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One or the other: under drought, grapevines do not express esca leaf symptoms

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Global viticulture has seen decreases in fruit yield and vine longevity over the past two decades. Our understanding of the underlying causes is limited by the complex interactions among the different factors involved and the technical challenges that limit investigations of these interactions. In Bortolami *et al.* (2021a)[1] we investigated the interaction between two main drivers of grapevine decline, drought and vascular disease (esca), monitoring esca leaf symptom development and vine physiology in Sauvignon blanc during both stresses. We found that drought conditions inhibited esca leaf symptom development revealing the key role of plant water status in esca pathogenesis and opening new perspectives into water use management in the context of climate change.

Links between grapevine hydraulics and esca leaf symptoms

Esca disease is one of the grapevine trunk diseases affecting vines and inducing yield losses and shortened plant lifespan[2], with an estimated economic loss of 1 billion euros in 2014 in France[3]. The causal fungal pathogens live and decay the perennial woody organs (trunk, arms, and multi-year canes), and induce the characteristic tiger-stripe symptoms in the leaves[4]. However, how pathogens induce leaf symptoms and how environmental conditions (especially drought and temperature) affect esca incidence is still an open question. We recently showed that esca leaf symptoms are linked to a loss in hydraulic conductivity (i.e., water transport) in leaves and in stems of the current year[5]. This discovery pointed out the key role of plant hydraulic functioning and xylem anatomy (the water transporting tissue) in the disease process. We then hypothesized that plant-water relations are the cornerstone of esca leaf symptom expression and that modified water availability (specifically during drought) might induce different levels of esca symptom expression. Indeed, the esca related pathogens live in the xylem[6], and their activity should be affected by the water status of the plant.

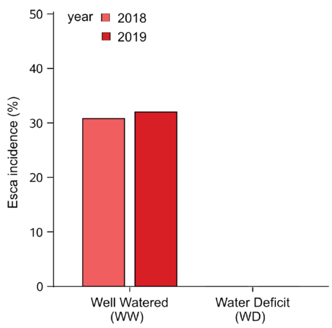
Solving the problem of studying esca under controlled conditions

Classical methods to study esca disease under controlled conditions would require the ability to reproduce the disease by inoculation of one (or more) of the esca-related pathogens in healthy grapevines, usually in rooted cuttings. However, such methods have failed to reliably reproduce the leaf symptoms hampering our understanding of esca. In our studies[1, 5], we uprooted 30-years old Sauvignon blanc plants from an experimental vineyard located at INRAE, Villenave d'Ornon, France. Each plant used in this study was monitored for esca symptom expression during the previous six years. During the experiments, plants were then divided according to whether they had never expressed symptoms (previously asymptomatic, pA), or had expressed symptoms at least once (previously symptomatic, pS). Plants were transplanted directly into 20-liter pots right before budbreak in fine clay medium (Klasmann Deilmann substrate 4:264). With this method we obtained mature plants in pots with known histories of esca disease expression. This allowed us to monitor the physiology of esca symptomatic plants under a controlled environment.

Grapevines never expressed esca leaf symptoms during a moderate to severe drought

During two consecutive seasons, we subjected half (n=25/51) of the plants to a moderate to severe level of drought. This water deficit condition was maintained for three months (July to October) by checking the predawn water potential (kept at -1 MPa on average), and by watering once every two-three days the exact amount of water lost via transpiration. The other half of the plants were well-watered, being watered every other day to field (i.e., pot) capacity. During both years we observed that none of the plants under water deficit expressed esca leaf symptoms, while under well-watered conditions around 30 % of the plants expressed symptoms in both years (Figure 1). This result is very unlikely due to chance; the likelihood of having not a single droughted plant express symptoms during the 2 years of study was less than 1 in 100 million.

Since the underlying mechanisms of this phenomenon are still unknown and need to be explored further, we can speculate about different future scenarios. In our study the drought intensity was moderate-severe resulting in very low plant transpiration but the xylem integrity was preserved (i.e., the critical thresholds inducing xylem embolism were not reached). We can expect that in the case of an



	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)

FIGURE 1. Effect of the watering regime on the percentage of Sauvignon blanc plants expressing esca leaf symptoms in 2018 and 2019. In the table, the plants are grouped by their watering regime (WW and WD plants) and by their disease history between 2012 and the year before the experimentation: plants that never expressed symptoms (pA) and plants that have expressed symptoms at least once (pS). Ratios present the number of symptomatic plants the year of experimentation in each category over the total number of plants of the category in each of the two different years. Adapted from Bortolami *et al.* (2021a)[1].

