# 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 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, grapevine trunk disease, multi-trait phenotyping, pathogenicity, phenotypic diversity, *Vitis vinifera*

42 ## Introduction

43 The domesticated grapevine *Vitis vinifera* L. ssp. *vinifera* has a high level of genetic and phenotypic
44 diversity, generated naturally by recombination, hybridisation, and mutation events, as well as
45 through human-assisted selection. More than 5,000 cultivars are currently registered (This *et al.*,
46 2006), although only a small proportion are widely cultivated worldwide (Anderson and Aryal, 2013).
47 Cultivar diversity is now considered an excellent tool for managing abiotic and biotic pressures in a
48 sustainable manner (Merdinoglu *et al.*, 2018; Wolkovich *et al.*, 2018). There is therefore a need to
49 improve our understanding of the variability between cultivars by phenotyping cultivars for a wide
50 range of traits. Several stress-related traits, including carbon isotope discrimination in berry juice at
51 maturity (δ13C; Plantevin *et al.*, 2022), cold hardiness (Ferguson *et al.*, 2014), and susceptibility to
52 pests and diseases (Boso *et al.*, 2011; Gaforio *et al.*, 2011; Paňitrur-De La Fuente *et al.*, 2018), have
53 already been studied in a range of cultivars. The susceptibility of the grapevine vascular system to
54 various stresses has also recently been studied. Xylem and hydraulic traits have been phenotyped in
55 a range of *Vitis* genotypes of different origins and levels of drought tolerance (Dayer *et al.*, 2022;
56 Lamarque *et al.*, 2023) or resistance to vascular diseases (Pouzoulet *et al.*, 2020; Fanton and
57 Brodersen, 2021).

58 Vascular biotic stresses include grapevine trunk diseases, which are responsible for substantial yield
59 losses in vineyards worldwide (Gramaje *et al.*, 2018). One such disease is esca, which is detected in
60 the vineyards through the summer expression of foliar symptoms and yield losses (Lecomte *et al.*,
61 2012). Esca pathogenesis has been associated with various types of trunk necrosis (Mugnai *et al.*,
62 1999) probably involving a complex community of fungal pathogens (Bruez *et al.*, 2014). This
63 community includes a few key pathogens from both Ascomycota (including *Phaeomoniella*
64 *chlamydospora* and *Phaeoacremonium minimum*) and Basidiomycota (e.g. *Fomitiporia*
65 *mediterranea*). However, no direct role in foliar symptom onset has ever been demonstrated for any

66 of these pathogens, which are present in both healthy and necrotic wood tissues (Bruez *et al.*, 2016)
67 and in both symptomatic leaves and asymptomatic plants (Hofsteter *et al.*, 2012; Bruez *et al.*, 2014;
68 Bortolami *et al.*, 2019). These fungi probably also interact with bacteria (Bruez *et al.*, 2020) and seem
69 to be restricted to the perennial organs (Bortolami *et al.*, 2019).

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

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

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

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

114 and dieback on the one hand, and phenological and ecophysiological traits, such as key phenological
115 stages, nitrogen status at flowering, pruning weight, and δ13C, a proxy of water use efficiency, on
116 the other.

117

118 ## Materials and methods

119 ### 1. Common garden experimental vineyard

120 The VitAdapt vineyard (as described by Destrac-Irvine and van Leeuwen 2016) was designed as a
121 common garden, and is located at the *Institut National de Recherche pour l'Agriculture,*
122 *l'alimentation et l'Environnement* (INRAE) research station (Villenave d'Ornon, Nouvelle-
123 Aquitaine, France), at 44°47'23.83 N'', 0°34'39.3' W'. This vineyard, on a sandy-gravel soil, was
124 planted with 52 genotypes (47 *Vitis vinifera* L. cultivars and 5 *Vitis* hybrids). In this study, 45 *V.*
125 *vinifera* L. cultivars, and one hybrid of several *Vitis* species — Hibernal, an F2 progeny of a Seibel
126 7053 x Riesling cross (Vitis International Variety Catalogue - VIVC; www.vivc.de) — were
127 monitored. Among them, 28 were red-berried cultivars and 18 were white-berried cultivars
128 (Supplementary Table S1). All plants were grafted onto Selection Oppenheim 4 (SO4) clone 761
129 rootstocks and planted at a density of 5,555 vines/ha, corresponding to a spacing of 1.8 m between
130 adjacent rows and 1 m between adjacent vines. Eight cultivars were first planted in 2010, all the others
131 being first planted in 2009 (Supplementary Table S1). Each cultivar was tested for major viral
132 diseases before planting, and only non-contaminated material was planted. All vines were pruned
133 according to the double guyot system and grown without irrigation. Pests and diseases were controlled
134 by an integrated management programme, and weeds were controlled by mechanical tillage beneath
135 the row. Cover crops were planted in every other row, alternating from year to year. The VitAdapt
136 vineyard was organized into a five-randomised block design to account for soil variability. Each block

137 comprised one subplot per cultivar, in which 10 vines were planted in two adjacent rows. In this
138 study, only four blocks were monitored, resulting in a total of 184 subplots (1,840 vines; 40 per
139 cultivar, 46 cultivars) subjected to ecophysiological monitoring and esca and dieback monitoring for
140 six and seven years, respectively.
141

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

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

154 Three epidemiological metrics were calculated from the data collected at subplot scale for esca foliar
155 expression and vine dieback. The incidence of esca foliar symptoms was calculated as the proportion
156 of the total number of productive plants (i.e. excluding totally apoplectic and dead plants, as well as
157 young replanted vines) displaying typical esca foliar symptoms. The cumulative incidence of foliar
158 symptoms was also calculated as the proportion of the productive vines expressing esca foliar
159 symptoms in at least one of the seven years monitored. The mean severity of esca foliar symptoms
160 was calculated at subplot scale, by averaging the score attributed to each symptomatic vine of the

subplot. Finally, the incidence of plant dieback was calculated as the proportion of mature plants (i.e. excluding young replanted vines) with at least one unproductive arm (i.e. apoplectic or dead). During the plant phenotyping process in the field, no *a priori* assumption was made concerning the cause of plant dieback, which may have multiple abiotic or biotic causes.

