# 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 $\delta 13C$ 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.

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36  Together, these results provide new insight into the potential of genetic resources for use in the

37  sustainable management of grapevine trunk diseases and open up new perspectives for studying the

38  pathological and physiological determinants of their incidence.

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40  **Keywords**: Ecophysiology, grapevine trunk disease, multi-trait phenotyping, pathogenicity,

41  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 cultivars for a wide range of traits. Several stress-related traits, including carbon isotope discrimination in berry juice at maturity ($\delta13C$; 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 diseases (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

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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.

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## 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.

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**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

8

161    subplot. Finally, the incidence of plant dieback was calculated as the proportion of mature plants (i.e.

162    excluding young replanted vines) with at least one unproductive arm (i.e. apoplectic or dead). During

163    the plant phenotyping process in the field, no *a priori* assumption was made concerning the cause of

164    plant dieback, which may have multiple abiotic or biotic causes.



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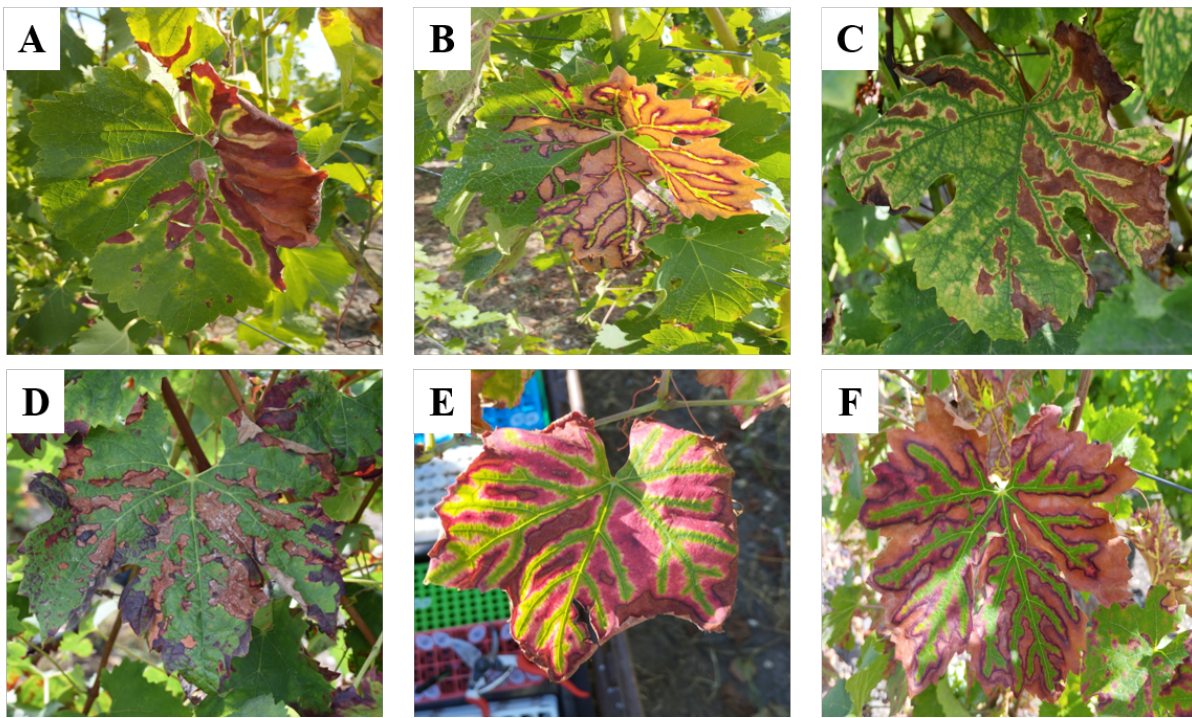
**Figure 1. Examples of various foliar phenotypes for esca on different *Vitis vinifera* cultivars grown in a common garden experimental vineyard**

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.

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**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.

**3.1. Monitoring of phenological stages**

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

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

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

**3.3. N-tester measurements**

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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

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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

