The Ecological Impacts Of Nitrogen Deposition: Insights From The Carnivorous Pitcher Plant *Sarracenia purpurea*

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Burning of Fossil Fuels

Nitrogen oxides NO$_x$

Use of Synthetic Fertilizers

Nitrate NO$_3$
Ammonium NH$_4$
The diagram illustrates the changes in teragrams of nitrogen from 1900 to 2000. It shows the total anthropogenic nitrogen fixed, fertilizer nitrogen, and NOx nitrogen. The natural range is depicted by the shaded area. The graph indicates a significant increase in anthropogenic nitrogen starting around 1960, with a rapid rise in the late 20th century.
Inorganic nitrogen wet deposition from nitrate and ammonium, 2001

Sites not pictured:
- AK01 0.2 kg/ha
- AK03 0.1 kg/ha
- HI99 0.9 kg/ha
- VI01 0.9 kg/ha

National Atmospheric Deposition Program/National Trends Network
http://nadp.sws.uiuc.edu
Sarracenia purpurea
The Northern Pitcher Plant
Effects of N Deposition

- **Individual**
  - Altered morphology
  - Changes in reproduction, survivorship

- **Population**
  - Increased long-term extinction risk
  - Changes in short-term dynamics

- **Community**
  - Changes in abundance and composition
  - Proteomic early-warning indicators
Effects of N Deposition on Carnivorous Plants

- Life History
- Effects on Individuals
- Effects on Populations
- Effects on Communities
- The Role of Ecologists
Effects of N Deposition on Carnivorous Plants

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Carnivorous plants: well-known, but poorly studied
Carnivory in plants

- Phylogenetically diverse
- Morphological, chemical adaptations for attracting, capturing, digesting arthropods
- Common in low N habitats
- Poor competitors for light, nutrients
The Northern Pitcher Plant
*Sarracenia purpurea*

- Perennial plant of low-N peatlands
- Lifespan 30-50 y
- Arthropod prey capture in water-filled pitchers
- Diverse inquiline community in pitchers
The Inquilines

Sarraceniopus gibsoni

Wyeomyia smithii

Blaesoxipha fletcheri

Habrotrocha rosa

Metriocnemus knabi
Inquiline food web

Food web of *Sarracenia* inquilines

Trophic Level

IV

III

II

I

0

- **Protozoa**
- **Algae**
- **Bacteria**
- **Detritus**
- **Yeast**
- **Midges, Mites**
- **Mosquito**
- **Rotifer**
- **Flesh Fly**

Captured Insects
Phylloodia

- Flat leaves
- No prey capture
- High concentration of chlorophyll, stomates
- Photosynthetically more efficient than pitchers
Flowering Stalks

- Single stalk per rosette
- Flowering after 3 to 5 years
- Bumblebee, fly pollinated
- Short-distance dispersal of seeds
Leaf Senescence

- Leaves persist 2-3 years
- Production of new leaves in following spring
- Annual increase in rosette diameter
Effects of N Deposition on Carnivorous Plants

• Life History
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• The Role of Ecologists
Anthropogenic N additions alter growth and morphology
Nutrient Treatments

- Distilled H\textsubscript{2}O
- Micronutrients
  - Low N (0.1 mg/L)
  - High N (1.0 mg/L)
  - Low P (0.025 mg/L)
  - High P (0.25 mg/L)
- N:P(1) Low N + Low P
- N:P(2) Low N + High P
- N:P(3) High N + Low P

Nutrient Source:
Micronutrients: Hoaglands
N: NH\textsubscript{4}Cl
P: NaH\textsubscript{2}PO\textsubscript{4}
Anthropogenic N additions alter growth and morphology

Increasing N
Effects of Anthropogenic N additions

• Increased production of phyllodia
• Phenotypic shift from carnivory to photosynthesis
• Increased probability of flowering
Contrasting effects of anthropogenic N vs. N derived from prey
Food Addition Experiment

- Ecological “press” experiment
- Food supplemented with house flies
- Treatments: 0, 2, 4, 6, 8, 10, 12, 14 flies/week
- Plants harvested after one field season
Food additions do not alter growth and morphology.