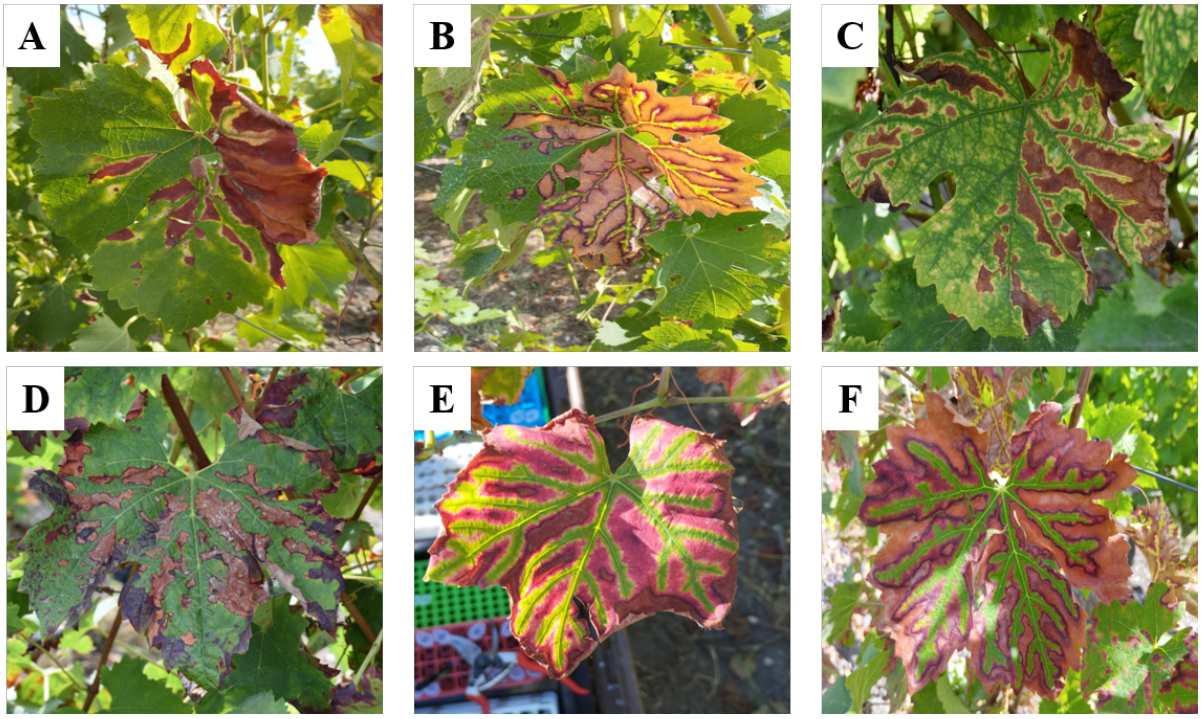



**Figure 1. Examples of various foliar phenotypes for esca on different *Vitis vinifera* cultivars grown in a common garden experimental vineyard**

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.

172 **3. Phenotyping of ecophysiological and phenological traits**

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

176 **3.1. Monitoring of phenological stages**

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

184 **3.2. Carbon isotope discrimination ($\delta^{13}C$)**

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

193 **3.3. N-tester measurements**

194 N-tester measurements were performed at flowering (as defined above), which is considered to be a
195 key stage for nitrogen assimilation by grapevines (Celette and Gary, 2013), on 30 leaves of each
196 cultivar in each of the four blocks, according to the manufacturer's protocol (Yara, Oslo, Østland,
197 Norway). Briefly, each leaf was clamped with the device, for the measurement of transmittance (at
198 wavelengths of 650 and 960 nm), which provides a standardised index of chlorophyll content that can
199 be used as a proxy for vine nitrogen status. As a means of accounting for cultivar-specific nitrogen-
200 status behaviour under similar conditions, raw values were transformed according to varietal rounded
201 corrections. The mean value for Sauvignon Blanc was similar to the mean value across all varieties,
202 so this cultivar was used as the reference variety for this index. For each cultivar, the difference
203 between the mean value for all available years for the cultivar (2015-2021 for 35 cultivars; 2020-
204 2021 for the other 11), and the mean value for Sauvignon Blanc was calculated. An Ascendant
205 Hierarchical Classification (AHC) method was then applied to the N-tester values to group the
206 cultivars and obtain an average correction for all the cultivars of a single group. The N-tester value
207 of each cultivar was then corrected with the correction coefficient for its group, as described in
208 Supplementary Table S3. Five years of data were included in subsequent analyses, from 2017 to 2021.

209 **3.4. Pruning weight quantification**

210 Pruning weight was quantified during the winter for all varieties in each of the four blocks. For each
211 cultivar, two measurements were made for each block, by averaging the value three central vines of
212 a row (i.e. six vines per subplot). Only the wood from the previous growing season removed from the
213 plants during pruning was weighed. All measurements were performed during the same period of the
214 year in each year: between January 15th and 30th. Six years of data were included in this study, from
215 2017 to 2022.
216

217 **4. Data analysis**

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

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

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

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

239 For all these analyses, linear models (LM) or linear mixed models (LMM) were used for response
240 variables following a normal distribution (i.e. foliar symptom severity). For binomial response

