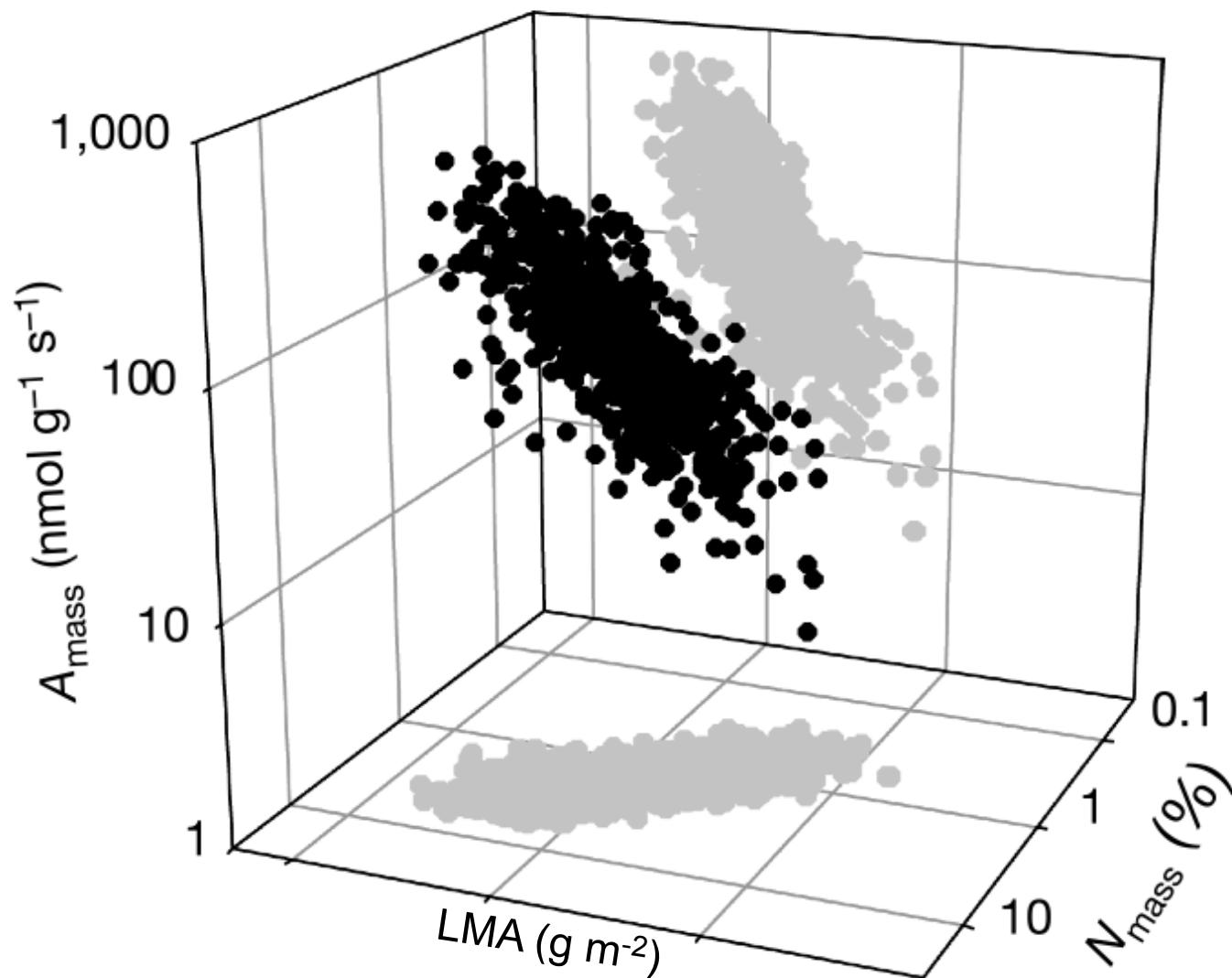


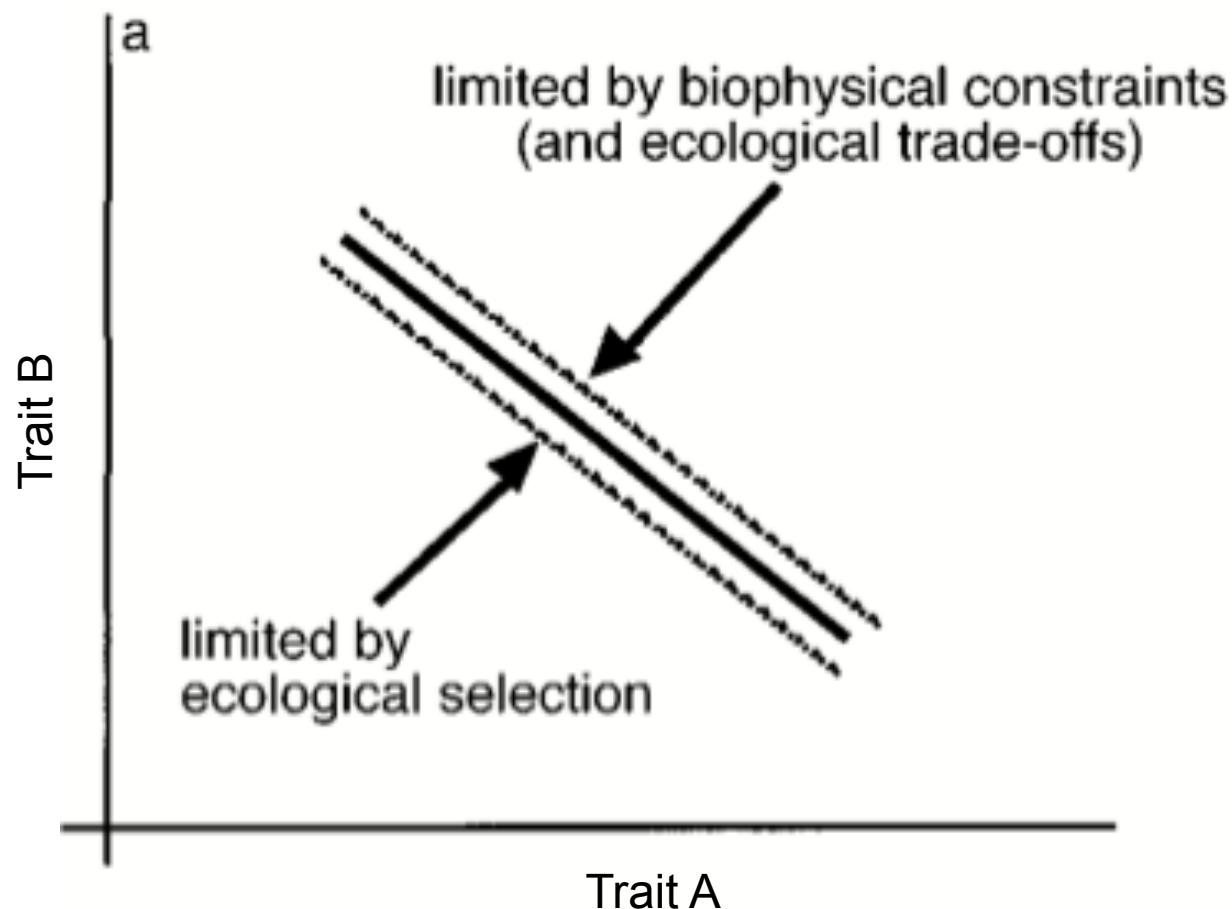
The origin of the leaf economics spectrum

Benjamin Blonder

28 March 2012

a

variation through a hyperellipsoid²⁴. A remarkable 82% of all variation in A_{mass} , LMA and N_{mass} across species lay along the first principal axis in three-trait space (Fig. 2a). Because some of the residual 18% must be measurement variation, 82% represents a minimum estimate of the dominance of this single spectrum in explaining variation across plant species worldwide. Further three-



