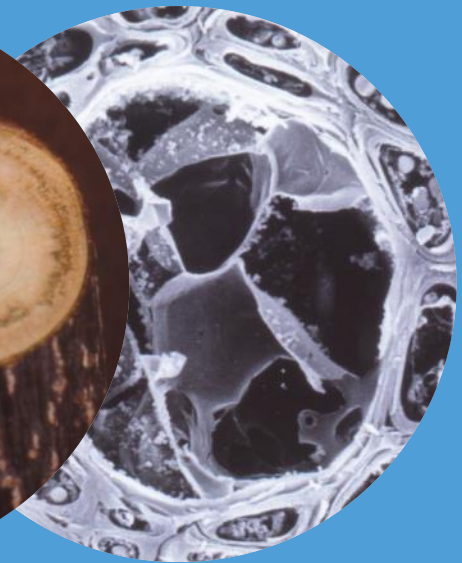
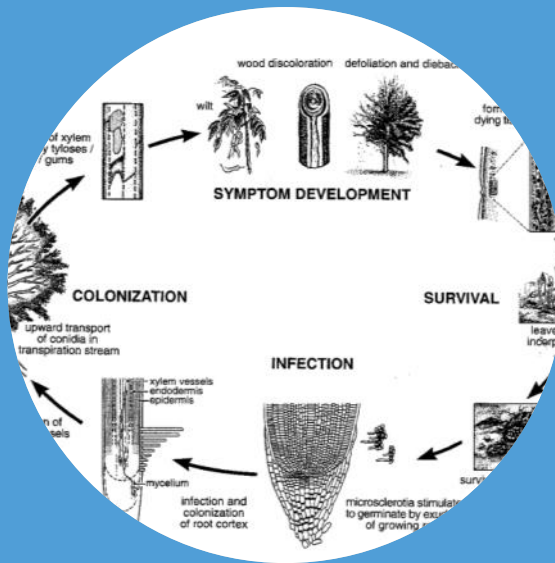


Spatial and temporal aspects of Verticillium wilt in trees and resistance against *V. dahliae*

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Göttingen, May 6th 2013



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Symptoms in woody hosts

■ 3 main types of effects:

- Leaf symptoms: wilt, discolouration, defoliation, drying/necrosis
- Vascular symptoms: discolouration of xylem, plugging of vessels
- Decline: stunting, dieback, death
- Occasionally: elongated dead areas of bark on stem/branches;
flower and fruit mummification



Tree hosts of VW

Forest/street/shade trees		Fruiting species	
Host	Non-host	Host	Non-host
<i>Acer</i> <i>Aesculus</i> <i>Ailanthus</i> <i>Castanea</i> <i>Catalpa</i> <i>Cercis</i> <i>Fraxinus</i> <i>Liriodendron</i> <i>Magnolia</i> <i>Robinia</i> <i>Tilia</i> <i>Ulmus</i>	<i>Alnus</i> <i>Betula</i> <i>Fagus</i> <i>Populus</i> <i>Quercus</i> <i>Salix</i>	<i>Coffea</i> <i>Cydonia</i> <i>Olea</i> <i>Persea</i> <i>Pistacia</i> <i>Prunus</i> <i>Rubus</i> <i>Theobroma</i>	<i>Malus</i> <i>Pyrus</i>

Cause of VW in trees: *V. dahliae* (“microsclerotial form of Vaa”)



Tree hosts and damage

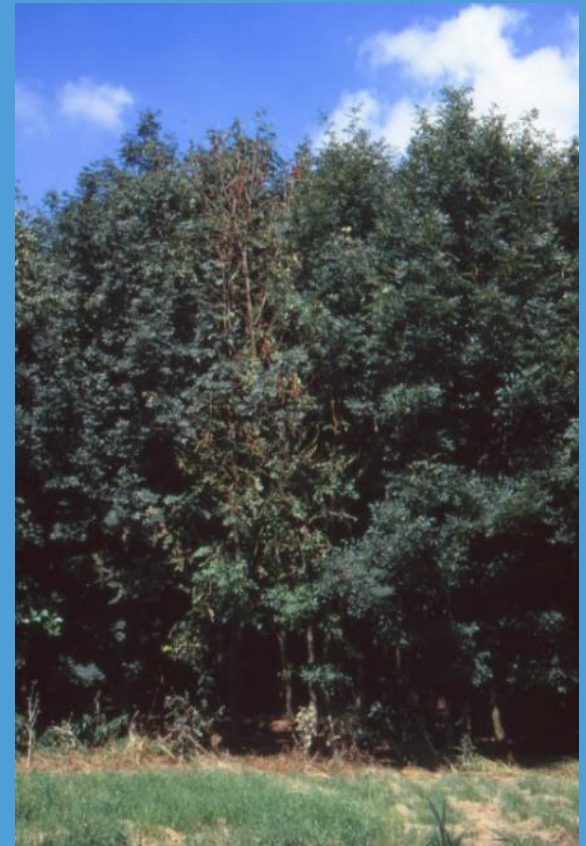
■ Different categories

- Fruit production: olive, stone fruits, pistachio
- Tree nursery: shade trees & ornamentals
- Urban and Landscape trees
- Forest trees ???



Verticillium wilt in forest stands ?

