Towards a universal model for ecosystem–atmosphere carbon and water exchanges

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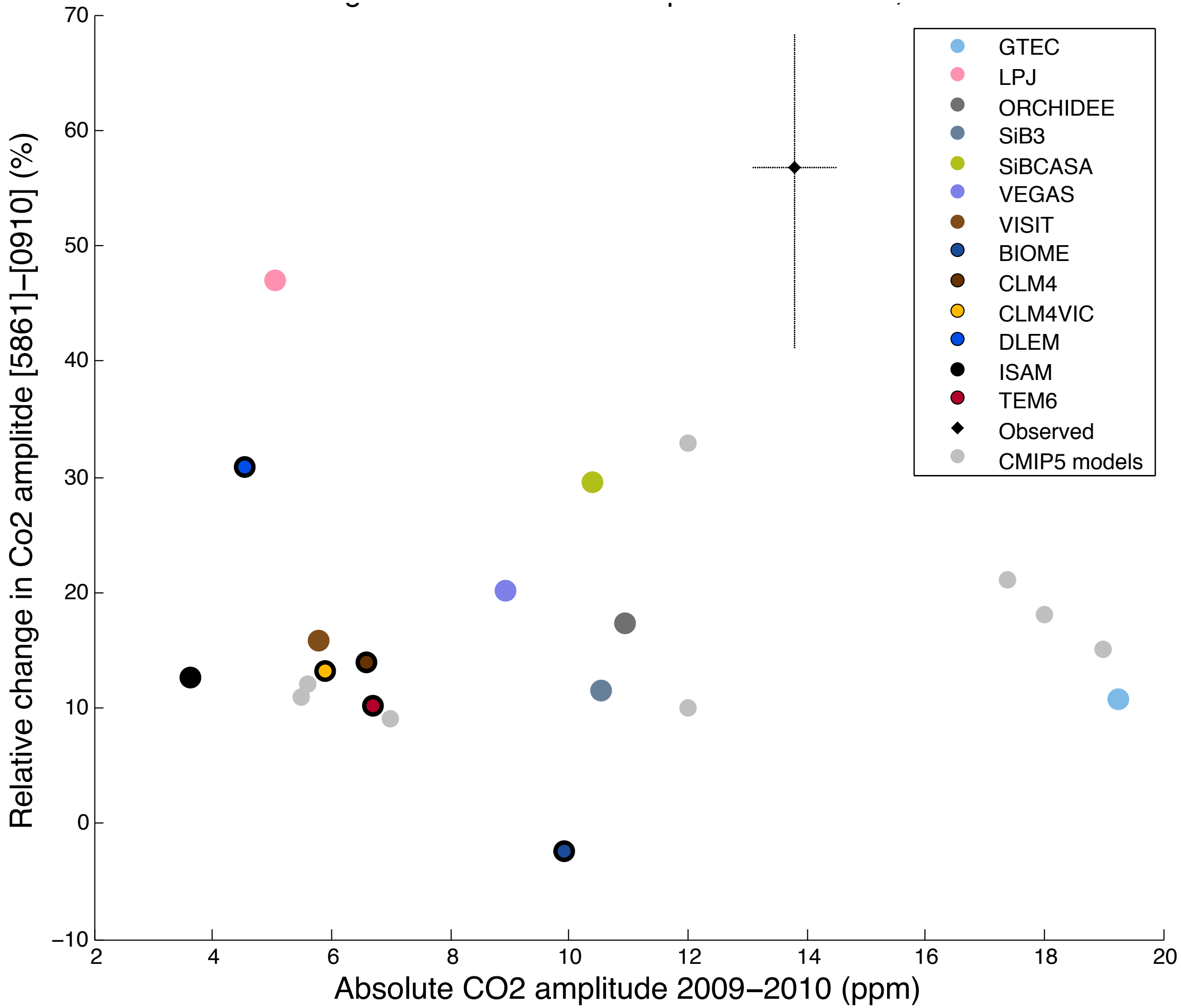
CO_2 seasonal cycle: *models differ, none are right*



Graven et al. (2013) *Science*

R Thomas *et al.* (in revision) *GRL*

Why do we need a universal model?

- Current models have too many parameters, and *still* fail key benchmark tests
- New theory and observations on plants and ecosystems support a different model structure:

  fewer (not more!) PFTs

  fewer parameters

  universal principles
- Simpler models embodying clear hypotheses are more useful for science and prediction

Evolutionary optimality: a basis for theory in ecosystem science

- The “missing law” of biology in Earth System models
- Natural selection is ubiquitous and *extremely* effective

  “Nothing in biology makes any sense except in the light of evolution” – T. Dobzhansky

- Explicit hypotheses can be quantitatively tested

Acclimation: bridging time scales

- Variation of parameters over days, weeks and months
- Variation of parameters across environments
- Short-term response ≠ longer-term response (fundamental, and generally ignored)
    - *example: plant respiration – almost flat response to temperature*
    - *may be the cause of the seasonal cycle problem?*
    - *also applies to photosynthesis*

What acclimation **is**

- Optimization of a phenotypically plastic trait

What acclimation is **not**

- An effect that *goes away* (cf. "downregulation" in response to enhanced CO_2: V_{cmax} declines, A_{net} increases ...)
- An idiosyncratic effect, making modelling even more complex
  - ➢ *it makes modelling **simpler,** by predicting universal relationships!*

Predictability of the c_i:c_a ratio (χ)

The "exchange rate" between CO_2 and water

- Least-cost hypothesis: minimize $a(E/A) + b(V_{cmax}/A)$
- This results in:

$$\chi_{opt} = \Gamma^*/c_a + (1 - \Gamma^*/c_a).\ \xi/(\xi + \sqrt{D})$$

where:

$$\xi = \sqrt{[b(K + \Gamma^*)/1.6a]}$$

$$K = K_C\,(1 + O/K_O)$$

$$a = r_s h^2 \rho_s \eta / 2(\Delta\psi) k_s \rho_w$$

$$b = \text{constant}$$

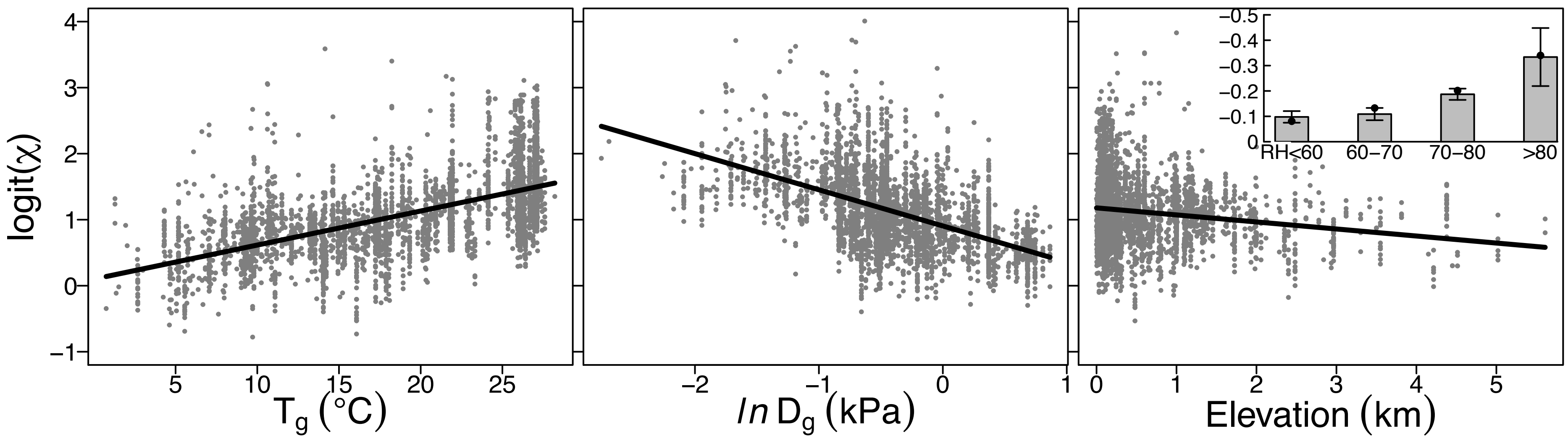
H Wang *et al. Nature Plants* (in revision)
bioRxiv http://dx.doi.org/10.1101/040246

ln $\chi/(1-\chi)$ *versus* environmental predictors (from global $\delta^{13}C$ data: > 3500 measurements)

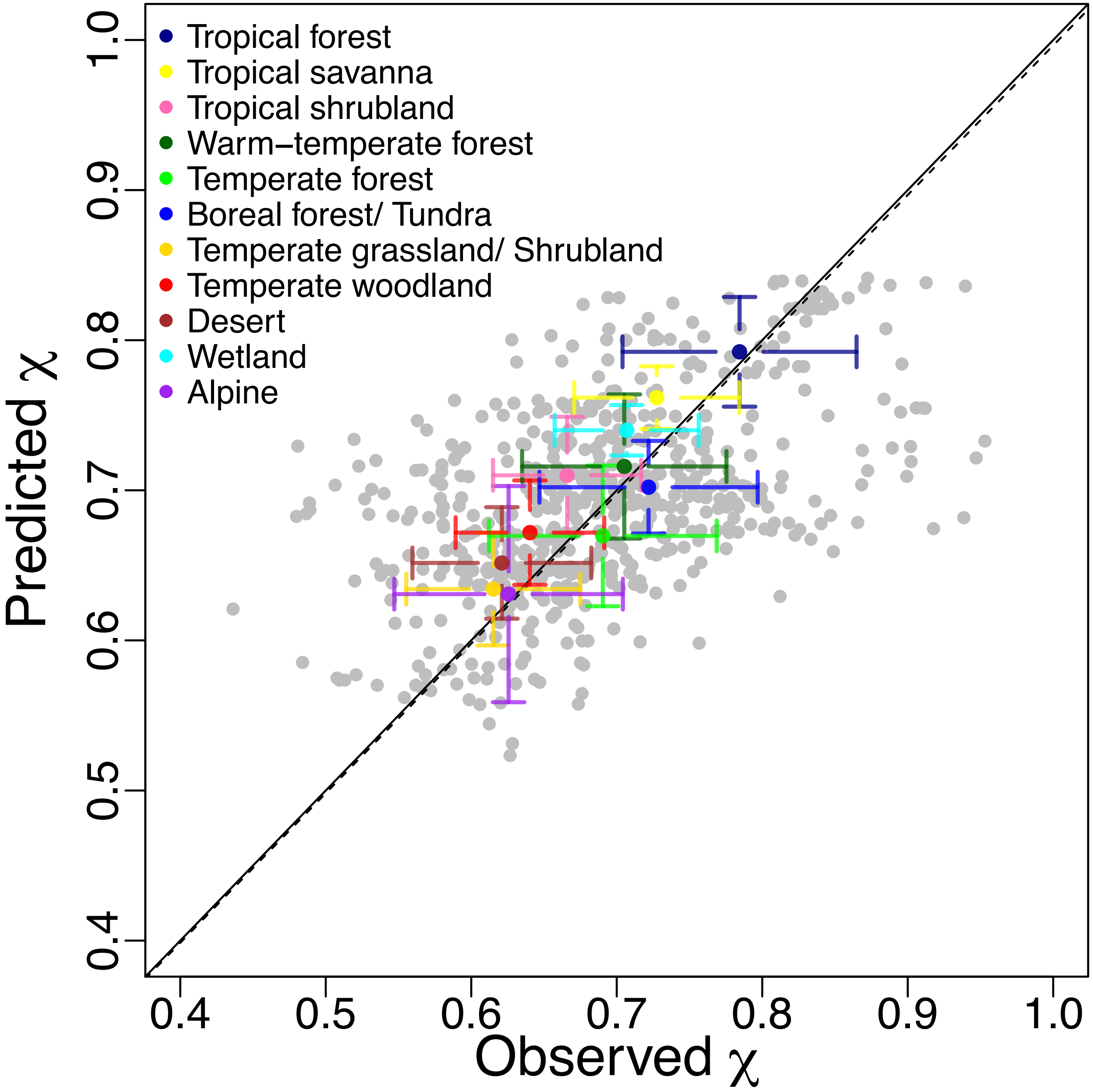
	predicted	fitted
temperature (K)	0.054	0.052 ± 0.006
ln vpd	–0.5	–0.55 ± 0.06
elevation (km)	–0.08	–0.11 ± 0.03

