Large gradient of susceptibility to esca disease revealed by long-term monitoring of 46 grapevine cultivars in a common garden vineyard

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Abstract

Grapevine (*Vitis vinifera* L.) is prone to many fungal diseases, including esca, a severe vascular disease threatening the wine sector and for which there is no cost-effective cure. Susceptibility to esca varies between cultivars in different infection conditions. It may therefore be possible to use the genetic diversity of grapevine cultivars to mitigate disease impact. However, the genetic component of esca susceptibility has rarely been investigated in the vineyard, and the specific mechanisms and varietal traits underlying esca susceptibility remain unknown.

In this study, we monitored the incidence and severity of esca foliar symptoms and plant dieback (apoplexy and mortality) at plant level for seven years, on 46 cultivars planted in an experimental common garden, to separate the genetic component of esca susceptibility from the effects of environment and cropping practices. We observed a broad gradient of varietal susceptibility, with a mean incidence of 0 to 26% of vines expressing esca foliar symptoms depending on the variety. This gradient remained similar across years and, unlike the severity of foliar symptoms, the incidence of grapevine dieback was significantly correlated with that of foliar symptoms. We detected a significant but weak and very localised phylogenetic signal for the incidence of esca foliar symptoms in this panel of cultivars.

We then explored the relationships between epidemiological metrics and ecophysiological and phenological traits phenotyped on the same plot. Esca disease incidence was negatively correlated with δ13C across cultivars, suggesting that varieties with higher water use efficiency are less prone to the expression of esca symptoms on leaves. Moreover, the least vigorous cultivars were among the least susceptible, although this relationship was not significant. By contrast, neither phenological stages nor nitrogen status were significantly predictive of cultivar susceptibility to the disease.

Together, these results provide new insight into the potential of genetic resources for use in the sustainable management of grapevine trunk diseases and open up new perspectives for studying the pathological and physiological determinants of their incidence.

Keywords: Ecophysiology, disease incidence, grapevine trunk disease, pathogenesis, phenotypic diversity, *Vitis vinifera*

Introduction

The domesticated grapevine *Vitis vinifera* L. ssp. *vinifera* has a high level of genetic and phenotypic diversity, generated naturally by recombination, hybridisation, and mutation events, as well as through human-assisted selection. More than 5,000 cultivars are currently registered (This *et al.*, 2006), although only a small proportion are widely cultivated worldwide (Anderson and Aryal, 2013). Cultivar diversity is now considered an excellent tool for managing abiotic and biotic pressures in a sustainable manner (Merdinoglu *et al.*, 2018; Wolkovich *et al.*, 2018). There is therefore a need to improve our understanding of the variability between cultivars by phenotyping them for a wide range of traits. Several stress-related traits, including carbon isotope discrimination in berry juice at maturity (δ13C; Plantevin *et al.*, 2022), cold hardiness (Ferguson *et al.*, 2014), and susceptibility to pests and diseases (Boso *et al.*, 2011; Gaforio *et al.*, 2011; Paňitrur-De La Fuente *et al.*, 2018), have already been studied in a range of cultivars. The susceptibility of the grapevine vascular system to various stresses has also recently been studied. Xylem and hydraulic traits have been phenotyped in a range of *Vitis* genotypes of different origins and levels of drought tolerance (Dayer *et al.*, 2022; Lamarque *et al*., 2023) or resistance to vascular pathogens (Pouzoulet *et al.*, 2020; Fanton and Brodersen, 2021).

Vascular biotic stresses include grapevine trunk diseases, which are responsible for substantial yield losses in vineyards worldwide (Gramaje *et al.*, 2018). One such disease is esca, which is detected in the vineyards through the summer expression of foliar symptoms and yield losses (Lecomte *et al.*, 2012). Esca pathogenesis has been associated with various types of trunk necrosis (Mugnai *et al.*, 1999) probably involving a complex community of fungal pathogens (Bruez *et al.*, 2014). This community includes a few key pathogens from both Ascomycota (including *Phaeomoniella chlamydospora* and *Phaeoacremonium minimum*) and Basidiomycota (e.g. *Fomitiporia mediterranea*). However, no direct role in foliar symptom onset has ever been demonstrated for any of these pathogens, which are present in both healthy and necrotic wood tissues (Bruez *et al.*, 2016)

66 and in both asymptomatic and symptomatic plants (Hofsteter *et al.*, 2012; Bruez *et al.*, 2014). These
67 fungi probably also interact with bacteria (Bruez *et al.*, 2020) and seem to be restricted to the perennial
68 organs (Bortolami *et al.*, 2019).

69 Foliar symptoms are associated with xylem hydraulic failure and impaired photosynthesis (Bortolami
70 *et al.*, 2019, 2021a; Ouadi *et al.*, 2021; Dell'Acqua *et al.*, 2023). The incidence of esca foliar
71 symptoms is probably affected by multiple factors (as reviewed in Claverie *et al.*, 2020), including
72 plant age, pedoclimatic conditions, viticulture practices, the plant- and soil-associated microbiota,
73 and the plant material. The genetic diversity of the grapevine response to esca may be associated with
74 differences in phenotypic characteristics (ecophysiology, phenology) at cultivar level. Based on what
75 we now know about plant-to-plant variability within a single cultivar, mineral status, water status and
76 plant phenology are promising avenues to be explored. The incidence of esca increases following
77 foliar applications of nutrient sprays, which suggests that a higher nutrient content in the leaves may
78 be associated with a higher incidence of esca (Calzarano *et al.*, 2009). High levels of grapevine
79 transpiration may facilitate the translocation of pathogenic toxins and metabolites throughout the vine
80 (Bortolami *et al.*, 2021b). Differences in phenology can interfere with the co-ordination between
81 ontogenic susceptibility and favourable climatic periods for disease development (Serra *et al.*, 2018).

82 The susceptibility of grapevine cultivars to trunk pathogens and diseases, especially esca, has been
83 assessed with three methods. The first one reports varietal susceptibility to fungal infection and
84 involves phenotyping the internal necrotic lesions that develop after artificial inoculation with one or
85 more fungal species, such as *P. chlamydospora* (e.g. Pouzoulet *et al.*, 2017, 2020; Martínez-Diz *et*
86 *al*., 2019) and, to a lesser extent, *P. minimum* (Feliciano *et al.*, 2004; Gubler *et al.*, 2004). However,
87 the results obtained by this method are not readily transferable to field conditions, particularly as
88 fungal inoculations do not reproduce foliar symptoms (Claverie *et al.*, 2020). The second method is
89 the monitoring of esca incidence (e.g. proportion of plants presenting foliar symptoms or dieback) in

90 a network of productive vineyards, over an entire region, or even at the national scale (Bruez *et al.*,
91 2013). However, one of the major limitations of this approach is the large number of confounding
92 factors, such as viticulture practices, climatic conditions, soil type, plant age, and rootstock. These
93 biases can be overcome, making it possible to compare grapevine cultivars within the same climatic
94 and cultural context, by monitoring a single experimental vineyard planted with a set of cultivars over
95 multiple years. In the last decade, such experimental setups have been used to compare numerous
96 cultivars in common environments (e.g. Murolo and Romanazzi, 2014). However, no experiment to
97 date has been purposely designed to take into account pedoclimatic microvariability and the origin of
98 the plant material, both of which could account for a significant amount of the variability in disease
99 susceptibility (Kovács *et al.*, 2017; Gramaje *et al.*, 2018). As a result, limited information is currently
100 available regarding cultivar differences in terms of the incidence of esca foliar symptoms and dieback
101 in a common environment. Are the differences between cultivars consistent between years? What are
102 the ecophysiological drivers of esca susceptibility at cultivar level?

103 In this study, we focused on the genetic component of grapevine susceptibility to esca foliar
104 symptoms and dieback, independent of *terroir* effects, and on the mechanisms potentially underlying
105 differences between cultivars. We monitored the incidence and severity of esca foliar symptoms and
106 plant dieback, and a range of phenological and ecophysiological traits in a common garden
107 experimental vineyard planted with 46 cultivars, over periods of seven and six years, respectively.
108 This design made it possible to study cultivar-specific variability without bias due to other factors,
109 such as year, soil, plant material origin, and viticulture practices. We first investigated the range of
110 cultivar susceptibility to esca foliar symptoms and grapevine dieback. We then explored multiple
111 correlations between different traits and years, to assess the temporal consistency of the ranking of
112 varieties for susceptibility. Finally, we investigated the relationships between esca foliar symptoms
113 and dieback on the one hand, and phenological and ecophysiological traits, such as key phenological

stages, nitrogen status at flowering, pruning weight, and δ13C, a proxy of water use efficiency, on the other.

Materials and methods

1. Common garden experimental vineyard

The VitAdapt vineyard (as described by Destrac-Irvine and van Leeuwen, 2016) was designed as a common garden, and is located at the *Institut National de Recherche pour l'Agriculture, l'alimentation et l'Environnement* (INRAE) research station (Villenave d'Ornon, Nouvelle-Aquitaine, France), at 44°47'23.83 N'', 0°34'39.3' W'. This vineyard, on a sandy-gravel soil, was planted with 52 genotypes (47 *Vitis vinifera* L. cultivars and 5 *Vitis* hybrids). In this study, 45 *V. vinifera* L. cultivars, and one hybrid of several *Vitis* species — Hibernal, an F2 progeny of a Seibel 7053 x Riesling cross (Vitis International Variety Catalogue - VIVC; www.vivc.de) — were monitored. Among them, 28 were red-berried cultivars and 18 were white-berried cultivars (Supplementary Table S1). All plants were grafted onto Selection Oppenheim 4 (SO4) clone 761 rootstock and planted at a density of 5,555 vines/ha, corresponding to a spacing of 1.8 m between adjacent rows and 1 m between adjacent vines. Eight cultivars were first planted in 2010, all the others being first planted in 2009 (Supplementary Table S1). Each cultivar was tested for major viral diseases before planting, and only non-contaminated material was planted. All vines were pruned according to the double guyot system and grown without irrigation. Pests and diseases were controlled by an integrated management programme, and weeds were controlled by mechanical tillage beneath the row. No specific management of trunk diseases was carried out. Cover crops were planted in every other row, alternating from year to year. The VitAdapt vineyard was organized into a five-randomised block design to account for variability in soil properties and pathogen inoculum. Thus,

137 we assume that all cultivars were exposed to similar risks of pathogen infection. Each block
138 comprised one subplot per cultivar, in which 10 vines were planted in two adjacent rows. In this
139 study, only four blocks were monitored, resulting in a total of 184 subplots (1,840 vines; 40 per
140 cultivar, 46 cultivars) subjected to ecophysiological monitoring and esca and dieback monitoring for
141 six and seven years, respectively. No artificial inoculation of trunk pathogens has been conducted in
142 this vineyard, and dead vines were regularly removed to prevent local hotspots of spore production.

143 **2. Monitoring of foliar symptoms of esca and plant dieback**

144 We monitored 1,840 vines individually by eye, to check for esca foliar symptoms (examples are
145 shown in Figure 1) and plant dieback (apoplexy and death), between 2017 and 2023. Evaluations
146 were performed one to three times per year, between early July and mid-September. For each
147 monitoring campaign, all the plants were inspected during a period of no more than one week. For
148 each vine, a score was assigned at individual arm level for the observed phenotype (asymptomatic,
149 presence of esca foliar symptoms/symptomatic, apoplectic, dead, young replanted vine, missing).
150 When foliar symptoms were observed, severity was scored by determining, for each arm, the
151 proportion of symptomatic shoots and the degree of leaf and berry dehydration (as described in
152 Supplementary Table S2). Briefly, the score attributed for each arm was either1 (light symptoms), 3
153 (moderate symptoms) or 5 (severe symptoms, i.e. 'tiger-striped' leaves and dried berries). In years
154 with multiple assessments, the maximum severity index was retained. To assign a score for each vine,
155 we averaged the score for each of its symptomatic arms.

156 Three epidemiological metrics were calculated from the data collected at subplot scale for esca foliar
157 expression and vine dieback. The incidence of esca foliar symptoms was calculated as the proportion
158 of the total number of productive plants (i.e. excluding totally apoplectic and dead plants, as well as
159 young replanted vines) displaying typical esca foliar symptoms. The cumulative incidence of foliar
160 symptoms was also calculated as the proportion of the productive vines having expressed esca foliar

161 symptoms in at least one of the seven years monitored. The mean severity of esca foliar symptoms
162 was calculated at subplot scale, by averaging the score attributed to each symptomatic vine of the
163 subplot. Finally, the incidence of plant dieback was calculated as the proportion of mature plants (i.e.
164 excluding young replanted vines) with at least one unproductive arm (i.e. apoplectic or dead). During
165 the plant phenotyping process in the field, no *a priori* assumption was made concerning the cause of
166 plant dieback, which may have multiple abiotic or biotic causes.

