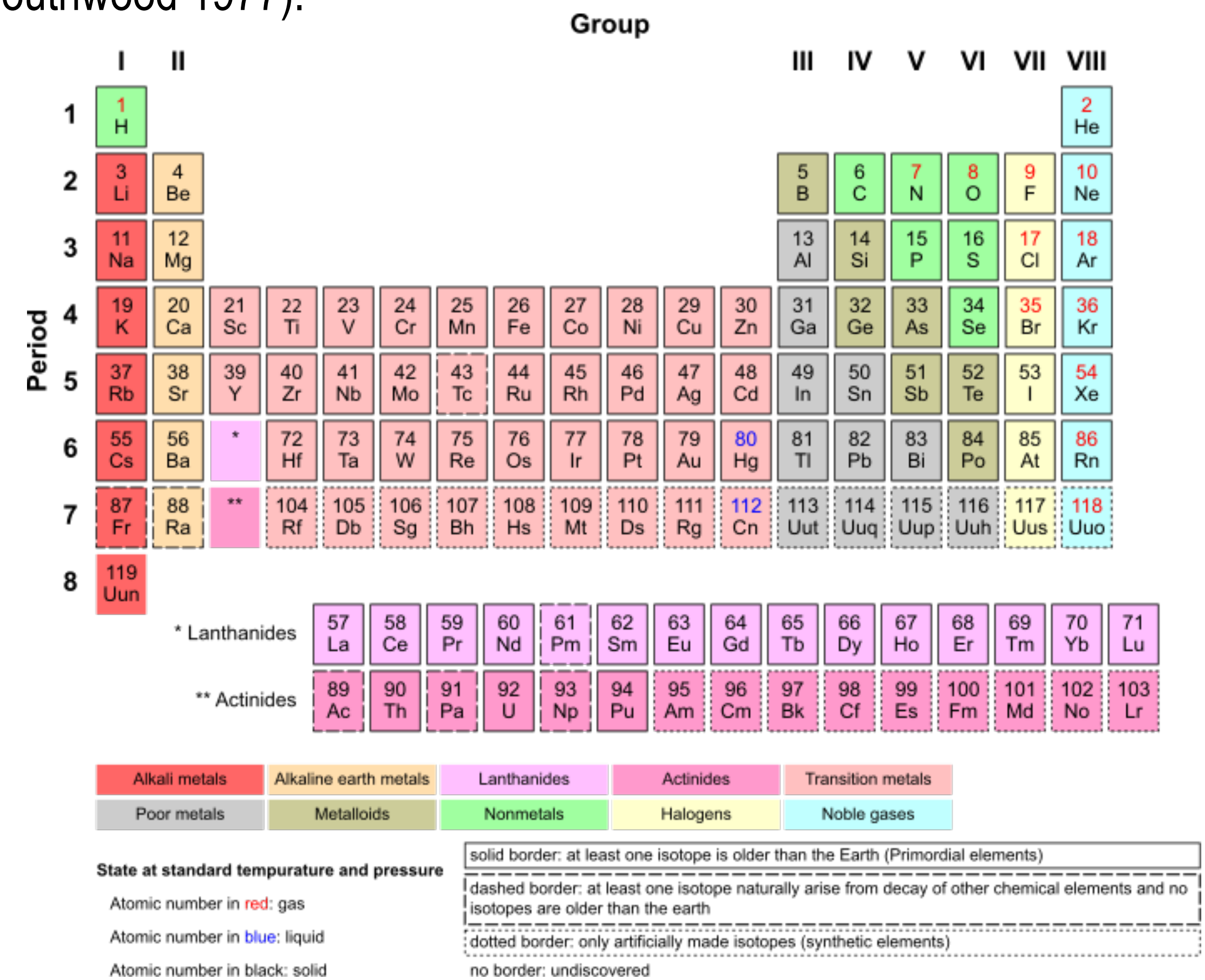
Which Traits *Matter*?

Functional Ecology 2-22-2012

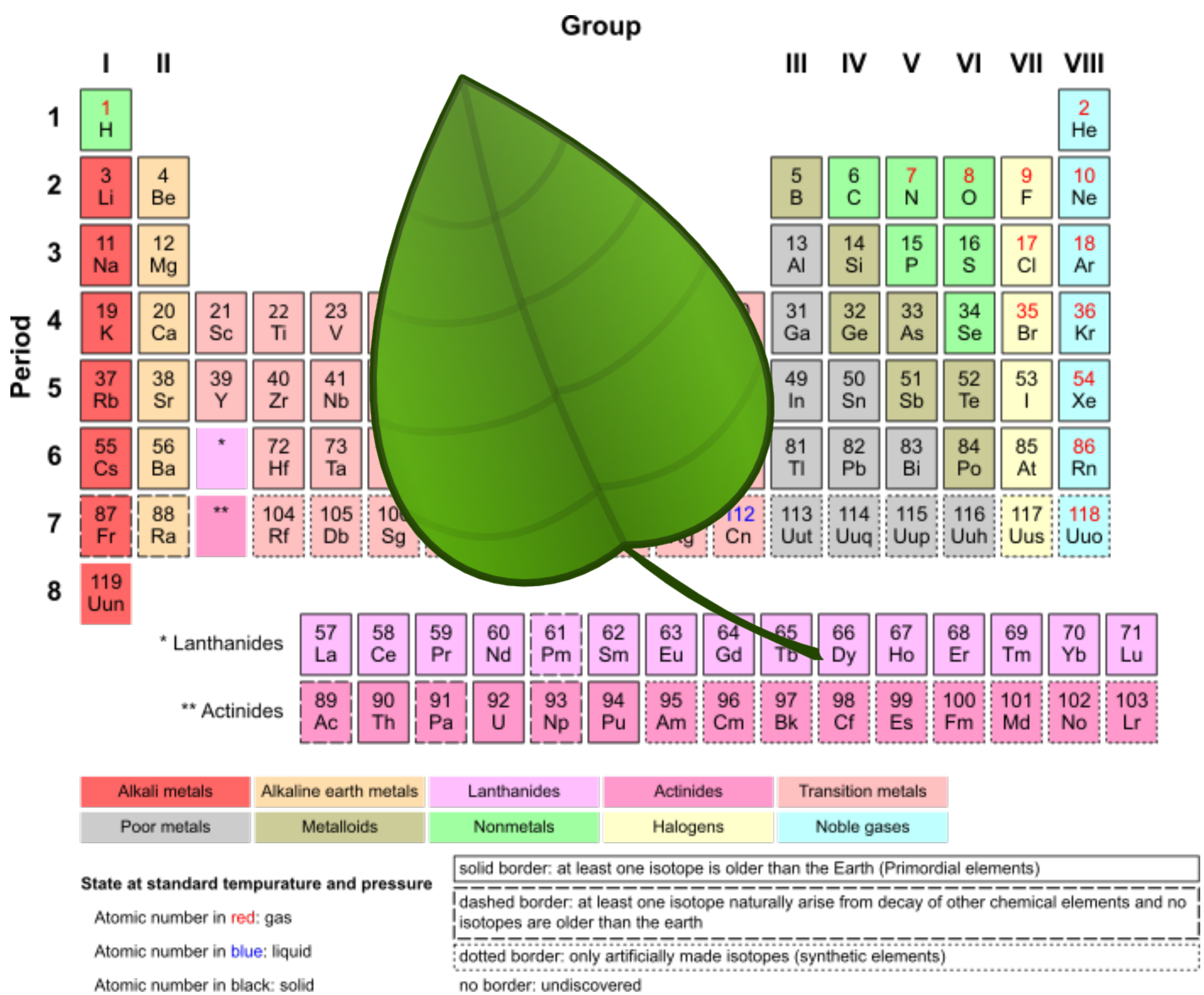
Loren Albert

“In some ways I think we may see ourselves at a similar point to the inorganic chemist before the development of the periodic table; then he could not predict, for example, how soluble a particular sulphate would be, or what was the likelihood of a particular reaction occurring. Each fact had to be discovered for itself and each must be remembered in isolation” (Southwood 1977).



