

*What to do once you've fitted a model
or, What can we do with these models?*

Predict trajectory of biomass through time

Derive absolute and relative growth rates

Correlate parameter estimates or growth rates
with other things, like seed size, or functional
traits

Determine which aspects of growth are most
affected by model parameters

Useful model outputs

Parameter values - eg, asymptotic size, beta, etc

Biomass at particular times

Absolute or relative growth rates

In all cases, must account for uncertainty in parameter estimates!

Inferences on relative growth rate (RGR)

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

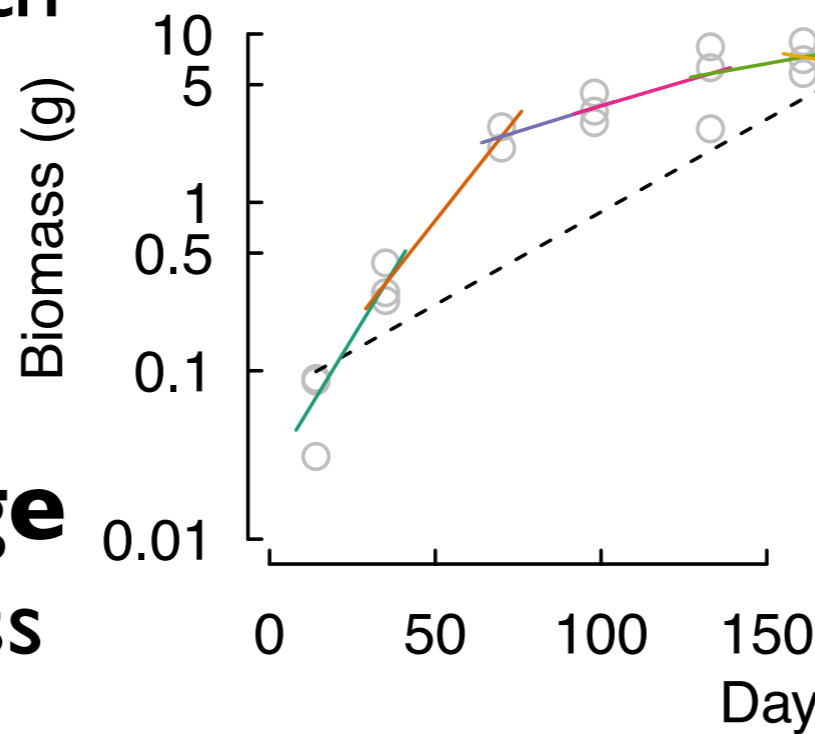
Assumes RGR is constant through time, which it never is.

Thus, this approach is **invalid** unless growth is perfectly exponential, which is unusual

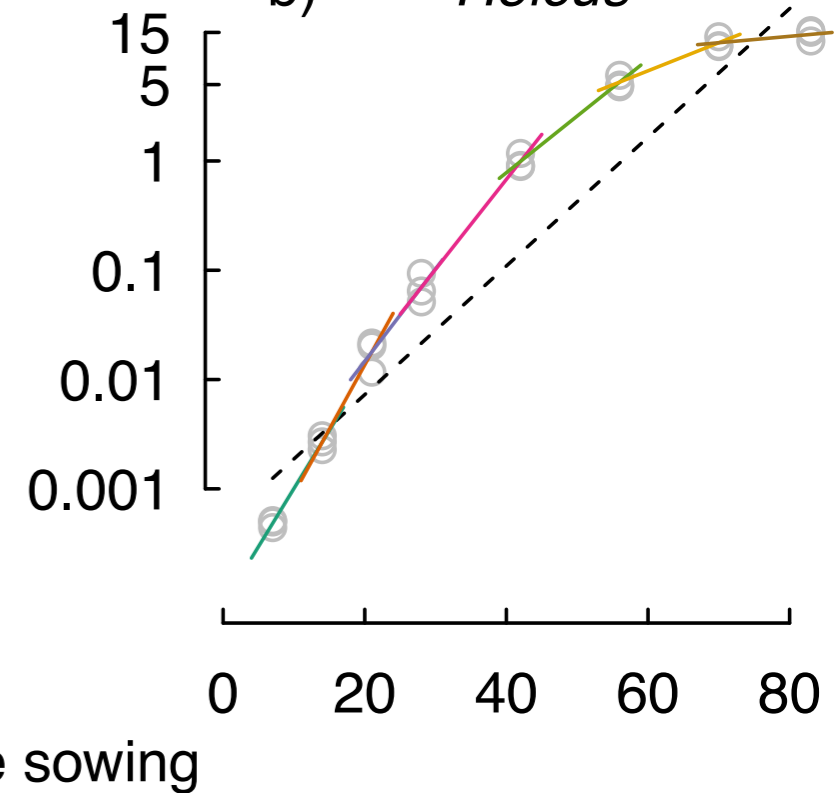
Growth rates **change** with time and biomass