$R^2 = 0.39$

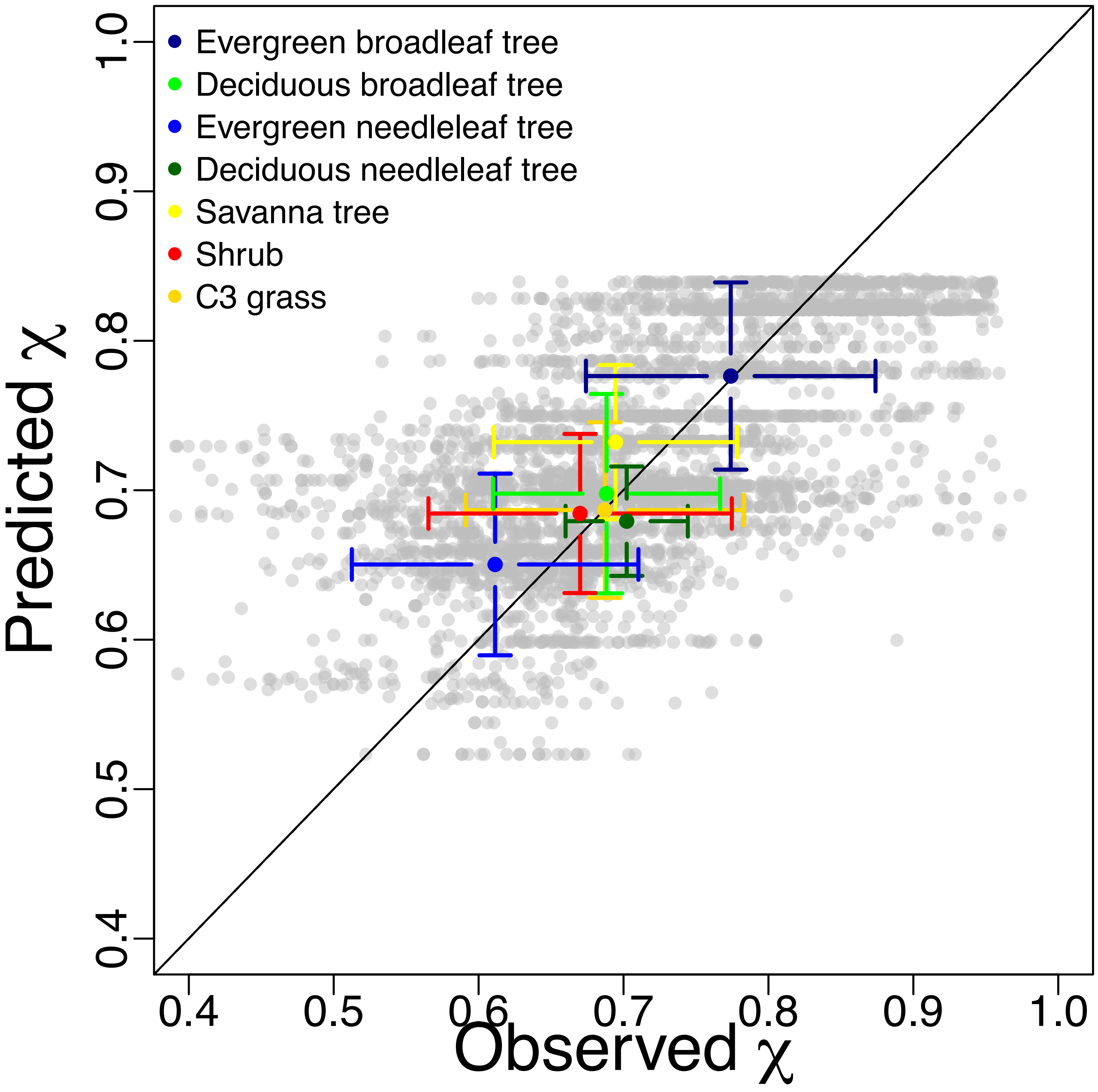
partial residual plots



(note dependence of elevation effect on relative humidity)



Tropical forest
Tropical savanna
Tropical shrubland
Warm−temperate forest
Temperate forest
Boreal forest/ Tundra
Temperate grassland/ Shrubland
Temperate woodland
Desert
Wetland
Alpine
Predicted χ
Observed χ
0.4
0.5
0.6
0.7
0.8
0.9
1.0



Evergreen broadleaf tree
Deciduous broadleaf tree
Evergreen needleleaf tree
Deciduous needleleaf tree
Savanna tree
Shrub
C3 grass
Predicted χ
Observed χ
0.4
0.5
0.6
0.7
0.8
0.9
1.0

A universal relationship

- Plant Functional Types have different c_i:c_a ratios **because they live in different climates**.

A universal relationship

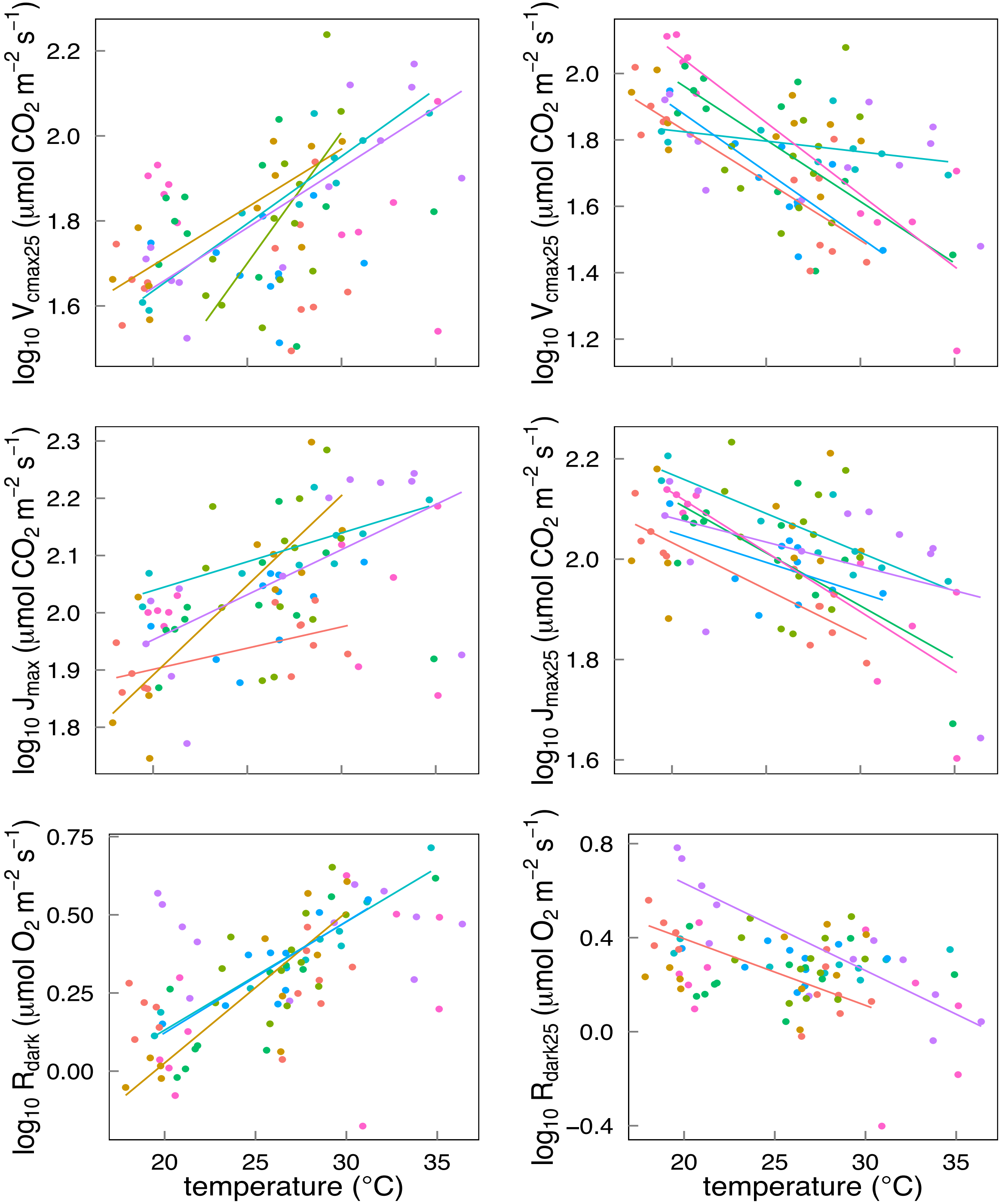
- PFTs have different c_i:c_a ratios **because they live in different climates**.
- Duh.

Predictability of carbon fixation capacity

The activity of the CO_2-fixing enzyme, Rubisco

- Predictions: V_{cmax} acclimates so as to make use of the available PAR (not less or more)

  - increases in proportion to PAR
  - increases **weakly** with temperature; less steeply than enzyme kinetics
  - value at standard temperature (e.g. 25˚C) **declines** with temperature



HF Togashi *et al.*
Functional Plant Ecology
(in revision)

Great Western
Woodlands, Australia

traits *versus* growth temperature

	predicted	fitted
$\ln V_{cmax}$	0.049*	0.033 ± 0.016
$\ln J_{max}$	0.024	0.025 ± 0.011
$\ln R_{dark}$	0.049	0.051 ± 0.016

*slope from Rubisco kinetics is 0.089

More (true) predictions

- higher V_{cmax} (and leaf N) in dry environments
- higher V_{cmax} (and leaf N) at high elevations
- lower V_{cmax} (and leaf N) at elevated CO_2: ‘down-regulation’

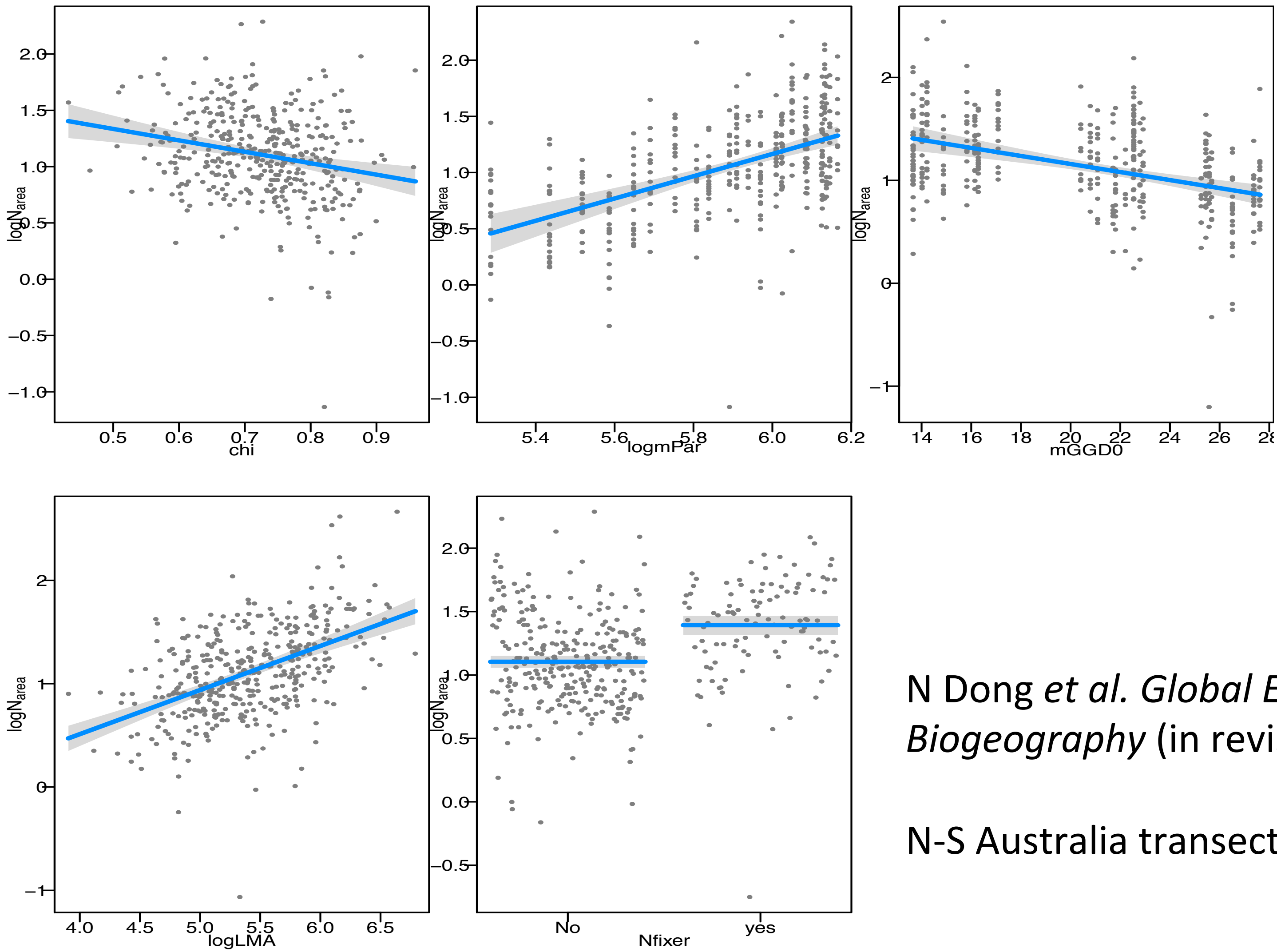
Predictability of leaf N content (ln N_{area})

	predicted	fitted
χ (from $\delta^{13}C$)	–0.62	–0.61 ± 0.25
ln PAR	1	0.87 ± 0.10
mean annual T	–0.048	–0.047 ± 0.007

