Esca disease: what we know and new research perspectives

Valérie HOFSTETTER and Katia GINDRO

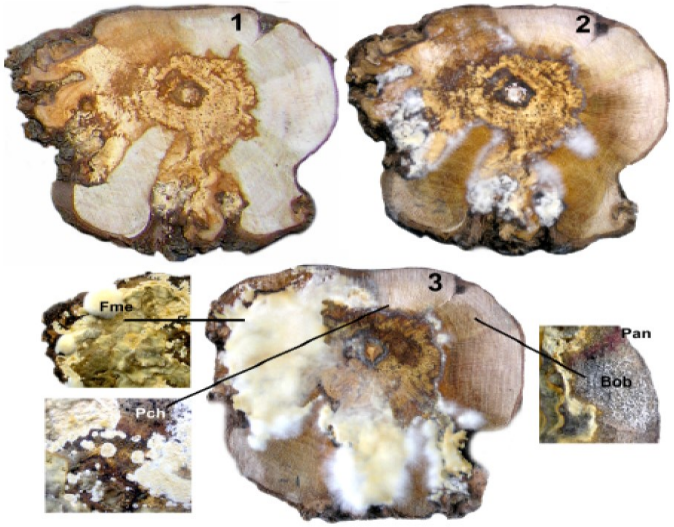
Agroscope

Agroscope

Esca is a grapevine wood disease (GTD)

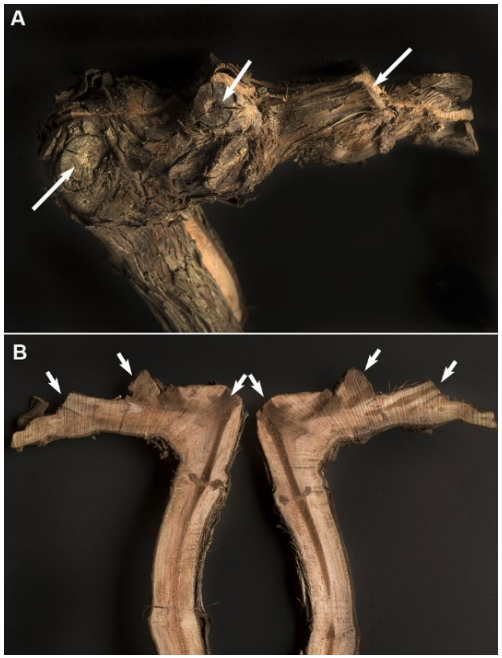
Present wherever grapes are grown and in almost all vineyards in the world. The **vast majority of affected plants die**.

Esca is considered a **fungal disease** because the **same fungal species** have been **repeatedly isolated from necrotic wood**.



Section of a trunk affected by the apoplectic form of esca with progressive development of fungi over time (1-3). Abbreviations: Fme: *Fomitiporia mediterranea*, Pch: *Phaeomoniella chlamydospora*, Pan: *Phaeoacremonium angustius*; Bob: *Botryosphaeria obtusa*)

Fungi associated with wood diseases **infect plants primarily through pruning wounds**.

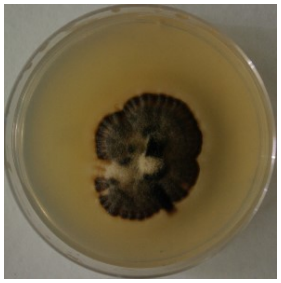


Eskalen A, Feliciano AJ, Gubler WD (2007) Susceptibility of grapevine pruning wounds and symptom development in response to infection by *Phaeoacremonium aleophilum* and *Phaeomoniella chlamydospora*. Plant Disease 91:1100–1104

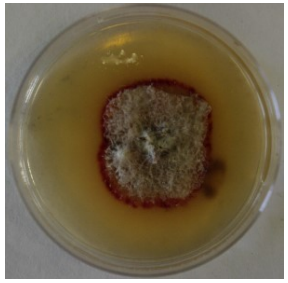
Agroscope

Most destructive grapevine wood diseases (GTD) in Europe

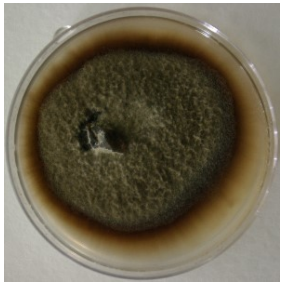
Esca (**as redefined by Surico 2009**) and "**young esca**" (= **Petri disease**)
Fungi : ***Phaeomoniella chlamydospora***, ***Phaeoacremonium spp.***, ***Fomitiporia mediterranea*** (in esca but not in young esca); ***Cadophora luteo-olivacea*** (Gramaje et al. 2011, Travadon et al. 2014).


