An introduction to the genus *Phytophthora*

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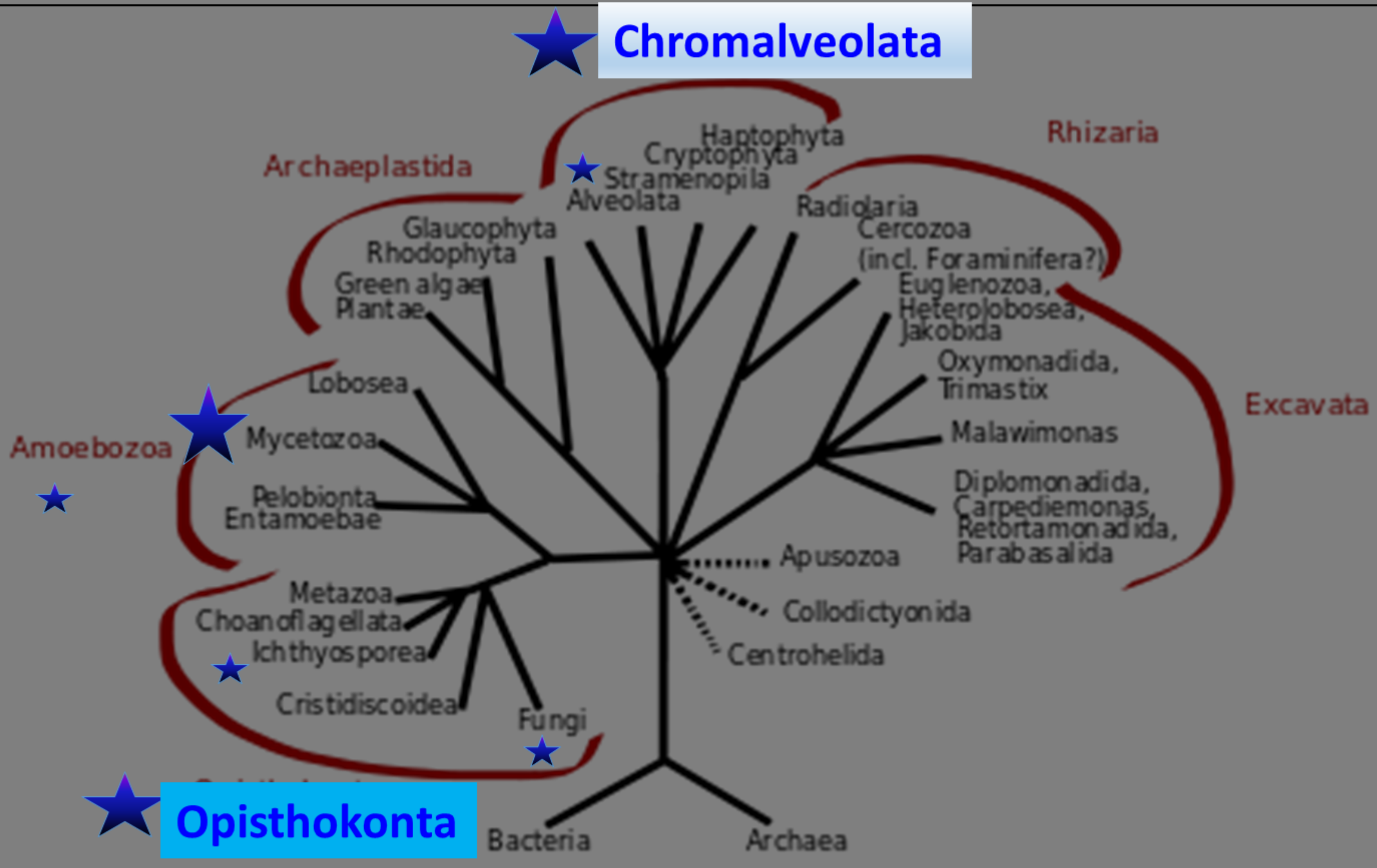
What are *Phytophthoras*?

- Fungi ?
- Fungus-like organisms?
- Water molds ?

Oomycota

- Belong to a kingdom that includes kelp and diatomes
- Kingdom used to be called Chromista (brown algae), it is now the Straminopila

Future classification systems are based on protozoan roots

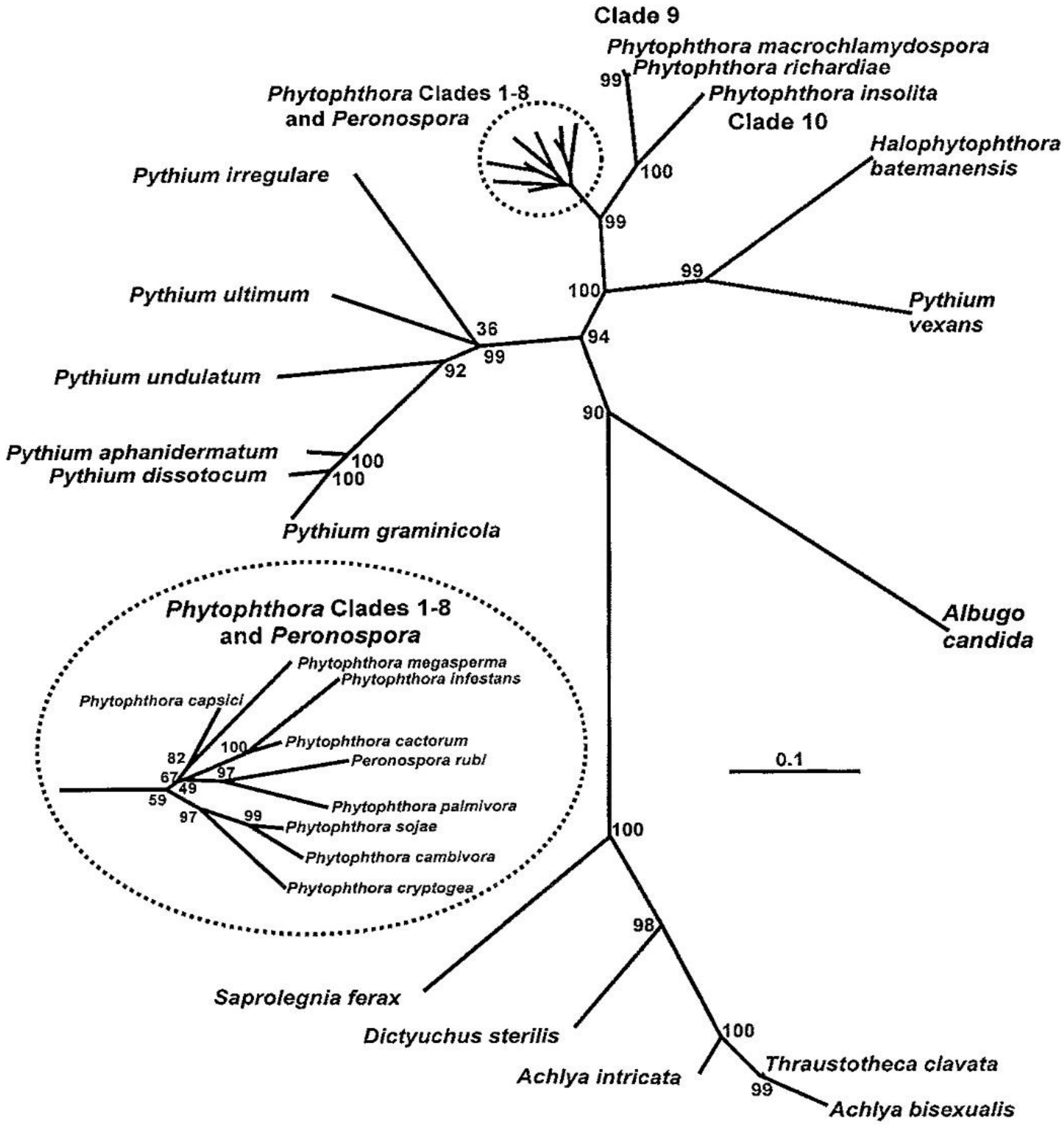


Wikipedia image

★ = historically included in study of "fungi"

Oomycota

- It includes many important plant pathogens:
  - *Peronospora*: mostly aerial
  - *Pythium*: mostly soilborne organisms
  - *Phytophthora*: mixed biology

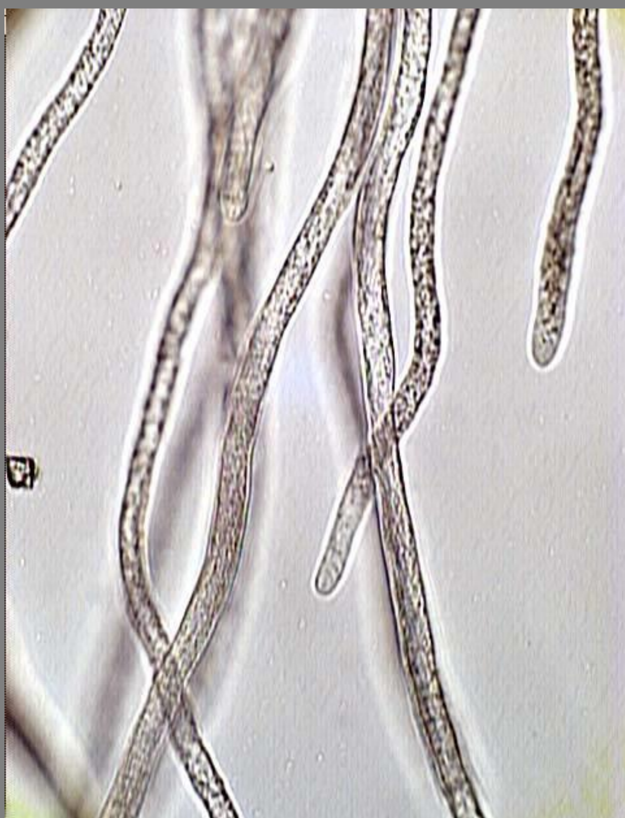


Clade 9
Phytophthora macrochlamydospora
Phytophthora richardiae
Phytophthora insolita
Clade 10
Phytophthora Clades 1-8 and Peronospora
Halophytophthora batemanensis
Pythium irregulare
Pythium ultimum
Pythium undulatum
Pythium aphanidermatum
Pythium dissotocum
Pythium graminicola
Pythium vexans
Albugo candida
Phytophthora megasperma
Phytophthora infestans
Phytophthora capsici
Phytophthora cactorum
Peronospora rubi
Phytophthora palmivora
Phytophthora sojae
Phytophthora cambivora
Phytophthora cryptogea
0.1
Saprolegnia ferax
Dictyuchus sterilis
Achlya intricata
Thraustotheca clavata
Achlya bisexualis

