

**Ecology and Evolutionary Biology
of Resistance
and Tolerance, Natural Systems**

Moderator: Bitty Roy

An Overview of Ecological and Evolutionary Research on Disease in “Natural” Systems

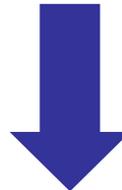
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University of Kansas



Forestry



Genetics



Plant – Pathogen Interactions



www.guardiantreeexperts.com/

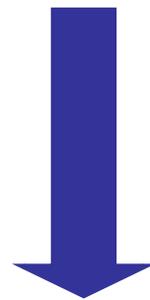


http://www.innovations-report.com/html/reports/agricultural_sciences/report-20778.html

Agriculture



Forestry



“Ecology and Evolutionary Biology”



Plant – Pathogen Interactions



www.ars.usda.gov/pandp/people/people.htm



www.fs.fed.us/psw/programs/ifg/wpbr/



(Photos from A. Laine, B. Roy)

Overlap between groups, but also three perspectives and sets of literature

Managed



**Unmanaged/
"Natural"**

Lower

Plant species diversity

Higher

Lower

Within a plant species:

--genetic diversity

Higher

Even-age

--age structure

Multi-age

Regular

--spacing

More
complex

**Plant dynamics
between years**

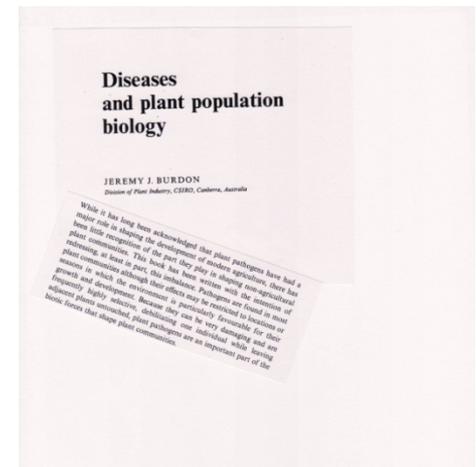
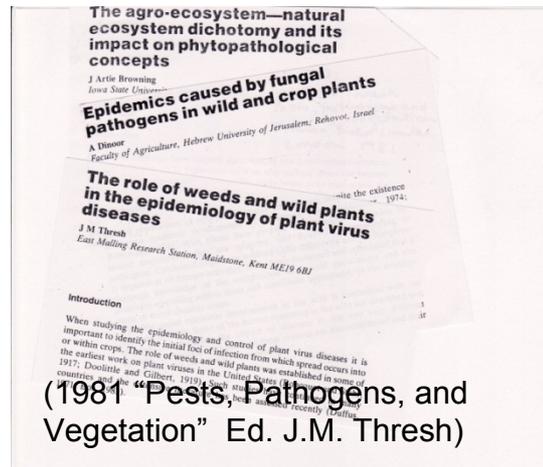
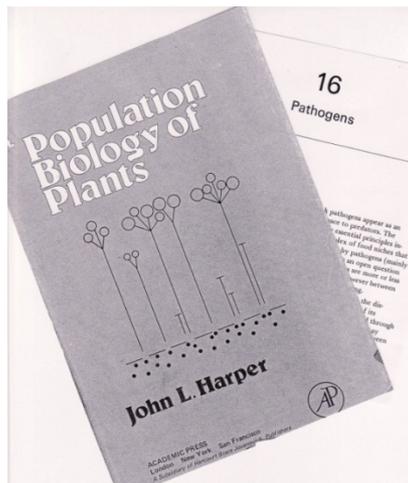
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Timeline: disease studies by “ecologists/evolutionary biologists”

- Historically, ignore pathogens (but see Haldane 1949)
- 1977: Harper
- 1970's – 1980's: crop vs. wild plant comparisons
- 1987: Burdon
- 1980's – present: increasing research interest



(1981) “Pests, Pathogens, and Vegetation” Ed. J.M. Thresh)

Research areas/Questions:

Studies of disease in relation to:

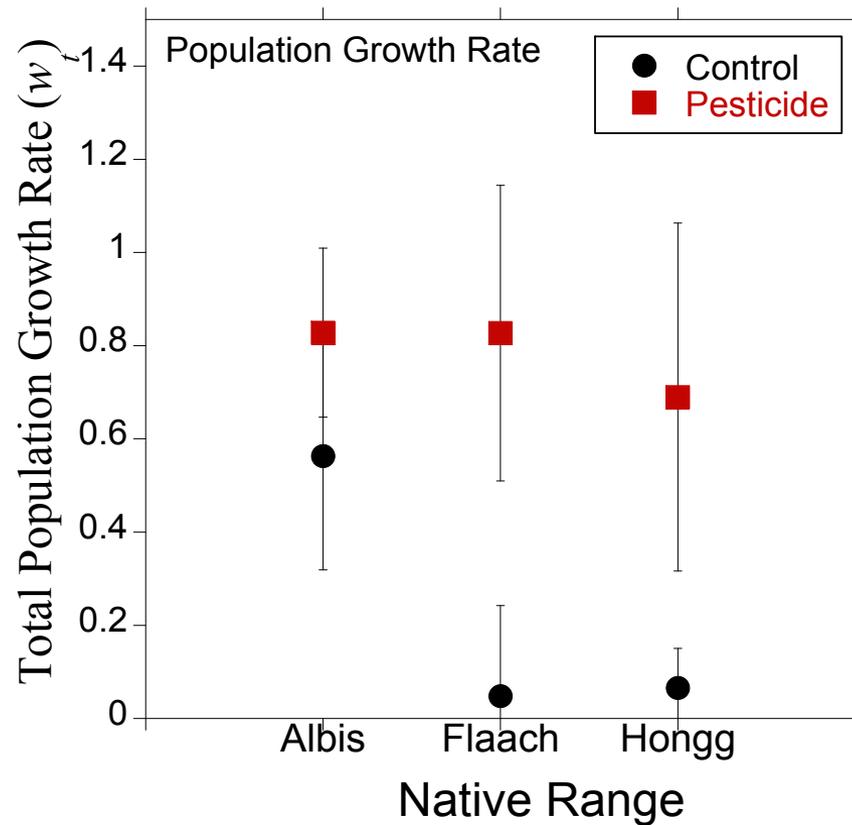
1. Plant population dynamics
2. Evolutionary interactions: plant - pathogen
3. Plant community composition
4. Global change and ecosystem function

Biases: -effects of pathogens on plants more than *vice versa*
-emphasis on fungi

(If interested, most references in Alexander (2010), *Plant Disease* 94:492-503)

Plant population dynamics: effects of disease on plant numbers and spatial distribution

- Experimental

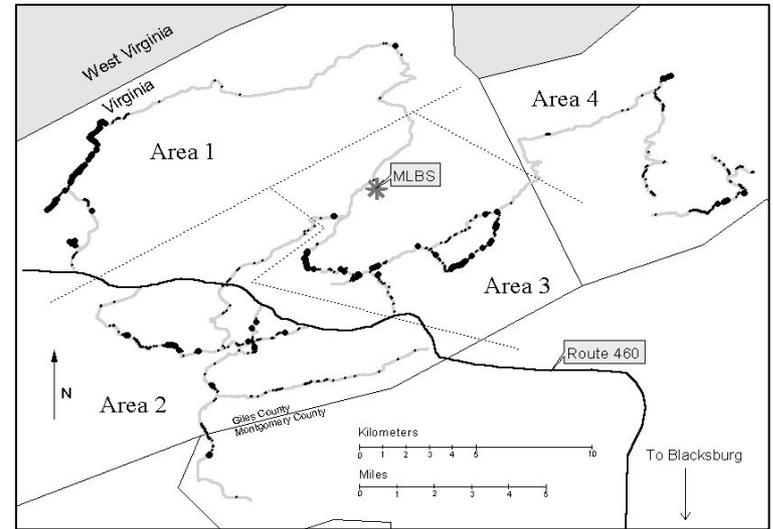


Photos from B. Roy

Plant population dynamics

-Long term observation and modeling

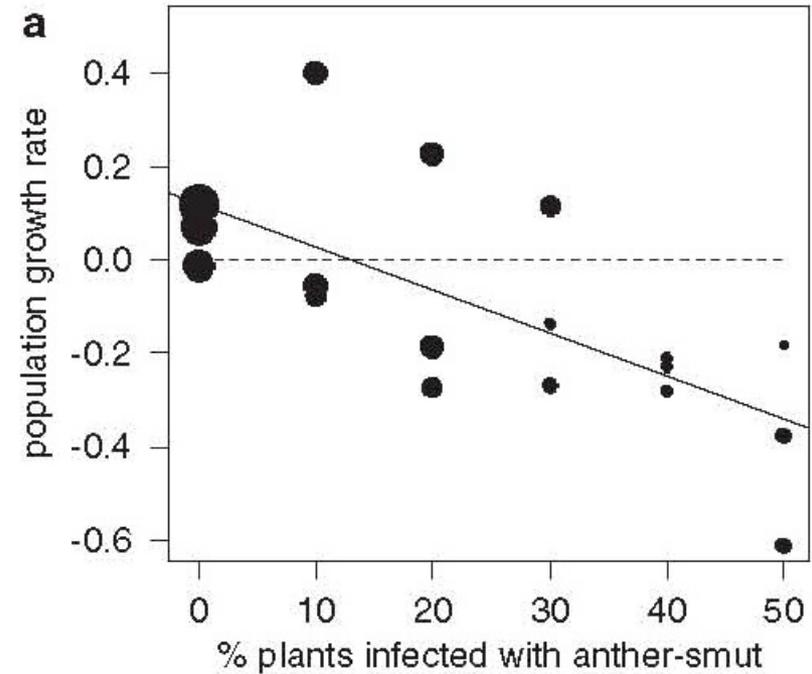
Antonovics et al. (1998), Antonovics (2004)



Silene/Microbotryum



Photo from M. Hood



Bernasconi et al. 2009

Plant population dynamics:

Changes in plant age/stage composition

(Davelos and Jarosz 2004)

Seed populations and seed bank persistence

(Eviner and Chapin 2003, Meyer et al. 2007, Beckstead et al. 2010)

Density-dependent effects and compensation

(Lively et al. 1995; Alexander and Mihail 2000)

Effects on plant metapopulation dynamics

(Antonovics et al. 1994, Antonovics 1999, Antonovics 2004)

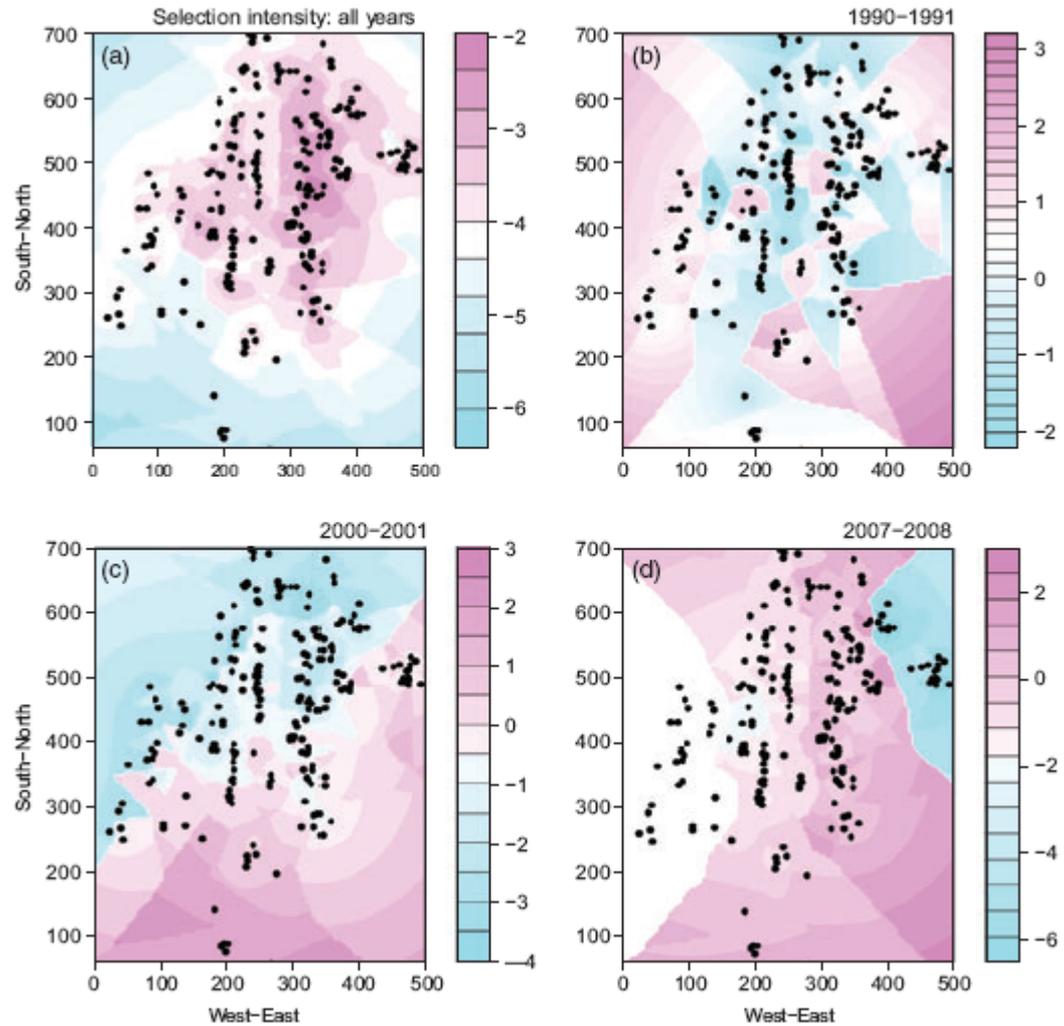
Temporal and spatial variation in disease