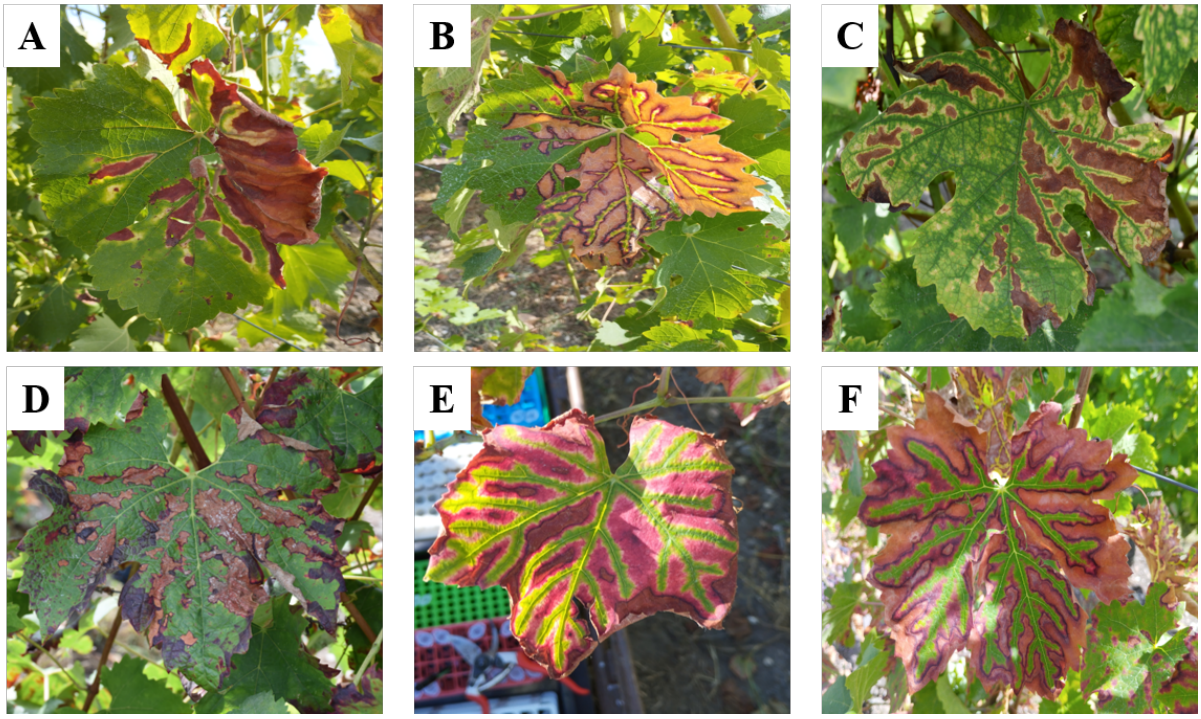


Figure 1. Examples of various foliar phenotypes for esca on different *Vitis vinifera* cultivars grown in a common garden experimental vineyard

A-C: white-berried cultivars (A) Muscadelle; (B) Chasselas; (C) Viognier. D-F: red-berried cultivars (D) Alvarinho; (E) Pinot Noir; (F) Cabernet Franc. Note that the disease status of a vine is determined by phenotyping the entire shoot, not just individual leaves.

3. Phenotyping of ecophysiological and phenological traits

We explored the mechanisms underlying cultivar susceptibility to esca and dieback, using cultivar phenology data and monitoring data for three ecophysiological traits collected at the subplot scale in the VitAdapt vineyard.

178 **3.1. Monitoring of phenological stages**

179 The phenological evaluation was performed visually, in the field, on 10 vines of each cultivar in each
180 of the four blocks, as described by Destrac-Irvine *et al.* (2019). Three different stages were monitored:
181 bud break, flowering and veraison. Notations were based on the BBCH scale (Lorenz *et al.*, 1995).
182 The bud-break stage corresponds to the date on which 50% of the buds have reached the BBCH 07
183 stage; the flowering stage corresponds to the date on which 50% of the flowers have reached the
184 BBCH 65 stage; and the veraison stage corresponds to the date on which 50% of the berries have
185 reached the BBCH 85 stage. Six years of data were included in this study, from 2017 to 2022.

186 **3.2. Carbon isotope discrimination ($\delta^{13}C$)**

187 We determined $\delta^{13}C$ levels in berry juice sugars obtained each year, at maturity, from 10 vines of
188 each cultivar in each of the four blocks, as described by Plantevin *et al.* (2022). All samples were
189 analysed in an external laboratory (UMR CNRS/Plateforme GISMO UMR 6282
190 BIOGEOSCIENCES *Université de Bourgogne*, 21000 Dijon, France). Briefly, the juice was
191 extracted and analysed on a Vario Micro Cube elemental analyser coupled in continuous flow mode
192 to an isotopic ratio mass spectrometer (IsoPrime, Elementar). Results are expressed according to the
193 Vienna Pee Dee Belemnite (VPDB) international reference. Six years of data were included in this
194 study, from 2017 to 2022.

195 **3.3. N-tester measurements**

196 N-tester measurements were performed at flowering (as defined above), which is considered to be a
197 key stage for nitrogen assimilation by grapevines (Celette and Gary, 2013), on 30 leaves of each
198 cultivar in each of the four blocks, according to the manufacturer's protocol (Yara, Oslo, Østland,
199 Norway). Briefly, each leaf was clamped with the device, for the measurement of transmittance (at
200 wavelengths of 650 and 960 nm), which provides a standardised index of chlorophyll content that can

be used as a proxy for vine nitrogen status. As a means of accounting for cultivar-specific nitrogen-status behaviour under similar conditions, raw values were transformed according to varietal rounded corrections. The mean value for Sauvignon Blanc was similar to the mean value across all varieties, so this cultivar was used as the reference variety for this index. For each cultivar, the difference between the mean value for all available years for the cultivar (2015-2021 for 35 cultivars; 2020-2021 for the other 11), and the mean value for Sauvignon Blanc was calculated. An Ascendant Hierarchical Classification (AHC) method was then applied to the N-tester values to group the cultivars and obtain an average correction for all the cultivars of a single group. The N-tester value of each cultivar was then corrected with the correction coefficient for its group, as described in Supplementary Table S3. Five years of data were included in subsequent analyses, from 2017 to 2021.

3.4. Pruning weight quantification

Pruning weight was quantified during the winter for all varieties in each of the four blocks. For each cultivar, two measurements were made for each block, by averaging the value three central vines of a row (i.e. six vines per subplot). Only the wood from the previous growing season removed from the plants during pruning was weighed. All measurements were performed during the same period of the year in each year: between January 15th and 30th. Six years of data were included in this study, from 2017 to 2022.

4. Data analysis

We first evaluated the effect of block on the three epidemiological metrics: esca foliar symptom incidence, esca foliar symptom severity, dieback incidence. Block was found to have a significant impact on the incidences of both foliar symptoms and dieback ($p = 0.03$ and $p = 10^{-5}$, respectively; Supplementary Figure S1). Thus, block was included in subsequent models as a random effect to account for this variability.

225 We assessed the effects of cultivar and year (entered as fixed effects) on the three epidemiological
226 metrics using three independent mixed modelling procedures, with block as a random effect. The
227 effect of berry skin colour (white/red) on the three epidemiological metrics was independently
228 modelled as a fixed factor, with cultivar and block as random effects.

229 We investigated the relationships between epidemiological metrics using mean values per cultivar
230 over blocks and years. This made it possible to model the average inter-variety variation of traits
231 independently of temporal and spatial variability. Correlations at cultivar level were assessed in
232 Pearson's correlation tests (i) between epidemiological metrics, (ii) between epidemiological metrics
233 for each single year, and (iii) between years for each single epidemiological metric. Independent
234 modelling procedures were performed for pairs of variables found to be significantly correlated.

235 The mean values per cultivar over blocks and years were also used to test the relationships between
236 quantitative ecophysiological and phenological traits on the one hand, and the three epidemiological
237 metrics on the other. Correlations between all pairs consisting of one epidemiological and one
238 phenotypic variable were tested in Pearson's correlation tests. Independent modelling was performed
239 for all pairs of variables found to be significantly correlated, with the epidemiological metric
240 modelled as the response variable, and the ecophysiological or phenological traits as fixed effects.

241 For all these analyses, linear models (LM) or linear mixed models (LMM) were used for response
242 variables following a normal distribution (i.e. foliar symptom severity). For binomial response
243 variables (i.e. the incidences of foliar symptoms and dieback), generalised linear models (GLM and
244 GLMM) were fitted, using the binomial family with "cloglog" links (accounting for a non-symmetric
245 distribution). Each model was graphically validated according to the normality of the residuals (QQ-
246 plot) and the homogeneity of the residual variance (residuals vs. fitted, residuals vs. predictors). All
247 analyses involving epidemiological metrics were conducted for the period 2017-2023, whereas
248 analyses including other phenotypic traits were conducted for the period 2017-2022. Analyses were

249 performed with R v.4.2.1 software (R Core Team, 2022) and the RStudio interface. Linear modelling
250 was performed with the "lme4" package (Bates *et al.*, 2015), and model validation was performed
251 with "DHARMa" (Hartig and Lohse, 2022). Correlation analyses were performed with the "corrplot"
252 package (Wei, Simko, 2021).
253

254 **5. Phylogenetic signal based on epidemiological metrics**

255 We built a phylogenetic classification of the 46 cultivars included in this study based on grapevine
256 genotyping data for 20 microsatellite markers (SSR), as described by Laucou *et al.* (2011). We used
257 the genetic distances between cultivars obtained from different hierarchical clustering analyses: two
258 classical methods for statistical clustering (i.e. Euclidean and Ward) and two methods adapted for
259 phylogenies (i.e. unweighted pair group method with arithmetic mean (UPGMA) and neighbour
260 joining (NJ)). For phylogenetic signal analysis, we visually inspected the four phylogenies and
261 selected the phylogeny best reflecting the known relationships between cultivars. All information on
262 kinship between the cultivars used in this work was based on the VIVC (www.vivc.de).

263 We searched for a phylogenetic signal in cultivar susceptibility to esca using methods based on
264 autocorrelations computed both on the global phylogenetic tree and local nodes of the phylogeny,
265 implemented in the "phylosignal" package (Keck *et al.*, 2016). A global Moran's I index was
266 calculated for each epidemiological metric and tested against the null hypothesis of an absence of
267 phylogenetic signal. Phylogenetic correlograms were then constructed to visualise the distribution of
268 this index over a gradient of phylogenetic distances and its confidence envelope based on
269 bootstrapping (1,000 repetitions). The local Moran's index I_i was also plotted alongside the
270 phylogeny to locate autocorrelation patterns more precisely through LIPA analysis. The existence of
271 local phylogenetic signals was assessed in a permutation-based test (999 repetitions).
272

Results

Global incidences of esca and dieback and changes over time

The mean incidence of esca foliar symptoms, for all cultivars, blocks, and years, was 7.3% (standard deviation, SD = 13.6%), with considerable variability (relative standard deviation, RSD = 185.4 %; Table 1). The mean cumulative incidence of esca foliar symptoms (i.e. observed in at least one year) was 30.5%, implying that almost one vine in three expressed esca foliar symptoms in at least one year. This value is five times higher than the mean annual incidence (Table 1). Foliar symptom severity had a mean score of 2.5 and was much less variable than the incidence of foliar symptoms (RSD = 59.4%; Table 1). Plant dieback had a mean incidence of 4.1%, which is lower than that of foliar symptom incidence by a factor of 1.8, but was much more variable (RSD = 233.0%; Table 1). An analysis of the declining vines showed that 16% expressed apoplexy on a single arm, 51% had a single dead arm, and 33% were totally unproductive (i.e. 11% totally apoplectic, 18% totally dead, and 4% with both phenotypes).

287 **Table 1. Overall statistics for esca and dieback epidemiological metrics in the VitAdapt**
288 **common garden experimental vineyard (Villenave d'Ornon, France) between 2017 and 2023**

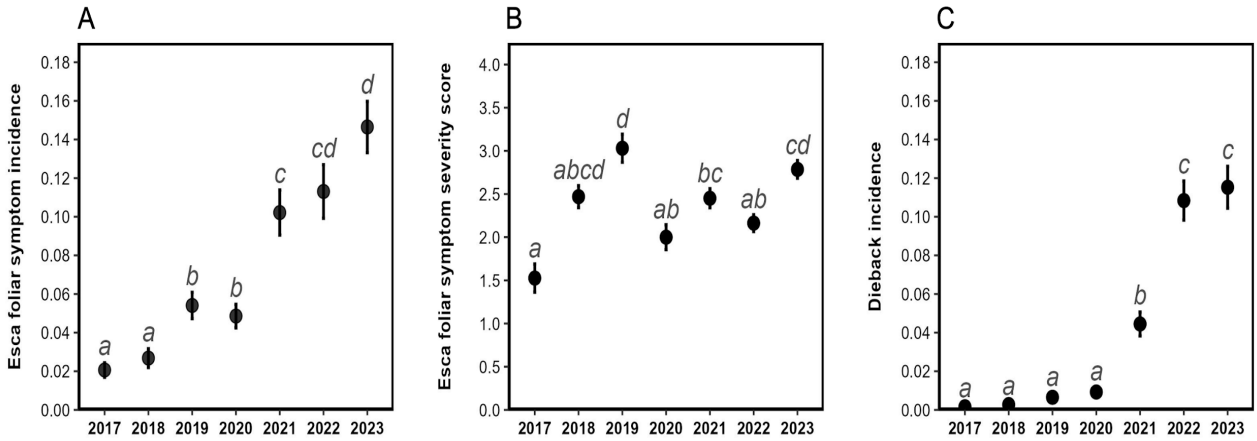
289 The statistics given are means, standard deviation, relative standard deviation, minimum and
290 maximum. Values are calculated for 1288 observations (46 cultivars; four blocks; seven years). The
291 severity index ranged from 1 (light esca foliar symptom on a single arm) to 5 (severe esca foliar
292 symptom on both arms) and was scored only for plants with symptoms.

