Life and Death in the Mines: Outbreak of the Aspen Leaf Miner in Interior Alaska

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Aspen leaf miner study acknowledgements

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Outline

• Natural history
• History of ALM outbreaks
• Effect of leaf mining on aspen
• ALM population trends
• Aspen defenses
• Climate and ALM overwintering
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Trembling aspen
(*Populus tremuloides*)

- Widespread across NA and from AK to Mexico
- Early successional species
- Asexual and sexual reproduction
Aspen leaf miner moth  
(*Phyllocnistis populiiella*)

- Geographic range
  - NA only
  - AK E across Canada to Atlantic
  - AK S to Kentucky, Utah, Colorado
- Host range - many species of *Populus*
Aspen leaf miner moth
(*Phyllocoenista populicella*)

- Univoltine
- Adults emerge in May before leaf-out, mate
- Lay eggs on both sides of new leaves
- Eggs digest cuticle, sink into leaf
Aspen leaf miner moth
(*Phyllocnistis populiiella*)

- Larvae restricted to one side of leaf
  - cannot switch sides
  - cannot exit and reenter
- Consume epidermal cells as move during instars I – III
- Separation of cuticle from mesophyll causes white appearance of mines
Aspen leaf miner moth

(Phyllocnistis populiiella)

• Instar IV non-feeding, spins webbing that folds leaf
• Pupate in leaf fold
• Adults emerge from folds in mid-June
• Adults overwinter in litter
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Aspen leaf miner infestation of Alaskan forests

R. Werner, US Forest Service flyovers
Aspen leaf miner infestation of Bonanza Creek LTER

Aspen leaf miners (N per m2 foliage)

Year

R. Werner, www.lter.uaf.edu and pers. comm.
Other outbreaks

- Yukon, North West Territories, British Columbia, Alberta late 1940s – late 1960s (Canadian FS - Forest Insect and Disease Surveys)

- Saskatchewan, Manitoba, Quebec, Maritimes, Newfoundland 1960s (FIDS)

- Alberta 1970s (Porter 1976)
History of ALM outbreaks

- ALM is a native species
- Subject to population irruption
- Previous Canadian outbreaks were long-lived (>decade)
Outline

- Natural history
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- **Effect of leaf mining on aspen**
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Aspen leaf miner moth 
(*Phyllocnistis populiella*)

- Epidermal mining is taxonomically restricted
- No previous studies on effects of epidermal mining on plant physiology or performance

Drawing - Condrashoff 1964
Bottom mining reduces photosynthesis

L. Defoliart, Wagner et al. in review
Bottom mining reduces photosynthesis

![Bar graph showing net photosynthesis at different surface mining conditions: Neither, Top, and Bottom.](image)

J. Schneiderheinze, Wagner et al. in review
Bottom mining disrupts stomatal function

• Hypothesis:
  – Photosynthetic potential near normal
  – Mined stomata unresponsive and shut
  – Decreased photosynthesis due to CO$_2$ limitation
Bottom mining disrupts stomatal function

Wagner, Defoliart, Doak, Schneiderheinze in review
Top mining affects water balance

% Leaf top mined

% Leaf $H_2O$
Leaf mining leads to early leaf abscission

Data: L. Defoliart
How does leaf mining affect aspen growth?

• Experimental reduction of leaf miner density
• 2 sites: Bonanza Creek and Ester Dome
• Spray insecticide just after leaf-out
• 2 – 10 fold reduction in mining on sprayed trees
• No significant non-target effects
Mining reduces aspen growth

Wagner, Defoliart, Doak, Schneiderheinze in review.
Mining reduces aspen growth

Wagner, Defoliart, Doak, Schneiderheinze in review.
Mining affects mortality?