19 year study, Swedish islands

Perennial herbaceous plant
and rust pathogen

“Hotspots”, and thus selective
pressure, change over time
and space

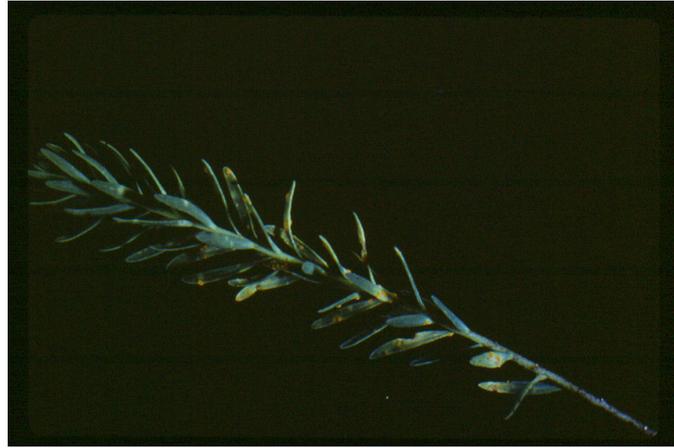
Smith et al. 2011



Other examples: Augspurger and Kelly 1984, Jarosz and Levy 1988, Carlsson et al. 1990, Antonovics et al. 1994, Thrall et al. et al. 2001, Carlsson-Granér and Thrall 2002, Smith et al. 2003, Antonovics 2004, Laine and Hanski 2006, Alexander et al. 2007, Reinhart and Clay 2009, Koslow and Clay 2010

2) Evolutionary interactions – plant/pathogen

Host resistance and tolerance; pathogen virulence



Linum/Melampsora

Alnus



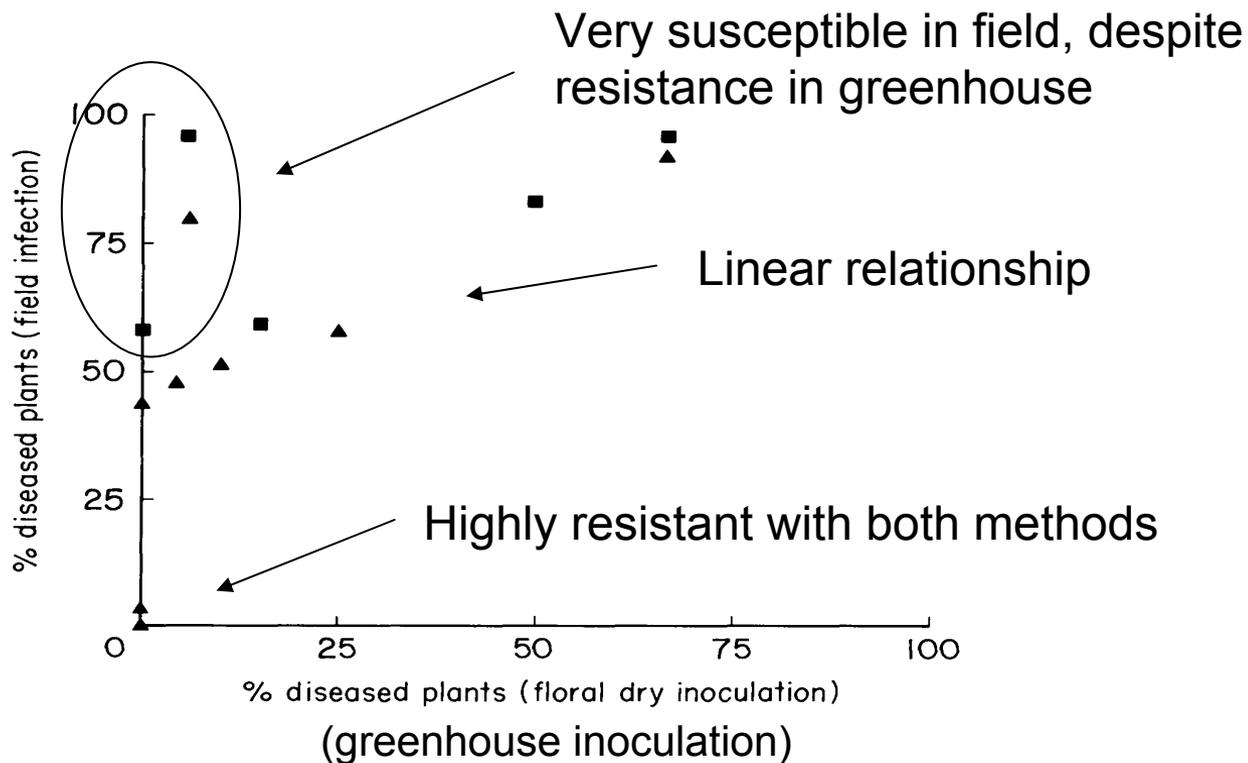
Photos from P. Thrall and B. Roy

(Dinoor 1977, Harry and Clarke 1986, Roy and Bierzychudek 1993, Simms 1993, Roy 1993, Jarosz and Burdon 1991, Thompson and Burdon 1992, Kelly 1994, Roy 1998, Roy et al. 2000, Roy and Kirchner 2000, Burdon et al. 2002, Thrall et al. 2002, Carr et al. 2003, Laine 2004, Carlsson-Granér and Pettersson 2005, Meyer et al. 2005, Carr et al. 2006, Inglese and Paul 2006, Barrett et al. 2007, Springer 2007, Koslow and Clay 2007, Barrett et al. 2009, Burdon and Thrall 2009, Gilbert and Parker 2010, Antonovics et al. 2010, Roux et al. 2010, Laine et al. 2011)

Interactions between ecology and genetics: relevance to populations

- Links between resistance structure and disease levels and/or plant population dynamics (*Thrall and Jarosz 1994, Alexander et al. 1996, Carlsson-Granér 1997; Thrall and Burdon 2000; Laine 2004, Springer 2007*)
- "Passive resistance" – heritable host traits other than resistance genes can affect field disease levels (*Alexander 1989, Alexander et al. 1993, Shykoff et al. 1994, Biere and Antonovics 1996; Giles et al. 2006*)

Example: role of variation in host floral traits (floral phenology, flower numbers) in field disease incidence



(Alexander et al. 1993)

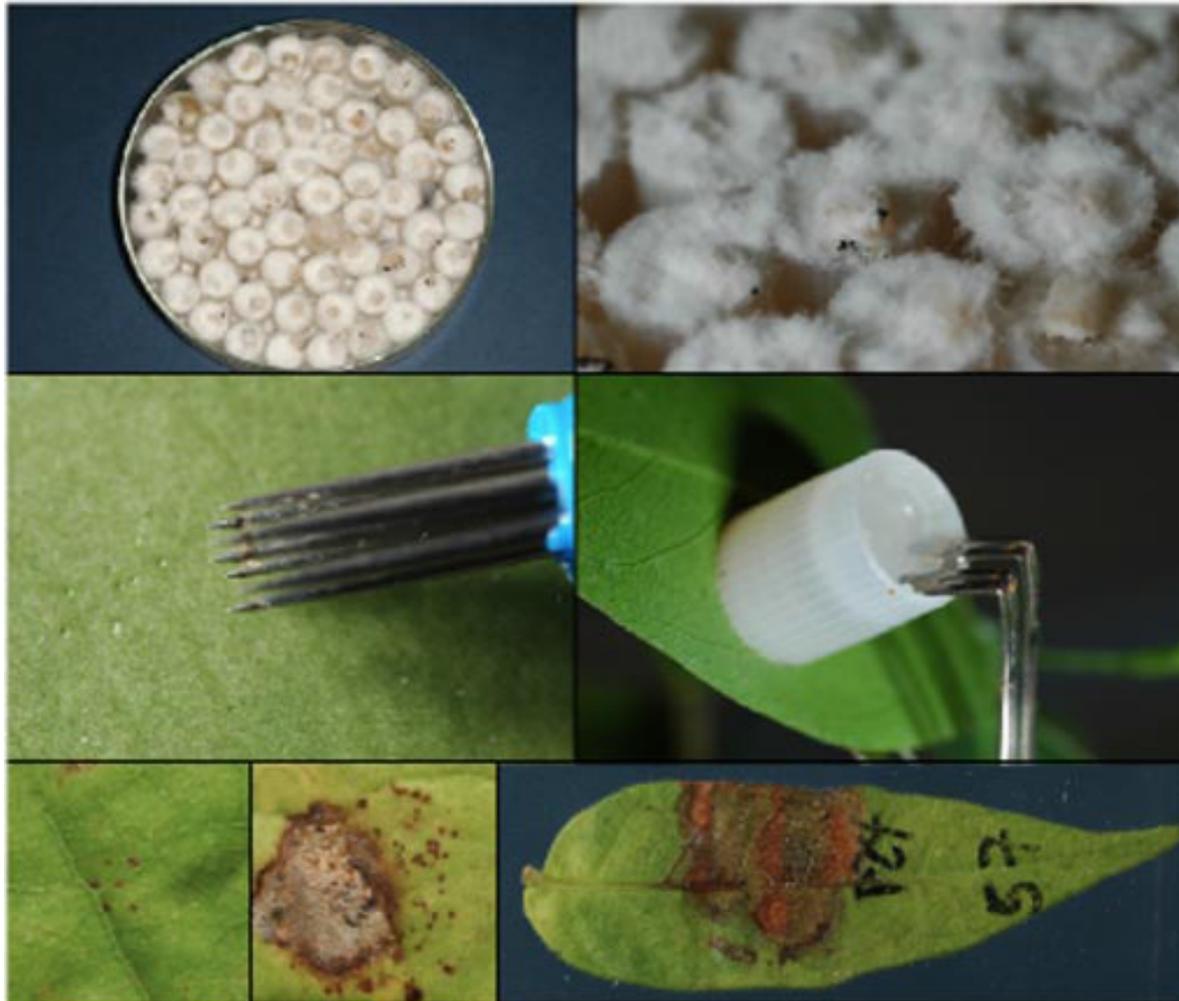
Interactions between ecology and genetics: relevance to communities

--Role of ecology, genetics, and phylogeny in host shifts (*Roy 2001, Antonovics et al. 2002, López-Villavicencio et al. 2005*)

--Genomics and viral prevalence across species (70% and 25% of samples across tropical forest and prairie communities have viral RNA (*Muthukumar et al. 2009, Roosinck et al. 2010*))

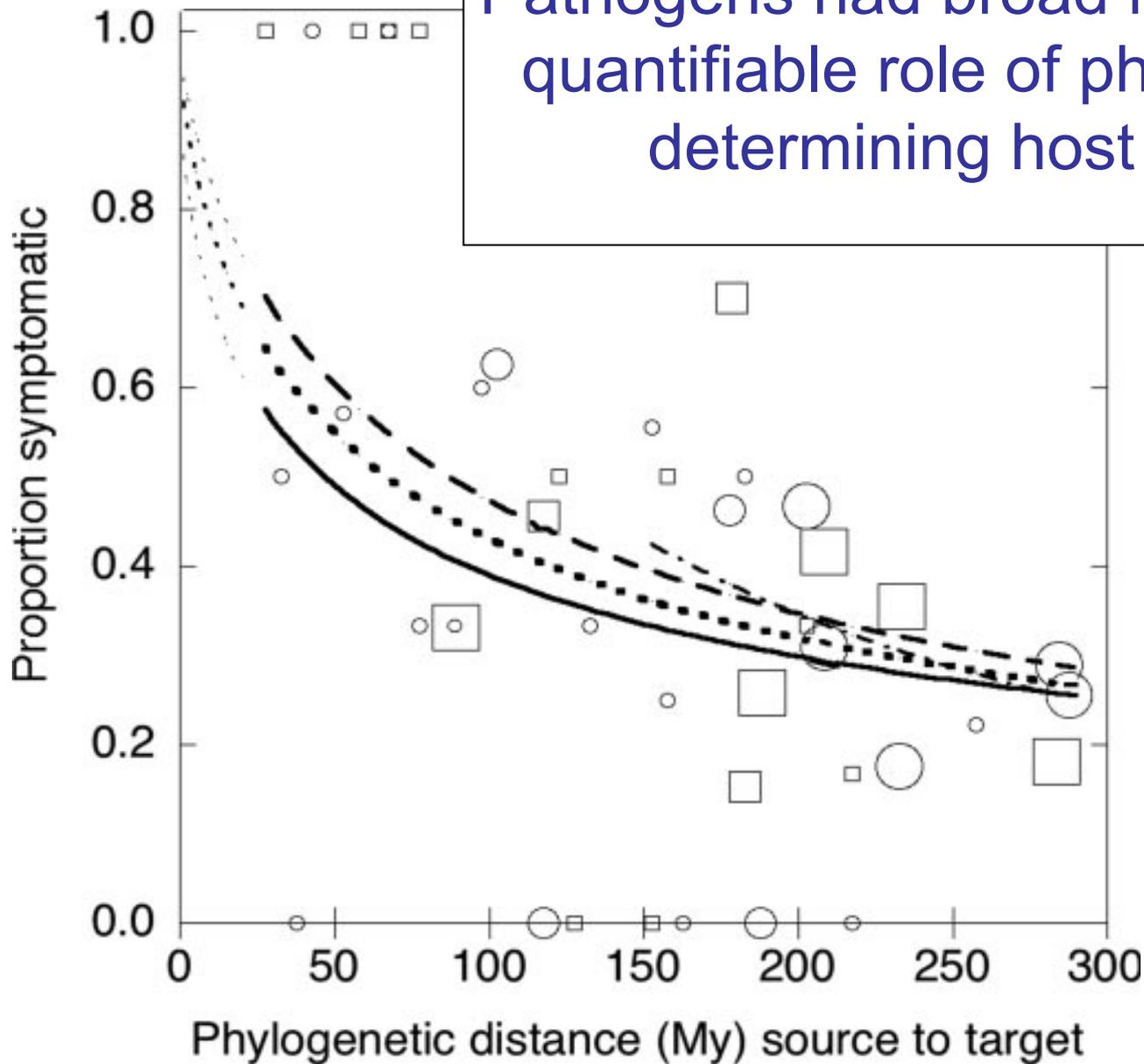
--Role of host phylogeny in plant-pathogen interactions and pathogen host range (*Webb et al. 2006, Gilbert and Webb 2007*)

