White pine blister rust:

An emergent disease caused by an introduced pathogen
The tree host: white pines

- Genus *Pinus*
- Hapoxylon subgroup
- Five-needled
- Eastern and western white pines, whitebark, sugar, limber, southwestern white, foxtail, bristlecone pines
- Whitebark is closely related to European stone pines, where rust is endemic (but there are questions on whether it is the same species)
In Western North America

- Nine species of white pines
- Eight are infected (*P. longaeva* is the only one without a report)
- Incidence of disease is not same across all species. E.g.: western white pine less resistant than Sugar pine. SP require wave years for infection to occur, that is years where Fall conditions have mild temperatures and rainfall
Five-needle pines in Europe

- *P. cembra*
- *P. sibirica*
- *P. strobus* (planted)
Blister rust cankers:

sugar pine

whitebark pine
Top kill in whitebark pine
Cronartium ribicola: the causal agent

• Complex system involving 5 spore stages and two hosts
  – Pinus and Ribes

• Introduced into North America around 1900 on infected eastern white pine stock; separate introductions on east and west coasts

• Native to Asia
Some details about introduction

- 1906 on East Coast, but there are records of many shipments from Germany and Holland, in multiple locations including the midwest
- 1910, Vancouver BC, One shipment documented from France but most reconstructions suggest more than a single introduction occurred
- Ribes also imported from Europe, but most ribes loose their foliage in fall, Introduction most likely to have happened through pines
Methods

- 4 collection sites of a single aecidia in West
  - 2 coastal sites (Manning Park, BC; Sacramento, NM)
  - 2 interior sites (Smallwood, BC; Shelter Bay, BC)

- 4 collection sites in the East
  - Ste-Camille, Quebec; Minden, Ontario; Little Grand Lake, NFLD; Moncton, New Brunswick
Results

- Among regions: West v. East (0.605)
  - Migration between east and west extremely low, less than 1 migrant per generation
- Among populations in regions (but markers were imperfect and fail to detect differences among western populations)
  - East (0.00 – 0.02)
  - West (0.00- 0.02)
- In Populations (0.493), a lot of sexual reproduction> No surprise because of rust cycle

<table>
<thead>
<tr>
<th>Hierarchical structurea</th>
<th>Source</th>
<th>df</th>
<th>Variance components</th>
<th>( \phi )-Statistics</th>
<th>Proportion of variance components (%)</th>
<th>( P ) valueb</th>
</tr>
</thead>
<tbody>
<tr>
<td>East (NFLD, QC, ON, NB) vs West (BC, NM)</td>
<td>Among regions</td>
<td>1</td>
<td>0.605</td>
<td>0.546</td>
<td>54.58</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td></td>
<td>Among populations in regions</td>
<td>6</td>
<td>0.011</td>
<td>0.021</td>
<td>0.97</td>
<td>0.076</td>
</tr>
<tr>
<td></td>
<td>In populations</td>
<td>262</td>
<td>0.493</td>
<td>0.556</td>
<td>44.45</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Interior BC vs Coastal BC</td>
<td>Among regions</td>
<td>1</td>
<td>0.000</td>
<td>0.000</td>
<td>0.00</td>
<td>0.78</td>
</tr>
<tr>
<td></td>
<td>Among populations in regions</td>
<td>1</td>
<td>0.008</td>
<td>0.044</td>
<td>4.49</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>In populations</td>
<td>105</td>
<td>0.174</td>
<td>0.032</td>
<td>95.51</td>
<td>&lt;0.001</td>
</tr>
</tbody>
</table>

a NFLD = Newfoundland, QC = Quebec, ON = Ontario, NB = New Brunswick, BC = British Columbia, and NM = New Mexico.

b Probability of obtaining equal or larger value determined by 1,000 random permutations of the treatments.
Shelter Bay = interior BC
Manning Park = interior BC
Smallwood = coastal BC
New Mexico Revisited