N Dong *et al. Global Ecology and Biogeography* (in revision)

N-S Australia transect

partial residual plots



N Dong *et al. Global Ecology and Biogeography* (in revision)

N-S Australia transect

Predictability of the J_{max}:V_{cmax} ratio

Ratio of investments in electron transport and carboxylation

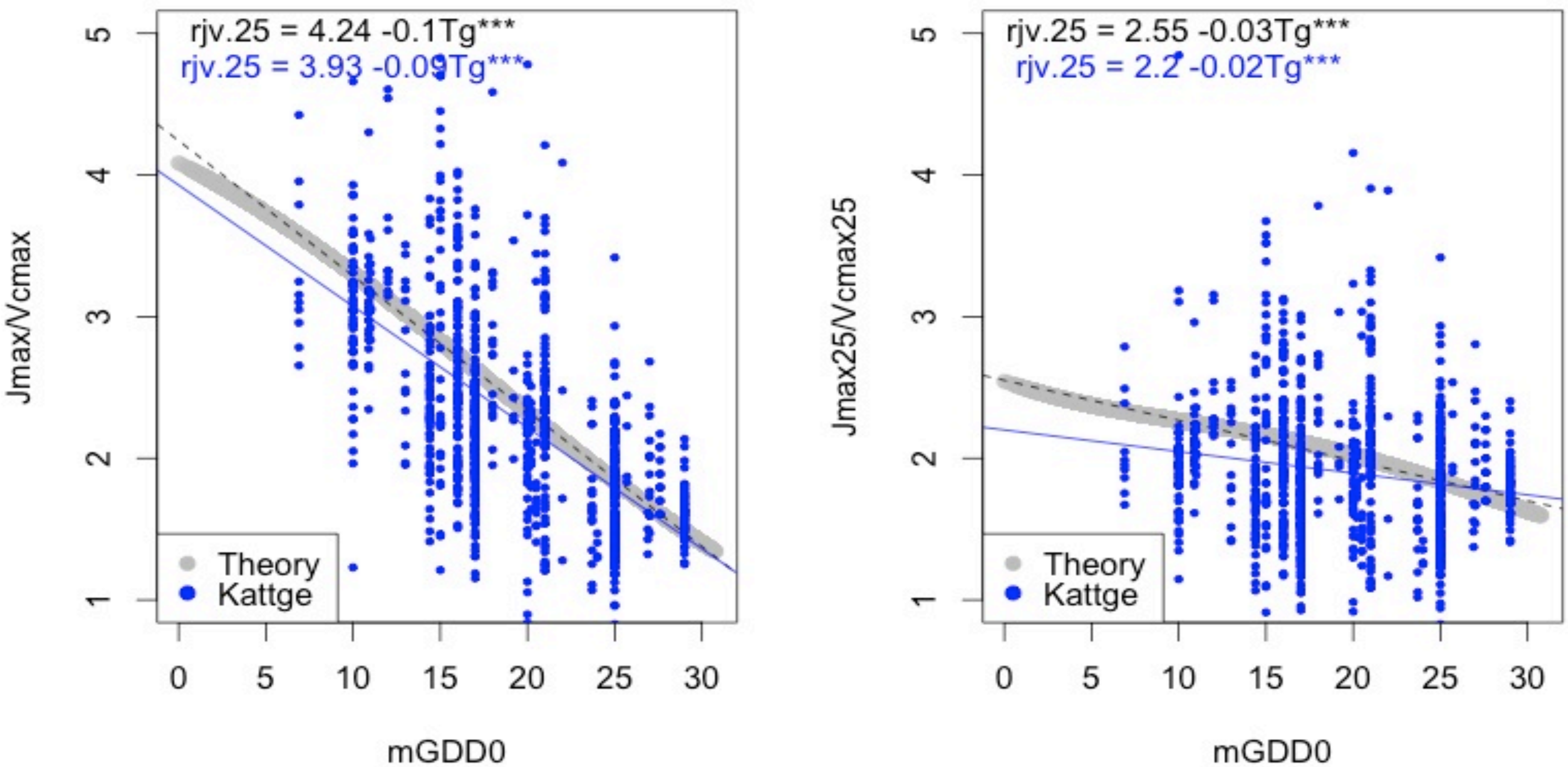
- J_{max} has a cost
- That's why the response of J to PAR is not linear
- Prediction based on the Smith formula for *J:*
  - *the ratio* J_{max}/V_{cmax} *has an optimum,*

    $J_{max} = 4\,k\,V_{cmax}$ *where*

    $k^3 = (1/c^*)\,(c_i - \Gamma^*)(c_i + 2\Gamma^*)^2/(c_i + K)^3$ and

    $c^* \approx 0.41$ (*from experimental data*)

J_{max}/V_{cmax} depends on growth temperature



H Wang *et al.* (unpublished results)

Predictability of GPP

Photosynthesis on a large scale

- A further consequence of the theory:
  - *GPP is proportional to absorbed PAR (Monteith 1977)*
- This is the foundation of LUE models!
- So now we can *predict* GPP, knowing *a*/*b* and *c**:
  - *Need satellite data on green vegetation cover (fAPAR)*
  - *Don't need PFTs, or any PFT-specific functions*
  - *Can predict environmental effects on LUE from first principles (including CO_2 effects)*

The universal GPP model

$$A_J = \varphi_0 I_{abs} m \sqrt{1 - \left(\frac{c^*}{m}\right)^{\frac{2}{3}}}$$

where

$$m = \frac{c_a - \Gamma^*}{c_a + 2\Gamma^* + 3\Gamma^* \sqrt{\frac{1.6 D \eta^*}{\beta\left(K + \Gamma^*\right)}}}$$

