A bestiary of non-linear functions for growth analysis

C. E. Timothy Paine[1], Toby Marthews[1,2], Deborah Vogt[1], Drew Purves[3], Mark Rees[4], Andy Hector[1], Lindsay Turnbull[1]

[1] Universität Zürich, Switzerland
[2] University of Oxford, UK
[3] Microsoft Research, UK
[4] University of Sheffield, UK

Objectives: Predict growth and associated rates

I am ecologist, not modeller. My desire is to generate ecological inferences.

For example...

Outcomes of competitive interactions

Rates of carbon accumulation

Rationale: Why revisit old topic?

Reviews

Causton, D. & Venus, J. (1981) *The biometry of plant growth.*

Hunt, R. (1982) *Plant growth curves: the functional approach to plant growth analysis*

Heinen, M. (1999) Analytical growth equations and their Genstat 5 equivalents. *Neth. J. Ag. Sci.*

Recent progress in fitting routines

nls (Nonlinear Least Squares)

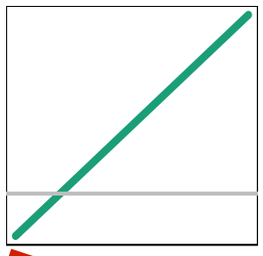
MCMC (Markov Chain Monte Carlo)

Reconsideration of the method of calculating RGR and other derived rates.

Back in the day, only linear, exponential and polynomial forms could be fit in linear model framework.

