

They assume an inherent economics in leaf, which could be described and quantified by revenues and expenditures per unit investment, measured by biomass or C, N or P.

*Figure 3 from Reich et al. (1997)

At the quick return end are species with high leaf nutrient concentrations, high rates of photosynthesis and respiration, short leaf lifetimes and low dry mass investment per leaf area

At the slow return end are species with long leaf lifetimes, expensive high LMA leaf construction, low nutrient concentrations, and low rates of photosynthesis and respiration.

Wright et al. 2004. Nature

Leaf Economics Spectrum

Mass-base leaf traits & Area-base leaf traits

$$Nmass=Narea*SLA \quad (or \; Nmass=Narea/LMA)$$

The same Narea can be combined with high Nmass and low LMA or low Nmass and high LMA (long-life leaf), which actually represents the total different environmental condition

Because of the covariation between leaf N and LMA, relationships between leaf N and other traits changed substantially when expressed on an area rather than on a mass basis

The coordination among leaf traits appears to be stronger and simpler on a mass basis than an area basis

Wright et al. 2004. Nature

Kikuzawa Model: a cost-benefit analysis

Origin: This model was developed to explain leaf habit, geographical distribution pattern of evergreen and deciduous trees

Key Issue: leaf age (or leaf longevity) are key to differentiate evergreen & deciduous trees

Main Assumption: Leaves, as a resource-gaining organ, produce or replace a leaf to maximize its life time net carbon gain.

Main Problem: is to find when the tree should replace its leaves, by which the net gain by a leaf per unit time over the entire life span is maximum
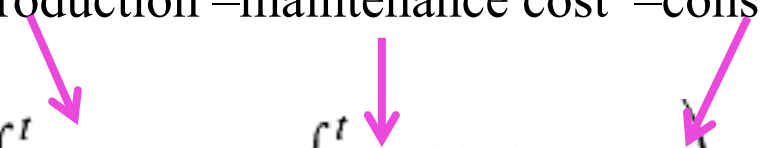
Kikuzawa. 1991. The American Naturist

Kikuzawa Model: a cost-benefit analysis

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$$g = G/t$$

Where g is the marginal gain, and G is the life time net gain by a leaf

G=lifetime photosynthetic production –maintenance cost –construction cost

$$g = (1/t)\left(\int_0^t p(t)dt - \int_0^t m(t)dt - C\right)$$

Where daily photosynthetic rate (p) is considered to be a monotonic decreasing function, while maintenance cost (m) is assumed to decrease in proportion to p.

$$p(t) = a(1 - t/b),$$

$$m(t) = m(1 - t/b)$$

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Kikuzawa also introduced the concept of **favorable period** f (yr; $0 < f \leq 1$) for photosynthesis alternate within a year, and in this case g is expressed as

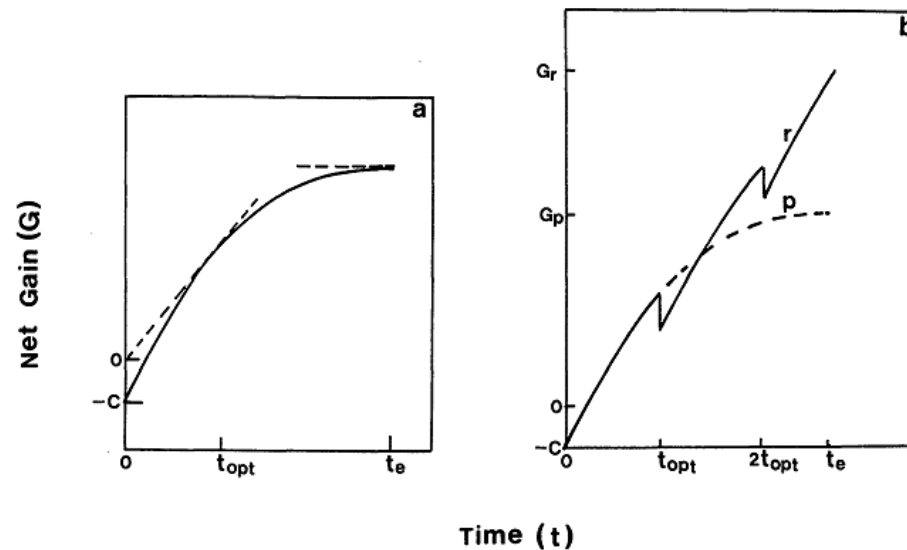$$g = (1/t)\left(\int_0^f p(t)dt + \int_1^{1+f} p(t)dt + \ldots + \int_{[t]}^t p(t)dt - \int_0^t m(t)dt - C\right)$$

e.g. t=2.5yr and f=0.5 yr

$$g = \frac{\int_0^{0.5} p(t)dt + \int_1^{1.5} p(t)dt + \int_2^{2.5} p(t)dt - \int_0^{2.5} m(t)dt - C}{2.5}$$