Increasing prey
N uptake **increases** with food level.
P uptake increases with food level
N:P ratio decreases with added food
Altered N:P ratios suggest P limitation under ambient conditions.

P limitation (Koerselman & Meuleman 1996, Olde Venternik et al. in press)
Anthropogenic N additions alter growth and morphology
Food additions do not alter growth and morphology.

Increasing prey
Contrasting effects of anthropogenic and natural sources of N

Anthropogenic N
- Altered N:P ratios
- Morphological shift
- Reduction in prey uptake

Prey N
- Uptake, storage of N & P
- No morphological shifts
- Continued prey uptake
Although *Sarracenia* has evolved adaptations for low N environments, chronic N deposition may have caused populations to be currently limited by P, not N.
Effects of N Deposition on Carnivorous Plants

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Study Sites

Molly Bog
44°30'N 72°45'30"W

Hawley Bog
42°34'31"N 72°53'23"W
Demography survey

- 100 adult, juvenile plants tagged at each site
- Plants censused and measured each year
- Seed plantings to estimate recruitment functions
Recruits

Juveniles

Adults

Flowering Adults

*Sarracenia* matrix model
Matrix Transition Model

\[ n_{t+1} = A n_t \]
# Population Projections

<table>
<thead>
<tr>
<th>Site</th>
<th>$r$ ( \text{individuals/individual-year} )</th>
<th>Doubling Time</th>
</tr>
</thead>
<tbody>
<tr>
<td>Hawley Bog</td>
<td>0.00456</td>
<td>152 y</td>
</tr>
<tr>
<td>Molly Bog</td>
<td>0.00554</td>
<td>125 y</td>
</tr>
<tr>
<td>Global human population</td>
<td>0.0138</td>
<td>~ 50 y</td>
</tr>
</tbody>
</table>
How do N and P concentrations affect population growth of *Sarracenia*?
Nutrient Addition Experiment

• 10 juveniles, 10 adults/treatment
• Nutrients added to leaves twice/month
• Nutrient concentrations bracket observed field values
• Nutrient treatments maintained 1998, 1999
• “Press” experiment
Nutrient Treatments

- Distilled H₂O
- Micronutrients
  - Low N (0.1 mg/L)
  - High N (1.0 mg/L)
  - Low P (0.025 mg/L)
  - High P (0.25 mg/L)
- N:P(1) Low N + Low P
- N:P(2) Low N + High P
- N:P(3) High N + Low P

Nutrient Source:
Micronutrients: Hoaglands
N: NH₄Cl
P: NaH₂PO₄
Effects of N additions

- Increased production of phyllodia
- Increased probability of flowering
- Decreased juvenile survivorship
Effects of Nitrogen on Demography: Results

• Population growth rates respond to different N and P regimes
• Population growth rate decreases in response to increasing N
• Population growth rate decreases in responses to increasing N:P
Modeling Long-term Environmental Change

- Observed N Deposition
- Time Series Modeling
- Long-term Forecast N(t)
- Transition Function
- Transition Matrix (t)
- Matrix Multiplication
- Population Time Series Extinction Risk Time to Extinction
- Population Structure (t)
Modeling Long-term Environmental Change

1. Observed N Deposition
2. Time Series Modeling
3. Long-term Forecast N(t)
4. Transition Function
5. Transition Matrix (t)
6. Matrix Multiplication
7. Population Structure (t)
9. Time to Extinction
N monitoring

- National Atmospheric Deposition Program
- \( \text{NH}_4, \text{NO}_3 \) measured as mg/l/yr
- Annual data 1984-1998
- Monitoring sites
  - Shelburne, VT
  - Quabbin, MA
## Regression Models