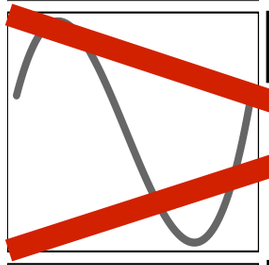
Now, many functions are treatable

Non-asymptotic

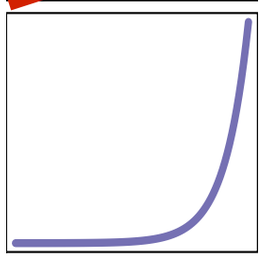


Linear

a

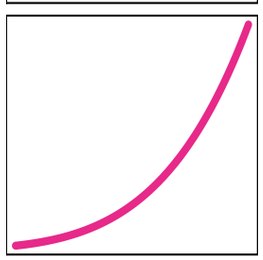


~~Polynomial~~



Exponential

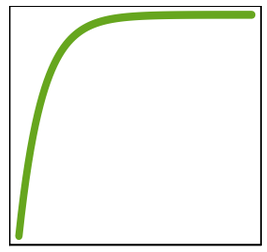
rM



Power-law

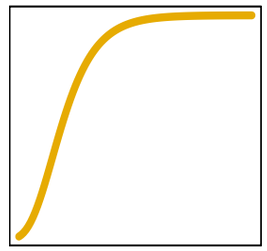
rM^{β}

Asymptotic



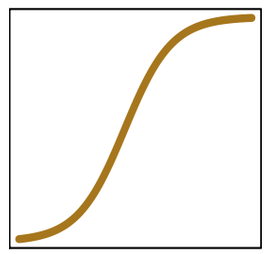
Monomolecular

$r(K - M)$



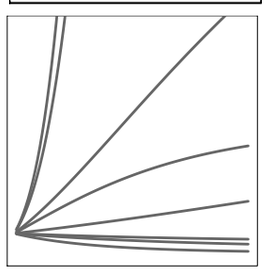
Gompertz

$rM(\ln K - \ln M)$



Logistic

$rM(1 - M/K)$



Von Bertalanffy

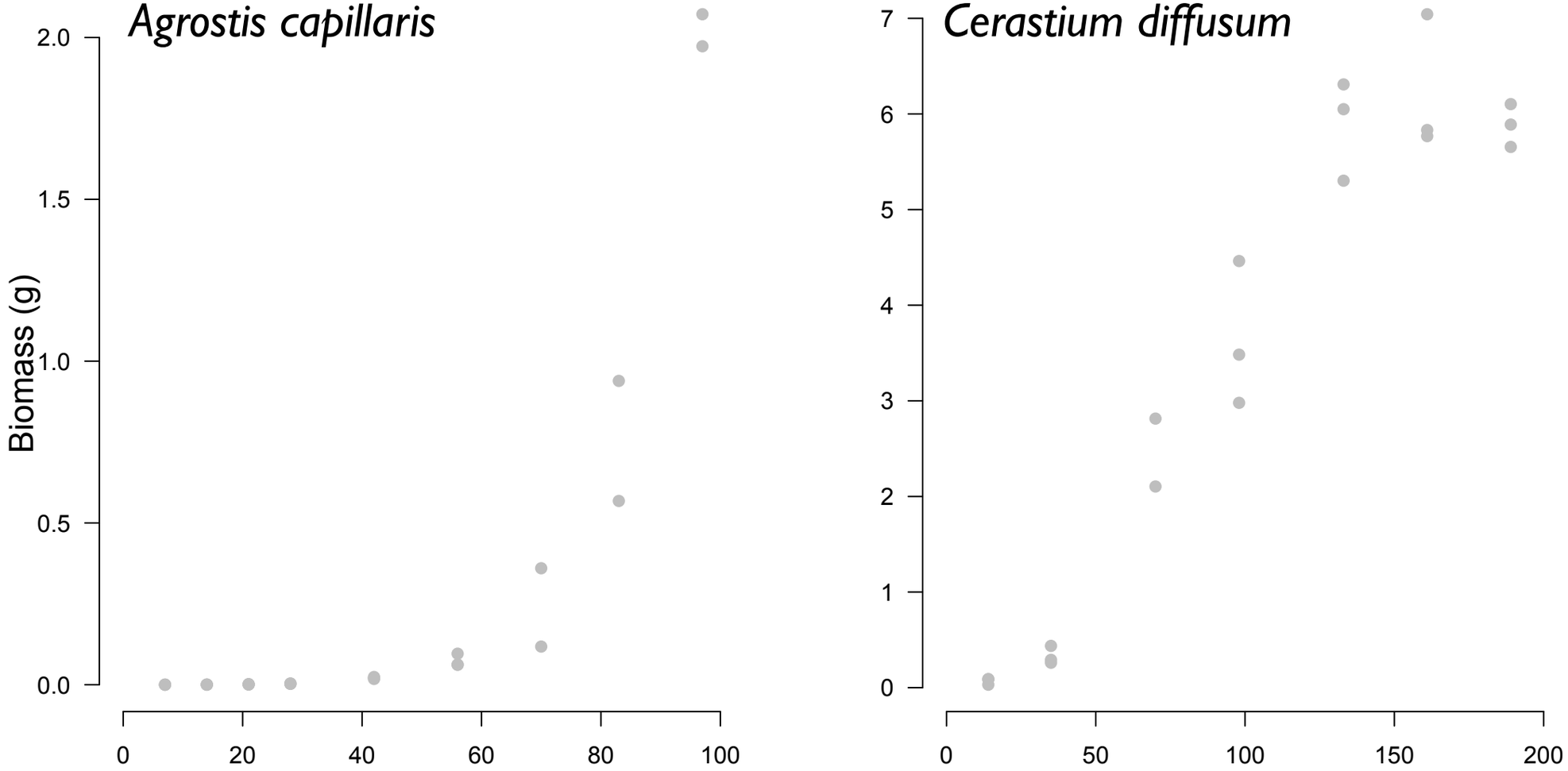