Kikuzawa. 1991. The American Naturist

Kikuzawa Model: a cost-benefit analysis

*Figure 1 from Kikuzawa (1991); schematic representation of net gain per leaf (G) to time (t) curve

maximize $g = (1/t)\left(\int_0^t p(t)dt - \int_0^t m(t)dt - C\right)$

$$t_{opt} = [2bC/(a - m)]^{1/2}$$

Kikuzawa. 1991. The American Naturist

Kikuzawa Model: a cost-benefit analysis

$$t_{opt} = [2bC/(a - m)]^{1/2}$$

(1) Leaf longevity is expected to be short when initial net photosynthetic rate of the leaf is large (Reich et al., 1997)

(2) Leaf longevity is long when the construction cost of the leaf is large (Coley, 1988)

(3) Leaf longevity is short when the decrease in net photosynthetic rate with time is large (Mastumoto, 1984)

*Figure 1 from Reich et al. (1997)
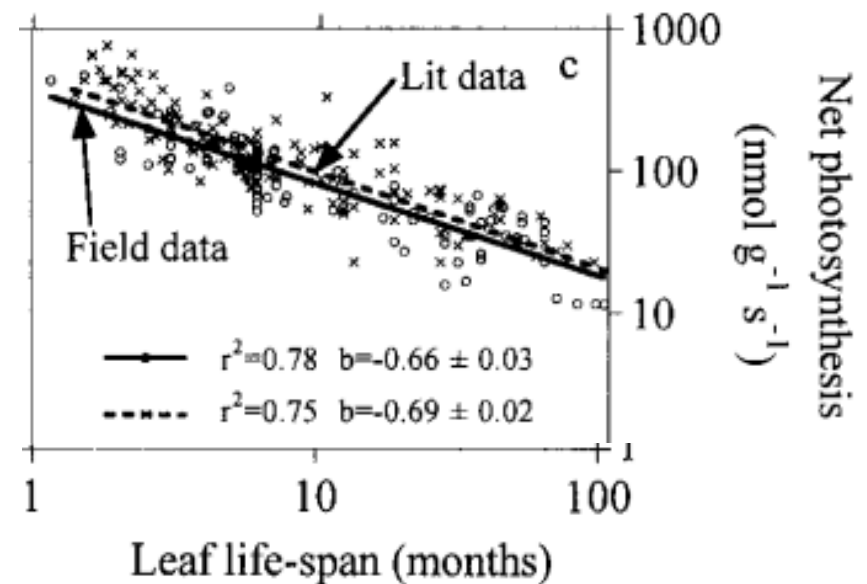
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Main Finding: $$t_{opt} = [2bC/(a - m)]^{1/2}$$

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The Time Value of Leaf Area

*Plant growth can be understood as a process of investment leading to returns and reinvestment.

*The revenue-stream is shaped by three variables:

(1) The light capture area per milligram dry mass invested, analogous to a potential rate of return on investment

(2) The longevity of the leaf, analogous to the expected duration of the revenue stream

(3) A time discount rate, quantifying the fact that light-capture area deployed in the immediate future is more valuable to the plant the same area deployed at some later time