In-situ inoculations in tropical forest using > 50 foliar fungal pathogens



(Gilbert and Webb 2007)

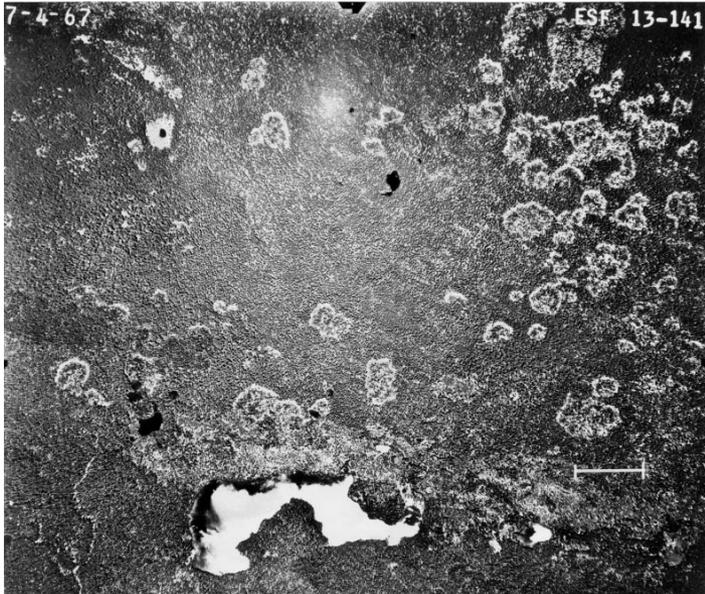
Pathogens had broad host ranges;
quantifiable role of phylogeny in
determining host range



(Gilbert and Webb 2007)

3) Plant community composition

Direct and indirect effects of pathogens on number of plant species per area and relative frequency



Mortality centers caused by *Phellinus weirii* in mountain hemlock forest

(picture from Hansen and Goheen 2000)



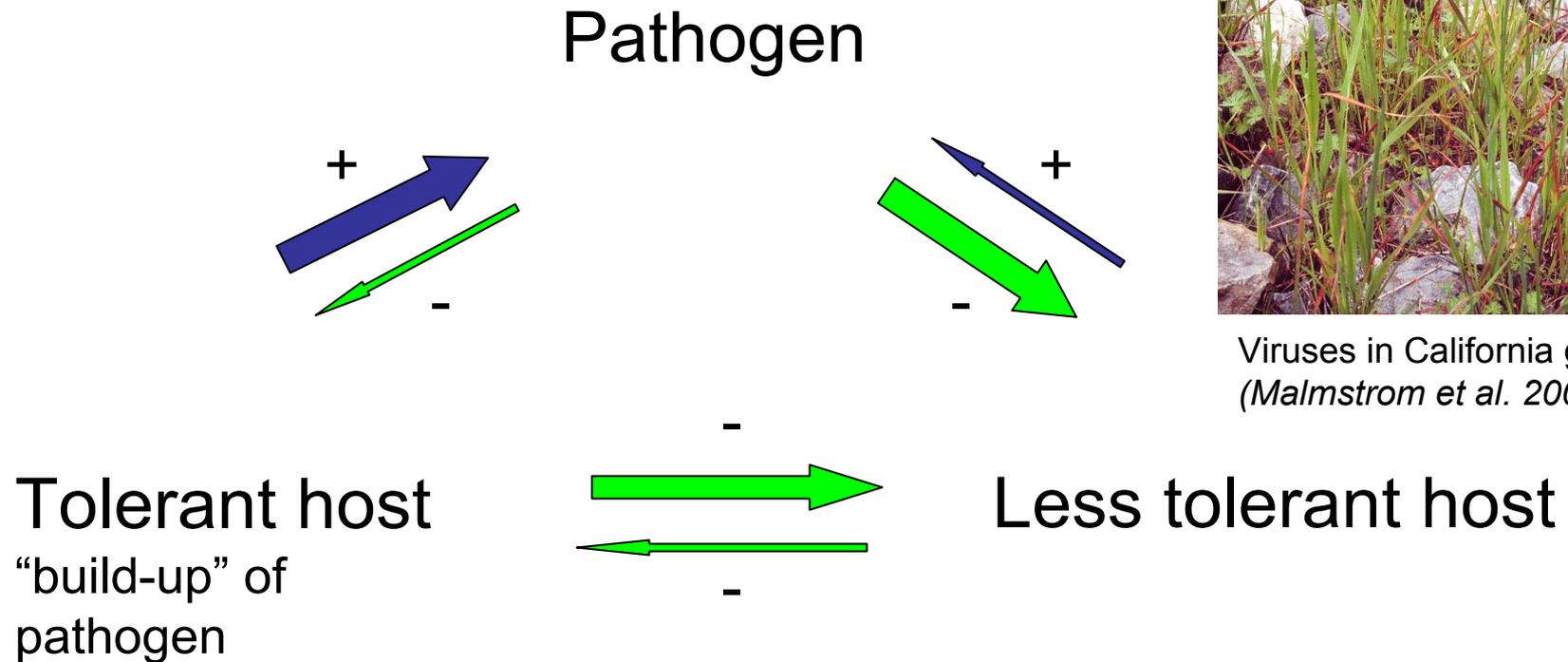
Lithocarpus densiflorus



Umbellularia californica

Sudden oak death - *Phytophthora ramorum*

Pathogens with multiple hosts: pathogen spillover and apparent competition *(Holt and Lawton 1994; Power and Mitchell 2004)*



Viruses in California grasses
(Malmstrom et al. 2005)

Cronin et al. 2010 – role of host physiological phenotype

Effects of the soil microbial community on plant community composition

Several models (negative feedback; Janzen-Connell interactions, negative density-dependence) address similar question:

-Consider plant species “A”: Does the presence/high density of species A contribute to the development of a soil microbial community that leads to low survival for individuals of species A (but not for species B, C, D...)?

Community implications: promote plant species diversity?

Most published studies are supportive.....

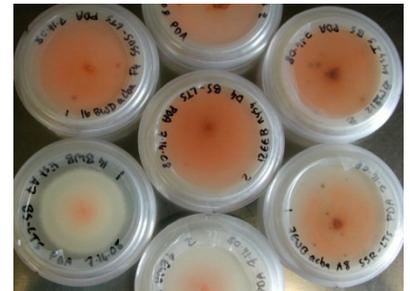
Van der Putten et al. 1993, Bever et al. 1997, Mills and Bever 1998, Holah and Alexander 1999, Packer and Clay 2000, Klironomos 2002, Bever 2003, Reynolds et al. 2003, Reinhardt et al. 2003, Petermann et al. 2008, Bagchi et al. 2010, Diez et al. 2010, Mangan et al. 2010, Swamy and Terborgh 2010)

But gaps in our knowledge:

- microbial community treated as “black box”
- role of generalists

M. Hersh: Host-specific effects can be generated by a generalist pathogen if differential:

- effects on survival of different hosts
- effects/patterns of coinfections

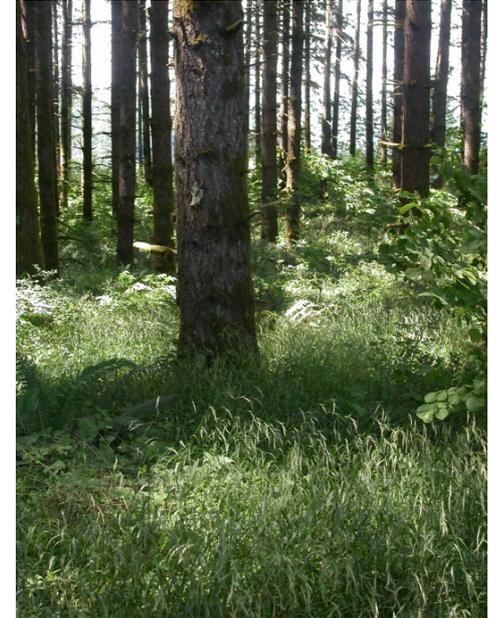


Disease and plant invasions

Does introduction of exotic plant species lead to “enemy release”?

-native site: pathogens regulate plant population

-introduced site: reduced pathogen presence and pressure



Eurasian grass in North American Forests – photo from B. Roy

Supporting evidence, but results are variable, and depend on system studied

(Reinhart et al. 2003, Agrawal et al. 2005, Mitchell et al. 2006, Parker and Gilbert 2007, van Kleunen and Fisher 2009, Mitchell et al. 2010, Diez et al. 2010, Roy et al. 2011)

Current work on invasion ecology and disease:

--Plant demography and population dynamics

(Chun et al. 2010, Roy et al. 2011)

--Roles of specialist versus generalist natural enemies

(Halbritter et al., in press)

--Explaining variation across species in enemy release

(Blumenthal et al. 2009)

--Accumulation of pathogens on introduced plant species

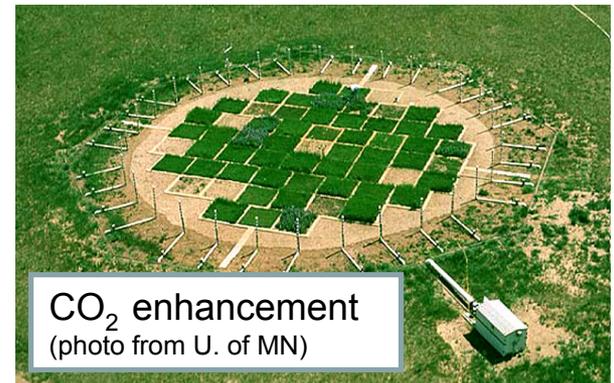
and evolutionary changes *(Diez et al. 2010,*

Gilbert and Parker 2010, Mitchell et al. 2010)

4) Global change and ecosystem function

Effects on disease levels:

- temperature, CO₂, nutrients (*Nordin et al. 1998, Strengbom et al. 2002, Mitchell et al. 2003, Roy et al. 2004, Strengbom et al. 2006, Tylianakis et al. 2008, Lau et al. 2008, Nordin et al. 2009*)



Genetic variation in response to environmental variables (*Laine 2007*)

Effects of disease on ecosystem function (*Mitchell 2003, Lovett et al. 2006, Eviner and Likens 2008*)

The future?