Credit: Armtuk via Wikimedia Commons. http://commons.wikimedia.org/wiki/File:Periodic_Table_Armtuk3.svg

Should we think more like chemists?



Credit: Periodic table: http://commons.wikimedia.org/wiki/File:Periodic_Table_Armtuk3.svg; Leaf: Open Clip Art Library

Why Relative Growth Rate?

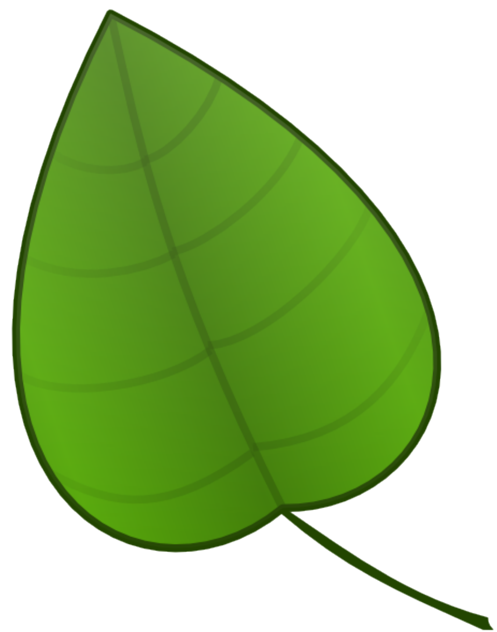
- Varies greatly…
  - Between plant species (e.g. Grime and Hunt 1975)
  - Between annuals and perennials (e.g. Garnier 1992).
- Can be used to predict ecosystem productivity (e.g. Vile et al. 2006, Lavorel and Garnier 2002)
- Can estimated based on measurable traits

Relative Growth Rate

Relative Growth Rate (RGR): "increase in plant weight per unit plant weight (W) already present and per unit time (t)." Poorter 1989

$$RGR = \frac{1}{W} * \frac{dW}{dt}$$

Units: $\dfrac{\text{mass}}{\text{mass*time}}$



Leaf: Open Clip Art Library

Poorter 1989

Three approaches to calculating RGR:

(1) RGR = NAR*LAR

Where…

NAR = Net assimilation Rate (the increase in plant weight per unit leaf area per unit time)

LAR = Leaf Area Ratio (specific leaf area*leaf weight ratio). LAR = LA/WL*WL/W

Poorter 1989

Three approaches to calculating RGR:

(1) RGR = NAR*LAR

(2) LAP = dLA/dW

(Leaf area partitioning is the leaf area increase per total plant weight increase)

Poorter 1989

Three approaches to calculating RGR:

(1) RGR = NAR*LAR

(2) LAP = dLA/dW

(3) RGR = NP*PNC

Where…

NP is dry weight increase per unit plant nitrogen per unit time.

PNC is plant nitrogen content (by weight).

Poorter 1989

Three approaches to calculating RGR:

(1) RGR = NAR*LAR

(2) LAP = dLA/dW

(3) RGR = NP*PNC

"The first method links in best with frequently measured parameters like rate of photosynthesis[…], chemical composition […], allocation (LWR) and morphology (SLA) into one composed formula."

Poorter 1989

How do NAR and LAR actually relate to RGR?

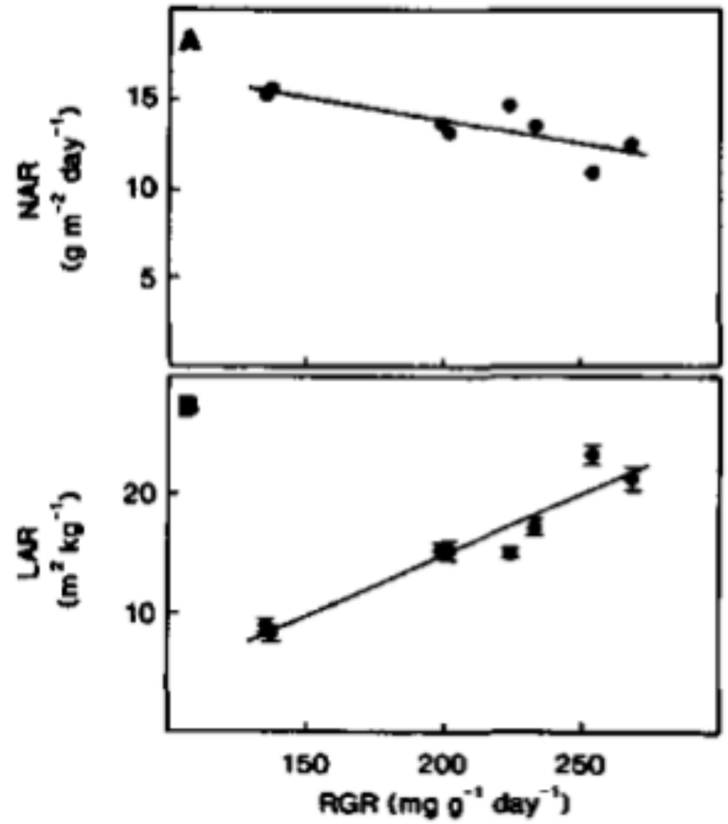


Fig. 1. A. Mean NAR of the eight species of Table 1 plotted against mean RGR. B. Idem for LAR. Error bars indicate the mean standard error at the different harvests within the growth period of 17 days (number of harvests = 6, n = 8). Total leaf area of species with needle-like leaves *(D. flexuosa, F. ovina)* was calculated as leaf blade length * the thickness in the middle of the leaf * π. For all species leaf area was determined as half the total leaf area.

Poorter 1989

How do NAR and LAR actually relate to RGR?

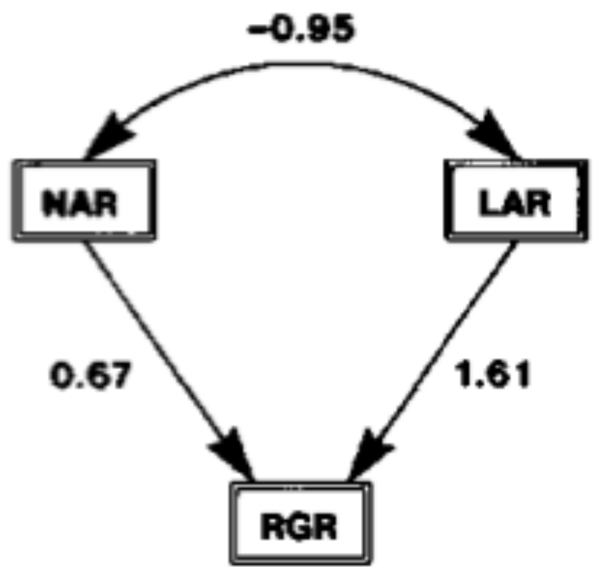


Fig. 2. Pathway analysis for the relations between RGR and its components. Values indicate the change in RGR (expressed in units standard deviation) as a result of a change of one unit standard deviation in NAR or LAR, both direct and indirect.