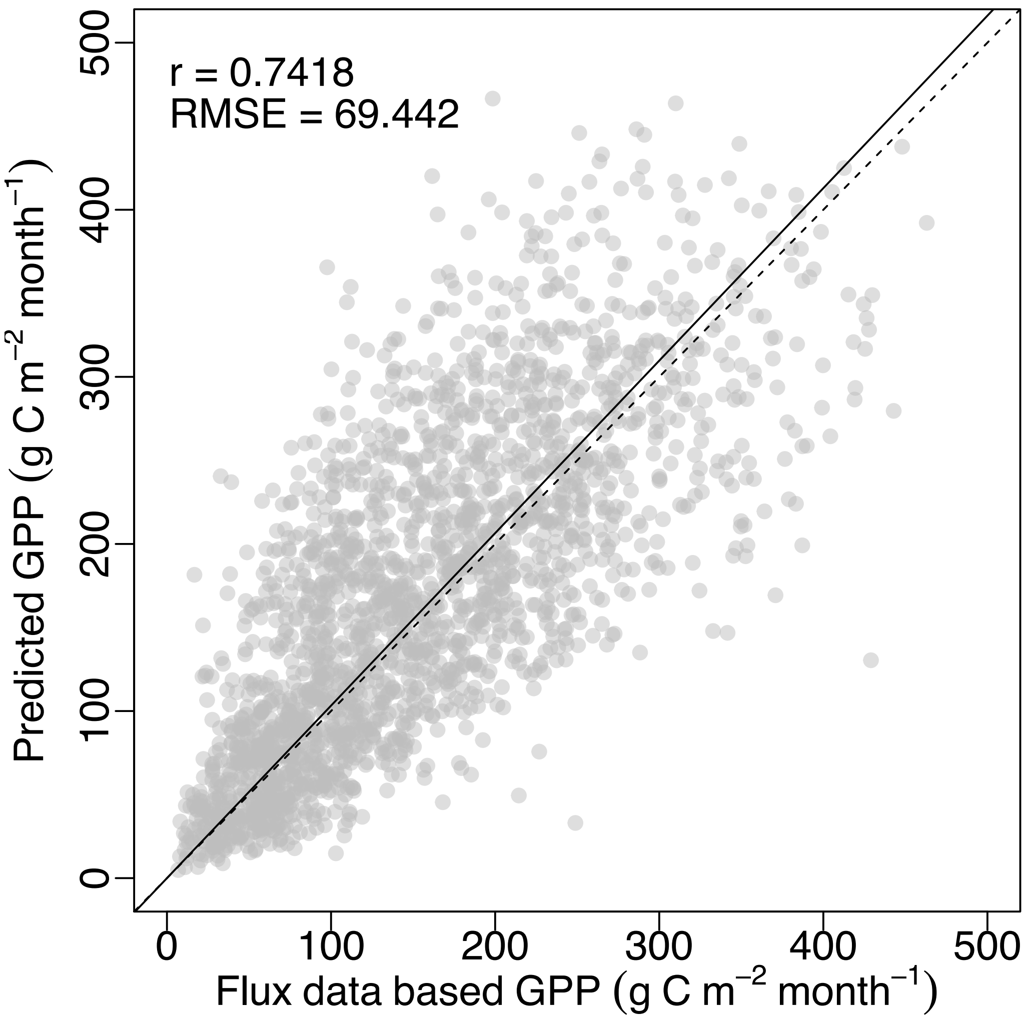
and

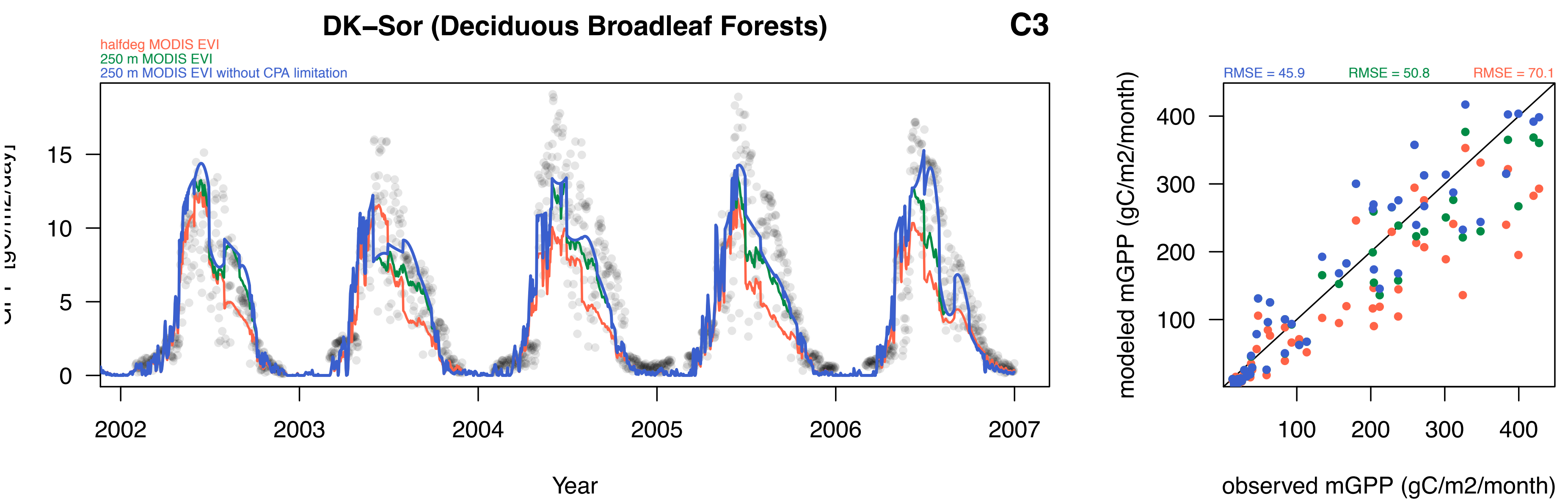
$\varphi_0 = 0.093$

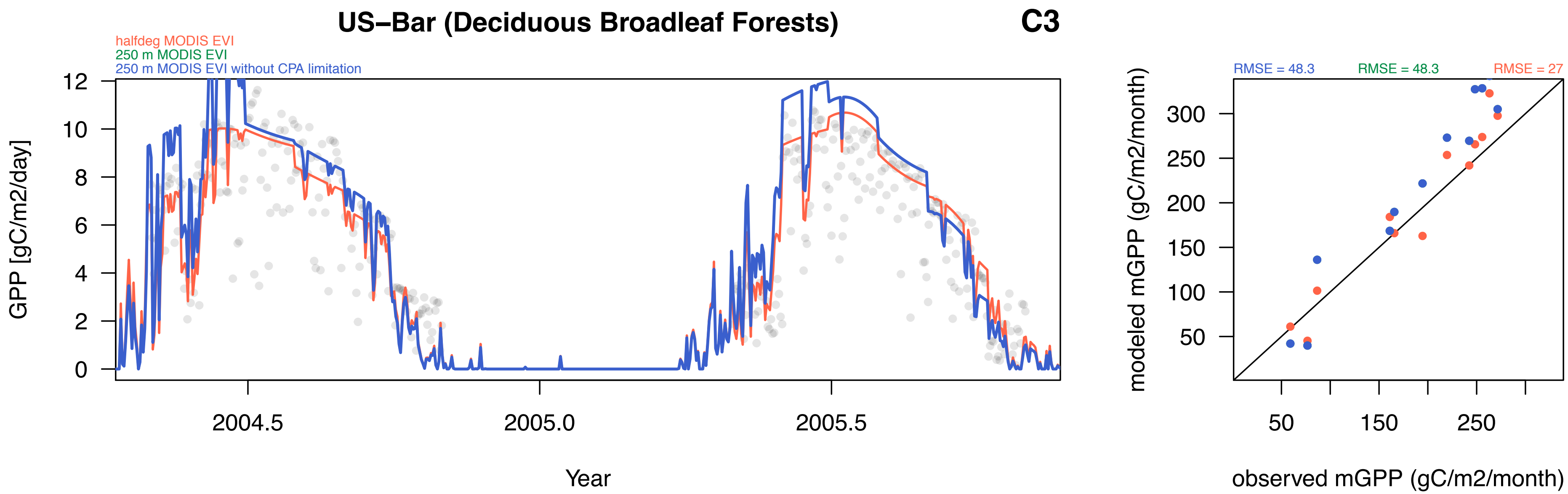
$c^* = 0.41$

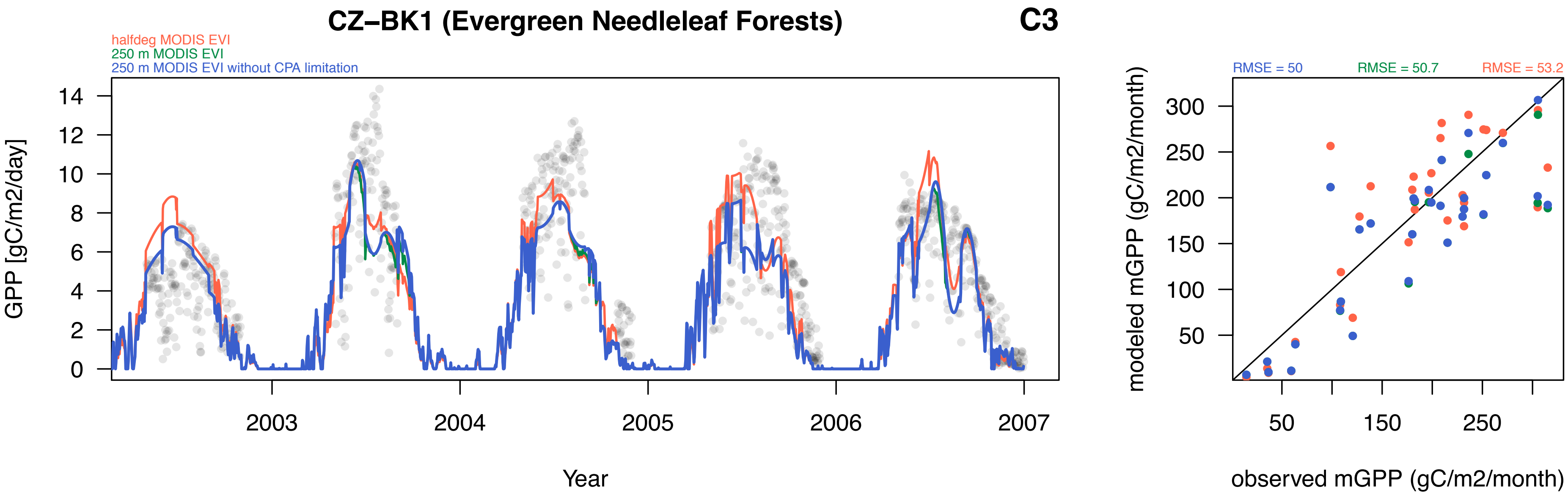
$\beta = b/a$ at $25^\circ\mathrm{C} = 240$

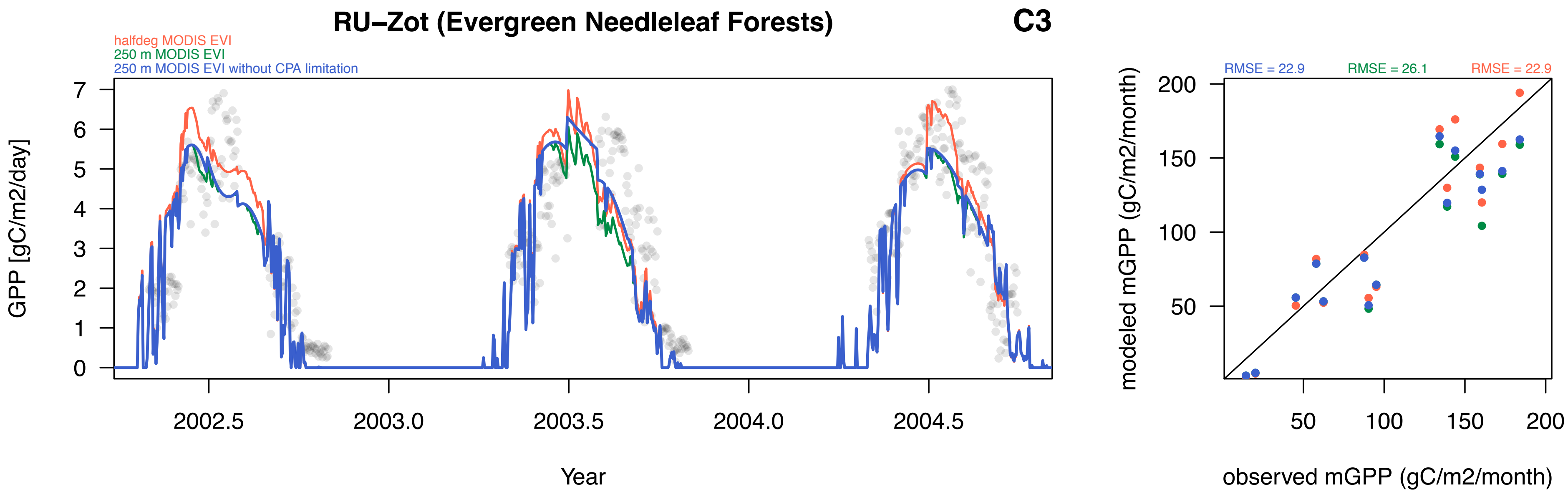
Global data-model comparison of monthly GPP

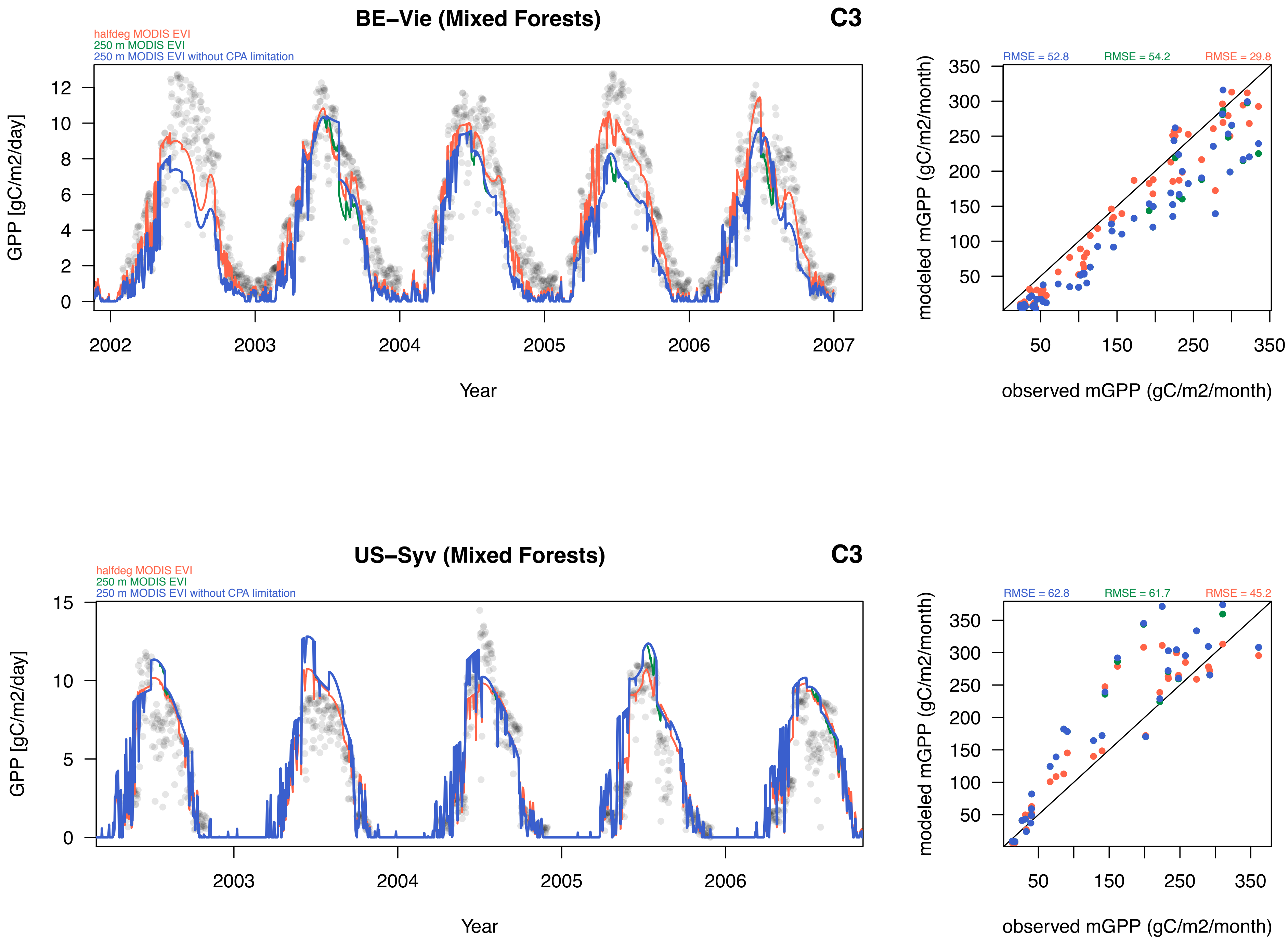


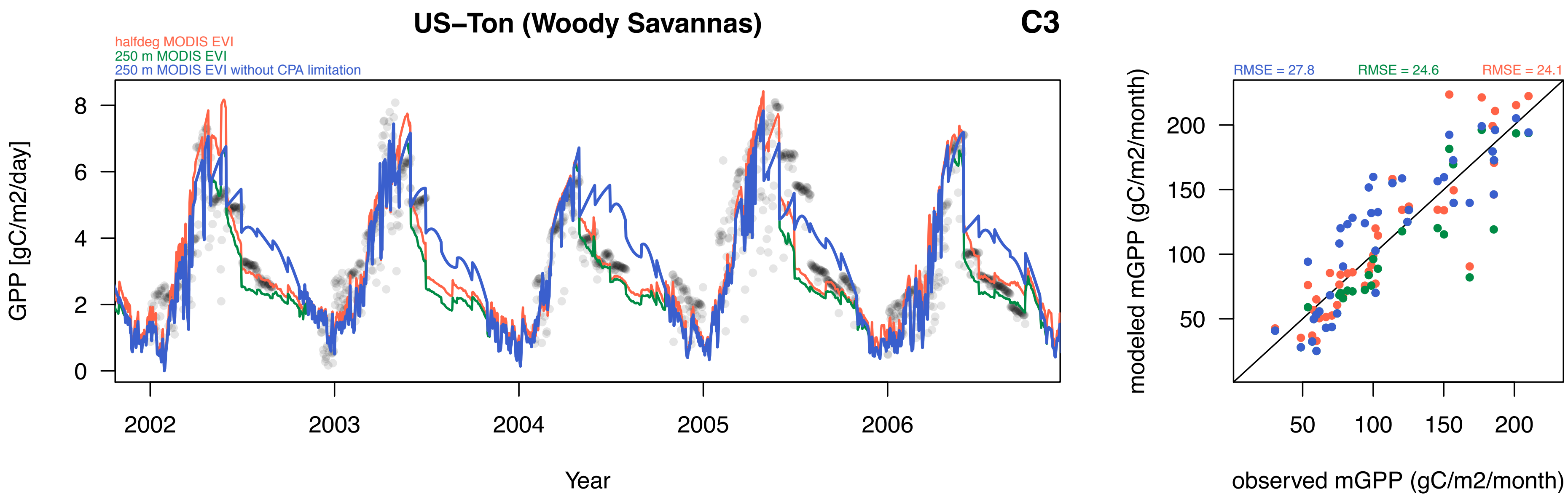

DK−Sor (Deciduous Broadleaf Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
Year
RMSE = 45.9
RMSE = 50.8
RMSE = 70.1
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)