TABLE 1. Estimated frequency of random amplified polymorphic DNA (RAPD) markers and expected heterozygosity ($H_j$) for populations of ascidia of Cronartium ribicola

<table>
<thead>
<tr>
<th>Population</th>
<th>$n^b$</th>
<th>OPA01-1700</th>
<th>OPA01-2000</th>
<th>OPC08-750</th>
<th>OPC08-900</th>
<th>OPE15-1600</th>
<th>OPK19-2000</th>
<th>OPK11-500</th>
<th>$H_j$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Manning Park (coastal BC)</td>
<td>55 (21)</td>
<td>0.963</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.203</td>
<td>0.000</td>
<td>0.069</td>
<td></td>
</tr>
<tr>
<td>Smallwood (interior BC)</td>
<td>37 (14)</td>
<td>1.000</td>
<td>0.987</td>
<td>1.000</td>
<td>1.000</td>
<td>0.987</td>
<td>0.410</td>
<td>0.077</td>
<td></td>
</tr>
<tr>
<td>Shelter Bay (interior BC)</td>
<td>16 (6)</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.969</td>
<td>1.000</td>
<td>0.000</td>
<td>0.009</td>
<td></td>
</tr>
<tr>
<td>Sacramento (NM)</td>
<td>45 (15)</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>1.000</td>
<td>0.000</td>
<td>0.000</td>
<td>0.000</td>
<td></td>
</tr>
<tr>
<td>Ste-Camille (Quebec)</td>
<td>30 (10)</td>
<td>0.417</td>
<td>1.000</td>
<td>0.966</td>
<td>0.610</td>
<td>0.733</td>
<td>0.375</td>
<td>0.490</td>
<td>0.347</td>
</tr>
<tr>
<td>Minden (Ontario)</td>
<td>30 (10)</td>
<td>0.522</td>
<td>1.000</td>
<td>0.983</td>
<td>0.522</td>
<td>0.582</td>
<td>0.455</td>
<td>0.553</td>
<td>0.369</td>
</tr>
<tr>
<td>Little Grand Lake (NFLD)</td>
<td>30 (10)</td>
<td>0.417</td>
<td>1.000</td>
<td>1.000</td>
<td>0.610</td>
<td>0.832</td>
<td>0.329</td>
<td>0.319</td>
<td></td>
</tr>
<tr>
<td>Mononton (New Brunswick)</td>
<td>30 (10)</td>
<td>0.564</td>
<td>0.969</td>
<td>0.985</td>
<td>0.641</td>
<td>0.655</td>
<td>0.440</td>
<td>0.313</td>
<td>0.344</td>
</tr>
</tbody>
</table>

$^a$ BC = British Columbia; NM = New Mexico; NFLD = Newfoundland. Quebec, Ontario, NFLD, and New Brunswick reproduced from Et-touil et al. (2); expected heterozygosity may differ from Et-touil et al. because two of the markers used in that study were not used here.

$^b$ Number of ascidia and number of trees in parentheses.

$^c$ Allele frequency for dominant RAPD markers was estimated according to the method of Lynch and Milligan (27); frequencies are those of the null allele.

- Sacramento, NM
- All fixed loci, absence of heterozygots
- Founder’s effect
- Low genetic differentiation = genetic bottleneck
Conclusions

• Eastern and western populations are not panmictic

• Barrier to gene flow between eastern and western populations
  – Great Plains – intense agriculture
  – 100 km absence of aecial and telial hosts
Factors affecting spread

- Founder population of pathogen (Germany vs. France)
- Number of introductions
- Species of white pines
- Amount of obligate alternate host *Ribes* and their distance from pines
- Climate: as it gets colder infection less successful (for instance moving inland and east in Easter North America)
- Weather: pine infection requires rainfall and moderate temperature in Fall, as we move South in the West these conditions happen only rarely, when they do we speak of WAVE YEAR
- Topography: the more rugged the more difficult the spread. Although while basidiospores only travel a few hundred yards or a few km in the presence of currents induced by lakes in mountainous areas, aeciopspores may be able to travel over 1000km
- Amount of resistance within species For instance in Sugar pine resistance is 1% in North and 8% in South CA, maybe due to resistance to *C. occidentale*, a rust of pinyon pines
C. ribicola life cycle