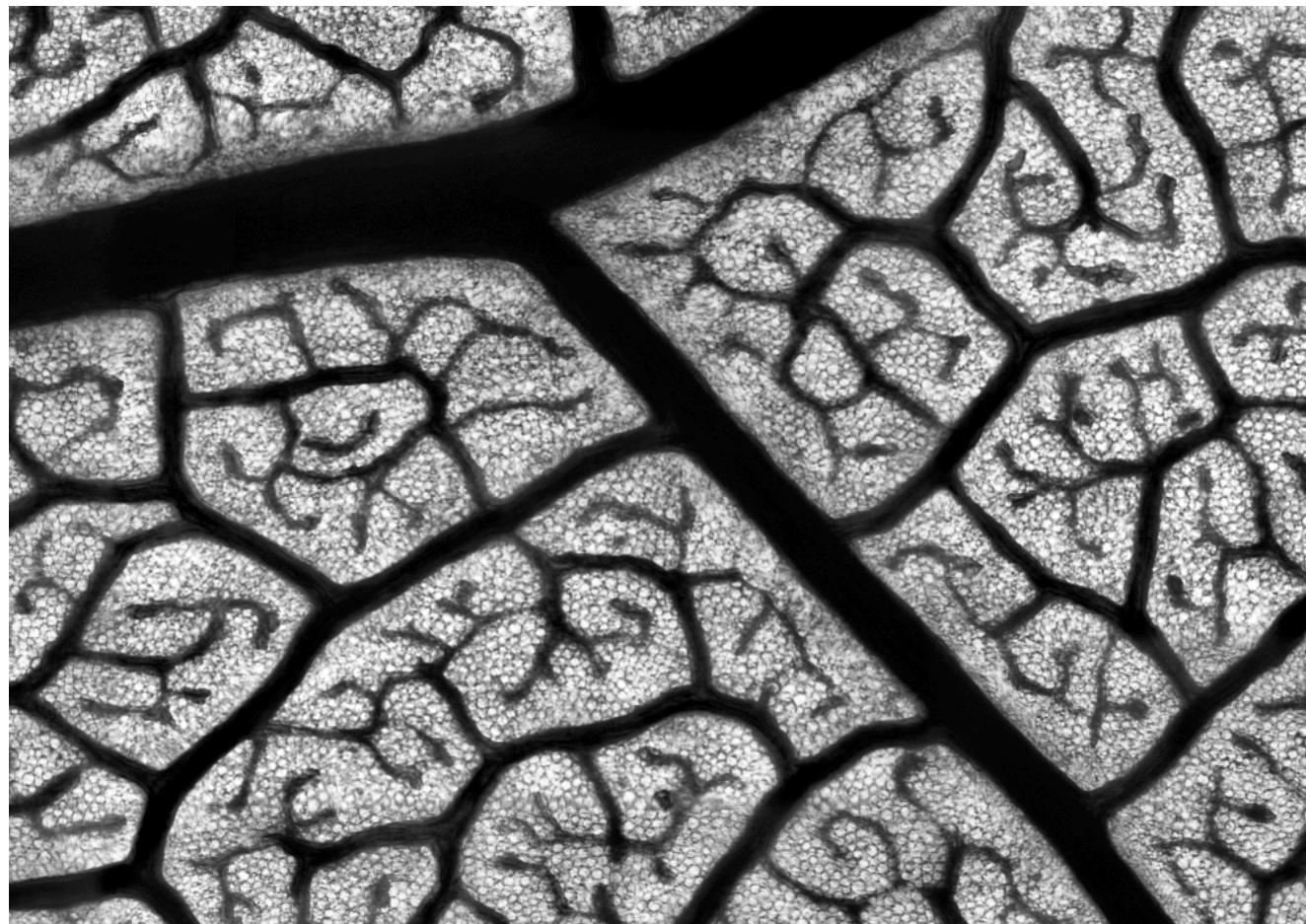


Mechanism – at what scale?

Marten van Valckenborch (1535-1612)

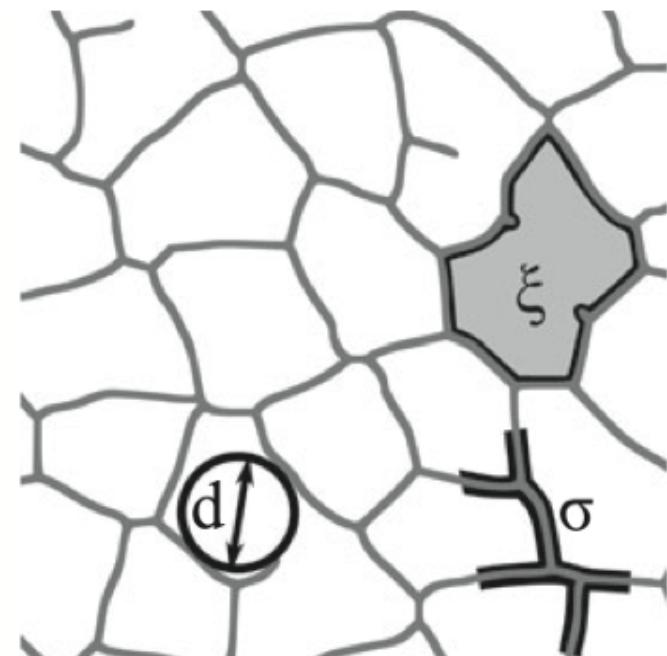
Paper	Mechanism	Scale	Evidence
Blonder ELE	Vein network tradeoffs	Physiology	Fits to global data & measurement of key trait
Blonder NP	Vein network tradeoffs	Physiology	Measurement of key trait & path analysis
Shipley Ecology	Structural tradeoffs and maximization of carbon gain	Physiology	Path analysis with global data
McMurtrie TP	Maximization of carbon gain	Physiology-environment	Fits to global & local data
Donovan TREE	Natural selection	Evolution	Measurement of selection coefficients and genetic constraints
Vasseur ELE	Pleiotropy	Genes	Forward genetics

1. Leaf veins (Blonder)



Central hypothesis

- The common architecture of all leaves causes venation-mediated structural tradeoffs that indirectly result in multiple leaf trait correlations



$$\text{LMA} = \pi r_V^2 (\rho_V - \rho_L) \sigma + \frac{2\rho_L}{k_0} d.$$

Veins are denser than other tissues

$$\begin{aligned} \text{LL} &= k_1 \delta \\ &= k_1 d \end{aligned}$$

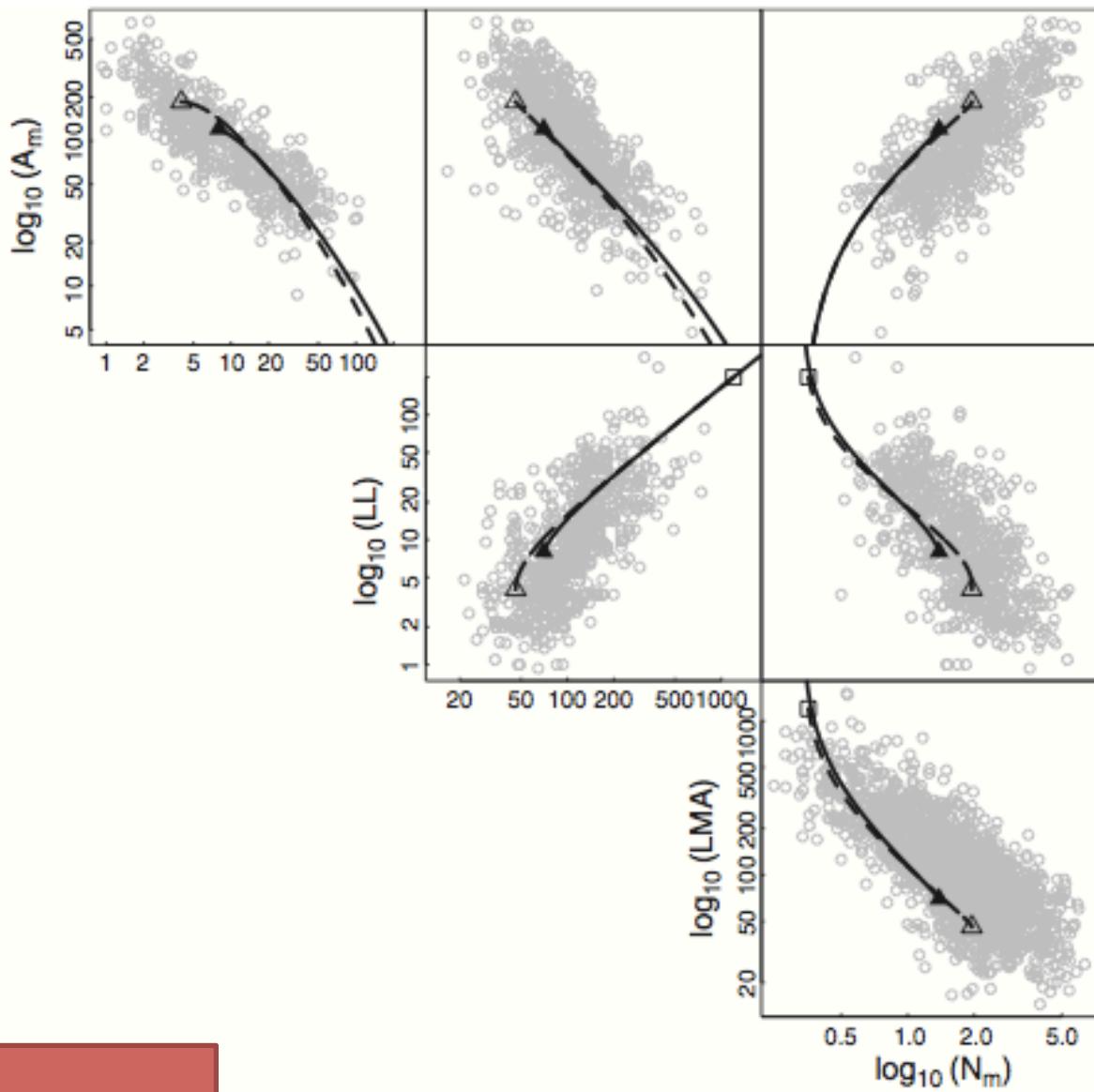
Thicker leaves are harder to damage

$$N_m = k_2 A_m + \frac{k_3}{k_0} \frac{2d - k_0 \pi r_V^2 \sigma}{\text{LMA}}$$

Nitrogen is not found in veins

$$A_m = \frac{[\pi c_0 D(1-b) k_0 n_s a_s \text{WUE}] \sigma}{[2\rho_L d + k_0 \pi r_V^2 (\rho_V - \rho_L) \sigma] [(\pi t_s + \sqrt{\pi a_s}) \sigma + 2a_s n_s \log \frac{d}{k_0 r_V}]}$$