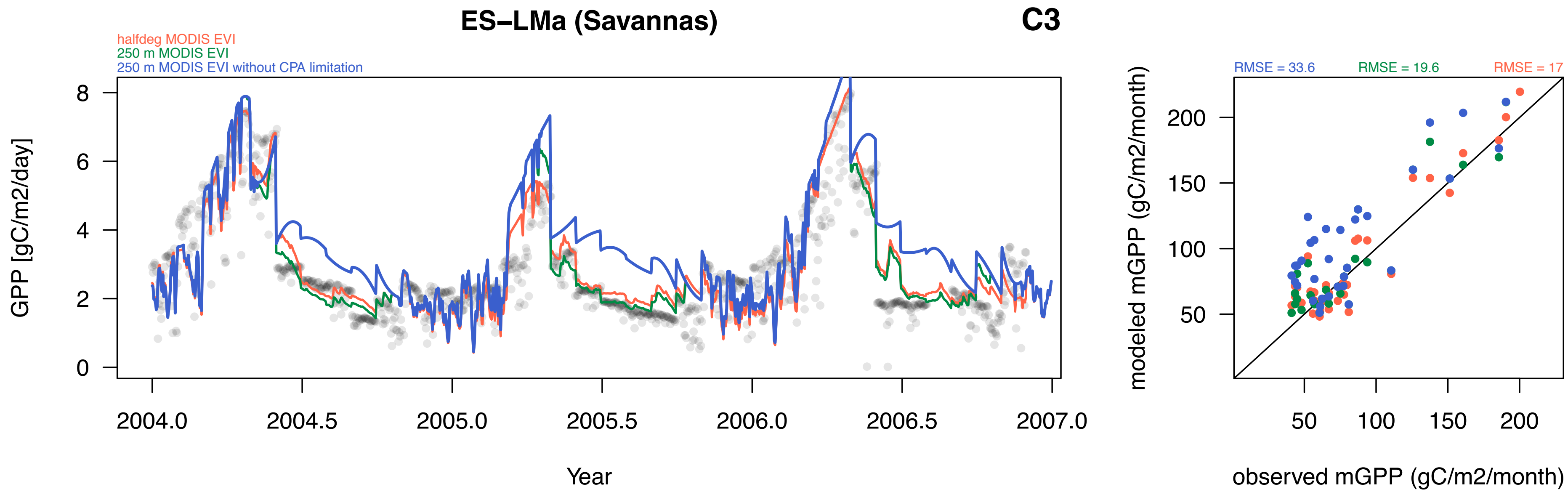

US−Bar (Deciduous Broadleaf Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 48.3
RMSE = 48.3
RMSE = 27
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)

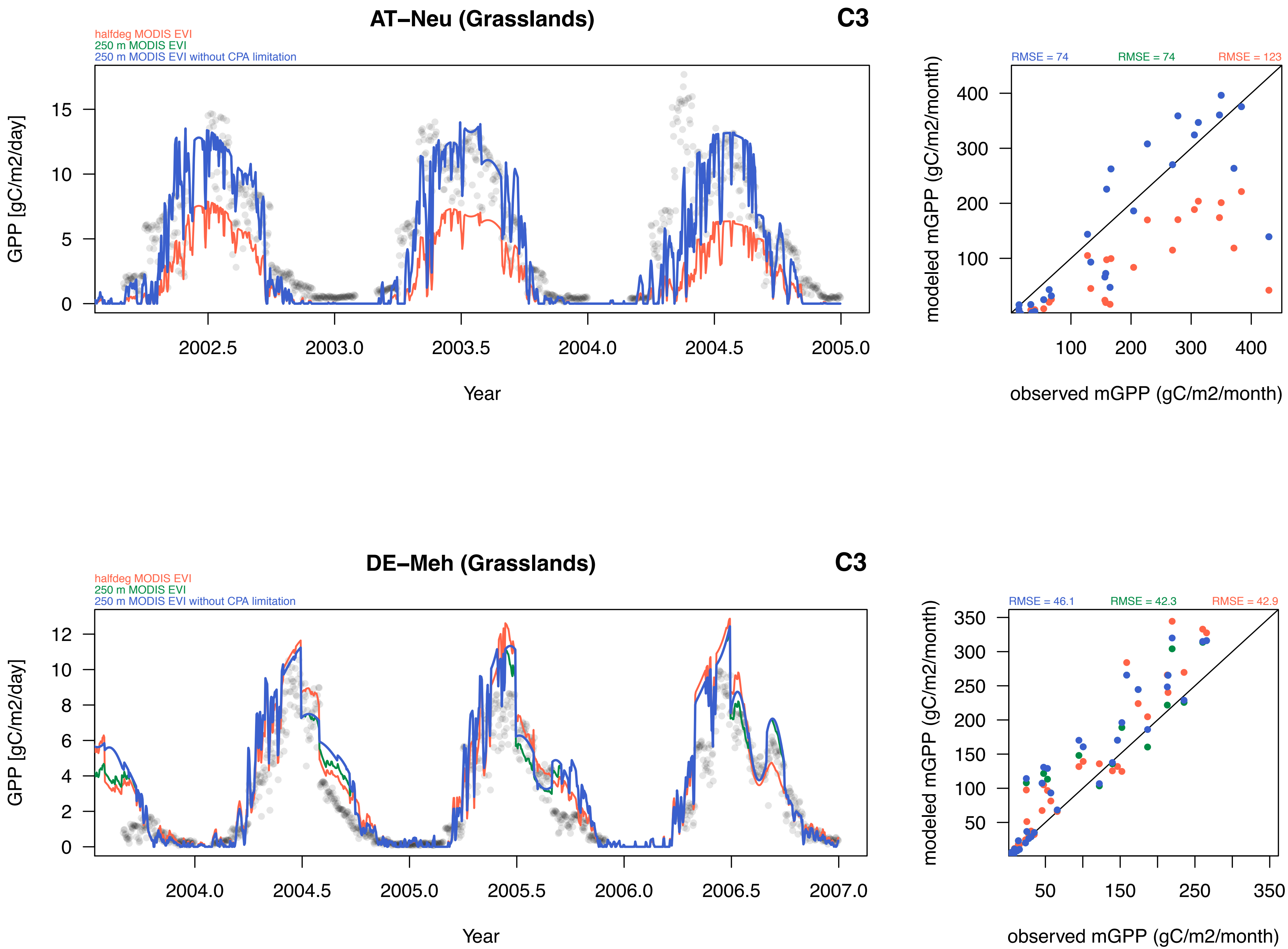

CZ–BK1 (Evergreen Needleleaf Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
0
2
4
6
8
10
12
14
2003
2004
2005
2006
2007
Year
RMSE = 50
RMSE = 50.7
RMSE = 53.2
modeled mGPP (gC/m2/month)
50
100
150
200
250
300
50
150
250
observed mGPP (gC/m2/month)

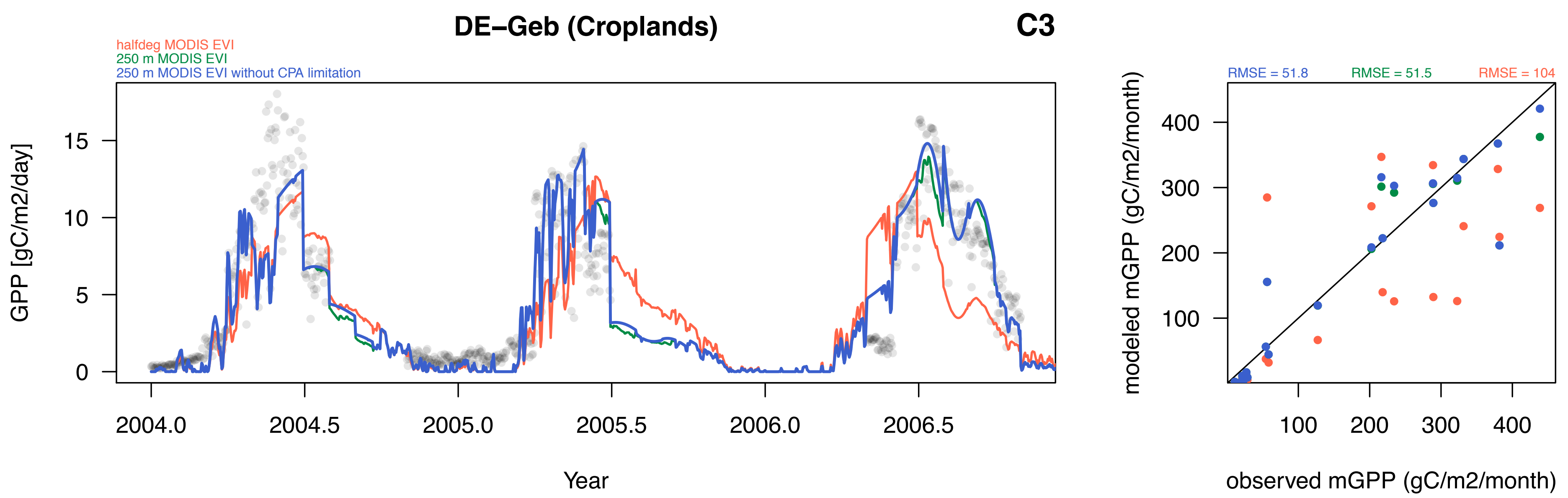

RU–Zot (Evergreen Needleleaf Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
0
1
2
3
4
5
6
7
2002.5
2003.0
2003.5
2004.0
2004.5
Year
RMSE = 22.9
RMSE = 26.1
RMSE = 22.9
modeled mGPP (gC/m2/month)
50
100
150
200
50
100
150
200
observed mGPP (gC/m2/month)


BE–Vie (Mixed Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 52.8
RMSE = 54.2
RMSE = 29.8
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)
US–Syv (Mixed Forests)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 62.8
RMSE = 61.7
RMSE = 45.2
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)