- NL; 1970's-1980's: VW of *Fraxinus excelsior*
 - Young forest plots in Flevopolders
 - Landscape / recreational plantings
 - Not in older forests

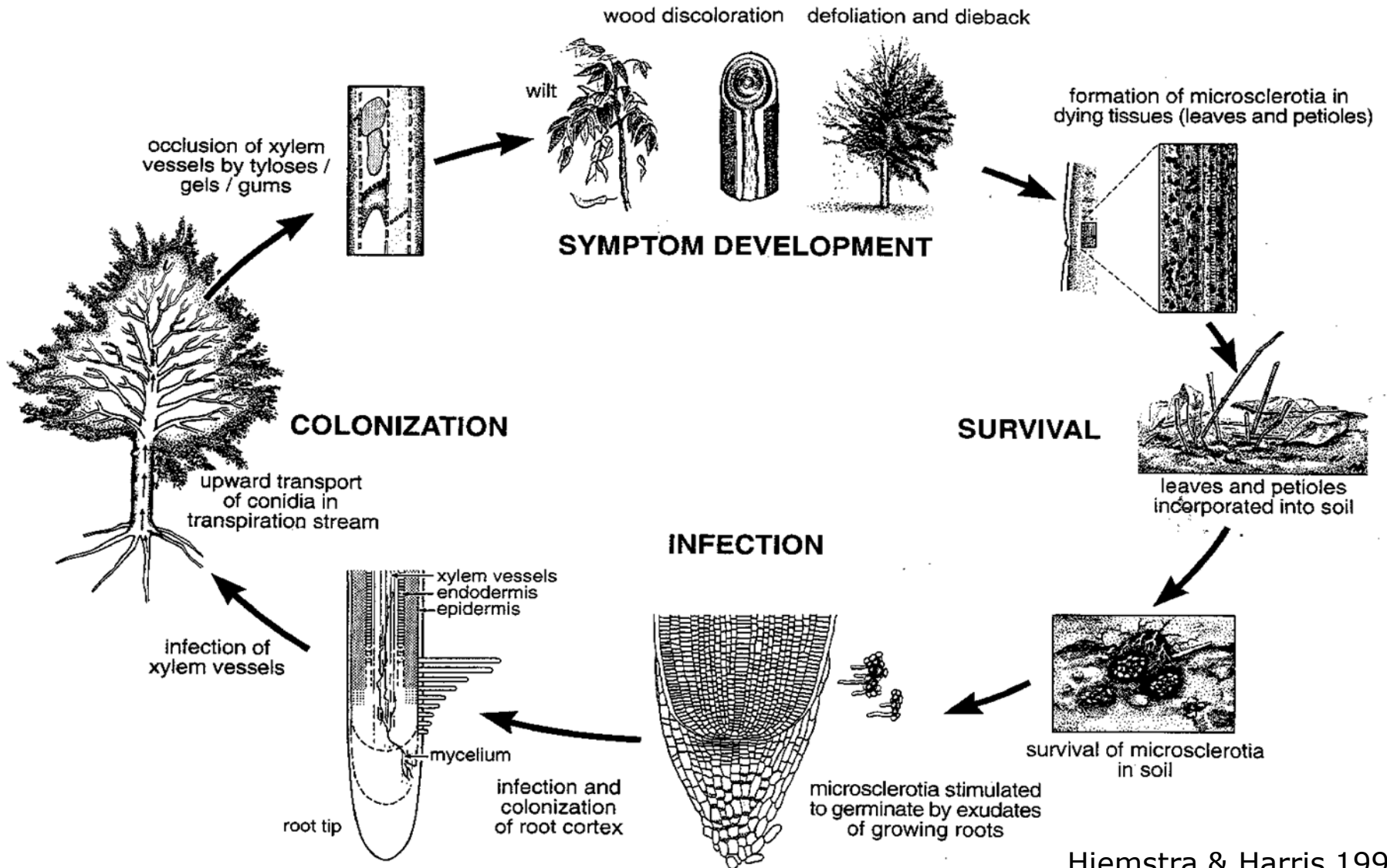


Verticillium wilt in forest stands ?

- Literature: very limited number of reports
 - *Ceanothus integerrimus* (Harrington & Cobb; 1984)
 - Coastal forest in California -- Vaa
 - *Liriodendron tulipifera* (Donahue & Morehart; 1978)
 - Urban and forest settings in Delaware -- Vd and Vaa
 - *Ailanthus altissima* (Schall and Davis; 2009)
 - Mixed hardwood forests in Pennsylvania – Vaa
→ *Verticillium nonalfalfae* !
- Mature (natural ?) forests VW very rare !!
 - Reason?



Disease cycle of *V. dahliae* in trees

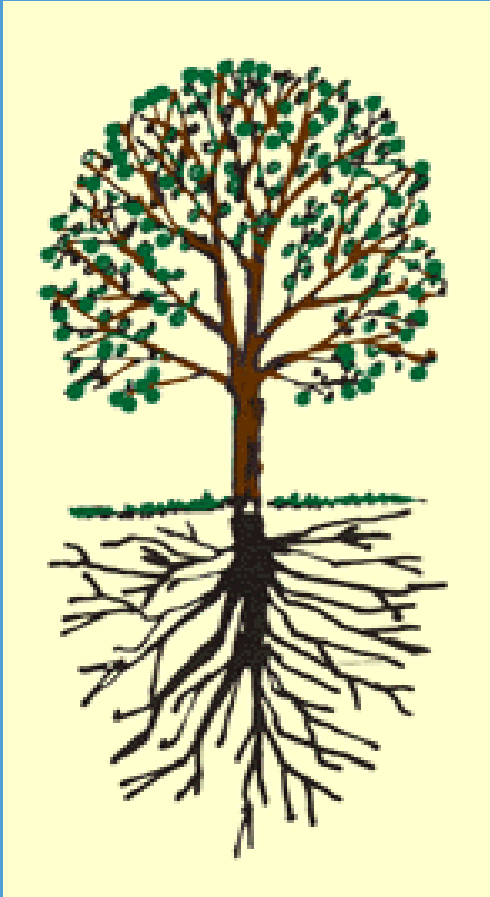


Special features of VW in trees

- Size of host
- Long-life of host
- Xylem anatomy



VW in Trees → Size effects



- Root system
 - covers large soil volume
 - each year major part fine roots renewed
 - roots not only in top layer
 - low IC → still contact many ms
- Damage threshold level often low
 - *Acer & Catalpa* (Goud, 2003):
5% damage threshold = 1-2 CFU/g soil
 - *Pistachio* (Ashworth & Zimmerman, 1976)
10-14% died at ID 1-2 ms/g soil
 - *Olive* ?