a) *Cerastium*



b) *Holcus*



Function-derived growth rates are **better**

How to use them?

Measure sizes at multiple times

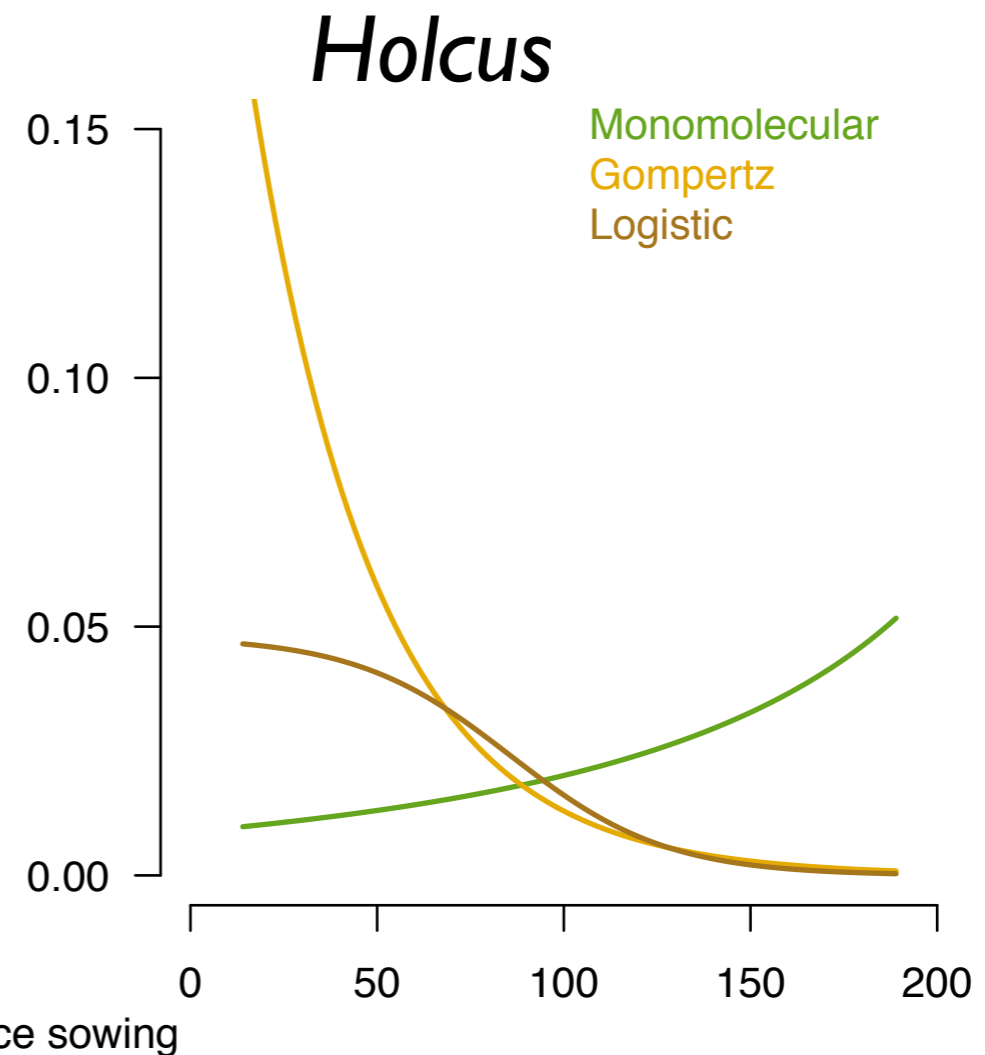
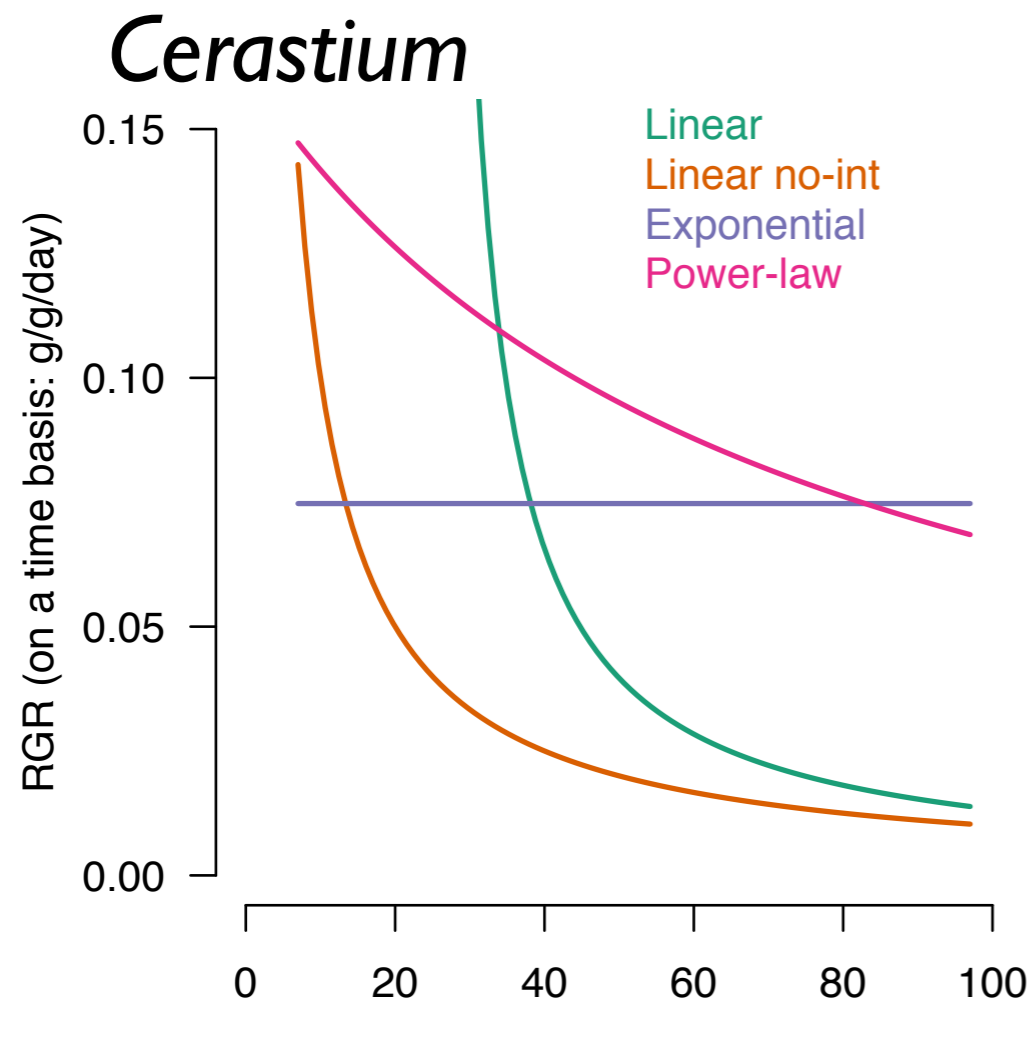
Fit a function