Poorter 1989

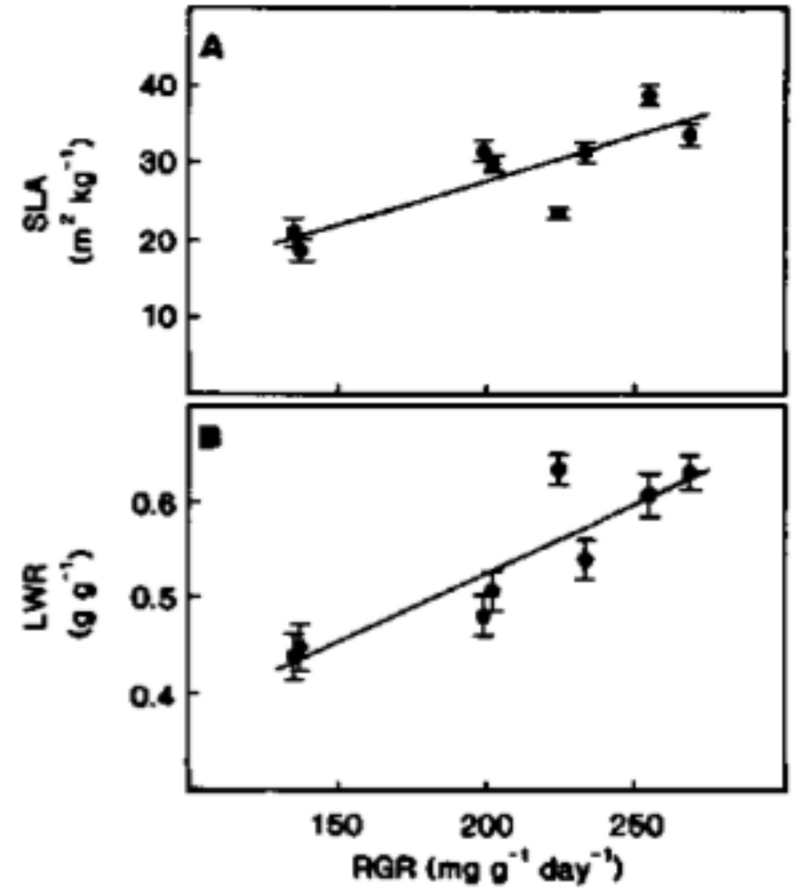


Fig. 3. A. Mean SLA of eight species plotted against mean RGR. B. idem for LWR.

LAR = LA/WL*WL/W

= SLA * LWR

Poorter 1989

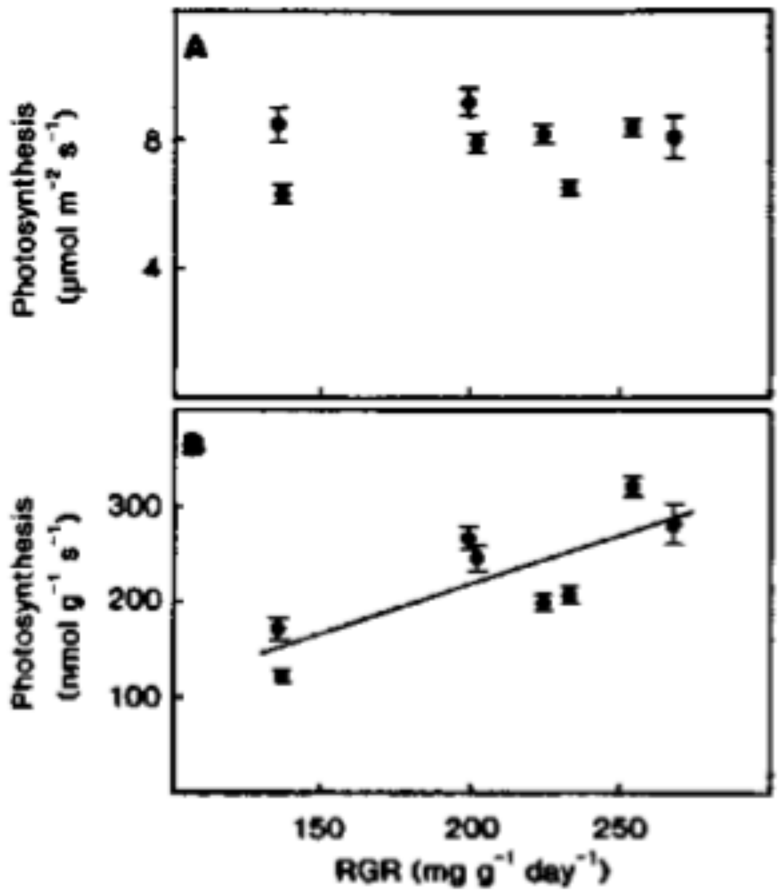


Fig. 5. A. Mean rate of photosynthesis, expressed on a leaf area basis, plotted against mean RGR for eight species. Photosynthesis was measured two times during the experimental period (n = 4), under the same conditions used for plant growth. B. Mean rate of photosynthesis expressed on a leaf dry weight basis.

Food for thought…

- Is the formula RGR = NAR*LAR still the most common way to analyze RGR?
- What about exudates and volatiles? Poorter says “there is almost no knowledge of the relation between RGR and exudates or volatiles”

$$NAR = \frac{1}{LA} \cdot \frac{dW}{dt} = CF * (PS - SR - RR) - EXU - VOL \qquad (3)$$

Where…

CF is a conversion factor (biomass/carbon weight ratio in newly formed material

EXU is exudates

VOL is volatiles

PS is photosynthesis

SR is shoot respiration

RR is root respiration

How much variation is there in RGR?