**FIGURE 15.5** Disease diagram of white pine blister rust caused by Cronartium ribicola. Drawn by Valerie Mortensen.
Cronartium ribicola—Causal Agent of White Pine Blister Rust

- WPBR is an exotic disease from EU

- Leaves above the canker die, causing branch/stem to break
- Opens site for decay fungus

**Fall:** fungus attacks needles

**Two Years Later:** Fungus spreads to branches and trunk

**Next Spring:** spores cause blisters and thus cankers

**Spore produced to transmit disease**
A Few Pathogen Details

- Infection occurs through stomata of needles of all age, if needle is on stem then infection directly leads to tree girdling. If needle on branch, it will cause branch death and then if it moves into stem it will cause stem girdling, if stem does not die before pathogen gets to stem...
- Because pathogen is obligate biotroph
- Overall Low genetic diversity in N.A. Sign of introduced disease
  - Diversity between subpopulations is greater in West because of rugged topography
  - Indicative of frequent founder events and little gene flow
- Genetic center: Asia
- To infect white pines: 48 hours <68 F, 100% relative humidity
Attempts to control WPBR

- Ribes eradication
  - More successful in East than West
- Use of Risk Zones for planting and management
  - Potential pitfalls: must also account for airflow patterns
- Pruning
  - Can be successful if infection caught 12 inches from main stem; costly; may need repeated entries; probably would not work in whitebark
- Genetics: probably most successful method
  - Sugar and western white pines
  - Whitebark pine work in progress
Ribes Eradication

- In East:
  - effective
  - well supported
  - easy

- In Lake States:
  - variable results

- In West:
  - difficult

Civilian Conservation Camps during the Depression,
Widespread mortality in western white pine
Why mortality appears in clusters if pine to pine infection does not occur?

1- Threshold of inoculum necessary for infections low in western white pine, so a single source can infect trees at various distance because dilution effects with distance are less pronounced

2- Resistance very infrequent (1 in a thousand)

3- Compounding effect of Mountain Pine Beetle
Pruning research in sugar pine before...
Pruning research in sugar pine...after
Eastern white pine (*P. strobus*)

- Largely cut over prior to rust, so loss due to rust minimal, but regenerating difficult
- Only tree where *Ribes* control was mildly successful
- Most land managers won’t risk it in high risk zones
Whitebark pine (*P. albicaulis*)

- High elevations in the western US and Canada
- Keystone species; slow growth
- Mutualistic relationship with Clark’s nutcracker
- Wildlife dependence on nuts
- Restoration treatments: a helping hand for a tree with a bleak future
Western white pine (*P. monticola*)

- Largely disappeared from the Inland Northwest, where it was once most valuable timber species
- Like eastern wp, avoided in plantings
- Changing species comp. and structure made forest more susceptible to fire, insects and other pathogens
Sugar pine (P. lambertiana)

- CA and PNW
- Tree of largest stature in mixed-conifer forests
- Few native pests, none causing such widespread mortality
- Also avoided in some planted settings
- Resistance 1% to 8%
Tree resistance

- Major gene for resistance
- Found in sugar, western white, and southwestern white so far
  - Thought to be gene-for-gene (because virulent race of pathogen neutralizes this gene)
  - Gene-for-gene typically indicates a pathosystem in which the host and pathogen have evolved over long time periods- so what is going on in this system?
A quick review of gene-for-gene resistance

