Nutrient availability determines forests’ carbon sequestration
- *A global synthesis*

Sara Vicca
Marcos Fernández-Martínez
Sebastiaan Luyssaert
Josep Peñuelas
Ivan Janssens
et al.

Universiteit Antwerpen

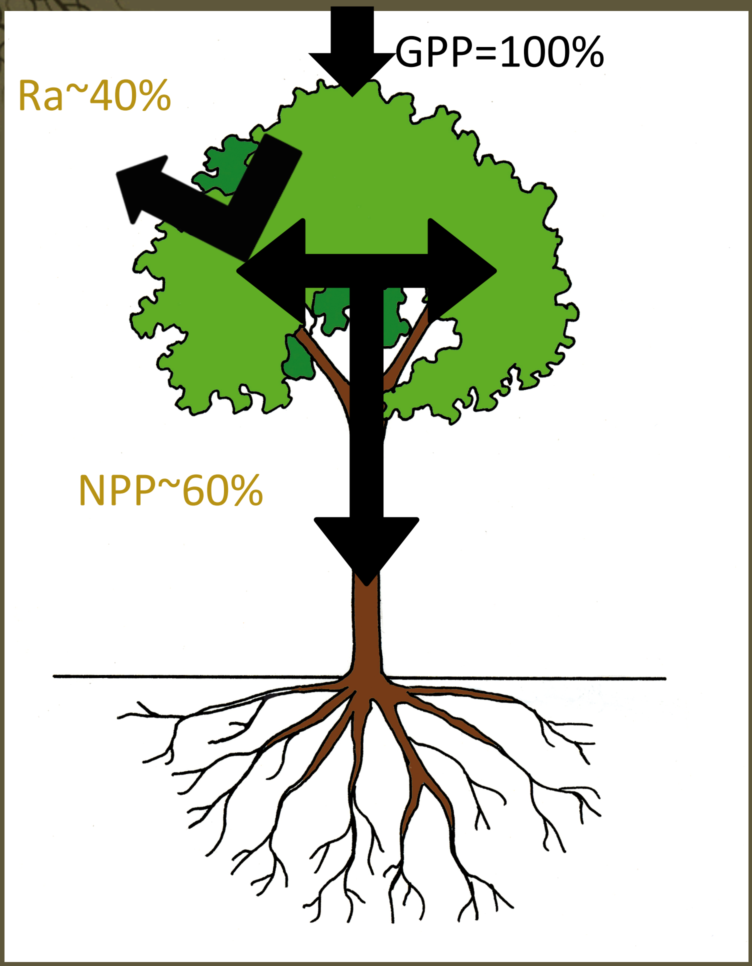
What happened previously

- Discussion: do plants respire a constant or variable fraction of the carbon assimilated during photosynthesis?
- Some scientists say yes (at long time scale):

CUE = 1-Ra:GPP

= NPP:GPP

~ 0.5-0.6



What happened previously

- Important argument for conservative CUE: photosynthesis and respiration are interdependent

ELSEVIER

Biochimica et Biophysica Acta 1366 (1998) 235–255

BIOCHIMICA ET BIOPHYSICA ACTA

BBA

Review

Interdependence between chloroplasts and mitochondria in the light and the dark

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Keywords: Chloroplast; Chlororespiration; Excess reductant; Metabolite exchange; Mitochondrion; Photosynthesis; Respiration

What happened previously

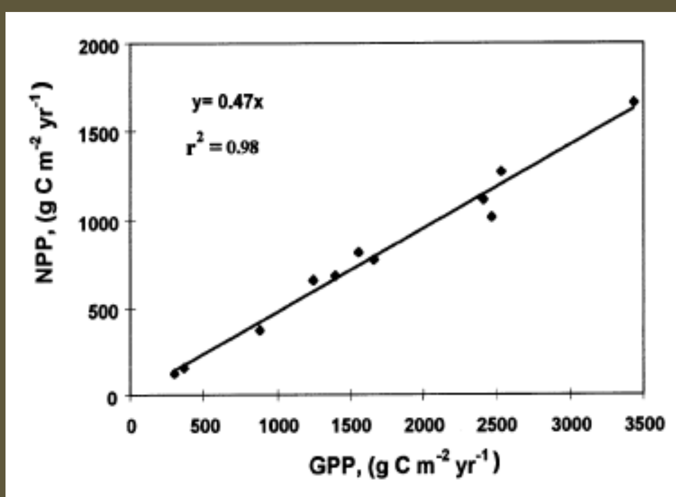
- Important argument for conservative CUE: photosynthesis and respiration are interdependent
- But.. Other scientists say CUE varies with climate, between species, ...

  Ra more T-sensitive than GPP

CUE constant? Difficult to measure

What happened previously

- FORESTS
- Waring et al (1998): NPP constant fraction of GPP; CUE ~ 0.47
- BUT! Artefact in calculations (Medlyn & Dewar, 1999)



Tree Physiology 18, 129–134

Net primary production of forests: a constant fraction of gross primary production?

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[1] *College of Forestry, Oregon State University, Corvallis, OR 97331-7501, USA*
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Received April 24, 1997

Summary Considerable progress has been made in our ability to model and measure annual gross primary production (GPP) by terrestrial vegetation. But challenges remain in estimating maintenance respiration (R_m) and net primary production (NPP). To search for possible common relationships, we assembled annual carbon budgets from six evergreen and one deciduous forest in Oregon, USA, three pine plantations in New South Wales, Australia, a deciduous forest in Massachusetts, USA, and a *Nothofagus* forest on the South Island of New Zealand. At all 12 sites, a standard procedure was followed to estimate annual NPP of foliage, branches, stems, and roots, the carbon expended in synthesis of these organs (R_g), their R_m, and that of previously produced foliage and sapwood in boles, branches, and large roots. In the survey, total NPP ranged from 120 to 1660 g C m^{-2} year^{-1}, whereas the calculated fraction allocated to roots varied from 0.22 to 0.63. Comparative analysis indicated that the total NPP/GPP ratio was conservative (0.47 ± 0.04 SD). This finding supports the possibility of greatly simplifying forest growth models. The constancy of the NPP/GPP ratio also provides an incentive to renew efforts to understand the environmental factors affecting partitioning of NPP above and belowground.

et al. 1997) are aimed at wider-scale simulations and treat radiation interception and canopy photosynthesis in less detail, these models still provide good estimates of GPP over longer intervals when compared against daily and monthly eddy flux data and annual whole-tree carbon balances (e.g., Waring et al. 1995, Williams et al. 1997). Landsberg and Gower (1996) have reviewed these models (except for MBL/SPA and MBL/CSA) and assessed their performance. They all recognize implicitly (or, in the case of BIOMASS, explicitly) that not all the photosynthetically active radiation absorbed by stands is effective in photosynthesis.

McMurtrie et al. (1994) proposed the term 'utilizable radiation' for the amount of photosynthetically active radiation that can be used by the canopy for photosynthesis. It is calculated by discounting the radiation absorbed by the canopy, determined by the ratio of average to maximum stomatal conductance, irrespective of whether reductions in conductance are caused by high vapor pressure deficits, low soil water content in the root zone, or subfreezing conditions. The procedure was described by Landsberg (1986) and has been applied by McMurtrie et al. 1994, Runyon et al. 1994, Waring et al. 1995 and Landsberg and Waring 1997.

What happened previously

- FORESTS
- DeLucia et al 2007: analysis of NPP:GPP in 60 forests around the globe
- CUE varied considerably

0.23<CUE<0.83

Global Change Biology (2007) 13, 1157–1167, doi: 10.1111/j.1365-2486.2007.01365.x

Forest carbon use efficiency: is respiration a constant fraction of gross primary production?