Trait	Statistical individual	mean	SD	RSD	min	max
Foliar symptom incidence	Observation (*n*=1288)	7.3%	13.6%	185.4%	0.0%	90%
Cumulative incidence over seven years	Cultivar (*n*=46)	30.5%	24.0%	74.4%	0.0%	78.5%
Foliar symptom severity index	Observation (*n*=858)	2.5	1.5	59.4%	1.0	5.0
Dieback incidence	Observation (*n*=1288)	4.1%	9.6%	233.0%	0.0%	71.4%

293

294 The incidences of esca and dieback increased significantly between 2017 and 2023, with the ageing
295 of the plot (from 7.8 to 13.8 years old on average). This temporal effect was highly significant for the
296 incidence of foliar symptoms ($p < 10^{-16}$). The incidences of esca and dieback in 2021 and 2022 were
297 significantly higher than those in the previous four years, with mean values almost six times higher
298 than those obtained in 2017. Finally, the highest incidences occurred in 2023, when the mean
299 incidence of foliar symptoms was more than seven times higher than that in 2017 (Figure 2A). A
300 similar pattern was observed for the incidence of dieback ($p < 10^{-16}$). Plant dieback rates were very
301 low during the first four years of monitoring, between 0% and 1%. The proportion of unproductive
302 plants was greatest in 2022 and 2023, when it was significantly higher than in all other years (Figure

303 2C). The severity of esca foliar symptoms also differed significantly between years ($p = 10^{-11}$).
304 However, severity did not follow a specific temporal pattern similar to that for incidence (Figure 2B).



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306 **Figure 2. Changes over time in the three variables related to esca foliar symptoms and dieback**
307 **for all cultivars from 2017 to 2023 (mean plant age increasing from 7.8 years in 2017 to 13.8**
308 **years in 2023)**

309 (A) Incidence of foliar symptoms of esca (mean ± SEM); (B) Severity of esca foliar symptoms
310 (mean ± SEM), i.e. mean severity index (according to the rating scale described in Supplementary
311 Table S2) calculated on the set of symptomatic plants; (C) Incidence of plant dieback (mean ± SEM).
312 The letters correspond to the groups of significance according to Tukey tests with an alpha risk of
313 5%.

314

315 **Esca incidence differs considerably between cultivars**

316 The incidence of esca foliar symptoms differed significantly between the 46 cultivars monitored from
317 2017 to 2023 ($p < 10^{-16}$). We found a large gradient of susceptibility to esca foliar symptoms, as four
318 grape varieties (Merlot, Petit Manseng, Tannat and Xinomavro) never expressed symptoms during
319 the seven years of monitoring whereas eight cultivars (Cabernet-Sauvignon, Castets, Tempranillo,

320 Sauvignon Blanc, Cabernet Franc, Mourvèdre, Saperavi and Chenin) had mean annual incidences
321 above 20% (Figure 3A).

322 Excluding the four cultivars with an overall incidence of zero, cumulative incidence ranged from
323 2.5% to 85%, and was 2.7 to 7 times higher than the mean incidence according to the cultivar (Figure
324 3A). The cumulative incidence of esca was highly correlated with the incidence of foliar symptoms
325 ($r = 0.95$; $p < 10^{-16}$).

326 The severity of esca foliar symptoms differed significantly between cultivars ($p = 0.04$) but the
327 variability was lower than that for incidence (Figure 3B). Each cultivar presenting esca foliar
328 symptoms could display any degree of disease severity, regardless of its mean incidence of foliar
329 symptoms.

330 The incidence of plant dieback also differed significantly between cultivars ($p < 10^{-16}$). Four cultivars
331 (Muscadelle, Petit Manseng, Prunelard, Petit Verdot) had no apoplectic or dead arms. The maximum
332 incidence, exceeding 20%, was recorded for Saperavi. The distribution of dieback phenotypes
333 differed between cultivars. For example, Castets was characterised by a higher incidence of apoplectic
334 arms than of dead arms, whereas the opposite pattern was observed for Chasselas (Figure 3C).
335 Berry colour had no significant effect on the incidence of either esca foliar symptoms or plant dieback
336 ($p = 0.95$ and $p = 1$, respectively; Figure 3A and 3C).

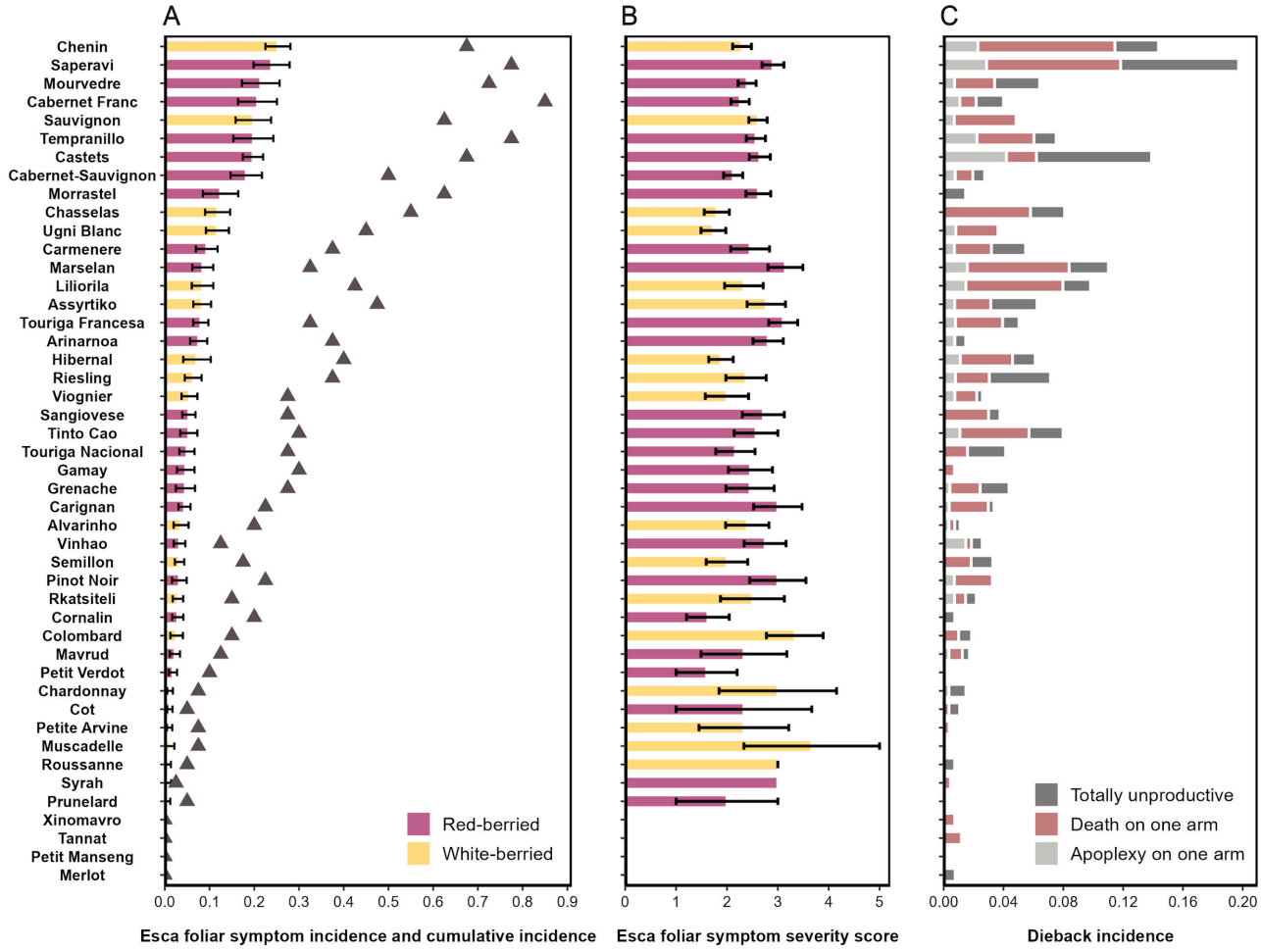

Figure 3. Variability of susceptibility to esca foliar symptoms and dieback among grapevine cultivars for the period 2017 to 2023.

(A) Mean incidence of esca foliar symptoms for the 46 cultivars monitored. Bars and error bars represent the means ± SEM and the grey triangles indicate the cumulative incidence over the seven years; (B) Range of severity of esca foliar symptoms in symptomatic plants only (mean ± SEM). The severity index, which ranged from 0 to 5, is described in Supplementary Material 2; (C) Range for the incidence of plant dieback. Light grey corresponds to plants with one apoplectic arm (total dehydration of the canopy). Red corresponds to plants with one dead arm. Dark grey corresponds to totally unproductive plants (apoplexy or death on both arms). Grapevine cultivars are ordered according to the mean incidence of foliar symptoms presented in (A). White-berried cultivars are shown in light yellow and red-berried cultivars are shown in dark purple.

Finally, the incidences of esca foliar symptoms and dieback were strongly correlated for each cultivar (r = 0.72; $p = 10^{-8}$; Supplementary Figure S2A). This relationship was strongest in years with an incidence of dieback of more than 4% (from 2021 to 2023), whereas it was marginal or non-significant in the preceding years (Figure 4). Despite this significant correlation, we were able to identify several cultivars with a greater expression of foliar symptoms than of dieback phenotypes, including Cabernet-Sauvignon, Sauvignon Blanc, Cabernet Franc and Morrastel. Several cultivars, including Castets, Marselan and Tinto Cao, displayed the opposite behaviour (Figure 3A and C).

By contrast, foliar symptom severity was not significantly correlated with either symptom incidence (r = 0.22, $p = 0.14$; Supplementary Figure S2B) or dieback incidence (r = 0.26, $p = 0.08$; Supplementary Figure S2C).

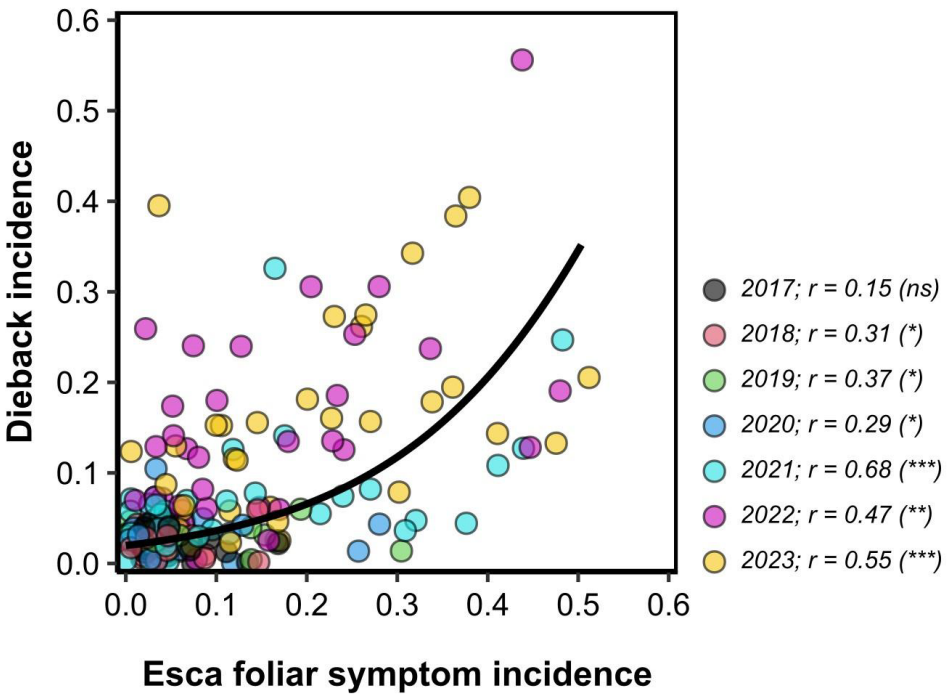

Figure 4. Relationship between the incidence of esca foliar symptoms and the incidence of dieback

Each dot corresponds to the value for a cultivar monitored during a single year. The regression line corresponds to a binomial model with a cloglog link fitted for all years (estimate = 6.11; $p < 10^{-16}$). Dots are coloured according to the year.