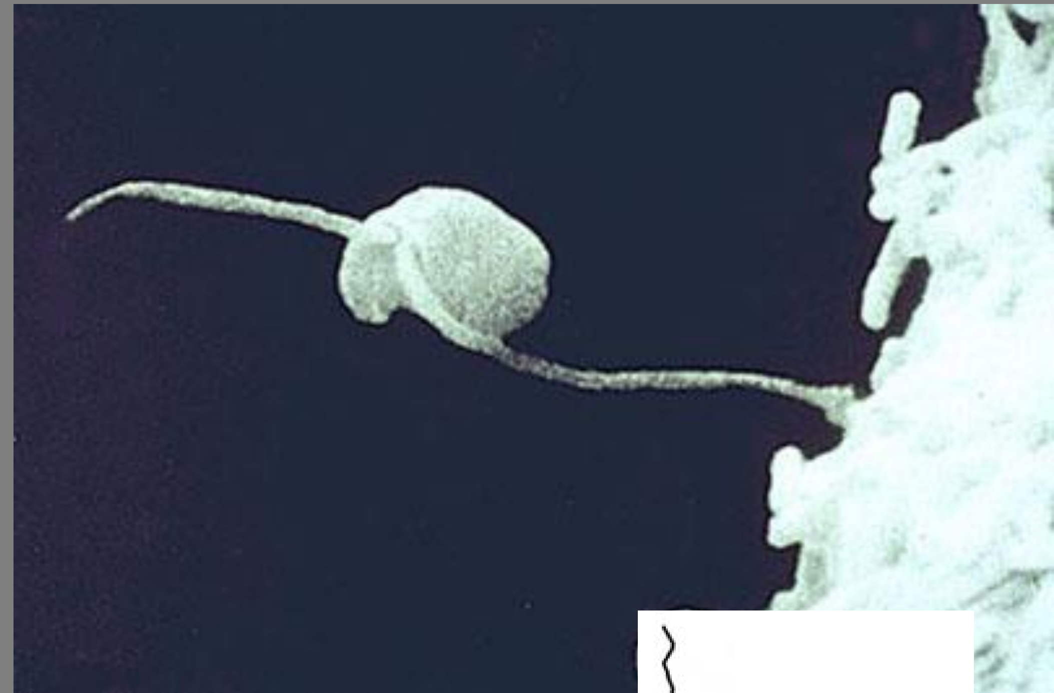
PHYLUM **Oomycota**

CLASS **Oomycete**

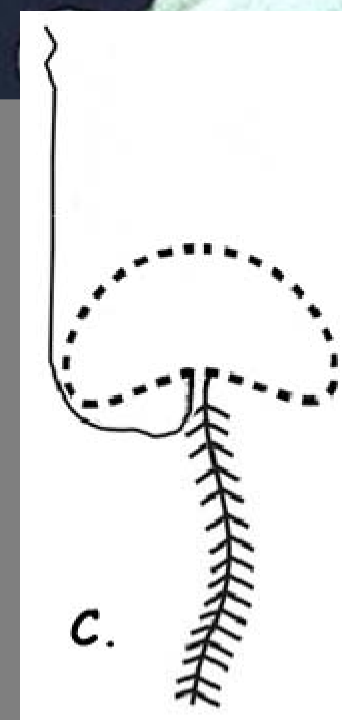
ORDER **Peronosporales**



coenocytic 2n mycelia



biflagellate zoospore



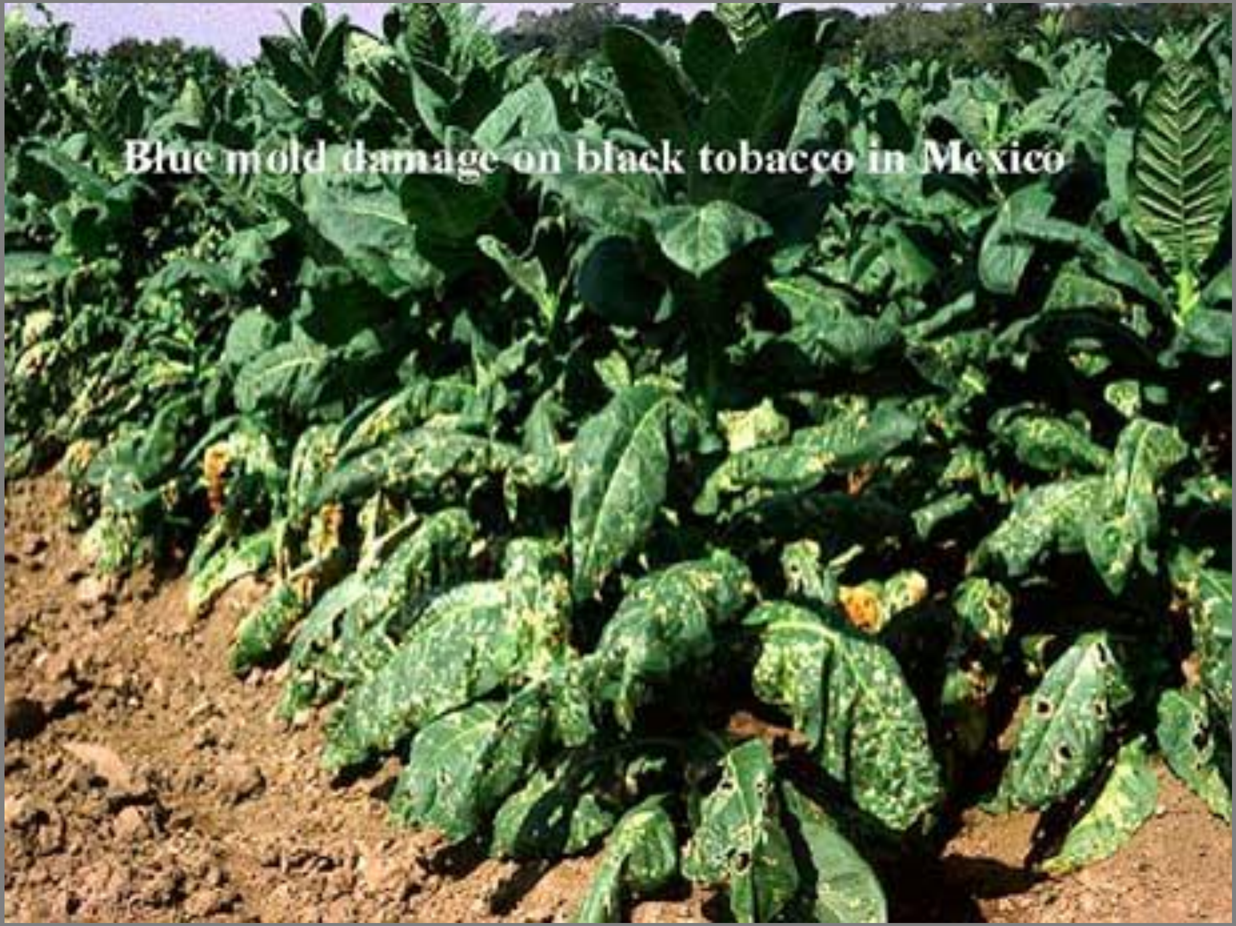
Oomycetes are <u>not</u> fungi

- Cellulose in cell wall
- Ploidy is 2n
- Result of sexual activity is oospore (2n)
- Meiosis, somatogamy, caryogamy all occur at the same time
- Water adapted biology, flagellate phase
- No septa, holocoenocytic hyphae

- Chitin in cell wall
- Ploidy is n, or n+n
- Result of sexual activity is a spore n
- Meiosis, somatogamy,caryogamy are usually interupted by vegetative (somatic phase)
- Better adapted for aerial transmission
- Septate hyphae

Blue mold of tobacco caused by *Peronospora tabacina*

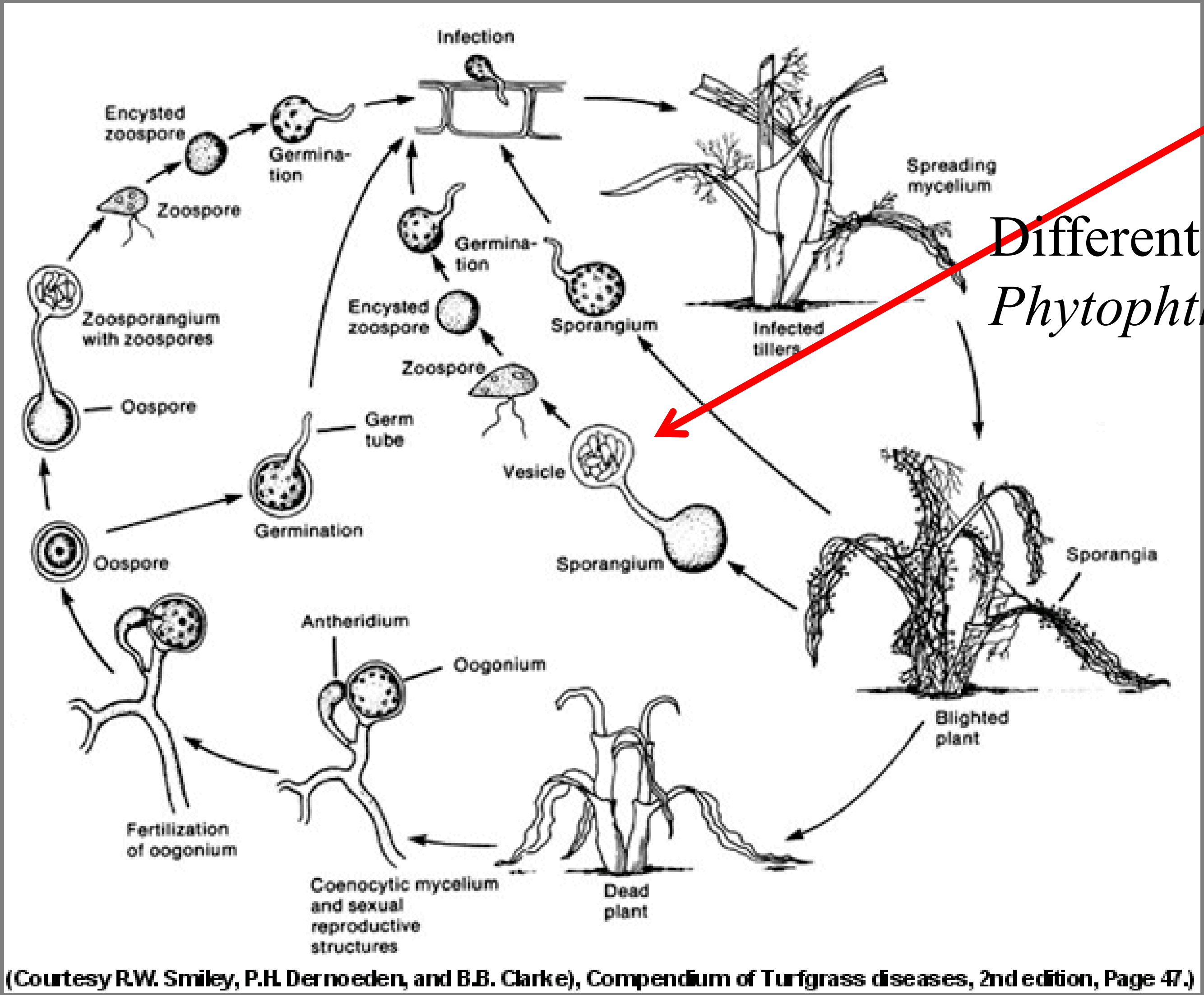
- Ability to travel aerially for hundreds of kilometers from Caribbean to Southern US
- Ability to predict arrival of inoculum based on weather pattern
- Some species capable of over-wintering in buds


Blue mold damage on black tobacco in Mexico

Phythium

- Mostly soilborne pathogens of plants, but at least one (*P. insidiosum*) causes a severe skin disease in mammals
- They are usually generalists, meaning they can affect a broad range of hosts
- Together with *Phytophthora*, *Rhizoctonia* and *Fusarium* responsible for a serious agricultural problem called damping off
- Some species are mycoparasites and have been used as biocontrol agents