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Abstract

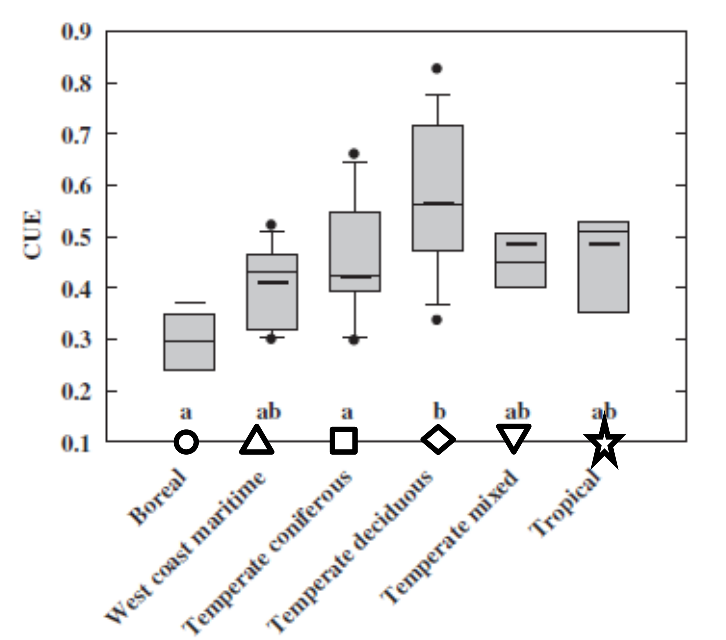
Carbon-use efficiency (CUE), the ratio of net primary production (NPP) to gross primary production (GPP), describes the capacity of forests to transfer carbon (C) from the atmosphere to terrestrial biomass. It is widely assumed in many landscape-scale carbon-cycling models that CUE for forests is a constant value of ~0.5. To achieve a constant CUE, tree respiration must be a constant fraction of canopy photosynthesis. We conducted a literature survey to test the hypothesis that CUE is constant and universal among forest ecosystems. Of the 60 data points obtained from 26 papers published since 1975, more than half reported values of GPP that were not estimated independently from NPP; values of CUE calculated from independent estimates of GPP were greater than those calculated from estimates of GPP derived from NPP. The slope of the relationship between NPP and GPP for all forests was 0.53, but values of CUE varied from 0.23 to 0.83 for different forest types. CUE decreased with increasing age, and a substantial portion of the variation among forest types was caused by differences in stand age. When corrected for age the mean value of CUE was greatest for temperate deciduous forests and lowest for boreal forests. CUE also increased as the ratio of leaf mass-to-total mass increased. Contrary to the assumption of constancy, substantial variation in CUE has been reported in the literature. It may be inappropriate to assume that respiration is a constant fraction of GPP as adhering to this assumption may contribute to incorrect estimates of C cycles. A 20% error in current estimates of CUE used in landscape models (i.e. ranging from 0.4 to 0.6) could misrepresent an amount of C equal to total anthropogenic emissions of CO_2 when scaled to the terrestrial biosphere.

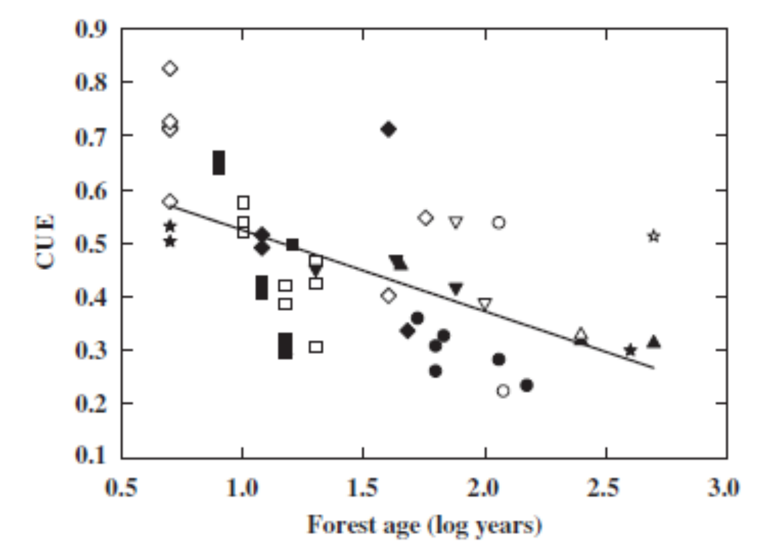
Keywords: age, biomass allocation, biome, carbon cycle, data synthesis, ecosystem, forest, gross primary production, net primary production, respiration

Received 6 September 2006; revised version received 1 January 2007 and accepted 2 February 2007

What happened previously

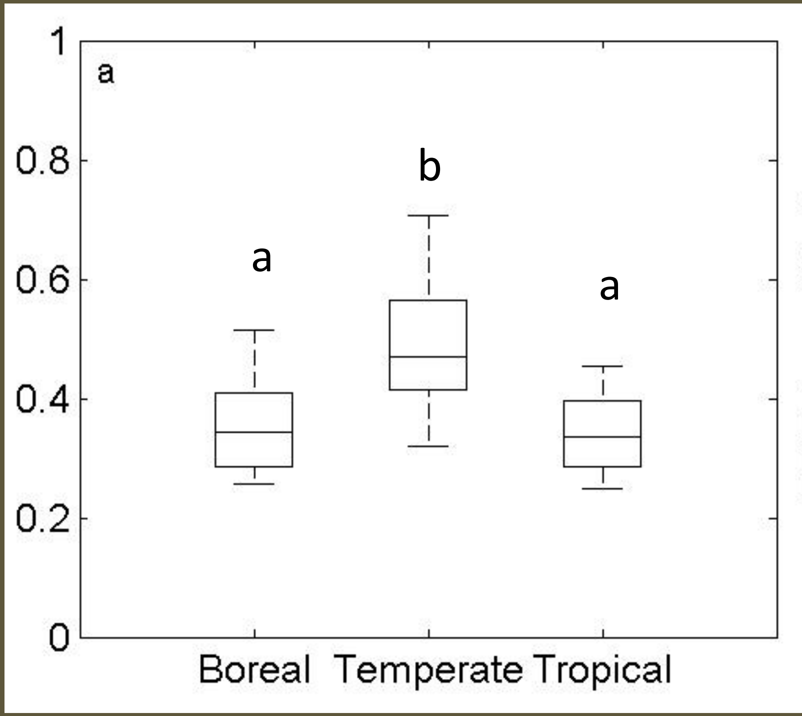
- Real driver of variation in CUE remained unclear due to confounding effects
  - Age effect confounded with forest type
  - Nitrogen deposition highest in temperate region
  - …
- In any case: assuming constancy of CUE seems inappropriate

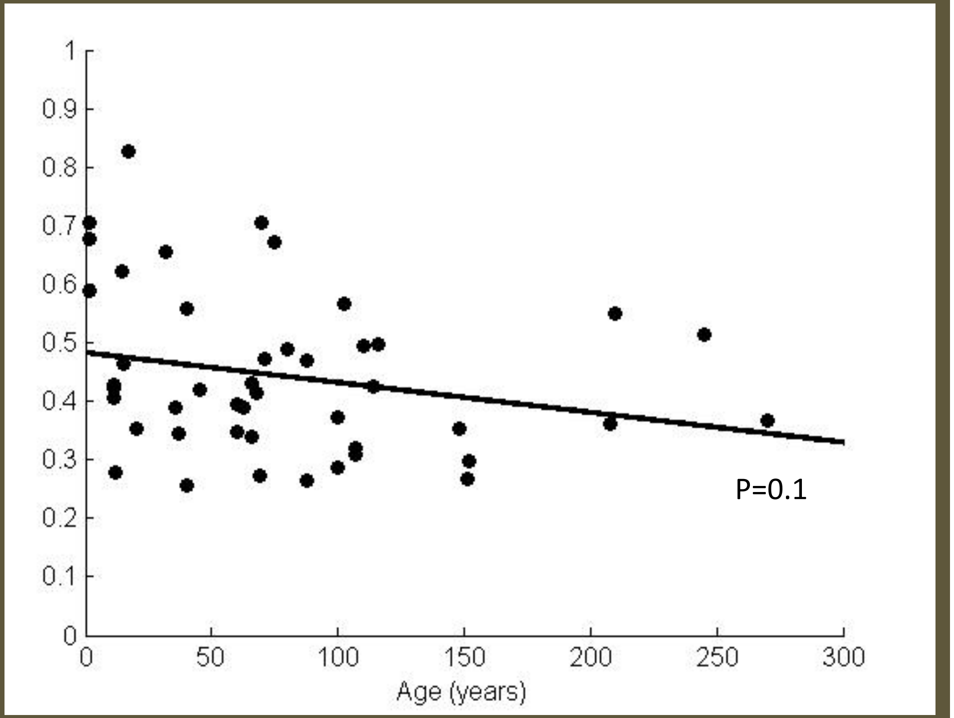




Can we solve this issue??