Take derivative of that function to obtain growth rates

Absolute growth rate: dM/dt

Relative growth rate: $1/M * dM/dt$

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



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

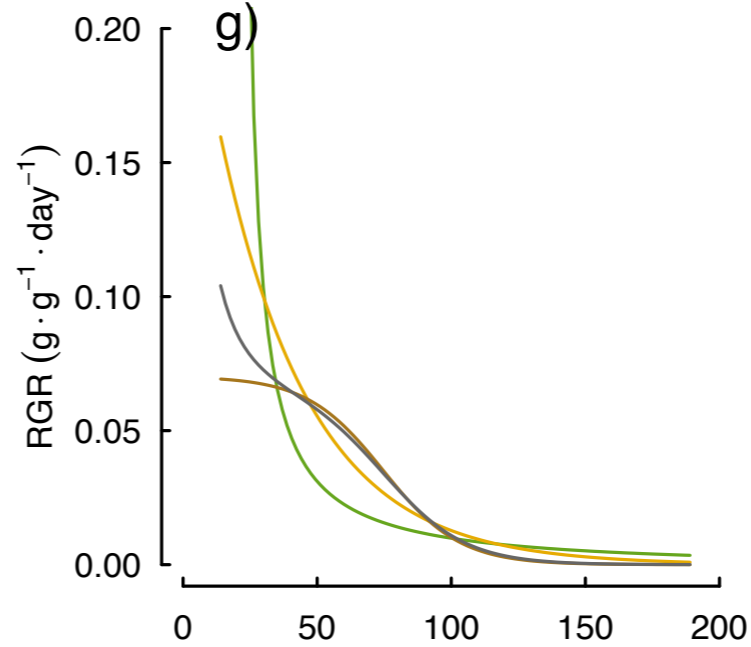
Choice of form affects the temporal pattern of RGR that you infer

RGR

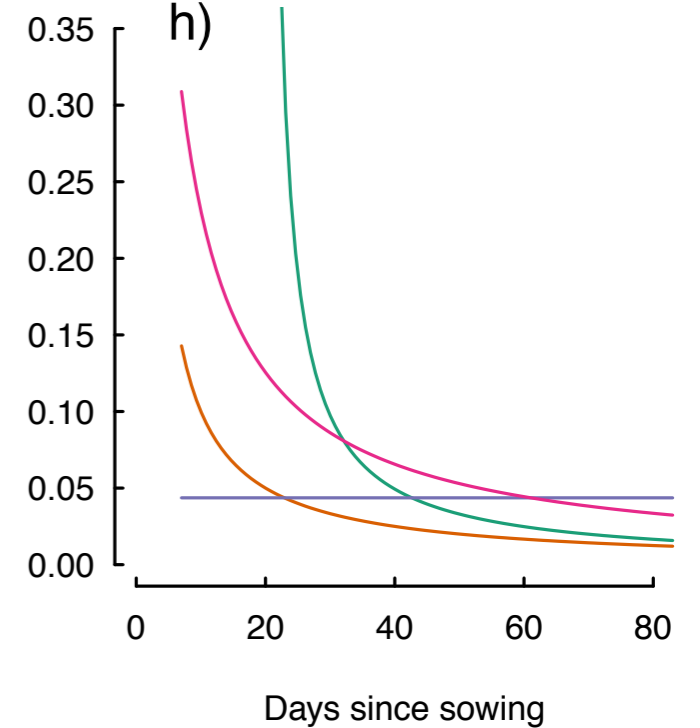
Deriving rates from functions also affects the pattern of RGR vs biomass - which differs from the temporal pattern, unless biomass and time are linearly related (which they're not)