Special features of VW in trees

- Size of host

- **Long-life of host**

- VW is mono-cyclic (year) BUT poly-cyclic (life-time)
 - repeated infections possible in life of tree
- Secondary inoculum may affect same tree





Secondary inoculum: *Acer platanoides*

Hiemstra, 1997



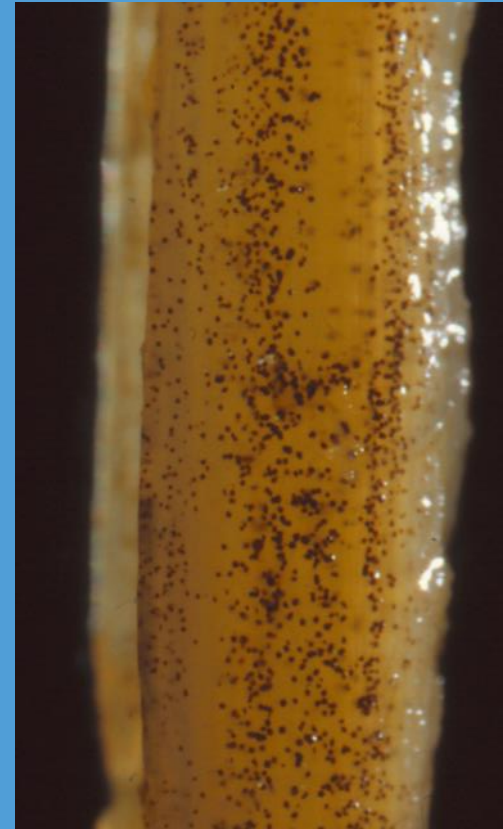
>50% petioles infected (10-94%)

inoculation experiment → 10% VW in young *A.plat.* trees



Secondary inoculum: *Fraxinus excelsior*

Rijkers *et al.*, 1997



14% of soil incubated petioles contained Vd ms
Avg 1500 ms/cm (not equally spread)



Secondary inoculum & trees

■ Petioles

- **Acer** (Zimm, 1918; Townsend *et al.*, 1990; Hiemstra, 1997): **50%**
- **Fraxinus** (Rijkers *et al.*, 1992) **14%**
- **Liriodendron** (Morehart & Melchior, 1982) +
- **Olea** (Tjamos&Botseas,1987: **68%**; Tjamos&Tsougriani,1990: **10%**)

■ Inflorescences

- **Olea** (Trapero *et al.*, 2011):
up to over **70 ppg** (peduncles) / **7 ppg** (flowers)

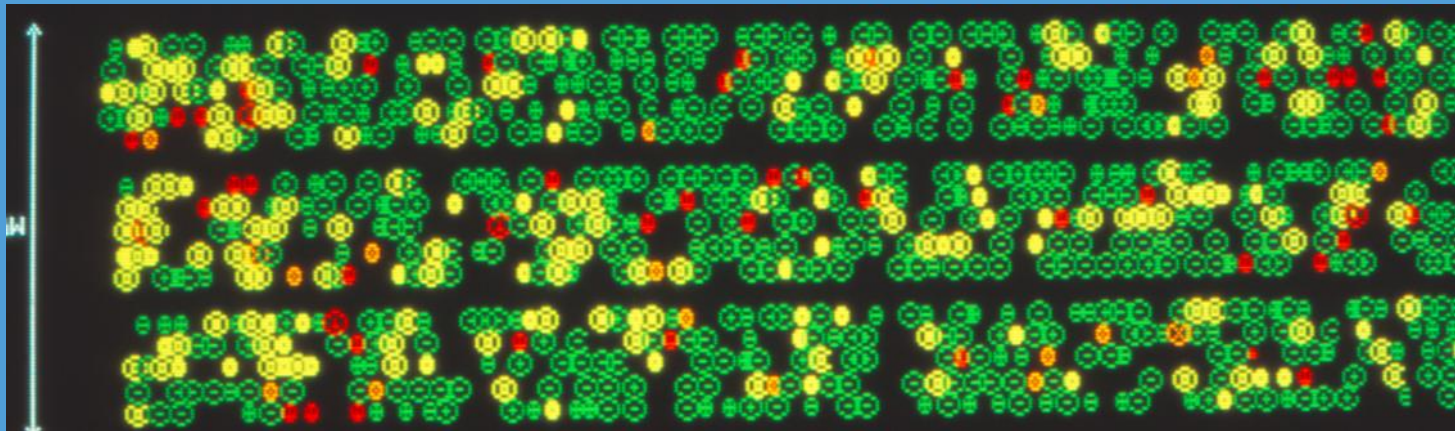
■ Sec. inoc. can substantially contribute to VW in trees



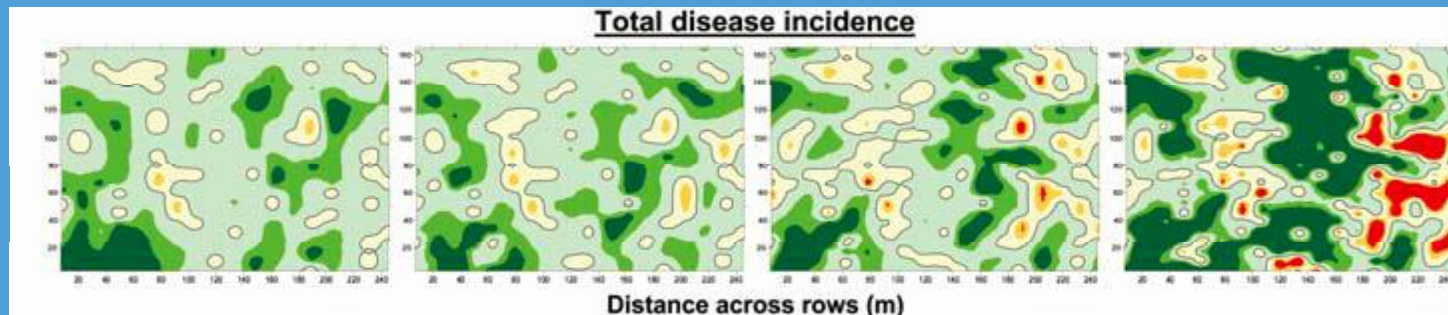
Distribution pattern of VW

- Patches of higher density superimposed on a general distribution at lower density