- Global forest database (Luyssaert et al 2007; n=49 for NPP:GPP analyses) shows similar patterns as observed by DeLucia et al 2007





Can we solve this issue??

- Global forest database (Luyssaert et al 2007; n=49 for NPP:GPP analyses) shows similar patterns as observed by DeLucia et al 2007
- IDEA:
  Global pattern was due to the unaccounted for NPP components: NPP = tree biomass production +
  - Fruits and seeds
  - Herbivory losses
  - Understory production
  - VOC emissions
  - Mycorrhizae
  - Exudates

Analyses

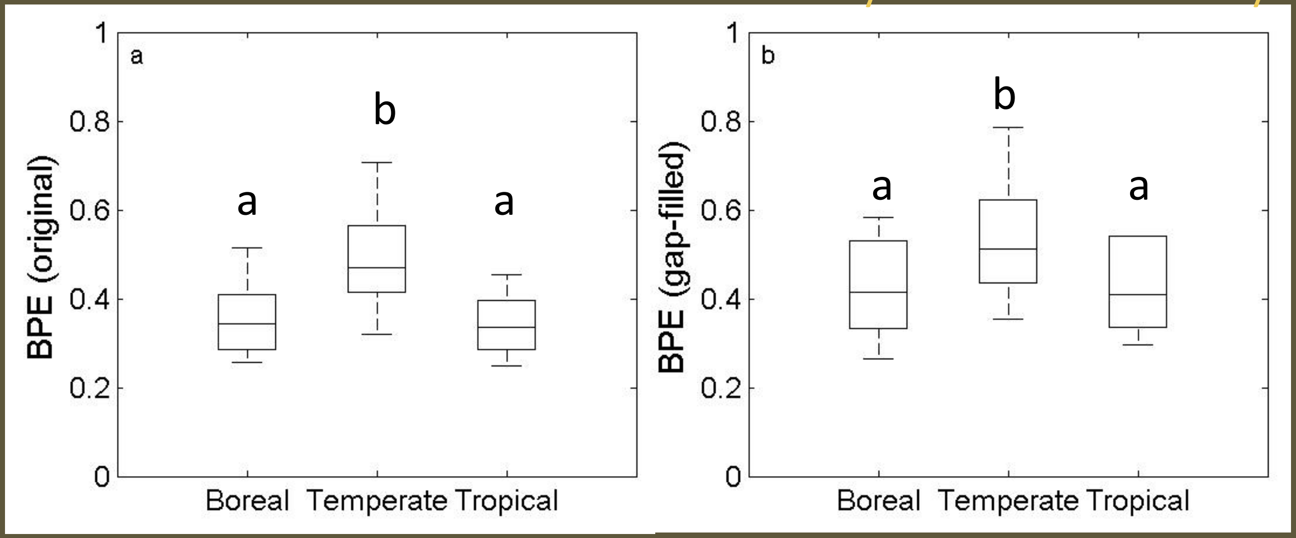
- DB included estimates for:
  - Fruits and seeds
  - Herbivory losses
  - Understory
- But no estimates available for
  - VOC emissions
  - Mycorrhizae
  - Exudates

Analyses

- New term:
  Biomass production:GPP = biomass production efficiency
  = BPE

Tree biomass only

Tree biomass + reproductive organs + herbivory losses + understory



Apparent contradiction with theory remains

Literature

- DB included estimates for:
  - Fruits
  - Herbivory losses
  - Understory
- But no estimates available for
  - VOC emissions → *usually < 5% of NPP*
  - Mycorrhizae → ***Can be large***
  - Exudates

(up to 30% of NPP; reviews by Hobbie et al., 2006 and Courty et al., 2010)

~ BPE=0.4 but NPP:GPP up to 0.6

Literature

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  - Exudates ***(up to 30% of NPP; reviews by Hobbie et al., 2006 and Courty et al., 2010)***

Up to 10% of NPP

~ BPE=0.4 but NPP:GPP up to 0.6

Literature

- Why would carbon allocation to mycorrhizae and exudates differ between forests?

NUTRIENTS

- Phillips & Fahey 2007: fertilization reduces mycorrhizal colonization in different tree species.
- Högberg et al 2010: fertilization reduces C allocation to soil biota by 60% in a boreal pine forest.
- Hobbie et al 2006 (review): fertilization reduces root exudation and symbionts by up to 22% of GPP.
- Treseder 2004 (review): P fertilization reduces mycorrhizal abundance by 32%
- Natural gradients in soil N content or atmospheric deposition: inversely related to mycorrhizal abundance, diversity, reproductive structures, … (Schulze et al 2000; Lilleskov et al 2002; Högberg et al 2003).

Literature

Can this help reconciling theory (constant CUE) and observations (variable BPE)?

If CUE is relatively constant

AND

we are missing a substantial fraction of NPP that is allocated to mycorrhizae and root exudates

We expect BPE to increase with increasing nutrient availability because mycorrhizae and exudates are tightly linked to nutrient availability

Analyses

- Does nutrient availability affect BPE??
  - No uniform measurements of nutrient availability currently available

Analyses

- Does nutrient availability affect BPE??
  - No uniform measurements of nutrient availability currently available
  - Nutrient classification based on different indicators:

			Indicators										Extra support
Site name	**ID**	**nutr. class**	**soil type**	**N soil**	**other nutr.**	**CEC/ exch. bases**	**N min.**	**pH**	**water status**	**flora**	**atm. dep.**	**history**	**report**
Bartlett	1	M		x			x						
Bornhoved Alder	2	L	x						x				x
Bornhoved Beech	3	M	x								x		
Cascade Head (1)	4	H		x									x
Cascade Head (1A)	5	H		x									x
Caxiuana	6	L			x	x							
Collelongo	7	H			x	x							x

Vicca et al., 2012
(Ecology Letters)

Analyses

- Does nutrient availability affect BPE??
  - No uniform measurements of nutrient availability currently available
  - Nutrient classification based on different indicators:
  - 49 forests → nutrient availability: 19 low
13 medium
17 high