The relationships between varietal patterns of susceptibility and genetic distances between cultivars are of borderline significance

Ward's genetic distances were calculated to test for the existence of a phylogenetic signal in the epidemiological metrics. The clustering based on these distances was highly consistent with known cultivar lineages. For esca foliar symptom incidence, a significant phylogenetic signal was highlighted at global level (I = -0.10; $p = 0.03$). For this trait, phylogenetic autocorrelation values were positive for short phylogenetic distances (Figure 5A). However, this signal was not very robust, had an extremely wide confidence envelope, and was significant only for very short phylogenetic distances (Figure 5A). The distribution of the local Moran's index I_i over the phylogeny revealed two hotspots of phylogenetic positive autocorrelation (i.e. nodes at which the local Moran's index value I_i was significant) (Figure 5B): (i) a node of six cultivars with low incidences (Prunelard, Cot, Tannat, Petit Verdot, Petite Arvine, and Cornalin); (ii) a node of cultivars with high incidences, three of which displayed a significant signal (Sauvignon Blanc, Morrastel and Carmenere). By contrast, this method revealed no phylogenetic autocorrelation for either foliar symptom severity (I = -0.02; $p = 0.52$) or the incidence of dieback (I = -0.02; $p = 0.30$).

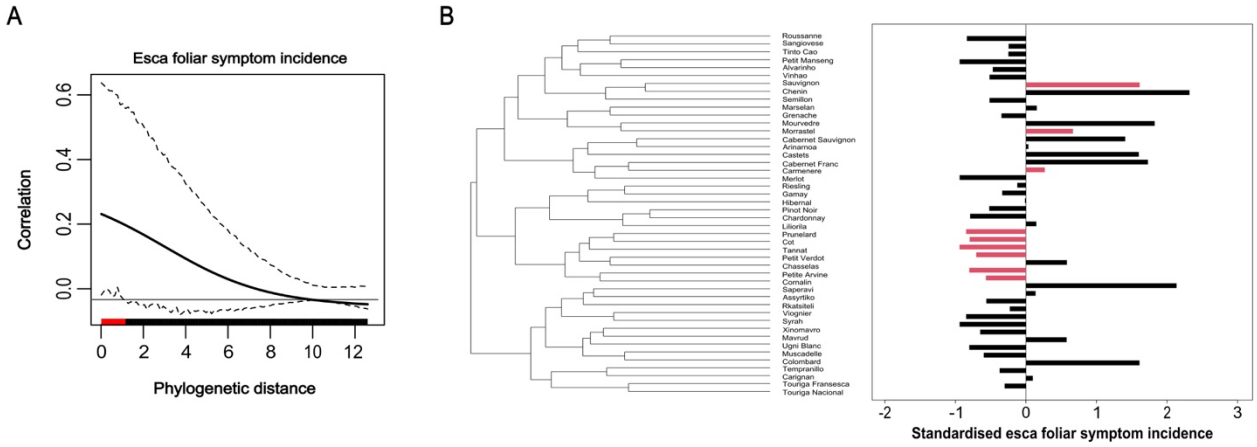

Figure 5. Relationship between genetic distance and the incidence of esca foliar symptoms for a panel of 46 grapevine cultivars

(A) Phylocorrelogram showing the change in Moran's I index (measuring phylogenetic autocorrelation) along a gradient of phylogenetic distances. Black lines represent Moran's I value. Dashed lines correspond to a confidence envelope at 95%, estimated from 1,000 bootstrap replicates. (B) Detection of the phylogenetic signal at a local scale over the phylogeny, by LIPA analysis. The dendrogram displaying genetic distances between cultivars is based on a set of 20 SSR markers. Bars correspond to standardised values (i.e. centred and scaled) for the mean incidence of esca foliar symptoms. Red bars correspond to tips for which the local Moran's index I_i was significant (i.e. $p < 0.05$ in a test based on permutations).

Varietal patterns of esca incidence remain constant over time

We investigated whether the incidence and severity of esca and plant dieback remained constant over time by performing two-by-two correlation analyses at cultivar level between the three epidemiological metrics, using the mean values for each of the six years of monitoring (a positive correlation indicates similar varietal patterns of incidence). For the incidence of foliar symptoms, all but one of the year-by-year correlations were clearly positive and significant, the exception being 2017 vs. 2022 (Figure 6A). For dieback incidence, all correlations were positive and all but five were

400 significant (Figure 6C). By contrast, no clear inter-annual correlation pattern was identified for foliar
401 symptom severity. Only three pairs of years displayed significant correlations, negative in one case
402 (2018 vs. 2019) and positive in the other two (2017 vs. 2022 and 2021 vs. 2023) (Figure 6B).

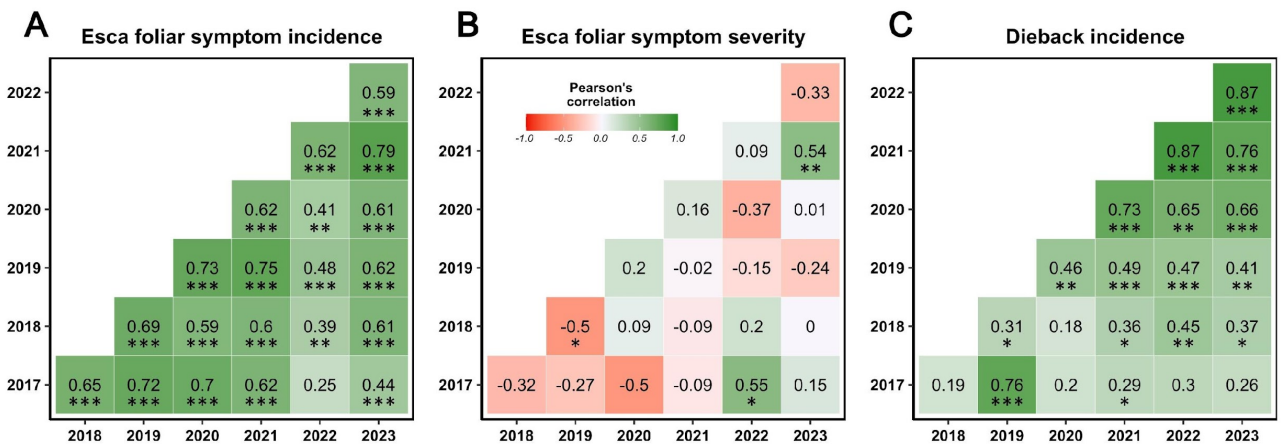

Figure 6. Inter-annual correlations of mean varietal values for the three variables related to esca foliar symptoms and dieback

(A) Foliar symptom incidence; (B) Severity of esca foliar symptoms, i.e. mean severity index (according to the rating scale described in Supplementary Material 2) calculated for the set of symptomatic plants; (C) Plant dieback incidence. Pearson's correlation coefficients marked with asterisks are significant at the 5% level; *: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$.

A low incidence of esca is associated with high water use efficiency and low vigour at cultivar scale

The relationships between the three epidemiological metrics and cultivar characteristics were explored by measuring six phenological and ecophysiological traits in the same vineyard: bud burst, flowering and veraison dates, $\delta^{13}C$, N-tester values at flowering, and pruning weight. The variability of these traits is presented in Supplementary Table S4. Globally, the range of variability for these traits was narrow, with RSD values ranging from 3.6% (for veraison date) to 30.2% (for pruning weight). Flowering date was positively correlated with both bud burst and veraison dates (r = 0.6 and r = 0.5, respectively; Supplementary Figure S3); we therefore retained flowering date as the only phenological variable.

421 Correlations between the mean values of the three epidemiological metrics and these four other
422 phenotypic traits were tested at cultivar level for the period 2017-2022 (Figure 7). $\delta^{13}C$ value at
423 harvest was significantly negatively correlated with foliar symptom expression, albeit weakly
424 (r = 0.33; $p = 0.03$; Figure 7A). Similarly, this trait was significantly negatively correlated with
425 dieback incidence (r = -0.32; $p = 0.03$; Figure 7I). In other words, cultivars with high water-use
426 efficiency (i.e. a less negative $\delta^{13}C$) were less susceptible to the expression of esca foliar symptoms
427 and dieback phenotypes. However, when this relationship was considered for each year separately,
428 the correlation between $\delta^{13}C$ and the incidence of foliar symptoms was significant only for 2022
429 (Supplementary Figure S4).

430 The relationship between the incidence of foliar symptoms and cultivar pruning weight was positive,
431 but not significant (r = 0.22; $p = 0.14$; Figure 7B). Despite the weak nature of this relationship, none
432 of the least vigorous cultivars had a high incidence of foliar symptoms.

433 There was a moderate negative correlation between these two ecophysiological traits ($\delta^{13}C$ and
434 pruning weight) at cultivar level (r = -0.49; $p = 10^{-5}$; Supplementary Figure S3).

435 N-tester values at flowering and cultivar phenology (flowering date) were not significantly correlated
436 with any of the three epidemiological metrics (Figure 7). All 12 correlations presented in Figure 7
437 were also tested at the subplot scale and similar trends were observed (*data not shown)*.

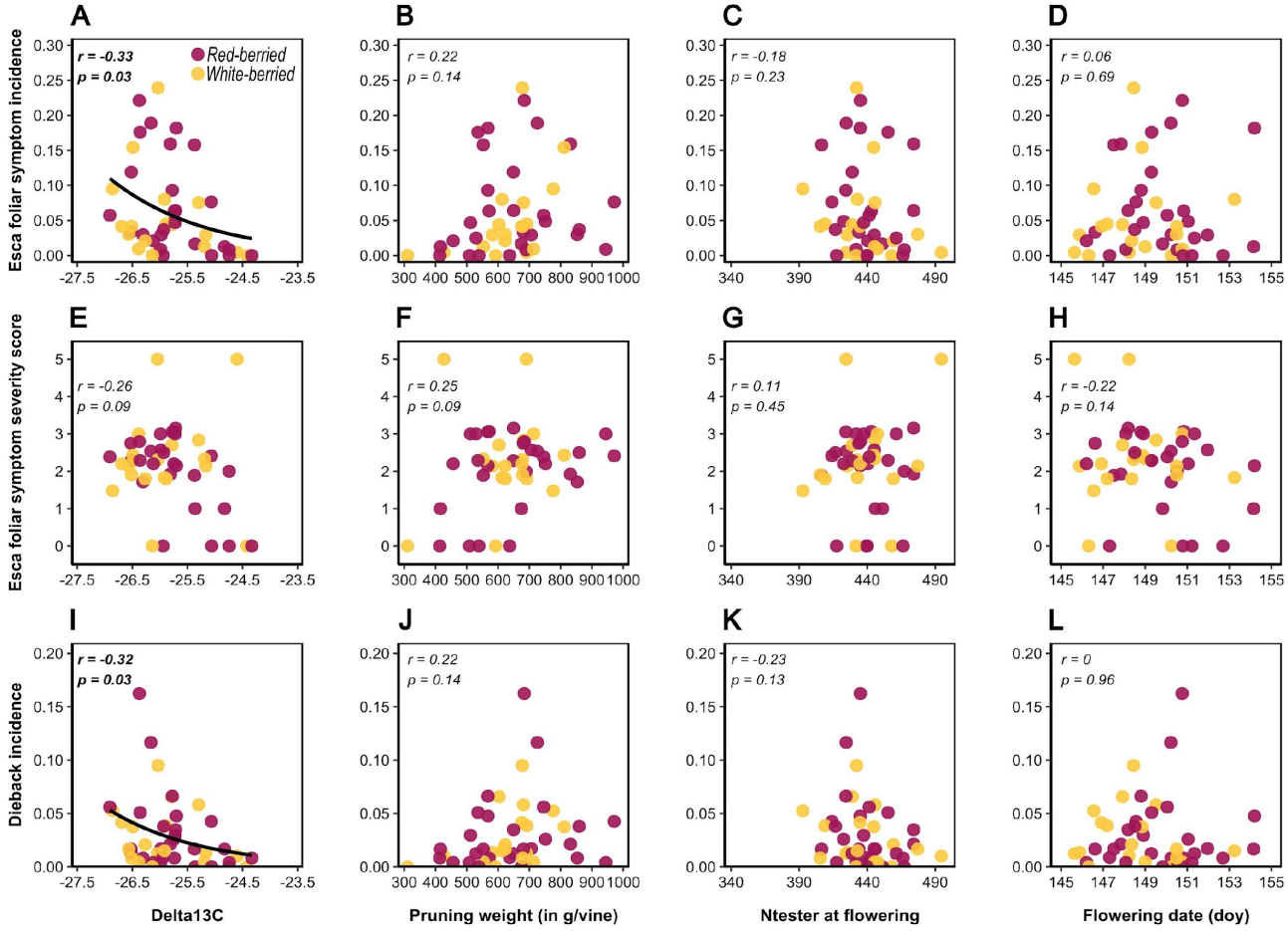

Figure 7. Relationships between three variables related to esca foliar symptom and dieback and four ecophysiological and phenological traits

Each dot corresponds to the value for a specific cultivar averaged over all years and blocks for the period 2017-2022. Pearson's correlation coefficients are indicated for each relationship. The regression line is provided for significant correlations only and corresponds to a binomial model with a cloglog link as follows: (A) estimate = -0.61; $p < 10^{-16}$; (E) estimate = -0.63; $p = 10^{-11}$. White-berried cultivars are shown in light yellow and red-berried cultivars are shown in dark purple.