Phaeomoniella chlamydospora

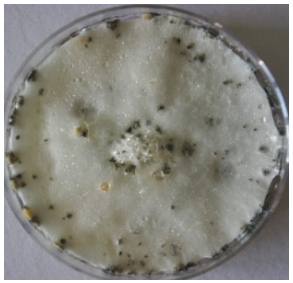

Phaeoacremonium mortoniae

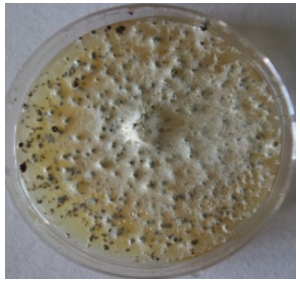

Phaeoacremonium viticola


Fomitiporia mediterranea

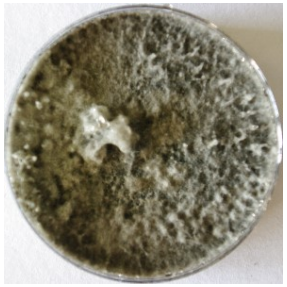

Cadophora luteo-olivacea

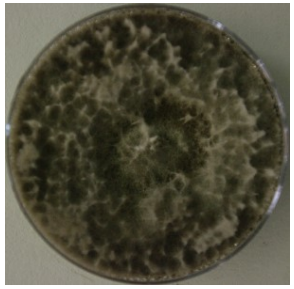
Eutypa dieback
Fungi: ***Eutypa lata , E. laevata*** (north of the USA) and other species of ***Eutypa*** and **Diaporthales** are involved in other continents.


Eutypa sp.


Eutypa lata

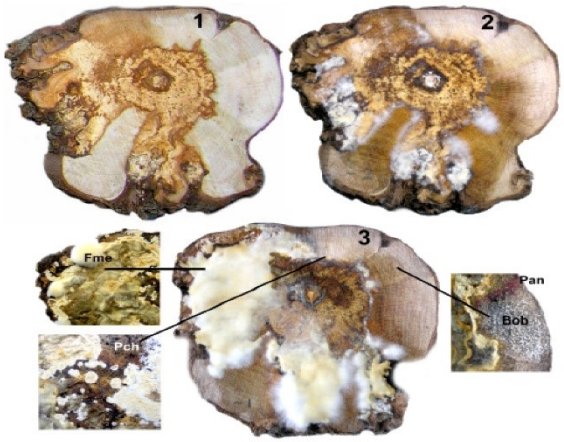
« Black dead arm » (BDA)
Fungi: ***Diplodia seriata*** (*Botryosphaeria obtusa*), ***Neofusicoccum parvum*** (*Botryosphaeria parva*) and other species of **Botryosphariaceae**.


Diplodia seriata


Neofusicoccum parvum

Why talk about wood diseases rather than just esca?

Leaf symptoms of **esca** (left) and **BDA** (right) are very similar (Luque *et al.* 2009, Viret & Gindro 2014)



The wood of **esca symptomatic plants** often shows **different types of necrosis** typical of **several GTDs**.

Several authors also believe that ***Eutypa lata*** (fungus responsible for **Eutypa dieback**) **may also play a role in esca expression** (Larignon & Dubos 1997, Lehoczky & Szabolcs 1983; Bertch *et al.* 2013)

The **redefinition of esca** by Surico (2009) is **questionable**

Main factors related to the incidence and severity of esca

1. **Fungi** associated with GTD : **action[s] mode[s]**?
   - **invasion** of healthy wood?
   - **toxins** production?
   - **virulence** (different pathotypes of the same species)

2. **Physiological accidents** related to **soil** and **climate conditions** ("terroir") and **cultivation practices** (management and pruning) **in relation or not to GTD fungi**?