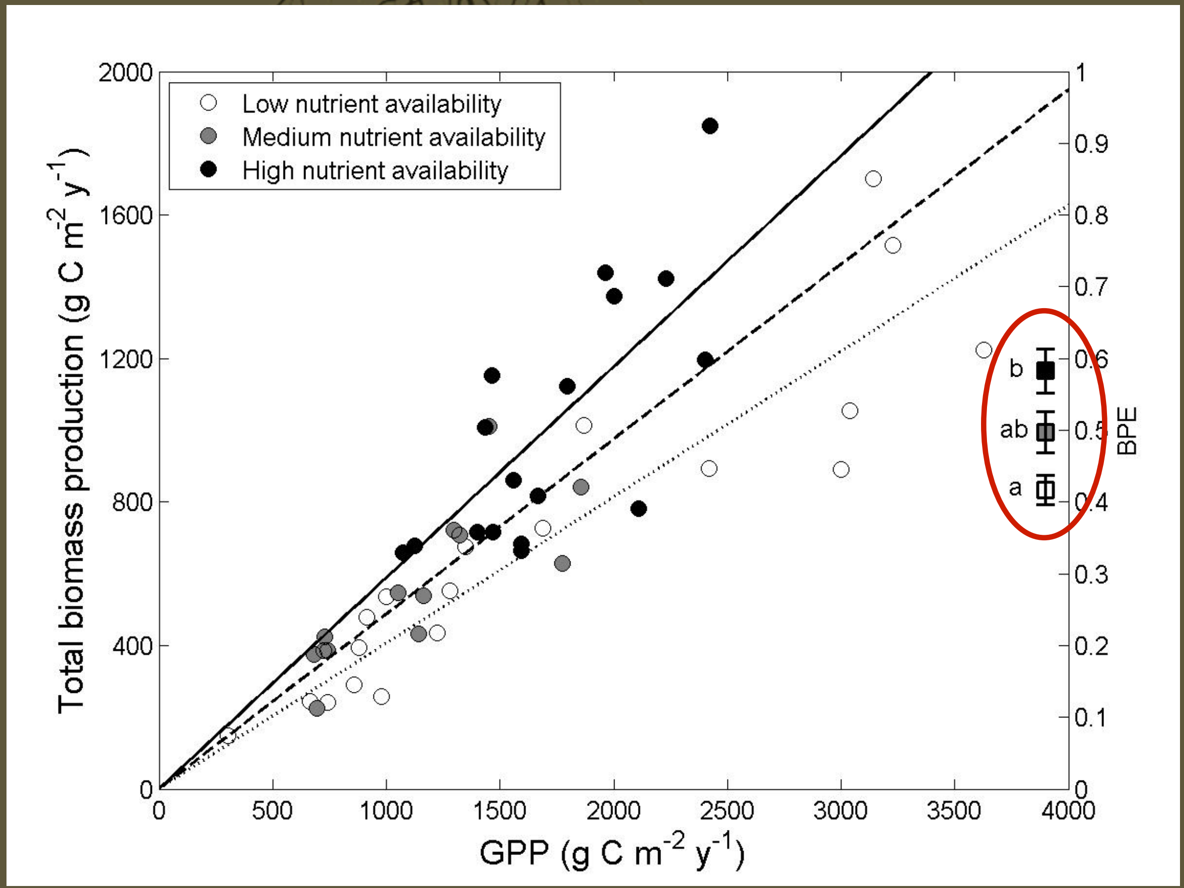
Results

- Nutrient effect on GPP and biomass production:
  - GPP increases ($p=0.05$)
  - Biomass production increases ($p<0.01$) – mainly wood

Climate zone, nutrient availability	GPP (g C m^{-2} y^{-1})	Biomass production (g C m^{-2} y^{-1})
Temperate, low	1320 (718)	565 (264)
Temperate, medium	1328 (372)	659 (208)
Temperate, high	1724 (408)	1008 (354)

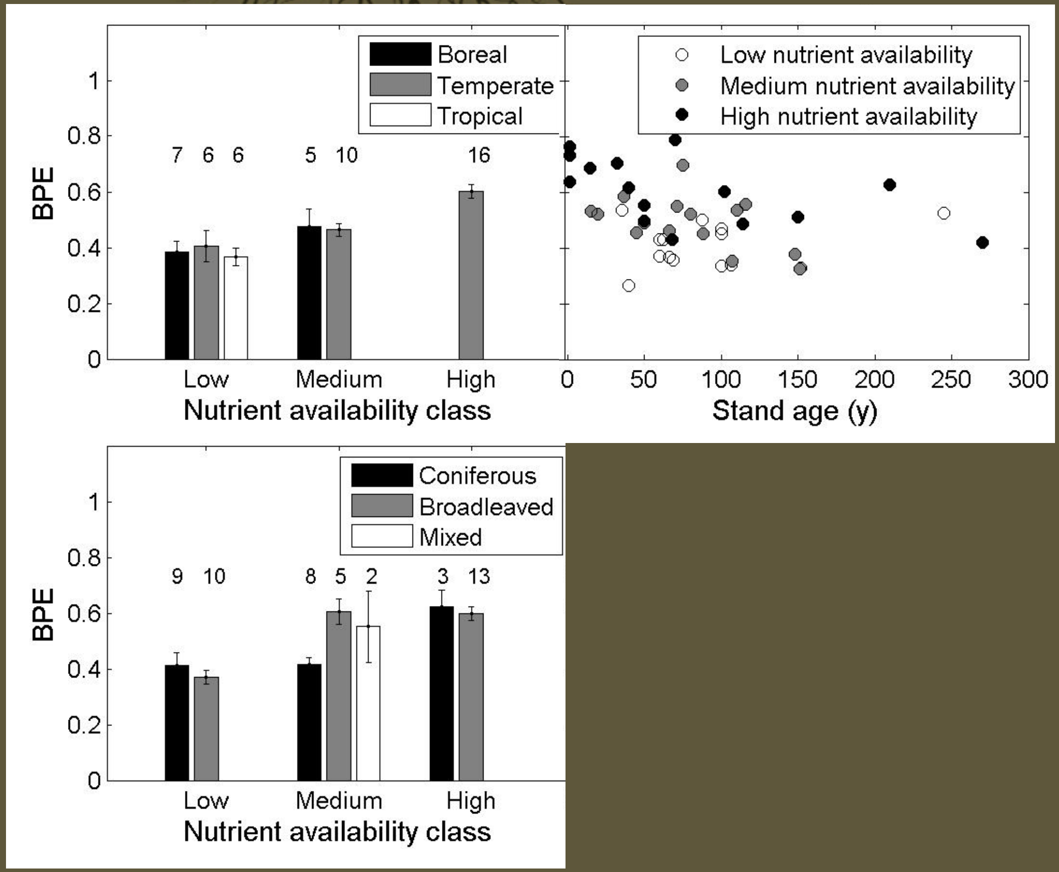
Results

- Nutrient effect on BPE:



Vicca et al., 2012
(Ecology Letters)

Results



Vicca et al., 2012
(Ecology Letters)

Conclusions (1)

- Nutrients were hidden drivers behind previously observed differences among climates, forest types and stand ages
- This may reconcile theory (CUE is constant) and observations (BPE varies substantially) if the nutrient availability reflects carbon allocation to mycorrhizae and exudates
- Data needed for CUE research: **total** NPP or Ra

Next question:

How does nutrient availability affect carbon balance in forests?

- ❑ What happens to decomposition rates?

nature geoscience

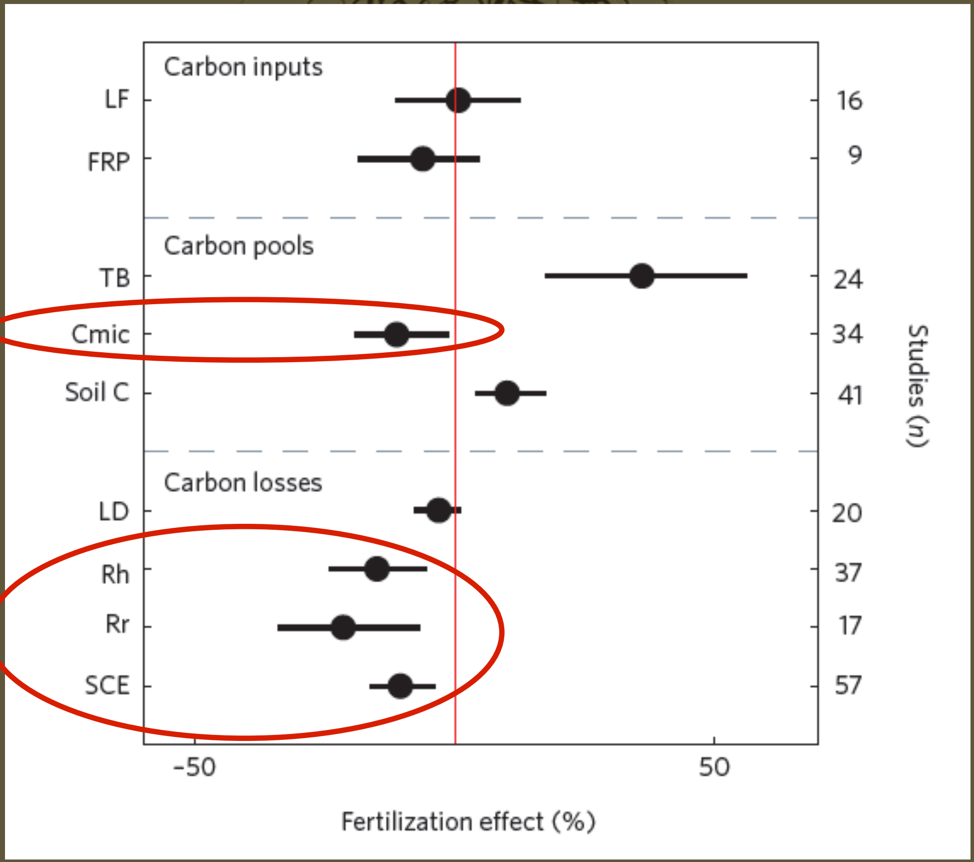
FOCUS | REVIEW ARTICLE
PUBLISHED ONLINE: 25 APRIL 2010 | DOI: 10.1038/NGEO844

Reduction of forest soil respiration in response to nitrogen deposition

I. A. Janssens[1]*, W. Dieleman[1], S. Luyssaert[2], J-A. Subke[3], M. Reichstein[4], R. Ceulemans[1], P. Ciais[2], A. J. Dolman[5], J. Grace[6], G. Matteucci[7], D. Papale[8], S. L. Piao[9], E-D. Schulze[4], J. Tang[10] and B. E. Law[11]