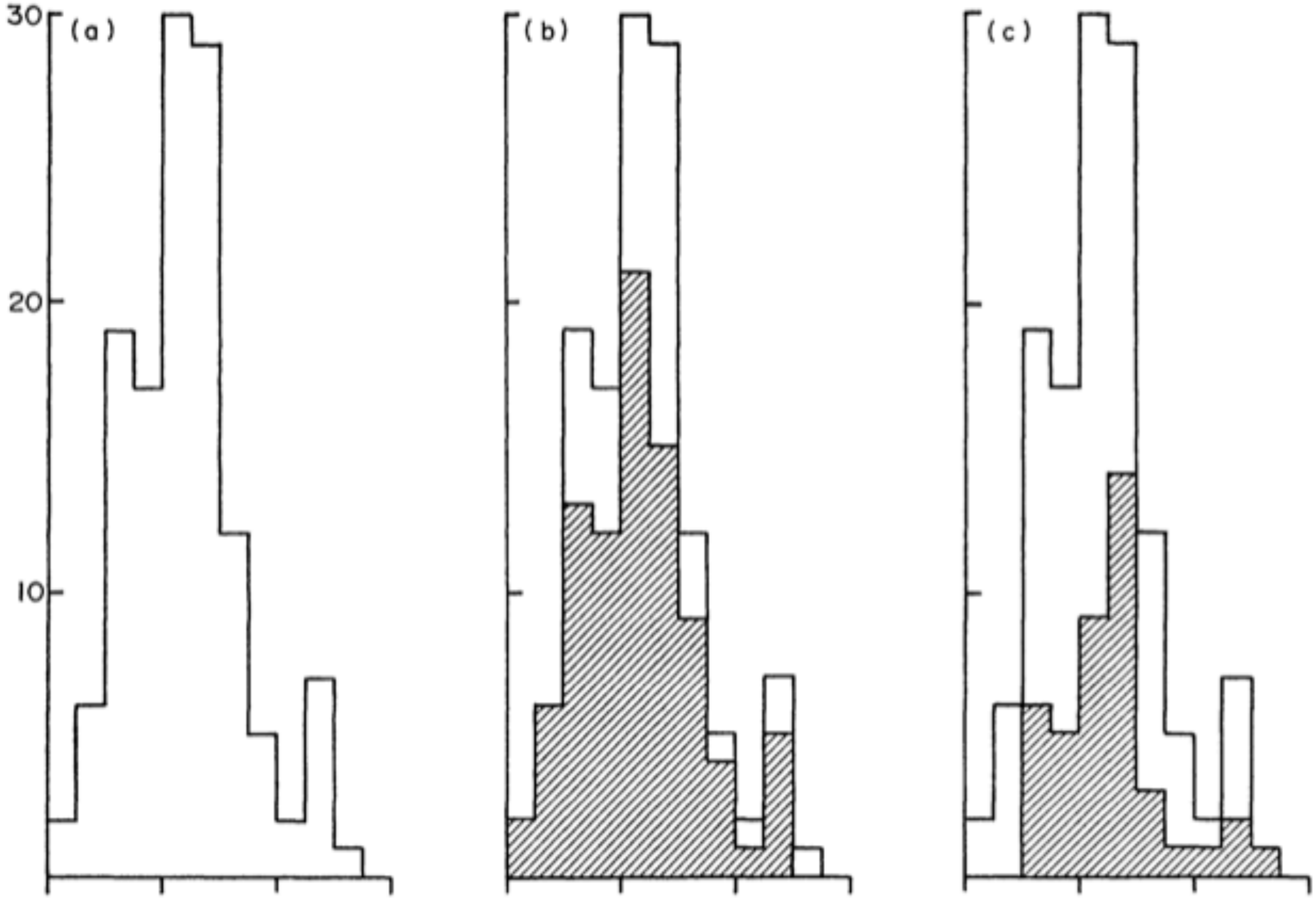
Grime and Hunt 1975

Table 5. *Values obtained for* $\mathbf{R_{max}}$ *and* $\bar{\mathbf{R}}$ *(week^{-1}); confidence limits (CL) are given at* $P<0{\cdot}05$

	R_{max}				$\bar{R}$			
	Value	Standard error	Lower CL	Upper CL	Value	Standard error	Lower CL	Upper CL
Acer pseudoplatanus	0·34	0·09	0·16	0·52	0·34	0·09	0·16	0·52
Achillea millefolium	1·96	0·11	1·71	2·21	1·70	0·09	1·49	1·90
Agropyron repens	1·21	0·05	1·11	1·33	1·21	0·05	1·11	1·33
Agrostis canina	1·41	0·08	1·23	1·59	1·41	0·08	1·23	1·59
A. stolonifera	1·48	0·10	1·26	1·70	1·48	0·10	1·26	1·70
A. tenuis	1·36	0·12	1·11	1·61	1·36	0·12	1·11	1·61
Aira praecox	0·87	0·07	0·73	1·00	0·87	0·07	0·73	1·00
Alopecurus geniculatus	1·24	0·07	1·10	1·38	1·24	0·07	1·10	1·38
A. pratensis	1·29	0·10	1·07	1·51	1·29	0·10	1·07	1·51
Anisantha sterilis	2·28	0·12	2·03	2·53	1·43	0·07	1·29	1·57
Anthoxanthum odoratum	0·94	0·08	0·77	1·11	0·94	0·08	0·77	1·11
Anthriscus sylvestris	0·52	0·07	0·38	0·66	0·52	0·07	0·38	0·66
Arabis hirsuta	1·32	0·12	1·05	1·60	1·32	0·12	1·05	1·60
Arenaria serpyllifolia	1·22	0·14	0·92	1·52	1·22	0·14	0·92	1·52
Arrhenatherum elatius	1·30	0·07	1·15	1·46	1·30	0·07	1·15	1·46
Betula pubescens	0·80	0·06	0·68	0·93	0·80	0·06	0·68	0·93
Bidens tripartita	1·89	0·09	1·71	2·06	1·30	0·12	1·06	1·55
*Brachypodium pinnatum**	1·03	0·09	0·85	1·20	1·03	0·09	0·85	1·20
B. sylvaticum	1·35	0·13	1·06	1·63	1·02	0·04	0·94	1·12
Briza media	1·11	0·06	0·97	1·24	1·11	0·06	0·97	1·24
Calluna vulgaris	0·35	0·05	0·25	0·45	0·35	0·05	0·25	0·45

List goes on for two and a half pages!

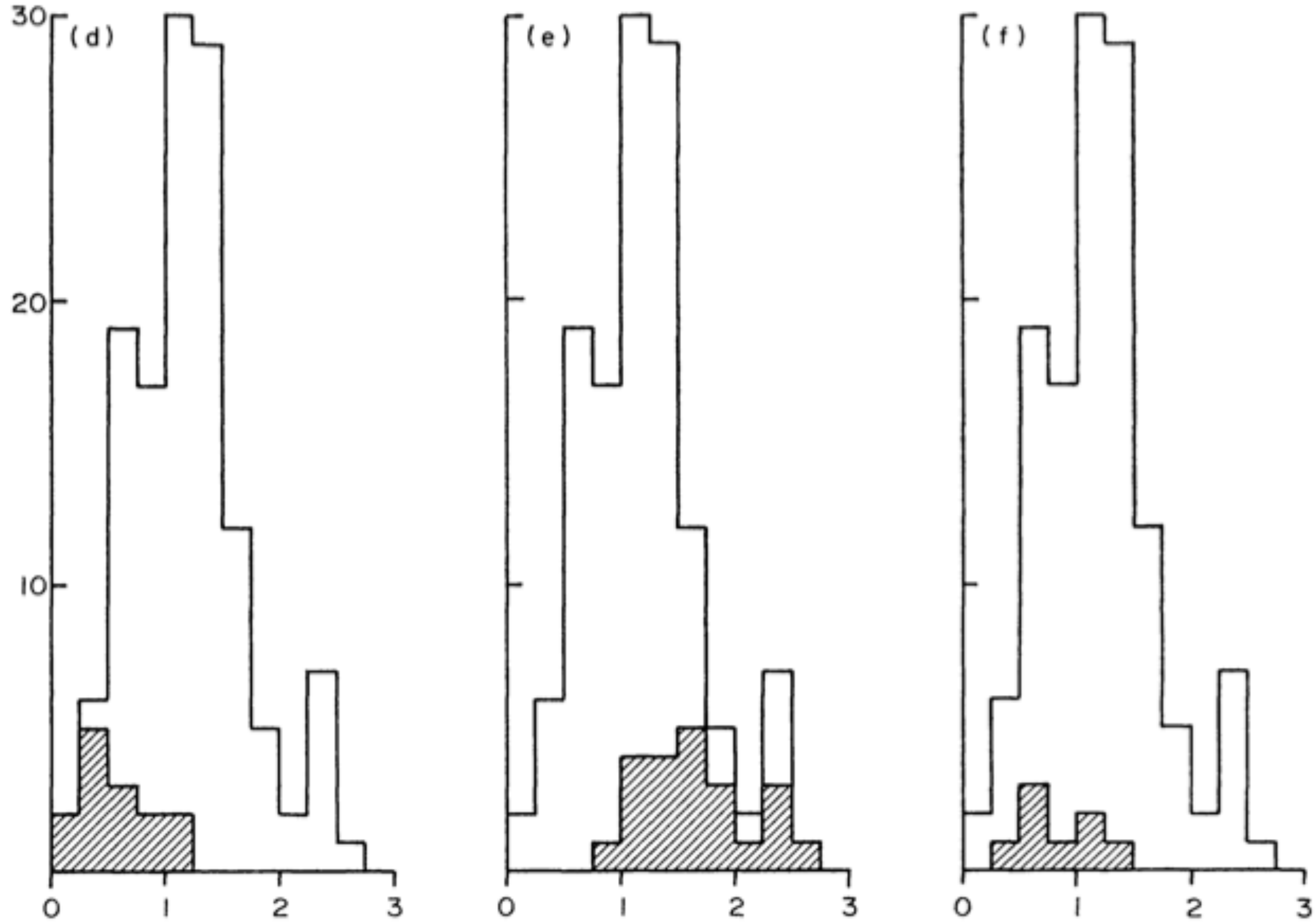
Grime and Hunt 1975



Whole sample | Dicots | Monocots

R_{max} (week^{-1})

Grime and Hunt 1975



Woody Species   Annual Species   Legumes

R_{max} (week^{-1})

Food for thought…

Ideally, to ensure measurement of the true $\mathbf{R}_{\mathbf{max}}$ of which each species is capable, estimations should be made under the growth conditions optimal for that species. In order to find these optimal conditions it would be necessary to subject each species to a wide range of factorially-combined levels of the necessary growth-factors (*sensu* Lockhart 1965) and then to adopt as $\mathbf{R}_{\mathbf{max}}$ the highest value of relative growth-rate, **R**, obtained from such a series of experiments. Even on a smaller scale than at present such a task would be totally impracticable. The environment selected for the measurement of $\mathbf{R}_{\mathbf{max}}$ in this large number of species therefore had to some extent to be a compromise between what was theoretically desirable and what was experimentally practicable.

