Soil nutrient competition: observations, theories, and implementation in earth system land model

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Overview

• Background
  – Why does competition occur?

• $^{15}\text{N}$ competition observations
  – What can we learn?

• Existing competition theories

• New competition theory

• Competition models vs. data
  – Tropical forests, alpine grassland, arctic tundra
Why does competition occur?

- N affect ecosystem C cycle
  - nitrogen-rich RuBisCO enzymes
  - nitrogen-rich extracellular enzymes
- P affect ecosystem C cycle
  - phosphorus-rich ATP
- Temperate and boreal
  - nitrogen limited
- Tropical forests
  - phosphorus limited

Schimel and Weintraub 2003
Competition hierarchy

Direct competition

Plant adjustment

Successional dynamics

Hour  week  month  year  decade
$^{15}\text{N}$ competition observations

![Graphs showing $^{15}\text{N}$ competition observations](image)
# Prevailing competition theories

<table>
<thead>
<tr>
<th>Competition Theory</th>
<th>Rationale</th>
<th>Implementation</th>
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</thead>
<tbody>
<tr>
<td><strong>CT1. No competition</strong></td>
<td>(1) Plants are nutrient limited; microbial decomposers are carbon limited.</td>
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<td>(2) Plants rely on inorganic nitrogen; microbial decomposers rely on organic nitrogen.</td>
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<tr>
<td><strong>CT2. Microbial decomposers outcompete plants</strong></td>
<td>(1) Microbial decomposers are ubiquitous.</td>
<td>(1) Separately simulate plant and microbial decomposer nutrient uptake.</td>
</tr>
<tr>
<td></td>
<td>(2) Microbial decomposers release inorganic nitrogen as “waste product” during soil organic matter decomposition.</td>
<td>(2) If soil inorganic nutrient is limited, immobilization is satisfied prior to plant uptake.</td>
</tr>
<tr>
<td><strong>CT3. Competition depends on pore-scale soil fertility heterogeneity</strong></td>
<td>(1) Plants do not completely lose the competition.</td>
<td>Explicit modeling of microsite scale soil fertility heterogeneity, nutrient diffusion, root-microbe interactions (~ mm spatial scale).</td>
</tr>
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<td>(2) Existence of plants exacerbates microbial nutrient limitation and suppress microbial immobilization at both microsite and whole-soil scales.</td>
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<tr>
<td><strong>CT4. Plant-microbe Relative Demand controls competition</strong></td>
<td>(1) Plant nutrient demand is a proxy of nutrient uptake capacity.</td>
<td>(1) Separately simulate plant and microbial decomposer nutrient uptake.</td>
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<td>(2) Expedient approach to implement competition in large-scale models.</td>
<td>(2) If soil inorganic nutrient is limited, both fluxes are down regulated proportional to demand.</td>
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<td>(3) No need to introduce parameters describing nutrient uptake and competition.</td>
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</table>
## Competition hypotheses in ESMs

<table>
<thead>
<tr>
<th>ESMs</th>
<th>Land component</th>
<th>Plant N uptake</th>
<th>Soil N immobilization</th>
<th>Competition</th>
</tr>
</thead>
<tbody>
<tr>
<td>BNU-ESM</td>
<td>CoLM + BNU-DGVM</td>
<td>$N_{demand} \cdot N_{stress}$</td>
<td>No gross mineralization and immobilization, net mineralization is directly calculated</td>
<td>Microbial decomposers outcompete plants</td>
</tr>
<tr>
<td>CESM</td>
<td>CLM4.5-BGC/CLM4-CN/CLM4-CNP</td>
<td>$N_{demand} \cdot N_{stress}$ or $N_{require} \cdot \min{N_{stress}, P_{stress}}$</td>
<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Relative Demand</td>
</tr>
<tr>
<td>ISPL</td>
<td>ORCHIDEE (now O-CN)</td>
<td>$V_{max} \cdot C_{root} \cdot [N_{av}] \cdot f_{T} \cdot f_{NC}$</td>
<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Microbial decomposers outcompete plants</td>
</tr>
<tr>
<td>GFDL</td>
<td>LM3 (now LM3-TAN)</td>
<td>$V_{max} \cdot C_{root} \cdot \frac{[N_{av}]}{K_{m} + [N_{av}]}$</td>
<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Microbial decomposers outcompete plants</td>
</tr>
<tr>
<td>HadGEM2</td>
<td>JULES (now JULES+ECOSSE)</td>
<td>$N_{demand} \cdot f_{T}$</td>
<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Microbial decomposers outcompete plants</td>
</tr>
<tr>
<td>MPI-ESM</td>
<td>JSBACH (now JSBACH-CNP)</td>
<td>$N_{demand} \cdot \min{N_{stress}, P_{stress}}$</td>
<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Relative Demand</td>
</tr>
<tr>
<td>NorESM</td>
<td>CLM-CN</td>
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<td>Carbon fluxes between soil organic matter pools scaled by their soil C:N ratios</td>
<td>Relative Demand</td>
</tr>
</tbody>
</table>
ECA Competition hypothesis: Enzyme-enzyme battle