Time basis

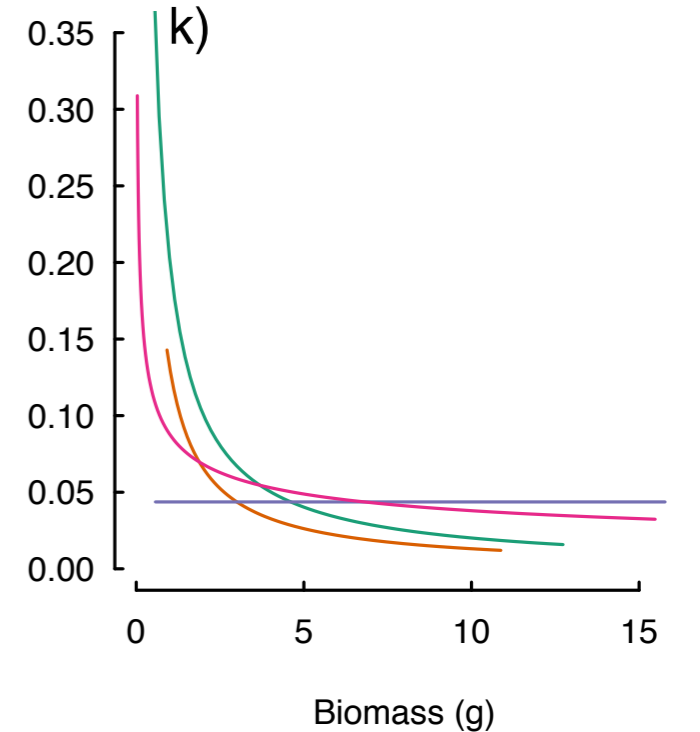
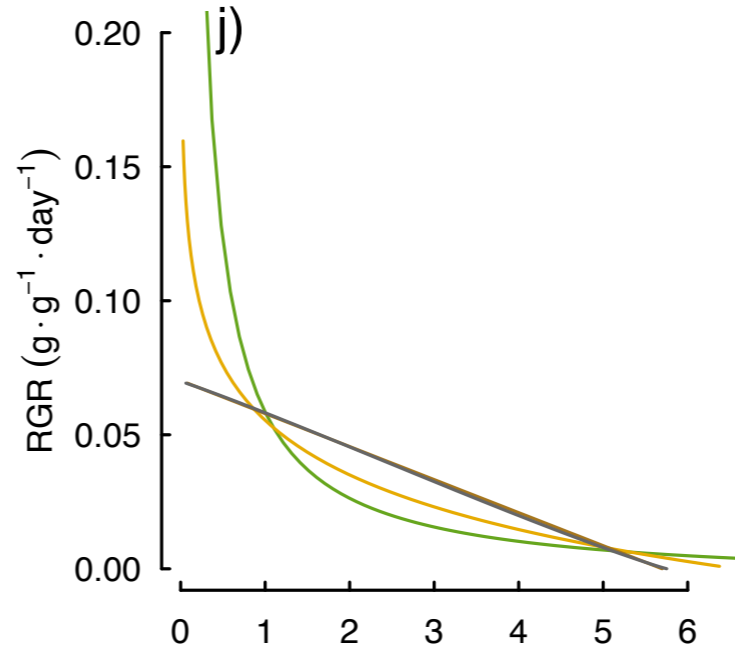
Cerastium