$\eta M^{\beta} - \kappa M$

von Bertalanffy 1957 *Quart Rev. Biol.*

Data for illustration

Agrostis capillaris

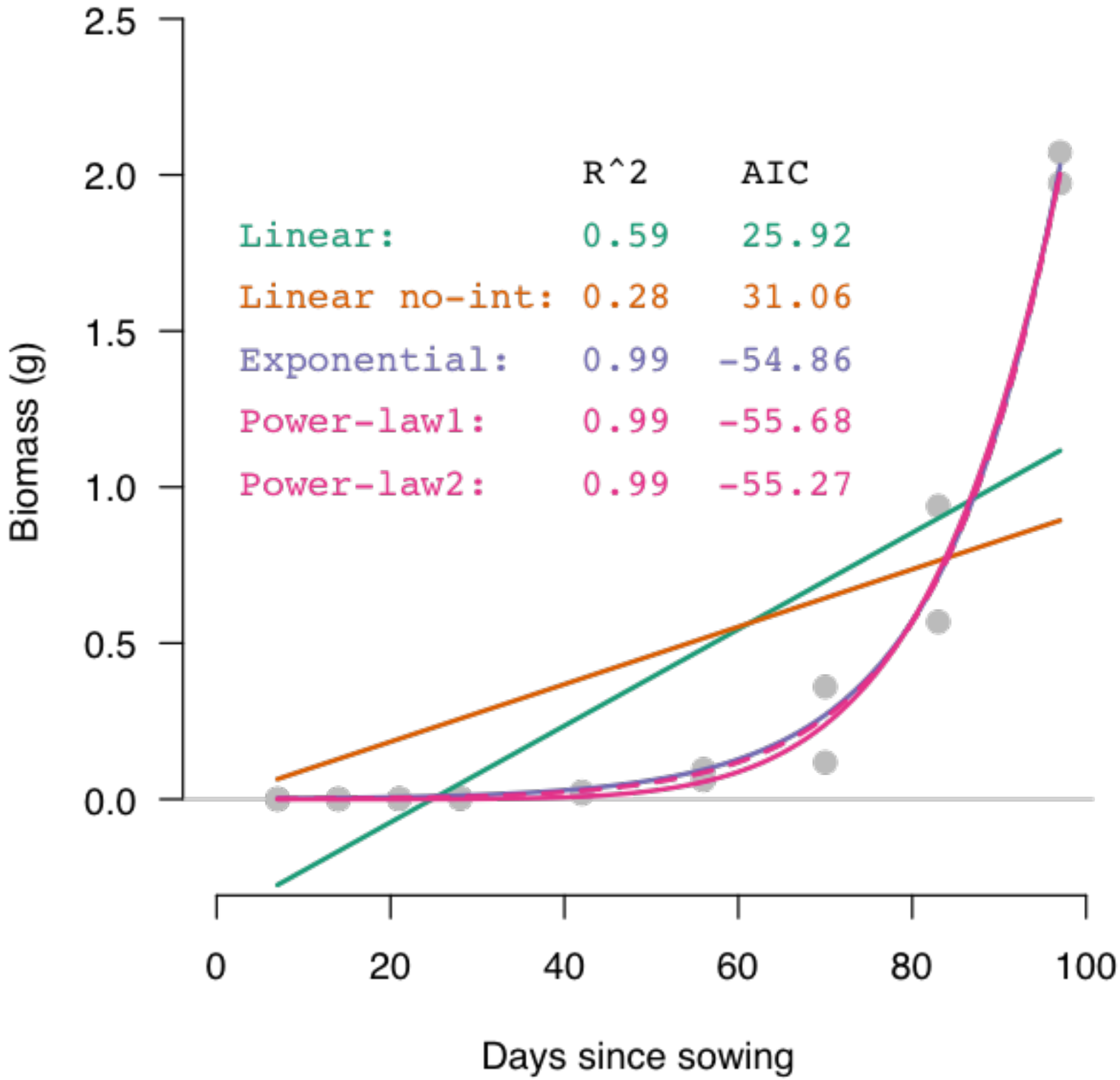
Cerastium diffusum



Hautier et al 2010, *J Ecology*

Turnbull et al 2008, *Ecology*

Non-asymptotic fits

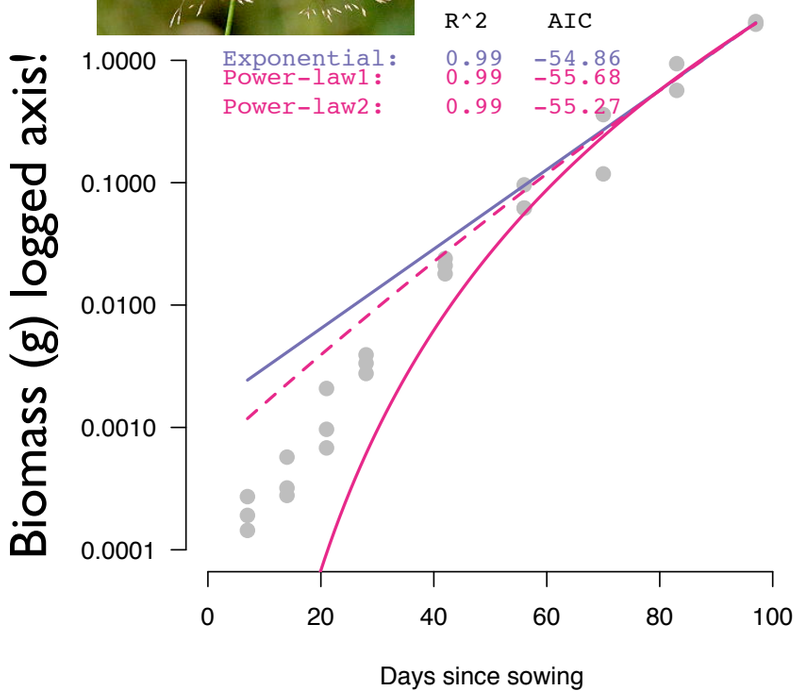


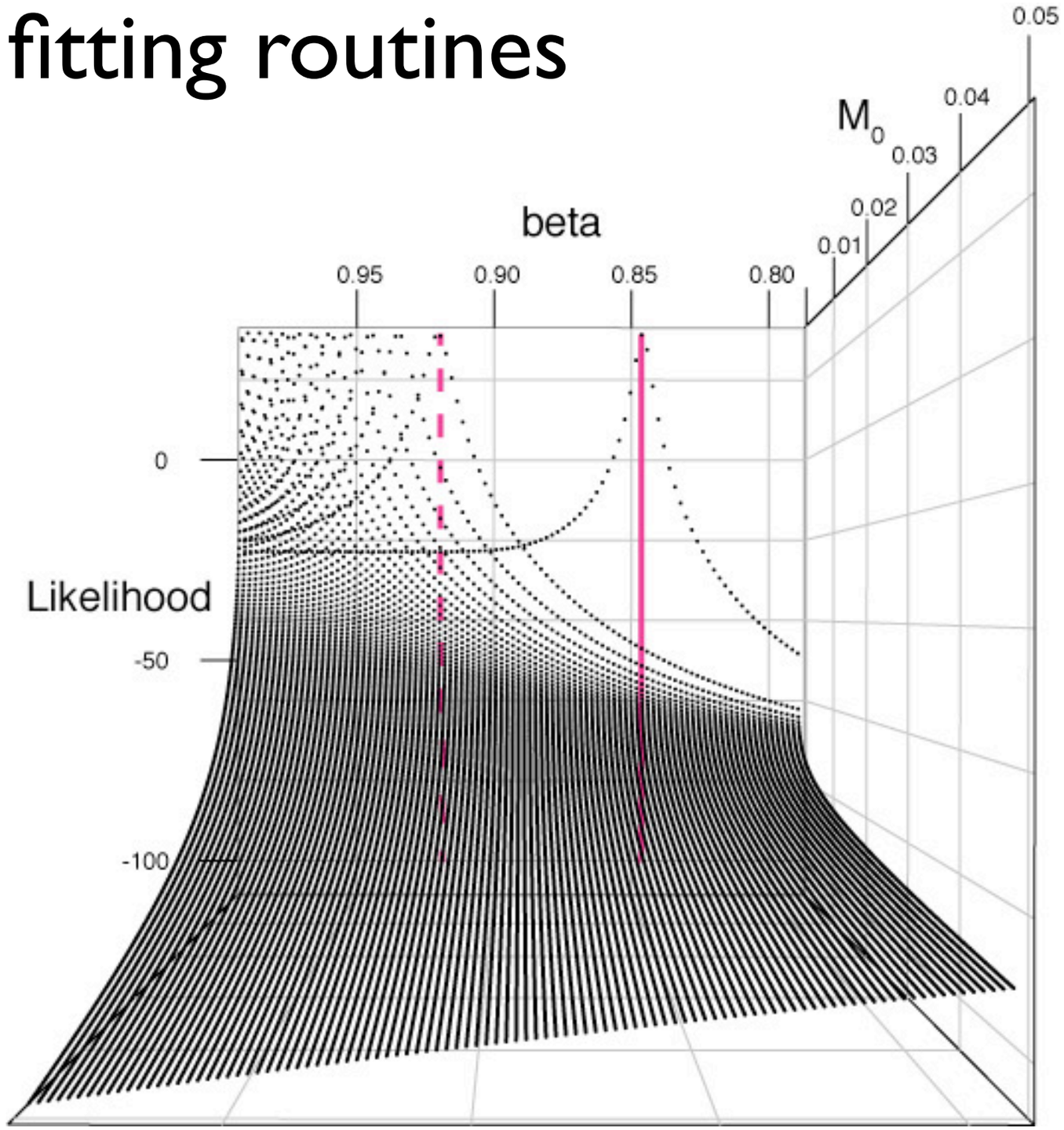
Agrostis capillaris

Here, exponential and power-law ‘tie’,
but power-law is generally preferred because flexible

Non-linear forms can be hard to fit.
Local minima confuse fitting routines

Agrostis capillaris





Solutions:

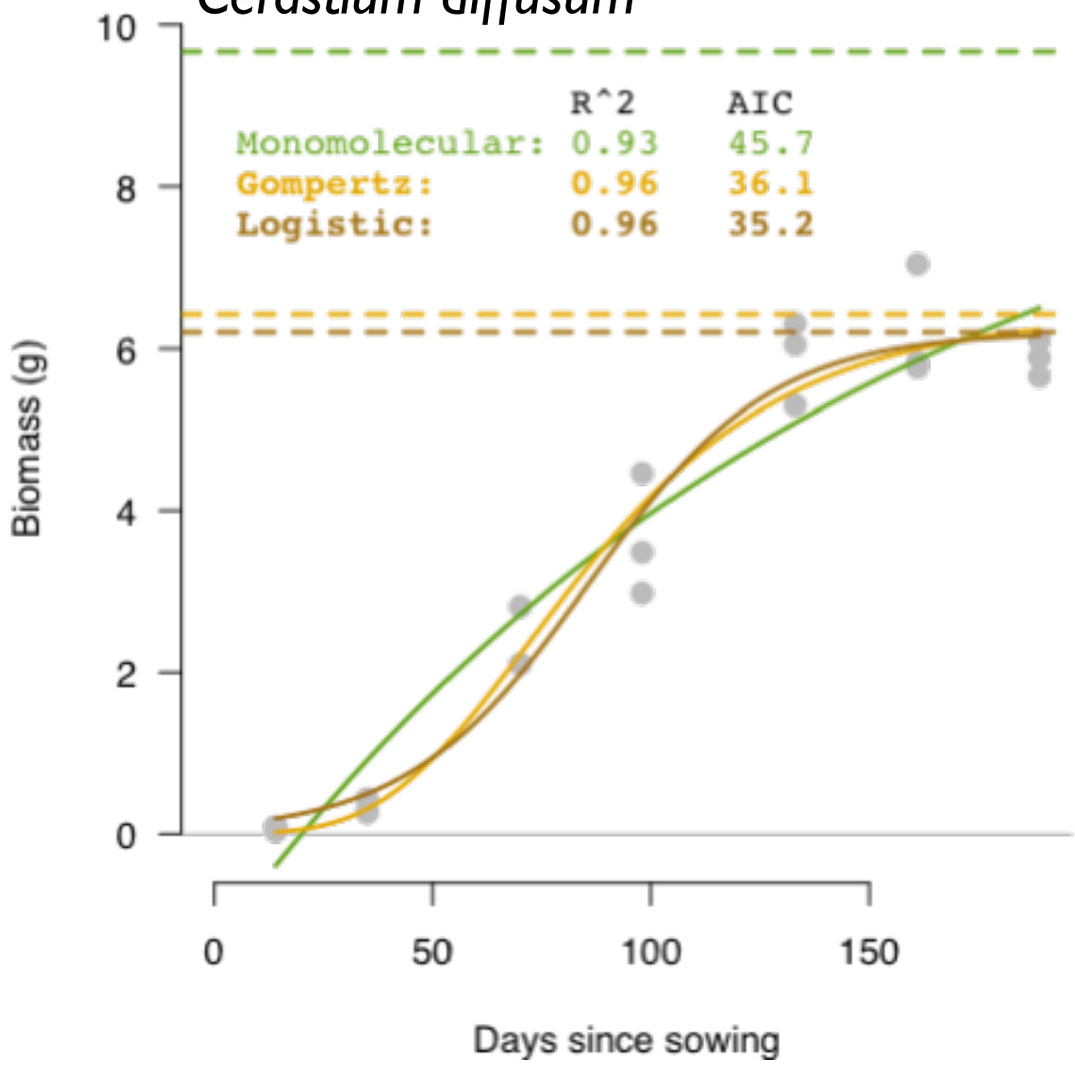
MCMC search

Brute-force search,

Fixing parameter values, other optimization routines

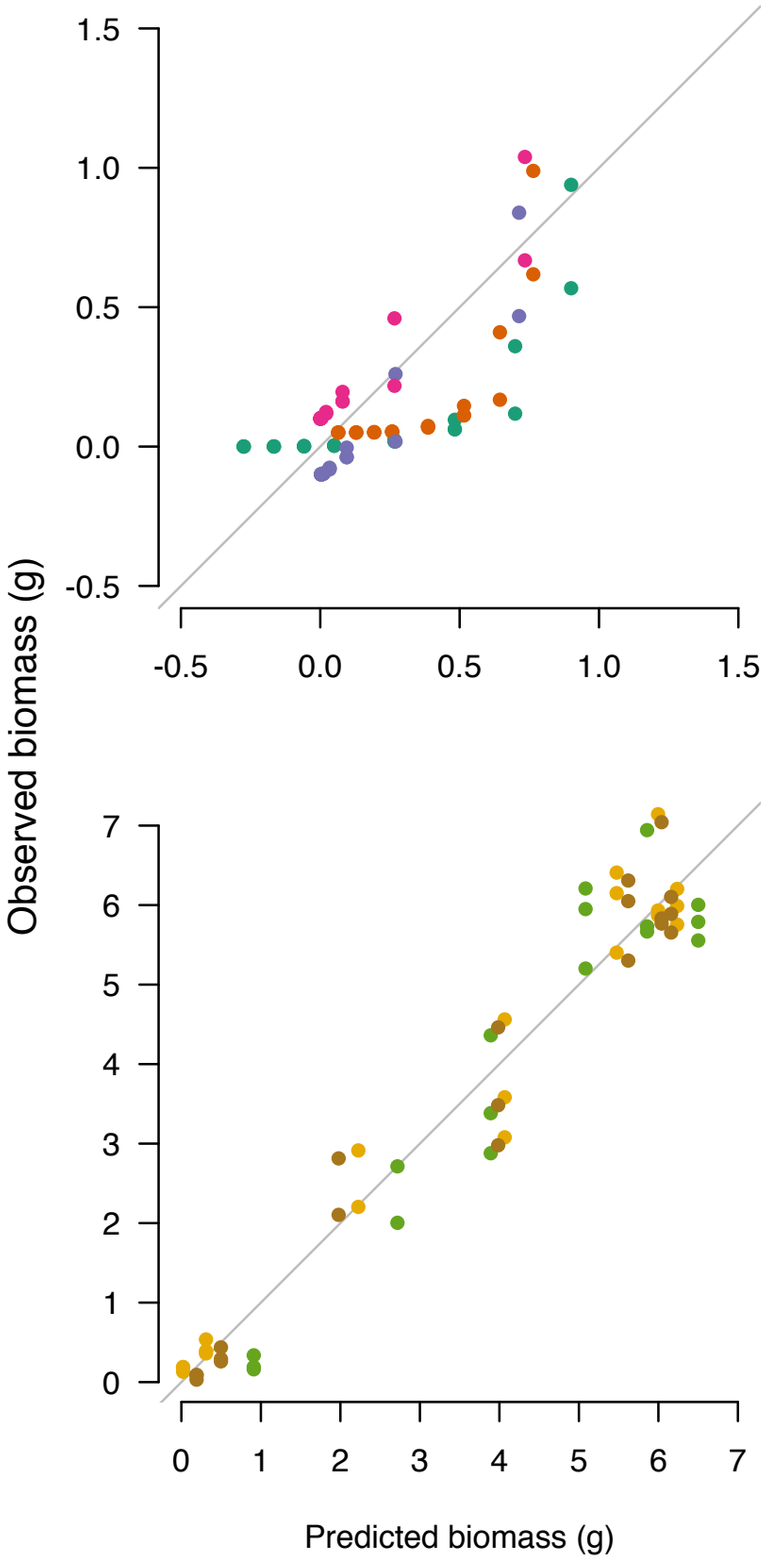
Asymptotic fits