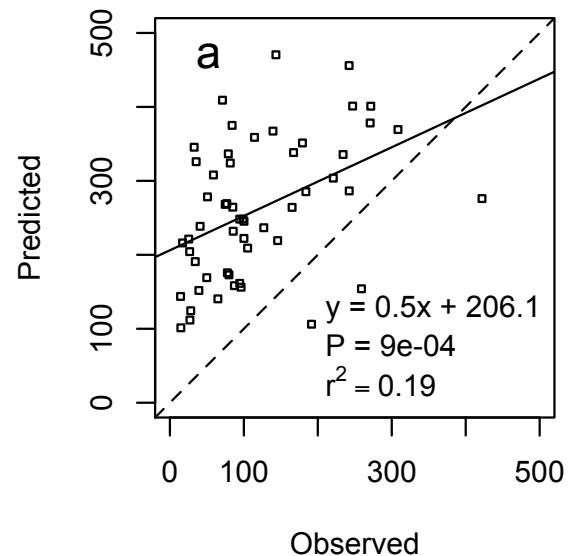
Water diffusion from veins limits carbon uptake



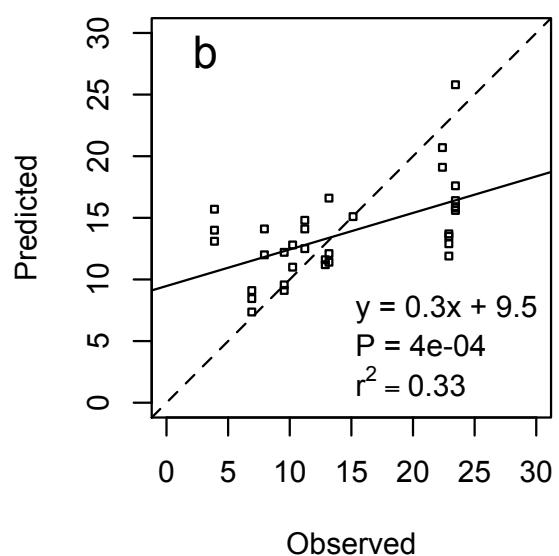
Fits to global data

Comparison to local data

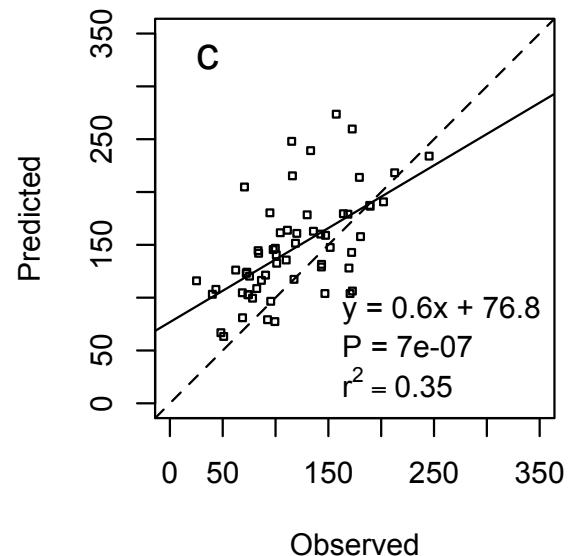
A_m (nmol C g $^{-1}$ s $^{-1}$)



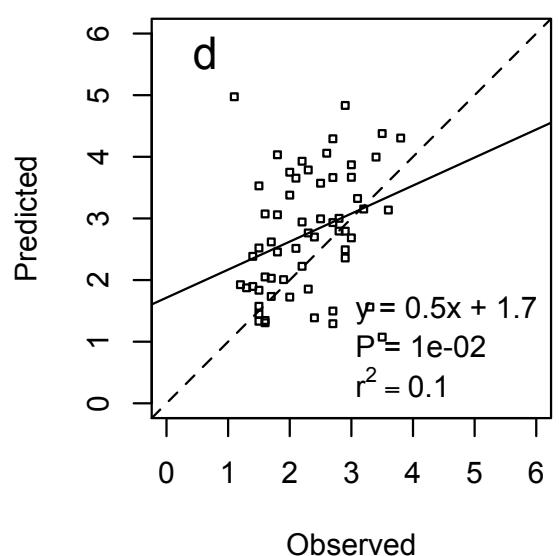
LL (mo)



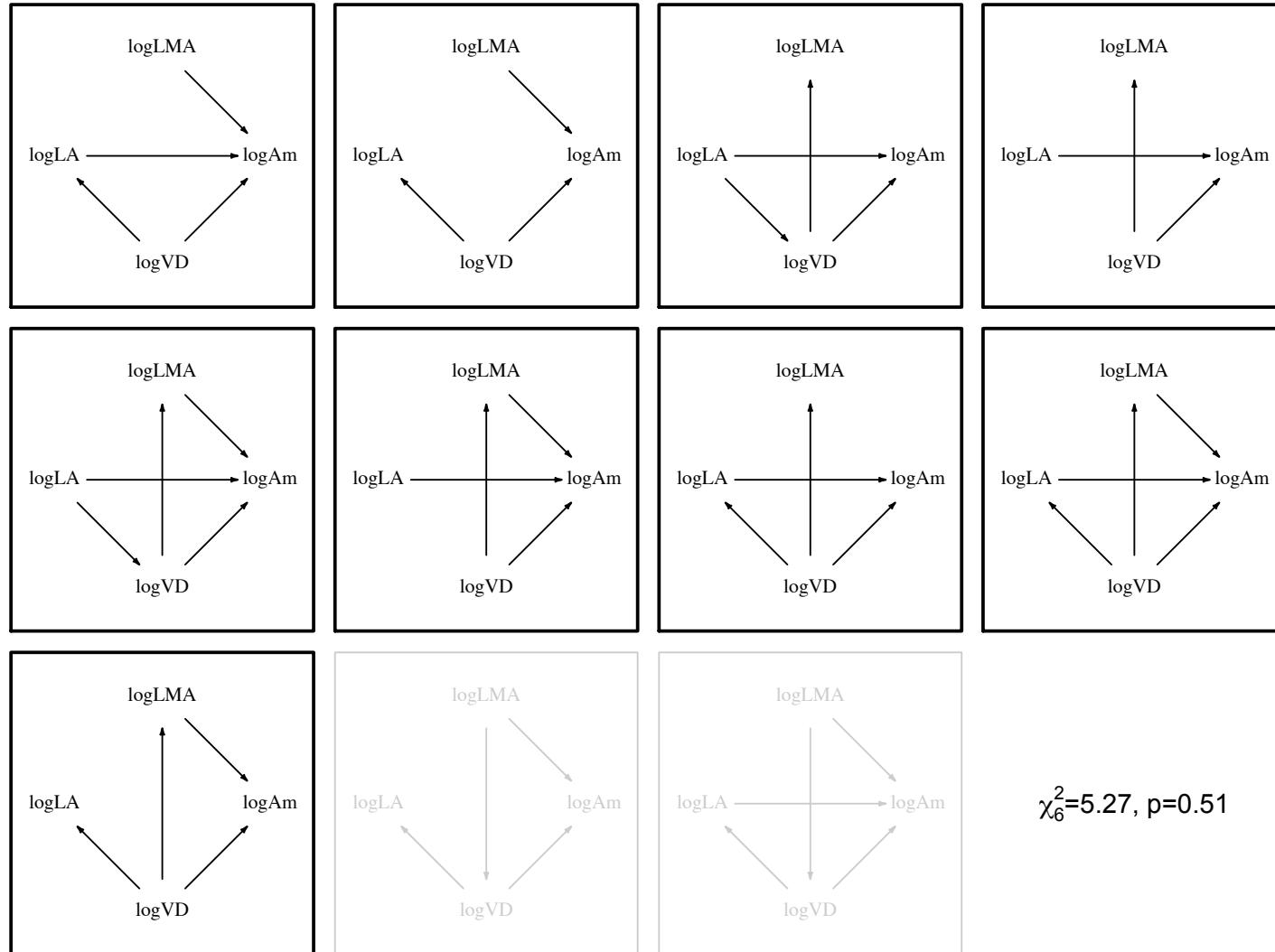
LMA (g m $^{-2}$)



N_m (%)