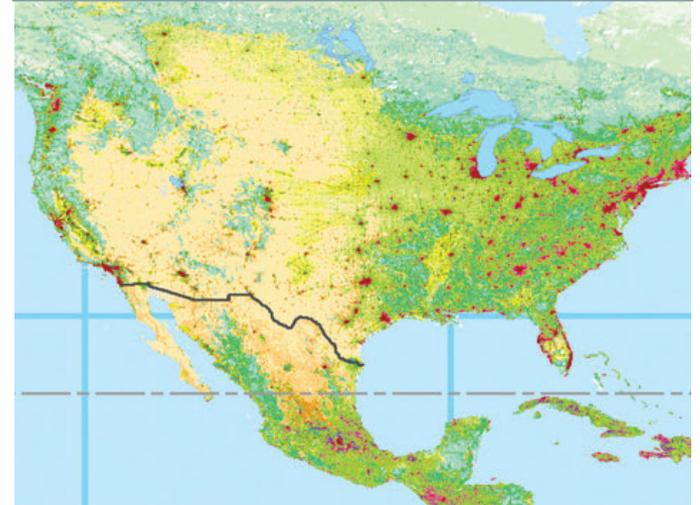
-Increasing importance of interface between agriculture/forestry and “natural” habitats

(Burdon and Thrall 2008, Fabiszewski et al. 2010)



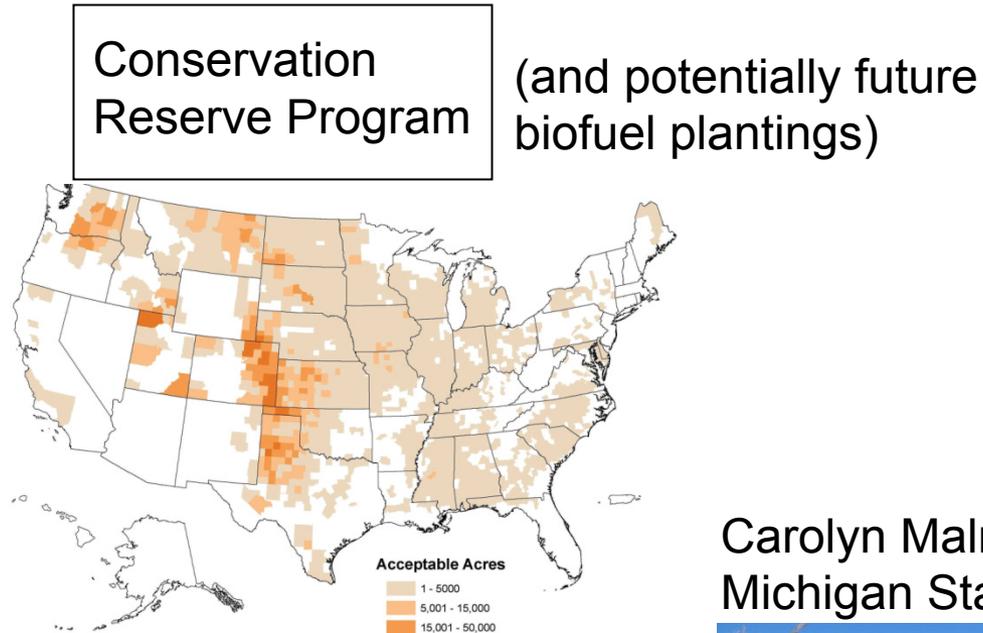
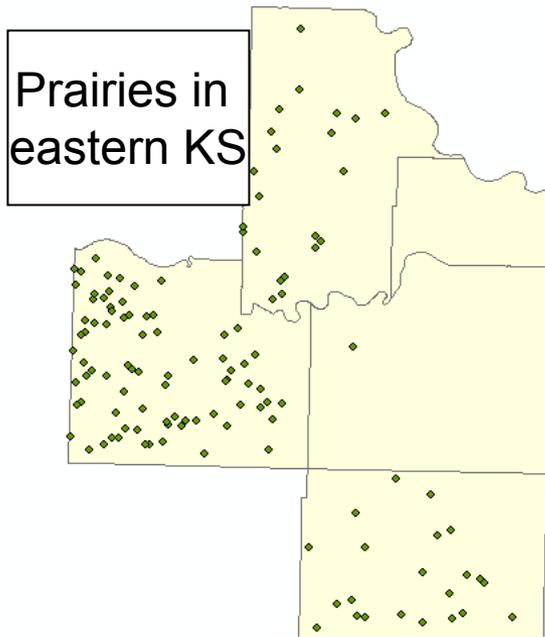
Virginiaplaces.org

Red (cities), Green (forest),
Yellow (crops), Tan (rangeland)



Anthropogenic biomes
(Ellis and Ramankutty 2008)

My current work: viral prevalence and diversity (switchgrass populations across managed/unmanaged habitat continuum)



http://www.apfo.usda.gov/Internet/FSA_File/su39book.pdf

Carolyn Malmstrom,
Michigan State University

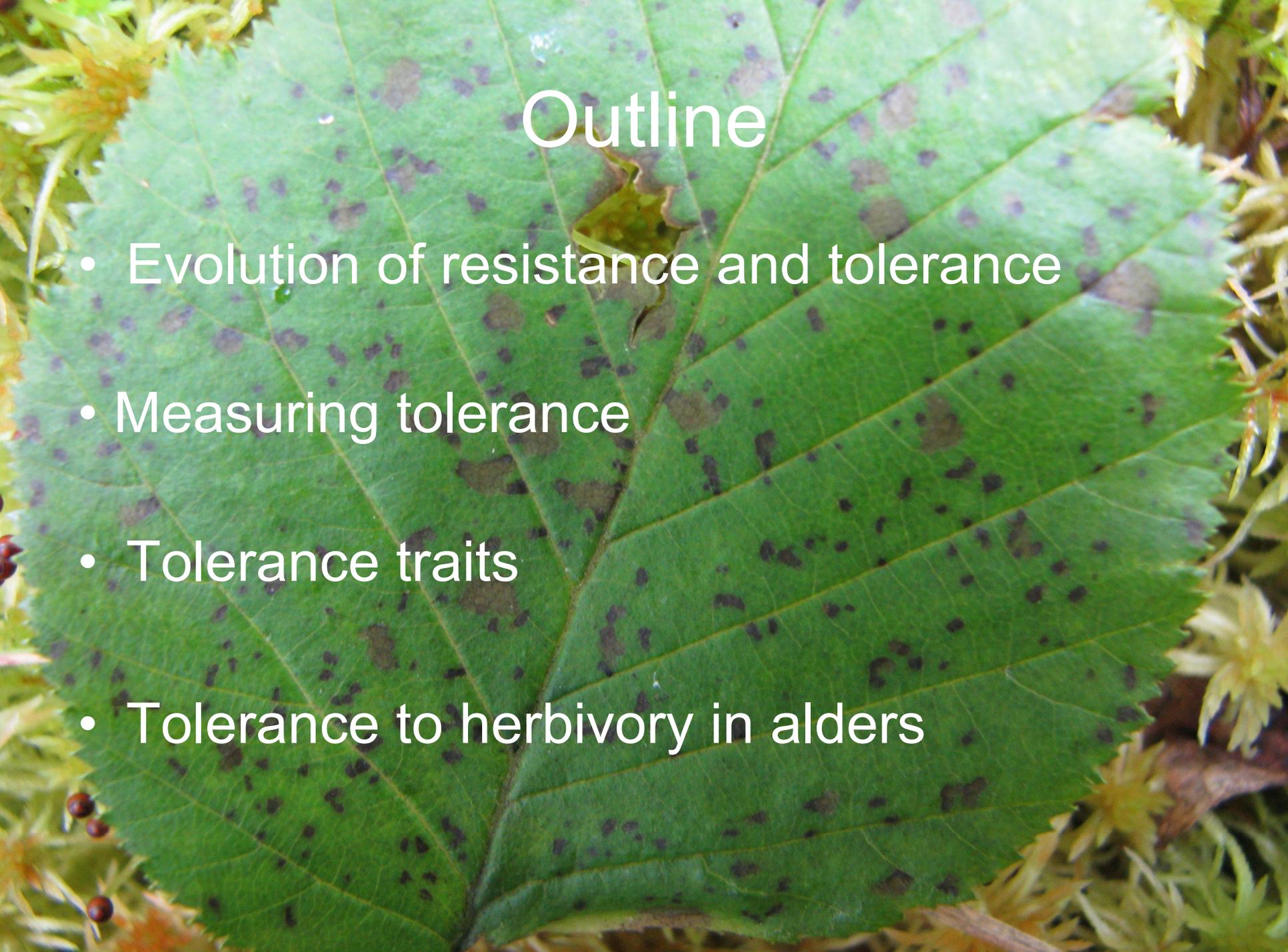


Tolerance and Trees

Bitty A Roy

University of Oregon



A close-up photograph of a green leaf with a prominent vein structure. The leaf is covered in numerous small, dark brown spots, likely due to herbivory or disease. A small, irregular hole is visible near the top center of the leaf. The leaf is surrounded by moss and other small plants, creating a natural, textured background.

Outline

- Evolution of resistance and tolerance
- Measuring tolerance
- Tolerance traits
- Tolerance to herbivory in alders