## Results

**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

15

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).
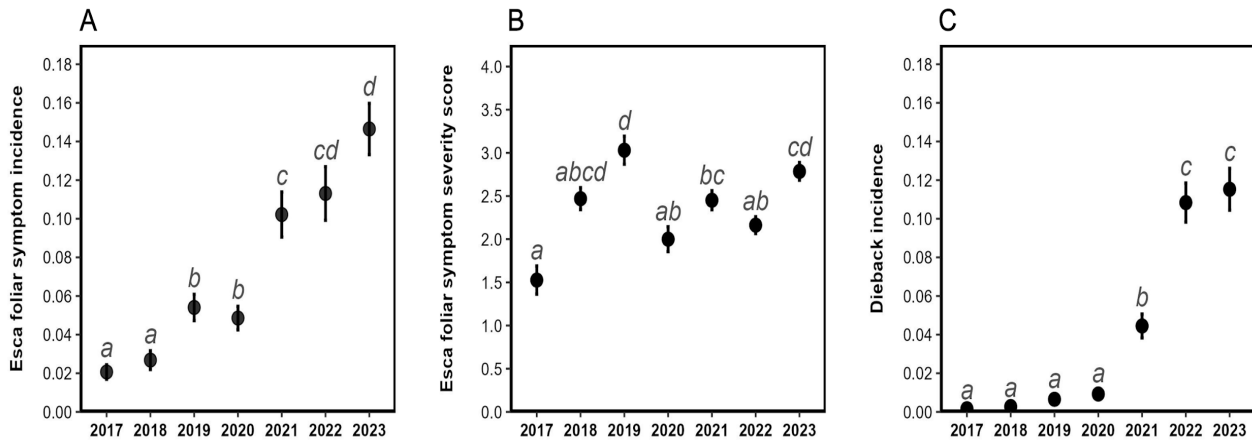


**Figure 2. Changes over time in the three variables related to esca foliar symptoms and dieback for all cultivars from 2017 to 2023 (mean plant age increasing from 7.8 years in 2017 to 13.8 years in 2023)**

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

**Esca incidence differs considerably between cultivars**

The incidence of esca foliar symptoms differed significantly between the 46 cultivars monitored from 2017 to 2023 ($p < 10^{-16}$). We found a large gradient of susceptibility to esca foliar symptoms, as four grape varieties (Merlot, Petit Manseng, Tannat and Xinomavro) never expressed symptoms during 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).

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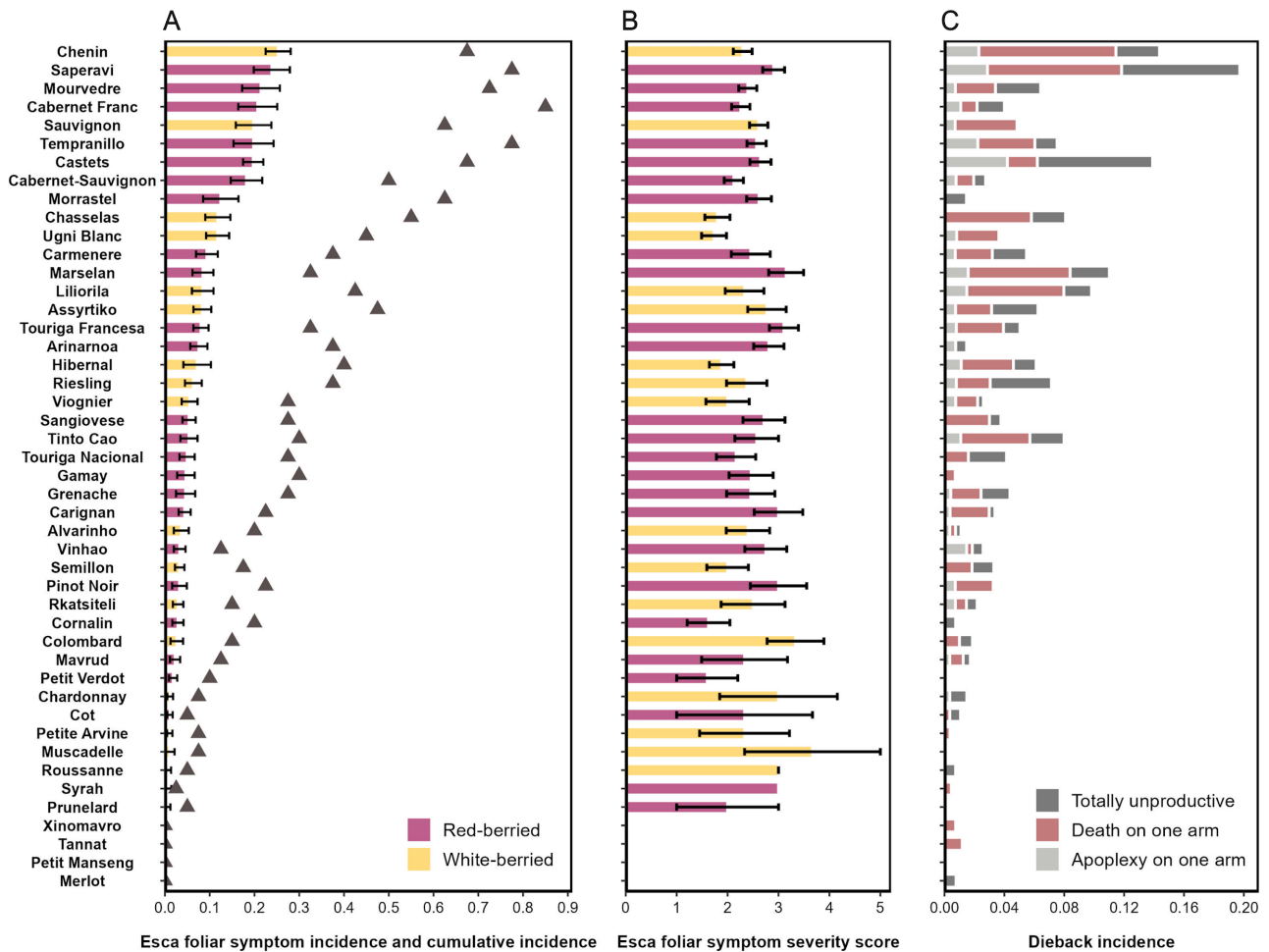
**Figure 3. Variability of susceptibility to esca foliar symptoms and dieback among grapevine cultivars for the period 2017 to 2023.**