Structural equation modeling of local data

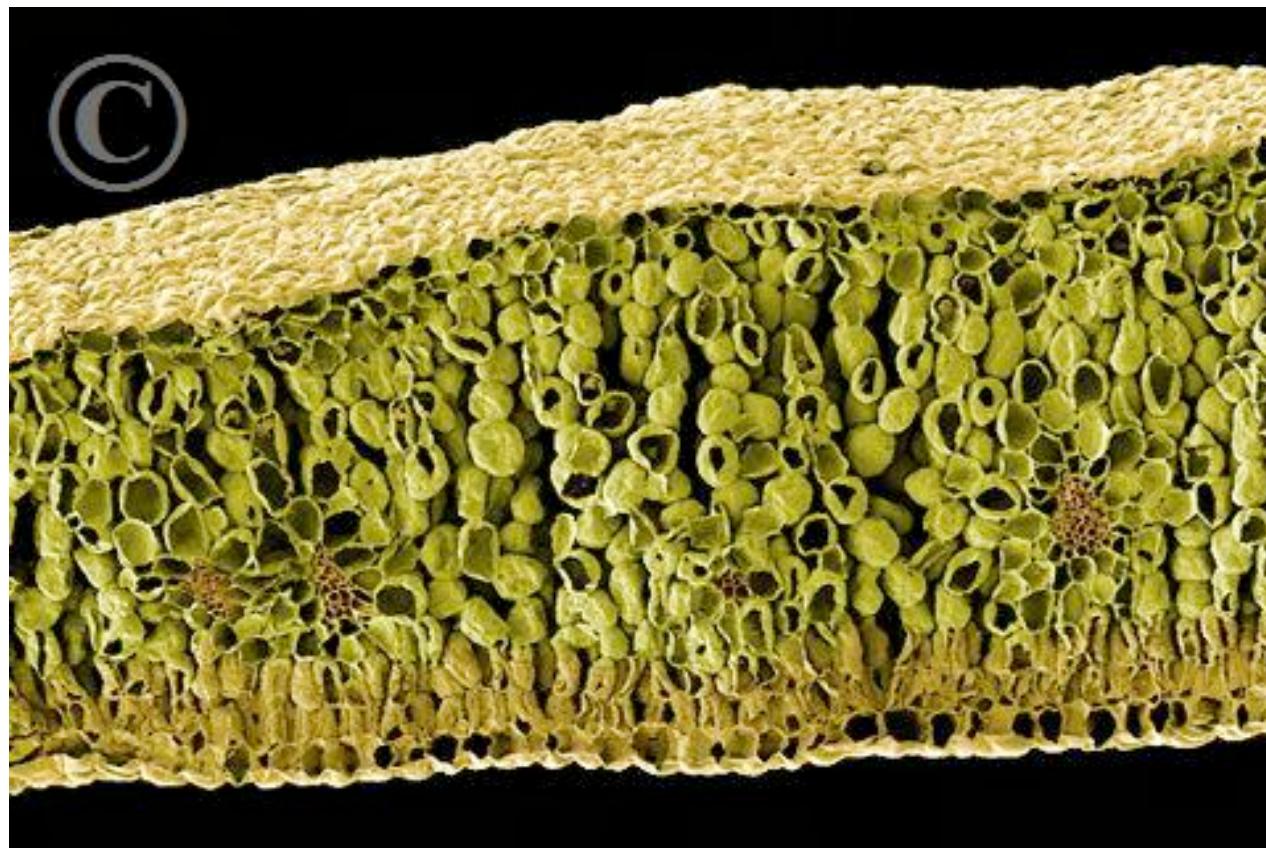


$$\chi^2_6 = 5.27, p = 0.51$$

Critical view

- Parsimonious explanation supported by data
- Mass partitioning in leaves may be more complex & involve other traits
- Leaf lifespan may not be a damage-controlled process

2. Structural tradeoffs (Shipley)

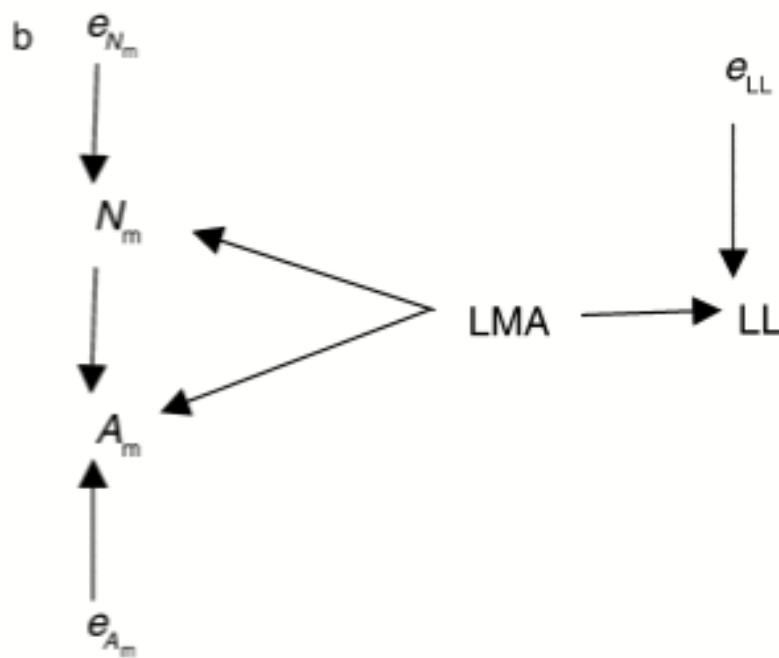
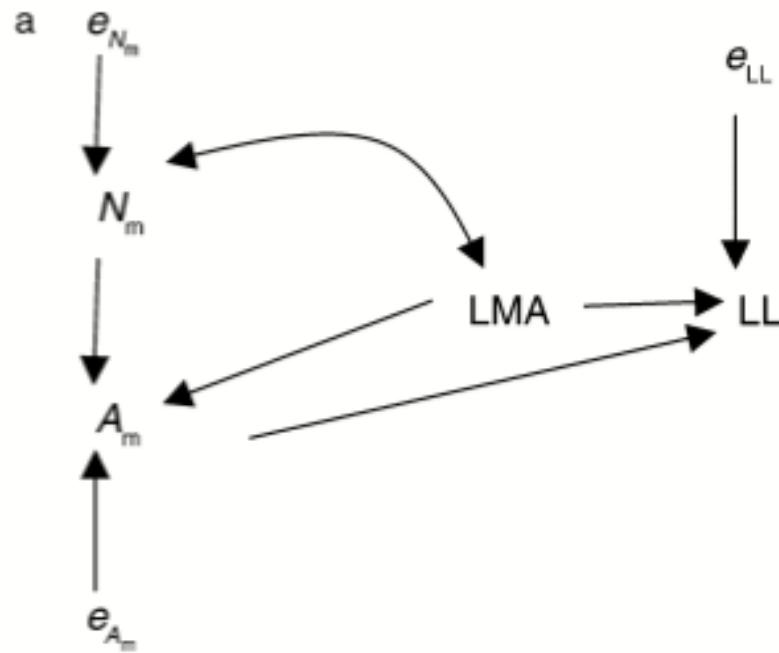


b745444 [RM] © www.visualphotos.com

Central hypothesis

A necessary trade-off between allocation to structural tissues versus liquid phase processes and an evolutionary trade-off between leaf photosynthetic rates, construction costs, and leaf longevity

Rejection of traits
directly causing other
traits



$$N_m \cong \frac{\bar{n}V_c}{dV_w}$$

$$A_m = \frac{A}{M_c + M_w} \cong \frac{\bar{a}V_c}{dV_w}$$

$$SLA \cong \frac{V_c + V_w + V_a}{T(dV_w)} = \frac{1}{d} \left(\frac{V_c}{TV_w} + \frac{1}{T} + \frac{V_a}{V_w} \right)$$

$$\Delta_m = \frac{\Delta}{M_c + M_w} \cong \frac{\Delta}{dV_w}$$

$$\cong \sum_i \delta_i \bar{e}_i \frac{V_c}{dV_w} + \frac{1}{d} \sum_j \delta_j \bar{e}_j.$$

Nitrogen found within cells

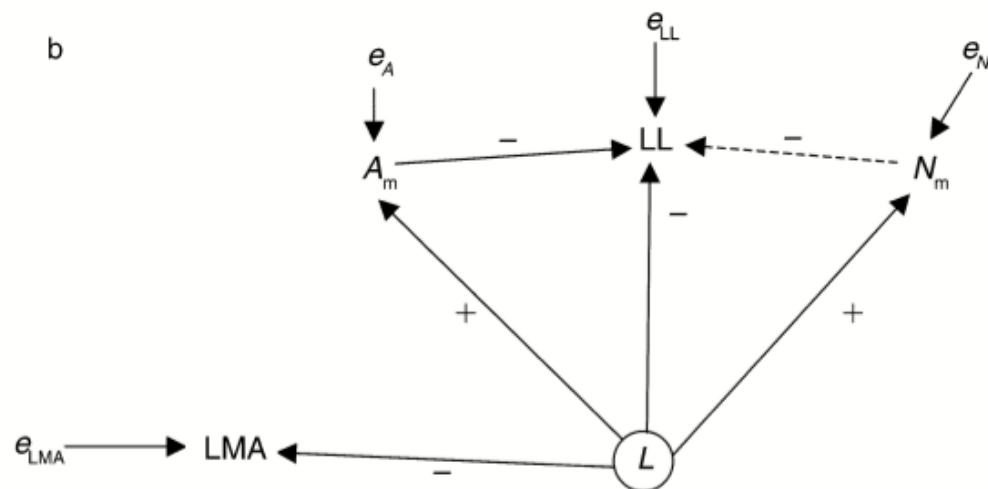
Photosynthesis proportional to chloroplast number density (i.e. # organelles / cell is proportional to cell volume)