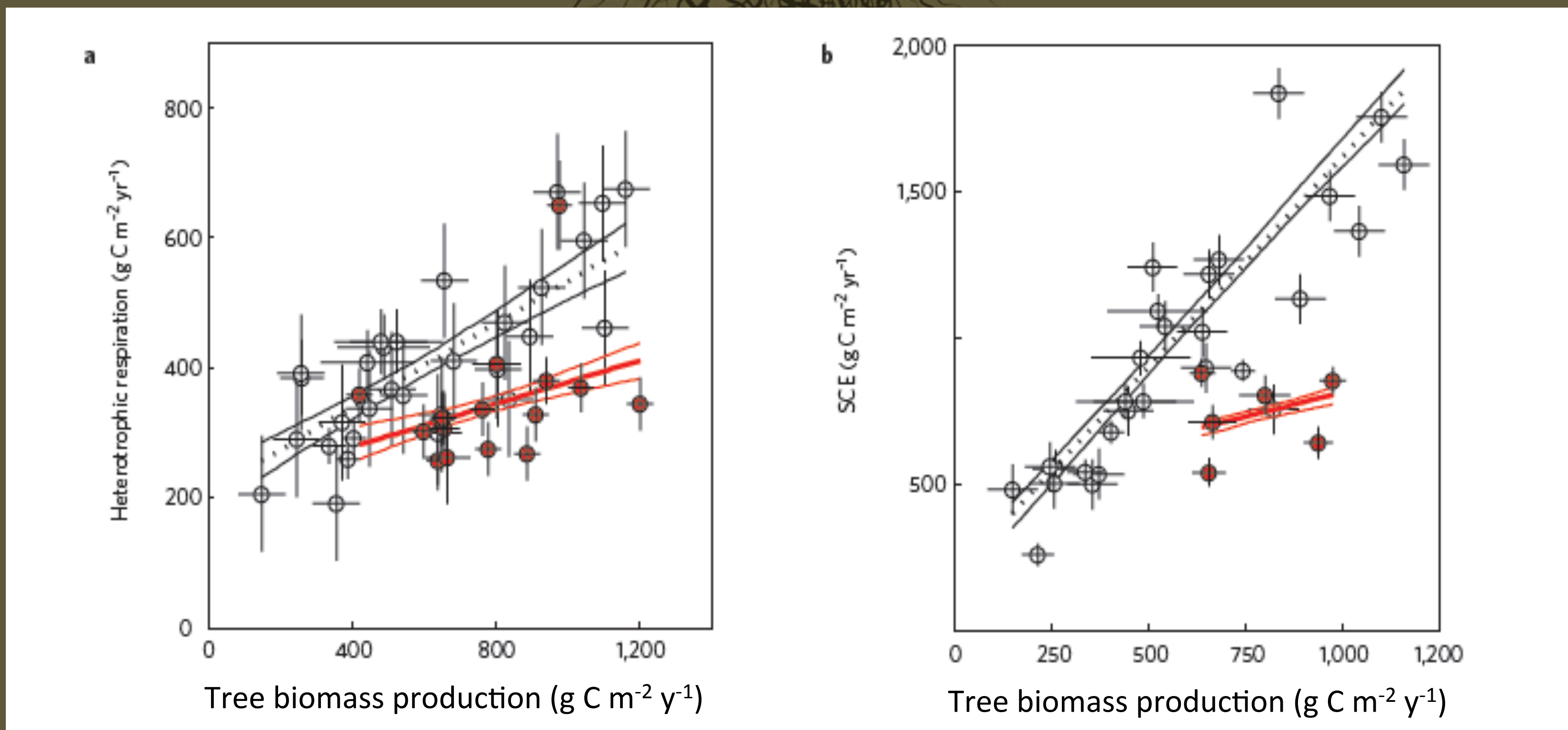
The use of fossil fuels and fertilizers has increased the amount of biologically reactive nitrogen in the atmosphere over the past century. As a consequence, forests in industrialized regions have experienced greater rates of nitrogen deposition in recent decades. This unintended fertilization has stimulated forest growth, but has also affected soil microbial activity, and thus the recycling of soil carbon and nutrients. A meta-analysis suggests that nitrogen deposition impedes organic matter decomposition, and thus stimulates carbon sequestration, in temperate forest soils where nitrogen is not limiting microbial growth. The concomitant reduction in soil carbon emissions is substantial, and equivalent in magnitude to the amount of carbon taken up by trees owing to nitrogen fertilization. As atmospheric nitrogen levels continue to rise, increased nitrogen deposition could spread to older, more weathered soils, as found in the tropics; however, soil carbon cycling in tropical forests cannot yet be assessed.

Fertilization manipulation experiments



Janssens et al., 2010
(Nature Geoscience)

Forest database



White = low N deposition

Red = high N deposition

Janssens et al., 2010
(Nature Geoscience)

Next question:

How does nutrient availability affect carbon balance in forests?

- ❑ What happens to decomposition rates?
  - ➢ Microbial activity and decomposition decrease when nutrient availability increases
- ❑ If BPE increases and microbial respiration decreases with increasing nutrient availability, does NEP increase? (NEP=GPP-Ra-Rh)

Analyses

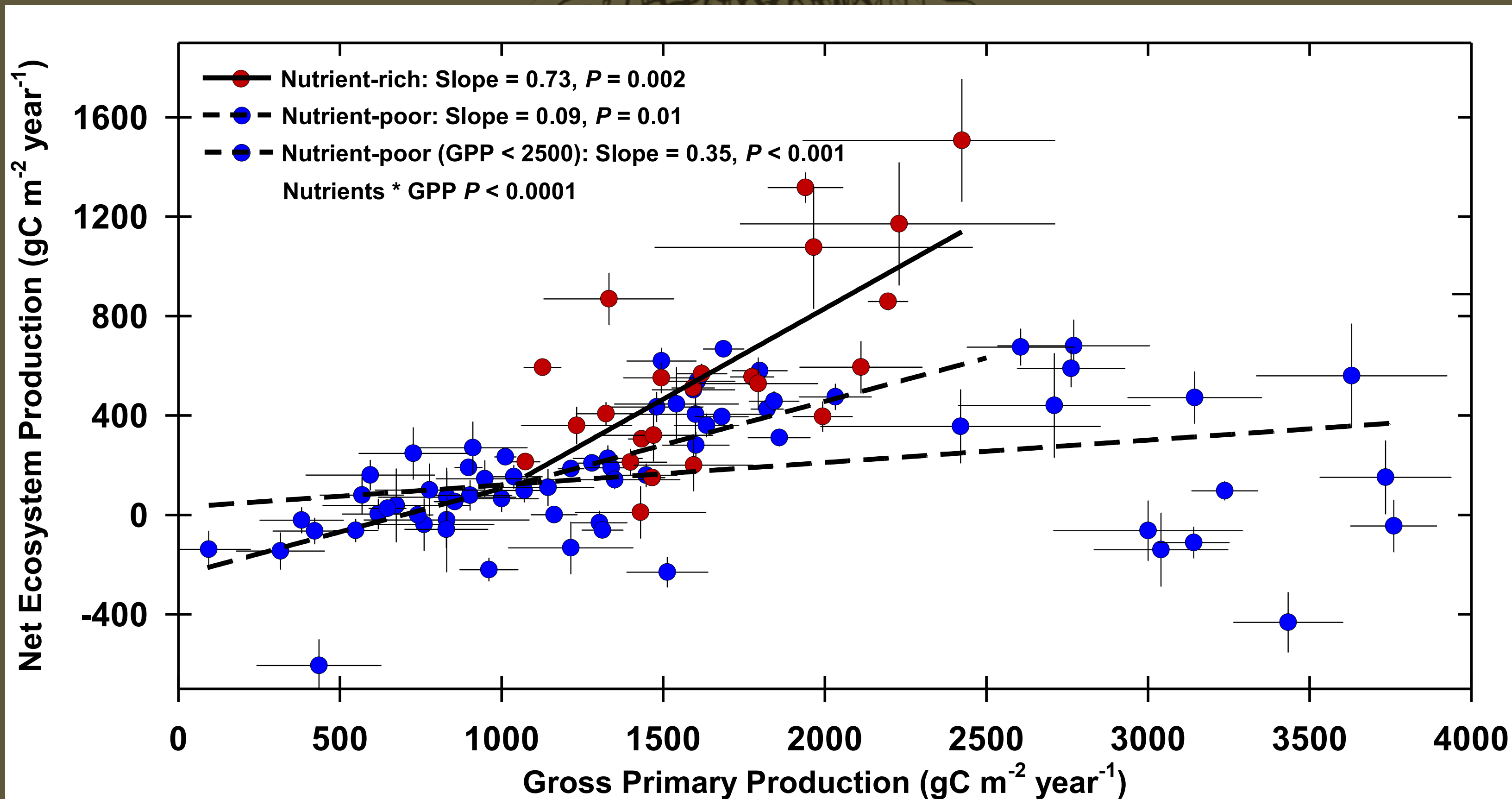
- 92 forests of low or high nutrient availability with NEP and GPP data available
- GLM to test drivers of NEP; predictor variables included:
    - Nutrient availability
    - Climate (MAP, MAT, WD)
    - Stand age
    - Management
    - GPP