Life cycle



Different than *Phytophthora*

Important structures

- **Sporangia**: size, shape, L:B, papillate or not, deciduous or not
- **Stalks**: length
- **Zoospores**. **Encysted zoospores**
- **Chlamydospores**: how are they carried (lateral vs. terminal), size, color, ornamentation
- **Oospores**
- **Hyphae:** swellings present or absent, linear or tormented
- **Colony morphology:** appressed vs aerial, fast-growing vs. slow-growing

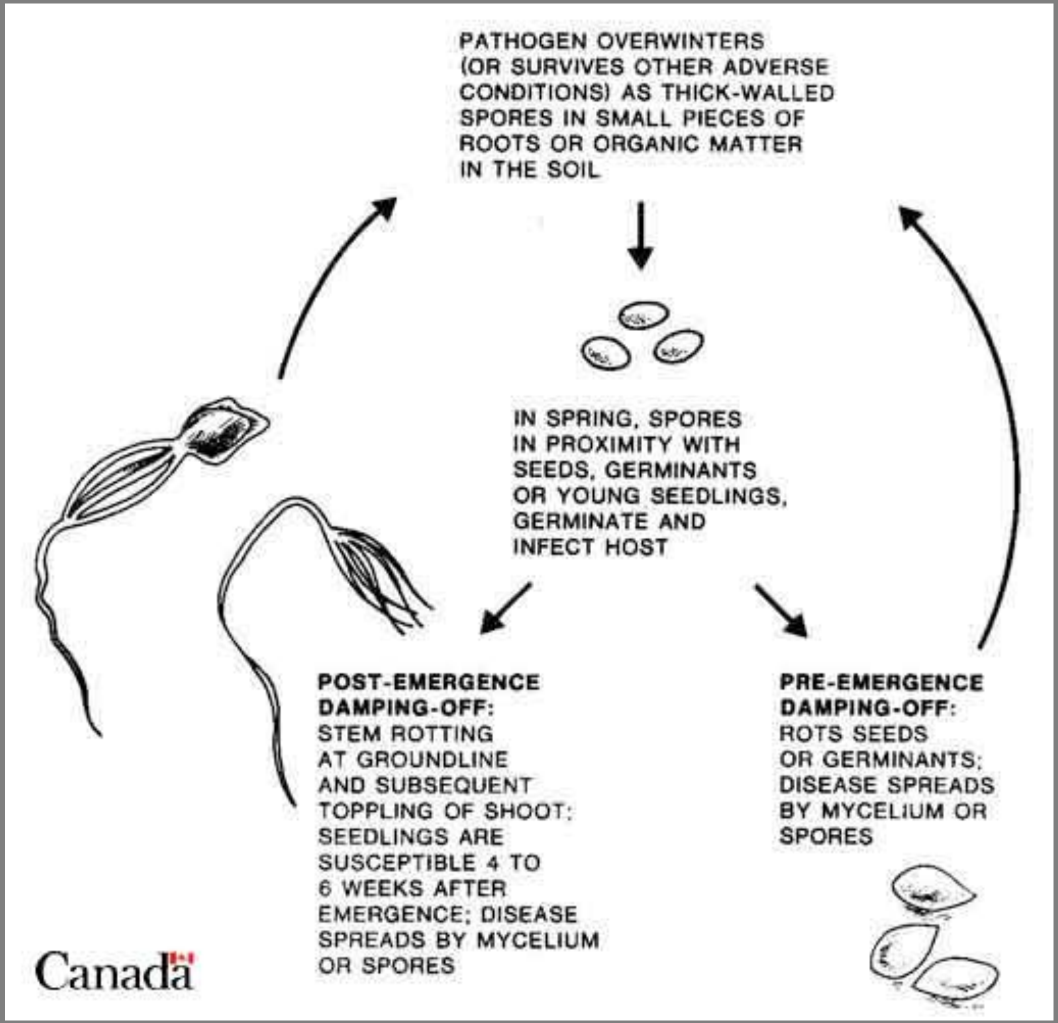
Damping off: because of generalist nature and of ability to overwinter, this is a serious issue in commercial facilities and in reforestation projects

- Pre-emergence
- Post emergence

Pre-emergence damping off in soybean

Post emergence damping off of yellow pine

Life history of damping off

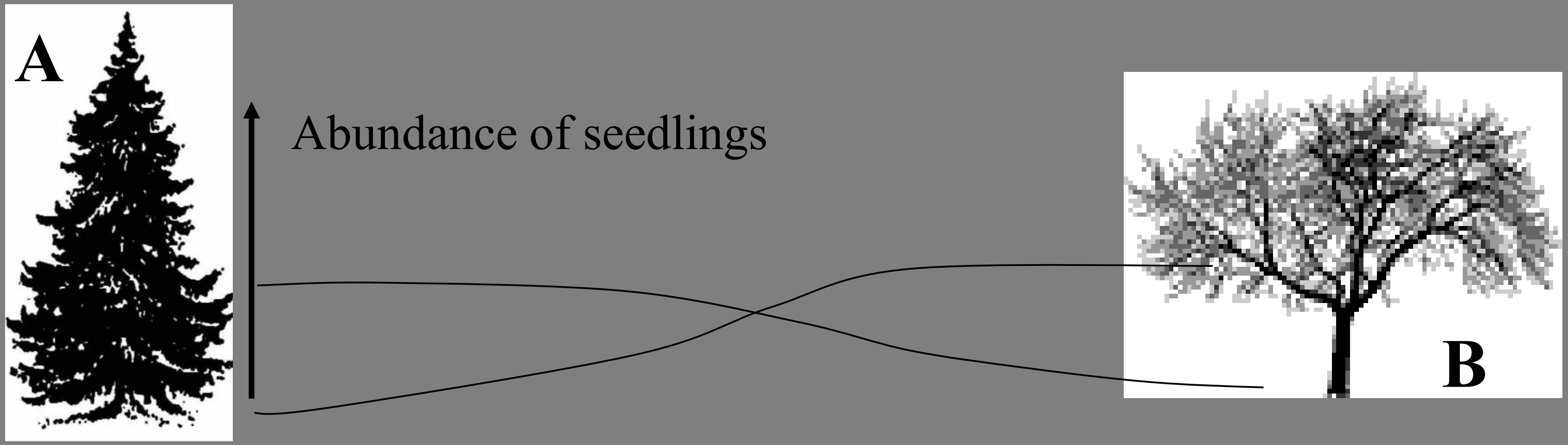


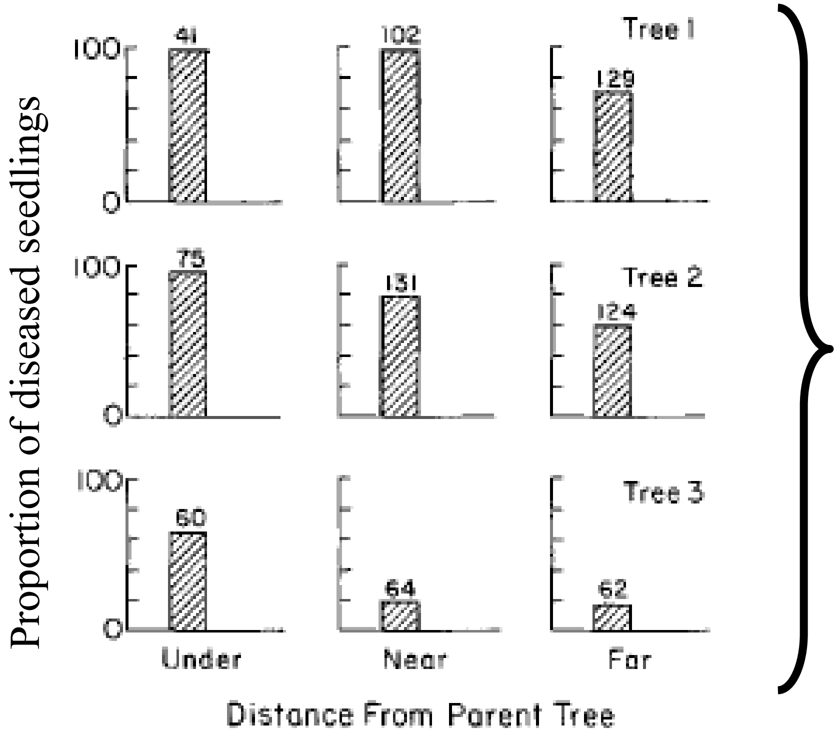
Key genus for the understanding of ecological role of soilborne microbes

- Negative feedback processes: progressive increase in reduction of % success of regeneration
- Optimal allocation of resources by culling seedlings that are less fit early on in the revegetation process thus bringing populations to viable density without wasting resources
- Major drivers of biodiversity: Janzen-Connell hypothesis

Janzen-Connell hypothesis

“Adults, by harboring host-specific pathogens and herbivores, will locally reduce the recruitment success of con-specific juveniles”





Lower mortality away from parent tree

Fig. 2. The proportion of seedlings of *Platypodium elegans* dying from damping-off disease in the distance-density experiment. Values represent totals summed for 4 replicates of a given treatment. The total number of seeds germinating is given above each bar. Shaded bars represent high density quadrats; unshaded bars represent low density quadrats

Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions

Carol K. Augspurger and Colleen K. Kelly
Department of Plant Biology, University of Illinois, Urbana, IL 61801, USA

Oecologia (Berlin) (1984) 61:211–217

Phytophthora

- Some important plant pathogens, with very well known history
  - *Phytophthora infestans* and the Irish potato famine
  - *Phytopthora cinnamomi* and the Jarrah dieback in Australia. Chestnut decline and littleleaf disease of pines in Southeastern USA

The Irish Potato Famine

- From 1845 to 1850
- *Phytophthora infestans*
- Resulted in the death of 750,000
- Emigration of over 2 million, mainly to the United States.

WOMAN BEGGING AT CLONAKILTY.

Phytophthora: "plant destructor"

- Best known pathogen whose long-distance transport linked to agriculture.
  - *Infected root-stocks*
  - *Infested soil*
  - *Infected plants*

100+ species of *Phytophthora*

- 60 until a few years ago, research accelerated, especially by molecular analyses
- Differentiated on basis of:
  - Type of sexual intercourse
  - Type of sexual activity
  - Number of hosts
  - Ideal temperature
  - Type of biology (soilborne, splash, airborne)
  - Evolutionary history (Waterhouse-Cooke)

Type of sexual strategy

Homothallic species, will produce both oogonia and antheridia and mate by themselves (hermaphrodite), low genetic variability. Strong inbreeding.

Heterothallic species need two individuals with different MATING TYPES. Normally defined as A1 and A2. Out-crossing species.

How do *Phytopthoras* “score”….