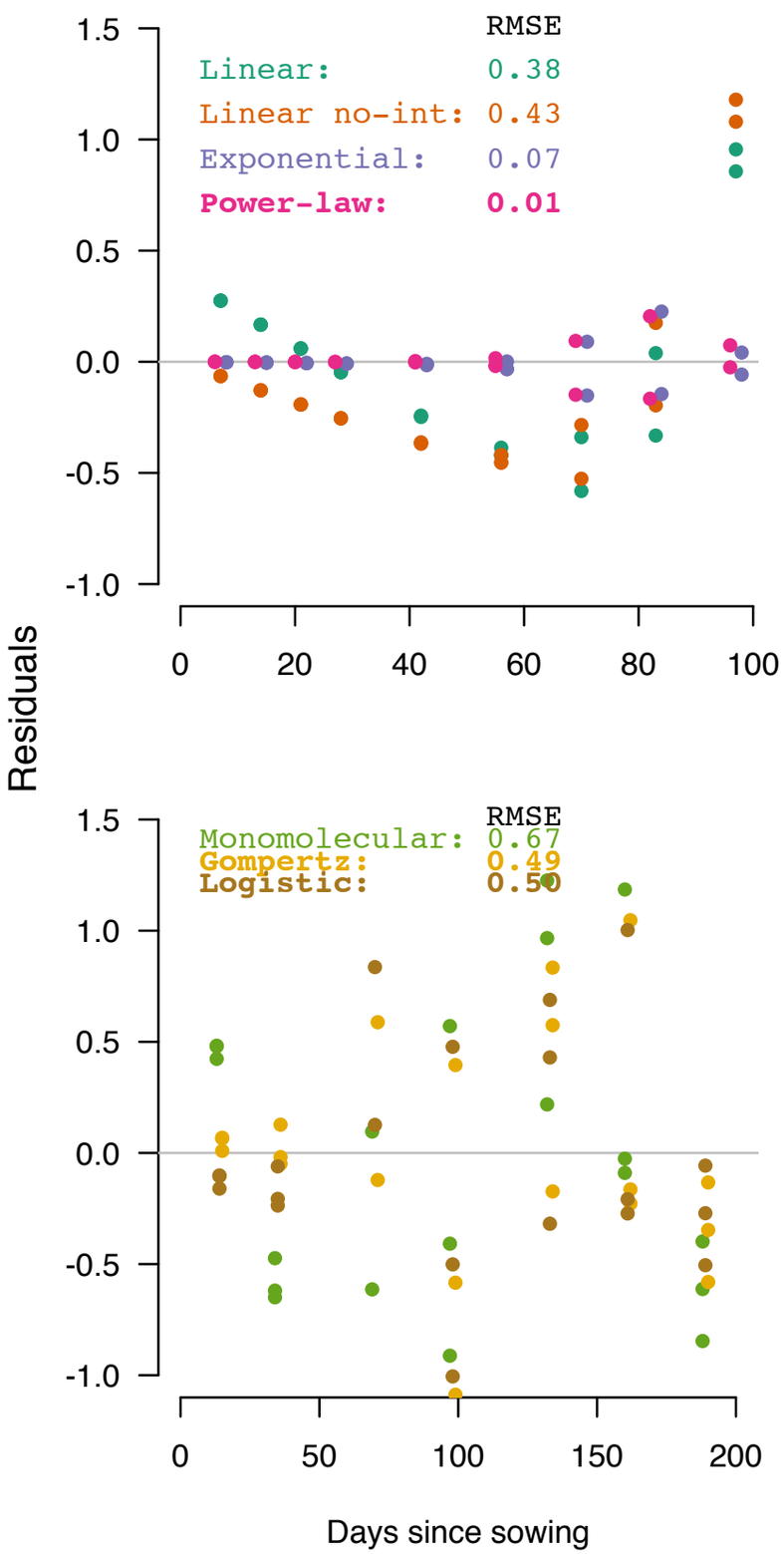
Cerastium diffusum



Here, logistic and Gompertz provide similar fits

Diagnostics





Agrostis capillaris

Cerastium diffusum

Use them!