Larger cells have proportionally less cell wall

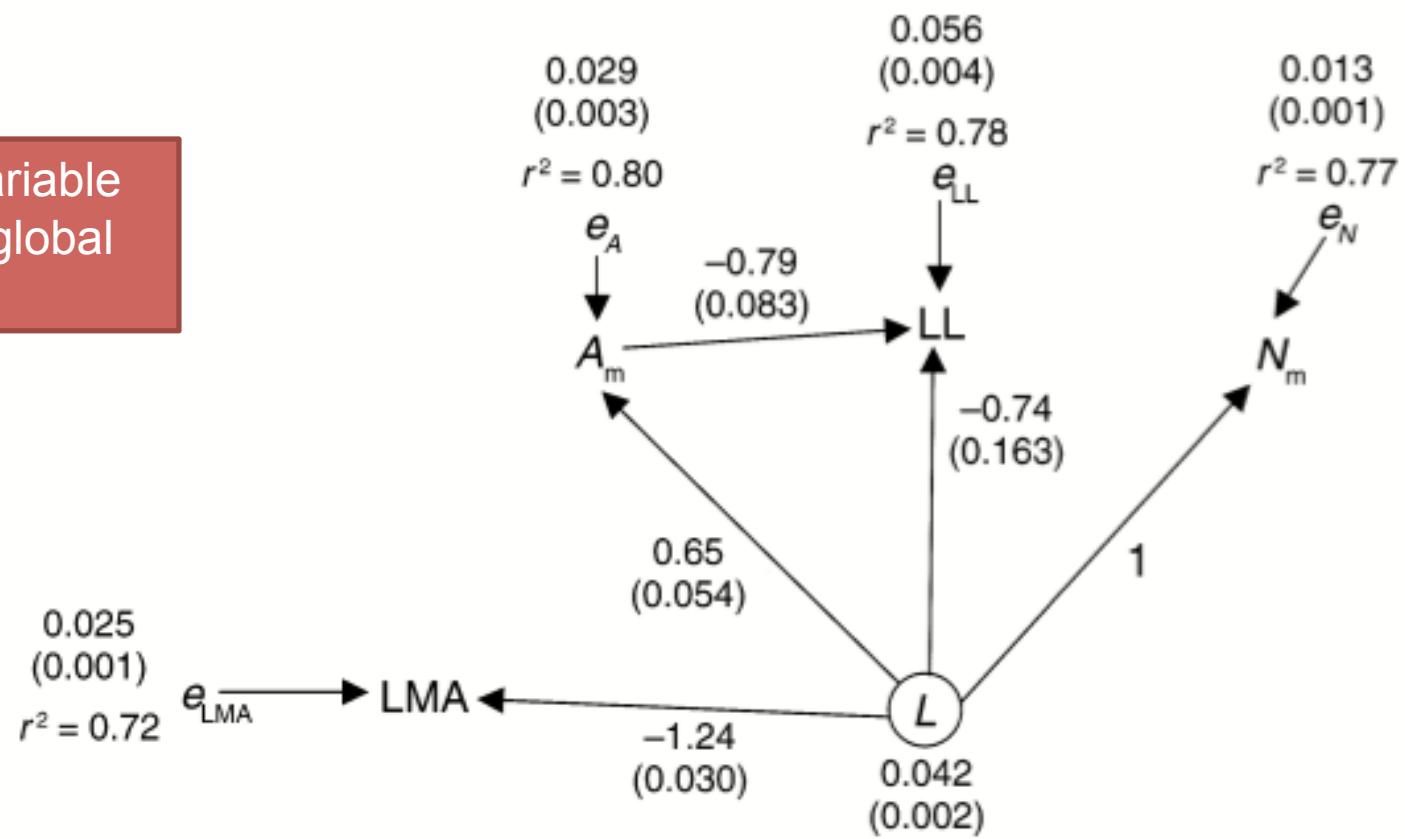
Cell volume and cell wall have different relative construction costs that require different payback times

Tradeoff: variation in cell size / cell number and cell wall thickness (V_c/V_w),

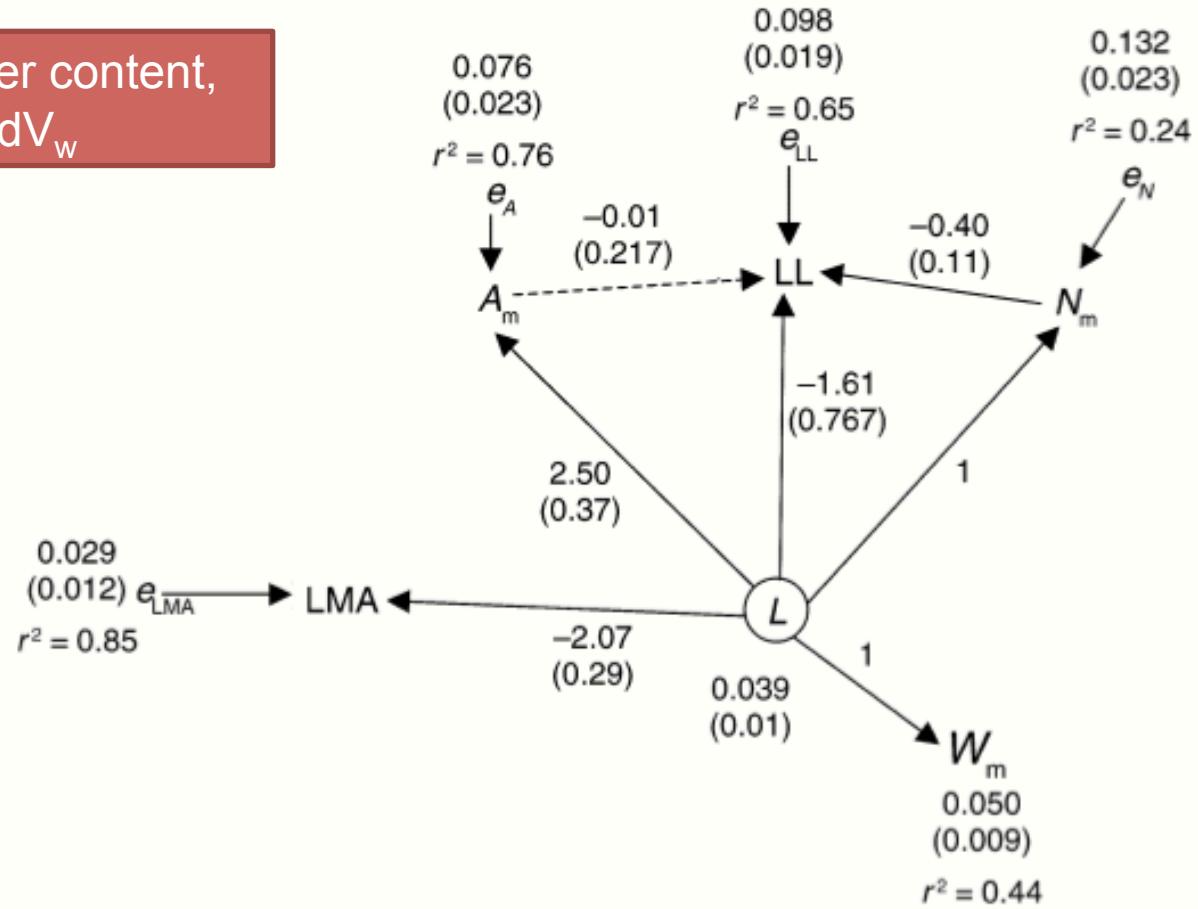
b



Tests with latent variable path analysis and global data



Tests with water content,
a proxy for V_c/dV_w



Critical view

- Parsimonious explanation
- Variable of interest never actually measured
- Model only useful for explaining relationships rather than predicting quantitative (nonlinear) form

3. Carbon maximization (McMurtrie)



Ansel Adams (untitled)

Central hypothesis

- MAXX: under the prevailing environmental resource constraints, plants with a given leaf lifespan τ will adjust their within-canopy profiles of leaf traits N_{area} and SLA, as well as their total canopy leaf area, so as to maximize the total amount of C exported from their canopies over the lifespan of leaves

$$X_{\text{tot}} = \int_0^{L_{\text{tot}}} X_{\text{area}}(L) dL$$

$$X_{\text{area}}(L) = A_{\text{area}}(L) - \frac{\omega}{\tau \cdot Y \cdot \text{SLA}(L)}$$

Maximize rate of carbon uptake over the entire canopy

$$U_{\text{tot}} = \int_0^{L_{\text{tot}}} U_{\text{area}}(L) dL$$

$$N_w(L) = b_0 + b_1 N_{\text{mass}}(L) = b_0 + b_1 X_{\text{area}}(L) \text{SLA}(L)$$

Subject to the constraint of fixed total nitrogen supply from the ground

$$U_{\text{area}}(L) = \frac{1-r}{\tau} N_{\text{area}}(L) + X_{\text{area}}(L) \alpha_w \frac{N_w(L)}{\omega}$$

Implies that rate of carbon gain per nitrogen used (XNUE) is also maximized for small/short plants