(Grime and Hunt 1975)

Is the measurement of Rmax any easier these days? Is it even more difficult as global change becomes more important?

Which characteristics allow annuals to grow more rapidly than perennials at the seedling stage?

Species	Life-form	Harvest times for calculation of plant parameters (days)
Brachypodium distachyon L.	annual	16,20,24
Brachypodium phoenicoides L.	perennial	20,24
Bromus hordeaceus L. } (*Bromus* 1 pair)	annual	16,20
Bromus erectus Huds. } (*Bromus* 1 pair)	perennial	16,20,24
Bromus madritensis L. } (*Bromus* 2 pair)	annual	12,16,20
Bromus ramosus Huds. } (*Bromus* 2 pair)	perennial	16,20,24
Hordeum murinum L.	annual	12,16
Hordeum secalinum Schreb.	perennial	16,20
Lolium rigidum Gaud.	annual	12,16,20
Lolium perenne L.	perennial	16,20,24
Poa annua L.	annual	20,24
Poa pratensis L.	perennial	20,24
Avena barbata Pott	annual	12,16
Dactylis glomerata L. (subsp. *hispanica* Roth)	perennial	20,24

(Garnier, E. 1992. Journal of Ecology, 80: 665-675.)

Which characteristics allow annuals to grow more rapidly than perennials at the seedling stage?

Measured/Calculated:

- Relative Growth Rates (RGR)
- Unit Leaf Rates (ULR)
  - Dry weight increment per day per unit leaf area (ULR_a)
  - Dry weight increment per day per unit dry weight (ULR_w)
- Leaf production rates (RLPR): number of leaves produced per unit time per leaf
- Allometric coefficients (K): slopes of the linear regressions of log(root dry weight) on log(shoot dry weight)
- Leaf weight ratio
- Sheath weight ratio
- Root weight ratio
- Specific leaf area
- Leaf area ratio
- Total Dry Weight percentage of whole plant, leaves, sheaths, roots.

(Garnier, E. 1992. Journal of Ecology, 80: 665-675.)

Which characteristics allow annuals to grow more rapidly than perennials at the seedling stage?

$RGR = ULR_a \times LWR \times SLA$

Where…

ULR_a = unit leaf rates: dry weight increment per day per unit leaf area

LWR = leaf weight ratio: the ratio between leaf weight and total plant weight

SLA = specific leaf area: the ratio of leaf area to leaf weight

(Garnier, E. 1992. Journal of Ecology, 80: 665-675.)

Results (Garnier et al. 1992)

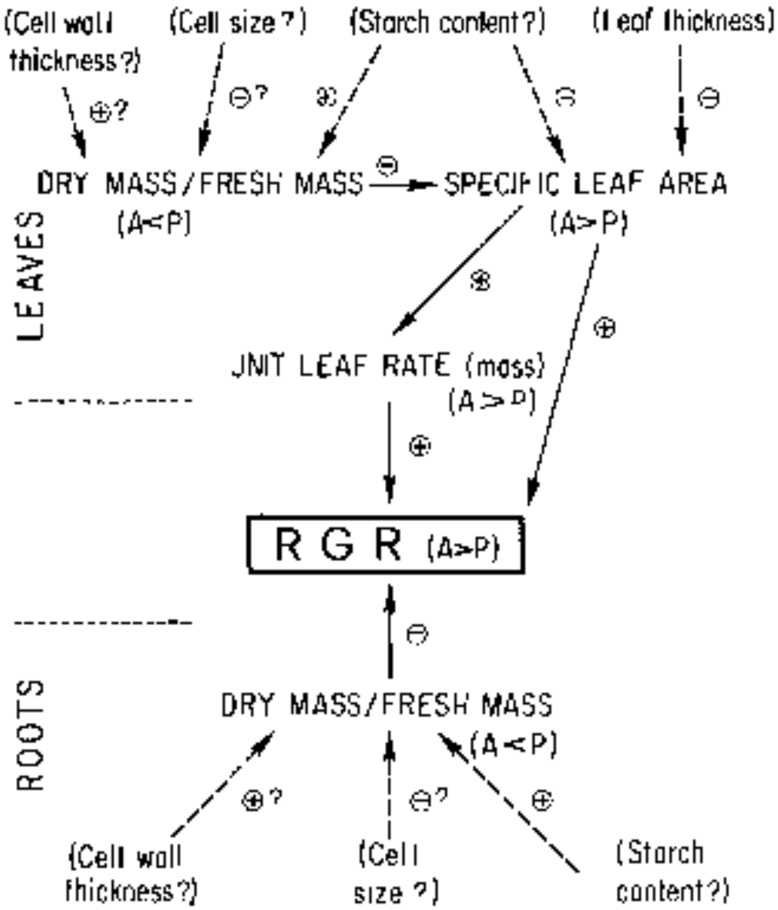


Fig. 5. Synthetic scheme summarizing the correlations found in the present study (solid lines). The dashed lines connected to parameters between brackets are correlations suggested from data or hypotheses found in the literature. These correlations do not necessarily imply direct causal relationships. A, annual; P, perennial.

- All production parameters were higher in annuals
- RGR significantly correlated with…
  - Specific leaf area
  - Unit leaf area
  - Leaf area ratio
  - Dry-weight:fresh-weight ratio of the whole plant
  - Dry-weight:fresh weight ratio of the roots

What is the relationship between RGR and ecosystem productivity?

Lavorel & Garnier 2002

$$NPP = \frac{\sum_{i=1}^{nspecies} N_i \times (Mf_i - Mo_i)}{\Delta T} \qquad \text{eqn 1}$$

Where…

N_i is the number of individuals of species i per unit ground area

Mf and Mo are the final and initial average biomasses of individuals of species i

ΔT is the period over which NPP is assessed

Lavorel & Garnier 2002

$$Mf_i = Mo_i \times e^{RGR_i \times (tf - to)_i} \qquad \text{eqn 2}$$

Where…

RGR_i is the average relative growth rate of species i

(tf-to) is the period of active growth of species i

Lavorel & Garnier 2002

Combining equations 1 and 2:

$$NPP = \frac{\sum_{i=1}^{nspecies} N_i \times Mo_i \times (e^{RGR_i \times (tf - to)_i} - 1)}{\Delta T} \qquad \text{eqn 3}$$

"NPP is controlled by the relative initial biomass of each species in the community (N_i x Mo_i; its carbon stock), the integrated functioning of each species (the outcome of carbon assimilation, nutrient uptake, allocation, etc.), and its phenology (duration of active growth period.)" (Lavorel and Garnier 2002).