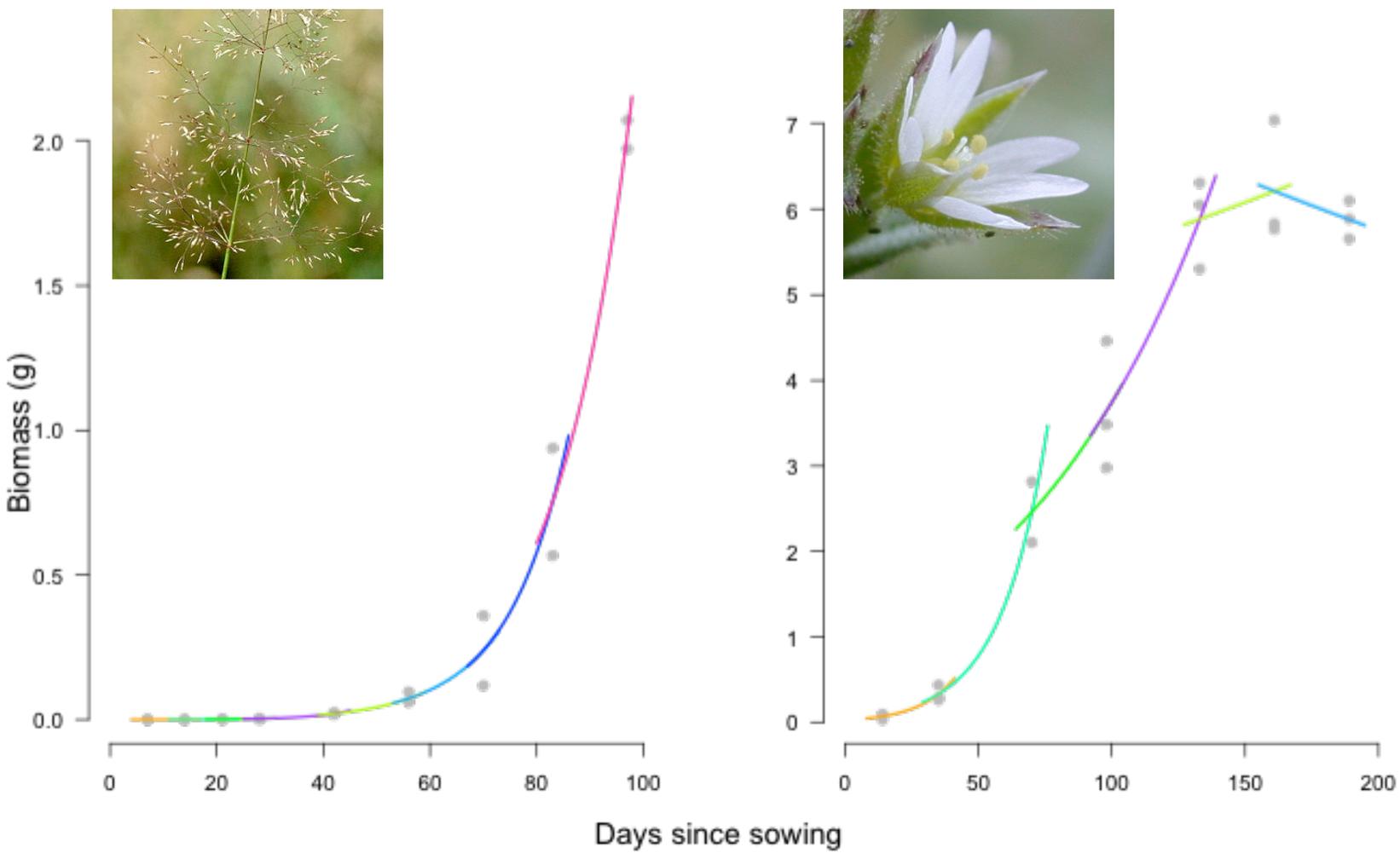
Inferences on relative growth rate (RGR)

Traditionally, $RGR = \frac{\ln(M_{t+1}) - \ln(M_t)}{\Delta t}$

This approach is **invalid** unless growth is perfectly exponential, which is unusual

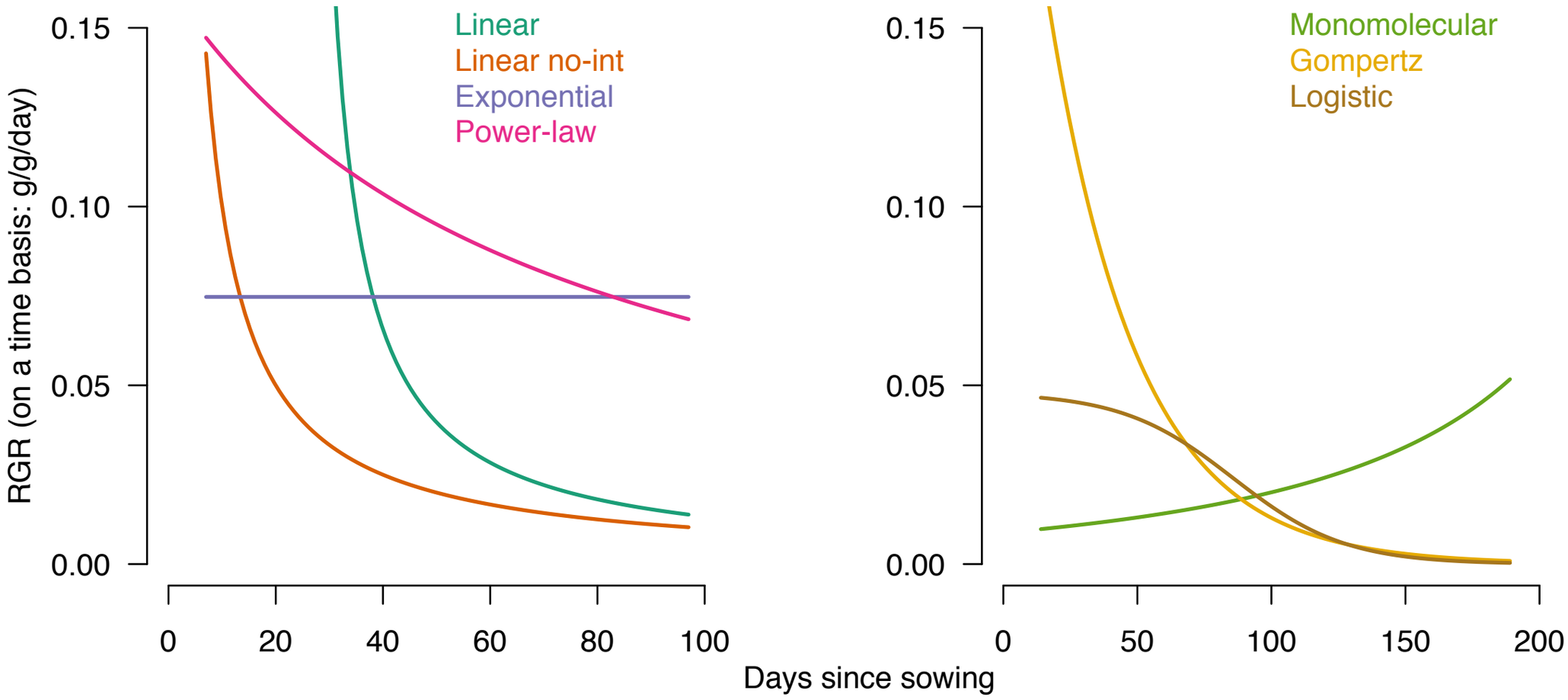
Cannot be extrapolated because no underlying function