- There has to be recognition of other sex, then foreplay, then sex
- Two mating types (A1 and A2) code for different lipids. Lipids are used to identify other sex
- Males and females thencommunicate through pheromones
- Antheridiol (Raper 1939) is produced by the female and stimulates in the male: a)- the production of the male organ antheridium; b)- the production of oogoniol that will then stimulate the female to produce the oogonia

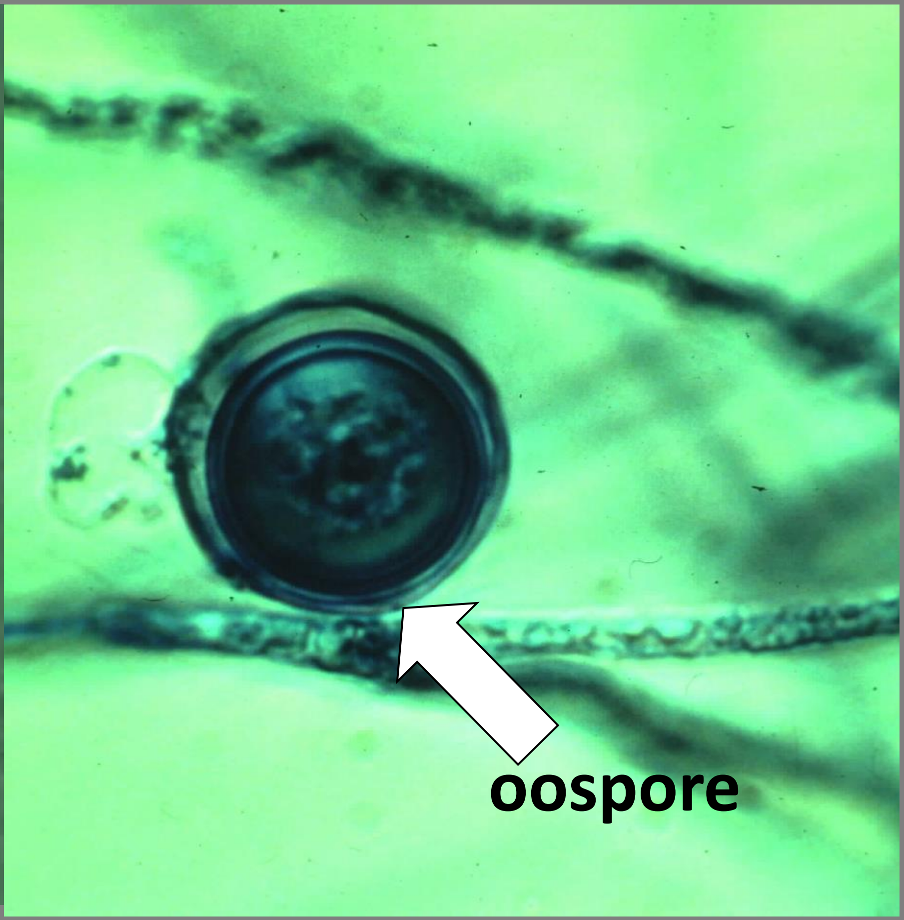
Nature of sexual contact

Oogonium (female sexual structure), trichogyne (receptive hyphae)

Antheridium (male sexual structure)

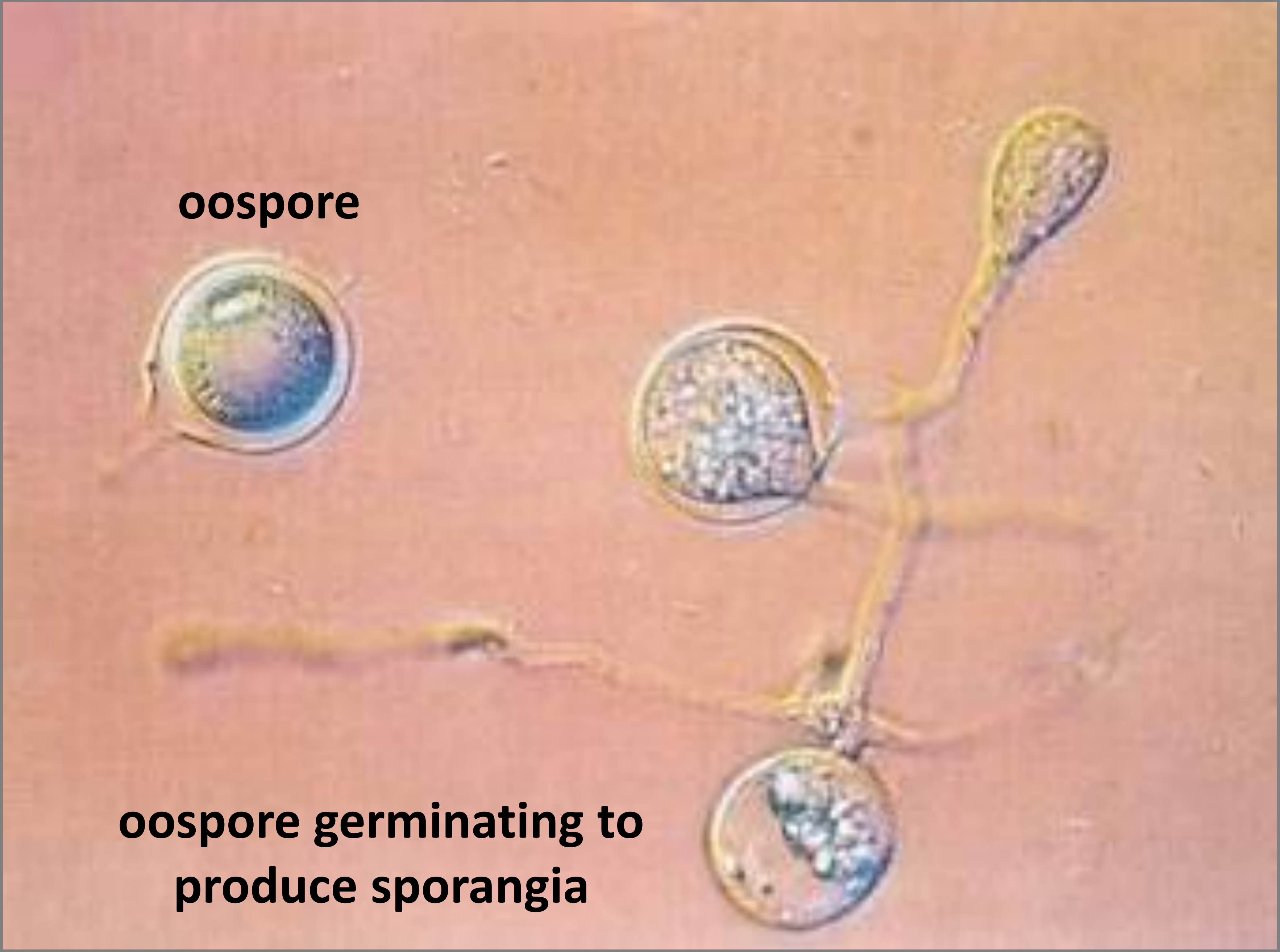
Amphiginous, Paragynous, Perigynous (based on how the two mate)

Sexual Reproduction



Two styles of attachment of antheridia and oogonia

amphigynous **paragynous**


oospore
oospore germinating to produce sporangia

Type of sexual strategy

In area of origin expectations are:

-Both mating types if heterothallic

-Sexual activity and large number of different genotypes

-If species is homothallic expectation is that populations in isolated areas should be different genetically because of lack of gene flow and genetic drift (basic Darwinian concept)

Type of sexual strategy

If species is exotic, expectations are:

-Often one mating type only, or mating types introduced at different times.

-Low genotypic diversity, prevalence of clonal lineages

-If species is homothallic expectation is that all individuals will be similar, because there has been no time for genetic differentiation

Type of sexual strategy

Why should we care about sex ?

-Ability to recombine alleles, better potential of adaptation to new conditions

-Ability to exchange genes with other individuals, if gene pool is large, it can be a great adaptive advantage

-For instance: ability to overcome the fungicide metalaxyl happened when A1 and A2 of *P. infestans* got together and reproduced.

More reasons to care about sex

- Oospores that are the end result of successful mating are extremely hardy, thick walled spores that act like survival structures capable of enduring extremely adverse conditions. Makes sanitation incredibly arduous
- Homothallic species tend to have a broader ecological range because they easily produce oospores

…and even more reasons to care about sex

- There may be different adaptive alleles linked to the two different mating types genes. These alleles may not be recombined but presence of both A1 and A2 means that populations can count on a broader array of genes
- *P. cinnamomi*: in general only A2 is found where pathogen is exotic. However A1 appears to be more aggressive on Camellias

However in the absence of sex…

- Genetically isolated populations undergo an independent evolution and adaptation resulting in so called lineages with dramatically different phenotypes

- Multiple introductions from different lineages can have dramatic impacts, yet very rarely are these lineages regulated independently

Number of hosts

- Single hosts, specialized: *P. sojae, P. lateralis*
- Multiple hosts, generalists: *P. cinnamomi* (3000 hosts!), *P. ramorum* (> 100). The evolution of extreme polyphagy is a stunning trait, really unique to this genus among pathogenic microbes. It implies the ability to overcome host-specific defenses that are wildly different

Phytophthora Genome Sequences Uncover Evolutionary Origins and Mechanisms of Pathogenesis

Brett M. Tyler,[1*] Sucheta Tripathy,[1] Xuemin Zhang,[1] Paramvir Dehal,[2,3] Rays H. Y. Jiang,[1,4] Andrea Aerts,[2,3] Felipe D. Arredondo,[1] Laura Baxter,[5] Douda Bensasson,[2,3,6] Jim L. Beynon,[5] Jarrod Chapman,[2,3,7] Cynthia M. B. Damasceno,[8] Anne E. Dorrance,[9] Daolong Dou,[1] Allan W. Dickerman,[1] Inna L. Dubchak,[2,3] Matteo Garbelotto,[10] Mark Gijzen,[11] Stuart G. Gordon,[9] Francine Govers,[4] Niklaus J. Grunwald,[12] Wayne Huang,[2,14] Kelly L. Ivors,[10,15] Richard W. Jones,[16] Sophien Kamoun,[9] Konstantinos Krampis,[1] Kurt H. Lamour,[17] Mi-Kyung Lee,[18] W. Hayes McDonald,[19] Mónica Medina,[20] Harold J. G. Meijer,[4] Eric K. Nordberg,[1] Donald J. Maclean,[21] Manuel D. Ospina-Giraldo,[22] Paul F. Morris,[23] Vipaporn Phuntumart,[23] Nicholas H. Putnam,[2,3] Sam Rash,[2,13] Jocelyn K. C. Rose,[24] Yasuko Sakihama,[25] Asaf A. Salamov,[2,3] Alon Savidor,[17] Chantel F. Scheuring,[18] Brian M. Smith,[1] Bruno W. S. Sobral,[1] Astrid Terry,[2,13] Trudy A. Torto-Alalibo,[1] Joe Win,[9] Zhanyou Xu,[18] Hongbin Zhang,[18] Igor V. Grigoriev,[2,3] Daniel S. Rokhsar,[2,7] Jeffrey L. Boore[2,3,26,27]

Draft genome sequences have been determined for the soybean pathogen *Phytophthora sojae* and the sudden oak death pathogen *Phytophthora ramorum*. Oömycetes such as these *Phytophthora* species share the kingdom Stramenopila with photosynthetic algae such as diatoms, and the presence of many *Phytophthora* genes of probable phototroph origin supports a photosynthetic ancestry for the stramenopiles. Comparison of the two species' genomes reveals a rapid expansion and diversification of many protein families associated with plant infection such as hydrolases, ABC transporters, protein toxins, proteinase inhibitors, and, in particular, a superfamily of 700 proteins with similarity to known oömycete avirulence genes.