- VW of *Fraxinus excelsior* in forests in NL (Hiemstra, 1995)



- VW of *Olea europaea* in orchards in SP (Navas et al., 2011)

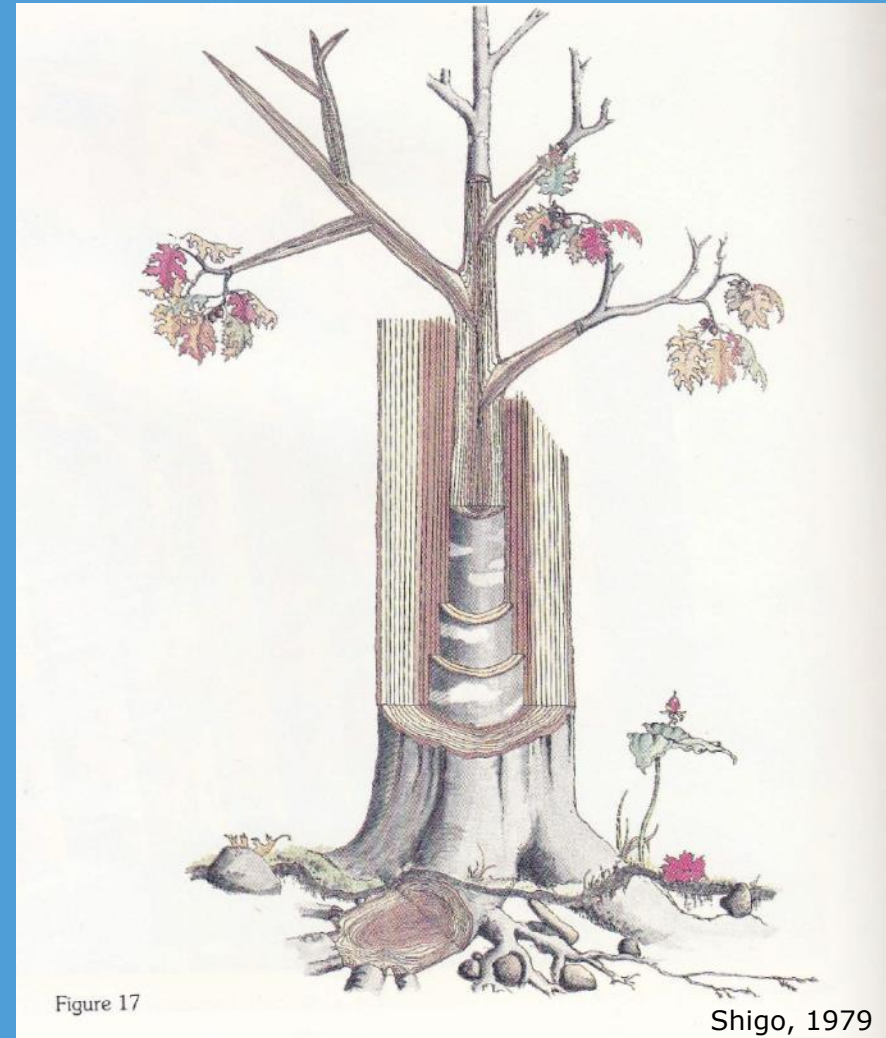
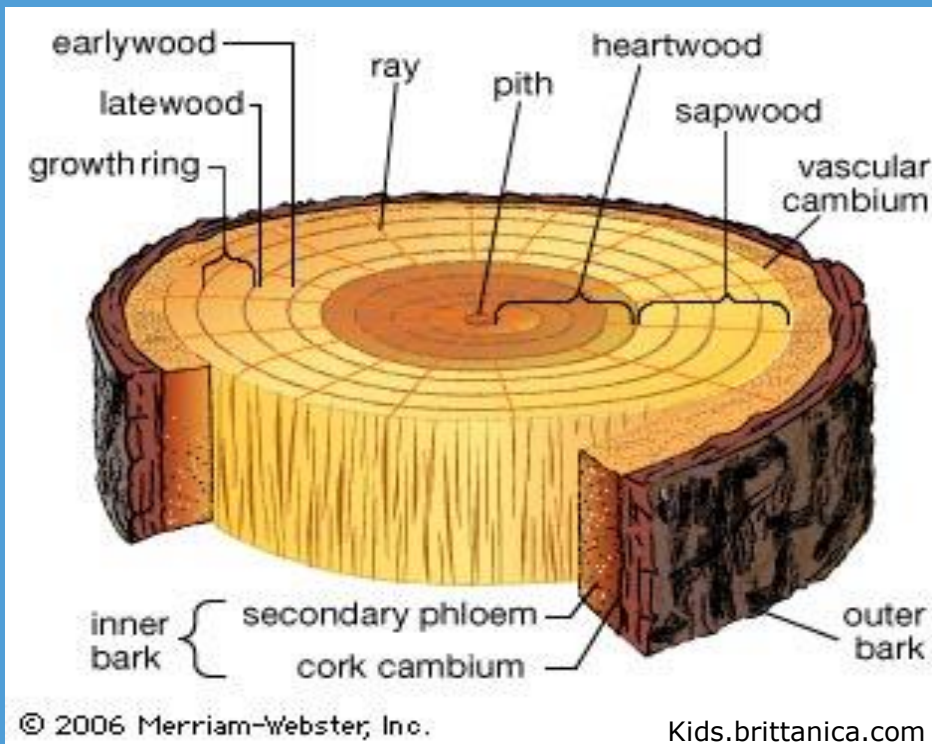
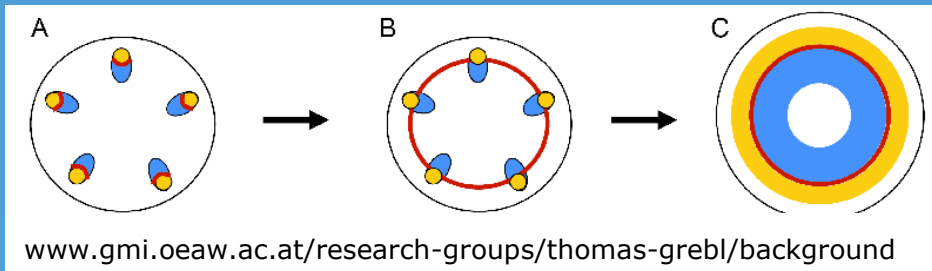