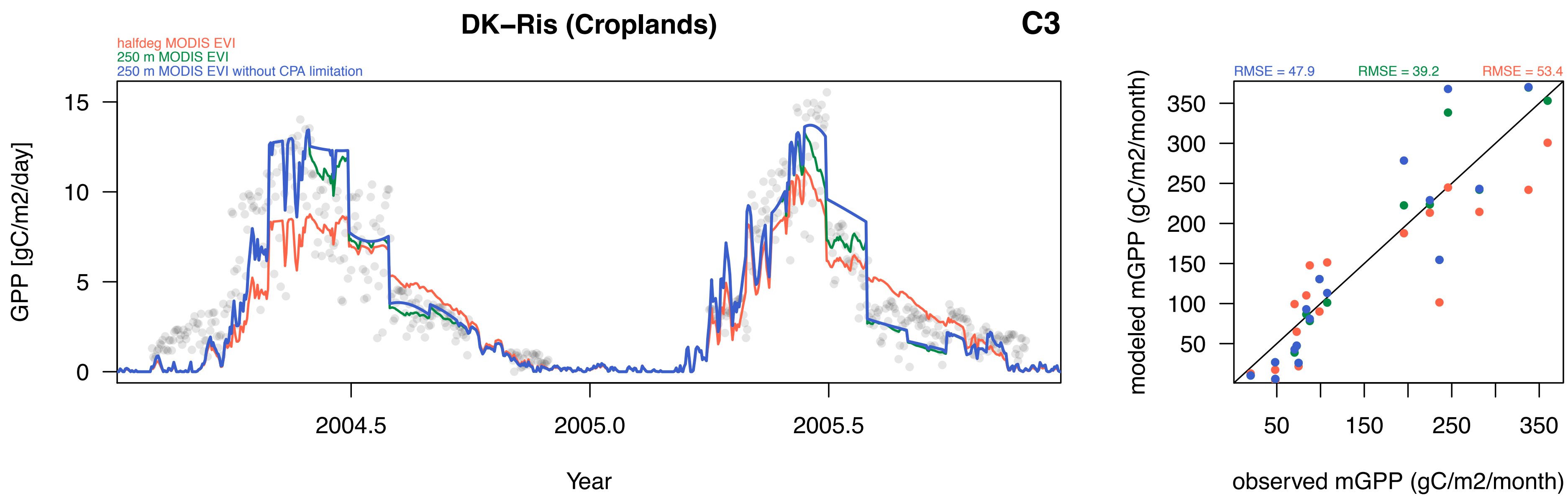

US–Ton (Woody Savannas)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 27.8
RMSE = 24.6
RMSE = 24.1
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)


ES–LMa (Savannas)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 33.6
RMSE = 19.6
RMSE = 17
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)

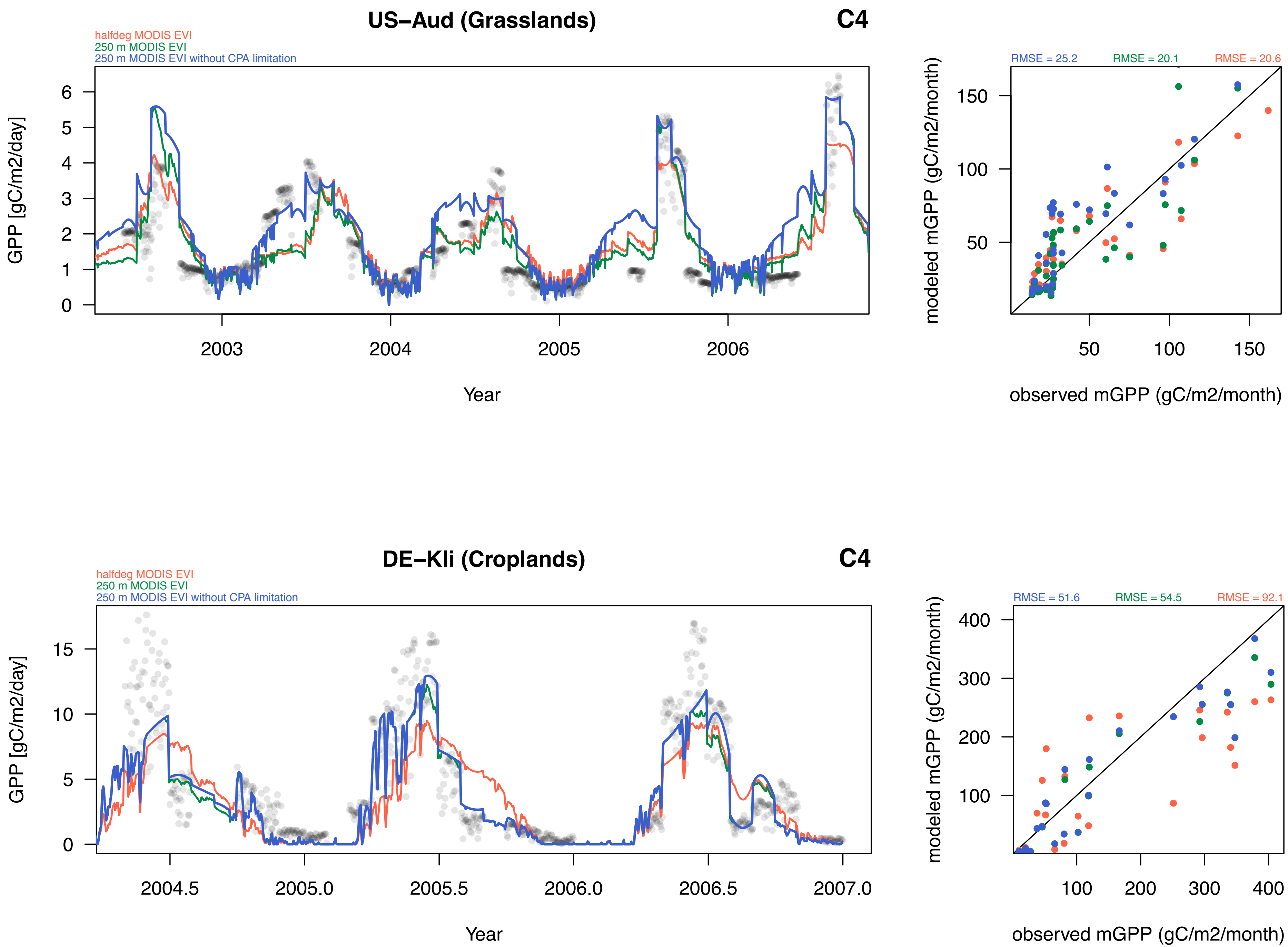

AT–Neu (Grasslands)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
2002.5
2003.0
2003.5
2004.0
2004.5
2005.0
RMSE = 74
RMSE = 74
RMSE = 123
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)
DE–Meh (Grasslands)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
2004.0
2004.5
2005.0
2005.5
2006.0
2006.5
2007.0
RMSE = 46.1
RMSE = 42.3
RMSE = 42.9
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)



DE–Geb (Croplands)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 51.8
RMSE = 51.5
RMSE = 104
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)



DK–Ris (Croplands)
C3
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 47.9
RMSE = 39.2
RMSE = 53.4
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)


US–Aud (Grasslands)
C4
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 25.2
RMSE = 20.1
RMSE = 20.6
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)
DE–Kli (Croplands)
C4
halfdeg MODIS EVI
250 m MODIS EVI
250 m MODIS EVI without CPA limitation
GPP [gC/m2/day]
Year
RMSE = 51.6
RMSE = 54.5
RMSE = 92.1
modeled mGPP (gC/m2/month)
observed mGPP (gC/m2/month)

Predictability of CO_2 effects

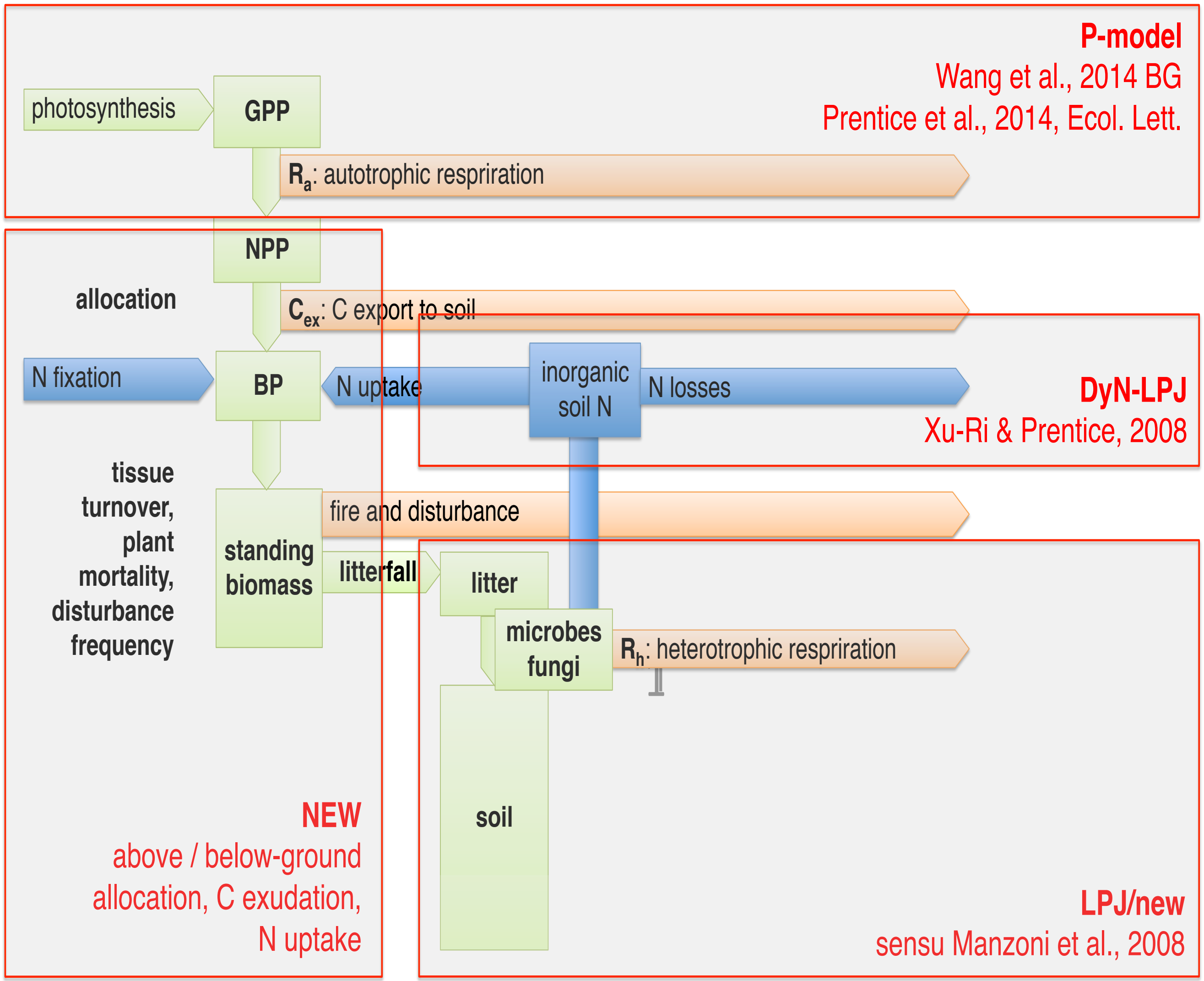
Comparison with Ainsworth & Long (2005) meta-analysis of FACE experiments (≈ 200 ppm CO_2 enhancement):

	meta-analysis	predicted
LUE	12.2 ± 9 %	15.2 %
WUE	54.3 ± 17 %	55 %
J_{max}/V_{cmax}	5.2 ± 2.8 %	9.8 %
g_s	–20 ± 3 %	15 %