(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.

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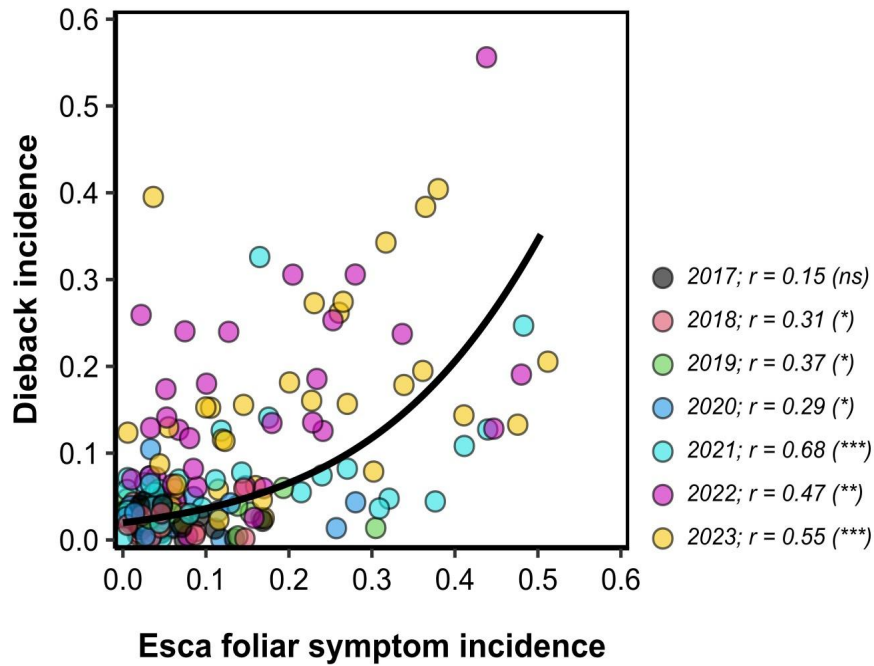
**Figure 4. Relationship between the incidence of esca foliar symptoms and the incidence of dieback**

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,

20

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



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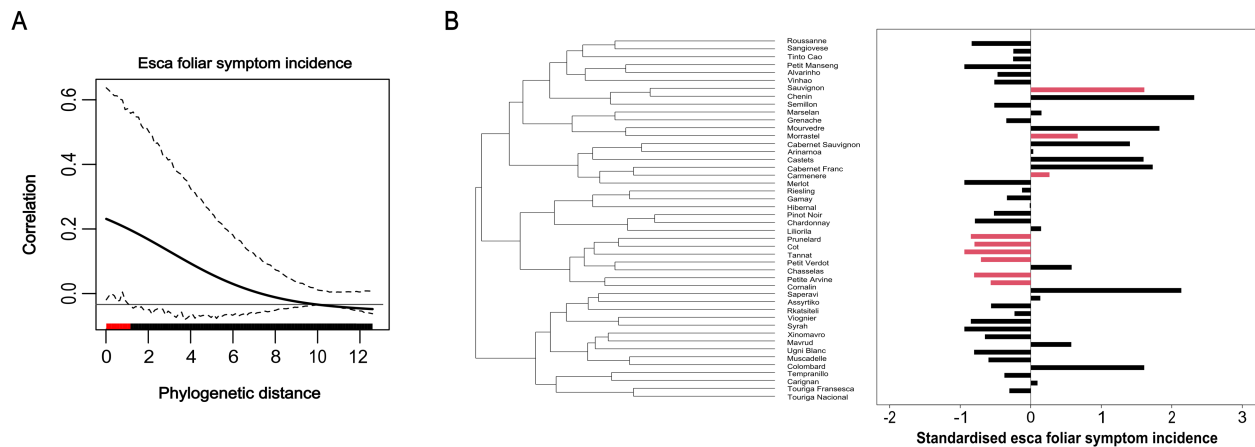
**Figure 5. Relationship between genetic distance and the incidence of esca foliar symptoms for a panel of 46 grapevine cultivars**