Single vs. multiple hosts

- Single-host species can spread more efficiently, depending on abundance and distribution of host
- Multi-host species may spread more slowly because not all hosts sporulate or because of different susceptibility among hosts (dilution effect)
- In the case of generalists it is important to understand susceptibility and infectiousness of each host

Generalist Phytophthoras

- Represent a challenge for modern society. How do you regulate 3000 host species? *P. ramorum* first generalist to be regulated, but current regulations probably are not sustainable in the long time
- Need to understand different role played by different hosts, and prioritize

Confirmed Susceptible Species

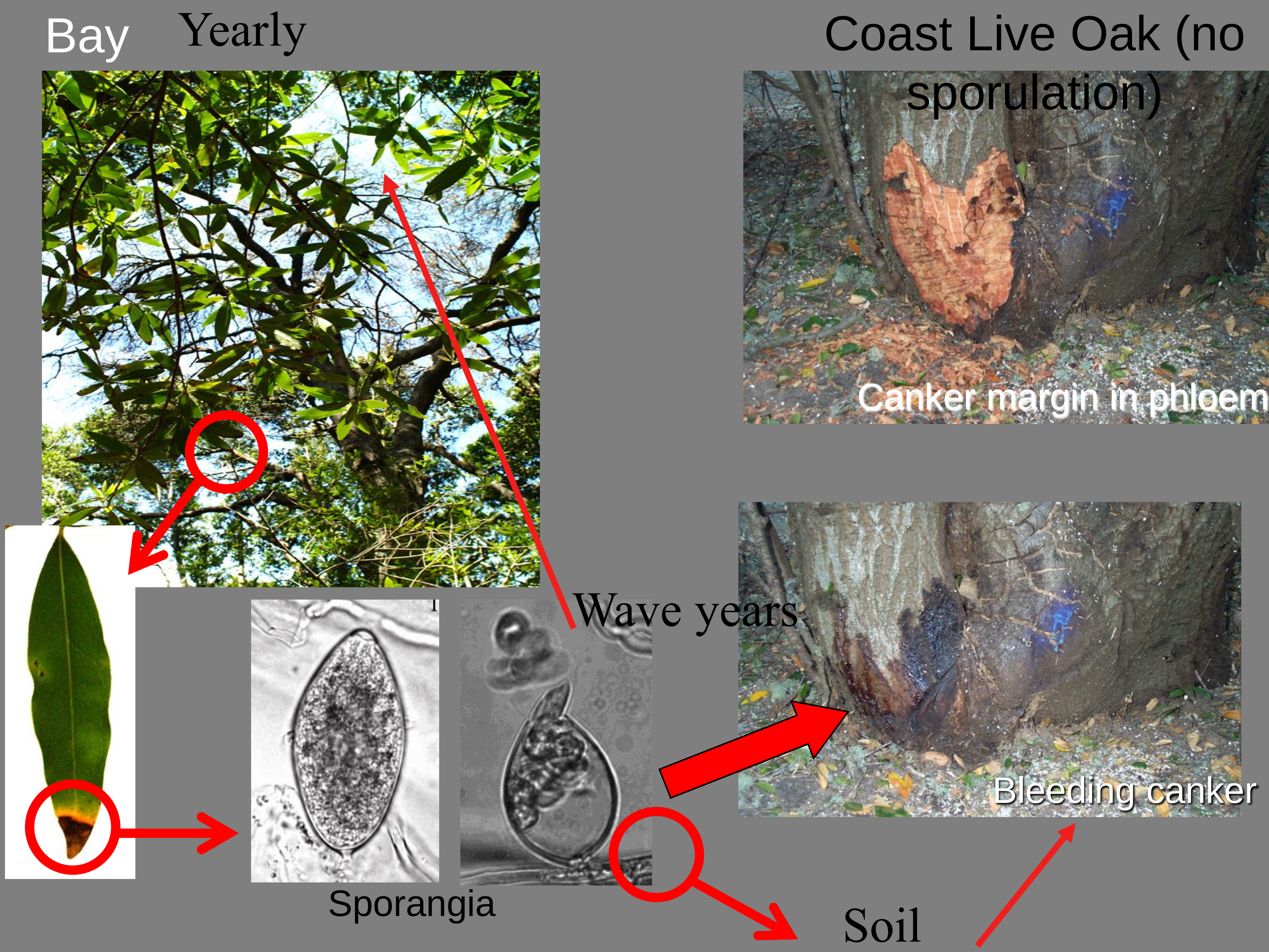
Andrew's clintonia bead lily
Ardisia
Bearberry
Bigleaf maple
Blueblossom
California bay laurel
California black oak
California buckeye
California coffeeberry
California hazelnut
California honeysuckle
California maidenhair fern
California nutmeg
California wood fern
Camellia species
Camphor tree
Canyon live oak
Cascara
Chinese witchhazel
Chinese guger tree
Coast live oak
Coast redwood
Dogwood species
Douglas fir
Eastern Joy Lotus Tree
European ash
European turkey oak
European yew
Evergreen huckleberry
Evergreen maple
False Solomon’s seal
Formosa firethorn
Fetterbush
Goat willow
Grand fir
Griselinia
Holly
Holly olive
Holm oak
Horse chestnut
Hybrid witchhazel
Japanese evergreen oak
Laurustinus
Leucothoe species
Lilac
Loropetalum species
Madrone
Magnolia varities
Manzanita
Michelia
Mountain laurel
Myrtle-leafed Distylium
Northern red oak
Oleander
Oregon ash
Oregon grape
Osmanthus
Pacific yew
Persian ironwood
Pieris varieties
Planetree maple
Poison oak
Prunus species
Red fir
Red lotus tree
Red tip photinia
Redwood ivy
Rhododendron species
Roble beech
Rosa species & hybrids
Rugosa rose
Salal
Salmonberry
Scotch heather
Scribbly gum
Sessile oak
Sheep laurel
Shreve’s oak
Southern red oak
Spicebush
Spike witch hazel
Spreading euonymus
Star magnolia
Strawberry tree
Striped bark maple
Sweet bay laurel
Sweet chestnut
Sweet Cicely
Sweet olive
Tanoak
Toyon
Viburnum varieties
Victorian box
Vine maple
Western maidenhair fern
Western starflower
White fir
Winter's bark
Witch hazel
Wood rose
Yew