Special features of VW in trees

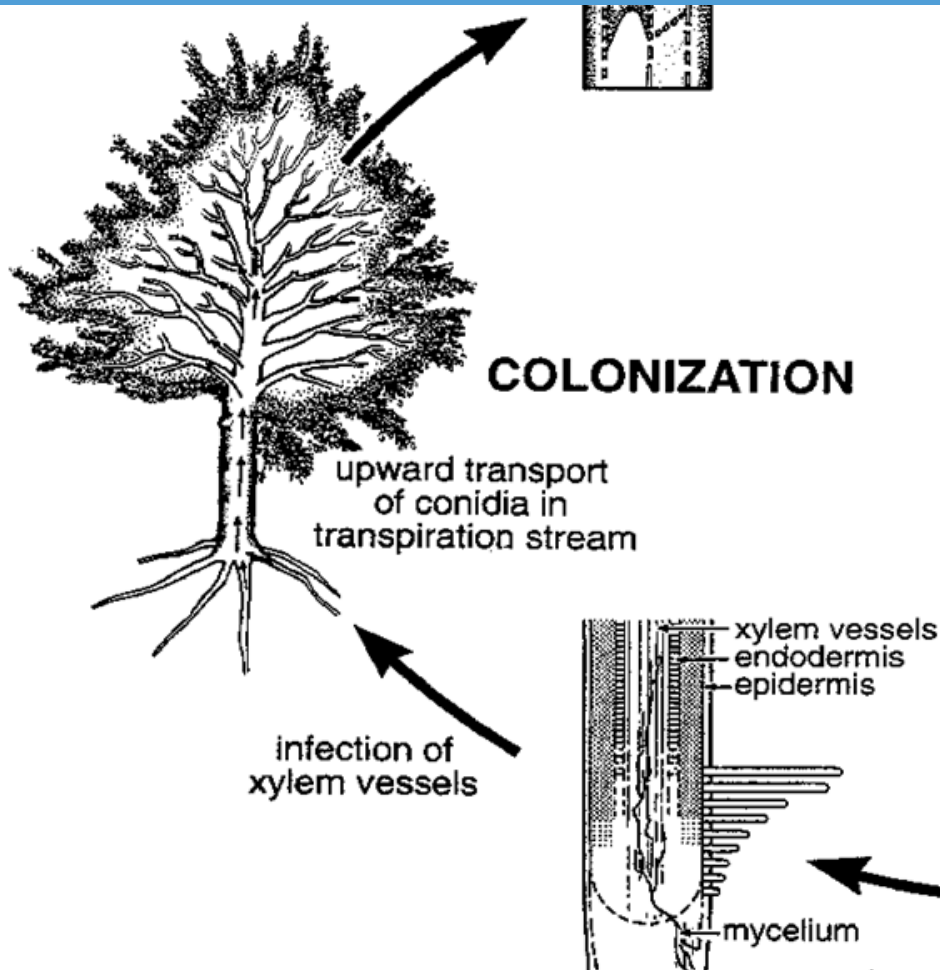
- Size of host
- Long-life of host & secondary inoculum
- **Xylem anatomy**
 - Anatomy affects colonization and symptom development
 - Annual production of new vascular tissue =
built-in mechanism for recovery
 - Anatomy may contribute to resistance