Resistance inhibits the occurrence or spread of infection



Tolerance limits the fitness consequences of infection when it occurs



Modeling Resistance & Tolerance

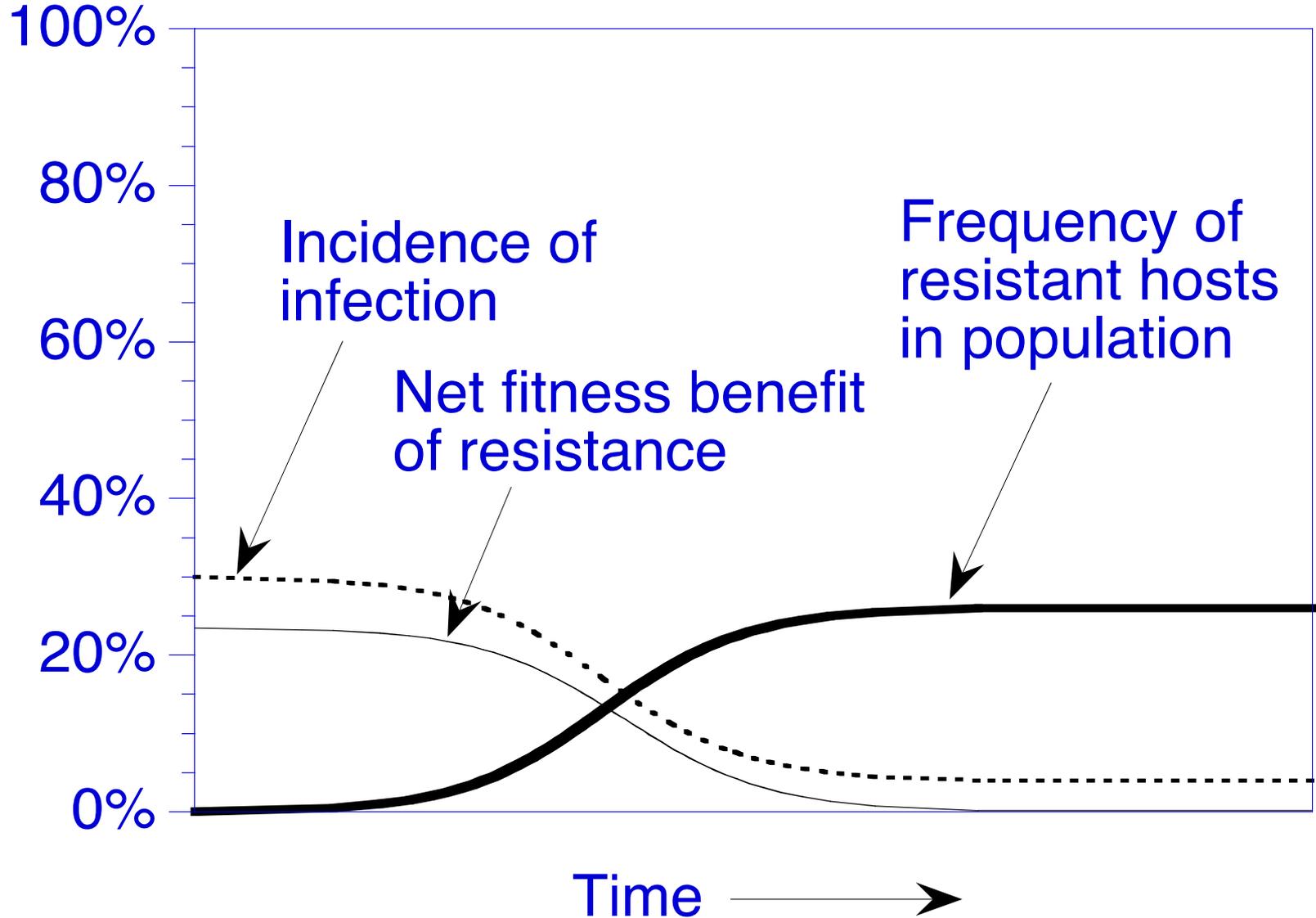


Jim Kirchner

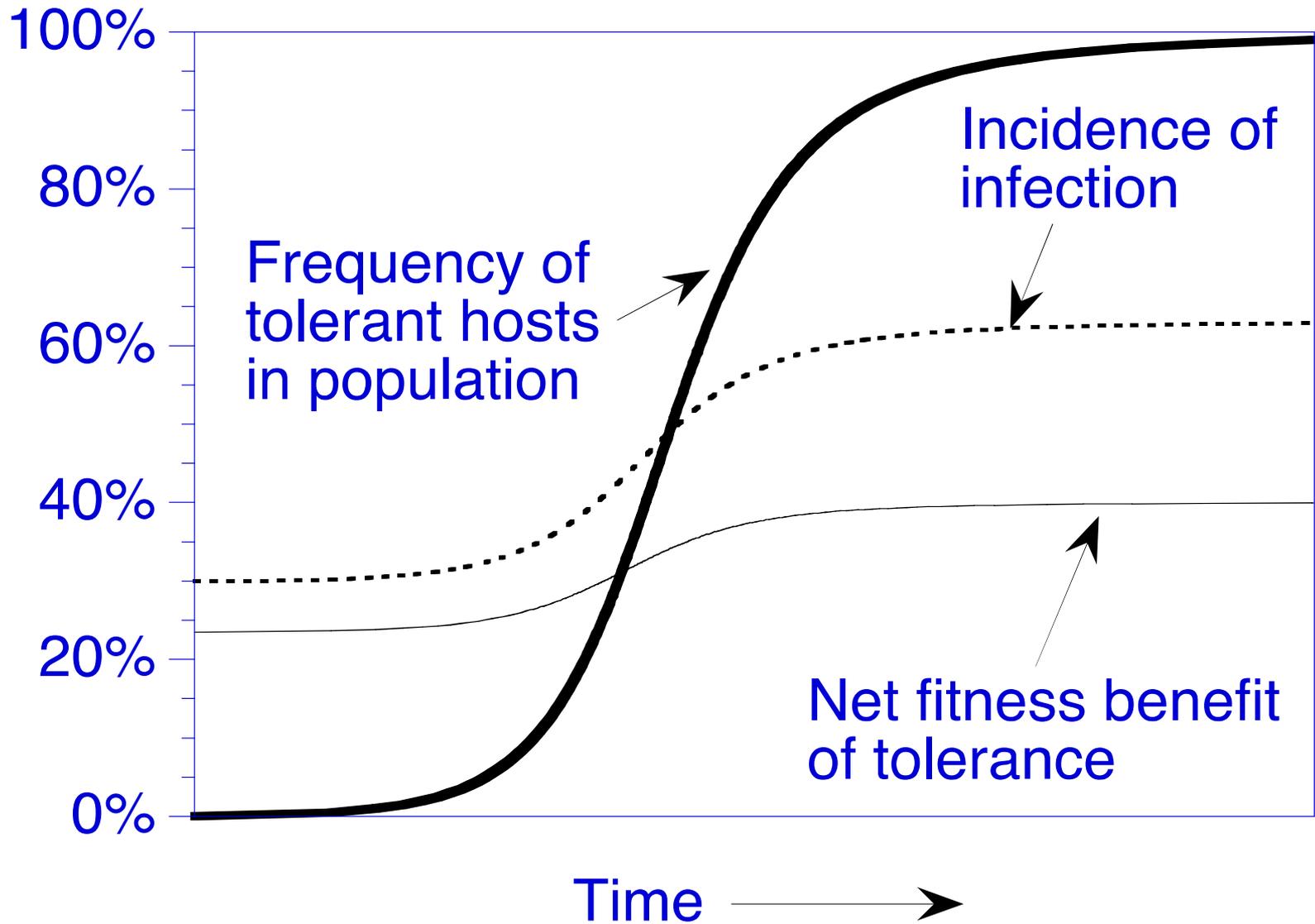
Parameters

- 30% initially infected
- Pathogen reduces longevity 50%
- 5% cost

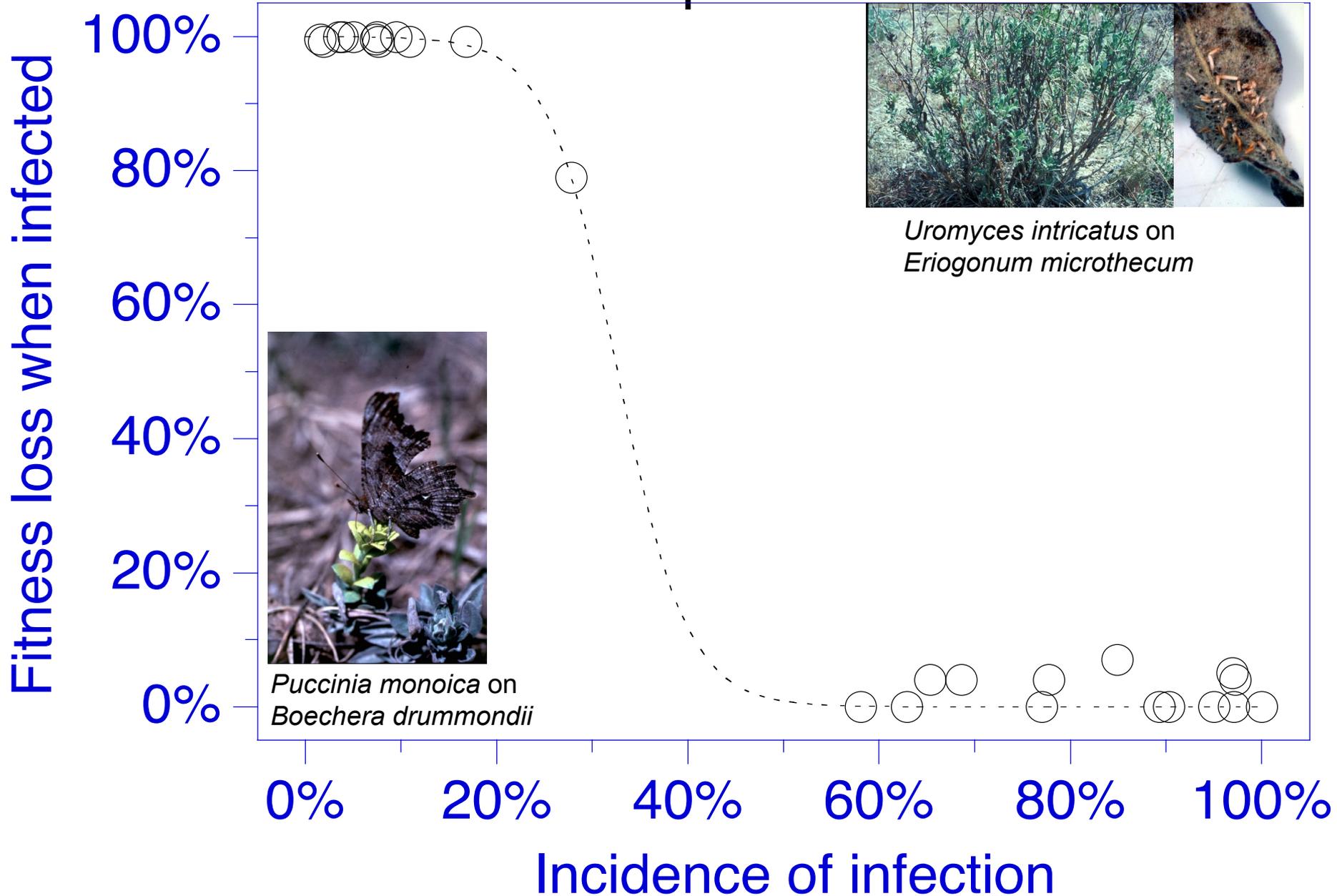
Resistance Dynamics



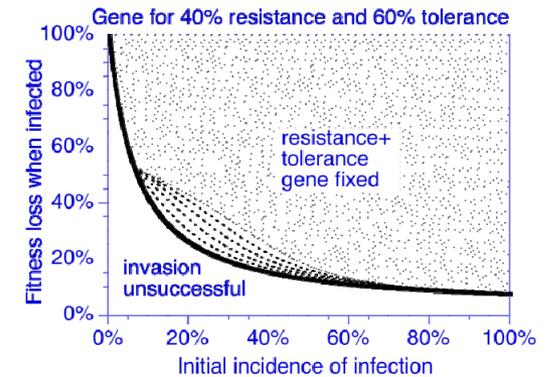
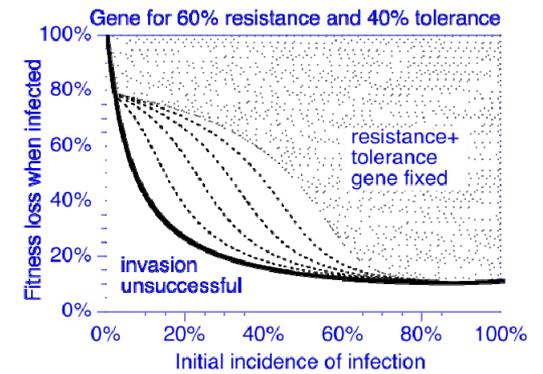
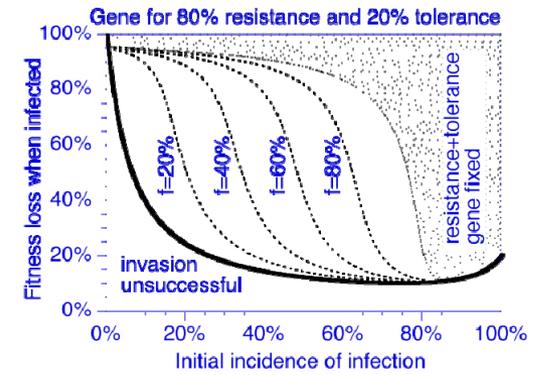
Tolerance Dynamics



Natural Populations



Traits that combine resistance and tolerance can be polymorphic



Combined Resistance and Tolerance

Healthy



Diseased

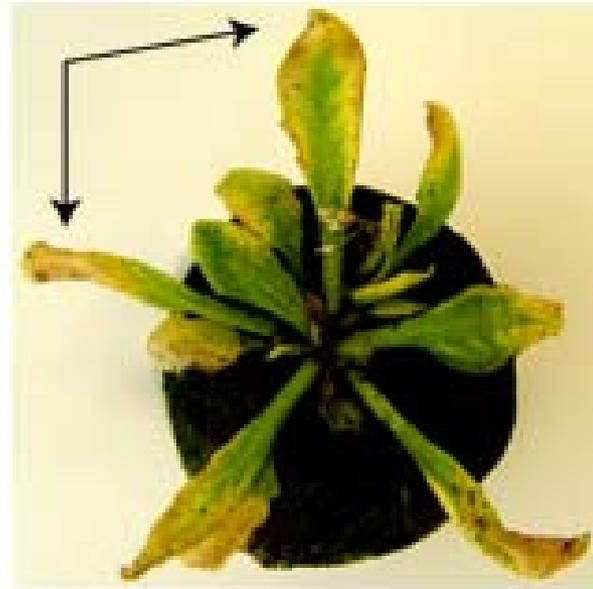
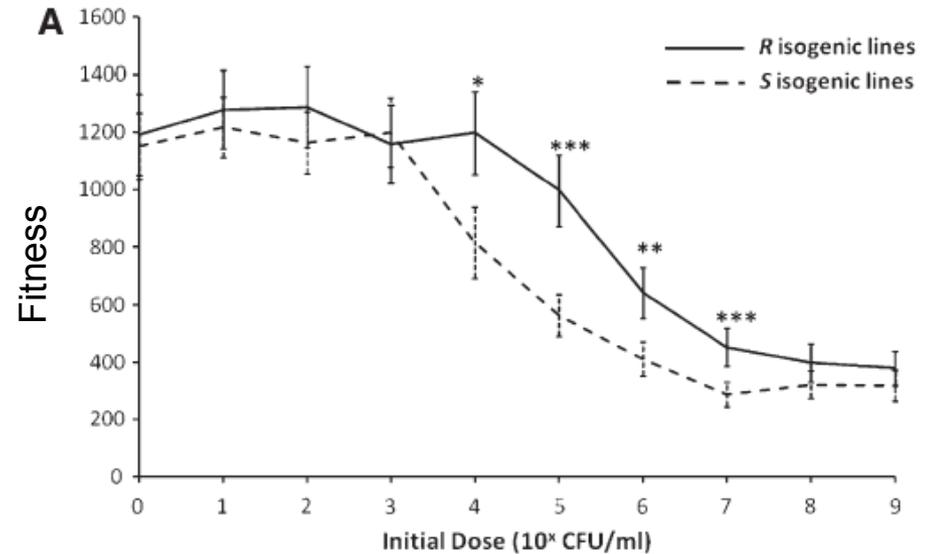
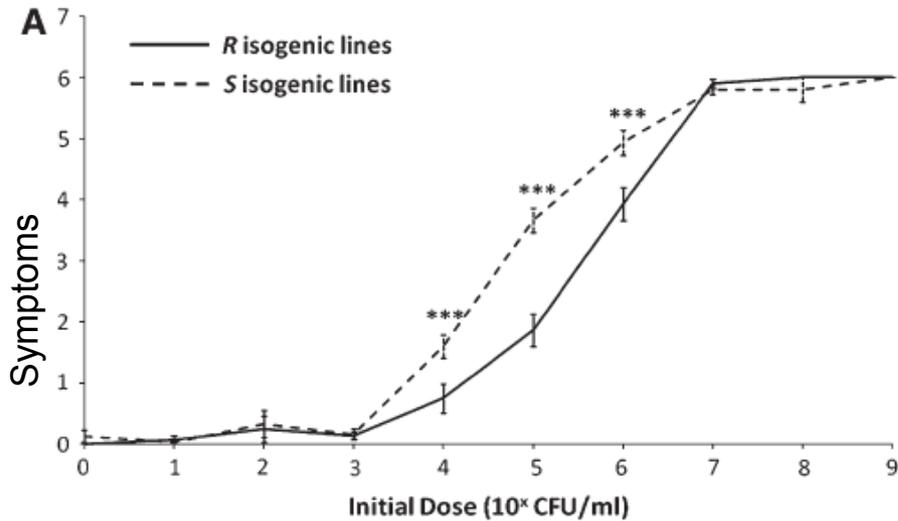
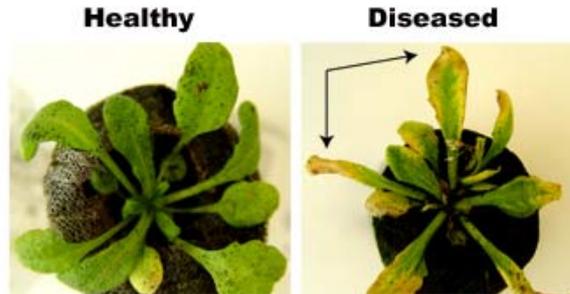