<table>
<thead>
<tr>
<th>Ordinary Least Squares (OLS)</th>
<th>( N_t = a + bt + e )</th>
</tr>
</thead>
<tbody>
<tr>
<td>First-order auto-regressive (AR-1)</td>
<td>( N_t = a + bN_{t-1} + e )</td>
</tr>
</tbody>
</table>
Modeling Long-term Environmental Change

- Observed N Deposition
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- Population Structure (t)
- Population Time Series
- Extinction Risk
- Time to Extinction
Modeling Demographic Transitions as a Function of Nitrogen
Modeling Long-term Environmental Change

- **Observed N Deposition**
- **Time Series Modeling** → **Long-term Forecast \( N(t) \)**
- **Transition Function** → **Transition Matrix \( t \)**
  - **Matrix Multiplication**
  - **Population Time Series**
  - **Extinction Risk**
  - **Time to Extinction**
- **Population Structure \( t \)**
Matrix Transition Model (changing environment)

\[ n_{t+1} = A_t n_t \]

- Population vector at time \( (t + 1) \)
- Sequentially changing transition matrix at time \( (t) \)
- Population vector at time \( (t) \)
## Estimated population size

<table>
<thead>
<tr>
<th>Stage</th>
<th>Number of individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Recruits</td>
<td>1500</td>
</tr>
<tr>
<td>Juveniles</td>
<td>23,500</td>
</tr>
<tr>
<td>Non-flowering Adults</td>
<td>1400</td>
</tr>
<tr>
<td>Flowering Adults</td>
<td>500</td>
</tr>
<tr>
<td>Scenario</td>
<td>Annual % Change</td>
</tr>
<tr>
<td>---------------</td>
<td>----------------</td>
</tr>
<tr>
<td>Best case</td>
<td>-4.7%</td>
</tr>
<tr>
<td>No change</td>
<td>0.0%</td>
</tr>
<tr>
<td>Small increase</td>
<td>1%</td>
</tr>
<tr>
<td>Worst case</td>
<td>4.7%</td>
</tr>
</tbody>
</table>
## Vermont Forecast

<table>
<thead>
<tr>
<th>Scenario</th>
<th>Annual % Change</th>
<th>( P (\text{ext}) ) at 100 y</th>
<th>Time to ext ((p = 0.95))</th>
</tr>
</thead>
<tbody>
<tr>
<td>Best case</td>
<td>-2.2%</td>
<td>0.158</td>
<td>&gt; 10,000 y</td>
</tr>
<tr>
<td>No change</td>
<td>0.0%</td>
<td>0.510</td>
<td>230 y</td>
</tr>
<tr>
<td>Small increase</td>
<td>1.0%</td>
<td>0.694</td>
<td>200 y</td>
</tr>
<tr>
<td>Worst case</td>
<td>2.2%</td>
<td>0.838</td>
<td>140 y</td>
</tr>
</tbody>
</table>
Projected Population Dynamics

![Graph showing population dynamics over years with data points for AR and OLS models.](image-url)
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• Effects on Communities
• The Role of Ecologists
Sarracenia Nutrient Feedback Loop

[Diagram]

- Arthropod Prey
- Atmospheric Deposition
- Inquiline Community
- Pitcher Nutrient Pool [N,P]
- Plant Growth
Sarracenia Nutrient Feedback Loop

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Sarracenia Nutrient Feedback Loop

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Sarracenia Nutrient Feedback Loop

Arthropod Prey

Atmospheric Deposition

Inquiline Community

Pitcher Nutrient Pool [N,P]

Plant Growth
Four-level Multi-Factorial Experiment

- Atmospheric N (8 levels)
- Prey supplement (yes, no)
- Top predator removal (yes, no)
- Nutrient exchange with plant (unmanipulated, isolated, control)
Nutrient exchange with the plant and top predators affect food web structure.
Sarracenia Nutrient Feedback Loop