Xylem anatomy of trees → Secondary growth



Colonization of tree body

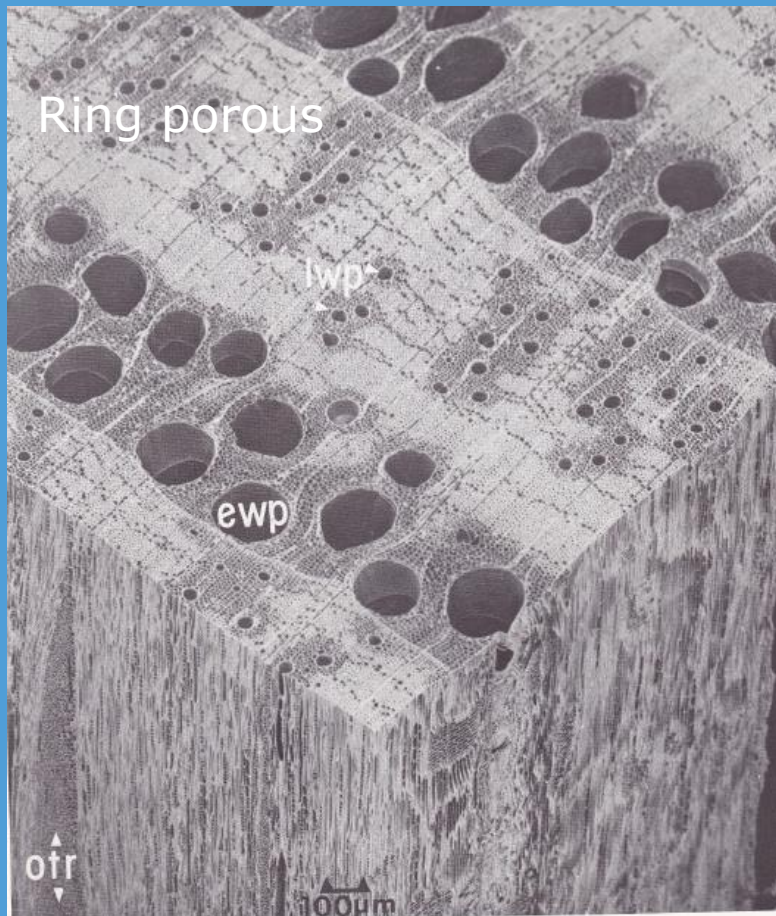


- Penetration of root
- Colonization of cortex
- Penetration of endodermis
- Entry into xylem
- Behaviour changes:
only in xylem vessels
conidia → fast upward transport
(see Prieto *et al.*, 2009)

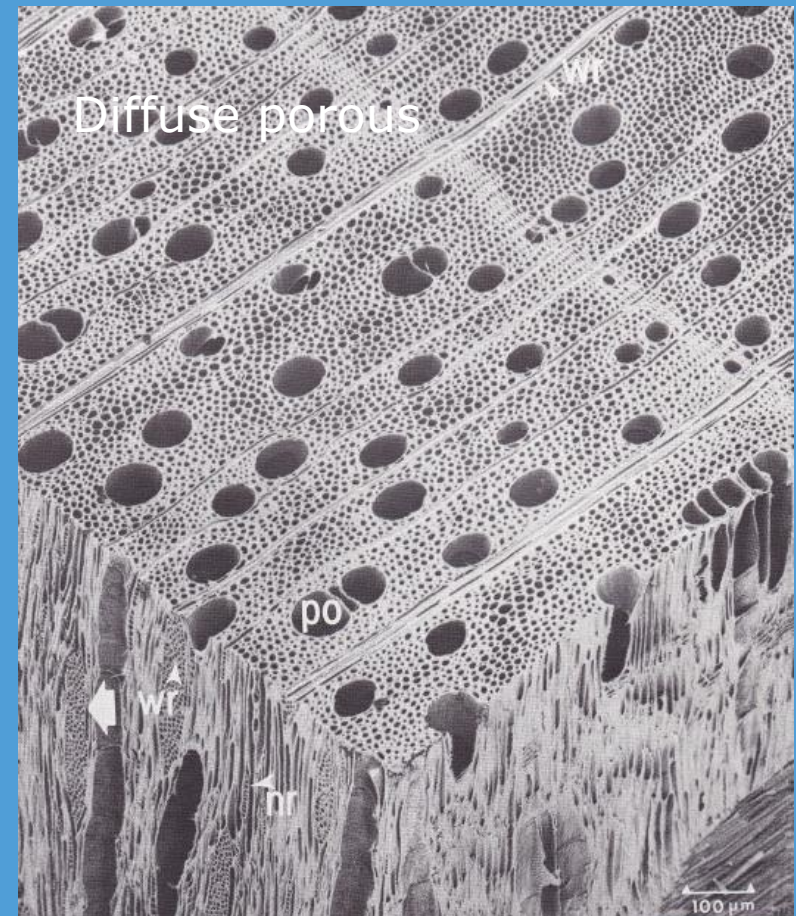


Xylem anatomy of trees

Core *et al.*, 1976



3 m; up to > 10 m
16-45 m/h



10 cm; up to 0.5 m
1-6 m/h



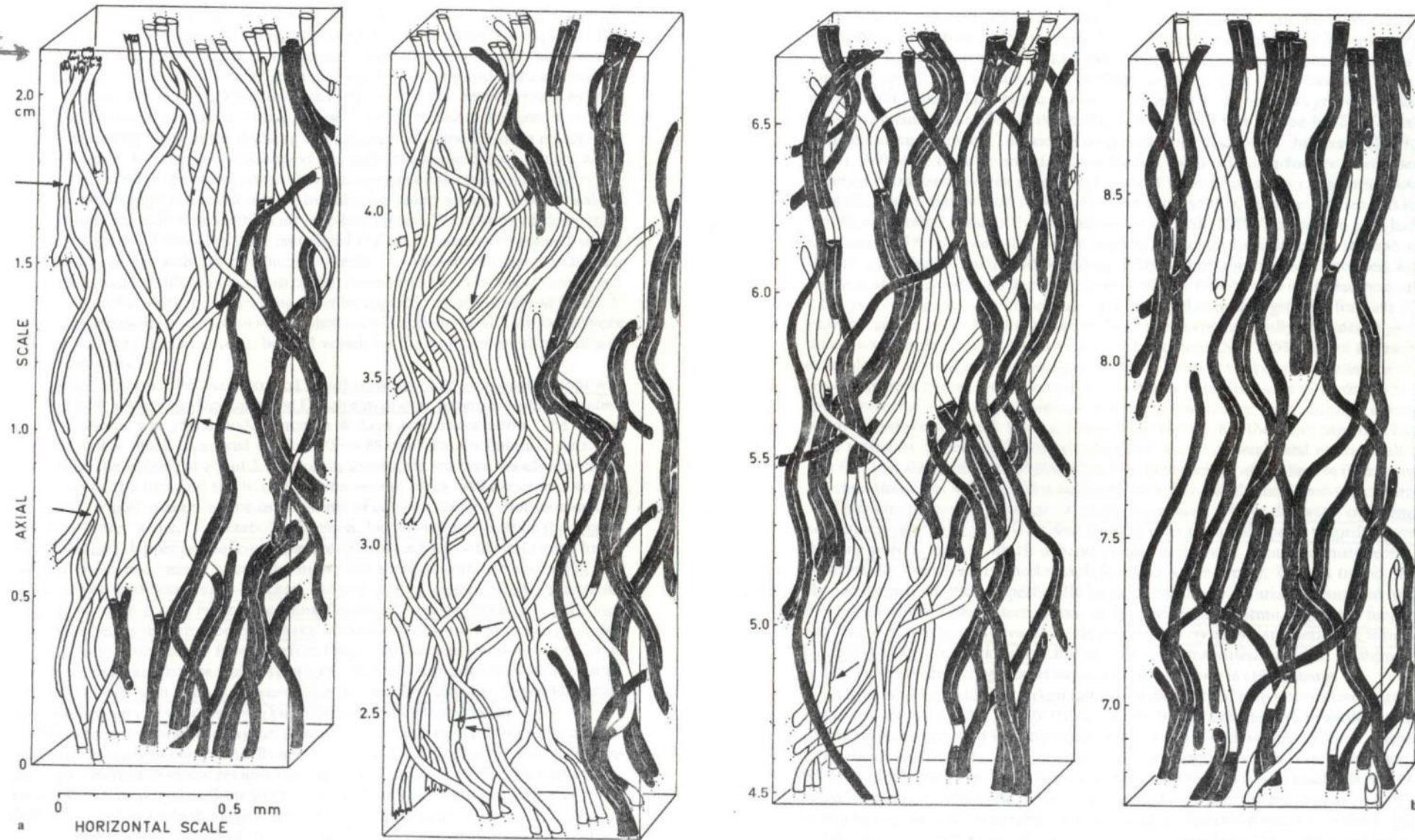
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Symposium 2013