• Experiment not designed for this purpose

• 5% mortality over 3 years
  – 3 control plants
  – 1 sprayed plant
Effects of ALM on aspen physiology and performance

- Bottom mining reduces photosynthesis
- Mechanism: stomata in mined areas cannot open normally
- Both top and bottom mining likely increase leaf permeability
  - Bottom mining – effects of stomatal closure override increases in cuticular permeability
- Mined leaves abscise earlier
- Mining reduces growth
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Leaf miner population trends

• Annual surveys:
  – Twice annually, 4 sites each, 20-40 trees/site
  – Here, discuss data from short trees only
  – May – egg number, egg scars (estimate of predation)
  – Late-June (pre-eclosion) - dissection of leaves, counts of live and dead leaf miners, forensic analysis
Leaf miner population trends

![Graph showing leaf miner population trends over years 2004 to 2007. The x-axis represents the years 2004 to 2007, and the y-axis represents eggs per leaf. The graph shows a decrease from 2004 to 2005, followed by an increase from 2005 to 2007. The data points are labeled with parentheses indicating the sample size: (4) for 2004, (3) for 2005, and (4) for 2006 and 2007.](image-url)
Leaf miner population trends

Survivors - pupae per leaf

2004 2005 2006 2007

(4) (1) (4) (4)
Leaf miner population trends

Survivorship (pupae/egg)

2004 2005 2006 2007

2004: 0.00 (4)
2005: 0.05 (1)
2006: 0.10 (4)
2007: 0.15 (4)
Leaf miner source of mortality

- Intraspecific competition
- Predators:
  - Ants (eggs, larvae, pupae)
  - Mites (eggs, larvae)
- Parasitoids (larvae and pupae)
Leaf miner population trends

![Graph showing survivorship (pupae/egg) from 2004 to 2007.](image-url)

- 2004: 0.00, (4)
- 2005: 0.05, (1)
- 2006: 0.10, (4)
- 2007: 0.15, (4)
Leaf miner sources of mortality

2006

2007

Alive
Dead – Unknown causes
Parasitized
Predation confirmed

Dead – Unknown causes
Leaf miner source of mortality (2007)

- 11% of leaf miner eggs eaten
- 84% of survivors died as larvae or pupae
- Most died of unknown causes as young, small larvae
- Possible contributions to unknown causes:
  - Competition
  - Mites
  - Disease
  - Phytochemistry
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Aspen defenses

• Extrafloral nectaries (EFNs) – attract predators and parasitoids

• Phytochemistry - Phenolic glycosides salicortin and tremulacian – toxic to some insect herbivores
Variation in aspen EFN expression

Frequency of leaves with EFNs varies within ramets, among ramets, with height, among clones.
Variation in EFN frequency among putative clones

Leaf positions 1-7
Aspen EFN visitors
Leaves with EFNs suffer lower mining damage
Effect of crawling predators (ants, mites)

- Experimental approaches
  - Crawling insect exclusion experiments
  - EFN blocks

- Both ants and mites deterred by tanglefoot; parasitoids are not

- B. Mortensen 2007
  - Simultaneous exclusion experiments at 9 sites
Effect of crawling predators (ants, mites)

a. Crawling predators reduce mining

Trt P<0.001*
EFNs P<0.001
Trt*EFNs n.s.
Effect of crawling predators (ants, mites)

b. Crawling predators are not responsible for EFN / no EFN mining difference
EFN frequency correlates with herbivory

B. Mortensen
EFN frequency appears to be increasing in recent years.

Aspen EFN frequency can be increased by experiment defoliation (Wooley et al. 2007).
What causes lower mining damage on EFN-bearing leaves?

• Oviposition—moths prefer leaves without EFNs

• Parasitoids target EFN leaves
Parasitoids

Parasitism: EFNs > no EFNs

Drawing from Condrashoff 1964
Parasitoids contribute to lower mining on EFN leaves
But do not account for EFN – no EFN mining difference!
What causes lower mining damage on EFN-bearing leaves?