Douglas-fir

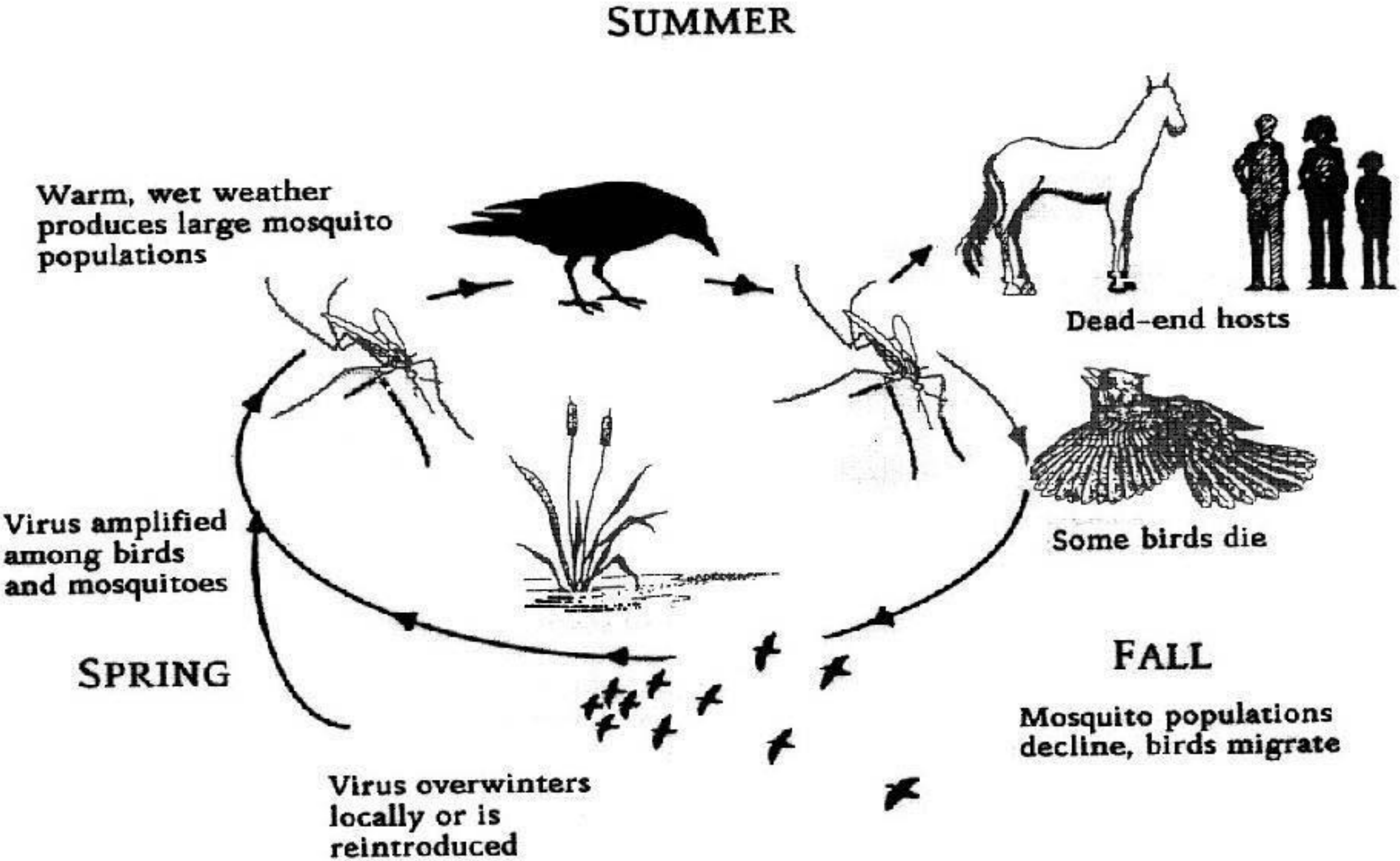
Buckeye

redwoods

Bay/Oak association



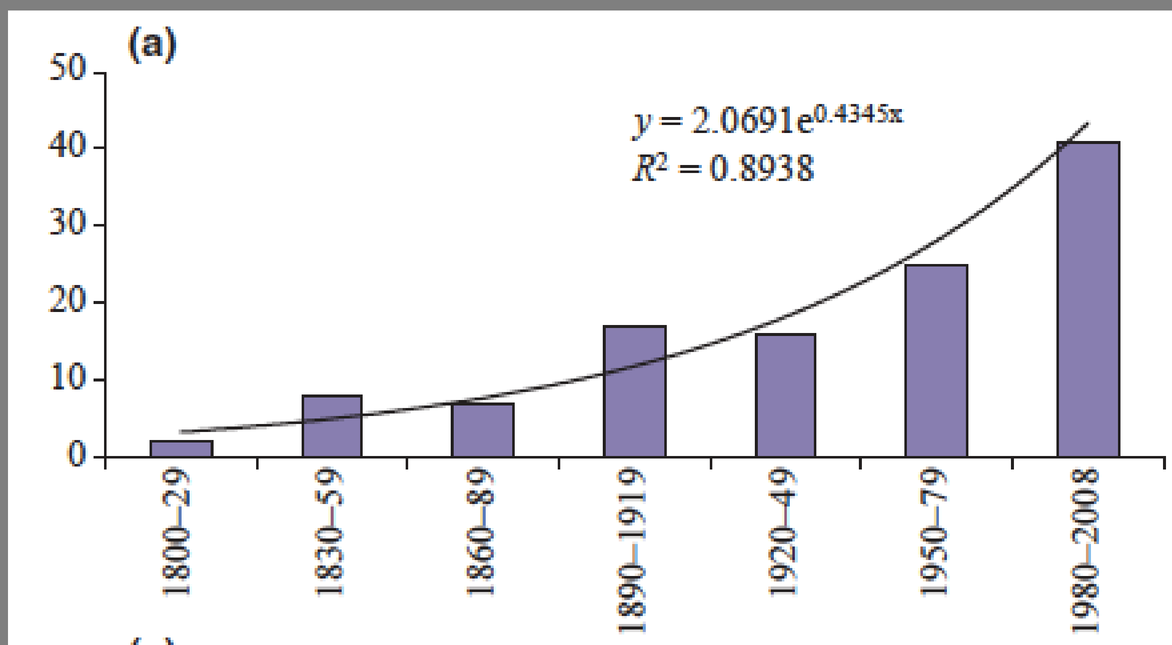
Life Cycle of the West Nile Virus



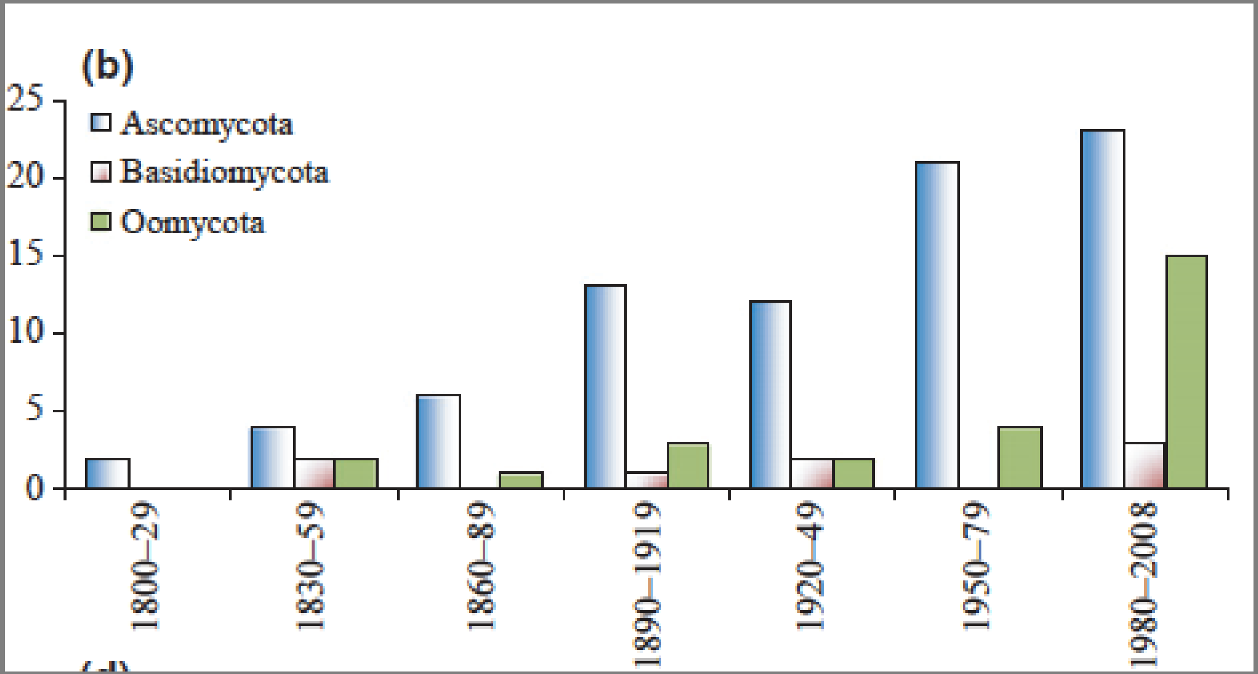
Research
New Phytologist

Biogeographical patterns and determinants of invasion by forest pathogens in Europe

A. Santini[1], L. Ghelardini[1], C.De Pace[2], M. L. Desprez-Loustau[3], P. Capretti[4], A. Chandelier[5], T. Cech[6], D. Chira[7], S. Diamandis[8], T. Gaitniekis[9], J. Hantula[10], O. Holdenrieder[11], L. Jankovsky[12], T. Jung[13], D. Jurc[14], T. Kirisits[15], A. Kunca[16], V. Lygis[17], M. Malecka[18], B. Marcais[19], S. Schmitz[5], J. Schumacher[20], H. Solheim[21], A. Solla[22], I. Szabò[23], P. Tsopelas[24], A. Vannini[25], A. M. Vettraino[25], J. Webber[26], S. Woodward[27] and J. Stenlid[28]

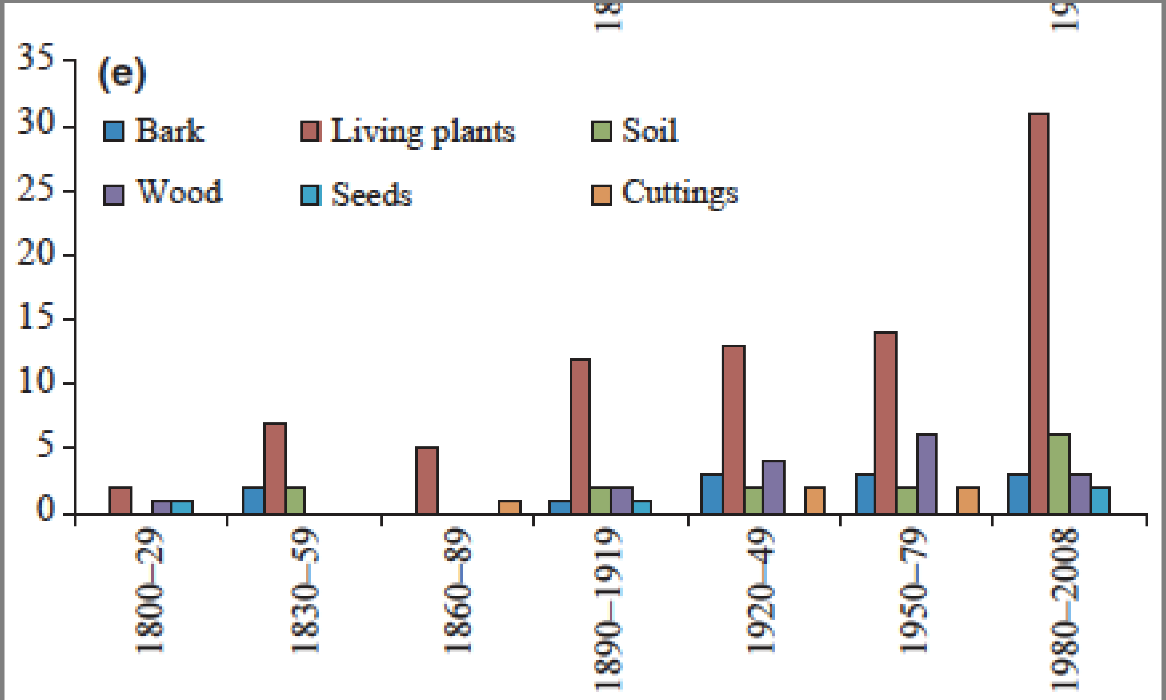


Number of Invasive Forest Pathogens



← Type of IFP

Pathway of introduction Of IFP →



Host species x pathogen genotype

- Diversity within a species of a pathogen and different epidemiological role of different hosts are key elements to be considered

Lineage, Temperature, and Host Species have Interacting Effects on Lesion Development in *Phytophthora ramorum*

C. A. Eyre, Forest Pathology and Mycology Laboratory, Department of Environmental Science, Policy and Management, University of California-Berkeley, Berkeley; **K. J. Hayden,** Forest Pathology and Mycology Laboratory, Department of Environmental Science, Policy and Management, University of California-Berkeley; INRA, Interactions Arbres–Microorganismes, UMR1136, F-54280 Champenoux, France; and Université de Lorraine, Interactions Arbres–Microorganismes, UMR1136, F-54500 Vandoeuvre-lès-Nancy, France; **M. Kozanitas,** Forest Pathology and Mycology Laboratory, Department of Environmental Science, Policy and Management, University of California-Berkeley; **N. J. Grünwald,** Horticultural Crops Research Laboratory, United States Department of Agriculture–Agricultural Research Service, Corvallis, OR; and **M. Garbelotto,** Forest Pathology and Mycology Laboratory, Department of Environmental Science, Policy and Management, University of California-Berkeley

Eyre, C. A., Hayden, K. J., Kozanitas, M., Grünwald, N. J., and Garbelotto, M. 2014. Lineage, temperature, and host species have interacting eff
on lesion development in *Phytophthora ramorum*. Plant Dis. 98:1717-1727.

Effect of variability within pathogen

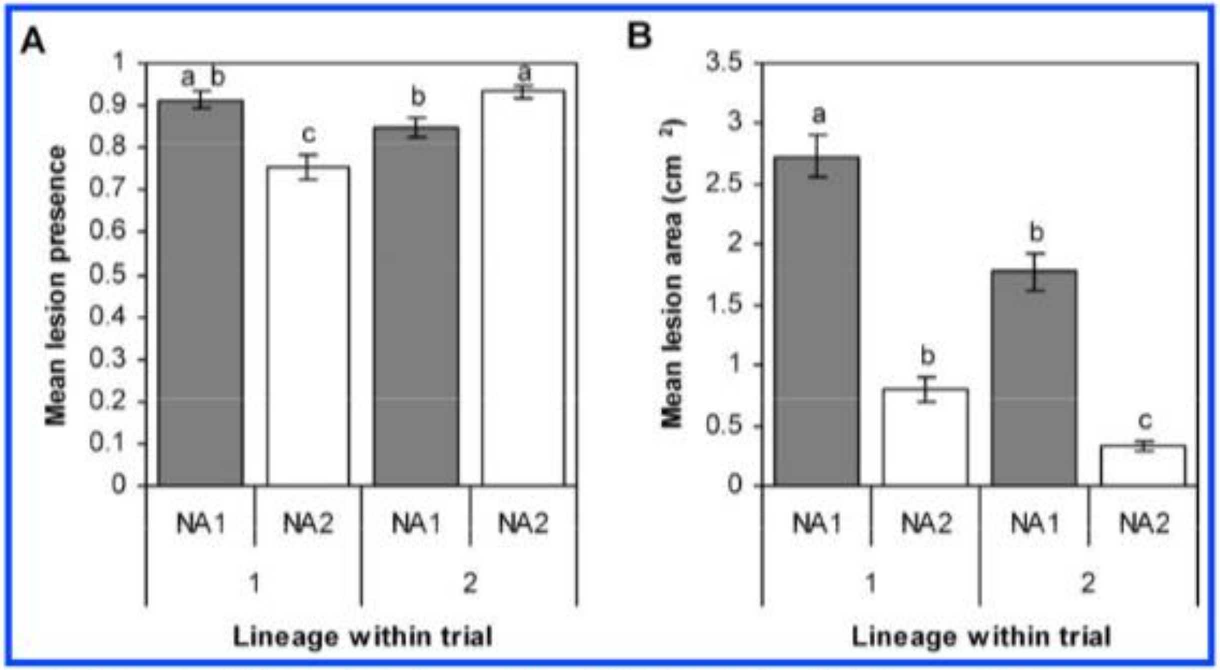


Fig. 3. Camellia detached-leaf zoospore inoculation assay testing lineages NA1 and NA2 in two trials (1 and 2). **A,** Frequency of lesion presence and **B,** mean lesion area (in square centimeters). Error bars are ± standard error of the mean. Different letters above bars in each plot indicate statistical difference (Tukey-Kramer honestly significant difference, $P < 0.05$).

Two different lineages of *Phytophthora ramorum* cause a disease of different severity on the same host

Host x Lineage x Temperature!