Holcus



Biomass basis



Calculation of AGR

Name	Model dM/dt	Biomass M time basis	AGR dM/dt time basis
Linear	a	$M_0 + at$	a
Exponential	rM	$M_0 e^{rt}$	$rM_0 e^{rt}$
Power-law	rM^β	$(M_0^{1-\beta} + rt(1-\beta))^{1/(1-\beta)}$	$r(M_0^{1-\beta} + rt(1-\beta))^{\beta/(1-\beta)}$
Monomolecular	$r(K - M)$	$K - e^{-rt}(K - M_0)$	$re^{-rt}(K - M_0)$
Logistic	$rM\left(1 - \frac{M}{K}\right)$	$\frac{M_0 K}{M_0 + (K - M_0)e^{-rt}}$	$\frac{rM_0 K e^{-rt}(K - M_0)}{(M_0 + e^{-rt}(K - M_0))^2}$
Four-parameter logistic	$rM\left(1 - \left(\frac{M}{K}\right)^{1/x_{mid}}\right)$	$M_0 + \frac{K - M_0}{1 + e^{x_{mid} - t/r}}$	$\frac{(K - M_0)e^{x_{mid} - t/r}}{r(1 + e^{x_{mid} - t/r})^2}$
Gompertz	$rM\left(\ln \frac{K}{M}\right)$	$K\left(\frac{M_0}{K}\right)^{e^{-rt}}$	$rK e^{-rt} \left(\frac{M_0}{K}\right)^{e^{-rt}} \ln \frac{K}{M_0}$

Looks ugly, but any AGR can be calculated by substitution, once solution to differential equation is known

Calculation of RGR

Name	Model dM/dt	RGR(dM/dt)/ M time basis	RGR (dM/dt)/ M mass basis
Linear	a	$\frac{a}{M_0 + at}$	$\frac{a}{M}$
Exponential	rM	r	r
Power-law	rM^β	$r(M_0^{1-\beta} + rt(1-\beta))^{-1}$	$rM^{\beta-1}$
Monomolecular	$r(K - M)$	$\frac{r(K - M_0)}{M_0 + K(e^{rt} - 1)}$	$\frac{r(K - M)}{M}$
Logistic	$rM\left(1 - \frac{M}{K}\right)$	$\frac{re^{-rt}(K - M_0)}{M_0 + e^{-rt}(K - M_0)}$	$r\left(1 - \frac{M}{K}\right)$
Four-parameter logistic	$rM\left(1 - \left(\frac{M}{K}\right)^{1/x_{mid}}\right)$	$\frac{(K - M_0)e^{x_{mid} - t/r}}{r(1 + e^{x_{mid} - t/r})^2} / M_0 + \frac{K - M_0}{1 + e^{x_{mid} - t/r}}$	$r\left(1 - \left(\frac{M}{K}\right)^{1/x_{mid}}\right)$
Gompertz	$rM\left(\ln \frac{K}{M}\right)$	$re^{-rt} \ln \frac{K}{M_0}$	$r \ln \frac{K}{M}$

RGR on a biomass basis is often cleaner to deal with, as well as often being more appropriate.

RGR on a biomass basis

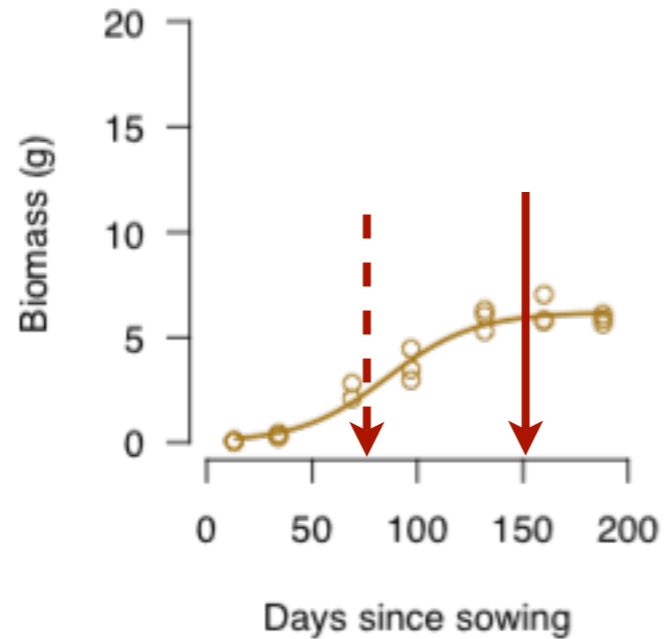
Often the more appropriate way to compare RGR among groups

Makes RGR independent of M_0

Compare groups at a certain reference mass, rather than a reference time.