- Oviposition—moths prefer leaves without EFNs
- Parasitoids target EFN leaves
- Palatability
Leaves with and without EFNs differ in physiology

Net Photosynthesis

(µmol CO₂ m⁻² s⁻¹)

No EFNs

EFNs

J. Schneiderheinze, unpubl.
Mining induces phenolic glycoside expression

12 days post egg-hatch

B. Young
EFN-bearing leaves have high constitutive phenolic concentrations

<table>
<thead>
<tr>
<th>Treatment</th>
<th>P-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>EFNs</td>
<td>&lt;0.01</td>
</tr>
<tr>
<td>EFNs*Trt</td>
<td>n.s.</td>
</tr>
</tbody>
</table>

B. Young
EFN-bearing leaves have higher phenolic concentrations across sites

<table>
<thead>
<tr>
<th>Site</th>
<th>Salicortin + Tremulacian (mg/g)</th>
</tr>
</thead>
<tbody>
<tr>
<td>BB</td>
<td>1</td>
</tr>
<tr>
<td>BS</td>
<td>2</td>
</tr>
<tr>
<td>CR</td>
<td>3</td>
</tr>
<tr>
<td>ED</td>
<td>4</td>
</tr>
<tr>
<td>RF</td>
<td>5</td>
</tr>
<tr>
<td>WR</td>
<td>6</td>
</tr>
</tbody>
</table>

- EFNs: P<0.001
- Site: P<0.001
- EFNs*Site: P<0.01

B. Young
What causes lower mining damage on EFN-bearing leaves?

- **Oviposition**—moths prefer leaves without EFNs

- **Parasitoids target EFN leaves**
  - Yes – significantly higher parasitism on mined leaves
  - But this does not account for differences in mining

- **Palatability**
  - Maybe
  - EFN leaves have higher phenolic concentrations
  - Effect on ALM mortality or feeding?
  - Aspen has mosaic of well-defended and weakly-defended leaves
EFN frequency correlates with herbivory

$r = -0.73$

B. Mortensen
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Has climate warming facilitated the current ALM outbreak?

- Known AK outbreaks coincided with warmer temperatures post-1975

- Study of ALM outbreak in Alberta 1970-1973 found overwinter mortality was key factor affecting population change

http://climate.gi.alaska.edu/
Has climate warming facilitated the current ALM outbreak?

Ability of leaf miners to sustain winter temperatures

• Behavior – where do moths overwinter?

• Physiology – how do moths cope with cold temperatures?
Moth overwintering behavior

Moths in leaf litter

Photo: Bryan Carlson
Moth overwintering behavior

• Standardized litter collections in 2007
• At multiple sites, litter samples of standard area:
  – Open
  – Aspen
  – White Spruce
  – Birch
  – Balsam popular
• Determine moths per m² litter
Moth overwintering behavior

• 85% of overwintering ALM under one non-host species - white spruce

• <10% under aspen

• Why?
  – Moths may shelter in crenulated bark in fall
  – Litter texture
  – Litter moisture much lower under spruce
  – But…temperatures may be lower as well
Moth overwintering physiology

- Moths do not survive freezing (Carlson, Sformo unpub.)

- Moths supercool (Carlson, Steiner, Sformo)

Photo T. Sformo
Moth overwintering physiology

Minimum litter temps
UAF, 2004-2006

Moth supercooling (range)

P. Steiner, B. Carlson, T. Sformo, Doak, Wagner, Barnes unpubl.
Moth overwintering physiology

Minimum annual O/M-H Temperatures

Mean moth supercooling temp - Nov

J. Yarie, http://www.lter.uaf.edu/
Has climate warming facilitated the current ALM outbreak?

• Moths have extraordinary abilities to supercool
• So far, cool about 10-25°C below minimum litter temperatures
• But temperatures colder in past, and only takes one cold night…
• Need to know:
  – Moth supercooling temperatures in winter, spring?
  – Temperatures of litter under spruce?
    • 85% of moths under spruce
    • Little snow
    • Litter temperature may be colder than data shown here
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- ALM is subject to irruptions of long duration
- Epidermal mining is unusual form of herbivory that affects gas exchange, reduces growth
- ALM in Fbks area are currently suffering reduced survivorship not due to parasitism, ant predation and perhaps due to increased mites populations, phenolic concentrations, disease
- EFNs attract mites, ants, parasitoids and provide diffuse defense to aspen leaves
- EFNs correlate with high levels chemical defense
- ALMs overwinter under spruce, supercool to <-35 C