Vile et al. 2006

$$\text{ANPP} = \frac{\text{live biomass in May} - \text{live biomass in February}}{t_{\text{May}} - t_{\text{February}}}, \quad (1)$$

Where…
t_{May} and $t_{February}$ are harvest dates

Vile et al. 2006

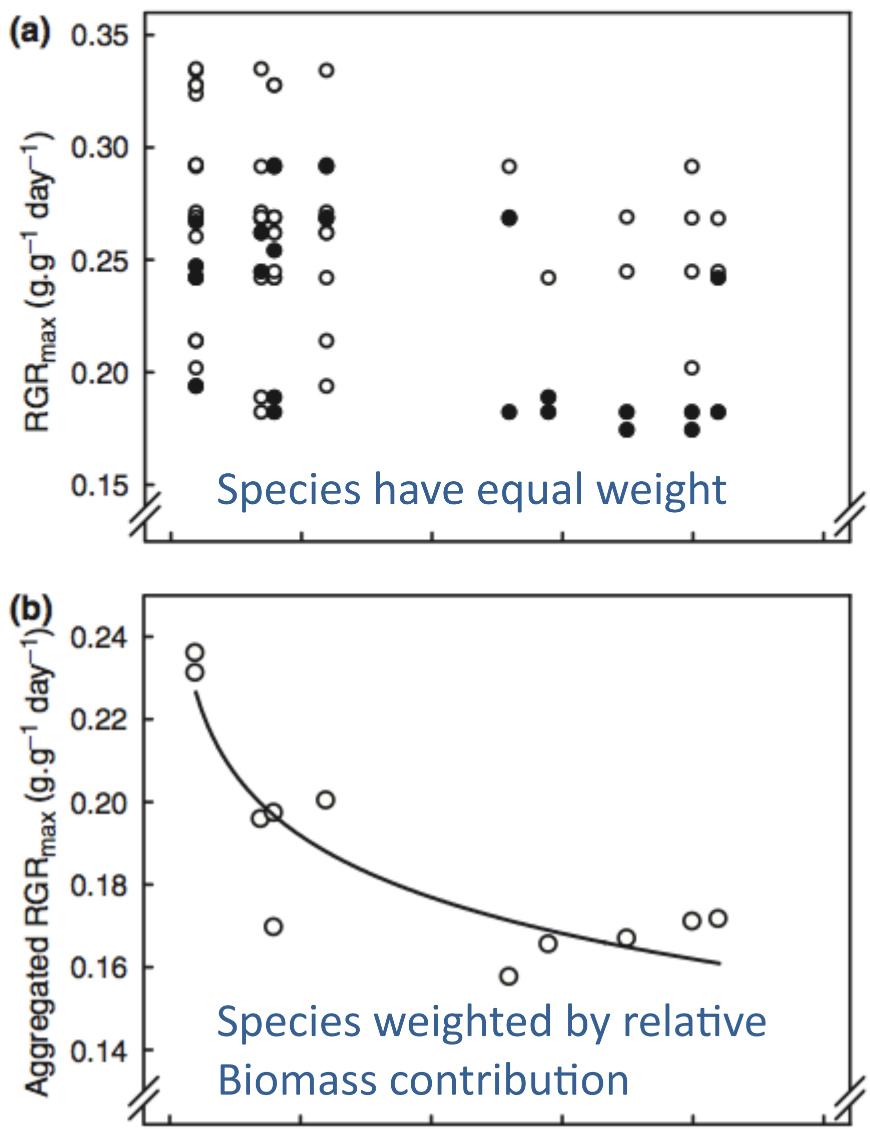
$$\mathrm{SANPP} = \frac{\log_{10}(\text{live biomass in May}) - \log_{10}(\text{live biomass in February})}{t_{\text{May}} - t_{\text{February}}} \tag{2}$$

Vile et al. 2006

$$\mathrm{RGR}_{\max-\mathrm{agg}j} = \sum_{i=1}^{n_j} P_{ij} \times \mathrm{RGR}_{\max i}, \qquad (3)$$

Where…
nj is the number of species sampled in community j
pij is the relative contribution of species i to the biomass of community j
RGR_{maxi} is the potential RGR of species i

Vile et al. 2006



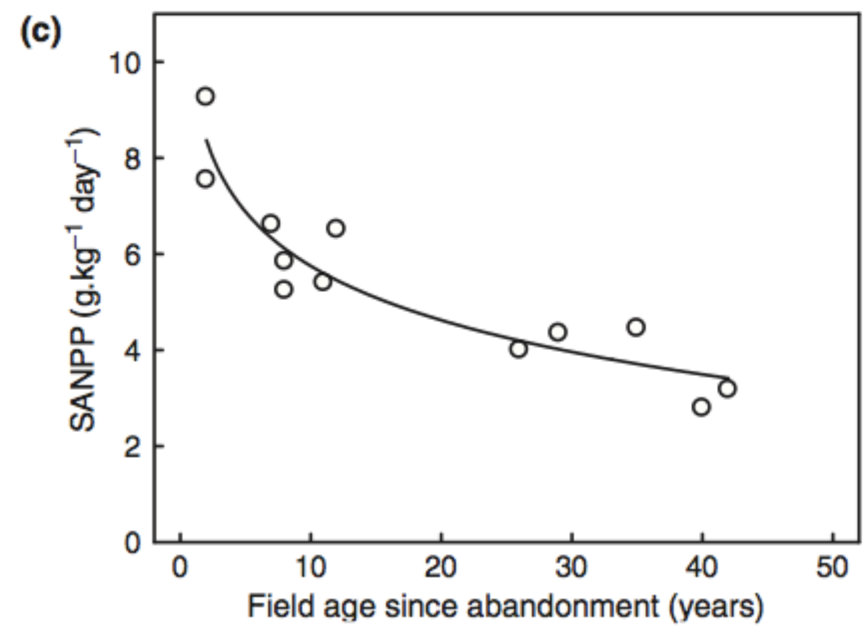


Figure 1 (a) Relationship between field age and potential maximum relative growth rate (RGR_{max}) for individual species. Solid symbols are for the two dominant species of each field; open symbols are for the other species. Pearson's correlation coefficients: for all species $r = -0.34$ ($n = 83$, $P = 0.002$), and for the two dominant species $r = -0.54$ ($n = 22$, $P = 0.008$). (b) Relationship between field age and RGR_{max} aggregated at the community level: $RGR_{max-agg} = -0.021 \log_{10}(\text{field age}) + 0.241$, $r^2 = 0.81$, $P < 0.001$, $n = 11$. (c) Relationship between field age and specific aboveground net primary productivity (SANPP): $\text{SANPP} = -1.63 \log_{10}(\text{fieldage}) + 9.50$, $r^2 = 0.87$, $P < 0.001$, $n = 12$. All x-data were back-transformed to draw the figures.