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increase in the frequency of drought events in the future, the incidence of esca would decrease. On the contrary, well-watered plants with high transpiration rates were expressing more symptoms during our experiment. Likewise, we hypothesize that increases in temperature with high soil water availability should increase the transpiration rates and possibly the expression of esca in the field. In this context, cultural practices such as irrigation, that can temporarily mitigate water deficit, could accelerate vine decline by esca.

Esca leaf symptoms do not affect grapevine anatomy over the long term

One of the most interesting characteristics of esca leaf symptoms is that the expression is not consistent year-to-year. Multiple field surveys have highlighted that plants showing symptoms during one season can be totally asymptomatic with green canopies the following season(s). We showed that the leaf symptom history of the plant does not influence several physiological parameters in asymptomatic plants[1, 5]. Asymptomatic plants exhibited the same hydraulic functioning and xylem anatomy in stems, regardless of whether they expressed esca leaf symptoms during one of the precedent seasons or not[5]. In the same vein, grapevine response to drought did not differ between plants that never expressed esca symptoms and those that had exhibited symptoms at least once over the previous six years (Figure 2). This finding suggests that the negative impact of esca leaf symptoms on the green tissue of the year (stems and leaves) is mostly limited to the season of disease expression.

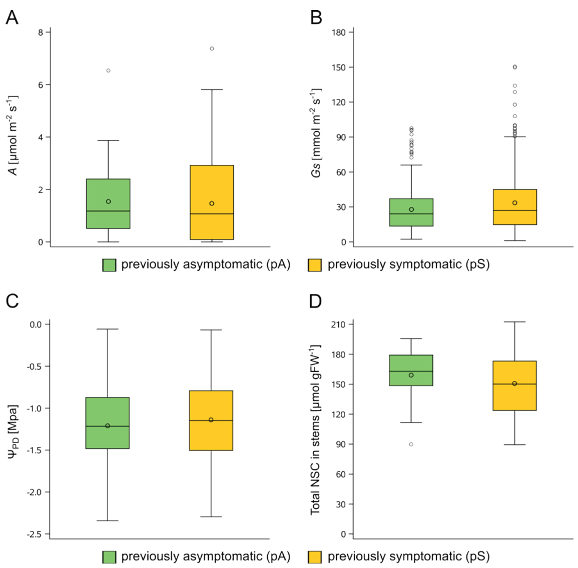

FIGURE 2. Effect of disease history on plant physiological response to drought. The colors represent the absence (pA, green) or presence (pS, yellow) of esca leaf symptoms during the preceding six seasons before submitting the plants to drought. (A) CO_2 assimilation (A, µmol m^{-2} s^{-1}), (B) whole plant stomatal conductance (Gs, mmol m^{-2} s^{-1}), (C) predawn water potential (Ψ_{PD}, MPa), (D) total Non Structural Carbohydrates in stems (µmol gFW^{-1}) after changing the watering regime. The disease history (pA versus pS) had no significant effect on any other recorded physiological parameter. Adapted from Bortolami *et al.* (2021a)[1].

Green regrowth after symptoms: a capacity of the plant to recover from esca?

All the plants that expressed leaf symptoms were able, two to five weeks after symptom expression, to generate new green leaves from secondary buds at the top of the symptomatic stems (Figure 3). This green regrowth was associated with a recovery on the whole-plant transpiration and a hydraulic functioning close to control asymptomatic plants[1]. More attention should be given to new shoots that are usually removed during the growing season. These new shoots, providing a new source of photosynthesis, might help the vine to mitigate the negative effects of esca on carbon reserves, yield, and plant longevity. Indeed, recent studies have suggested that minimal pruning might decrease trunk disease incidence[7], while intensive pruning could increase it[8]. Consequently, the effect of different trimming and pruning practices on esca symptomatic plants should be attentively studied during future field surveys.

FIGURE 3. A plant of *V. vinifera* cv Sauvignon blanc showing a green asymptomatic regrowth from secondary buds at the top of esca symptomatic shoots.

Integrative studies, a priority for understanding and preventing vineyard decline

Over the last 20 years, European vineyards are experiencing yield losses related to a general plant dieback[3]. Here we would like to highlight that stressors should not be considered independently in research programs if we are to understand the underlying mechanisms of grapevine dieback.

Indeed, as a perennial crop, grapevines experience several stresses during their lifetime, sometimes in sequence, sometimes simultaneously. It is time, using the technological advances that are given to us, to increase the number of integrative studies to better understand grapevine physiology in the field and how it (and we) will face the future climate change. ■

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