241 variables (i.e. the incidences of foliar symptoms and dieback), generalised linear models (GLM and
242 GLMM) were fitted, using the binomial family with "cloglog" links (accounting for a non-symmetric
243 distribution). Each model was graphically validated according to the normality of the residuals (QQ-
244 plot) and the homogeneity of the residual variance (residuals vs. fitted, residuals vs. predictors). All
245 analyses involving epidemiological metrics were conducted for the period 2017-2023, whereas
246 analyses including other phenotypic traits were conducted for the period 2017-2022. Analyses were
247 performed with R v.4.2.1 software (R Core Team, 2022) and the RStudio interface. Linear modelling
248 was performed with the "lme4" package (Bates *et al.*, 2015), and model validation was performed
249 with "DHARMa" (Hartig and Lohse, 2022). Correlation analyses were performed with the "corrplot"
250 package (Wei, Simko, 2021).
251

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

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

261 We searched for a phylogenetic signal in cultivar susceptibility to esca using methods based on
262 autocorrelations computed both on the global phylogenetic tree and local nodes of the phylogeny
263 implemented in the "phylosignal" package (Keck *et al.*, 2016). A global Moran's I index was
264 calculated for each epidemiological metric and tested against the null hypothesis of an absence of

265 phylogenetic signal. Phylogenetic correlograms were then constructed to visualise the distribution of
266 this index over a gradient of phylogenetic distances and its confidence envelope based on
267 bootstrapping (1,000 repetitions). The local Moran's index $I_i$ was also plotted alongside the
268 phylogeny to locate autocorrelation patterns more precisely through LIPA analysis. The existence of
269 local phylogenetic signals was assessed in a permutation-based test (999 repetitions).
270

271 ## Results

272 **Global incidences of esca and dieback and changes over time**

273 The mean incidence of esca foliar symptoms, for all cultivars, blocks, and years, was 7.5% (standard
274 deviation, SD = 13.6%), with considerable variability (relative standard deviation, RSD = 182.2%;
275 Table 1). The mean cumulative incidence of esca foliar symptoms (i.e. observed in at least one year)
276 was 30.5%, implying that almost one vine in three expressed esca foliar symptoms in at least one
277 year. This value is five times higher than the mean annual incidence (Table 1). Foliar symptom
278 severity had a mean score of 2.5 and was much less variable than the incidence of foliar symptoms
279 (RSD = 59.4%; Table 1). Plant dieback had a mean incidence of 4.1%, which is lower than that of
280 foliar symptom incidence by a factor of 1.8, but was much more variable (RSD = 233.0%; Table 1).
281 An analysis of the declining vines showed that 16% expressed apoplexy on a single arm, 51% had a
282 single dead arm, and 33% were totally unproductive (i.e. 11% totally apoplectic, 18% totally dead,
283 and 4% with both phenotypes).
284

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

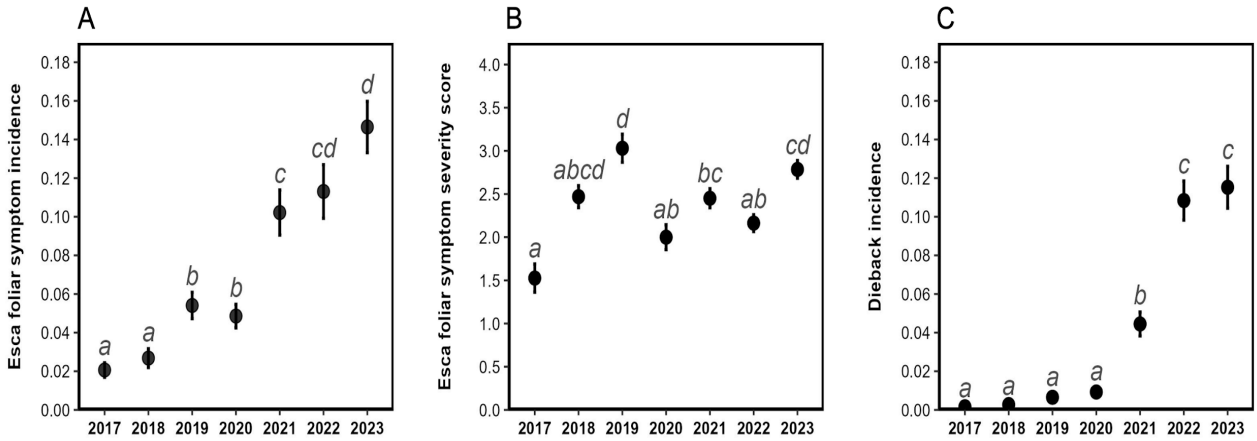
287 The statistics given are means, standard deviation, relative standard deviation, minimum and
288 maximum. Values are calculated for 1288 observations (46 cultivars; four blocks; seven years). The
289 severity index ranged from 1 (light esca foliar symptom on a single arm) to 5 (severe esca foliar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

| Trait | Statistical individual | mean | SD | CV | min | max |
|---|---|---|---|---|---|---|
| Foliar symptom incidence | Observation (*n*=1288) | 7.3% | 13.6% | 185.3% | 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% |

291

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

301 2C). The severity of esca foliar symptoms also differed significantly between years ($p = 10^{-11}$).
302 However, severity did not follow a specific temporal pattern similar to that for incidence (Figure 2B).




303

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

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

312

313 **Esca incidence differs considerably between cultivars**

314 The incidence of esca foliar symptoms differed significantly between the 46 cultivars monitored from
315 2017 to 2023 ($p < 10^{-16}$). We found a large gradient of susceptibility to esca foliar symptoms, as four
316 grape varieties (Merlot, Petit Manseng, Tannat and Xinomavro) never expressed symptoms during
317 the seven years of monitoring whereas eight cultivars (Chenin, Saperavi, Mourvèdre, Cabernet Franc,

318 Sauvignon, Tempranillo, Castets and Cabernet-Sauvignon) had mean annual incidences above 20%
319 (Figure 3A).

320 Excluding the four cultivars with an overall incidence of zero, cumulative incidence ranged from
321 2.5% to 85%, and was 2.7 to 7 times higher than the mean incidence according to the cultivar (Figure
322 3A). The cumulative incidence of esca was highly correlated with the incidence of foliar symptoms
323 ($r = 0.95$; $p < 10^{-16}$).