Results

NEP =

Predictor	estimate	p value	R^2
(intercept)	-1056	<0.01	
GPP	0.87	<0.01	0.18
AGE	4.76	<0.01	0.03
NUTRIENTS	934.9	<0.01	0.19
MAT	20.67	<0.01	0.09
GPP * AGE	-0.0029	<0.01	0.09
GPP * NUTRIENTS	-0.68	<0.01	0.15
AGE * NUTRIENTS	-1.86	0.018	0.01

Results



Fernández-Martínez et al,
under review for Nature

Next question:

How does nutrient availability affect carbon balance in forests?

- What happens to decomposition rates?
    - Microbial activity thus decomposition decrease when nutrient availability increases
- If BPE increases and microbial respiration decreases with increasing fertility, does NEP increase? (NEP=GPP-Ra-Rh)
    - **Yes**. NEP can only be high when nutrient availability is high

Conclusions

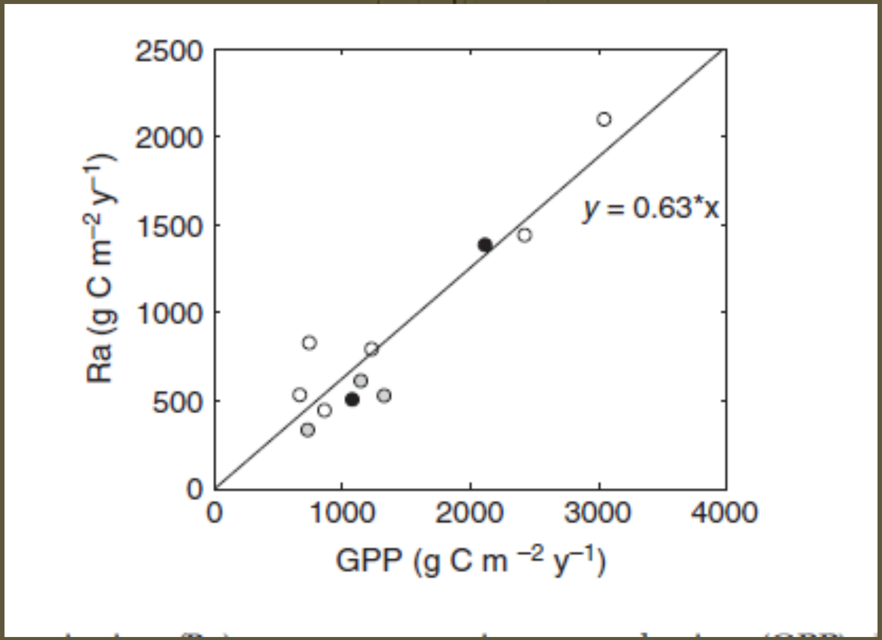
- CUE: still not sure if/how/why it varies among forests
- BPE increases with increasing nutrient availability. If missing NPP components are behind this, CUE is less variable than assumed from the data.
- NEP increases with increasing nutrient availability
- High carbon sequestration only possible when nutrient availability is high

Thanks for your attention

Extra

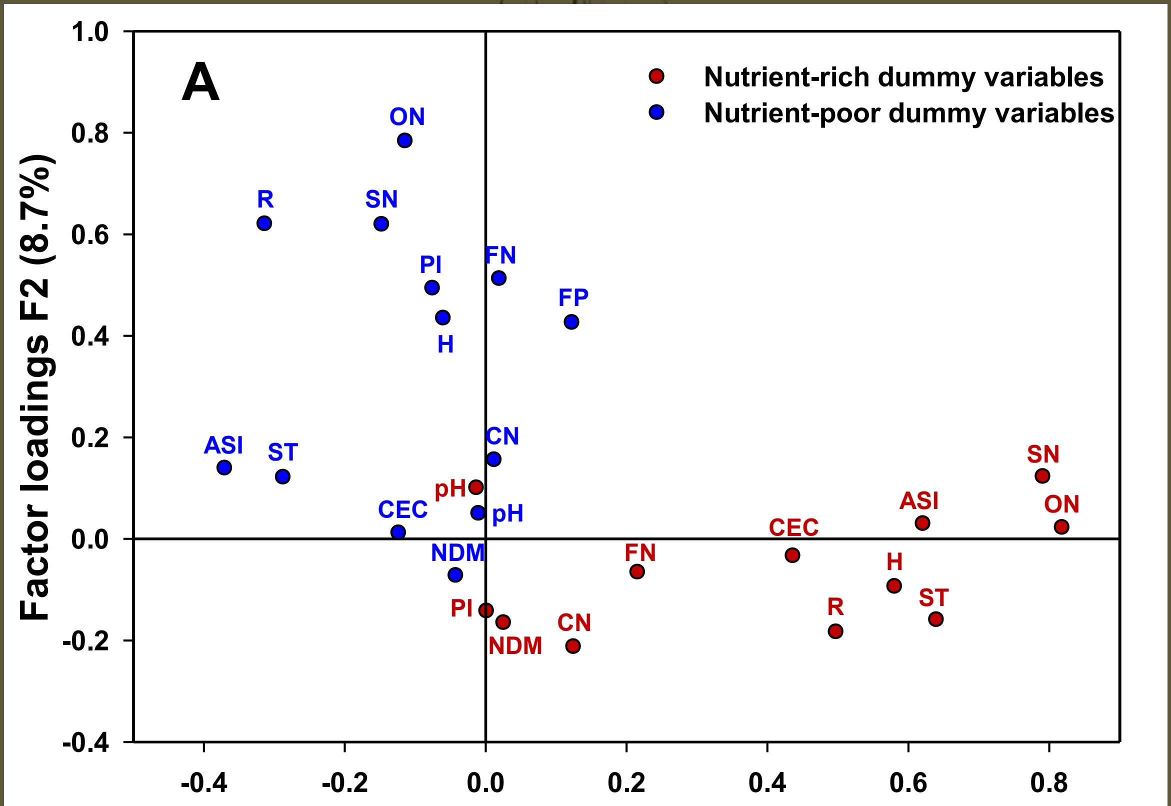
Climate zone, nutrient availability	GPP (g C m^{-2} y^{-1})	Biomass production (g C m^{-2} y^{-1})	BPE
Boreal, low	911 (184)	355 (124)	0.39 (0.10)
Temperate, low	1320 (718)	565 (264)	0.43 (0.05)
Tropical, low	2985 (591)	1233 (315)	0.41 (0.11)
Boreal, medium	803 (204)	390 (112)	0.49 (0.10)
Temperate, medium	1328 (372)	659 (208)	0.50 (0.11)
Temperate, high	1724 (408)	1008 (354)	0.58 (0.13)