Xylem vessel network

Zimmermann, 1983



Vessel network & distribution of conidia

- Passive transport by sapstream
 - Upward & tangential distribution
 - Extent depends on species
 - Influenced by active reaction of host
- Examples
 - Ash: strongly interconnected vessels (Zimmermann, 1983)
 - Olive: ind. roots strong connection with ind. branches (Lavee, 1996)



Xylem build-up enables recovery of trees

A.L. Shigo: **CODIT-model**

- highly compartmented
- active response
- “multiple” plant
- new xylem every year

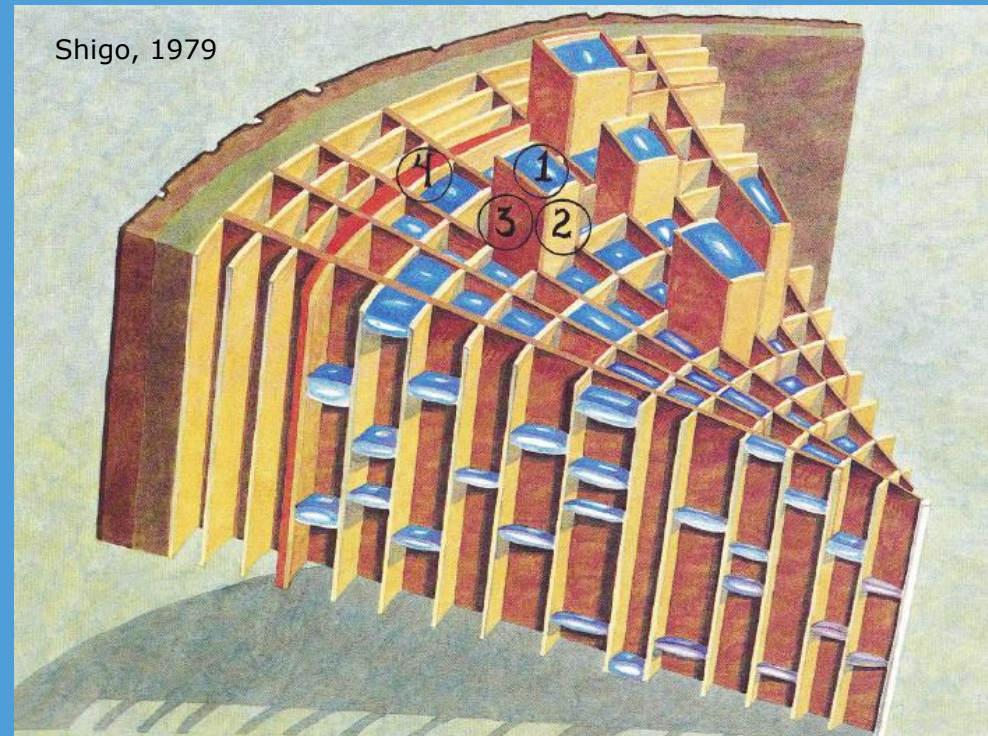
Tippett & Shigo, 1981:

Wall 1: vascular occlusions

Wall 2: margins of growth rings

Wall 3: sheets of ray cells

Wall 4: formation of barrier zone

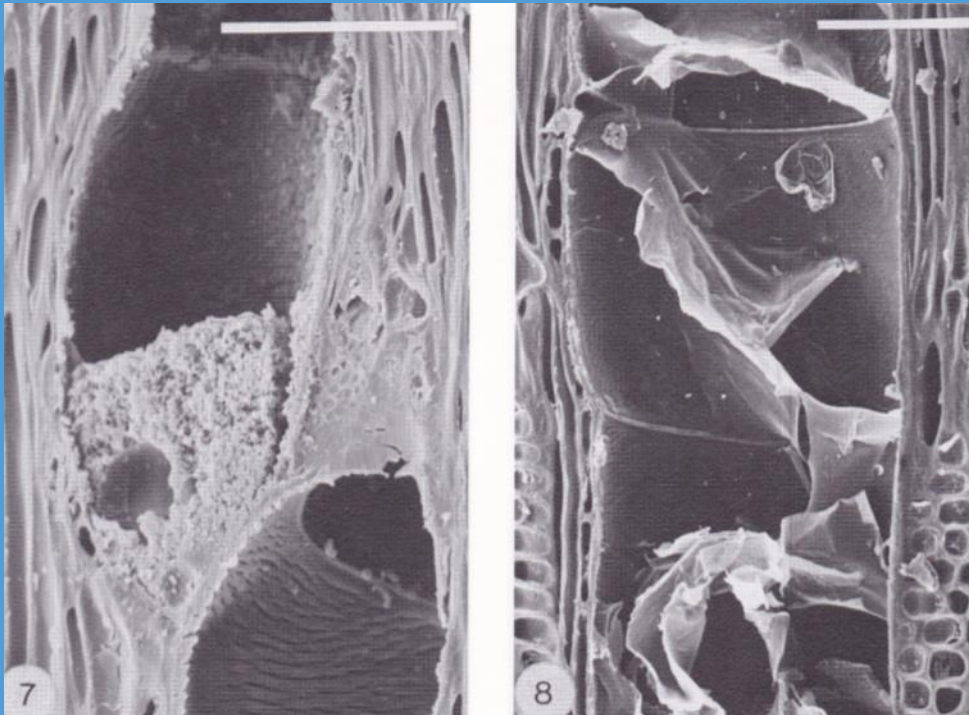


Recovery from VW in tree hosts

- Cherry Van der Meer, 1925
- Peach Ciccarese *et al.*, 1990
- Apricot Taylor & Flentje, 1968; Vigouroux & Castelain, 1969; Harrison & Glare, 1970
- Almond Cirulli *et al.*, 1998
- Cacao Emechebe *et al.*, 1974
- Olive Wilhelm & Taylor, 1965; Vigouroux, 1975
- Ash Hiemstra, 1995
- Maple Sinclair *et al.*, 1981



Active response of *Fraxinus excelsior*



Miller & Hiemstra, 1987

- Extensive vascular occlusion
- No barrier zone →
marginal parenchyma band



Recovery can be very effective

Ash (*Fraxinus excelsior*)

		% recovery	% dieback/dead
Natural infection	Forest trees	40	40
	Landscape trees	56	13
Inoculated trees		100	0

Hiemstra, 1995

- Infection type matters



Recovery can be very effective

Olive (*Olea europaea*)

		ND	D
Inoculated trees		86 %	24 %
	R	100	
	MS	90	83
	S	81	36
	ES	56	9

López-Escudero & Blanco-López, 2005

- Resistance level of cv
- Virulence of pathogen (D/ND)



Recovery - summary

■ Mechanism

- Confinement of pathogen
- Formation of new uninfected xylem
- Dieback/death only when pathogen reaches cambium
- Pathogen seems to “disappear” gradually

Anatomy provides structure and opportunity;

active response by host (and interaction with pathogen) is decisive

→ Link to Resistance



Resistance to VW

■ 2 types (Fradin & Thomma, 2006)

- Polygenic: alfalfa, cotton, potato, strawberry
- Single dominant R-gene: cotton, sunflower, potato, tomato

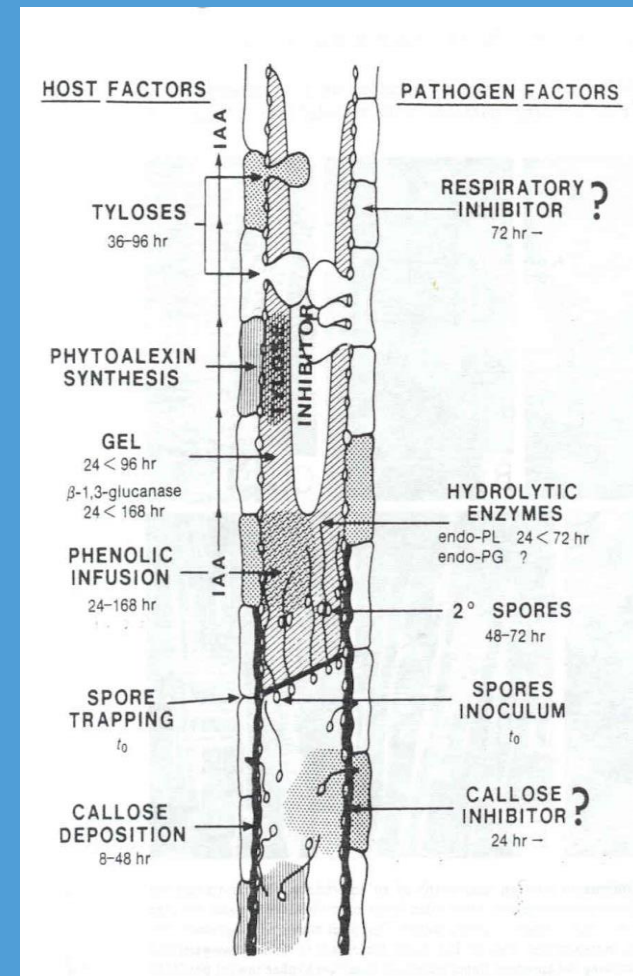
■ Tree hosts

- Long history of screening & selection for R
 - Olive, maple, prunus, pistacia
- No information on R-genes
- Processes similar as described for recovery
 - Anatomical factors contribute
 - Active response of the host decisive



Response of host

- Many mechanisms available
 - To avoid vascular infection
 - To block vascular distribution
 - To eliminate the pathogen once established
- Probably “there is no magic key to understanding all Verticillium infections” (J. Robb, 2007)
- Concept of time/space frame still valid and very useful



Beckman, 1984



Implications for integrated control

- Trees live long → prevent building-up of sec. inoculum
 - Make sure planting material is not infected
 - Remove diseased trees from new plantations
- Trees have a built-in recovery system
 - Pruning diseased branches may stimulate recovery
- Individuals often vary in susceptibility
 - Rootstock with increased level of resistance may protect susceptible commercially important cultivars



Thank you for your attention