- Arthropod Prey
- Atmospheric Deposition
- Inquiline Community
- Pitcher Nutrient Pool [N,P]
- Plant Growth
Inquilines → Nutrients

- Manipulate [N], [P] in leaves
- Orthogonal “regression” design
- Establish initial [] in a “pulse” experiment
Response Surface
Experimental Design

\[ N \]
\[ P \]

\[ \begin{array}{cccccccc}
N & 0 & 1 & 2 & 3 & 4 & 5 & 6 & 7 \\
0 &  &  &  &  &  &  &  &  \\
1 &  &  &  &  &  &  &  &  \\
2 &  &  &  &  &  &  &  &  \\
3 &  &  &  &  &  &  &  &  \\
4 &  &  &  &  &  &  &  &  \\
5 &  &  &  &  &  &  &  &  \\
6 &  &  &  &  &  &  &  &  \\
7 &  &  &  &  &  &  &  &  \\
\end{array} \]
Null Hypothesis
Community Regulation of Nutrients
Trajectories of N and P in 2001 nutrient pulse experiment

Leaf number 1

log(concentration of P in mg/L) vs log(concentration of N in mg/L)
**Sarracenia** Nutrient Feedback Loop

- **Arthropod Prey**
- **Atmospheric Deposition**
- **Inquiline Community**
- **Pitcher Nutrient Pool [N,P]**
- **Plant Growth**
Nutrients ↔ Inquilines

\[
\frac{dN}{dt} = f(N, I, t)
\]

\[
\frac{dI}{dt} = g(I, N, t)
\]
Sarracenia as a model system for studying eutrophication
Experimental enrichment and ecosystem collapse

![Graph showing dissolved oxygen over time with labels for Prey Addition, Eutrophic Collapse, and State change.](image)
Proteomic biomarkers as early warning indicators of state changes
Species Profiles of Top 30 Identified Proteins when Searching NRP NCBI Indexed Database

Unmanipulated Controls

Unmanipulated
Species Profiles of Top 30 Identified Proteins when Searching NRP NCBI Indexed Database

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Burning of Fossil Fuels

Use of Synthetic Fertilizers
Total anthropogenic N fixed

Fertilizer

Natural range

NOx
Ecology ≠ Environmental Science
Reasons for Studying Ecology
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• Natural History
Reasons for Studying Ecology

• Natural History
• Field Studies & Experiments
Reasons for Studying Ecology

• Natural History
• Field Studies & Experiments
• Statistics & Data Analysis
Population Growth Rate (Deterministic)

-0.15
-0.10
-0.05
0.00
0.05

Distilled Micros
Low N
High N
Low P
High P
NP (2)
NP (1)
NP (3)
Reasons for Studying Ecology

• Natural History
• Field Studies & Experiments
• Statistics & Data Analysis
• Modeling
\[
\frac{dN}{dt} = f(N, I, t)
\]
\[
\frac{dI}{dt} = g(I, N, t)
\]
Reasons for Studying Ecology

• Natural History
• Field Studies & Experiments
• Statistics & Data Analysis
• Modeling
• Collaboration
Aaron M. Ellison
Harvard Forest
Conclusions

• Anthropogenic deposition of N is a major ecological challenge
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• Carnivorous plants in ombrotrophic bogs are a model system
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• **Individual response**
  ➢ plants alter morphology and growth in response to N:P ratios
Conclusions

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• Carnivorous plants in ombrotrophic bogs are a model system
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• Population response
  ➢ N and P environments affect population growth rate
Conclusions

• Anthropogenic deposition of N is a major ecological challenge
• Carnivorous plants in ombrotrophic bogs are a model system
• Individual response
  ➢ plants alter morphology and growth in response to N:P ratios
• Population response
  ➢ N and P environments affect population growth rate
• Community response
  ➢ Further study of nutrient ↔ inquiline feedback loop