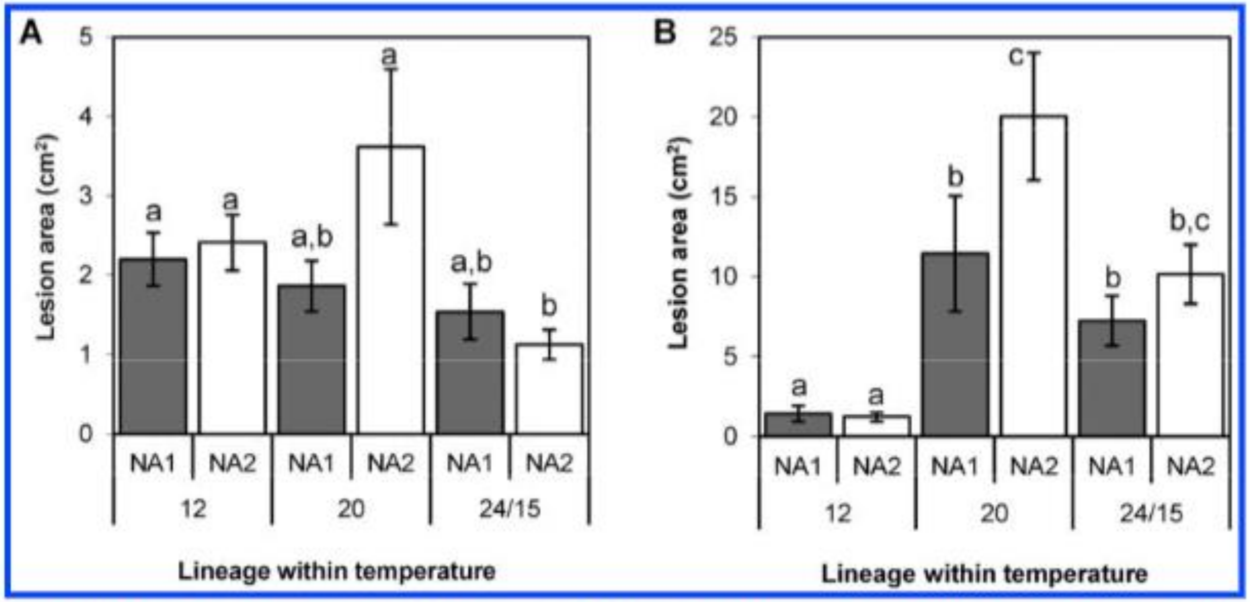


Fig. 6. Mean lesion area (in square centimeters) caused by zoospore suspensions of *Phytophthora ramorum* lineages NA1 and NA2 under three incubation conditions on leaves of **A,** bay laurel and **B,** 'Cunningham's White' rhododendron. Bars marked with different letters are significantly different at $P < 0.05$ by Tukey-Kramer's honestly significant difference. Error bars are ± standard error of the mean.

-Bays and Rhododendrons respond differently: bays remain very susceptible at low temperatures, not so for rhododendrons. This has implications for disease spread in colder climates

- At intermediate temperatures, NA2 is more aggressive

Oak root canker
(*Phytophthora cinnamomi*)

- **Species originally from PNG/Borneo/Sumatra, a common agricultural pathogen**
- **Soilborne, waterborne common in the wild in other parts of the US**
- **If host not extremely susceptible, predisposing factors needed for mortality to occur (e.g. oaks in Southern Europe)**
  - **Dry spell**
  - **Man-induced ecological alterations**

P. cinnamomi causes Littleleaf disease of pines on former-agricultural soils with hardpan in the Eastern US

Problem: Oak decline

Locations:

- Del Dios Area (Lake Hodges)
- County Parks
- Rural Areas


Oak Tree Survey at Del Dios

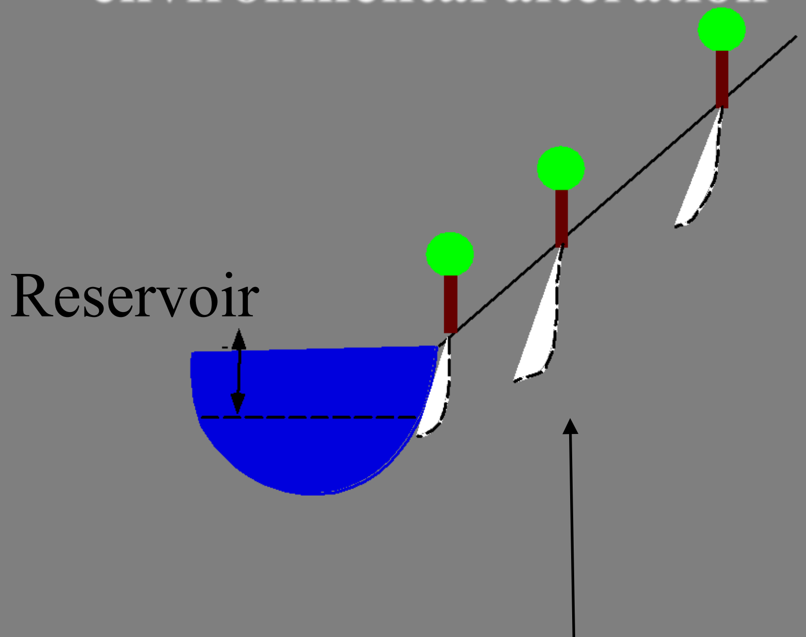
Results:

Of 474 *Quercus agrifolia* trees,
27% had bleeding cankers on the trunk.

Of 86 *Quercus engelmannii* trees,
none showed bleeding.

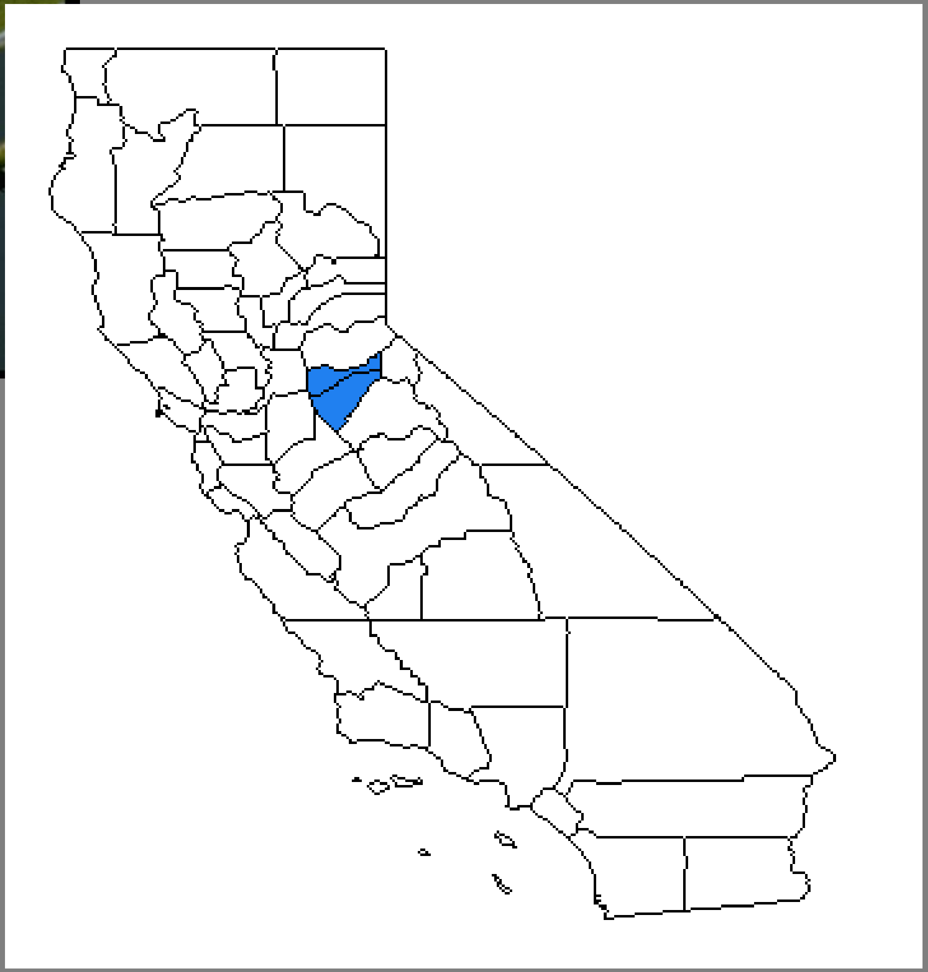
Example of man-induced environmental alteration

Phytophthora cinnamomi
Introduced on
Coast Live Oak
San Diego Co.



Oaks at mid-slope experience fluctuations in the water table level: if infected by *P. cinnamomi* become extremely weak and attractive to insects

Ione manzanita: endangered species



Ione
Extremely harsh ecosystems, serpentine soild (very acidic, rich in Fe++), mining operations

Two major components of plant cover are manzanitas:

A. viscida (white manzanita)
A. myrtifolia (ione manzanita)

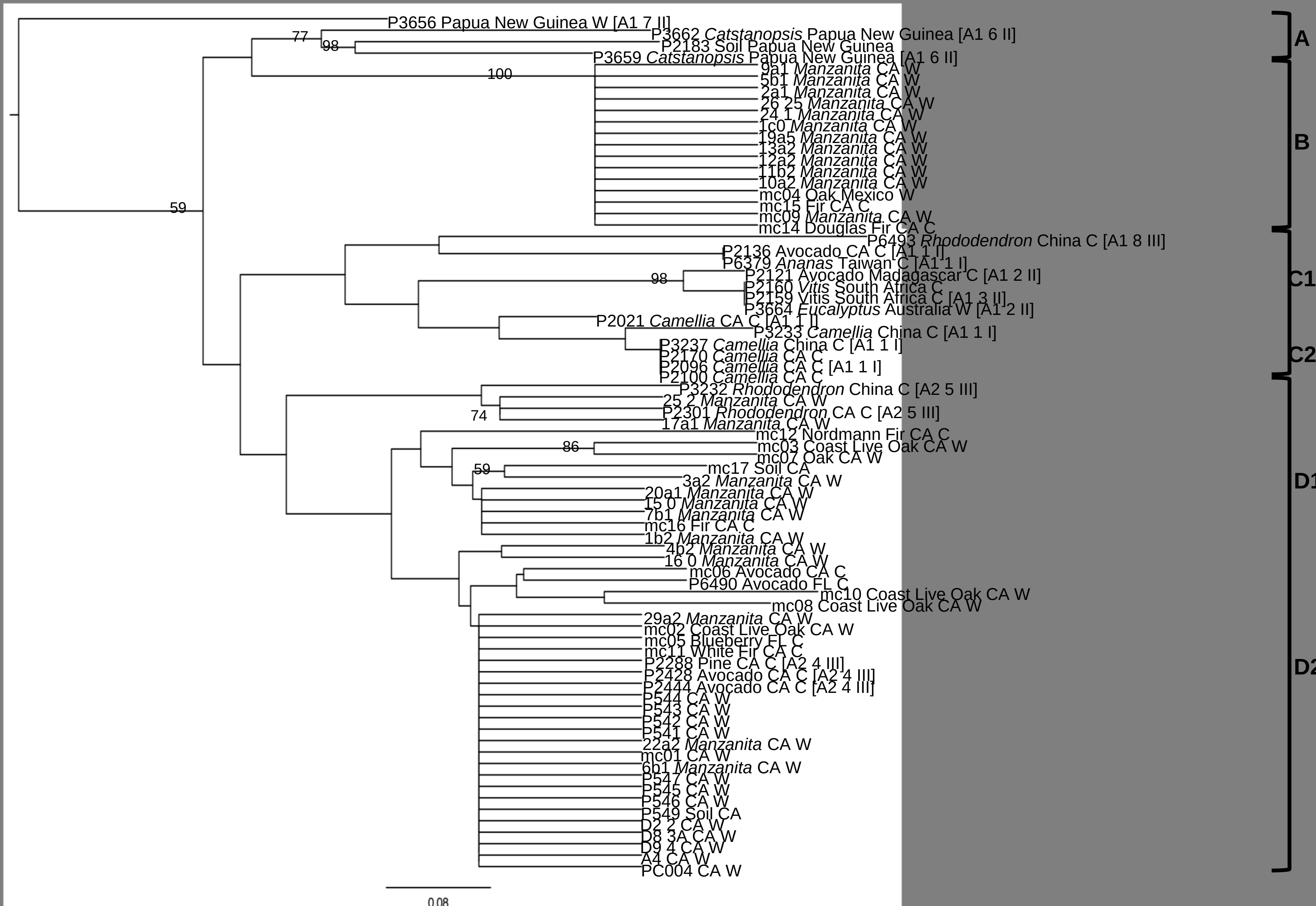
Ione manzanita is a rare endemic species of the Ione area, one that has well adapted to the local conditions, but it is currently in the list of US threatened species