Choice of reference mass or reference time also affects comparisons

↓ = Fert. matters
- - - = Or it doesn't



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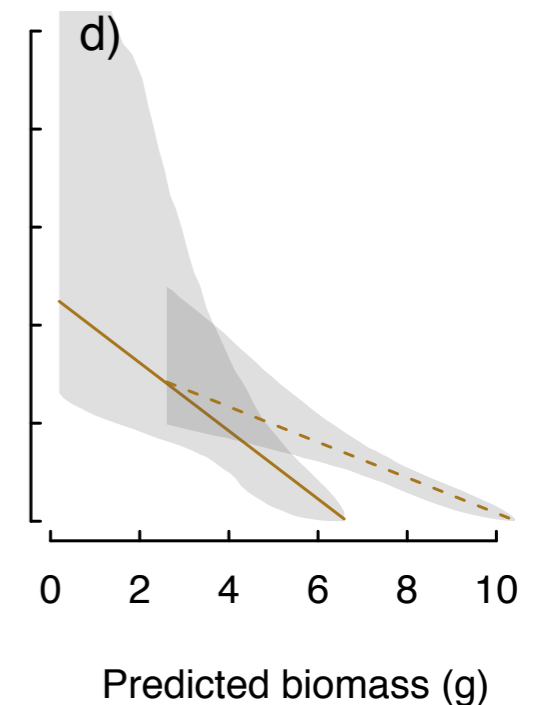
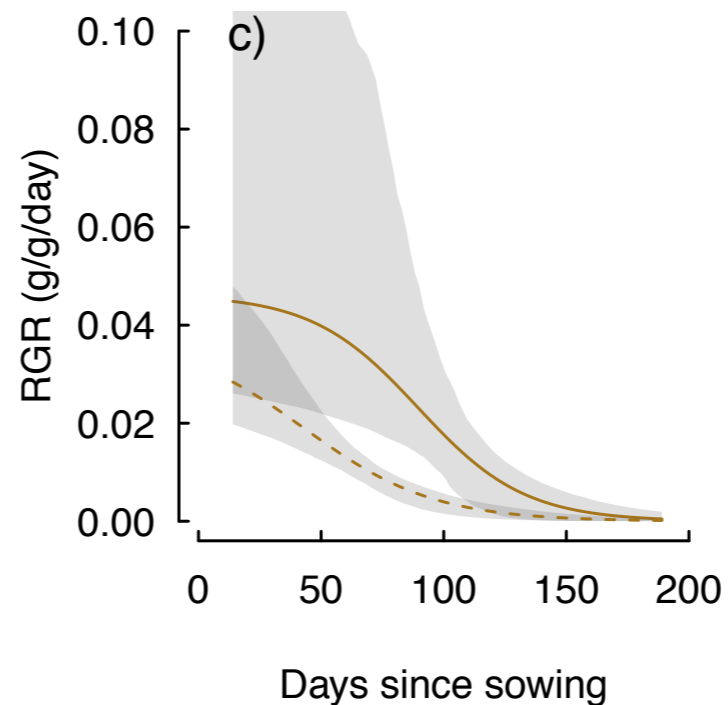
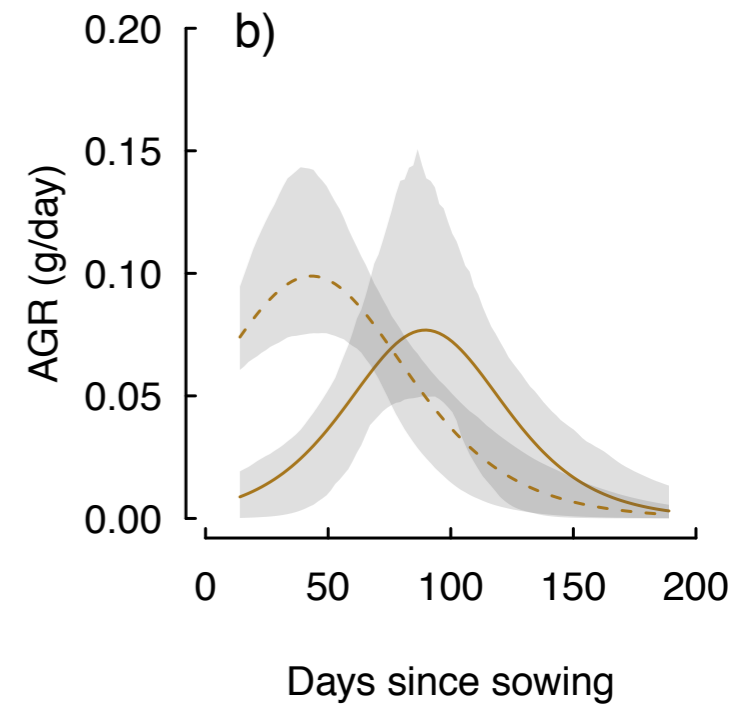
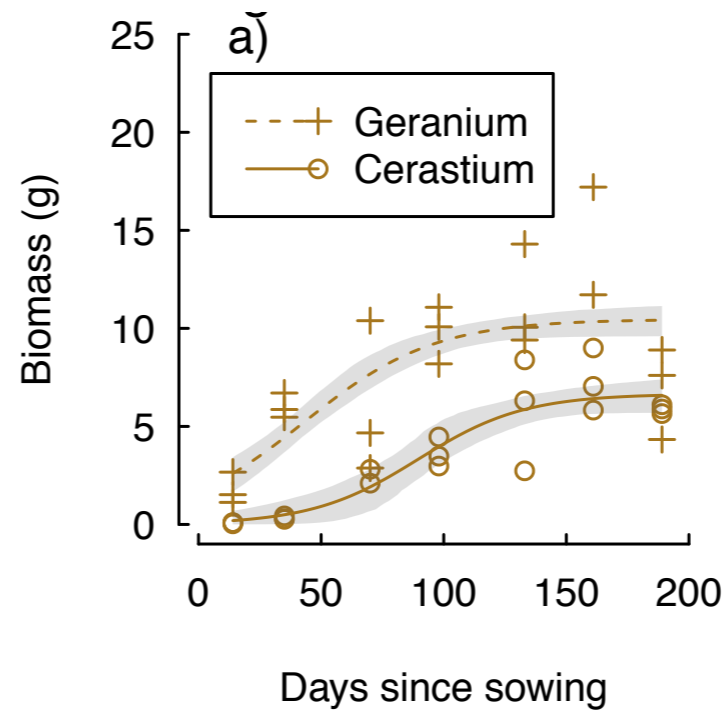
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Use **natural history** to choose times/masses for comparison

Propagation of uncertainty

We estimate parameter values. We do not know them exactly.

That uncertainty needs to be dealt with when making inferences on growth rates



Propagation of uncertainty- Population Prediction Intervals

General approach:

Obtain means and variance-covariance matrix for parameter estimates for each group of interest (here, two species).

Draw ~ 1000 random deviates from the multivariate normal distribution defined by those means & var-cov matrix.

Use those deviates to calculate 1000 RGR's, using the appropriate function. Take the 0.025th and 0.975th percentiles of the distribution of RGRs at every biomass (or time)