447 ## Discussion

448 In this study, we used a unique common garden experimental vineyard to assess inter-variety
449 variability in the expression of the vascular disease esca in grapevine. Our results indicate diverse
450 patterns of disease susceptibility among cultivars, with some cultivars displaying no foliar symptoms
451 in any of the seven years studied and others highly susceptible. We also identified key
452 ecophysiological traits correlated with susceptibility to esca disease, such as cultivar water use
453 efficiency (WUE) and vigour.

454 The results obtained with VitAdapt indicate that there is a high level of fairly stable cultivar-
455 associated variability in terms of esca expression. The long-term monitoring of the VitAdapt common
456 garden experimental vineyard revealed a significant variability of esca foliar symptoms and plant
457 dieback between the 46 grapevine cultivars. Several cultivars, only very rarely expressed foliar
458 symptoms or dieback phenotypes, whereas others, including several of high economic importance,
459 were much more strongly affected by esca and dieback. The use of a common garden design, even
460 with a limited number of plants per cultivar (n = 40), and the inclusion of a block effect in statistical
461 models, made it possible to prevent biases in the calculation of esca incidence due to the variability
462 of soils and viticulture practices. Our results provide new information for consideration in the
463 discussions of cultivar rankings for esca susceptibility obtained in previous multiregional and multi-
464 cultivar monitoring programmes. For example, Ugni Blanc, for which very high incidences were
465 recorded in the Charentes region (France; Bruez *et al.*, 2013), did not cluster among the most
466 susceptible cultivars in our vineyard, in which all cultivars were subjected to the same environment
467 and the same viticulture practices (e.g. double guyot pruning system). Bruez *et al.* (2013) showed
468 that, for a given cultivar, a large proportion of the residual variability is due to the growing area.
469 There are at least two possible explanations for this. First, there can be considerable climatic variation
470 between regions. Second, the incidence of esca disease may be affected by differences in viticulture

471 systems and practices from between regions (Lecomte *et al.*, 2018). This may be the case for Ugni
472 Blanc, which was analysed here in growth conditions different from those applying to productive
473 contexts in the Charentes region (France), where it is cultivated for the production of Cognac.

474 Our findings clearly confirmed a number of well-known trends, such as the large differences between
475 elite international cultivars, with Merlot (no foliar symptoms at all from eight to 14 years of age),
476 Syrah and Pinot Noir displaying low levels of susceptibility to esca, whereas Cabernet-Sauvignon,
477 Sauvignon Blanc, and Tempranillo were highly susceptible (consistent with the findings of Martínez-
478 Diz *et al.*, 2019; Csótó *et al.*, 2023). However, they also provide integrative ecophysiological and
479 esca susceptibility data for lesser-known varieties with promising tolerance to abiotic and biotic
480 stresses. For example, Xinomavro, which never expressed esca in our vineyard, was classified as
481 drought-tolerant by Plantevin *et al.* (2022) and is one of the latest ripening variety in VitAdapt (i.e. it
482 is comparable to Grenache and Carignan, *data not shown*). Conversely, Saperavi was found to be
483 highly prone to the expression of esca and dieback (apoplexy and death), and was also classified as
484 susceptible to drought (Plantevin *et al.*, 2022; Lamarque *et al.*, 2023). More detailed studies are now
485 required to determine whether these preliminary findings are also valid for other commercial clones
486 of these cultivars, and for combinations with different rootstocks, in contrasting productive contexts.
487 More generally, the extent to which esca expression varies between different clones of a single
488 cultivar remains unclear (Murolo and Romanazzi, 2014; Moret *et al.*, 2019). Zooming out to consider
489 the entire pool of *Vitis* spp. might also be promising, to move towards the integration of susceptibility
490 to trunk diseases as a key trait while selecting and planting both rootstocks (Gramaje *et al.*, 2010;
491 Murolo and Romanazzi, 2014) and hybrid cultivars. Here, the only hybrid variety studied, Hibernal,
492 was found to be of intermediate susceptibility. Comparing 104 interspecific hybrids of diversified
493 pedigrees with 201 *V. vinifera* cultivars, Csótó *et al.* (2023) demonstrated that the interspecific
494 hybrids were globally less susceptible to trunk diseases.

495 A global increase in esca expression was recorded over the course of the trial, for both foliar
496 symptoms and plant dieback, probably due to the ageing of the plants (from 8 years old at the start of
497 monitoring to 14 years old). The incidence of esca disease is known to increase when the plants are
498 about 10 years of age, generally reaching a maximum in plants between the ages of 15 and 25 years
499 (Kovács *et al.*, 2017; Etienne *et al.*, 2024). Moreover, our data confirm that the cumulative incidence
500 of esca foliar symptoms was much higher than the mean annual incidence, implying that, for a given
501 subplot, the vines presenting foliar symptoms of esca differ between years. These results, alongside
502 with previous findings, clearly indicate that it is essential to perform monitoring over several years
503 for field trials (Reis *et al.*, 2019).

504 Even though the incidence of esca increased over time, the relative ranking of the varieties remained
505 constant between years. As all cultivars were compared in similar environmental conditions, this
506 suggests that each cultivar has a constitutive level of susceptibility that is little affected by local
507 variations of esca disease pressure (which are, in turn, influenced by several traits relating to
508 pathogens, plants and environment; Claverie *et al.*, 2020). A first genetic locus associated with
509 grapevine susceptibility to fungal trunk pathogens was recently identified in *V. vinifera* cv.
510 'Gewurztraminer', based on internal symptoms (proportions of total necrosis and white rot) rather
511 than the monitoring of foliar symptoms and dieback (Arnold *et al.*, 2023). However, anatomical and
512 physiological traits may contribute to cultivar susceptibility. A high density of large vessels
513 (>100 µm) has been associated with enhanced susceptibility to *P.chlamydospora* following artificial
514 inoculation (Pouzoulet *et al.*, 2020). Based on the results of studies on very small numbers of
515 cultivars, we can also hypothesise that wood composition (see Rolshausen *et al.*, 2008 for *Eutypa*
516 *lata*, another fungal pathogen of wood) and secondary metabolism (see Lemaitre-Guillier *et al.*, 2020
517 for *Botryosphaeria* sp. diseases) may have an effect. Another non-mutually exclusive hypothesis

518 would be the existence of interspecific and intraspecific diversity in the microbial communities
519 interacting with different cultivars during plant pathogenesis (Laveau *et al.*, 2009; Bekris *et al.*, 2021).

520 As the genetic proximity between plant species and populations is often associated with common
521 susceptibilities to pathogens and pests (Gilbert *et al.*, 2015), we tested the hypothesis of closely
522 related cultivars having similar patterns of susceptibility to esca. We found a significant but weak
523 phylogenetic signal for esca susceptibility based on the incidence of foliar symptoms. This signal was
524 associated exclusively with local nodes of closely related cultivars and was similar for all four
525 clustering methods tested *(data not shown)*. This signal was not as robust as that likely to arise at
526 broader levels of grouping, and may be strongly affected by the choice of genetic markers. Based on
527 a local-scale analysis, the main hotspots of phylogenetic signal corresponded to a group of weakly
528 susceptible cultivars. Pedigrees were available for only two of these six cultivars, Cot being an
529 offspring of Prunelard in the VIVC. The relationships between the remaining varieties were less clear,
530 and they even came from contrasting locations (Bacilieri *et al.*, 2013). We can hypothesise that traits
531 reducing susceptibility to esca in grapevine cultivars are converging within this group of interest.
532 Susceptible cultivars were overrepresented at another node of the phylogeny: Sauvignon Blanc,
533 Chenin, Marselan, Mourvedre, Morrastel, Cabernet-Sauvignon, Castets, Cabernet Franc, Carmenere.
534 All these cultivars originate from Western and Central Europe, with six originating from South-
535 Western France (Bacilieri *et al.*, 2013). Most belong to the Savagnin and Cabernet Franc families.
536 Nevertheless, the signal on these branches appeared unstable (i.e. significant for only three cultivars).
537 Moreover, phylogenetic correlation did not apply to all members of a group or lineage, as represented
538 in the vineyard studied. Thus, despite promising findings, it is difficult to conclude that esca
539 susceptibility is clearly driven by phylogenetic patterns. Here, the genetic panel studied consisted of
540 cultivars belonging from a single species, *V. vinifera* L. (with the exception of the *Vitis* sp. hybrid
541 'Hibernal') and was not truly representative of the overall diversity of grapevine. The search for

542 genetic markers of trunk disease incidence would probably benefit from studies of specifically
543 designed diversity panels (e.g. Nicolas *et al.*, 2016).

544 Interestingly, the incidences of foliar symptoms and dieback were strongly and consistently correlated
545 between cultivars and years. This suggests that the cultivars with a high incidence of esca were also
546 those with a high proportion of apoplectic or dead plants. This finding echoes the work of Guérin-
547 Dubrana *et al.* (2013) in the Bordeaux region, which showed that, in Cabernet-Sauvignon, mortality
548 was higher in plants that had expressed esca symptoms in previous years. Nevertheless, other studies
549 have shown that this correlation is not always valid at plant level in individual cultivars. For instance,
550 Andreini *et al.* (2014) noted a discordance between esca symptom expression and plant mortality,
551 especially for Cabernet-Sauvignon. Dewasme *et al.* (2022) suggested that the impact of esca on the
552 mortality of this cultivar might be overestimated. Investigations of the mechanisms underlying foliar
553 symptoms and plant decline, especially at vascular level, would be a promising approach to clarifying
554 this issue.

555 Conversely, a lack of correlation was noted between the metrics reflecting disease incidence and those
556 reflecting the severity of foliar symptoms. There was also no clear varietal or temporal pattern for
557 foliar symptom severity. We hypothesise that a number of different mechanisms and factors underlie
558 these differences in severity levels. The link between incidence and severity has long been called into
559 question in plant science. These two traits are known to be positively correlated for a large number
560 of airborne fungal diseases (Seem, 1984). Nevertheless, no such relationship would be expected for
561 wilt diseases with symptoms occurring in organs (here, in leaves) distal to the infection area (here,
562 woody organs; Seem, 1984). Few studies have specifically tested this hypothesis for trunk disease
563 pathosystems, although several previous studies concluded that there was a positive correlation
564 between incidence and severity in a single (Calzarano *et al.*, 2018) or multiple cultivars (Romanazzi
565 *et al.*, 2009).

566 There have been many studies of the impact of esca disease on grapevine physiology, including plant
567 growth (Gramaje *et al.*, 2010; Dell'Acqua *et al.*, 2023), photosynthesis, water relations (Magnin-
568 Robert *et al.*, 2011; Bortolami *et al.*, 2021a,b), and phenology (Andreini *et al.*, 2013), but very little
569 effort has, as yet, been devoted to the opposite issue: the ecophysiological traits predicting esca
570 incidence or severity. Here, we found that a low incidence of esca appeared to be associated with high
571 water use efficiency and low vigour at the cultivar scale. At this same scale, $\delta^{13}C$ levels were
572 significantly negatively related to the incidences of both foliar symptoms and dieback. This indicator,
573 averaged over several years of contrasting water availability, is used as a proxy for varietal WUE
574 (Bchir *et al.*, 2016). Cultivars with higher WUE, likely associated with lower levels of stomatal
575 opening (Bota *et al.*, 2016), were found to be less prone to the expression of esca symptoms. The
576 underlying mechanism may be at least partly related to that proposed by Bortolami *et al.* (2021b) to
577 elucidate the antagonistic effects of drought and esca. Genotypes with a high WUE control their
578 transpiration much more strongly, thereby slowing the translocation of toxins from the trunk to the
579 leaves via the vascular apparatus. Di Marco and Osti (2008) drew similar conclusions for wood decay
580 in kiwifruit (*Actinidia deliciosa* var. deliciosa). However, in our case, this relationship was found to
581 be unstable over time. The strongest correlation was observed in 2022, a year combining high esca
582 intensity and low water availability. Indeed, it is known that the differences in WUE between varieties
583 can be exacerbated by drought conditions (Plantevin *et al.*, 2022), particularly when different plant
584 genotypes are planted in the same vineyard.

585 Water availability is considered a driver of esca disease expression. High water levels are considered
586 to activate esca expression (Bortolami *et al.*, 2021b; Monod *et al.*, 2023). In this study, the overall
587 increase in esca incidence over time (with the ageing of the vines) made it difficult to decipher
588 precisely the role of the water conditions in each year. Our findings suggest that, in our experimental
589 context, plant age makes a much greater contribution to esca incidence than plant water use. Etienne

590 *et al.* (2024) demonstrated that esca incidence reaches its maximum between 15 and 39 years old, for
591 most of the cultivars. Several factors related either to fungal colonisation (e.g. number of infection
592 cycles, wood microbiome) or to plant defence response (e.g. metabolism, wood properties) may
593 potentially explain these differences related to plant age (Dissanayake *et al.*, 2018; Fischer and
594 Peighami-Ashnaei, 2019).