Because of almost total susceptibility to soilborne *P. cinnamomi*

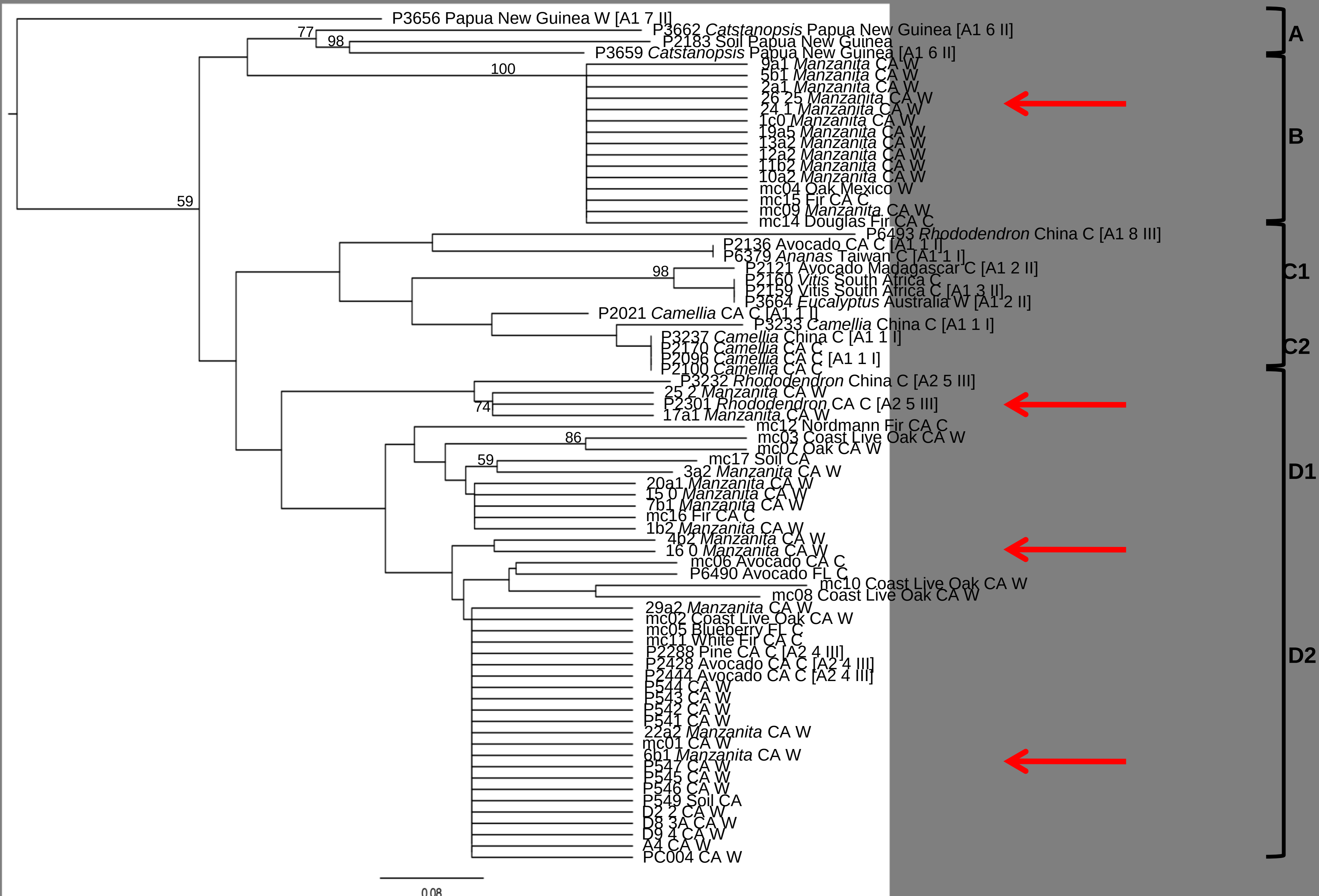
Genetic diversity of Pc in Ione is staggering, it includes all of the diversity present in California natural ecosystems

How can we explain this diversity?

- At least four introductions of four distinct strains
- Populations large enough that additional diversity generated locally (soil environment favorable to pathogen)
- One dominant strain is also present in Ca Christmas tree farms also matching a strain from a severe outbreak of oak mortality in Colima. This strain is novel


P3656 Papua New Guinea W [A1 7 II]
P3662 Catstanopsis Papua New Guinea [A1 6 II]
P2183 Soil Papua New Guinea
P3659 Catstanopsis Papua New Guinea [A1 6 II]
9a1 Manzanita CA W
5b1 Manzanita CA W
2a1 Manzanita CA W
26 25 Manzanita CA W
24 1 Manzanita CA W
1c0 Manzanita CA W
19a5 Manzanita CA W
13a2 Manzanita CA W
12a2 Manzanita CA W
11b2 Manzanita CA W
10a2 Manzanita CA W
mc04 Oak Mexico W
mc15 Fir CA C
mc09 Manzanita CA W
mc14 Douglas Fir CA C
P6493 Rhododendron China C [A1 8 III]
P2136 Avocado CA C [A1 1 I]
P6379 Ananas Taiwan C [A1 1 I]
P2121 Avocado Madagascar C [A1 2 II]
P2160 Vitis South Africa C
P2159 Vitis South Africa C [A1 3 II]
P3664 Eucalyptus Australia W [A1 2 II]
P2021 Camellia CA C [A1 1 I]
P3233 Camellia China C [A1 1 I]
P3237 Camellia China C [A1 1 I]
P2170 Camellia CA C
P2096 Camellia CA C [A1 1 I]
P2100 Camellia CA C
P3232 Rhododendron China C [A2 5 III]
25 2 Manzanita CA W
P2301 Rhododendron CA C [A2 5 III]
17a1 Manzanita CA W
mc12 Nordmann Fir CA C
mc03 Coast Live Oak CA W
mc07 Oak CA W
mc17 Soil CA
3a2 Manzanita CA W
20a1 Manzanita CA W
15 0 Manzanita CA W
7b1 Manzanita CA W
mc16 Fir CA C
1b2 Manzanita CA W
4b2 Manzanita CA W
16 0 Manzanita CA W
mc06 Avocado CA C
P6490 Avocado FL C
mc10 Coast Live Oak CA W
mc08 Coast Live Oak CA W
29a2 Manzanita CA W
mc02 Coast Live Oak CA W
mc05 Blueberry FL C
mc11 White Fir CA C
P2288 Pine CA C [A2 4 III]
P2428 Avocado CA C [A2 4 III]
P2444 Avocado CA C [A2 4 III]
P544 CA W
P543 CA W
P542 CA W
P541 CA W
22a2 Manzanita CA W
mc01 CA W
6b1 Manzanita CA W
P547 CA W
P545 CA W
P546 CA W
P549 Soil CA
D2 2 CA W
D8 3A CA W
D9 4 CA W
A4 CA W
PC004 CA W
77
98
100
59
98
74
86
59
0.08
A
B
C1
C2
D1
D2

Manzanita


P3656 Papua New Guinea W [A1 7 II]
P3662 *Catstanopsis* Papua New Guinea [A1 6 II]
P2183 Soil Papua New Guinea
P3659 *Catstanopsis* Papua New Guinea [A1 6 II]
9a1 *Manzanita* CA W
5b1 *Manzanita* CA W
2a1 *Manzanita* CA W
26 25 *Manzanita* CA W
24 1 *Manzanita* CA W
1c0 *Manzanita* CA W
19a5 *Manzanita* CA W
13a2 *Manzanita* CA W
12a2 *Manzanita* CA W
11b2 *Manzanita* CA W
10a2 *Manzanita* CA W
mc04 Oak Mexico W
mc15 Fir CA C
mc09 *Manzanita* CA W
mc14 Douglas Fir CA C
P6493 *Rhododendron* China C [A1 8 III]
P2136 Avocado CA C [A1 1 I]
P6379 *Ananas* Taiwan C [A1 1 I]
P2121 Avocado Madagascar C [A1 2 II]
P2160 *Vitis* South Africa C
P2159 Vitis South Africa C [A1 3 II]
P3664 *Eucalyptus* Australia W [A1 2 II]
P2021 *Camellia* CA C [A1 1 I]
P3233 *Camellia* China C [A1 1 I]
P3237 *Camellia* China C [A1 1 I]
P2170 *Camellia* CA C
P2096 *Camellia* CA C [A1 1 I]
P2100 *Camellia* CA C
P3232 *Rhododendron* China C [A2 5 III]
25 2 *Manzanita* CA W
P2301 *Rhododendron* CA C [A2 5 III]
17a1 *Manzanita* CA W
mc12 Nordmann Fir CA C
mc03 Coast Live Oak CA W
mc07 Oak CA W
mc17 Soil CA
3a2 *Manzanita* CA W
20a1 *Manzanita* CA W
15 0 *Manzanita* CA W
7b1 *Manzanita* CA W
mc16 Fir CA C
1b2 *Manzanita* CA W
4b2 *Manzanita* CA W
16 0 *Manzanita* CA W
mc06 Avocado CA C
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mc10 Coast Live Oak CA W
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mc02 Coast Live Oak CA W
mc05 Blueberry FL C
mc11 White Fir CA C
P2288 Pine CA C [A2 4 III]
P2428 Avocado CA C [A2 4 III]
P2444 Avocado CA C [A2 4 III]
P544 CA W
P543 CA W
P542 CA W
P541 CA W
22a2 *Manzanita* CA W
mc01 CA W
6b1 *Manzanita* CA W
P547 CA W
P545 CA W
P546 CA W
P549 Soil CA
D2 2 CA W
D8 3A CA W
D9 4 CA W
A4 CA W
PC004 CA W
77
98
100
59
98
74
86
59
0.08
A
B
C1
C2
D1
D2

How can we explain such a severe effect on manzanita spp.?

- Host is very susceptible
- Multiple lineages of the pathogen were introduced. Because lineages are different there is synergism resulting in higher infection levels
- One lineage is novel and it has been reported in a serious outbreak in Colima, Mexico, in new outbreaks in Christmas tree farms in California and in Ione