3. **Plant genetics**: **grape cultivars** (or even clones of the same variety) **show variable sensitivities to GTD**.

1. Fungi: action(s) mode(s)?

Most scientists working on GTD consider the fungi involved as **latent pathogens**.

A **latent pathogen** can live for a long time in a host plant without generating symptoms but will, at some point, be responsible for the **appearance of disease symptoms**.

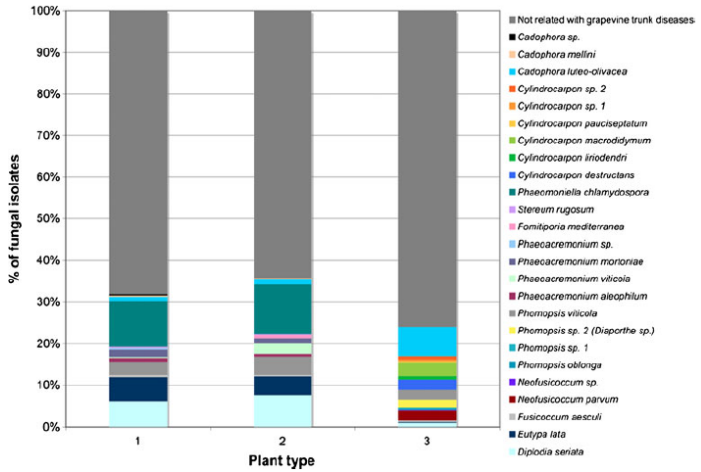
To do this, **the fungus must change its behavior** by becoming either **invasive** and/or producing **toxins**.

Hypothesis 1: invasion of healthy wood by GTD fungi?

Hypothesis 2: production of **phytotoxic compounds** by GTD fungi?

Hypothesis 3: diseased plants host **more virulent pathotypes** of GTD fungi than asymptomatic plants?

Hypothesis 1: invasion of healthy wood by GTD fungi?



1. Asymptomatic plants
2. Esca symptomatic plants
3. Nursery plants

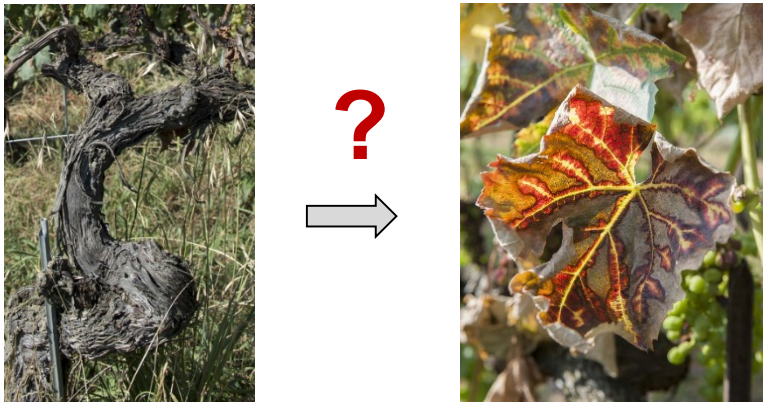
The rate of **wood colonization** by GTD-associated fungi is **very similar in esca and healthy plants**.
(Bruez *et al.* 2014, Del Frari *et al.* 2019, Hofstetter *et al.* 2012)

The **grafting material** does **not host esca pathogens**, but **other grapevine pathogens** such as *Cylindrocarpon* spp. (Black foot disease), *Cadophora* spp. (young esca) and *Phomopsis* spp. (Phomopsis dieback)
(Eichmeier *et al.* 2018, Hofstetter *et al.* 2012)

However, **after one growing season**, **esca-associated species are isolated**
(Eichmeier *et al.* 2018)

Hypothesis 2: production of phytotoxic compounds by GTD fungi?

GTD-associated fungi all produce secondary metabolites
that are phytotoxic (Andolfi *et al.* 2011, Bertsch *et al.* 2013).



GTD-associated fungi live exclusively in the wood of grapevine (they have never been isolated from the leaves): the foliar symptoms can therefore only result from the **transport** of these **phytotoxic compounds from the wood to the leaves** by the vascular system of the plant and in **sufficient quantity** to generate the foliar symptoms.