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

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

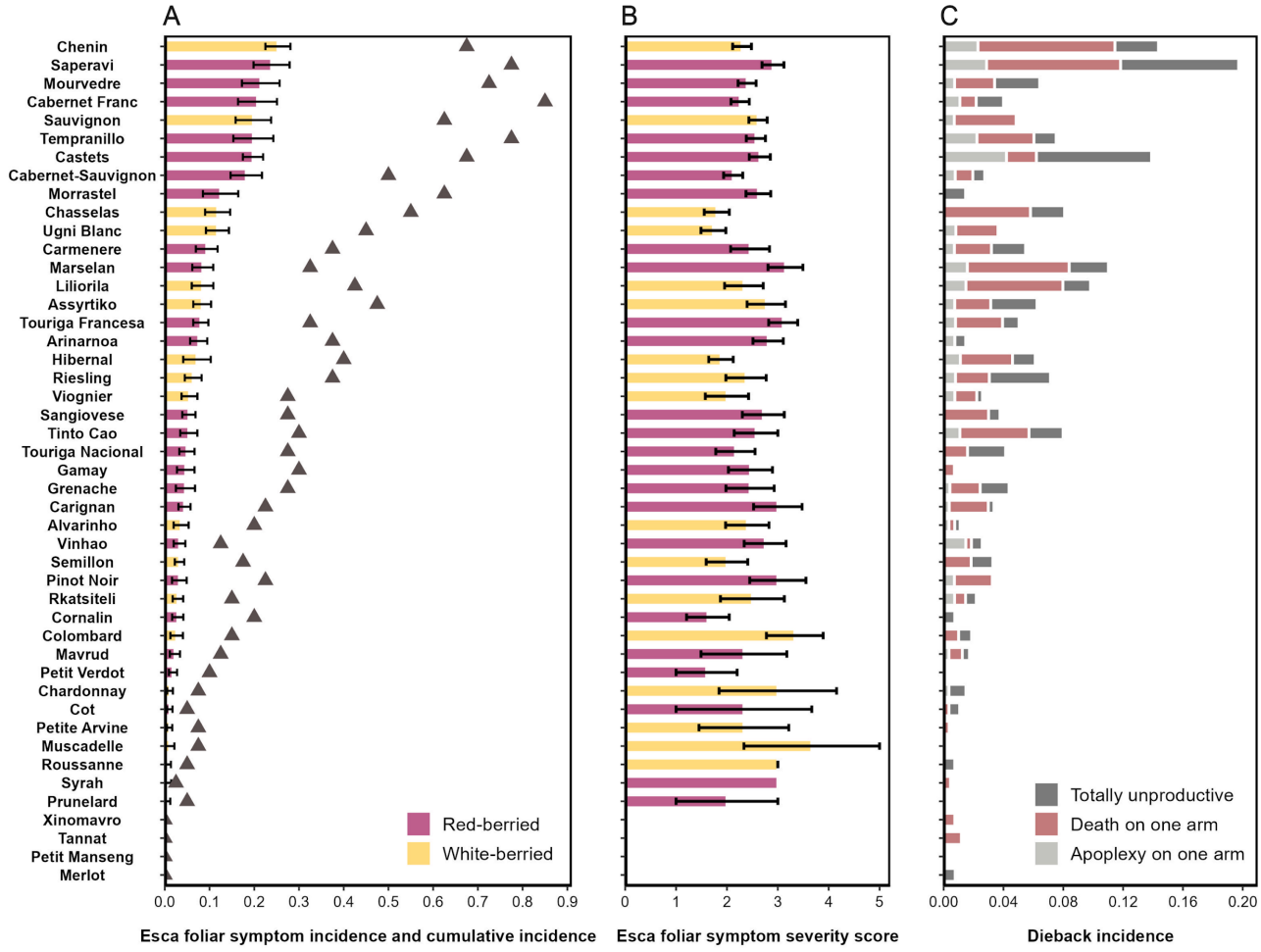



**Figure 3. Variability of susceptibility to esca foliar symptoms and dieback among grapevine cultivars for the period 2017 to 2023.**

(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.

