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

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

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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 1650 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 below ground.

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 $0.23 < \text{CUE} < 0.83$
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: $$\text{NPP} = \text{tree biomass production} +$$
  - 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

Apparent contradiction with theory remains
• DB included estimates for:
  – Fruits
  – Herbivory losses
  – Understory
• But no estimates available for
  – VOC emissions  \( \text{usually} < 5\% \text{ of NPP} \)
  – Mycorrhizae  \( \text{Can be large} \)
  – Exudates  \( \text{(up to} 30\% \text{ of NPP; reviews by Hobbie et al., 2006 and Courty et al., 2010)} \)
  \( \sim BPE=0.4 \text{ but } NPP:GPP \text{ up to 0.6} \)
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  → *Can be large*  
    (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*
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).
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
• Does nutrient availability affect BPE??
  – No uniform measurements of nutrient availability currently available
  – Nutrient classification based on different indicators:

<table>
<thead>
<tr>
<th>Site name</th>
<th>ID</th>
<th>nutr. class</th>
<th>soil type</th>
<th>N</th>
<th>soil</th>
<th>other nutr.</th>
<th>CEC/ exch. bases</th>
<th>N min.</th>
<th>pH</th>
<th>water status</th>
<th>flora</th>
<th>atm. dep.</th>
<th>history</th>
<th>report</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bartlett</td>
<td>1</td>
<td>M</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Bornhoved Alder</td>
<td>2</td>
<td>L</td>
<td>x</td>
<td>x</td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bornhoved Beech</td>
<td>3</td>
<td>M</td>
<td>x</td>
<td>x</td>
<td></td>
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</tr>
<tr>
<td>Cascade Head (1)</td>
<td>4</td>
<td>H</td>
<td>x</td>
<td></td>
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<tr>
<td>Cascade Head (1A)</td>
<td>5</td>
<td>H</td>
<td>x</td>
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</tr>
<tr>
<td>Caxiuana</td>
<td>6</td>
<td>L</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Collelongo</td>
<td>7</td>
<td>H</td>
<td>x</td>
<td>x</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

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

<table>
<thead>
<tr>
<th>Climate zone, nutrient availability</th>
<th>GPP (g C m⁻² y⁻¹)</th>
<th>Biomass production (g C m⁻² y⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Temperate, low</td>
<td>1320 (718)</td>
<td>565 (264)</td>
</tr>
<tr>
<td>Temperate, medium</td>
<td>1328 (372)</td>
<td>659 (208)</td>
</tr>
<tr>
<td>Temperate, high</td>
<td>1724 (408)</td>
<td>1008 (354)</td>
</tr>
</tbody>
</table>
Results

- Nutrient effect on BPE:

Vicca et al., 2012
(Ecology Letters)
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?
Reduction of forest soil respiration in response to nitrogen deposition


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

Janssens et al., 2010
(Nature Geoscience)

White = low N deposition
Red = high N deposition
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

$$\text{NEP} =$$

<table>
<thead>
<tr>
<th>Predictor</th>
<th>estimate</th>
<th>p value</th>
<th>$R^2$</th>
</tr>
</thead>
<tbody>
<tr>
<td>(intercept)</td>
<td>-1056</td>
<td>$&lt;0.01$</td>
<td></td>
</tr>
<tr>
<td>GPP</td>
<td>0.87</td>
<td>$&lt;0.01$</td>
<td>0.18</td>
</tr>
<tr>
<td>AGE</td>
<td>4.76</td>
<td>$&lt;0.01$</td>
<td>0.03</td>
</tr>
<tr>
<td>NUTRIENTS</td>
<td>934.9</td>
<td>$&lt;0.01$</td>
<td>0.19</td>
</tr>
<tr>
<td>MAT</td>
<td>20.67</td>
<td>$&lt;0.01$</td>
<td>0.09</td>
</tr>
<tr>
<td>GPP * AGE</td>
<td>-0.0029</td>
<td>$&lt;0.01$</td>
<td>0.09</td>
</tr>
<tr>
<td>GPP * NUTRIENTS</td>
<td>-0.68</td>
<td>$&lt;0.01$</td>
<td>0.15</td>
</tr>
<tr>
<td>AGE * NUTRIENTS</td>
<td>-1.86</td>
<td>0.018</td>
<td>0.01</td>
</tr>
</tbody>
</table>
Results