$$g = (1/t) \left(\int_0^t p(t)dt - \int_0^t m(t)dt - C \right)$$

Westoby et al. 2000. The American Naturist

The Time Value of Leaf Area

Why do species with lower SLA not evolve toward higher value?
A likely answer is that low-SLA species, investigating more mass per unit leaf area, build leaves with greater life span
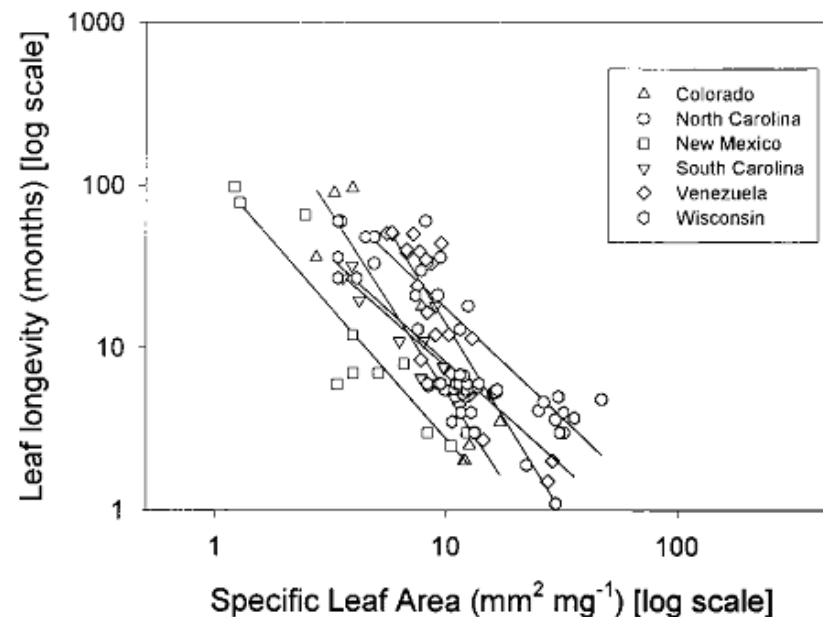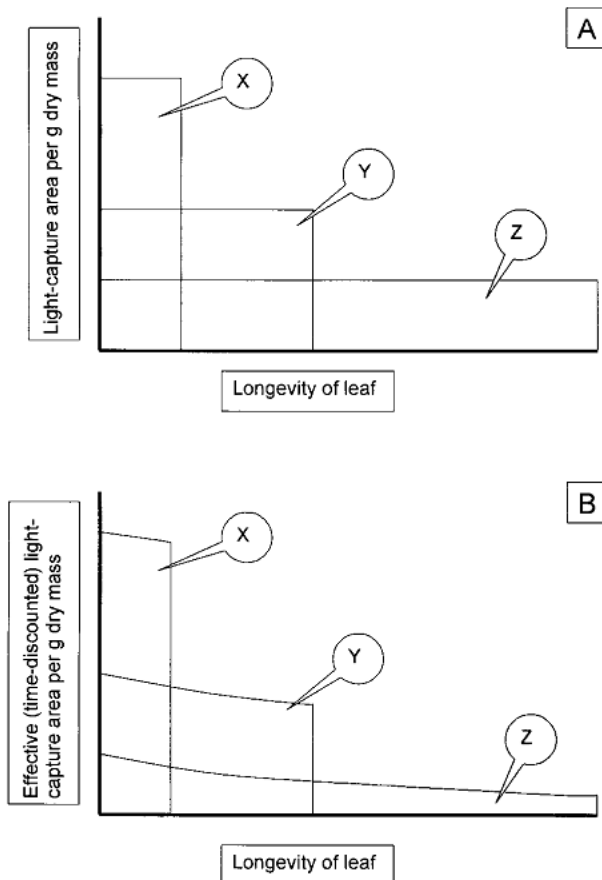

Figure 1: Cross-species relationships between leaf longevity (mo) and specific leaf area (mm² mg⁻¹), from data in Reich et al. (1999).

The Time Value of Leaf Area

Time discounting effect and the time value of leaf area

Future persistence of leaf area should less valuable than immediate production of leaf area

(1) reduced revenue from older leaves, due to overshading

(2) 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

(3) There is the risk that the plant will no longer be alive to benefit

(4) Opportunity cost effect

Westoby et al. 2000. The American Naturist

The Time Value of Leaf Area

Goals of this paper:

(1) Approximately what level of time discounting would have the effect of setting the expected level of SLA at some intermediate level