347

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

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

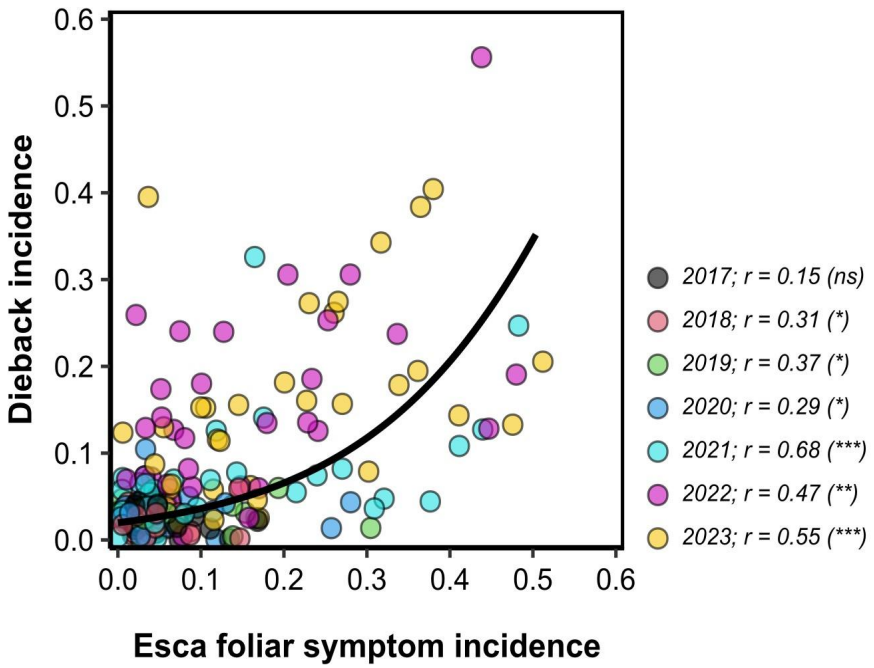


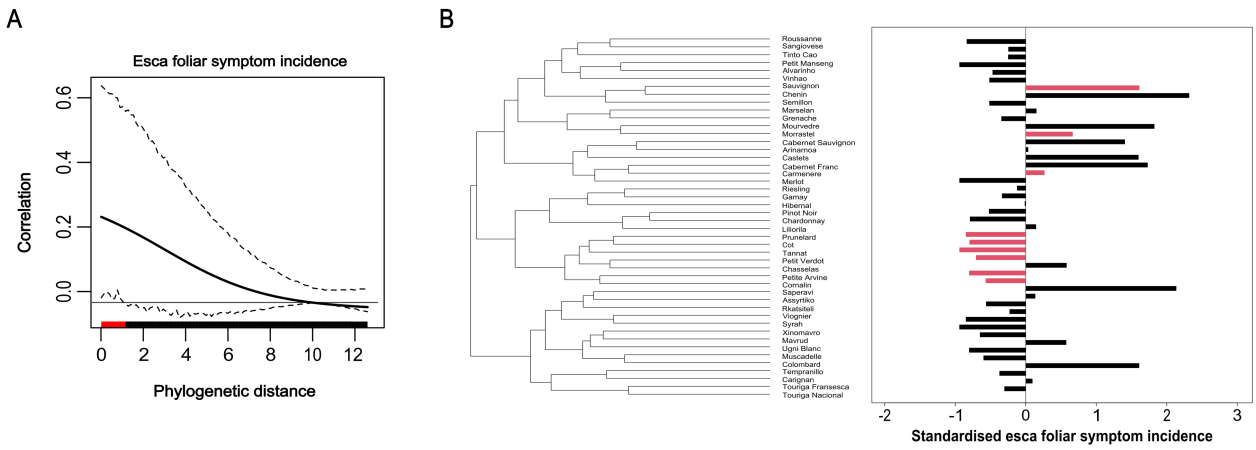

**Figure 4. Relationship between the incidence of esca foliar symptoms and the incidence of dieback**

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,

372 had an extremely wide confidence envelope, and was significant only for very short phylogenetic
373 distances (Figure 5A). The distribution of the local Moran's index $I_i$ over the phylogeny revealed two
374 hotspots of phylogenetic positive autocorrelation (i.e. nodes at which the local Moran's index value
375 $I_i$ was significant) (Figure 5B): (i) a node of six cultivars with low incidences (Prunelard, Cot, Tannat,
376 Petit Verdot, Petite Arvine, and Cornalin); (ii) a node of cultivars with high incidences, three of which
377 displayed a significant signal (Sauvignon, Morrastel, Carmenere). By contrast, this method revealed
378 no phylogenetic autocorrelation for either foliar symptom severity (I = -0.02; $p = 0.52$) or the
379 incidence of dieback (I = -0.02, $p = 0.30$).
380




381

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

384 (A) Phylocorrelogram showing the change in Moran's I index (measuring phylogenetic
385 autocorrelation) along a gradient of phylogenetic distances. Black lines represent Moran's I value.
386 Dashed lines correspond to a confidence envelope at 95%, estimated from 1,000 bootstrap replicates.
387 (B) Detection of the phylogenetic signal at a local scale over the phylogeny, by LIPA analysis. The
388 dendrogram displaying genetic distances between cultivars is based on a set of 20 SSR markers. Bars
389 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 significant (Figure 6C). By contrast, no clear inter-annual correlation pattern was identified for foliar symptom severity. Only three pairs of years displayed significant correlations, negative in one case (2018 vs. 2019) and positive in the other two (2017 vs. 2022 and 2021 vs. 2023) (Figure 6B).

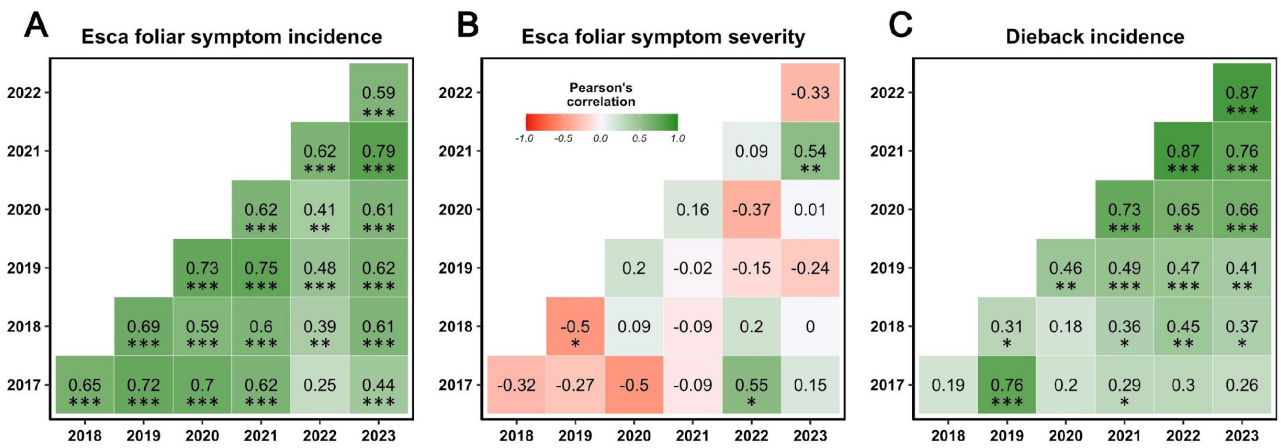



**Figure 6. Inter-annual correlations of mean varietal values for the three variables related to esca foliar symptoms and dieback**

(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 (r = -
424 0.33; $p = 0.03$; Figure 7A). Similarly, this trait was significantly negatively correlated with dieback
425 incidence (r = -0.32; $p = 0.03$; Figure 7I). In other words, cultivars with high water- use efficiency
426 (i.e. a less negative $\delta^{13}C$) were less susceptible to the expression of esca foliar symptoms and dieback
427 phenotypes. However, when this relationship was considered for each year separately, the correlation
428 between $\delta^{13}C$ and the incidence of foliar symptoms was significant only for 2022 (Supplementary
429 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)*.