<table>
<thead>
<tr>
<th>Pathogen genotype</th>
<th>Host genotype</th>
<th>Pathogen genotype</th>
<th>Host genotype</th>
</tr>
</thead>
<tbody>
<tr>
<td>RR</td>
<td>R</td>
<td>RR</td>
<td>R</td>
</tr>
<tr>
<td>RR</td>
<td>rr</td>
<td>RR</td>
<td>rr</td>
</tr>
<tr>
<td>VV</td>
<td>-</td>
<td>VV</td>
<td>+</td>
</tr>
<tr>
<td>Vv</td>
<td>-</td>
<td>Vv</td>
<td>+</td>
</tr>
<tr>
<td>v</td>
<td>+</td>
<td>v</td>
<td>+</td>
</tr>
<tr>
<td>w</td>
<td>+</td>
<td>w</td>
<td>+</td>
</tr>
</tbody>
</table>
Lesion types: sugar pine
Additional types of tree resistance

• Sugar pine
  – Slow rusting resistance - many components of resistance combined into a single phenotypic expression, exhibited as amount and type of infection with moderately strong inheritance and independently inherited expressions (low infection # and high infection abortion)
  – Ontogenetic resistance - another phenotypic expression that develops as the tree ages; under genetic controls; offspring may be fully susceptible
Additional types of tree resistance, cont’d

• Western white pine
  – Slow canker growth - non race specific trait; produces abnormally small cankers; may reduce pruning necessity (due to success)
  – Reduced needle lesion frequency - also non race specific trait; few individual infection sites per seedling; may only be juvenile trait (seen in cotyledons)
Evaluation of longevity of control practices

- Race of pathogen able to overcome major gene resistance in Sugar pine already present. Slow resistance or combination of two may be more durable approach.
Influence of Host Resistance on the Genetic Structure of White Pine Blister Rust Fungus in the Western United States

Richardson, Klopfenstein, Zambino, McDonald, Geils, Carris
Purpose

1) Examine genetic diversity within and among population of western N.America
2) Effects of host resistance on C. ribicola
3) Identify loci that behave as if linked to loci undergoing environmental selection
Material + Methods

- Sampling of isolates from 6 sites
- B= merry creek: multigenic resistant, D= happy camp: major gene resistant
Results

- Low number of polymorphic loci among 148 C. ribicola isolates
- Heterozygosity
  - Highest at MC
  - Lowest at HC
- \( F_{st} = 0.082 \) among sites, significant
Discussion
Effects of host resistance on C. ribicola

Merry Creek (multigenic resistant trees):
had highest heterozygosity

Happy Camp (major gene resistant trees):
had

lower heterozygosity

- Selection for rust isolates carrying vc1 because all trees have cr1.
Results

• Possibly 3 populations of C. Ribicola in Western US

• Loci GFAC57B had very high Fst among different sites.
Discussion
Identify loci undergoing environmental selection

• GTAC57B could be linked to genes under selection.
Mortality and decline of white pine not only due to WPBR

- Fire suppression: most wp species like open spaces created by fire and are fire-adapted. With lack of fire, site are encroached by shade tolerant species and white pine regeneration is limited
- Insect (mountain pine beetle) outbreaks. When populations of this insect become large they attack healthy trees as well. Effect of WPBT and mountain pine beetle is more than the sum of the two
- Dothistroma needle blight can cause outbreaks, however both Dothistroma and insect outbreaks may be cyclical and natural
- Global warming
Consequences of wp mortality

- Group of species that is extremely adaptable, and that in western North America, depending on latitude, goes from sea level to tree-line

- High market value: white pines timber is king. In past times it was the best timber to build ships’ masts. One of the reasons for the secession of American territories

- It includes the oldest living organism on earth (Bristlecone pine)

- In the Rockies it is essential for survival of Clark’s nutcracker and Grizzly bears. In the West, white pines are diversity hotspots
"In North America, white pine blister rust has caused more damage and costs more to control than any other conifer disease. Since the 1920's, millions of dollars have been spent on the eradication of the alternate host, *Ribes*, and thousands of white pine stands have been severely damaged. In the western United States and Canada, some stands have been completely destroyed. When the main stem of a tree is invaded, death is only a question of time."

Robert F. Sharpf, U.S. Department of Agriculture Handbook 521 (p.85)