The **effects** of most **fungal metabolites** on plants are still **very poorly known**.

Another possibility is that the **phytotoxic compounds originate from wood degraded by fungi**.
A **mixture** of these compounds (**fungal and wood by-products**) could maybe cause esca **foliar symptoms**.

Hypothesis 2: production of phytotoxic compounds by GTD fungi?

Leaf symptoms may also result from **toxins produced only when certain species of fungi come into confrontation in the wood**. Fungi are known to engage in **chemical warfare** with each other when placed in **co-culture**
(Bertrand *et al.* 2014).

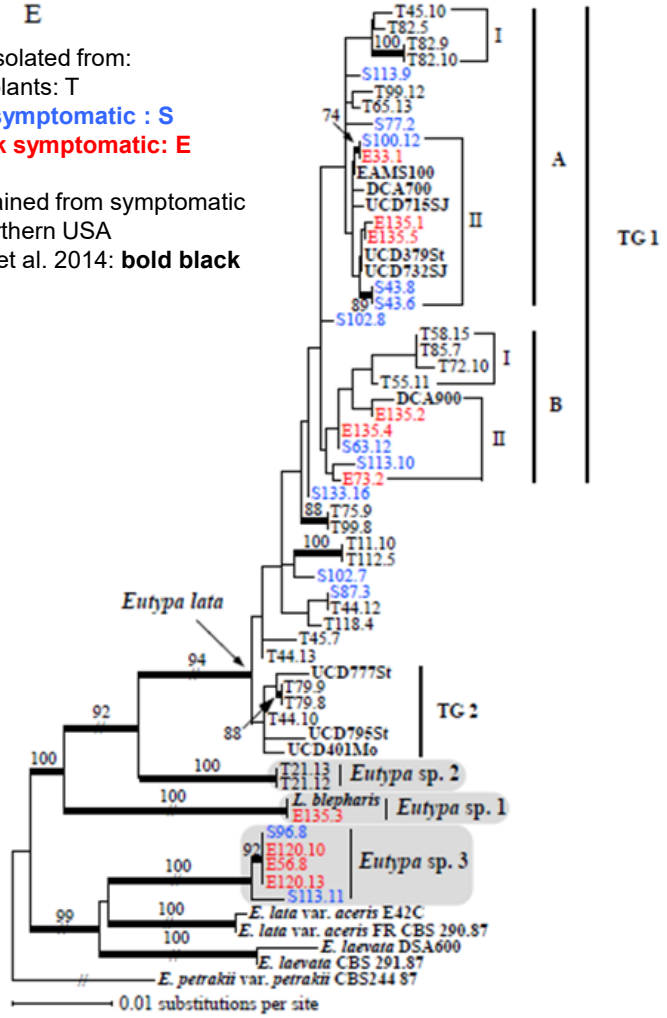
This hypothesis could also explain the **discontinuous nature of esca** in the vineyard. Even if all plants have the same fungal community, **symptoms may only appear when certain species come into contact in the wood.**

Hypothesis 3. Difference in virulence between individuals of the same GTD fungal species and/or between different species of the same genus?

E

Fungal strains isolated from:
Asymptomatic plants: T
Esca dieback symptomatic : S
Eutypa dieback symptomatic: E

Sequences obtained from symptomatic plants in the northern USA by Rolshausen et al. 2014: **bold black**



Two groups of ***E. lata*** isolates:
TG1 and TG2

(Rolshausen *et al.* 2014)

E. lata strains isolated from **diseased plants** (see groups **A II** and **B II**) do **not** cluster with those isolated from **healthy plants** (**A I** and **B1**).

These results suggest that **some strains** of ***E. lata*** may be **more virulent** than others.

(Hofstetter *et al.* in prep)

This hypothesis **has not been tested** on **esca-associated** fungi.