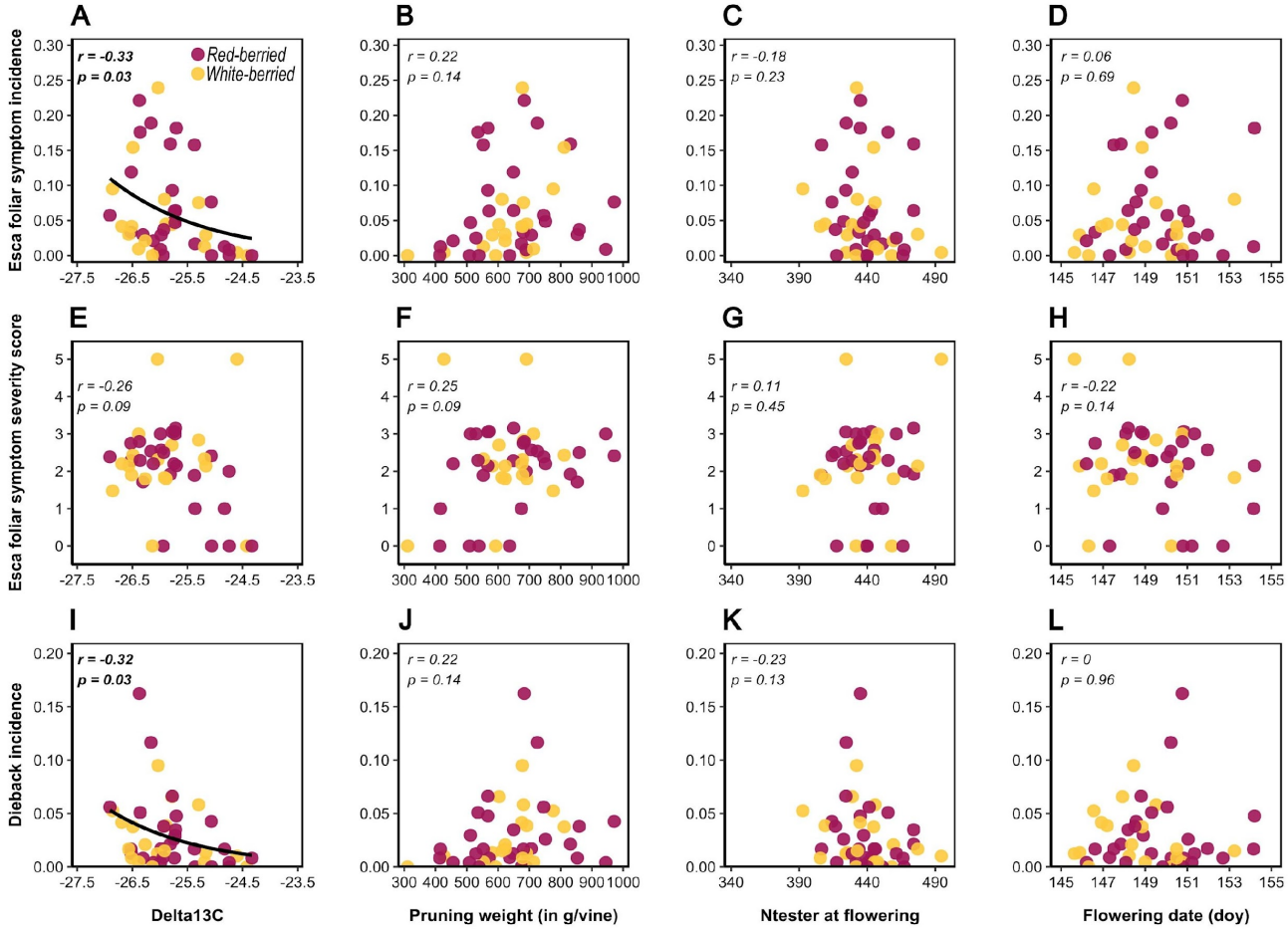



**Figure 7. Relationships between three variables related to esca foliar symptom and dieback and four ecophysiological and phenological traits**

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 focused on esca, a fungal vascular disease of grapevine of growing concern. We
449 used a unique common garden vineyard to assess inter-variety variability in the expression of esca
450 disease. Our results indicate diverse patterns of susceptibility among cultivars, with some cultivars
451 displaying no foliar symptoms in any of the seven years studied and others highly susceptible. We
452 also identified key ecophysiological traits correlated with susceptibility to esca disease, such as
453 cultivar water use 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 revealed a significant variability of esca foliar symptoms and plant dieback between the 46
457 grapevine cultivars. Several cultivars only very rarely expressed foliar symptoms or dieback
458 phenotypes, whereas others, including several of high economic importance, were much more
459 strongly affected by esca and dieback. The use of a common garden design and the inclusion of a
460 block effect in statistical models made it possible to prevent possible biases in the calculation of esca
461 incidence due to the variability of soils and viticulture practices. Our results provide new information
462 for consideration in the discussions of cultivar rankings for esca susceptibility obtained in previous
463 multiregional and multicultivar monitoring programmes. For example, Ugni Blanc, for which very
464 high incidences were recorded in the Charentes region (France; Bruez *et al.*, 2013), did not cluster
465 among the most susceptible cultivars in our vineyard, in which all cultivars were subject to the same
466 environment and the same viticulture practices (e.g. double guyot pruning system). Bruez *et al.* (2013)
467 showed that, for a given cultivar, a large proportion of the residual variability is due to the growing
468 area. There are at least two possible explanations for this. First, there can be considerable climatic
469 variation between regions. Second, the incidence of esca disease may be affected by differences in
470 viticulture systems and practices from between regions (Lecomte *et al.*, 2018). This may be the case

471 for Ugni Blanc, which was analysed here in growth conditions different from those applying to
472 productive contexts in the Charentes region (France), where it is cultivated for the production of
473 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 high levels of resistance 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 resistance to
490 trunk diseases as a key trait while selecting and planting both rootstocks (Gramaje *et al.*, 2010; Murolo
491 and Romanazzi, 2014) and hybrid cultivars. Here, the only hybrid variety studied, Hibernal, was
492 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 more tolerant 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 (Mugnai *et al.*, 1999; Kovács *et al.*, 2017). Moreover, our data indicate 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 clearly
502 indicate that it is essential to perform monitoring over several years for field trials (Reis *et al.*, 2019).