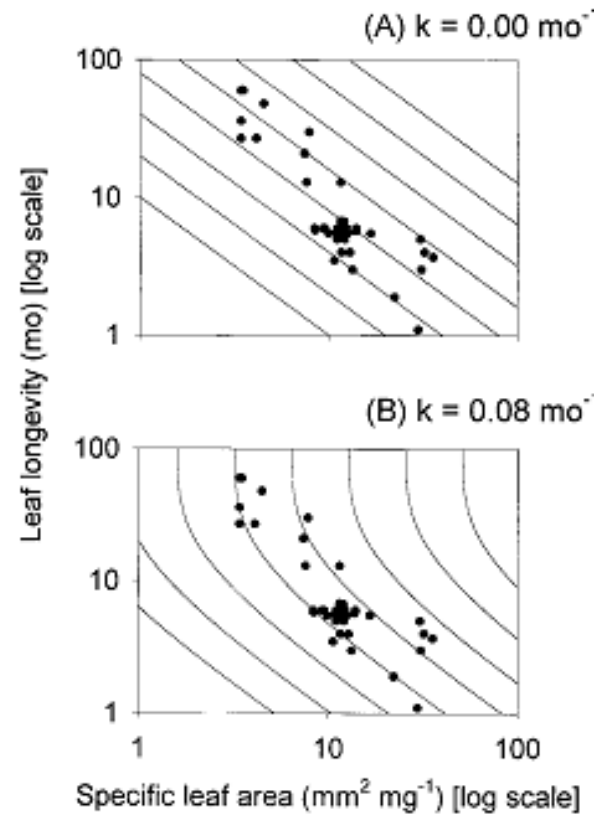(2) When time discounting is taken into account, is SLA predicted to have a narrow and clear-cut optimum

Westoby et al. 2000. The American Naturist

The Time Value of Leaf Area

Equal-Benefit-Set Formulation

$$R = \int_{0}^{longev} \left(E \times SLA \times e^{-kt} \right) dt,$$
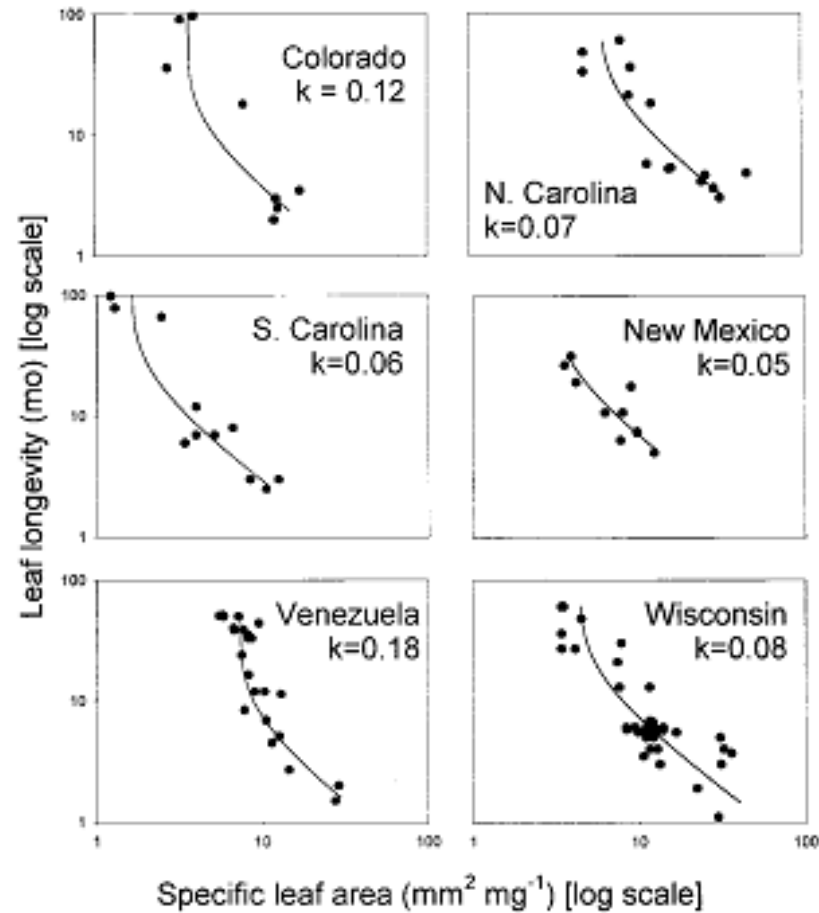
$$R = \frac{E \times SLA}{k} \left[1 - e^{(-k)longev} \right].$$

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

(A) k = 0.00 mo'

(B) k = 0.08 mo'

Leaf longevity (mo) [log scale]

Specific leaf area (mm^2 mg^{-1}) [log scale]

Westoby et al. 2000. The American Naturist

The Time Value of Leaf Area

Westoby et al. 2000. The American Naturist

Summary

A pattern was found: global convergence of plant traits

Two Theories were proposed: Leaf economics and cost-benefit analysis

Equal benefit theory was proposed to explain the interspecific variation of leaf traits at local scale