EXTRA

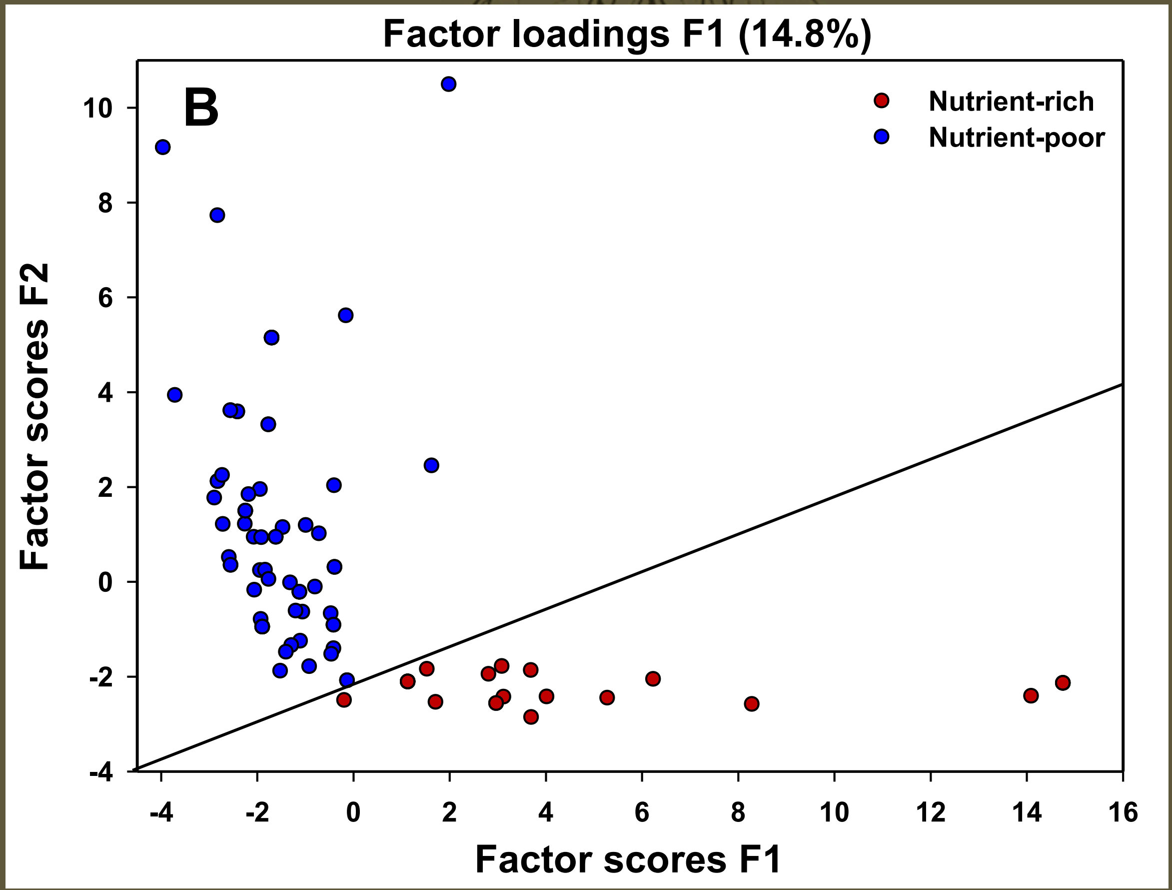


2500
2000
1500
1000
500
0
0
1000
2000
3000
4000
y = 0.63*x
Ra (g C m⁻² y⁻¹)
GPP (g C m −2 y−1)

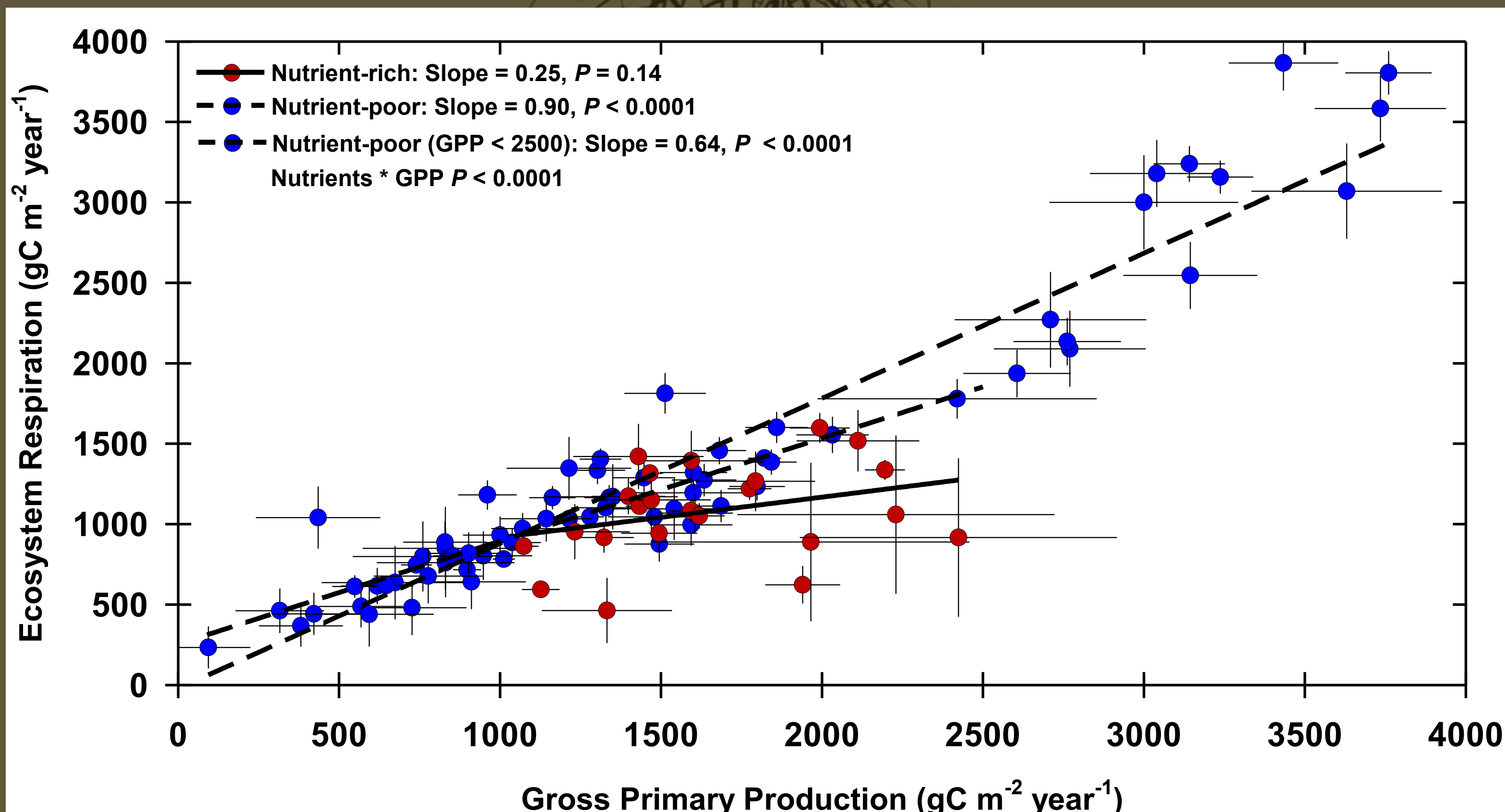
EXTRA


A
Nutrient-rich dummy variables
Nutrient-poor dummy variables
Factor loadings F2 (8.7%)
1.0
0.8
0.6
0.4
0.2
0.0
-0.2
-0.4
-0.4
-0.2
0.0
0.2
0.4
0.6
0.8
ON
R
SN
PI
FN
FP
H
ASI
ST
CN
pH
CEC
NDM
CN
FN
CEC
ASI
SN
ON
H
R
ST
PI
NDM