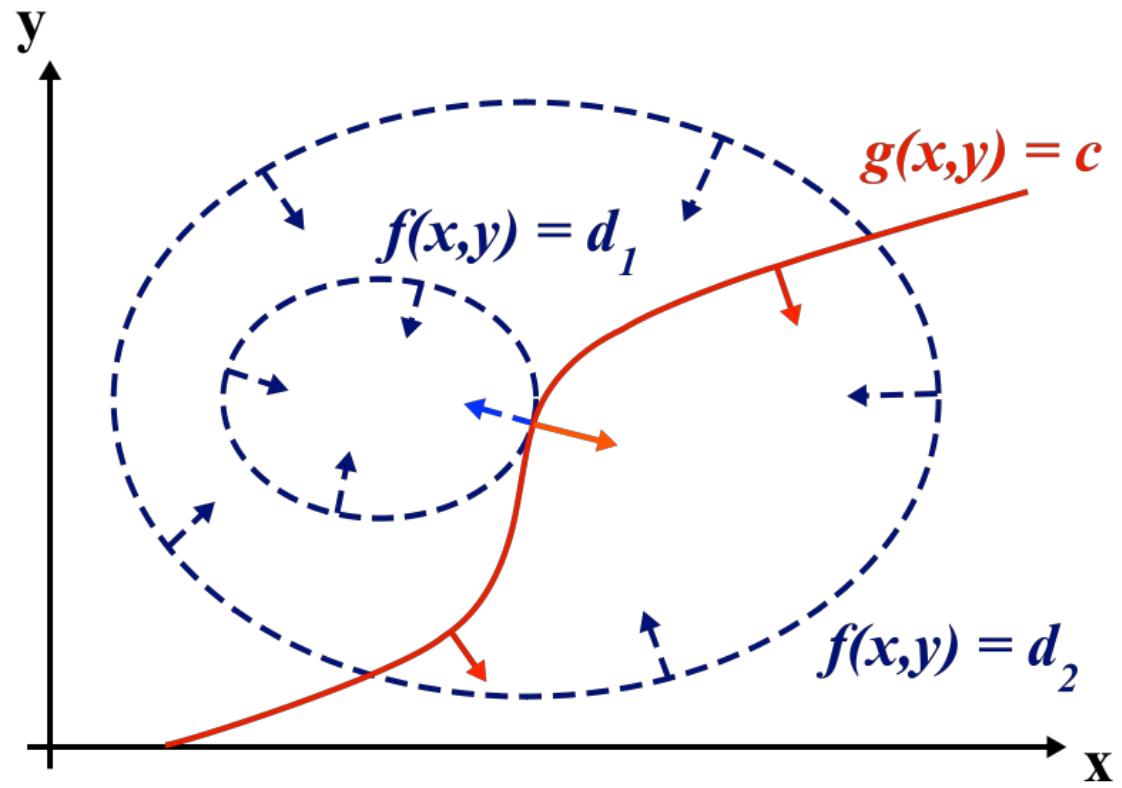
$$A_{\text{area}} = m_C h (A_{\text{area-sat}} f(q) - R_0 N_{\text{area}})$$

where $m_C = 12 \times 10^{-3}$ kg C (mol CO₂)⁻¹, $q = \pi k \alpha P_{\text{in}} e^{-kL} / h A_{\text{area-sat}}$ and

$$f(q) = \frac{2}{\pi} \int_0^{\pi/2} dx \frac{2q \sin x}{1 + q \sin x + \sqrt{(1 + q \sin x)^2 - 4\theta q \sin x}} \quad (\text{A5})$$

Carbon uptake is a function of canopy depth and light availability

A, SLA, N, τ are all emergent outcomes of the optimization process achieved by Lagrange multipliers



Lagrange multipliers

To maximize $f(x,y)$ with the constraint $g(x,y)=c$, find the point where the gradient of f and g are proportional:

$$\nabla_{x,y}f = -\lambda \nabla_{x,y}g$$

$$\nabla_{x,y}f = \left(\frac{\partial f}{\partial x}, \frac{\partial f}{\partial y} \right)$$

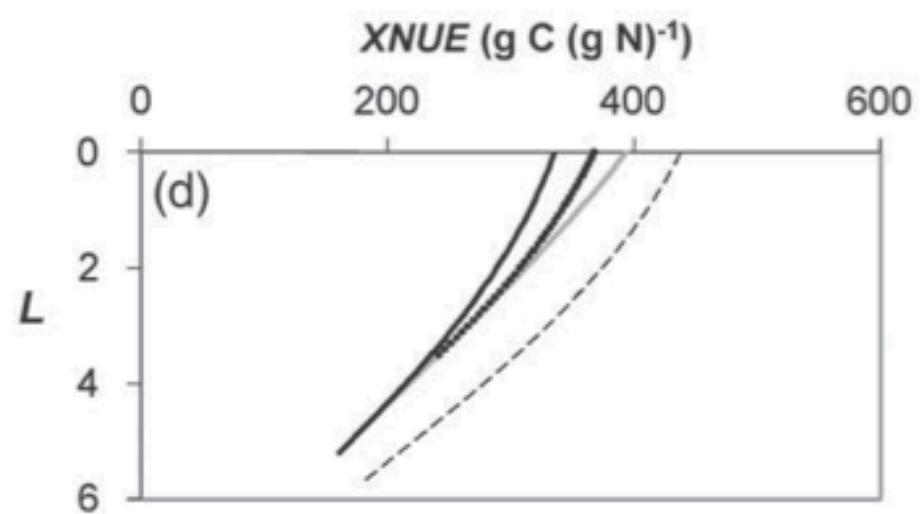
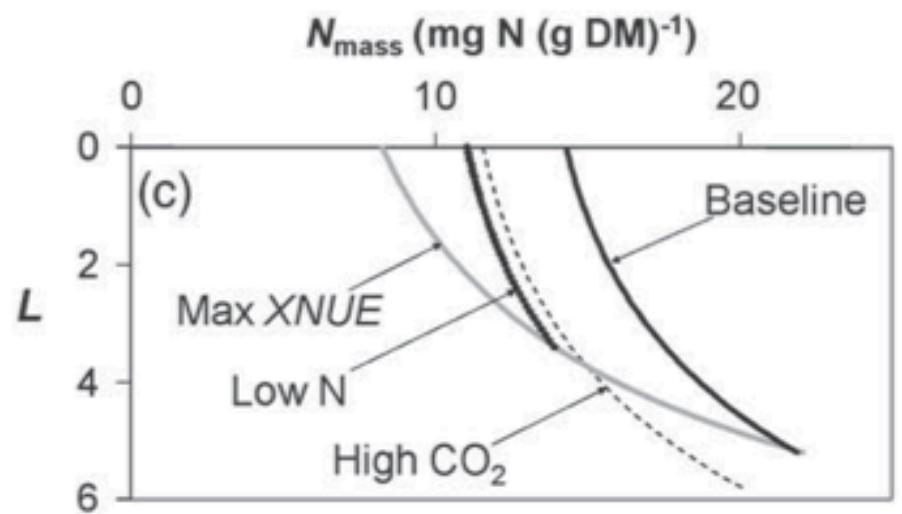
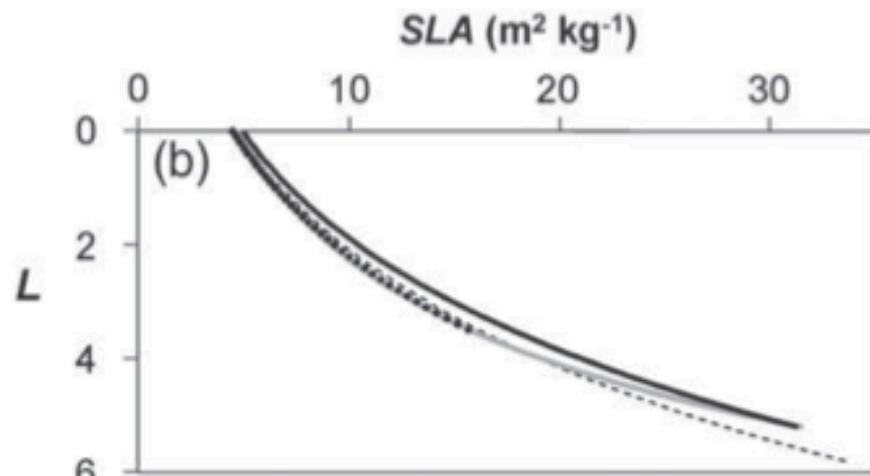
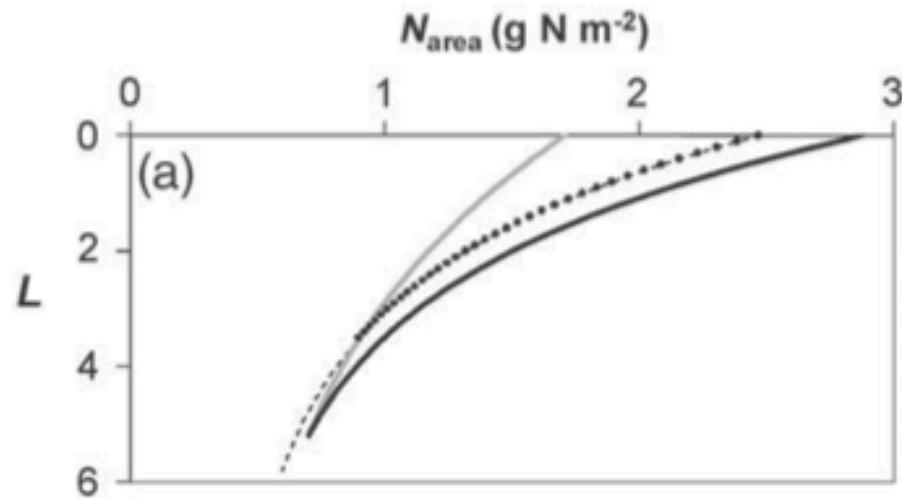
$$\nabla_{x,y}g = \left(\frac{\partial g}{\partial x}, \frac{\partial g}{\partial y} \right)$$