Allocation: from GPP to biomass production

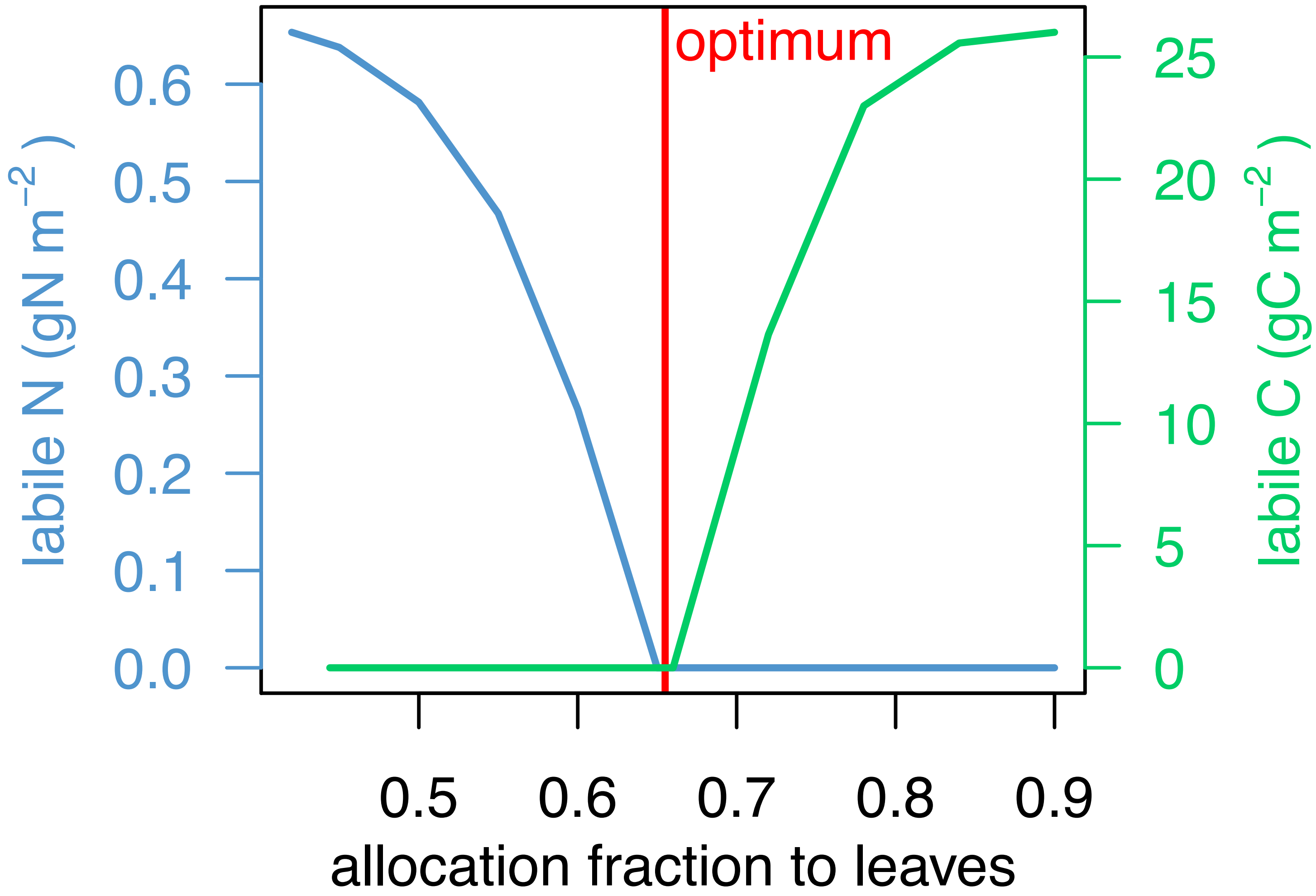
- Maintenance of functional and stoichiometric balance ≠ fixed allocation fractions
- Key to C-N cycle coupling: optimal allocation

Components of SOFUN

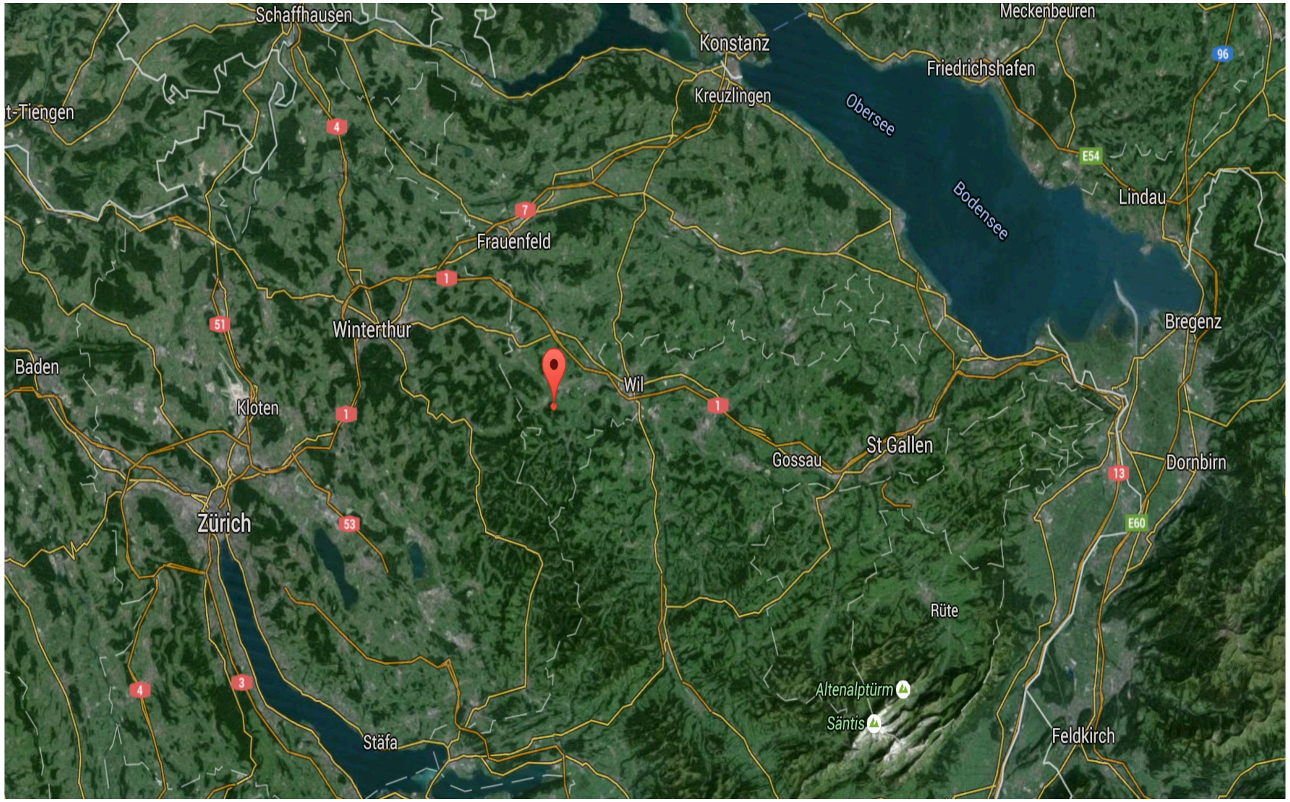


B. Stocker *et al.*, unpublished

Stoichiometric balance

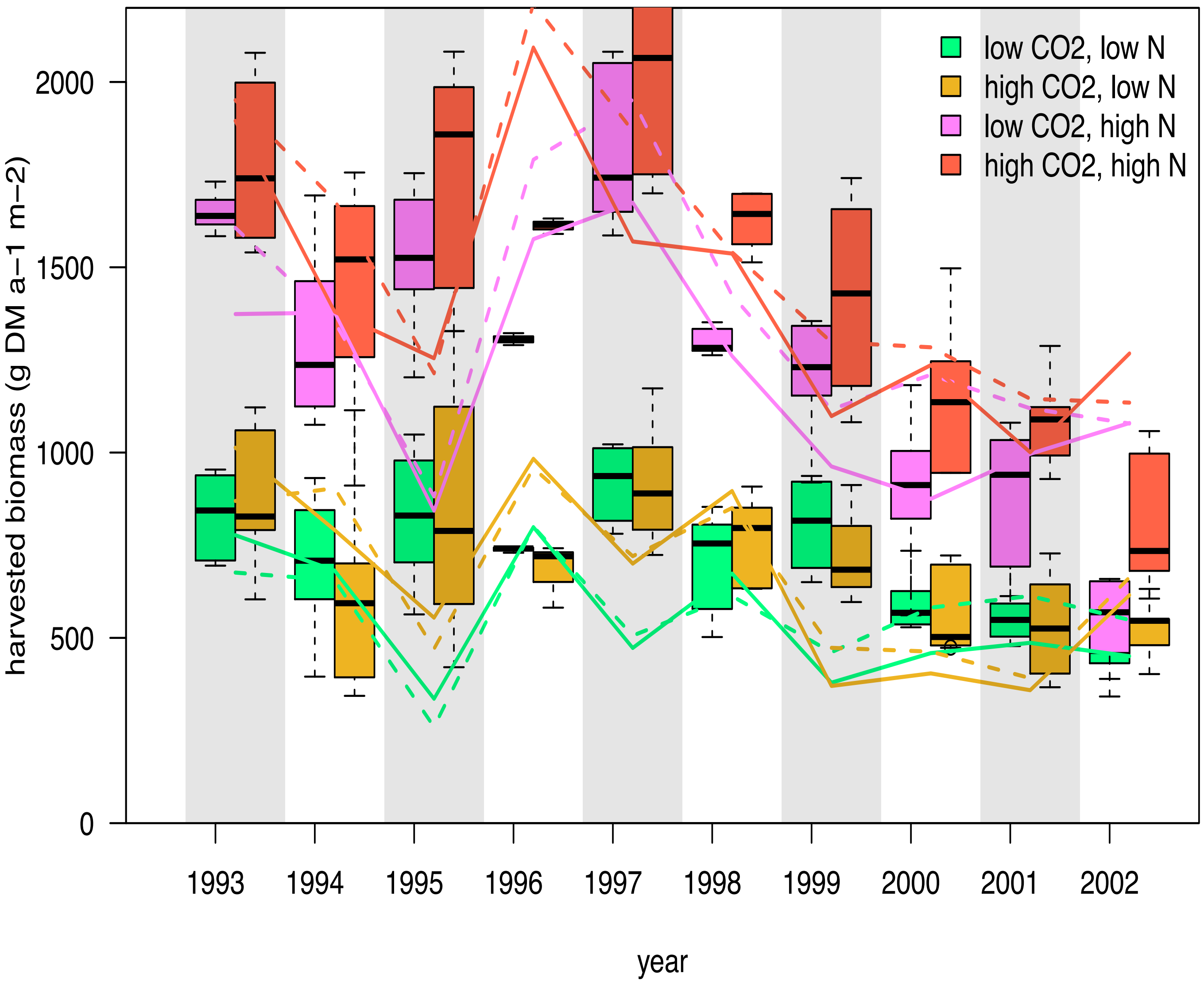


SwissFACE (Lüscher *et al,* 2004 *GCB*)

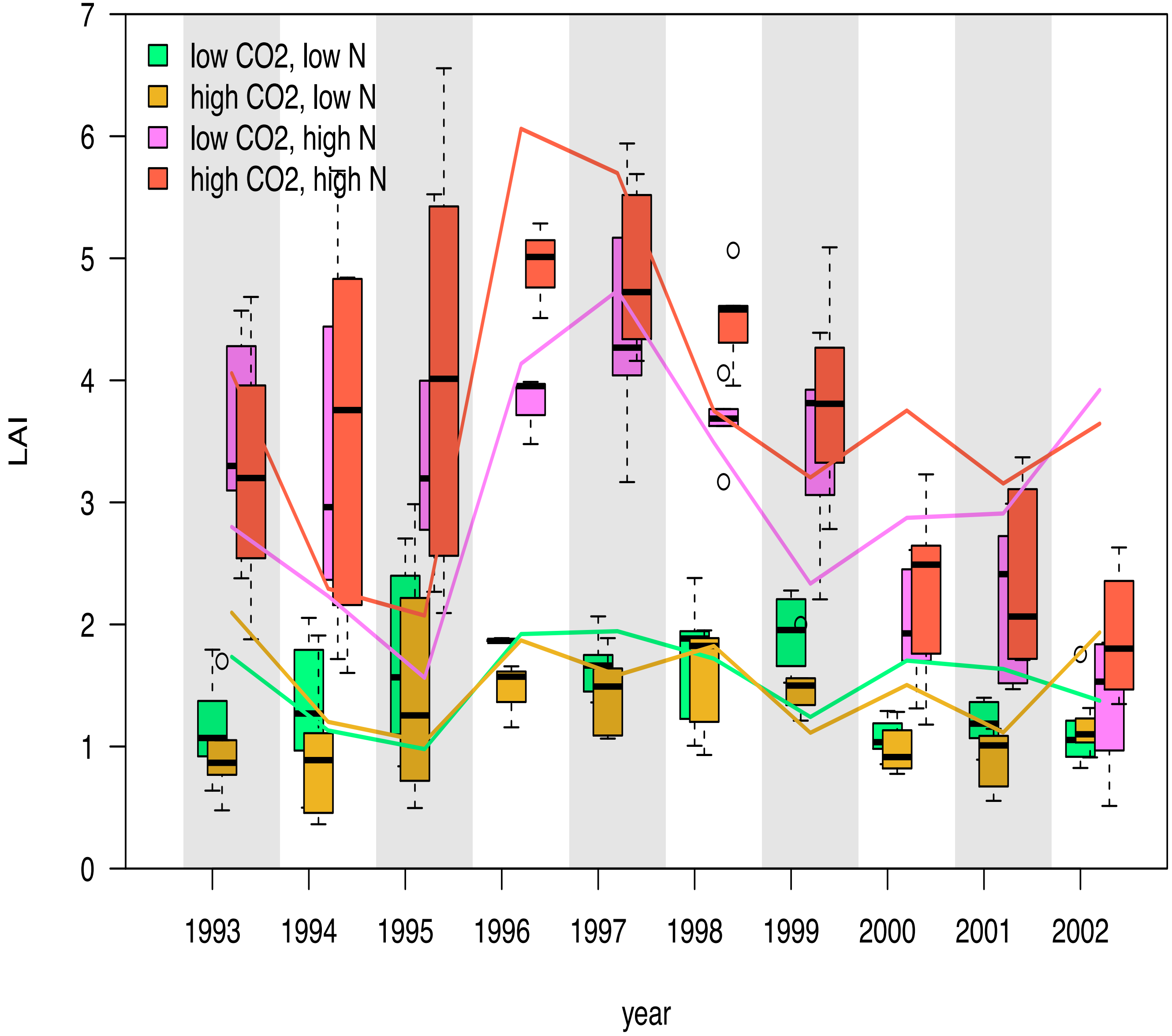


- temperate grassland
- factorial CO_2 x N-fertilization experiment
- modelled with daily climate and CO_2, actual N-fertilization and harvest
- no parameter tuning to fit the results