595 The least vigorous cultivars appear to be grouped among the cultivars least susceptible to esca. This
596 relationship has already been suggested for trunk diseases, but never clearly demonstrated. It may
597 reflect the narrower xylem vessels of less vigorous vines, increasing compartmentalisation efficiency
598 and decreasing susceptibility to wood pathogens (Pouzoulet *et al.*, 2020). We found that $\delta^{13}C$ levels
599 and pruning weight were negatively correlated. In particular, a set of weakly susceptible cultivars of
600 low vigour were found to have less negative values for $\delta^{13}C$ (e.g. Petit Manseng, Tannat, Mavrud,
601 Colombard). We suggest that the tandem action of these two traits in the prediction of esca incidence
602 is not a coincidence. As discussed in previous studies, these cultivars are more able to decrease their
603 hydraulic conductivity markedly and rapidly in response to non-optimal water conditions, thus
604 ensuring larger hydraulic safety margins but constraining plant growth and productivity (Torrez-Ruiz
605 *et al.*, 2024). Nevertheless, this relationship is ambiguous, and depends on water availability. Our
606 findings are consistent with those of Tambussi *et al.* (2007), who found that, for common cereals,
607 plants with a lower WUE have a competitive advantage for growth and productivity in climates with
608 rainfall occurring during the growing season (here, a temperate oceanic climate).

609 Esca disease expression is also considered to be positively correlated with leaf nitrogen status
610 (Calzarano *et al.*, 2009; Li, 2015) through a roughly twofold mechanism that has already been
611 discussed for plants (e.g. Mur *et al.*, 2017; Sun *et al.*, 2020) involving modifications to plant
612 metabolism (e.g. enhanced vigour) and a favouring of fungal development and pathogenicity. In our
613 experimental vineyard, normalised nitrogen index was not a determinant of varietal susceptibility to

614 esca. As nitrogen status and vigour were only weakly correlated in this dataset (Supplementary
615 Material 7), it seems likely that the variability of nitrogen status was limited in this trial, potentially
616 accounting for the lack of correlation between vine nitrogen status and esca symptoms. This result
617 and those of Monod *et al.* (2023), who demonstrated a negative correlation between nitrogen status
618 and esca severity in a single cultivar growing in contrasting conditions, claim for more research,
619 across a wide range of genotypes and growing conditions, to explore the link between vine mineral
620 status and the incidence of trunk diseases.

621 Finally, we found no significant effect of phenology on the variability of esca expression between
622 varieties. There have been few studies of the links between trunk diseases and phenology. Serra *et al.*
623 (2018) assumed that phenology affects esca expression in relation to climatic variables. As foliar
624 symptoms emerge only between fruit set and veraison and accumulate through the summer season in
625 a systematic progressive sigmoidal pattern (Lecomte *et al.*, 2024), we can hypothesise that varietal
626 shifts in phenological stage may influence cultivar-specific patterns of esca expression, particularly
627 when climatic conditions fluctuate sharply. Monitoring over a time scale finer than one year would
628 improve our understanding of the interaction between grapevine phenology and disease dynamics.

629 Conclusion

630 This study, making use of a unique experimental facility, adds to our knowledge of the contribution
631 of genetic diversity to the sustainable management of grapevine dieback. Our findings confirm the
632 utility of performing pluriannual monitoring in natural conditions, within common garden
633 experimental vineyards, for accurate comparisons of susceptibility to trunk diseases between
634 cultivars. The ranking of varieties for susceptibility, based on the incidence of esca foliar symptoms,
635 was consistent with the findings of a previous field trial conducted in Italy (Murolo and Romanazzi,
636 2014; Figure 8A). A weaker correlation was also identified with the ranking obtained in a network of

French vineyards (Figure 8B). Correlations were tested with the ranking of varietal susceptibility to other grapevine diseases. The susceptibility to *flavescence dorée*, caused by a phytoplasma, was significantly correlated with esca susceptibility (eight cultivars in common with VitAdapt; $\tau = 0.76$; $p = 10^{-3}$; Eveillard *et al.*, 2016), while the susceptibility to the fungal trunk disease Eutypa dieback was not (29 cultivars in common; $\tau = 0.23$; $p = 0.11$; Sosnowski *et al.*, 2022). No correlation was found on VitAdapt between the incidence of esca foliar symptoms and the incidence of symptoms associated with *Botrytis cinerea* (an aerial necrotrophic fungus) on bunches at harvest (22 cultivars in common; $\tau = -0.22$; $p = 0.15$; Paňitrur-De La Fuente *et al.*, 2018). Interestingly, no correlation was found between the ranking of varieties for the incidence of esca foliar symptoms in VitAdapt and the susceptibility gradients obtained by artificially inoculating cuttings with wood pathogens such as *P. chlamydospora* (Pouzoulet *et al.*, 2020; Figure 8C) or *Neofusicoccum parvum* (*unpublished data*; Figure 8D). This confirms that the susceptibility of grapevine genotypes to trunk diseases cannot be assessed solely on the basis of inoculations under control conditions, as already discussed by several authors (e.g. Sosnowski *et al.*, 2007; Reis *et al.*, 2019).

Furthermore, susceptibility to trunk diseases is potentially plastic in response to the environment. To facilitate the selection of the most suitable cultivars for each production context, it therefore seems necessary to combine (i) replication of such monitoring under contrasting conditions and (ii) modelling-based approaches, integrating epidemiological, physiological and pedoclimatic variables. Within this framework, a complementary strategy would involve monitoring a single cultivar in multiple environments (see Monod *et al.*, 2023). Finally, we recommend tackling the highly multifactorial nature of plant dieback through integrative approaches taking multiple factors, such as other pests and diseases, climatic hazards, soil fertility and technical management, into account.

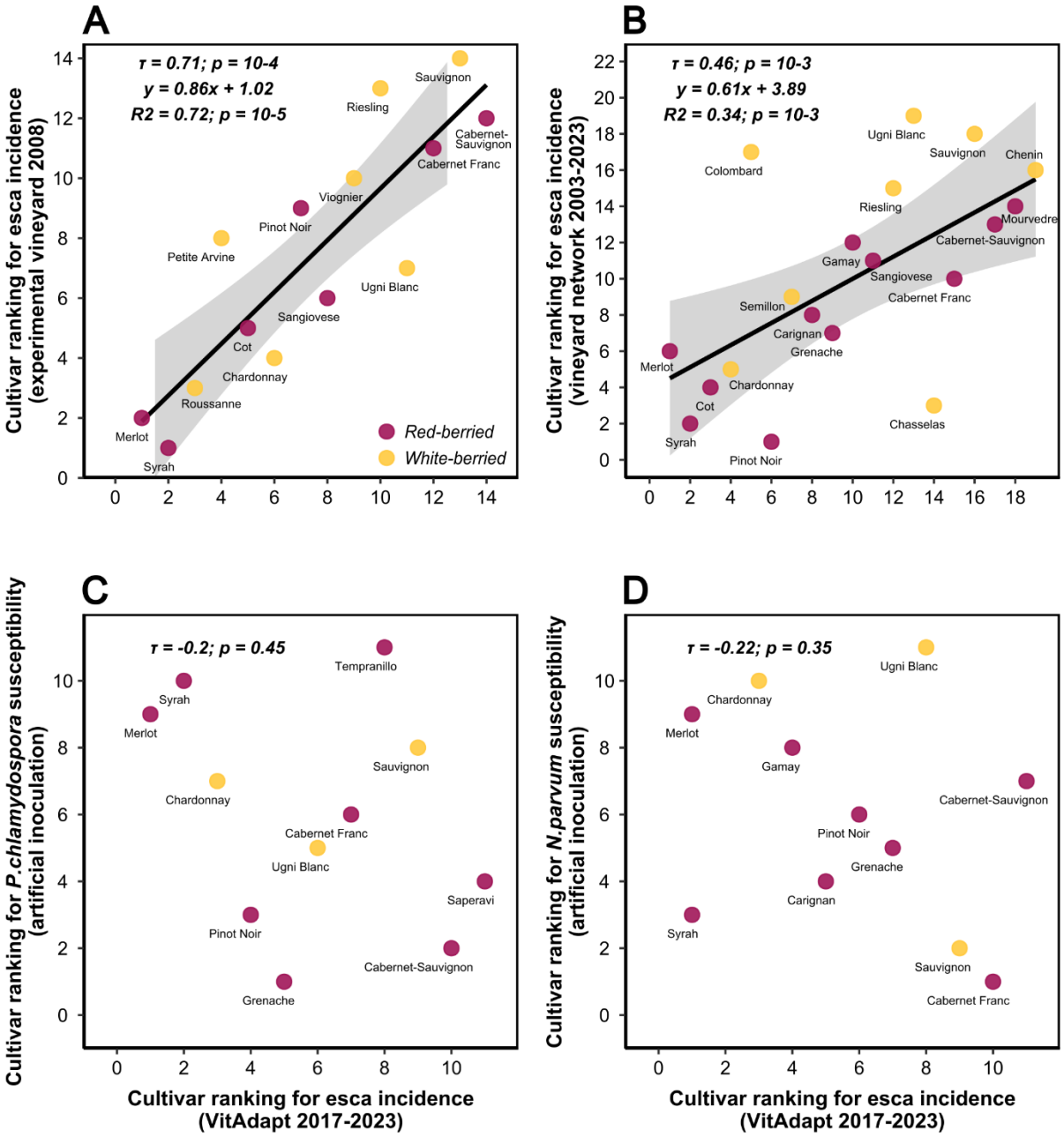

Figure 8. Scatterplots showing the relationships between cultivar ranks for susceptibility to esca and wood pathogens as assessed in this work and reported in previous publications.

Each dot corresponds to the ranking of a cultivar in a given study, for the range of cultivars common to the two studies compared. (A) Relationship between the cultivar rankings obtained in this study

and those obtained by Murolo and Romanazzi (2014) in a one-year (2008) study monitoring of esca foliar symptom expression in an experimental vineyard in Italy (14 cultivars common to the two studies). The regression line corresponds to a linear model, and the standard error is provided; (B) Relationship between the cultivar rankings obtained in this study and those obtained by Etienne *et al.* (2024), in a study over six years (2003-2023) monitoring esca foliar symptom expression in a network of 2084 vineyards located in French grape-producing areas (19 cultivars common to the two studies); (C) Relationship between the cultivar rankings obtained in this study and those obtained by Pouzoulet *et al.* (2020) by phenotyping the length of stem necrosis induced by *Phaeomoniella chlamydospora* after 12 weeks of incubation (11 cultivars common to the two studies). Rank-based Kendall's correlation coefficients are indicated for each relationship; (D) Relationship between the cultivar rankings obtained in this study and those obtained by phenotyping the length of stem necrosis induced by *Neofusicoccum parvum* after 28 weeks of incubation (*unpublished data;* 11 cultivars common to the two studies). Rank-based Kendall's correlation coefficients are indicated for each relationship.

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Competing Interests statement

The authors have no competing interests to declare.

References

Anderson, K., & Aryal, N. R. (2013). *Which Winegrape Varieties are Grown Where? : A global empirical picture*. University of Adelaide Press. https://www.jstor.org/stable/10.20851/j.ctt1t304tz

Andreini, L., Cardelli, R., Bartolini, S., Scalabrelli, G., & Viti, R. (2014). Esca symptoms appearance in *Vitis vinifera* L. : Influence of climate, pedo-climatic conditions and rootstock/cultivar combination. *Vitis*, *53*(1), 33-38.

Andreini, L., Guarino, L., Viti, R., & Scalabrelli, G. (2013). Evaluation of the effect of esca disease on bud break in *Vitis vinifera* L. : Possible relationship between cultivars and rootstocks. *VITIS - Journal of Grapevine Research*, 52(1), 33-40. https://doi.org/10.5073/vitis.2013.52.33-40

Arnold, G., Prado, E., Dumas, V., Butterlin, G., Duchêne, E., Avia, K., & Merdinoglu, D. (2023). *Discovery of a locus associated with susceptibility to esca dieback in grapevine* (p. 2023.10.20.563213). bioRxiv. https://doi.org/10.1101/2023.10.20.563213

Bacilieri, R., Lacombe, T., Le Cunff, L., Di Vecchi-Staraz, M., Laucou, V., Genna, B., Péros, J.-P., This, P., & Boursiquot, J.-M. (2013). Genetic structure in cultivated grapevines is linked to geography and human selection. *BMC Plant Biology*, *13*(1), 25. https://doi.org/10.1186/1471-2229-13-25

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, *67*, 1-48. https://doi.org/10.18637/jss.v067.i01

Bchir, A., Escalona, J. M., Gallé, A., Hernández-Montes, E., Tortosa, I., Braham, M., & Medrano, H. (2016). Carbon isotope discrimination (δ13C) as an indicator of vine water status and water use efficiency (WUE) : Looking for the most representative sample and sampling time. *Agricultural Water Management*, *167*, 11-20. https://doi.org/10.1016/j.agwat.2015.12.018

Bekris, F., Vasileiadis, S., Papadopoulou, E., Samaras, A., Testempasis, S., Gkizi, D., Tavlaki, G., Tzima, A., Paplomatas, E., Markakis, E., Karaoglanidis, G., Papadopoulou, K. K., & Karpouzas, D. G. (2021). Grapevine wood microbiome analysis identifies key fungal pathogens and potential interactions with the bacterial community implicated in grapevine trunk disease appearance. *Environmental Microbiome*, *16*(1), 23. https://doi.org/10.1186/s40793-021-00390-1

Bortolami, G., Farolfi, E., Badel, E., Burlett, R., Cochard, H., Ferrer, N., King, A., Lamarque, L. J., Lecomte, P., Marchesseau-Marchal, M., Pouzoulet, J., Torres-Ruiz, J. M., Trueba, S., Delzon, S., Gambetta, G. A., & Delmas, C. E.