Better: Measure size at multiple times, and fit functions



With a function, $RGR = \frac{1}{M}\frac{dM}{dt}$

Unless growth is exponential
(then RGR = r), RGR **varies** with time / mass



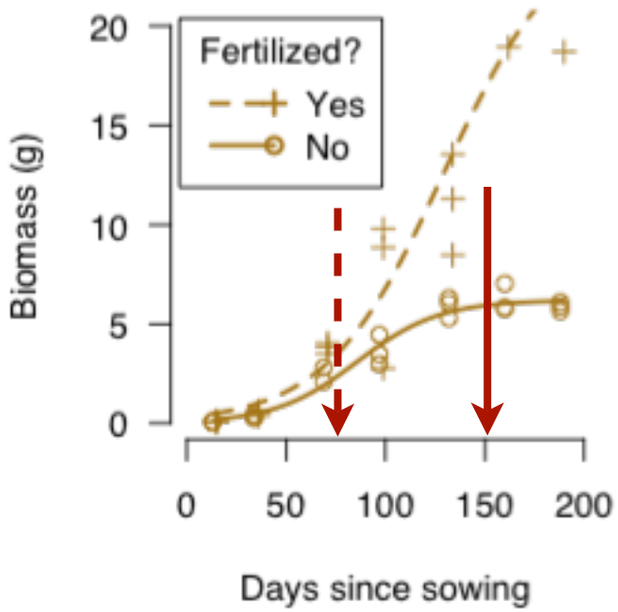
Important, since **growth slows** as non-photosynthetic biomass accumulates

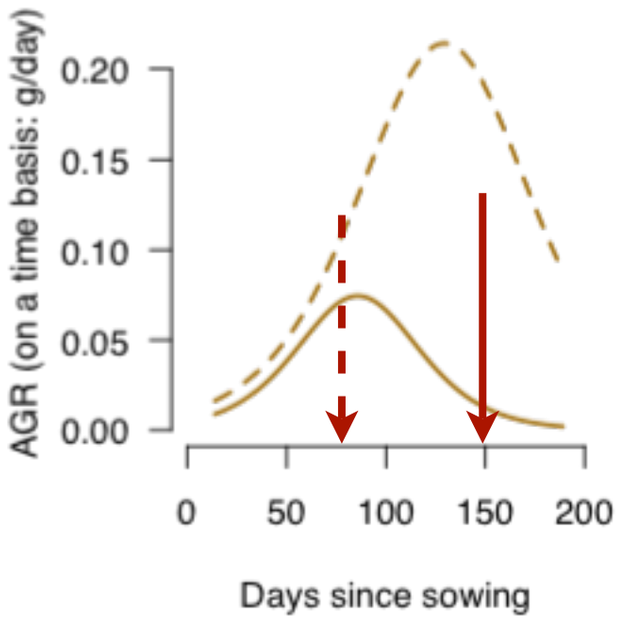
Choice of form affects inferred temporal pattern of RGR

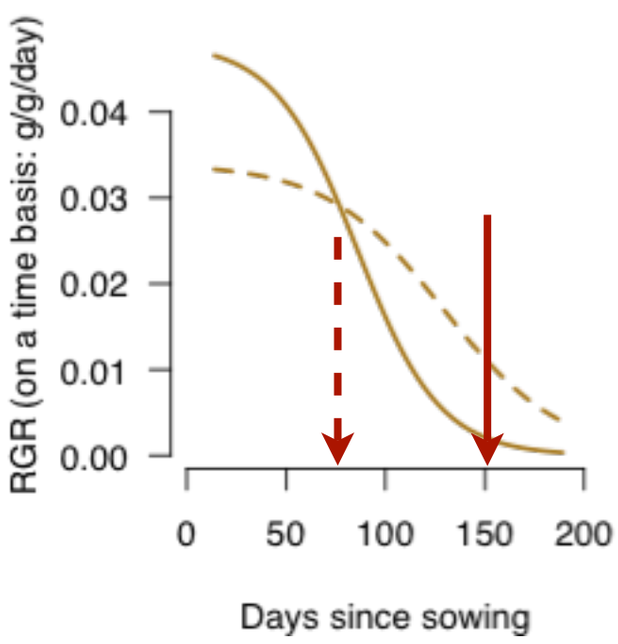
Choice of reference mass or reference time also affects comparisons