EXTRA

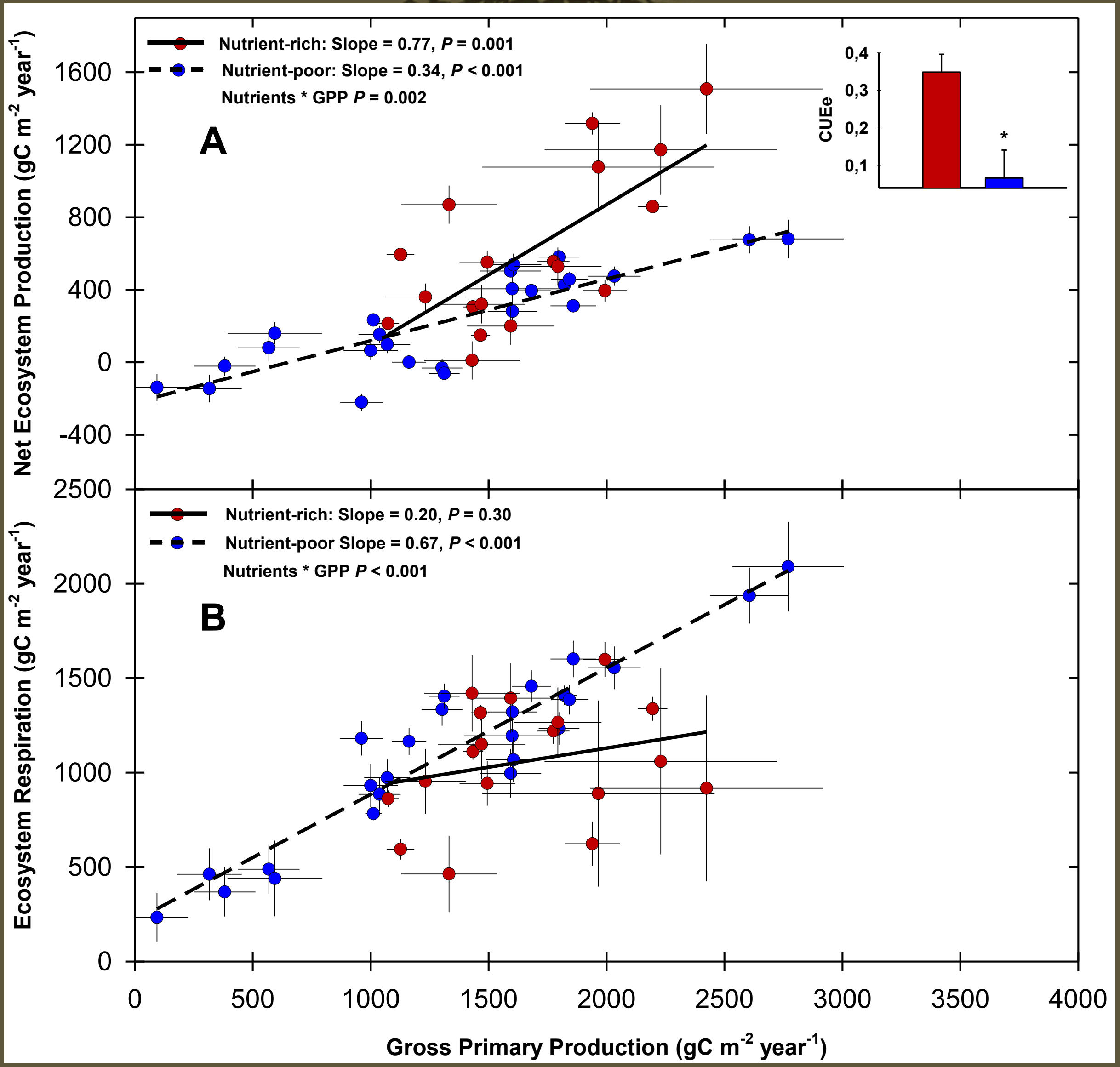

Factor loadings F1 (14.8%)
B
Nutrient-rich
Nutrient-poor
Factor scores F2
Factor scores F1
10
8
6
4
2
0
-2
-4
-4
-2
0
2
4
6
8
10
12
14
16

EXTRA



Nutrient-rich: Slope = 0.25, P = 0.14
Nutrient-poor: Slope = 0.90, P < 0.0001
Nutrient-poor (GPP < 2500): Slope = 0.64, P < 0.0001
Nutrients * GPP P < 0.0001
Ecosystem Respiration (gC m-2 year-1)
Gross Primary Production (gC m-2 year-1)
0
500
1000
1500
2000
2500
3000
3500
4000

EXTRA

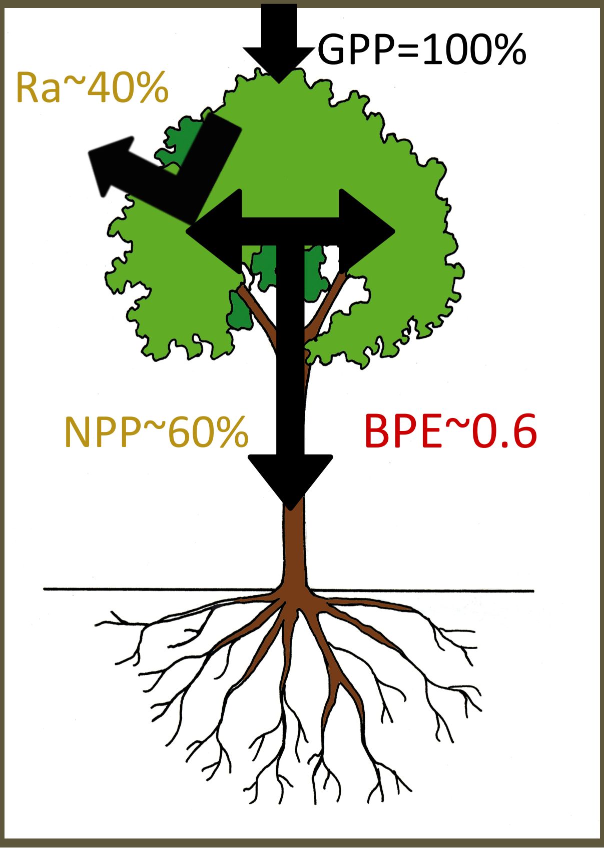


Nutrient-rich: Slope = 0.77, P = 0.001
Nutrient-poor: Slope = 0.34, P < 0.001
Nutrients * GPP P = 0.002
A
CUEe
0,4
0,3
0,2
0,1
*
Net Ecosystem Production (gC m-2 year-1)
1600
1200
800
400
0
-400
Nutrient-rich: Slope = 0.20, P = 0.30
Nutrient-poor Slope = 0.67, P < 0.001
Nutrients * GPP P < 0.001
B
Ecosystem Respiration (gC m-2 year-1)
2500
2000
1500
1000
500
0
0
500
1000
1500
2000
2500
3000
3500
4000
Gross Primary Production (gC m-2 year-1)

Literature

Can this help reconciling theory (constant CUE) and observations (variable BPE)?

No missing NPP components



Literature

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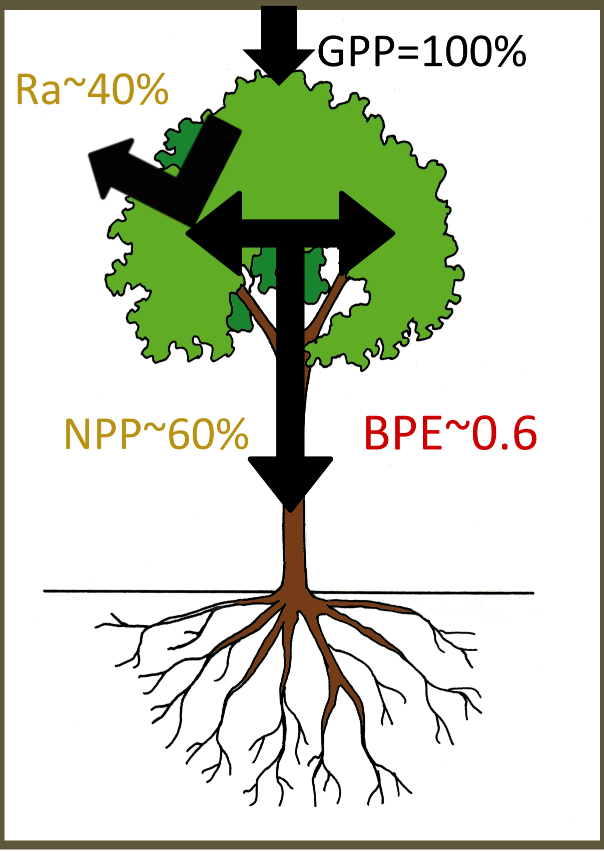

30% of NPP to mycorrhizae and exudates