L. (2021a). Seasonal and long-term consequences of esca grapevine disease on stem xylem integrity. *Journal of Experimental Botany*, *72*(10), 3914-3928. https://doi.org/10.1093/jxb/erab117

Bortolami, G., Gambetta, G. A., Cassan, C., Dayer, S., Farolfi, E., Ferrer, N., Gibon, Y., Jolivet, J., Lecomte, P., & Delmas, C. E. L. (2021b). Grapevines under drought do not express esca leaf symptoms. *Proceedings of the National Academy of Sciences*, *118*(43), e2112825118. https://doi.org/10.1073/pnas.2112825118

Bortolami, G., Gambetta, G. A., Delzon, S., Lamarque, L. J., Pouzoulet, J., Badel, E., Burlett, R., Charrier, G., Cochard, H., Dayer, S., Jansen, S., King, A., Lecomte, P., Lens, F., Torres-Ruiz, J. M., & Delmas, C. E. L. (2019). Exploring the Hydraulic Failure Hypothesis of Esca Leaf Symptom Formation. *Plant Physiology*, *181*(3), 1163-1174. https://doi.org/10.1104/pp.19.00591

Boso, S., Alonso-Villaverde, V., Gago, P., Santiago, J. l., & Martínez, M. c. (2011). Susceptibility of 44 grapevine (*Vitis vinifera* L.) varieties to downy mildew in the field. *Australian Journal of Grape and Wine Research*, *17*(3), 394-400. https://doi.org/10.1111/j.1755-0238.2011.00157.x

Bota, J., Tomás, M., Flexas, J., Medrano, H., & Escalona, J. M. (2016). Differences among grapevine cultivars in their stomatal behavior and water use efficiency under progressive water stress. *Agricultural Water Management*, 164, 91-99. https://doi.org/10.1016/j.agwat.2015.07.016

Bruez, E., Baumgartner, K., Bastien, S., Travadon, R., Guérin-Dubrana, L., & Rey, P. (2016). Various fungal communities colonise the functional wood tissues of old grapevines externally free from grapevine trunk disease symptoms. *Australian Journal of Grape and Wine Research*, *22*(2), 288-295. https://doi.org/10.1111/ajgw.12209

Bruez, E., Lecomte, P., Grosman, J., Doublet, B., Bertsch, C., Fontaine, F., Ugaglia, A., Teissedre, P.-L., Costa, J.-P. D., Guerin-Dubrana, L., & Rey, P. (2013). Overview of grapevine trunk diseases in France in the 2000s. *Phytopathologia Mediterranea*, *52*(2), 262-275. https://doi.org/10.14601/Phytopathol_Mediterr-11578

Bruez, E., Vallance, J., Gautier, A., Laval, V., Compant, S., Maurer, W., Sessitsch, A., Lebrun, M.-H., & Rey, P. (2020). Major changes in grapevine wood microbiota are associated with the onset of esca, a devastating trunk disease. *Environmental Microbiology*, *22*(12), 5189-5206. https://doi.org/10.1111/1462-2920.15180

Bruez, E., Vallance, J., Gerbore, J., Lecomte, P., Costa, J.-P. D., Guerin-Dubrana, L., & Rey, P. (2014). Analyses of the Temporal Dynamics of Fungal Communities Colonizing the Healthy Wood Tissues of Esca Leaf-Symptomatic and Asymptomatic Vines. *PLOS ONE*, *9*(5), e95928. https://doi.org/10.1371/journal.pone.0095928

Calzarano, F., Amalfitano, C., Seghetti, L., & Cozzolino, V. (2009). Nutritional status of vines affected with esca proper. *Phytopathologia Mediterranea*, 48(1), 20-31. https://doi.org/10.14601/Phytopathol_Mediterr-2872

Calzarano, F., Osti, F., Baránek, M., & Di Marco, S. (2018). Rainfall and temperature influence expression of foliar symptoms of grapevine leaf stripe disease (esca complex) in vineyards. *Phytopathologia Mediterranea*, *47*, 488-505. https://doi.org/10.14601/Phytopathol_Mediterr-23787

Celette, F., & Gary, C. (2013). Dynamics of water and nitrogen stress along the grapevine cycle as affected by cover cropping. *European Journal of Agronomy*, *45*, 142-152. https://doi.org/10.1016/j.eja.2012.10.001

Claverie, M., Notaro, M., Fontaine, F., & Wery, J. (2020). Current knowledge on Grapevine Trunk Diseases with complex etiology : A systemic approach. *Phytopathologia Mediterranea*, *59*(1), 29-53. https://doi.org/10.36253/phyto-11150

Csótó, A., Nagy, A., Laurinyecz, N., Nagy, Z. A., Németh, C., Németh, E. K., Csikász-Krizsics, A., Rakonczás, N., Fontaine, F., Fekete, E., Flipphi, M., Karaffa, L., & Sándor, E. (2023). Hybrid *Vitis* Cultivars with American or Asian Ancestries Show Higher Tolerance towards Grapevine Trunk Diseases. *Plants*, *12*(12), 2328. https://doi.org/10.3390/plants12122328

Dayer, S., Lamarque, L. J., Burlett, R., Bortolami, G., Delzon, S., Herrera, J. C., Cochard, H., & Gambetta, G. A. (2022). Model-assisted ideotyping reveals trait syndromes to adapt viticulture to a drier climate. *Plant Physiology*, *190*(3), 1673-1686. https://doi.org/10.1093/plphys/kiac361

Dell'Acqua, N., Gambetta, G. A., Delzon, S., Ferrer, N., Lamarque, L. J., Saurin, N., Theodore, P., & Delmas, C. E. L. (2023). Mechanisms of grapevine resilience to a vascular disease : Investigating stem radial growth, xylem development, and physiological acclimation. *Annals of Botany*, 23, 1-15. https://doi.org/10.1093/aob/mcad188

Destrac-Irvine, A., Barbeau, G., Resseguier, L. de, Dufourcq, T., Dumas, V., Cortazar-Atauri, I. G. de, Ojeda, H., Saurin, N., Leeuwen, C. van, & Duchêne, É. (2019). Measuring the phenology to more effectively manage the vineyard. *IVES Technical Reviews, Vine and Wine*. https://doi.org/10.20870/IVES-TR.2019.2586

Destrac-Irvine A., van Leeuwen C. (2016). VitAdapt: an experimental program to study the behavior of a wide range of Vitis vinifera varieties in a context of climate change in the Bordeaux vineyards. Climwine, sustainable grape and wine production in the context of climate change, 11-13 April 2016, Bordeaux. Full text proceedings paper, 165-171.

Dewasme, C., Mary, S., Darrieutort, G., Roby, J.-P., & Gambetta, G. A. (2022). Long-Term Esca Monitoring Reveals Disease Impacts on Fruit Yield and Wine Quality. *Plant Disease*, *106*(12), 3076-3082. https://doi.org/10.1094/PDIS-11-21-2454-RE

Di Marco, S., & Osti, F. (2008). Foliar Symptom Expression of Wood Decay in *Actinidia deliciosa* in Relation to Environmental Factors. *Plant Disease*, *92*(8), 1150-1157. https://doi.org/10.1094/PDIS-92-8-1150

Etienne, L., Fabre, F., Martinetti, D., Frank, E., Michel, L., Bonnardot, V., Guérin-Dubrana, L., & Delmas, C. E. L. (2024). *Exploring the role of cultivar, year and plot age in the incidence of grapevine trunk diseases : Insights from 20 years of regional surveys in France* (p. 2024.03.19.585220). bioRxiv. https://doi.org/10.1101/2024.03.19.585220

Eveillard, S., Jollard, C., Labroussaa, F., Khalil, D., Perrin, M., Desqué, D., Salar, P., Razan, F., Hévin, C., Bordenave, L., Foissac, X., Masson, J. E., & Malembic-Maher, S. (2016). Contrasting Susceptibilities to Flavescence Dorée in *Vitis vinifera*, Rootstocks and Wild *Vitis* Species. *Frontiers in Plant Science*, 7, 1762. https://doi.org/10.3389/fpls.2016.01762

Fanton, A. C., & Brodersen, C. (2021). Hydraulic consequences of enzymatic breakdown of grapevine pit membranes. *Plant Physiology*, *186*(4), 1919-1931. https://doi.org/10.1093/plphys/kiab191

Feliciano, A., Eskalen, A., & Gubler, W. (2004). Differential susceptibility of three grapevine cultivars to *Phaeoacremonium aleophilum* and *Phaeomoniella chlamydospora* in California. *Phytopathologia Mediterranea*, *43*, 66-69. https://doi.org/10.14601/Phytopathol_Mediterr-1727

Ferguson, J. C., Moyer, M. M., Mills, L. J., Hoogenboom, G., & Keller, M. (2014). Modeling Dormant Bud Cold Hardiness and Budbreak in Twenty-Three *Vitis* Genotypes Reveals Variation by Region of Origin. *American Journal of Enology and Viticulture*, *65*(1), 59-71. https://doi.org/10.5344/ajev.2013.13098

Gaforio, L., García-Muñoz, S., Cabello, F., & Muñoz-Organero, G. (2011). Evaluation of susceptibility to powdery mildew (*Erysiphe necator*) in *Vitis vinifera* varieties. *VITIS - Journal of Grapevine Research*, 50(3), 123-126. https://doi.org/10.5073/vitis.2011.50.123-126

Gilbert, G. S., Briggs, H. M., & Magarey, R. (2015). The Impact of Plant Enemies Shows a Phylogenetic Signal. *PLOS ONE*, *10*(4), e0123758. https://doi.org/10.1371/journal.pone.0123758

Gramaje, D., García-Jiménez, J., & Armengol, J. (2010). Field Evaluation of Grapevine Rootstocks Inoculated with Fungi Associated with Petri Disease and Esca. *American Journal of Enology and Viticulture*, *61*(4), 512-520. https://doi.org/10.5344/ajev.2010.10021

Gramaje, D., Úrbez-Torres, J. R., & Sosnowski, M. R. (2018). Managing Grapevine Trunk Diseases With Respect to Etiology and Epidemiology : Current Strategies and Future Prospects. *Plant Disease*, *102*(1), 12-39. https://doi.org/10.1094/PDIS-04-17-0512-FE

Gubler, W., Thind, T., Feliciano, A., & Eskalen, A. (2004). Pathogenicity of *Phaeoacremonium aleophilum* and *Phaeomoniella chlamydospora* on Grape Berries in California. *Phytopathologia Mediterranea*, *43*, 70-74. https://doi.org/10.14601/Phytopathol_Mediterr-1735

Guerin-Dubrana, L., Labenne, A., Labrousse, J. C., Bastien, S., Rey, P., & Gégout-Petit, A. (2013). Statistical analysis of grapevine mortality associated with esca or Eutypa dieback foliar expression. *Phytopathologia Mediterranea*, 52(2), 276-288. https://doi.org/10.14601/Phytopathol_Mediterr-11602

Hartig, F., & Lohse, L. (2022). *DHARMa : Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models* (0.4.6) [Software]. https://cran.r-project.org/web/packages/DHARMa/index.html

Hofstetter, V., Buyck, B., Croll, D., Viret, O., Couloux, A., & Gindro, K. (2012). What if esca disease of grapevine were not a fungal disease? *Fungal Diversity*, *54*(1), 51-67. https://doi.org/10.1007/s13225-012-0171-z

Keck, F., Rimet, F., Bouchez, A., & Franc, A. (2016). phylosignal : An R package to measure, test, and explore the phylogenetic signal. *Ecology and Evolution*, *6*(9), 2774-2780. https://doi.org/10.1002/ece3.2051

Kovács, C., Balling, P., Bihari, Z., Nagy, A., & Sándor, E. (2017). Incidence of grapevine trunk diseases is influenced by soil, topology and vineyard age, but not by *Diplodia seriata* infection rate in the Tokaj Wine Region, Hungary. *Phytoparasitica*, *45*(1), 21-32. https://doi.org/10.1007/s12600-017-0570-5