503 Even though the incidence of esca increased over time, the relative ranking of the varieties remained
504 constant between years. As all cultivars were compared in similar environmental conditions, this
505 suggests that each cultivar has a constitutive level of resistance that is little affected by local variations
506 of esca disease pressure (which are, in turn, influenced by several traits relating to pathogens, plants
507 and environment; Claverie *et al.*, 2020). A first genetic locus associated with grapevine susceptibility
508 to trunk diseases was recently identified in *V. vinifera* cv. 'Gewurztraminer', based on internal
509 symptoms (proportions of total necrosis and white rot) rather than the monitoring of foliar symptoms
510 and dieback (Arnold *et al.*, 2023). However, anatomical and physiological traits may contribute to
511 cultivar susceptibility. A high density of large vessels (>100 µm) has been associated with enhanced
512 susceptibility following artificial inoculation (Pouzoulet *et al.*, 2020). Based on the results of studies
513 on very small numbers of cultivars, we can also hypothesise that wood composition (see Rolshausen
514 *et al.*, 2008 for *Eutypa lata*, another fungal pathogen of wood) and secondary metabolism (see
515 Lemaitre-Guillier *et al.*, 2020 for *Botryosphaeria* sp. diseases) may have an effect. Another non-
516 mutually exclusive hypothesis would be the existence of interspecific and intraspecific diversity in
517 the microbial communities interacting with different cultivars during plant pathogenesis (Laveau *et*
518 *al.*, 2009; Bekris *et al.*, 2021).

519 As the genetic proximity between plant species and populations is often associated with common
520 susceptibilities to pathogens and pests (Gilbert *et al.*, 2015), we tested the hypothesis of closely
521 related cultivars having similar patterns of susceptibility to esca. We found a significant but weak
522 phylogenetic signal for esca susceptibility based on the incidence of foliar symptoms. This signal was
523 associated exclusively with local nodes of closely related cultivars and was similar for all four
524 clustering methods tested *(data not shown)*. This signal was not as robust as that likely to arise at
525 broader levels of grouping and may be strongly affected by the choice of genetic markers. Based on
526 a local-scale analysis, the main hotspots of phylogenetic signal corresponded to a group of weakly
527 susceptible cultivars. Pedigrees were available for only two of these six cultivars, Cot being an
528 offspring of Prunelard in the VIVC. The relationships between the remaining varieties were less clear,
529 and they even came from contrasting locations (Bacilieri *et al.*, 2013). We can hypothesise that traits
530 reducing susceptibility to esca in grapevine cultivars are converging within this group of interest.
531 Susceptible cultivars were overrepresented at another node of the phylogeny: Sauvignon, Chenin,
532 Marselan, Mourvedre, Morrastel, Cabernet-Sauvignon, Castets, Cabernet Franc, Carmenere. All
533 these cultivars originate from Western and Central Europe, with six originating from South-Western
534 France (Bacilieri *et al.*, 2013). Most belong to the Savagnin and Cabernet Franc families.
535 Nevertheless, the signal on these branches appeared unstable (i.e. significant for only three cultivars).
536 Moreover, phylogenetic correlation did not apply to all members of a group or lineage, as represented
537 in the vineyard studied. Thus, despite promising findings, it is difficult to conclude that esca
538 susceptibility is clearly driven by phylogenetic patterns. Here, the genetic panel studied consisted of
539 cultivars belonging from a single species, *V. vinifera* L. (with the exception of the *Vitis* sp. hybrid
540 'Hibernal') and was not truly representative of the overall diversity of grapevine. The search for
541 genetic markers of trunk disease incidence would probably benefit from studies of specifically
542 designed diversity panels (e.g. Nicolas *et al.*, 2016).

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

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

565 There have been many studies of the impact of esca disease on grapevine physiology, including plant
566 growth (Gramaje *et al.*, 2010; Dell'Acqua *et al.*, 2023), photosynthesis, water relations (Magnin-

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

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

589 The least vigorous cultivars appear to be grouped among the cultivars least susceptible to esca. This
590 relationship has already been suggested for trunk diseases, but never clearly demonstrated. It may

591 reflect the narrower xylem vessels of less vigorous vines, increasing compartmentalisation efficiency
592 and decreasing susceptibility to esca (Pouzoulet *et al.*, 2020). We found that $\delta^{13}C$ levels and pruning
593 weight were negatively correlated. In particular, a set of weakly susceptible cultivars of low vigour
594 were found to have less negative values for $\delta^{13}C$ (e.g. Petit Manseng, Tannat, Mavrud, Colombard).
595 We suggest that this tandem action of these two traits in the prediction of esca incidence is not a
596 coincidence. As discussed in previous studies, these cultivars are more able to decrease their hydraulic
597 conductivity markedly and rapidly in response to non-optimal water conditions, thus ensuring larger
598 hydraulic safety margins but constraining plant growth and productivity (Torrez-Ruiz *et al.*, 2024).
599 Nevertheless, this relationship is ambiguous, and depends on water availability. Our findings are
600 consistent with those of Tambussi *et al.* (2007), who found that, for common cereals, plants with a
601 lower WUE have a competitive advantage for growth and productivity in climates with rainfall
602 occurring during the growing season (here, a temperate oceanic climate).