\[ S + E_{\text{plant}} \xrightleftharpoons[k^-_{\text{plant}}]{k^+_{\text{plant}}} C_{\text{plant}} \xrightarrow[k^+_{\text{plant}}]{k^-_{\text{plant}}} P + E_{\text{plant}} \]

\[ S + E_{\text{mic}} \xrightleftharpoons[k^-_{\text{mic}}]{k^+_{\text{mic}}} C_{\text{mic}} \xrightarrow[k^+_{\text{mic}}]{k^-_{\text{mic}}} P + E_{\text{mic}} \]
Substrate diffusivity limitation

1. Explicit modeling of nutrient heterogeneity

2. Implicitly aggregated diffusivity limitation in kinetics parameter (model $K_M \neq$ observed $K_M$)
Tropical forest sites

<table>
<thead>
<tr>
<th>Data Sets</th>
<th>Dose</th>
<th>Competitors</th>
<th>Duration</th>
<th>References</th>
</tr>
</thead>
<tbody>
<tr>
<td>$^{25}$PO$_4$</td>
<td>10 $\mu$g$^{-1}$</td>
<td>I. Mineral</td>
<td></td>
<td></td>
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<tr>
<td>fertilization</td>
<td></td>
<td>II. Decomposing</td>
<td></td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>surface</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>microbe</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$^{15}$NH$_4$</td>
<td>4.6 $\mu$g$^{-1}$</td>
<td>I. Plant</td>
<td></td>
<td></td>
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<tr>
<td>fertilization</td>
<td></td>
<td>II. Decomposing</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>III. Nitrifier</td>
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<td></td>
<td></td>
<td>24h</td>
<td></td>
<td>[Templer et al., 2008]</td>
</tr>
<tr>
<td>$^{15}$NO$_3$</td>
<td>0.92 $\mu$g$^{-1}$</td>
<td>I. Plant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>fertilization</td>
<td></td>
<td>II. Decomposing</td>
<td></td>
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<tr>
<td></td>
<td></td>
<td>microbe</td>
<td></td>
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<td></td>
<td></td>
<td>24h</td>
<td></td>
<td>[Templer et al., 2008]</td>
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</tbody>
</table>
Alpine grassland site

$^{15}$N-NH$_4^+$/$^{15}$N-NO$_3^-$ fertilization study (24~48 h)
Xu et al., 2011
Arctic tundra sites: $^{15}$N tracer data

- **Extractable NH$_4$-N**
  - (g N / m$^3$ soil)
  - Soil depth increment (cm):
    - 0-5
    - 5-10
    - 10-15
    - 15-20
    - 20-25
    - 25-30
    - 30-35

- **Organic soil**
- **Mineral soil**

**Live fine-root biomass**
- Carex aquatilis
- Eriophorum angustifolium
- Salix rotundifolia
  - Soil depth increment (cm):
    - 0-5
    - 5-10
    - 10-15
    - 15-20
    - 20-25
  - Live fine-root biomass (g root /m$^3$ soil)
Competitive traits

- **Carex**: competitive species
  - High affinity nitrogen carrier enzyme (low KM) (McRoy 1975)
- **Salix**: competitive species
  - Mycorrhizal fungi (Kroehler 1988)
- **Eriophorum**: uncompetitive species
  - Low affinity nitrogen carrier enzyme (high KM) (Leadley 1997)
  - No mycorrhizal fungi (Lavoie 2005)
Root trait data

- Root nitrogen uptake kinetics parameter
- Root depth
  - Canadell 1996 (global)
  - Iversen 2015b (tundra)
- Root density profile
  - Zeng 2001
  - Schenk 2002
- Mycorrhizal fungi association
  - Soudzilovskaia 2015
Conclusions

- There are multiple competition theories (MIC win, RD, micropore-to-micropore, no competition)
- Two of them are not applicable in ESM (micropore-to-micropore, no competition)
- Two of them are not successful in ESM (MIC win, RD)
- The new competition theory (ECA) is best one so far.
Thanks!

Questions?