Lamarque, L. J., Delmas, C. E. L., Charrier, G., Burlett, R., Dell'Acqua, N., Pouzoulet, J., Gambetta, G. A., & Delzon, S. (2023). Quantifying the grapevine xylem embolism resistance spectrum to identify varieties and regions at risk in a future dry climate. *Scientific Reports*, *13*(1), 7724. https://doi.org/10.1038/s41598-023-34224-6

Laucou, V., Lacombe, T., Dechesne, F., Siret, R., Bruno, J.-P., Dessup, M., Dessup, T., Ortigosa, P., Parra, P., Roux, C., Santoni, S., Varès, D., Péros, J.-P., Boursiquot, J.-M., & This, P. (2011). High throughput analysis of grape genetic diversity as a tool for germplasm collection management. *Theoretical and Applied Genetics*, *122*(6), 1233-1245. https://doi.org/10.1007/s00122-010-1527-y

Laveau, C., Letouze, A., Louvet, G., Bastien, S., & Guerin-Dubrana, L. (2009). Differential aggressiveness of fungi implicated in esca and associated diseases of grapevine in France. *Phytopathologia Mediterranea*, 48(1), 32-46. https://doi.org/10.14601/Phytopathol_Mediterr-2873

Lecomte, P., Bénétreau, C., Diarra, B., Meziani, Y., Delmas, C., & Fermaud, M. (2024). Logistic modeling of summer expression of esca symptoms in tolerant and susceptible cultivars in Bordeaux vineyards. *OENO One*, *58*(1). https://doi.org/10.20870/oeno-one.2024.58.1.7571

Lecomte, P., Darrieutort, G., Liminana, J.-M., Comont, G., Muruamendiaraz, A., Legorburu, F.-J., Choueiri, E., Jreijiri, F., El Amil, R., & Fermaud, M. (2012). New Insights into Esca of Grapevine : The Development of Foliar Symptoms and Their Association with Xylem Discoloration. *Plant Disease*, *96*(7), 924-934. https://doi.org/10.1094/PDIS-09-11-0776-RE

Lecomte, P., Diarra, B., Carbonneau, A., Rey, P., & Chevrier, C. (2018). Esca of grapevine and training practices in France : Results of a 10-year survey. *Phytopathologia Mediterranea*, *57*(3), 472-487. https://doi.org/10.14601/Phytopathol_Mediterr-22025

Lemaitre-Guillier, C., Fontaine, F., Roullier-Gall, C., Harir, M., Magnin-Robert, M., Clément, C., Trouvelot, S., Gougeon, R. D., Schmitt-Kopplin, P., & Adrian, M. (2020). Cultivar- and Wood Area-Dependent Metabolomic Fingerprints of Grapevine Infected by Botryosphaeria Dieback. *Phytopathology®*, *110*(11), 1821-1837. https://doi.org/10.1094/PHYTO-02-20-0055-R

Li, S. (2015). *Modélisation spatio-temporelle pour l'esca de la vigne à l'échelle de la parcelle* [Phdthesis, Université de Bordeaux]. https://theses.hal.science/tel-01793300

Lorenz, D. h., Eichhorn, K. w., Bleiholder, H., Klose, R., Meier, U., & Weber, E. (1995). Growth Stages of the Grapevine : Phenological growth stages of the grapevine (*Vitis vinifera* L. ssp. *vinifera*)—Codes and descriptions according to the extended BBCH scale. *Australian Journal of Grape and Wine Research*, *1*(2), 100-103. https://doi.org/10.1111/j.1755-0238.1995.tb00085.x

Magnin-Robert, M., Letousey, P., Spagnolo, A., Rabenoelina, F., Jacquens, L., Mercier, L., Clément, C., & Fontaine, F. (2011). Leaf stripe form of esca induces alteration of photosynthesis and defence reactions in presymptomatic leaves. *Functional Plant Biology*, *38*(11), 856-866. https://doi.org/10.1071/FP11083

Martínez-Diz, M. del P., Díaz-Losada, E., Barajas, E., Ruano-Rosa, D., Andrés-Sodupe, M., & Gramaje, D. (2019). Screening of Spanish *Vitis vinifera* germplasm for resistance to *Phaeomoniella chlamydospora*. *Scientia Horticulturae*, *246*, 104-109. https://doi.org/10.1016/j.scienta.2018.10.049

Merdinoglu, D., Schneider, C., Prado, E., Wiedemann-Merdinoglu, S., & Mestre, P. (2018). Breeding for durable resistance to downy and powdery mildew in grapevine. *OENO One*, *52*(3), 203-209. https://doi.org/10.20870/oeno-one.2018.52.3.2116

Monod, V., Zufferey, V., Wilhelm, M., Viret, O., Gindro, K., Croll, D., & Hofstetter, V. (2023). *A systemic approach allows to identify the pedoclimatic conditions most critical in the susceptibility of a grapevine cultivar to esca/Botryosphaeria dieback* (p. 2023.05.23.541976). bioRxiv. https://doi.org/10.1101/2023.05.23.541976

Moret, F., Lemaître-Guillier, C., Grosjean, C., Clément, G., Coelho, C., Negrel, J., Jacquens, L., Morvan, G., Mouille, G., Trouvelot, S., Fontaine, F., & Adrian, M. (2019). Clone-Dependent Expression of Esca Disease Revealed by Leaf Metabolite Analysis. *Frontiers in Plant Science*, *9*. https://www.frontiersin.org/article/10.3389/fpls.2018.01960

Mugnai, L., Graniti, A., & Surico, G. (1999). Esca (Black Measles) and Brown Wood-Streaking : Two Old and Elusive Diseases of Grapevines. *Plant Disease*, *83*(5), 404-418. https://doi.org/10.1094/PDIS.1999.83.5.404

Mur, L. A. J., Simpson, C., Kumari, A., Gupta, A. K., & Gupta, K. J. (2017). Moving nitrogen to the centre of plant defence against pathogens. *Annals of Botany*, *119*(5), 703-709. https://doi.org/10.1093/aob/mcw179

Murolo, S., & Romanazzi, G. (2014). Effects of grapevine cultivar, rootstock and clone on esca disease. *Australasian Plant Pathology*, *43*(2), 215-221. https://doi.org/10.1007/s13313-014-0276-9

Nicolas, S. D., Péros, J.-P., Lacombe, T., Launay, A., Le Paslier, M.-C., Bérard, A., Mangin, B., Valière, S., Martins, F., Le Cunff, L., Laucou, V., Bacilieri, R., Dereeper, A., Chatelet, P., This, P., & Doligez, A. (2016). Genetic diversity, linkage disequilibrium and power of a large grapevine (*Vitis vinifera* L) diversity panel newly designed for association studies. *BMC Plant Biology*, *16*, 74. https://doi.org/10.1186/s12870-016-0754-z

Ouadi, L., Bruez, E., Bastien, S., Yacoub, A., Coppin, C., Guérin-Dubrana, L., Fontaine, F., Domec, J.-C., & Rey, P. (2021). Sap Flow Disruption in Grapevine Is the Early Signal Predicting the Structural, Functional, and Genetic Responses to Esca Disease. *Frontiers in Plant Science*, *12*. https://www.frontiersin.org/articles/10.3389/fpls.2021.695846

Paňitrur-De La Fuente, C., Valdés-Gómez, H., Roudet, J., Acevedo-Opazo, C., Verdugo-Vásquez, N., Araya-Alman, M., Lolas, M., Moreno, Y., & Fermaud, M. (2018). Classification of winegrape cultivars in Chile and France according to

their susceptibility to *Botrytis cinerea* related to fruit maturity. *Australian Journal of Grape and Wine Research*, *24*(2), 145-157. https://doi.org/10.1111/ajgw.12315

Plantevin, M., Gowdy, M., Destrac-Irvine, A., Marguerit, E., Gambetta, G. A., & Leeuwen, C. van. (2022). Using δ13C and hydroscapes for discriminating cultivar specific drought responses. *OENO One*, *56*(2). https://doi.org/10.20870/oeno-one.2022.56.2.5434

Pouzoulet, J., Rolshausen, P. E., Charbois, R., Chen, J., Guillaumie, S., Ollat, N., Gambetta, G. A., & Delmas, C. E. L. (2020). Behind the curtain of the compartmentalization process : Exploring how xylem vessel diameter impacts vascular pathogen resistance. *Plant, Cell & Environment*, *43*(11), 2782-2796. https://doi.org/10.1111/pce.13848

Pouzoulet, J., Scudiero, E., Schiavon, M., & Rolshausen, P. E. (2017). Xylem Vessel Diameter Affects the Compartmentalization of the Vascular Pathogen *Phaeomoniella chlamydospora* in Grapevine. *Frontiers in Plant Science*, *8*. https://www.frontiersin.org/article/10.3389/fpls.2017.01442

R Core Team. (2022). *R: A Language and Environment for Statistical Computing* [Software]. R Foundation for Statistical Computing. https://www.R-project.org/

Reis, P., Pierron, R., Larignon, P., Lecomte, P., Abou-Mansour, E., Farine, S., Bertsch, C., Jacques, A., Trotel-Aziz, P., Rego, C., & Fontaine, F. (2019). Vitis Methods to Understand and Develop Strategies for Diagnosis and Sustainable Control of Grapevine Trunk Diseases. *Phytopathology®*, *109*(6), 916-931. https://doi.org/10.1094/PHYTO-09-18-0349-RVW

Rolshausen, P. E., Greve, L. C., Labavitch, J. M., Mahoney, N. E., Molyneux, R. J., & Gubler, W. D. (2008). Pathogenesis of Eutypa lata in grapevine : Identification of virulence factors and biochemical characterization of cordon dieback. *Phytopathology*, *98*(2), 222-229. https://doi.org/10.1094/PHYTO-98-2-0222

Romanazzi, G., Murolo, S., Pizzichini, L., & Nardi, S. (2009). Esca in young and mature vineyards, and molecular diagnosis of the associated fungi. *European Journal of Plant Pathology*, *125*(2), 277-290. https://doi.org/10.1007/s10658-009-9481-8

Seem, R. C. (1984). Disease Incidence and Severity Relationships. *Annual Review of Phytopathology*, *22*(1), 133-150. https://doi.org/10.1146/annurev.py.22.090184.001025

Serra, S., Ligios, V., Schianchi, N., Prota, V., & Scanu, B. (2018). Expression of grapevine leaf stripe disease foliar symptoms in four cultivars in relation to grapevine phenology and climatic conditions. *Phytopathologia Mediterranea*, 57(3), 337-568. https://doi.org/10.14601/Phytopathol_Mediterr-24088

Sosnowski, M.R., Ayres, M.R., McCarthy, M.G., & Scott, E.S. (2022). Winegrape cultivars (*Vitis vinifera*) vary in susceptibility to the grapevine trunk pathogens *Eutypa lata* and *Diplodia seriata*. *Australian Journal of Grape and Wine Research*, 28(1), 166-174. https://doi.org/10.1111/ajgw.12531

Sosnowski, M. R., Lardner, R., Wicks, T. J., & Scott, E. S. (2007). The Influence of Grapevine Cultivar and Isolate of *Eutypa lata* on Wood and Foliar Symptoms. *Plant Disease*, *91*(8), 924-931. https://doi.org/10.1094/PDIS-91-8-0924

Sun, Y., Wang, M., Mur, L. A. J., Shen, Q., & Guo, S. (2020). Unravelling the Roles of Nitrogen Nutrition in Plant Disease Defences. *International Journal of Molecular Sciences*, *21*(2), 572. https://doi.org/10.3390/ijms21020572

Tambussi, E. a., Bort, J., & Araus, J. l. (2007). Water use efficiency in C3 cereals under Mediterranean conditions : A review of physiological aspects. *Annals of Applied Biology*, *150*(3), 307-321. https://doi.org/10.1111/j.1744-7348.2007.00143.x

This, P., Lacombe, T., & Thomas, M. R. (2006). Historical origins and genetic diversity of wine grapes. *Trends in Genetics*, *22*(9), 511-519. https://doi.org/10.1016/j.tig.2006.07.008

Torres-Ruiz, J. M., Cochard, H., Delzon, S., Boivin, T., Burlett, R., Cailleret, M., Corso, D., Delmas, C. E. L., De Caceres, M., Diaz-Espejo, A., Fernández-Conradi, P., Guillemot, J., Lamarque, L. J., Limousin, J.-M., Mantova, M., Mencuccini, M., Morin, X., Pimont, F., De Dios, V. R., … Martin-StPaul, N. K. (2024). Plant hydraulics at the heart of plant, crops and ecosystem functions in the face of climate change. *New Phytologist*, *241*(3), 984-999. https://doi.org/10.1111/nph.19463

Wei T, Simko V (2021). *R package 'corrplot': Visualization of a Correlation Matrix*. (Version 0.92), https://github.com/taiyun/corrplot.

Wolkovich, E. M., García de Cortázar-Atauri, I., Morales-Castilla, I., Nicholas, K. A., & Lacombe, T. (2018). From Pinot to Xinomavro in the world's future wine-growing regions. *Nature Climate Change*, *8*(1), 29-37. https://doi.org/10.1038/s41558-017-0016-6