2. May esca result from physiological accidents?

Pedoclimatic factors are known to **influence the expression of esca** (Dubos et al. 2002)

Soils with a **high water retention capacity** (deep and clayey soils). **Climatic variations during the summer** (**alternation** of **humid and cool** periods with **hot and dry** periods, leading the vine to an important production of leaves and vegetal cover and thus to a strong **evapotranspiration leading to a gas embolism**).
(Fischer 2003; Surico, Mugnai and Marchi 2006)

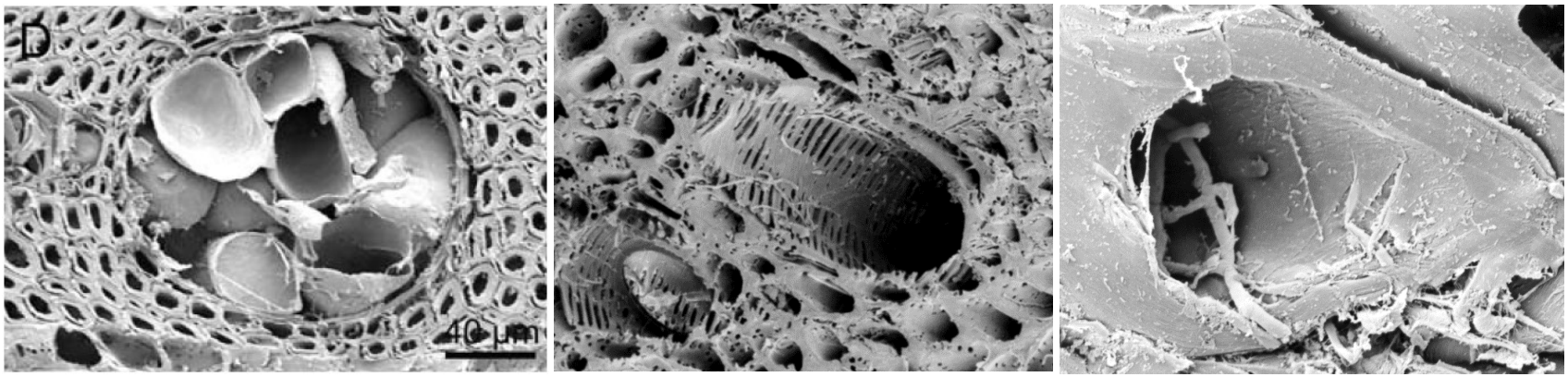
Do **esca leaves symptoms** and **apoplexy** result from a **hydraulic failure**?

1. Occlusion of the **xylem vessels** by **fungi,** by **tyloses and gels** or **both?**

2. Gas embolism resulting from a **too strong evapotranspiration**?

2. May esca result from physiological accidents?

The **vine** is a **liana** and **does not cover** its **wounds with a callus** unlike other woody plants.



PRUNING-INDUCED TYLOSE DEVELOPMENT IN STEMS OF CURRENT-YEAR SHOOTS OF VITIS VINIFERA (VITACEAE)
QIANG SUN, THOMAS L. ROST, AND MARK A. MATTHEWS. 2006, Americann Journal of Botany

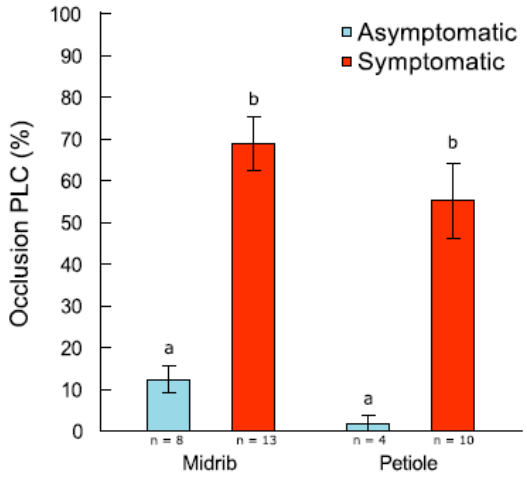
When injured (pruning wounds, mechanical injuries, frost) **vine produces huge quantities** of **tylose** (in **summer**) or **pectin gels** (in **winter**)

Fungi do not degrade tyloses but **pectin gels** are **excellent substrates** for fungi

May esca result from physiological accidents?

(Bortolami *et al* 2019)

Transplantation of **adult plants, symptomatic of esca** in large pots in order to **test the hypothesis of physiological accident** (loss of hydraulic conductance). The authors used non destructive techniques to **visualise in vivo the content** (**air embolism, occlusions**) and **functionality of vessels** in petioles and midribs of esca symptomatic leaves.