Which is equivalent to solving

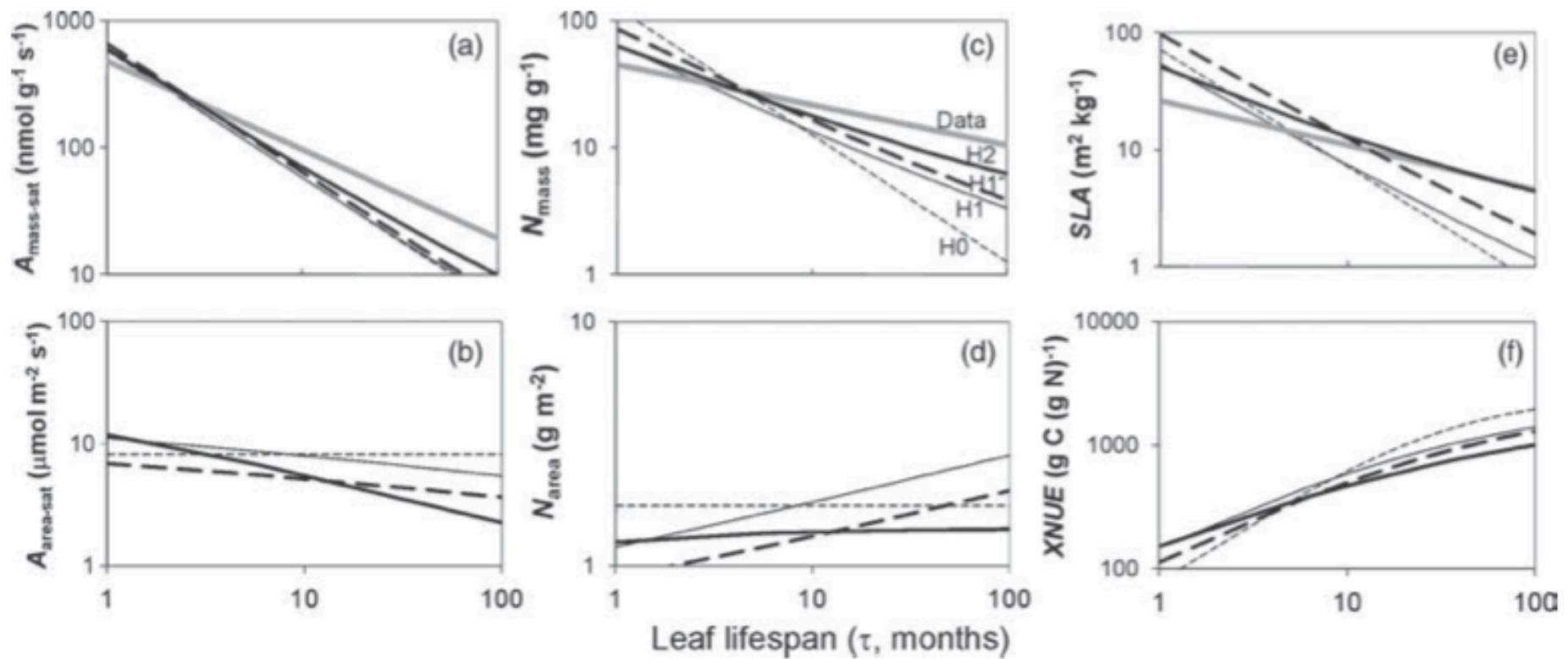
$$\nabla_{x,y,\lambda}\Lambda(x,y,\lambda) = 0.$$

$$\Lambda(x,y,\lambda) = f(x,y) + \lambda \cdot (g(x,y) - c),$$

Predictions under altered resource supply states qualitatively match experiment



Leaf economic spectrum correlations are replicated under H1 (slope of A/N relationship decreases with lifespan) – the black long dash line



Critical view

- Couples leaf processes to environment & is highly predictive
- Large amount of complexity and # of parameters required in model
- Extensive *post-hoc* modification to improve fit

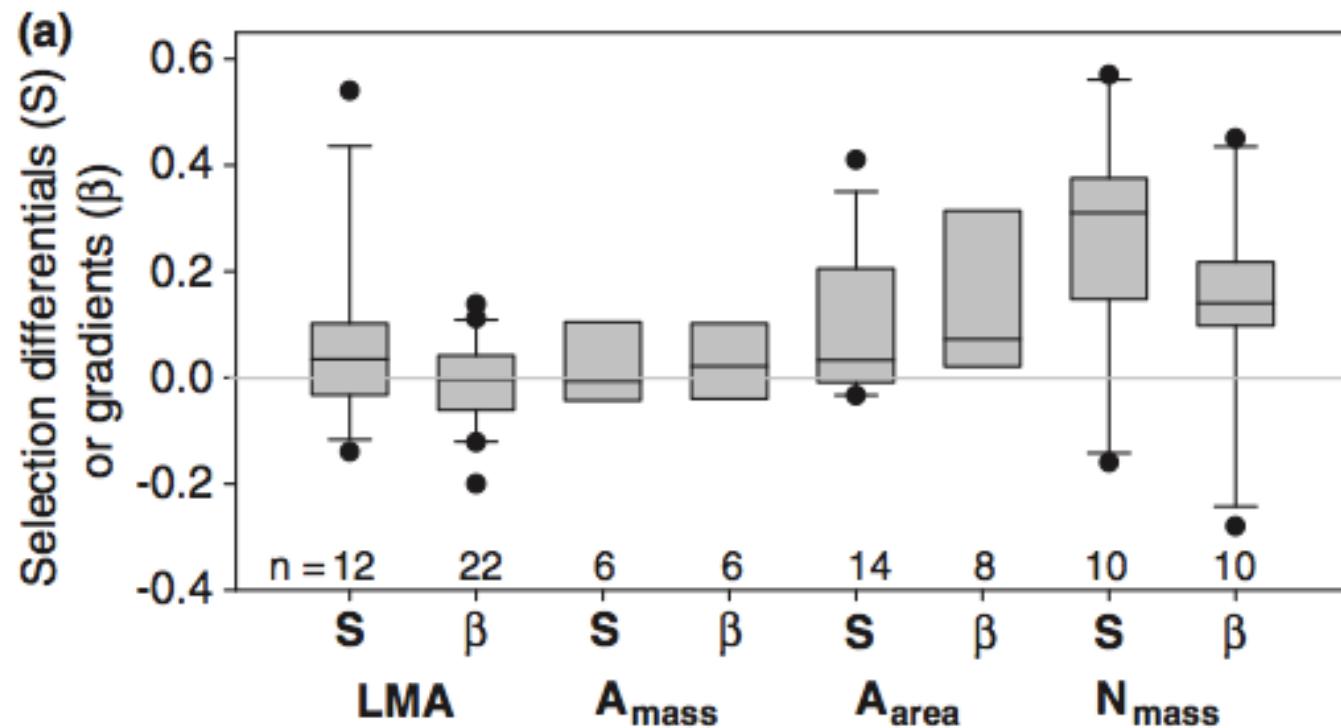
4. Evolutionary causes (Donovan)