603

604 Esca disease expression is also considered to be positively correlated with leaf nitrogen status
605 (Calzarano *et al.*, 2009; Li, 2015) through a roughly twofold mechanism that has already been
606 discussed for plants (e.g. Mur *et al.*, 2017; Sun *et al.*, 2020) involving modifications to plant
607 metabolism (e.g. enhanced vigour) and a favouring of fungal development and pathogenicity. In our
608 experimental vineyard, normalised nitrogen index was not a determinant of varietal susceptibility to
609 esca. As nitrogen status and vigour were only weakly correlated in this dataset (Supplementary
610 Material 7), it seems likely that the variability of nitrogen status was limited in this trial, potentially
611 accounting for the lack of correlation between vine nitrogen status and esca symptoms. This result
612 and those of Monod *et al.* (2023), who demonstrated a negative correlation between nitrogen status
613 and esca severity in a single cultivar growing in contrasting conditions in different vineyards, argue

614 in favour of a reconsideration, across a wide range of genotypes and growing conditions, of the link
615 between vine mineral status and the incidence of trunk disease.

616 Finally, we found no significant effect of phenology on the variability of esca expression between
617 varieties. There have been few studies of the links between trunk diseases and phenology. Serra *et al.*
618 (2018) assumed that phenology affects esca expression in relation to climatic variables. As foliar
619 symptoms emerge only between fruit set and veraison and accumulate through the summer season in
620 a systematic progressive sigmoidal pattern (Lecomte *et al.*, 2024), we can hypothesise that varietal
621 shifts in phenological stage may influence cultivar-specific patterns of esca expression, particularly
622 when climatic conditions fluctuate sharply. Monitoring over a time scale finer than one year would
623 improve our understanding of the interaction between grapevine phenology and disease dynamics.

## 624 Conclusion

625 This study, making use of a unique experimental facility, adds to our knowledge of the contribution
626 of genetic diversity to the sustainable management of grapevine dieback. Our findings confirm the
627 utility of performing pluriannual monitoring in natural conditions, within common garden
628 experimental vineyards, for accurate comparisons of susceptibility to trunk diseases between
629 cultivars. The ranking of varieties for susceptibility, based on the incidence of esca foliar symptoms,
630 was consistent with the findings of a previous field trial conducted in Italy (Murolo and Romanazzi,
631 2014; Figure 8A). A weaker correlation was also identified with the ranking obtained in a network of
632 French vineyards (Figure 8B). By contrast, no correlation was found with the susceptibility gradient
633 obtained by artificially inoculating cuttings with *P. chlamydospora* (Pouzoulet *et al.*, 2020; Figure
634 8C). This confirms that the susceptibility of grapevine genotypes to trunk diseases cannot be assessed
635 solely on the basis of inoculations under control conditions, as already discussed by several authors
636 (e.g. Sosnowski *et al.*, 2007; Reis *et al.*, 2019). Furthermore, susceptibility to trunk diseases is

potentially plastic in response to the environment. It therefore seems necessary to replicate such monitoring under contrasting conditions, to facilitate the selection of the most suitable cultivars for each production context. 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.

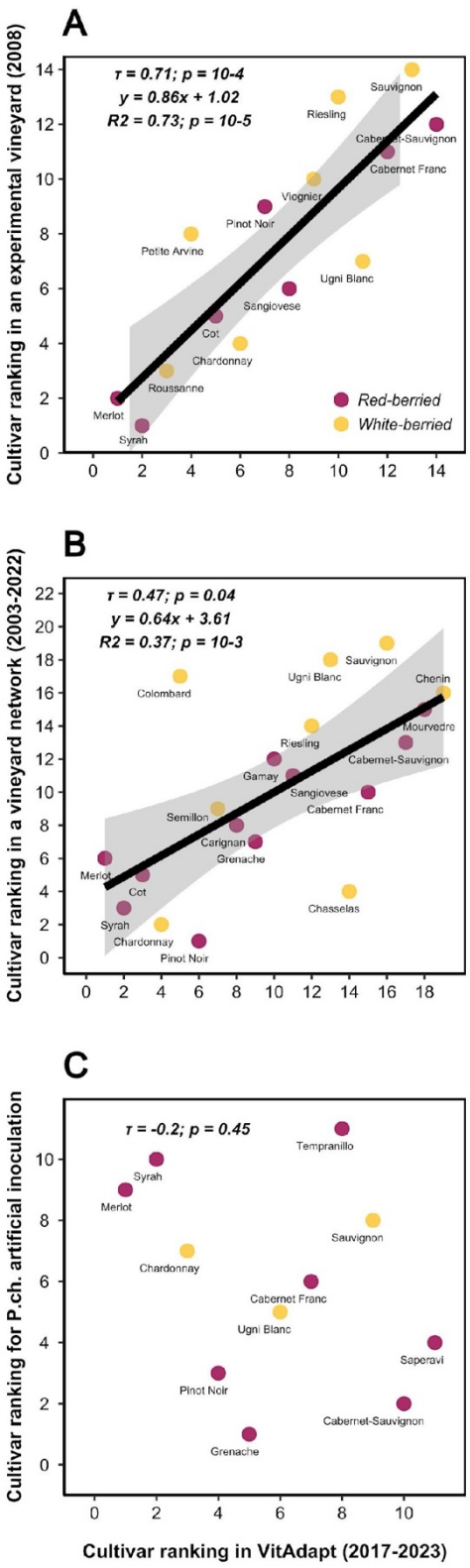



**Figure 8. Scatterplots showing the relationships between cultivar ranks for susceptibility to esca as assessed in this work and reported in previous publications.**

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 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.* (unpublished data), in a study over six years (2003-2022) monitoring 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.

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## Competing Interests statement

The authors have no competing interests to declare.

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