The percentage of **vessels occlusion** is **much higher** in **esca symptomatic** plants than is asymptomatic plants

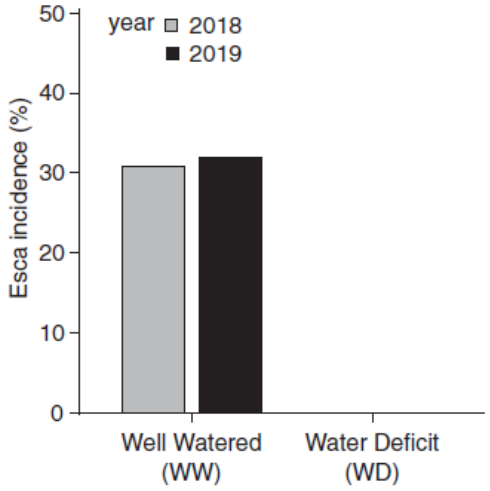
However there is **no significant relationship** between
the **severity of symptoms**
and the **percentage of hydraulic conductance loss** due to occluded vessels in the leaves.

Leaf symptoms do **not result** from **gas embolism.**

Leaf symptom development is associated with **vascular occlusions (by tyloses and gels)** that are likely **elicited at a distance from fungi living in the trunk**.

May esca result from physiological accidents?

(Bortolami *et al* 2021)



	Well-watered (WW)		Water deficit (WD)	
	pA	pS	pA	pS
Esca leaf symptom incidence in 2018	14% (2/14)	50% (6/12)	0% (0/13)	0% (0/12)
Esca leaf symptom incidence in 2019	33% (4/12)	31% (4/13)	0% (0/13)	0% (0/13)

Several authors hypothesized that **vascular pathogenic fungi** and **water deficit induced** the **same mechanisms before plant death**.

The **results** of this study **largely reject this hypothesis**; these two stresses induce **distinct physiological responses**.

Esca does **not alter** the **long-term sensitivity of plants to drought**.

Drought and **vascular disease** could act **synergistically** over the longer term to plant decline.

May esca results from physiological accidents?

The susceptibility of different grape cultivars to esca is variable.

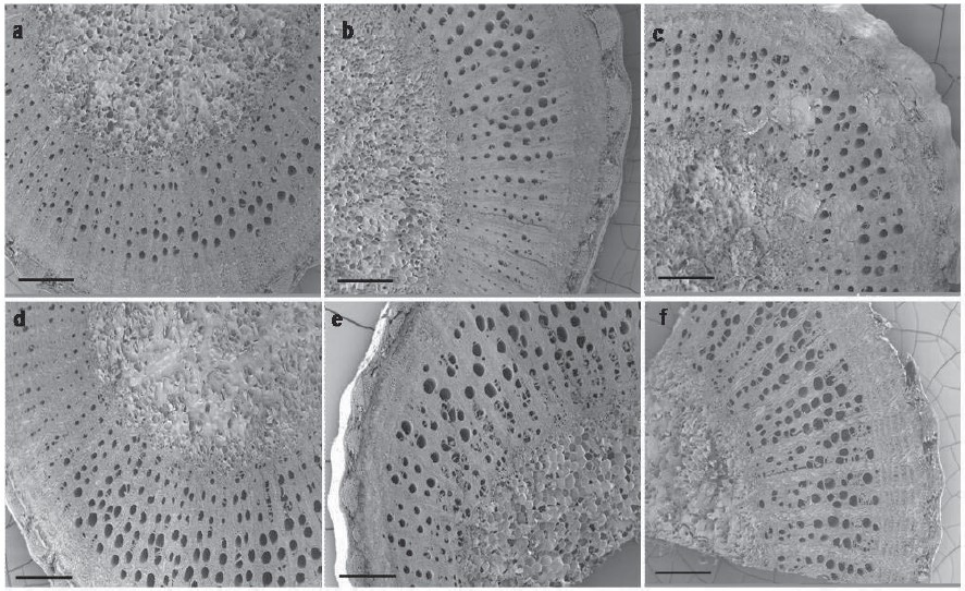
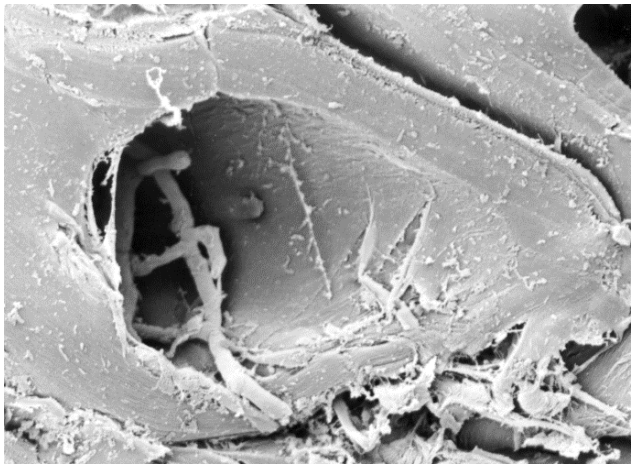