Vile et al. 2006

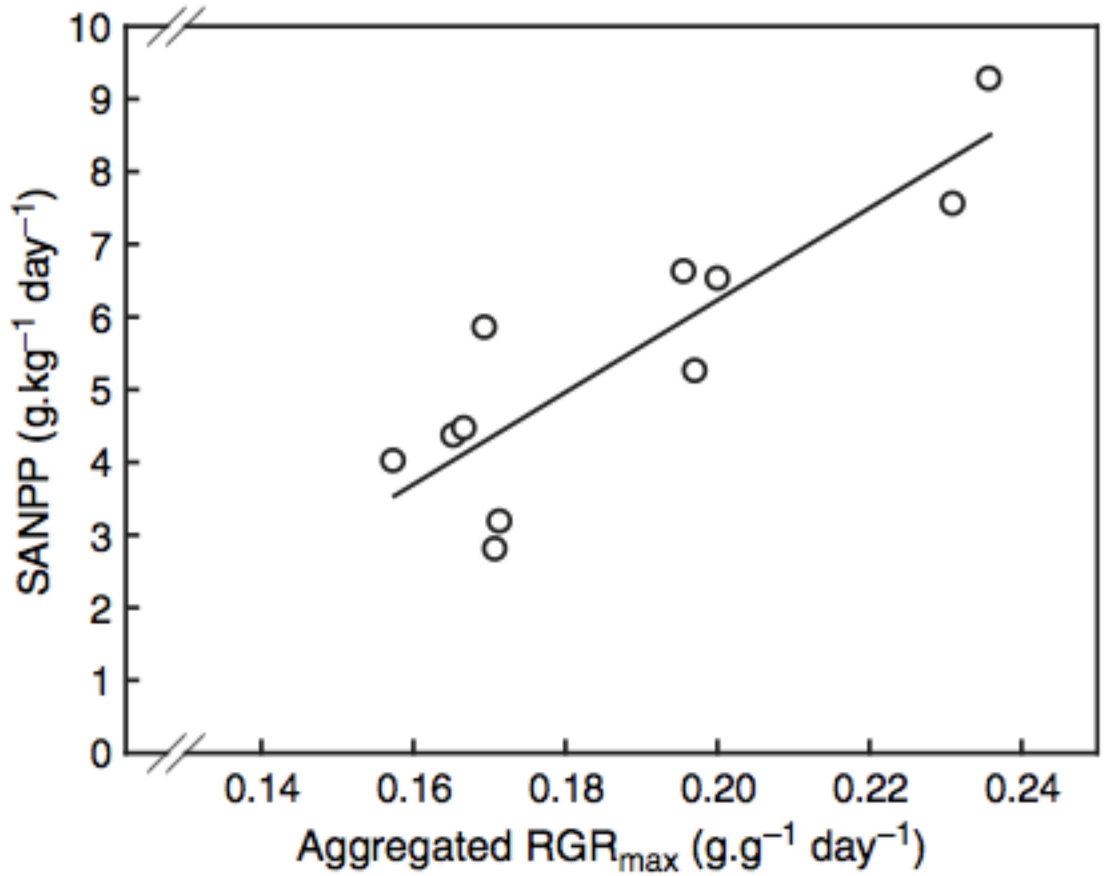


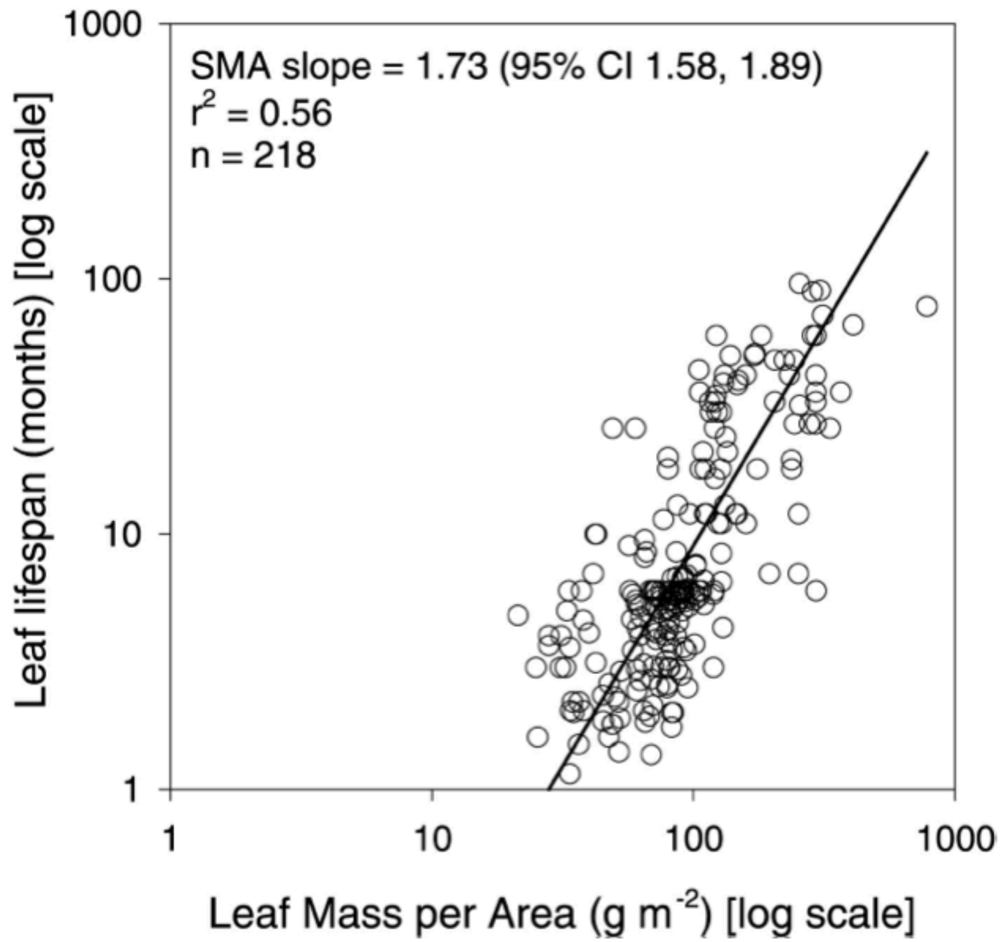
Figure 2 Relationship between specific net primary productivity (SANPP) and potential relative growth rate aggregated at the community level ($RGR_{max-agg}$): SANPP = 63.4 $RGR_{max-agg}$ − 6.45, $r^2 = 0.77$, $P = 0.001$, $n = 11$.

Other traits that *matter*

Westoby et al. 2002

First dimension of variation: LMA-LL

218 species, multiple habitats



Westoby et al. 2002

First dimension of variation: LMA-LL

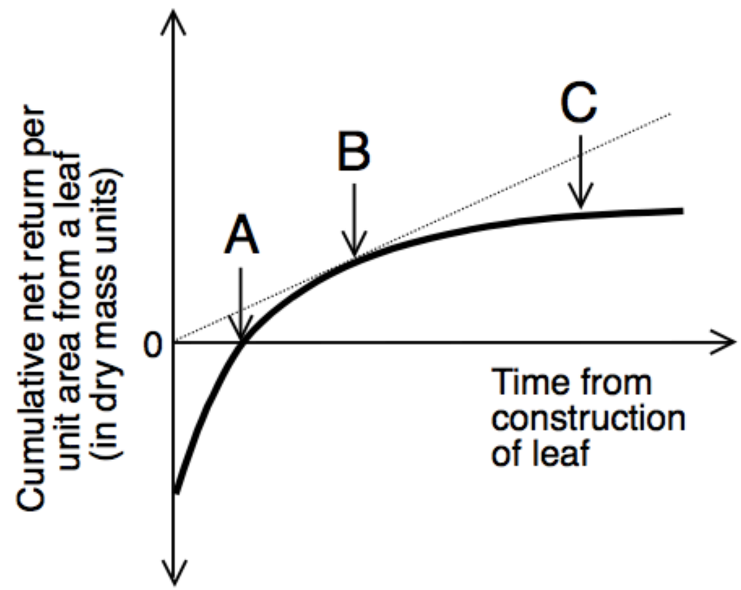


Figure 2 Essentials of existing theory for leaf lifespan (Kikuzawa 1995). Curve shows cumulative dry-mass return from a unit leaf area, net of costs of leaf respiration and of root and stem activity to support the leaf's photosynthesis. Curve is initially negative owing to construction costs (leaf mass per area), then increases through a leaf's lifetime. Payback time for the investment is at A. Net dry-mass return per time per leaf area is the slope of a line from the origin to the curve. It is maximized at the lifespan B. This optimum at B, and also payback time A, shift to longer lifespan if the cumulative dry-mass gain curve is shallower (slow-revenue environments) or if the initial investment is greater (higher leaf mass per area). At C, approximately, the leaf is no longer returning net dry-mass revenue.