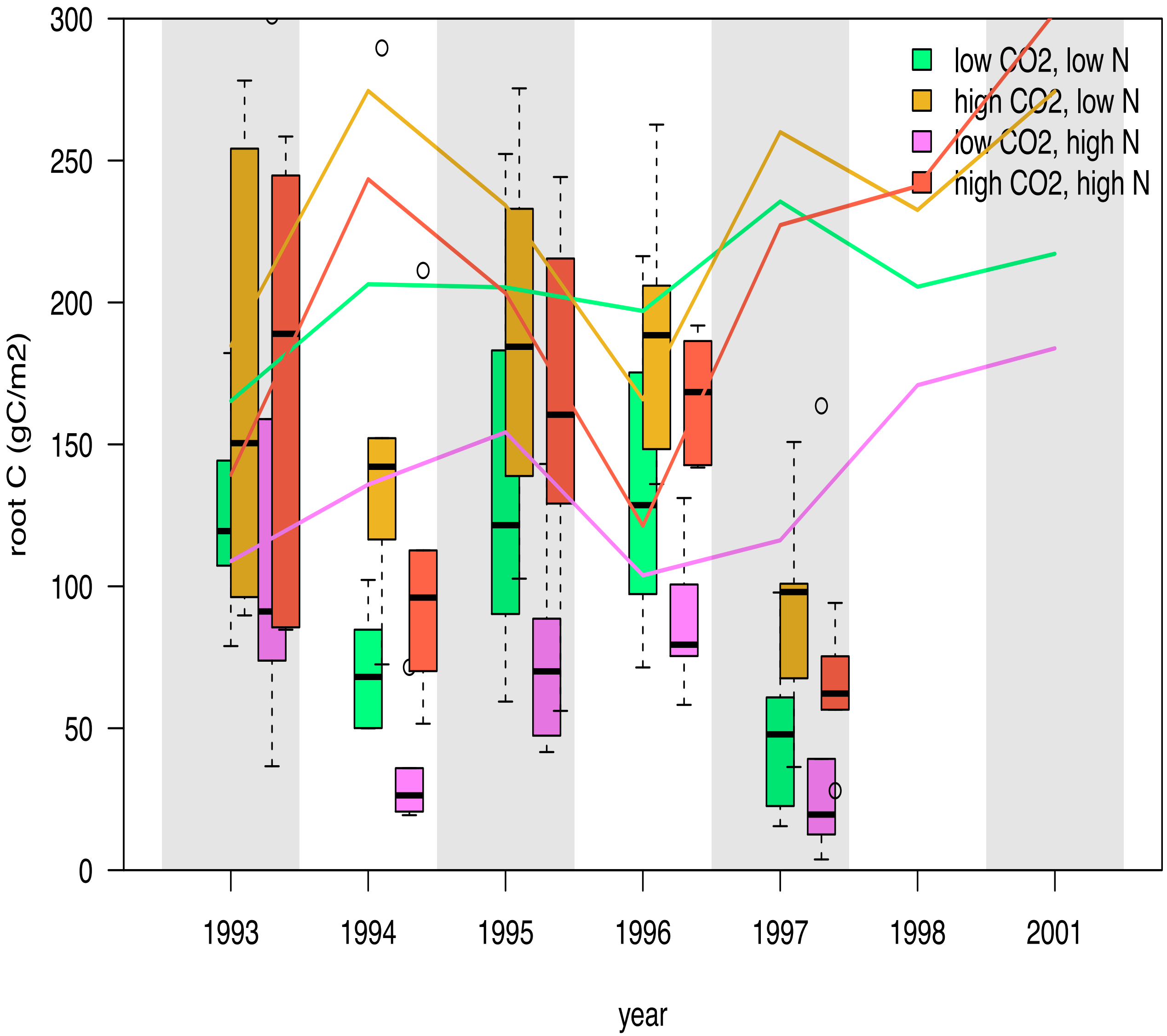
Swiss FACE: harvested biomass



Swiss FACE: LAI

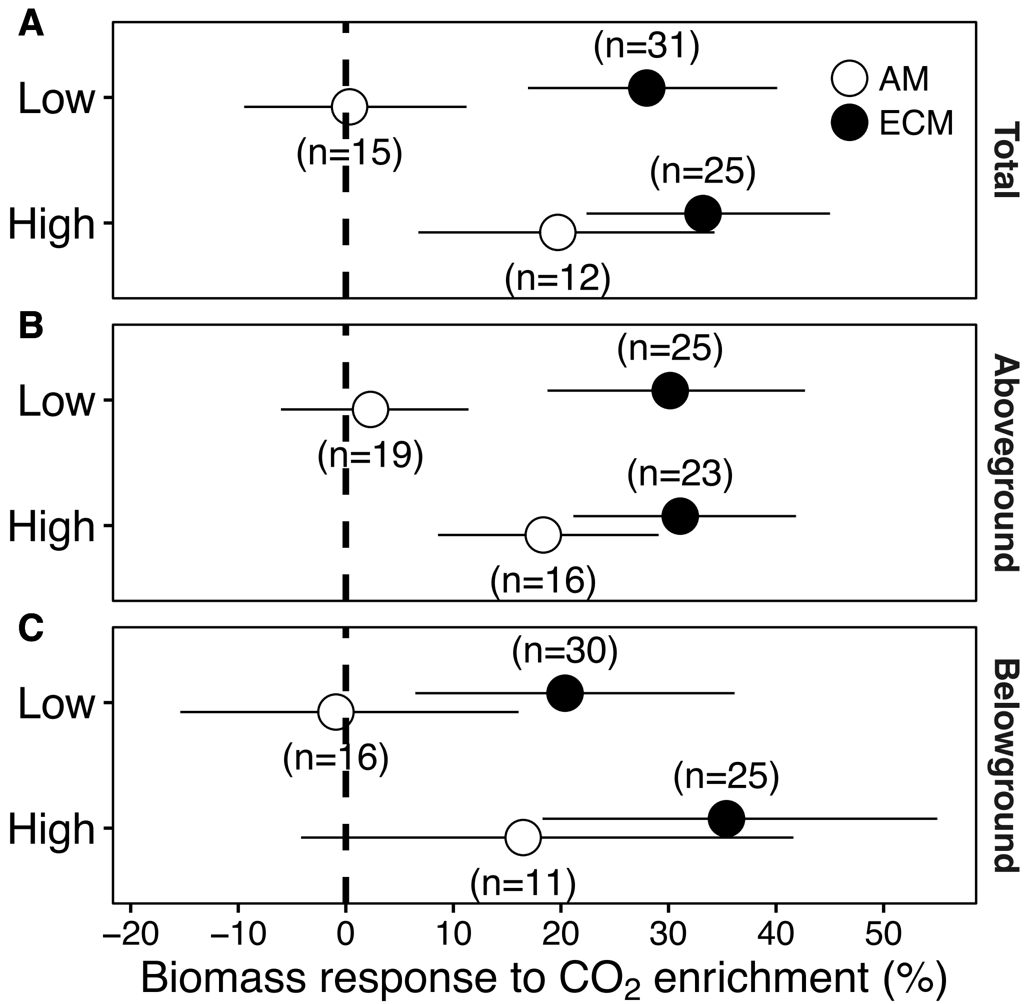


Swiss FACE: root mass



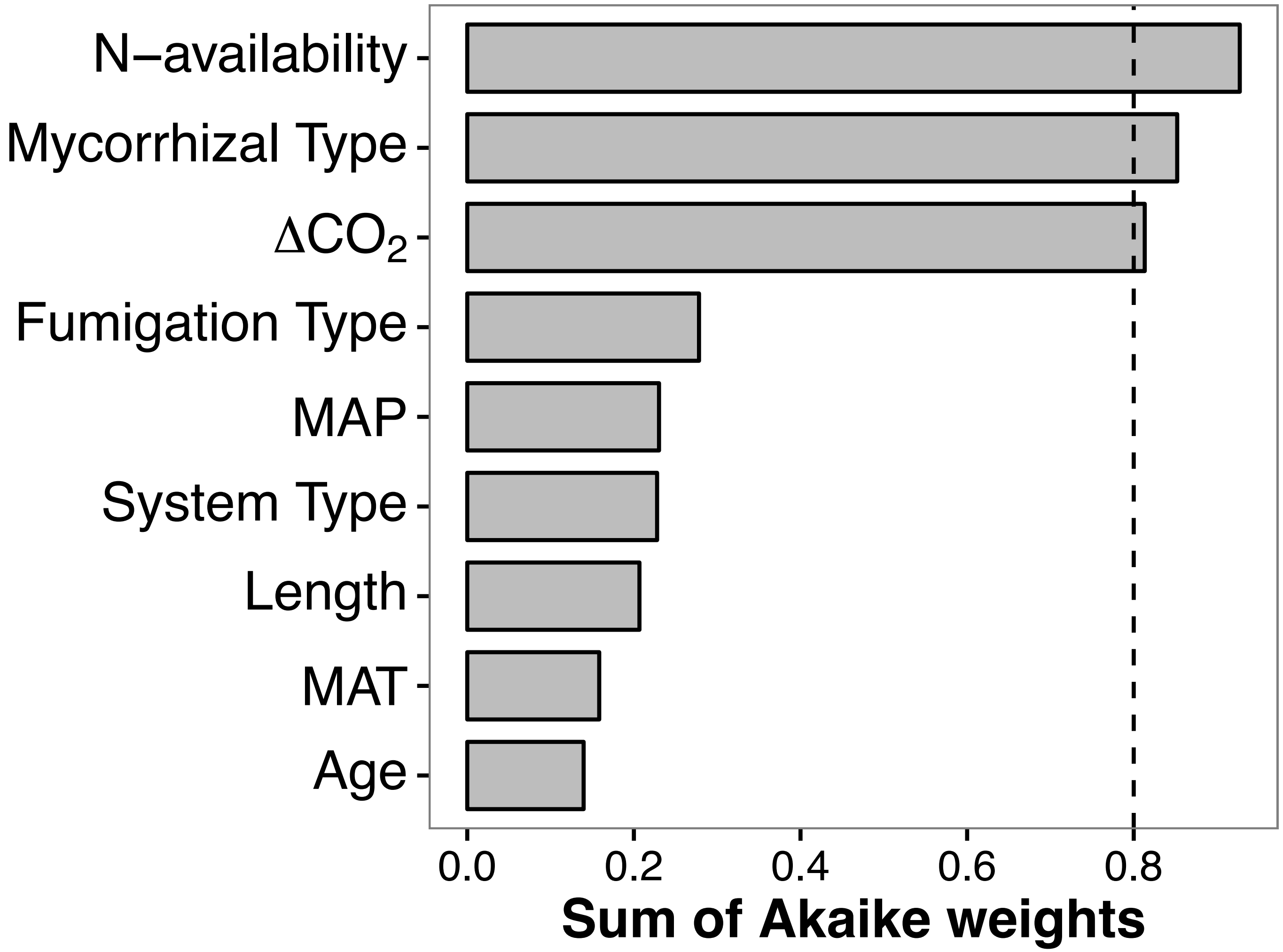
Why do some N-limited ecosystems respond/ not respond to enhanced CO_2?

It's the mycorrhizae, stupid!



Terrer *et al.* (2016) *Science*

It's the mycorrhizae, stupid!



Terrer *et al.* (2016) *Science*

Conclusions

- GPP can be predicted from fAPAR with a single, universal equation.
- $E = 1.6\, g_s\, D$, where $g_s = (A/c_a)/(1 - \chi)$...
    - *transpiration is predictable in the same way.*
- CO_2 effects can be predicted with the same equation.
- The next big challege is to ‘close the loop’ between GPP and fAPAR, requiring a comprehensive treatment of allocation.