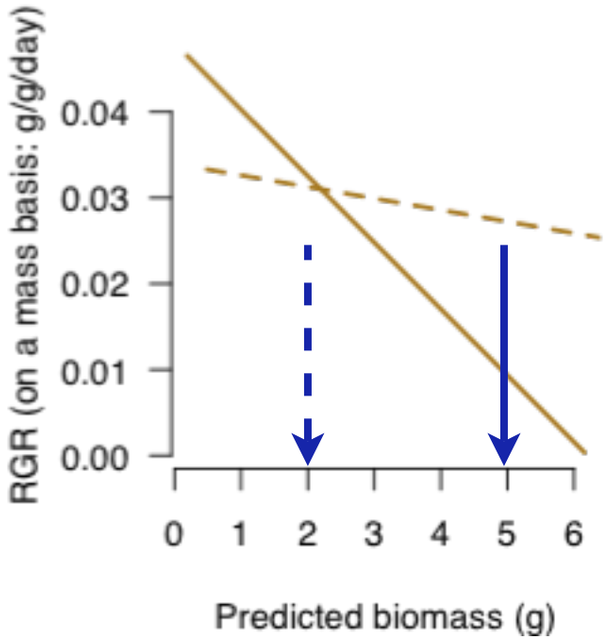
↓ = Fert. matters

⇣ = Or it doesn't









Use
natural history
to choose times/masses for comparison

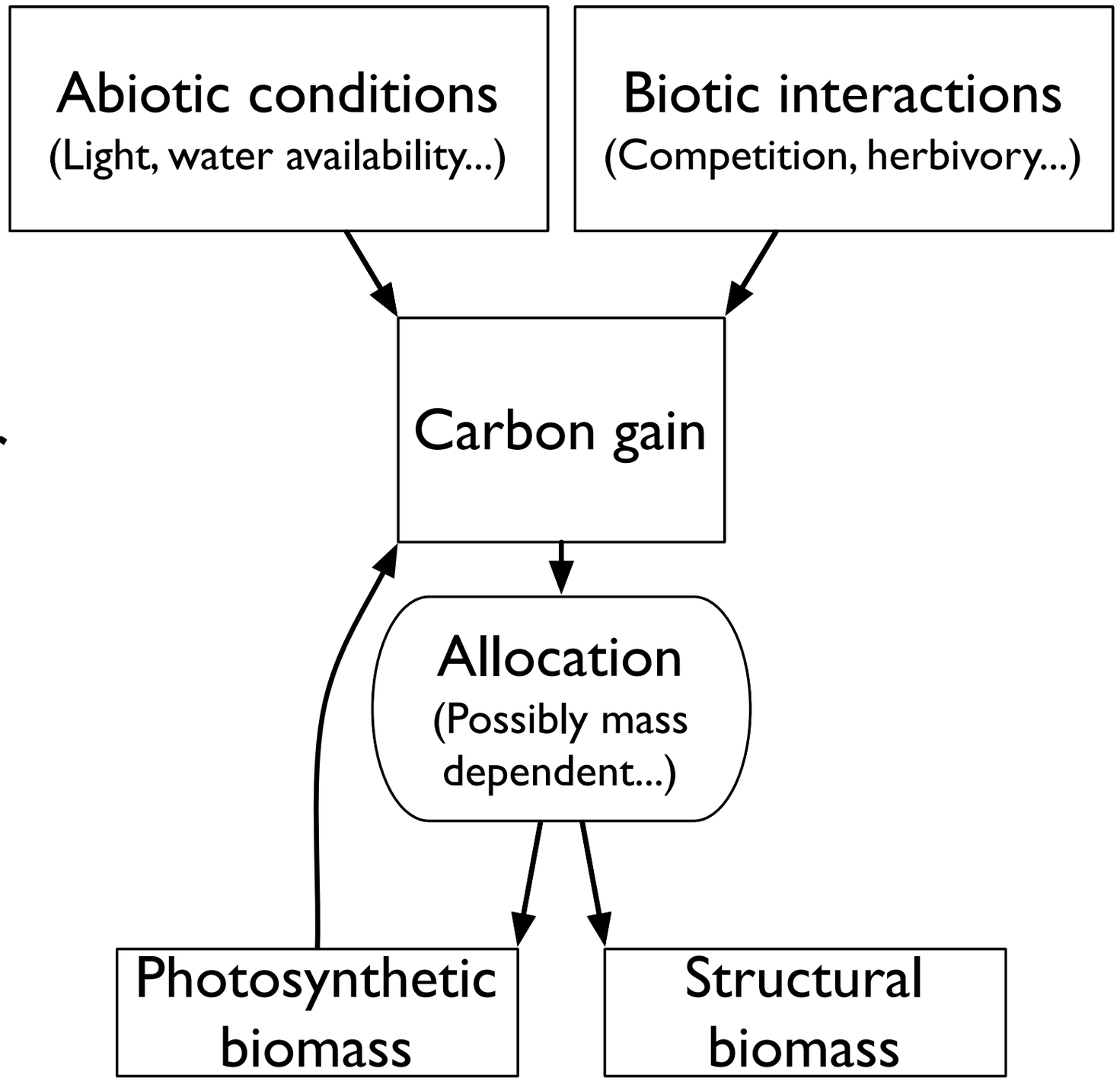
Mechanistic models for plant growth

Bespoke models for hypothesis testing

Incorporate data **from any source**

Requires **MCMC** for parameter estimation

Example:
Turnbull et al 2008 *Ecology*



Recommendations

1. Let **data** and **natural history** of system guide experimental design, data collection, and analysis

2. Measure **few** plants at each of **many** time points

3. Measure **often** when plants are growing **rapidly**

4. Fit **functions** to growth data

5. Prefer **flexible** forms, despite difficulty in fitting parameters

Code, etc available:
tim.paine@ieu.uzh.ch