Westoby et al. 2002

First dimension of variation: LMA-LL

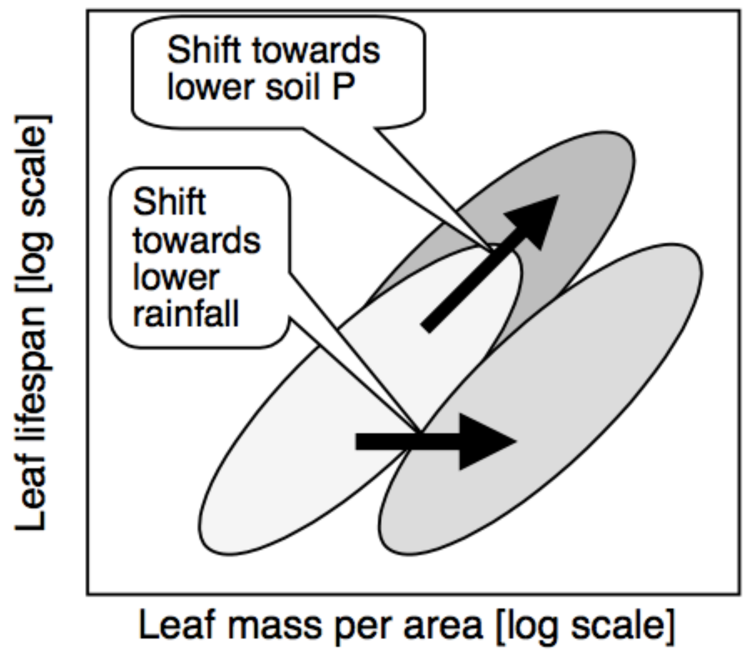


Figure 3 Schematic of leaf lifespan: leaf mass per area (LMA) relationships observed by Wright et al. (2002). Each oval cloud represents the scatter of species in a given habitat. Species occurring at lower soil P tend to have higher LMA, and leaf lifespan is also higher, corresponding to the same LMA-LL relationship observed across species within habitat. Species occurring at lower rainfall also tend to higher LMA but have shifted to a parallel relationship achieving shorter leaf lifespan for a given LMA.

Westoby et al. 2002

Second dimension of variation:
Seed mass and
Seed output

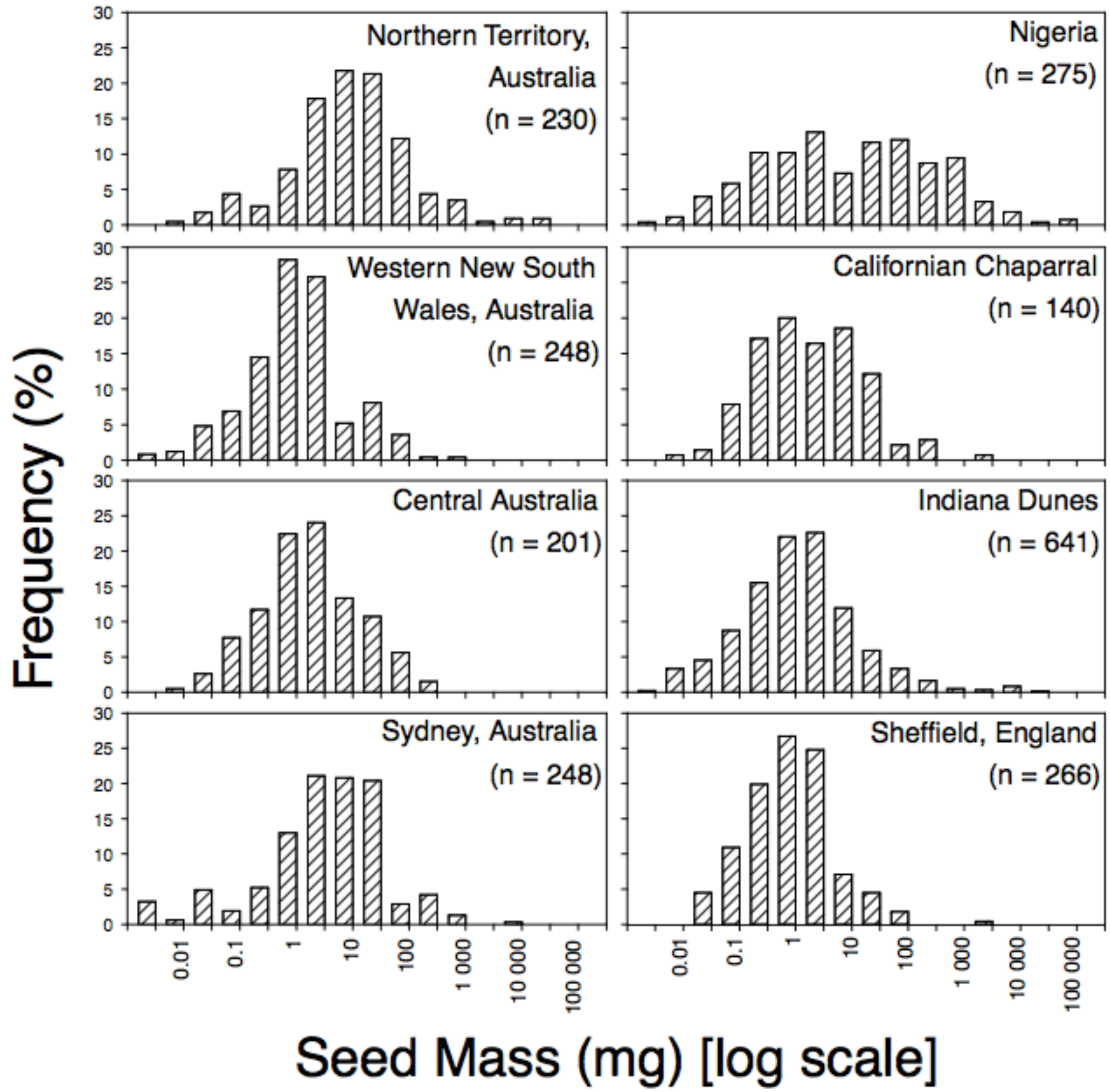


Figure 4 Cross-species frequency distributions of individual seed mass for several locations (Leishman et al. 2000). Two bars per order of magnitude of seed mass.

Westoby et al. 2002

- Third dimension: Leaf-size and twig size
  - Thicker stems associated with larger leaves
  - Hydraulic and mechanical reasons for this
- Fourth dimension: Potential canopy height
  - Game theory
  - Costs and benefits

Citations

Garnier, E. 1992. Growth analysis of congeneric annual and perennial grass species. *Journal of Ecology*. 80(4):665-675.

Grime, J., and R. Hunt. 1975. Relative Growth-Rate: its range and adaptive significance in a local flora. *The Journal of Ecology*. 63(2): 393-422.

Lavorel, S. and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology*. 16: 545-556.

Poorter, H. 1989. Interspecific variation in relative growth rate: on ecological causes and physiological consequences. *Causes and consequences of variation in growth rate and productivity of higher plants*. Edited by H. Lambers et al. pp 45-68.

Westoby, M., D. Falster, A. Moles, P. Vesk, and I. Wright. 2002. Plant Ecological Strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics.* 33: 125-159.

Vile, D., B. Shipley, and E. Garnier. 2006. Ecosystem productivity can be predicted from relative growth rate and species abundance. *Ecology Letters*. 9: 1061-1067.