Gross Primary Production (gC m$^{-2}$ year$^{-1}$)

Net Ecosystem Production (gC m$^{-2}$ year$^{-1}$)

Nutrient-poor: Slope = 0.09, $P = 0.01$

Nutrient-rich: Slope = 0.73, $P = 0.002$

Nutrients * GPP $P < 0.0001$

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
### Climate zone, nutrient availability

<table>
<thead>
<tr>
<th>Climate zone, nutrient availability</th>
<th>GPP (g C m(^{-2}) y(^{-1}))</th>
<th>Biomass production (g C m(^{-2}) y(^{-1}))</th>
<th>BPE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Boreal, low</td>
<td>911 (184)</td>
<td>355 (124)</td>
<td>0.39 (0.10)</td>
</tr>
<tr>
<td>Temperate, low</td>
<td>1320 (718)</td>
<td>565 (264)</td>
<td>0.43 (0.05)</td>
</tr>
<tr>
<td>Tropical, low</td>
<td>2985 (591)</td>
<td>1233 (315)</td>
<td>0.41 (0.11)</td>
</tr>
<tr>
<td>Boreal, medium</td>
<td>803 (204)</td>
<td>390 (112)</td>
<td>0.49 (0.10)</td>
</tr>
<tr>
<td>Temperate, medium</td>
<td>1328 (372)</td>
<td>659 (208)</td>
<td>0.50 (0.11)</td>
</tr>
<tr>
<td>Temperate, high</td>
<td>1724 (408)</td>
<td>1008 (354)</td>
<td>0.58 (0.13)</td>
</tr>
</tbody>
</table>
Factor loadings F1 (14.8%)

-0.4  -0.2  0.0  0.2  0.4  0.6  0.8

Factor loadings F2 (8.7%)

-0.4  -0.2  0.0  0.2  0.4  0.6  0.8  1.0

Nutrient-rich dummy variables
Nutrient-poor dummy variables

ON  R  PI  FN  H  FP  SN  CN  CEC  ST  ASI  pH  NDM

Factor scores F1

-4  -2  0  2  4  6  8  10  12  14  16

Factor scores F2

-4  -2  0  2  4  6  8  10  12  14  16

A

Nutrient-rich dummy variables
Nutrient-poor dummy variables
Factor loadings F1 (14.8%)

Factor loadings F2 (8.7%)

Nutrient-rich dummy variables
- N
- P
- F
- H
- F
- C
- C
- H
- N
- D

Nutrient-poor dummy variables
- A
- S
- N
- C
- T
- A
- R
- H
- S
- N

Factor scores F1
- A
- B
- C
- D

Factor scores F2
- E
- F
- G
- H

Nutrient-rich
- Red
- Nutrient-poor
- Blue
Gross Primary Production (gC m\(^{-2}\) year\(^{-1}\))

Ecosystem Respiration (gC m\(^{-2}\) year\(^{-1}\))

Nutrients * GPP

- 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 \(P < 0.0001\)
EXTRA

Net Ecosystem Production (gC m\(^{-2}\) year\(^{-1}\))

Gross Primary Production (gC m\(^{-2}\) year\(^{-1}\))

Ecosystem Respiration (gC m\(^{-2}\) year\(^{-1}\))

Nutrient-poor Slope = 0.34, \(P < 0.001\)

Nutrient-rich: Slope = 0.77, \(P = 0.001\)

Nutrient-rich: Slope = 0.20, \(P = 0.30\)

Nutrients \(\times\) GPP \(P = 0.002\)

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

No missing NPP components
Can this help reconciling theory (constant CUE) and observations (variable BPE)?

No missing NPP components

30% of NPP to mycorrhizae and exudates