(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

21

390    symptoms. Red bars correspond to tips for which the local Moran's index $I_i$ was significant (i.e.

391    $p < 0.05$ in a test based on permutations).

392

**Varietal patterns of esca incidence remain constant over time**

394    We investigated whether the incidence and severity of esca and plant dieback remained constant over

395    time by performing two-by-two correlation analyses at cultivar level between the three

396    epidemiological metrics, using the mean values for each of the six years of monitoring (a positive

397    correlation indicates similar varietal patterns of incidence). For the incidence of foliar symptoms, all

398    but one of the year-by-year correlations were clearly positive and significant, the exception being

399    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).
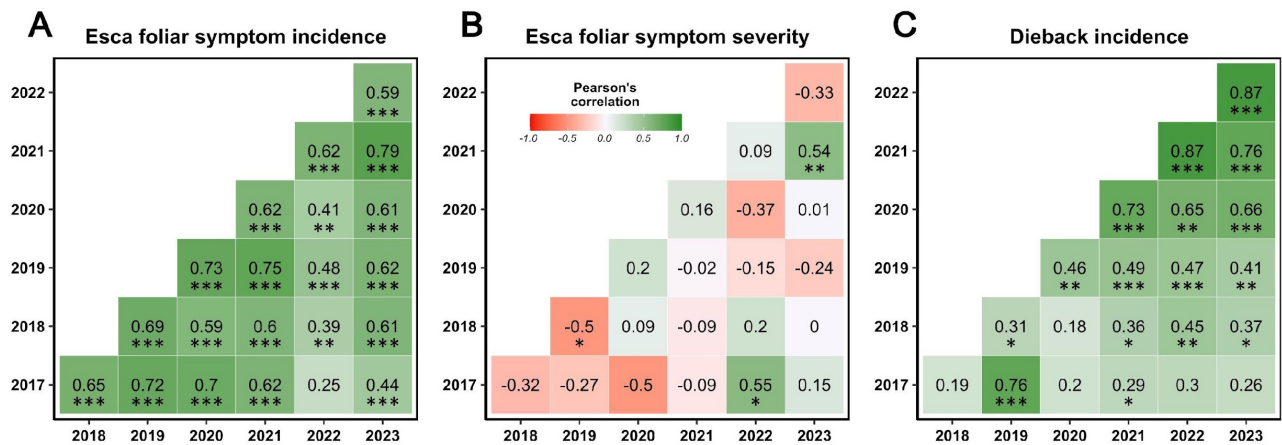
**Figure 6. Inter-annual correlations of mean varietal values for the three variables related to esca foliar symptoms and dieback**

(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.

23

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*).