Fig. 3. Example SEM images of vessels surface in semi-thin section dormant canes. a, Chasselas; b, Gamay; c, 3309 (rootstock); d, Gamaret; e, Arvine; f, Humagne. Scale bar=1 mm.



Casieri L, Hofstetter V, Viret O, Gindro K, (2009). Fungal communities living in the wood of different cultivars of young *Vitis vinifera* plants. *Phytopathol. Mediterr.* 48, 73–83

The **difference in vessel size** between the **graft** and the **rootstock** could favor physiological accidents. The **larger vessels** could also favor the transport of **fungal spores** (**occlusion**).

3. **Plant genetics**: different **grape varieties** (or even clones of the same variety) **show variable sensitivities** to GTD.

(Graniti et al., 2000)

Two recent studies suggest that the **expression of esca** is **dependent** on the **genetic variability** of the vine **within the same species** (**"clone dependent"**).
(Murolo & Romanazzi, 2014 [Sauvignon]; Moret et al. 2019 [Chardonnay])

However, the **results** of these two studies are **contradictory.** While Murolo and Romanazzi observed a **clone dependent** esca expression **for Sauvignon** but **not for Chardonnay**, Moret et al. found a clone dependant expression of esca for **Chardonnay**.

What are the main factors leading to the expression of esca?

To understand esca, a systemic approach including the study of **epidemiology, fungal community and their metabolomics, grapevine physiology and genomics, all in relation to soil and climatic conditions** ("terroir") is necessary.

The SAVI Vaud-Agroscope-University of Neuchâtel project was designed to understand the **reasons for the decline** of **Gamaret**, a **grape variety with variable susceptibility to esca** (21 plots in different terroirs in the French-speaking part of Switzerland; study of the **fungal community** and of the **physiological state of the plants** on each plot in link with **pedoclimatic conditions**)

GTD control: Mycoviruses of fungi associated with GTD?

The **grapevine virome** is **dominated by mycoviruses** (Rwahnih et al. 2011).

Two studies (Yu et al. 2015, Wang *et al.* 2014) showed that the presence of **particular viruses in pathogenic fungi** (*Botrytis cinerea* and *Botryosphaeria dothidea*, respectively) could make them **hypovirulent**.

Yu et al. 2015. Novel hypovirulence-associated RNA mycovirus in the plant-pathogenic fungus *Botrytis cinerea*: molecular and biological characterization. *Appl Environ Microbiol*. 81(7):2299-310

Wang et al. 2014. Hypovirulence of the phytopathogenic fungus *Botryosphaeria dothidea*: 2 associations with a co-infecting chrysovirus and a partitivirus. *J. Virol.* 88(13):7517-27

Introducing hypovirulent fungal strains into grapevines (naturally virused strains or strains inoculated with such viruses) could be a way to **control GTD.**

Collaborators

Agroscope

Katia Gindro

Vivian Zufferey

Pierre-Henri Dubuis

SAVI

Olivier Viret

(Responsable du centre de compétence vitivinicole à Marcelin; Service de l'agriculture et de la viticulture (SAVI) du canton de Vaud).

Daniel Croll
Université de Neuchâtel

Vinciane Monod

Anne-Lise Fabre

MNHN Paris

Bart Buyck

Thanks for your attention!