Photo: Jorge Vivanco

Arabidopsis thaliana infected by *Pseudomonas syringae*

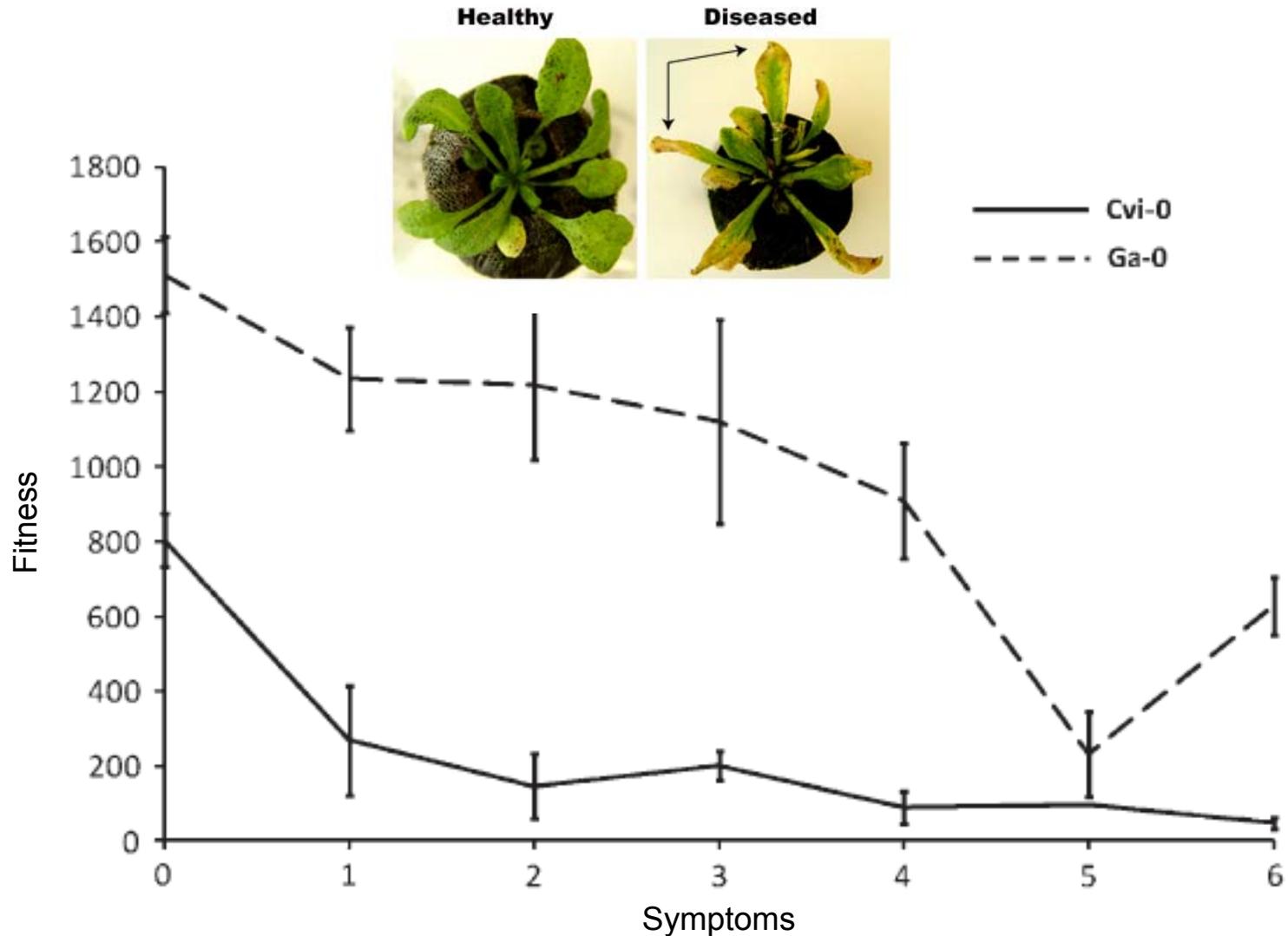
Rpm1 resistance and AvrRpm1 avirulence

Combined Resistance and Tolerance



Resistance influence on fitness: resistant lines have fewer symptoms, leading to higher fitness

Combined Resistance and Tolerance



Natural variation in tolerance among accessions within the Susceptible group

Summary

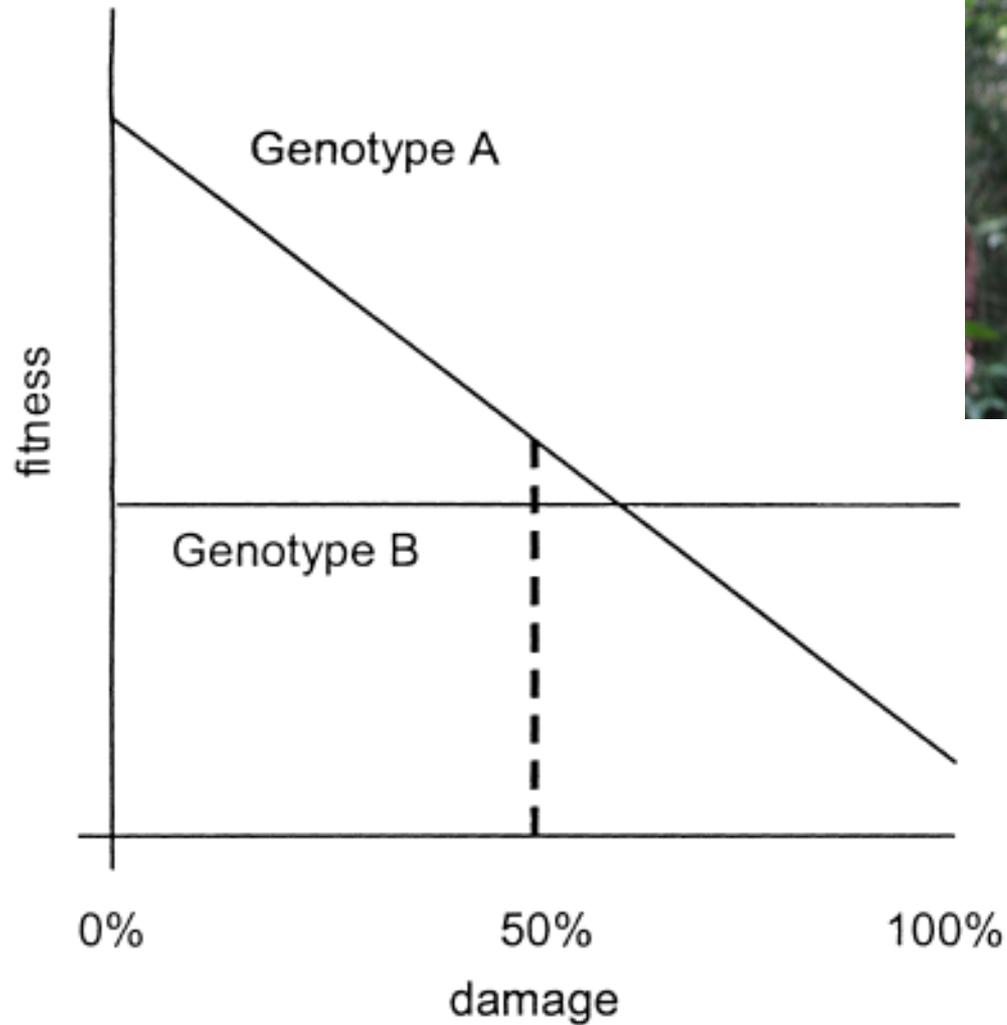
Dynamics of Resistance and Tolerance

- Where tolerance occurs it is likely to be fixed
- Where resistance occurs it is likely to be polymorphic
- Traits that combine resistance and tolerance are likely to be polymorphic

Tolerance Implications

- Less likely to select for aggressive pathogens
- More likely to be “durable” than resistance
- Aesthetics of appearance

Measuring tolerance



When yield is not decreased by damage is it due to

Pathogen virulence
(virulence=pathogen caused
decrease in host fitness)

OR

host tolerance
(compensation)?



Measuring tolerance

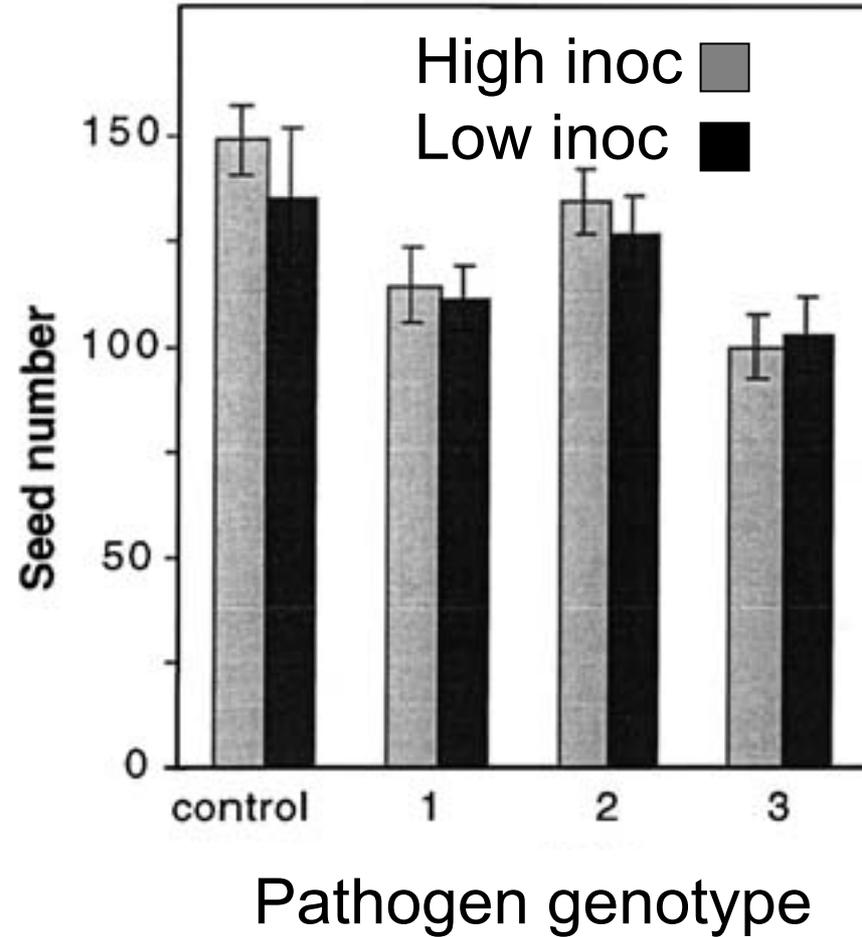
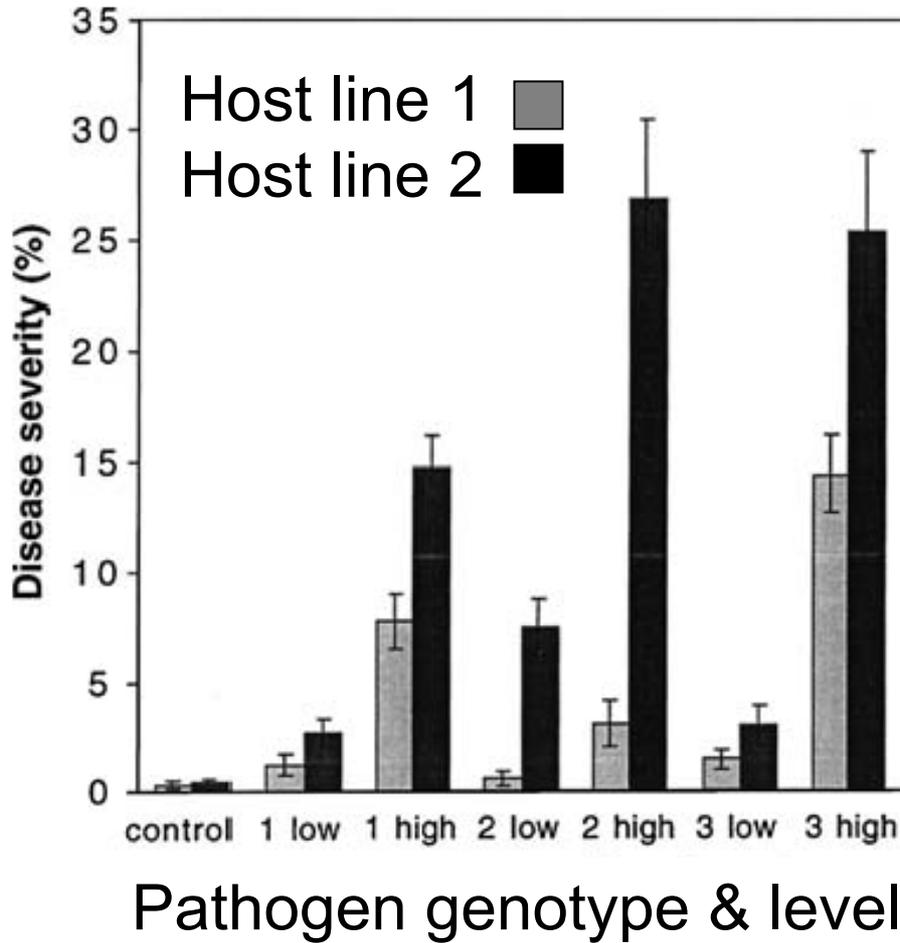