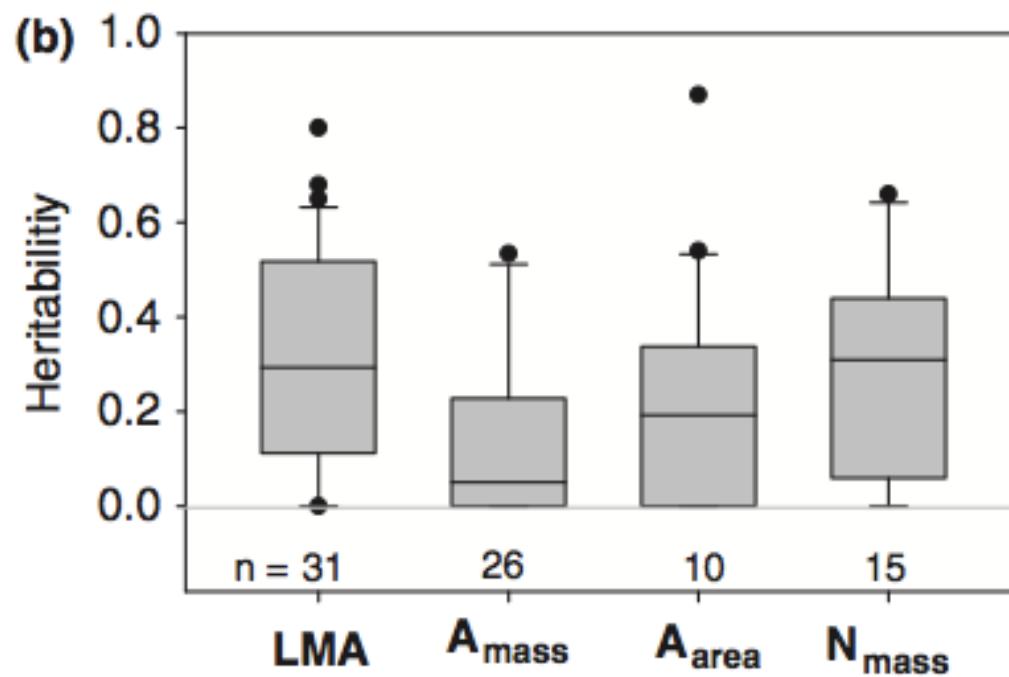
Central result

- There was significant selection for leaf traits on both ends of the WLES spectrum, as well as significant genetic variation for these traits. In addition, genetic correlations between WLES traits were variable in strength and direction. These data suggest that genetic constraints have had a smaller role than selection in the evolution of the WLES.

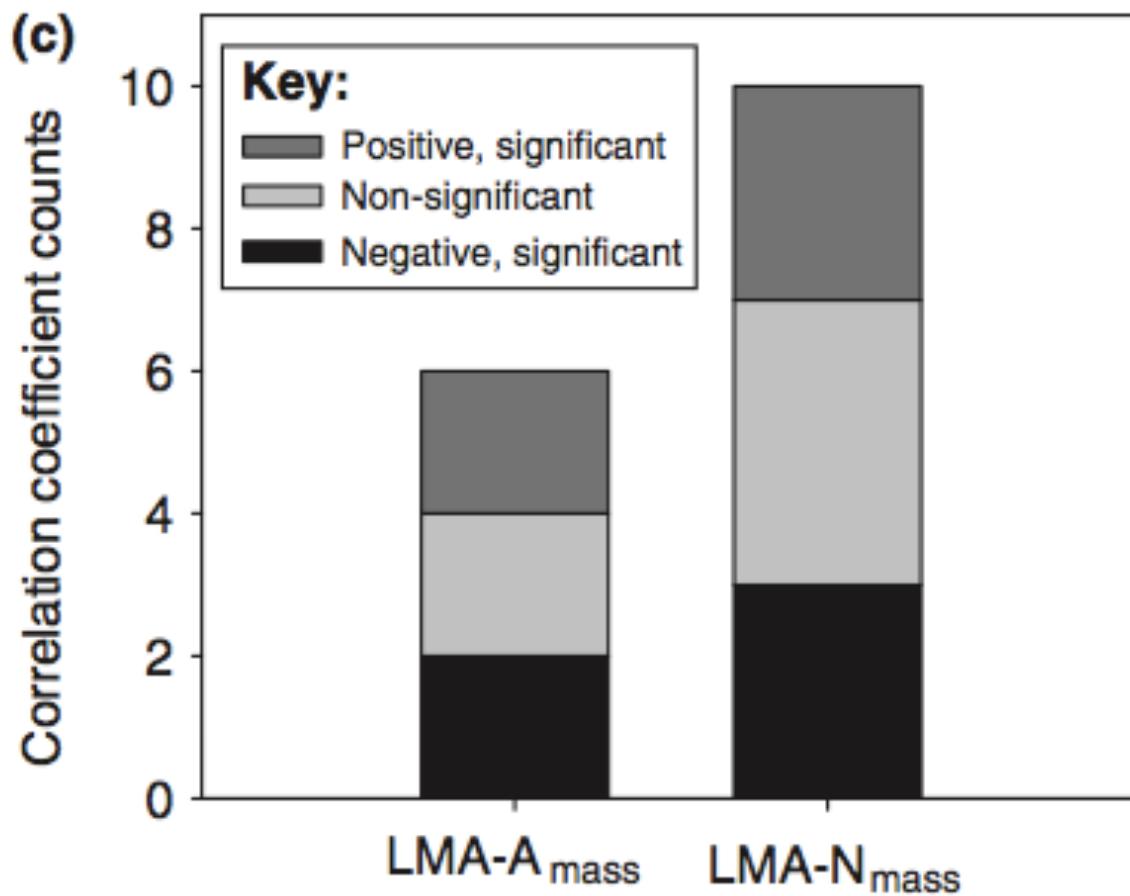
Selection gradients are high and could cause trait response



Leaf traits are heritable



Genetic correlations are highly variable



Critical view

- Proposed artificial selection / trait manipulations are likely very difficult
- Evolutionary perspective does not explain the precise form of observed selection gradients

5. Genetics (Vasseur)

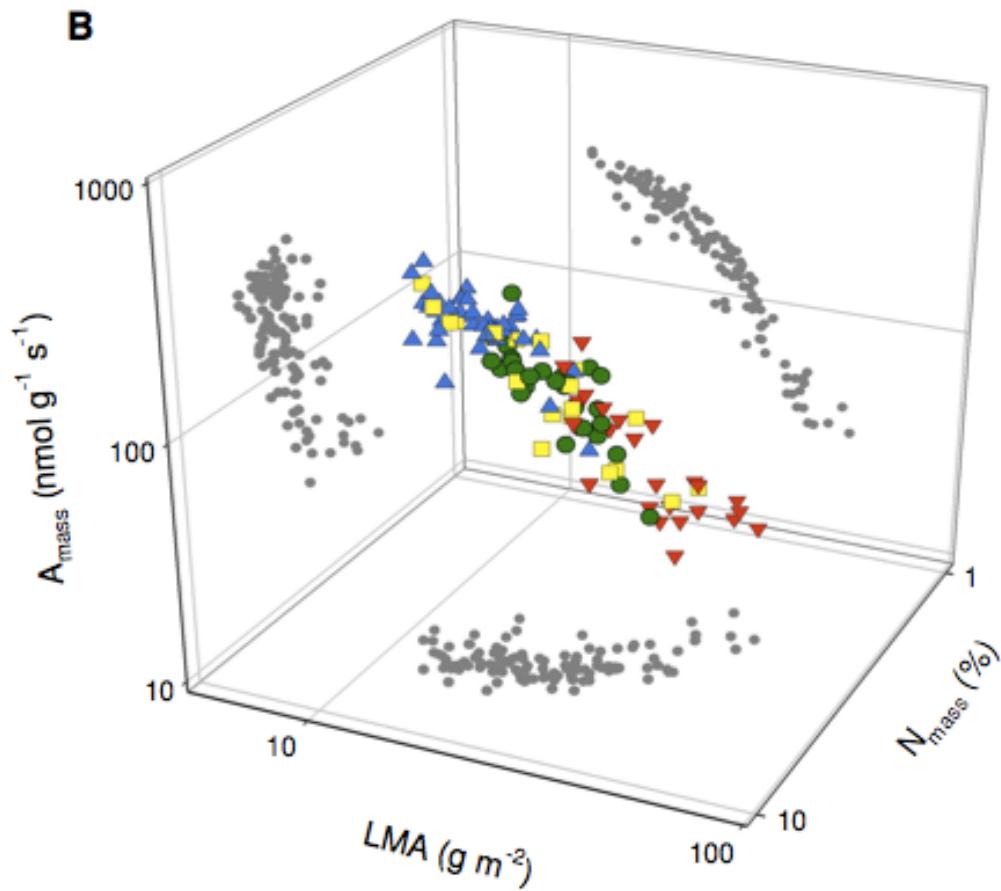


Photo at CNRS (France) – photo courtesy Brian Enquist

Economic traits are heritable

	<i>M</i>	<i>G</i>	θ_q	Age at flowering	<i>A_{mass}</i>	LMA	<i>H²</i>	EDI (%)	FLG (%)
<i>M</i>							0.94	26.8	28.8
<i>G</i>	0.98						0.92	36.6	30.6
θ_q	-0.98	-0.96					0.95	44.2	33.0
Age at flowering	0.96	0.91	-0.97				0.91	38.2	34.6
<i>A_{mass}</i>	-0.92	-0.86	0.94	-0.95			0.90	39.4	29.0
LMA	0.94	0.93	-0.94	0.93	-0.93		0.84	33.7	31.3
<i>N_{mass}</i>	-0.60	-0.53	0.66	-0.67	0.72	-0.66	-	18.6	17.9

New genotypes fall on global leaf economics spectrum axes



Critical view

- Recapitulation of global interspecific relationships within genotypes of one species
- Unclear if there is fitness cost to phenotypes not on tradeoff axis
- Physiological basis of tradeoffs (e.g. effects of multiple genes) remains unclear

Broad questions

- What is the appropriate scale for understanding these trait correlations?
- Does natural selection act on model equations, on model parameters, or both?
- What determines a species' particular combination of traits in a community and in an environment?
- Are leaf trait correlations independent of other parts the plant phenotype?