Stéphanie Schürch



Mycosphaerella graminicola
(Septoria blotch) on wheat

Measuring tolerance



Both pathogen virulence and host tolerance are tested with ANCOVA

Source of variation	df	Seed number		
		MS	<i>F</i> value	<i>p</i> > <i>F</i>
Path. genotype	2	2115	1.18	0.3467
Block	5	1857		
Error 1	10	1789		
Line	1	24,511	97.80	<0.0001
Line * PG	2	130	0.14	0.8659
Disease severity	1	405	0.45	0.5040
Line * D. severity	1	3611	4.00	0.0470
PG * D. severity	2	649	0.72	0.4891
Line * PG * D. sev.	2	1437	1.59	0.2064
Biomass	1	243,679	269.76	<0.0001
Error 2	186	903		

Potential Tolerance Traits

- increase chlorophyll concentration
- increase size of new leaves
- advance timing of bud break
- delay senescence of infected tissue
- increase nutrient uptake
- sap flow and water relations

Water relations in green alder *Alnus viridis* susp. *fruticosa*

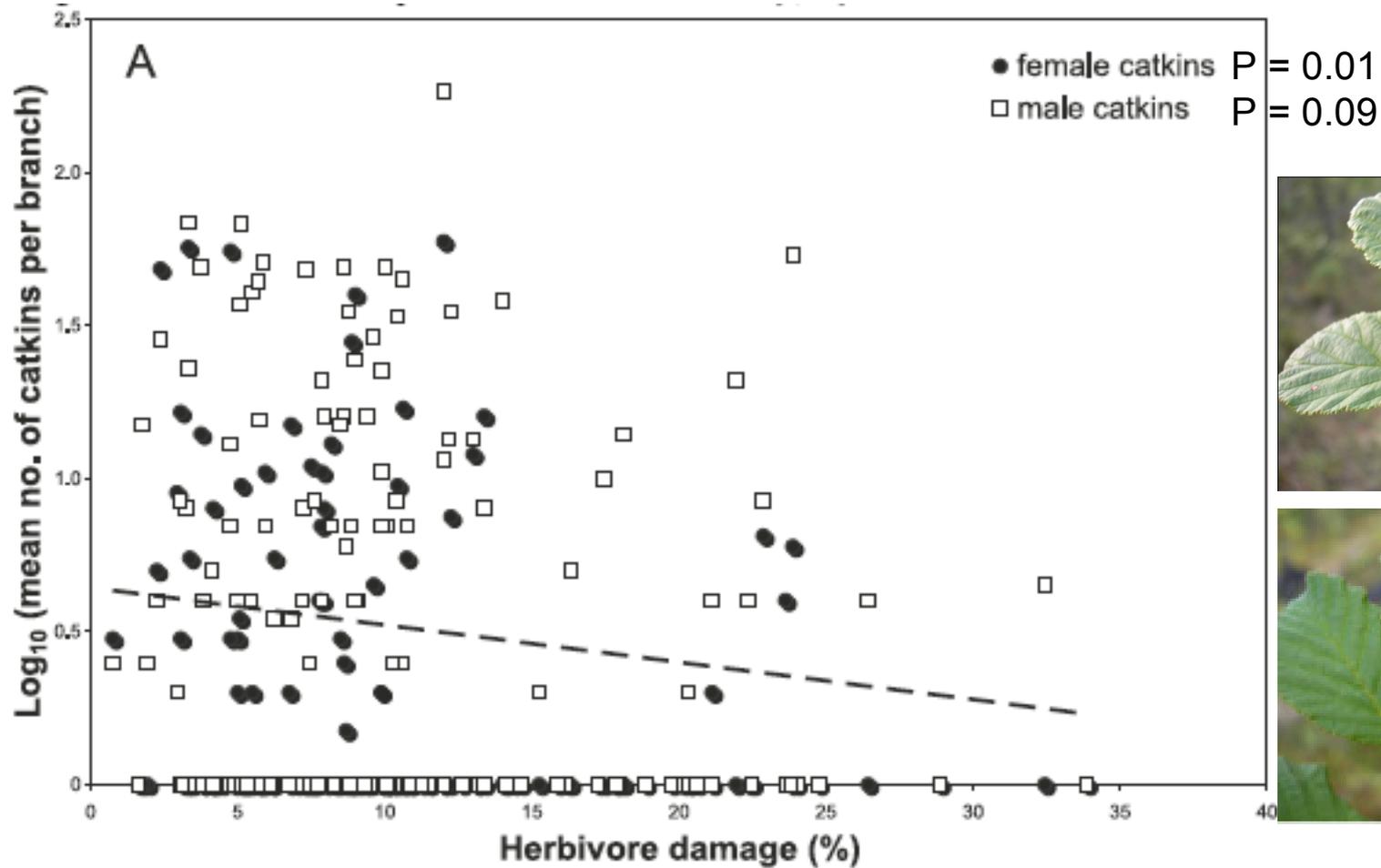


Christa Mulder

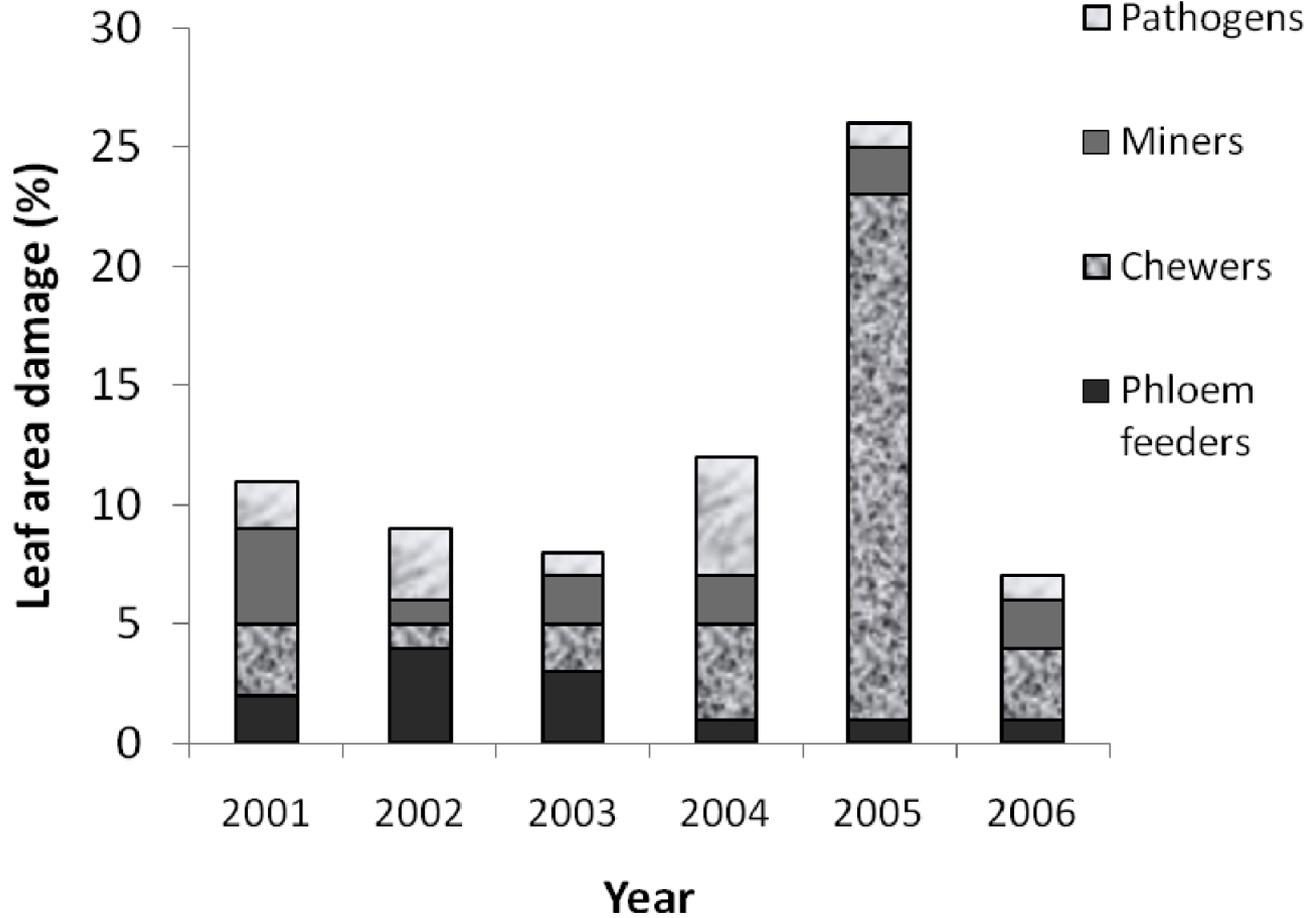


Jenny Rohrs-Richey

Herbivory reduces fitness



Alders are attacked by insects and pathogens



Can they compensate for damage?



Jenny Rohrs-Richey



Rohrs-Richey

Can they compensate?



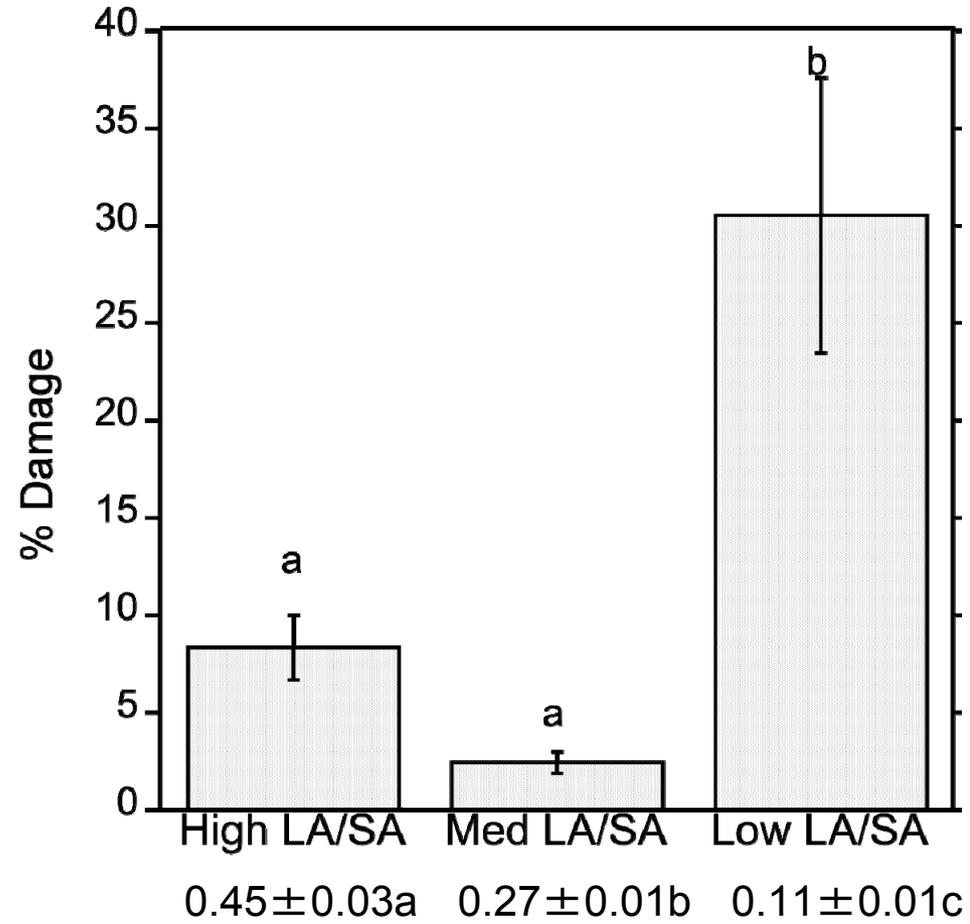
Leaf Area:Sapwood area =Demand:Supply



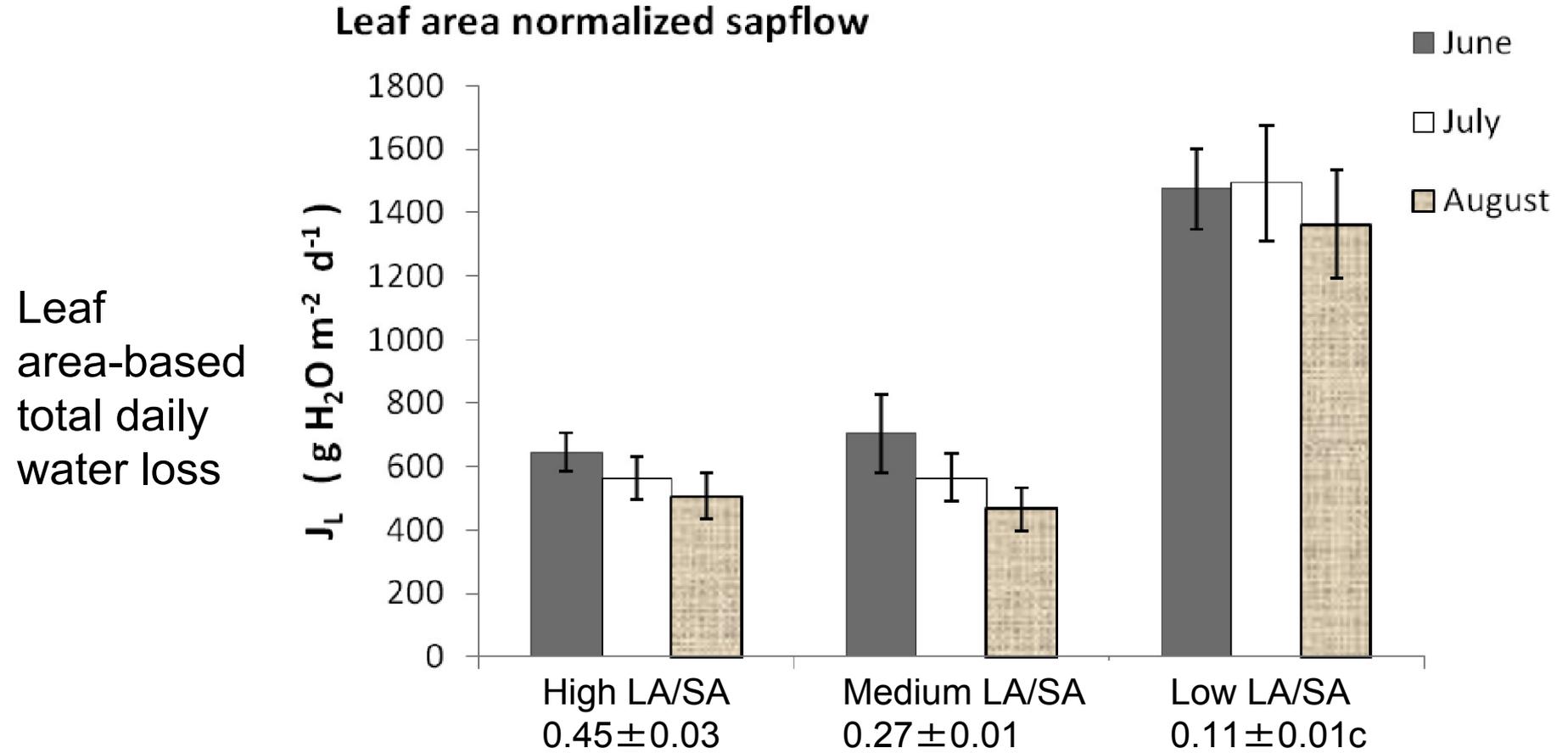
High	Medium	Low
$0.45 \pm 0.03a$	$0.27 \pm 0.01b$	$0.11 \pm 0.01c$

Low=reduced canopy water demand relative to the supplying sapwood area

Damage highest for lowest LA/SA



Compensation: Sapflow highest for lowest LA/SA



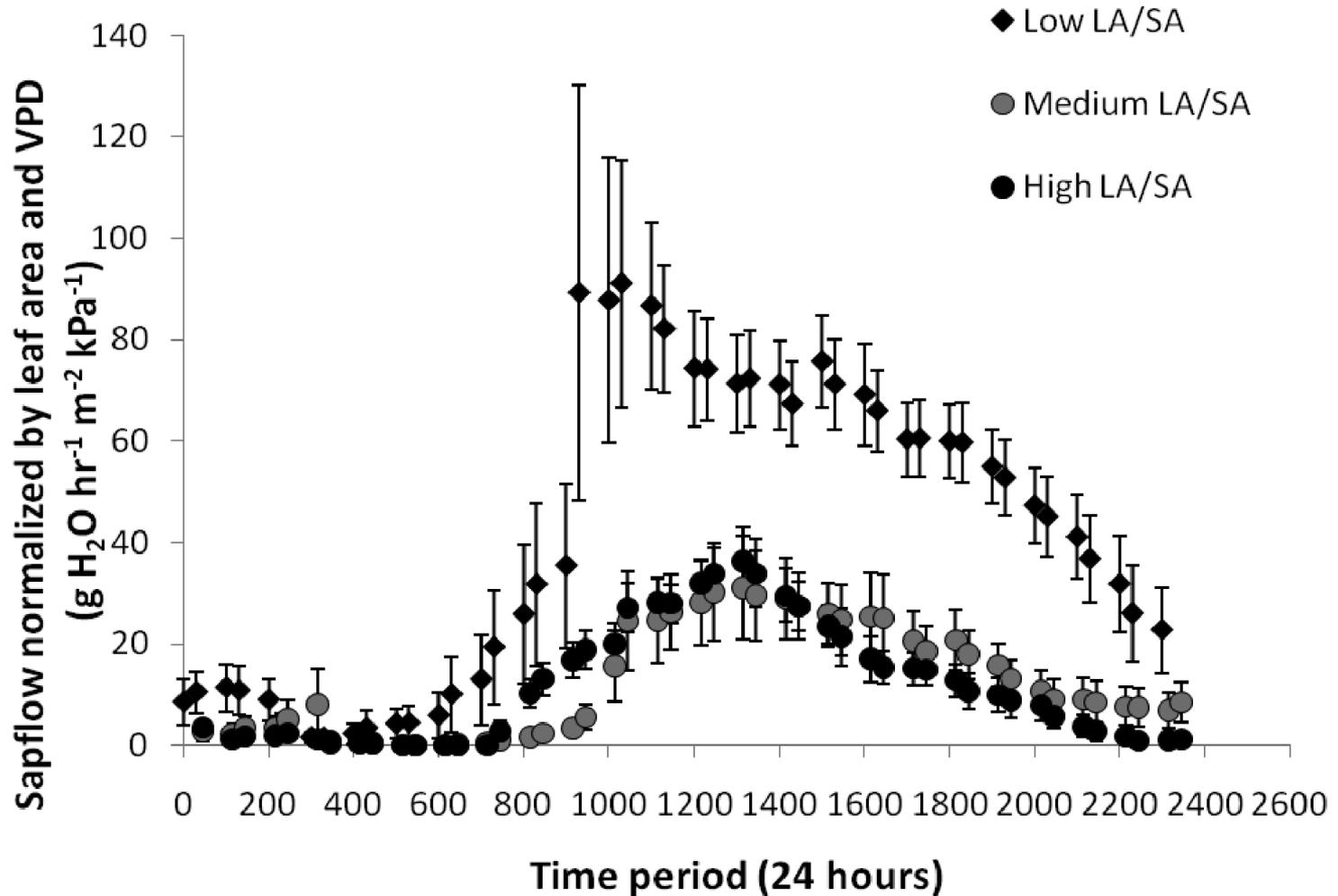
Compensation:

Enhanced water loss in low LA/SA is related to increased photosynthesis

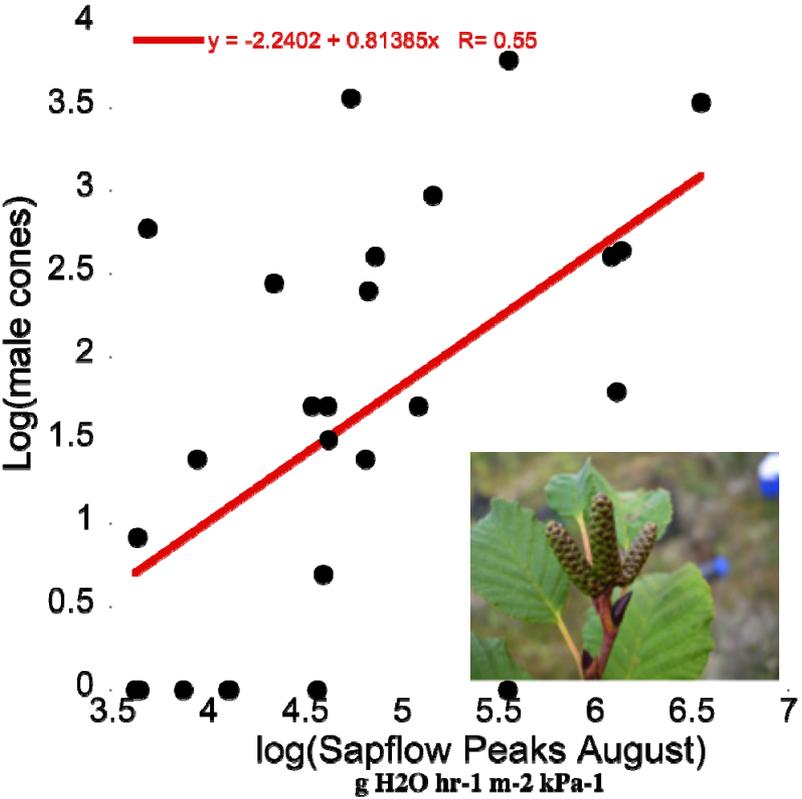


	L LA/SA	Hi LA/SA
Leaf N/unit mass increase	22%	6%
Specific leaf area (thickness)	8%	0%

Peak sapflow likely critical

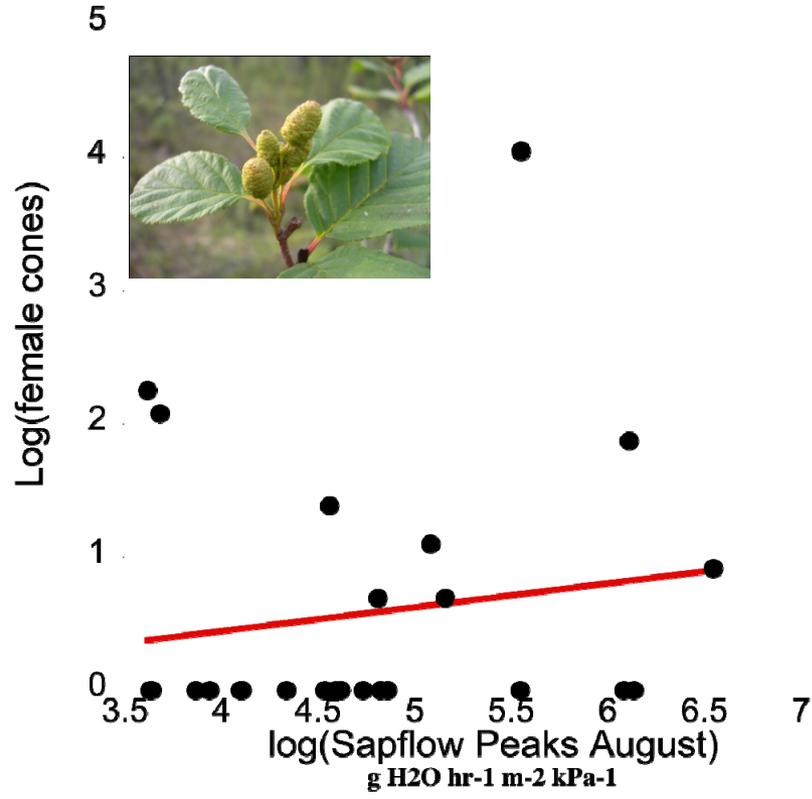


Sapflow is positively associated with male reproduction



P=0.0037

19/27 trees



P=0.4619

9/27 trees

Conclusion

- In alder herbivory-related declines in the LA/SA ratio were followed by a compensatory cascade of physiological changes leading to tolerance.
- Tolerance, the ability to survive, grow, and reproduce when attacked by pests, should receive more breeding attention.

Acknowledgements



Stéphanie Schürch



Jenny Rohrs Richey
& Christa Mulder



Jim Kirchner

Field Assistance: Kai Blaisdell, Michelle Burrell, Elise Glenn,
June Keay, Sabine Güsewell, Becky Mueller, Julie Stewart,
Dan Uliassi

Funding: DOE WESTGEC (Alder work)

Swiss National Fund (Tolerance model)

Caffeine: Alaska Coffee Roasting Co.