24
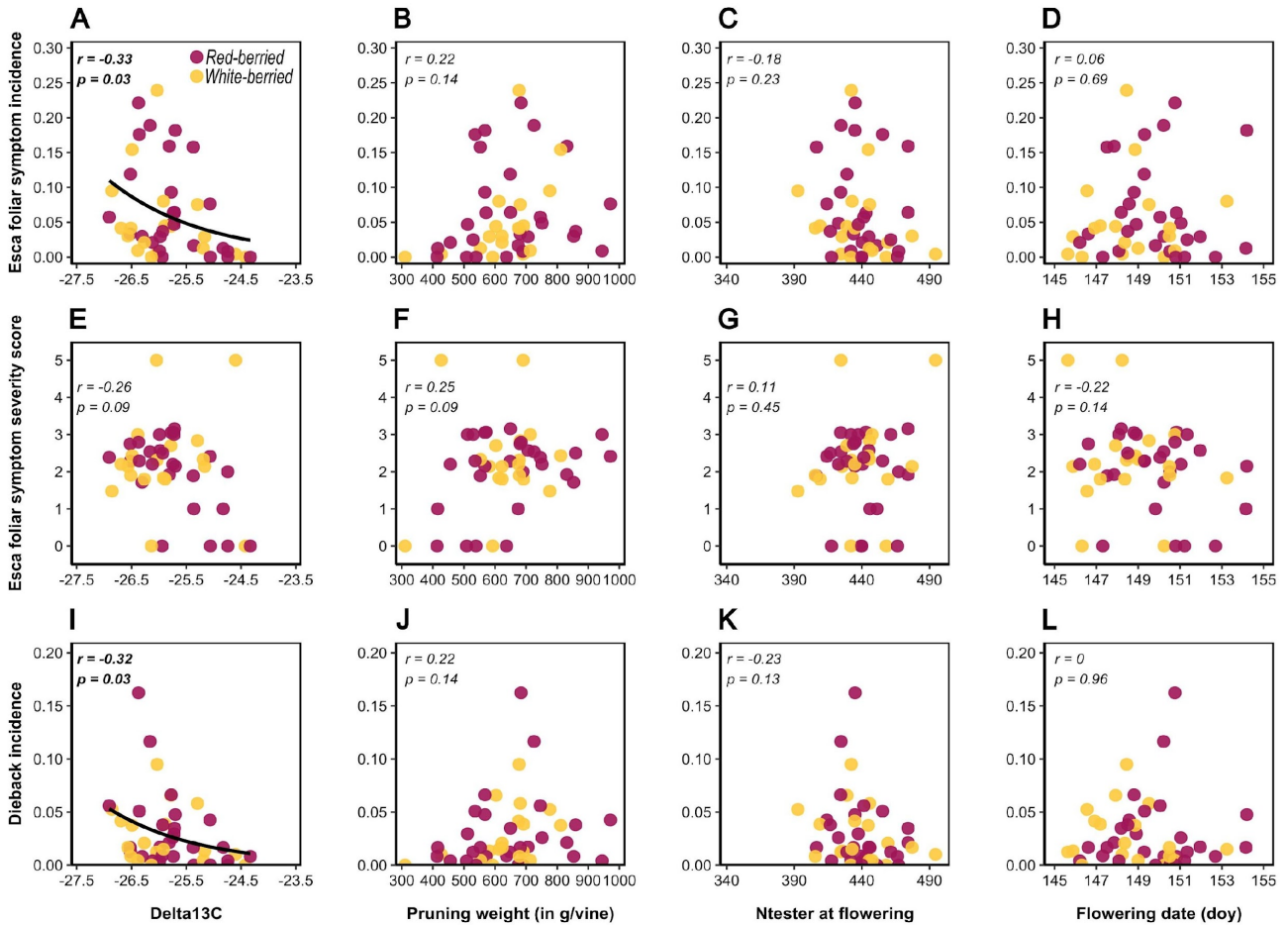
**Figure 7. Relationships between three variables related to esca foliar symptom and dieback and four ecophysiological and phenological traits**

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.

## Discussion

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

The results obtained with VitAdapt indicate that there is a high level of fairly stable cultivar-associated variability in terms of esca expression. The long-term monitoring of the VitAdapt common garden revealed a significant variability of esca foliar symptoms and plant dieback between the 46 grapevine cultivars. Several cultivars only very rarely expressed foliar symptoms or dieback phenotypes, whereas others, including several of high economic importance, were much more strongly affected by esca and dieback. The use of a common garden design and the inclusion of a block effect in statistical models made it possible to prevent possible biases in the calculation of esca incidence due to the variability of soils and viticulture practices. Our results provide new information for consideration in the discussions of cultivar rankings for esca susceptibility obtained in previous multiregional and multicultivar monitoring programmes. For example, Ugni Blanc, for which very high incidences were recorded in the Charentes region (France; Bruez *et al.*, 2013), did not cluster among the most susceptible cultivars in our vineyard, in which all cultivars were subject to the same environment and the same viticulture practices (e.g. double guyot pruning system). Bruez *et al.* (2013) showed that, for a given cultivar, a large proportion of the residual variability is due to the growing area. There are at least two possible explanations for this. First, there can be considerable climatic variation between regions. Second, the incidence of esca disease may be affected by differences in viticulture systems and practices from between regions (Lecomte *et al.*, 2018). This may be the case

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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.

27

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

637 potentially plastic in response to the environment. It therefore seems necessary to replicate such

638 monitoring under contrasting conditions, to facilitate the selection of the most suitable cultivars for

639 each production context. Within this framework, a complementary strategy would involve monitoring

640 a single cultivar in multiple environments (see Monod *et al.*, 2023).

641 Finally, we recommend tackling the highly multifactorial nature of plant dieback through integrative

642 approaches taking multiple factors, such as other pests and diseases, climatic hazards, soil fertility

643 and technical management, into account.

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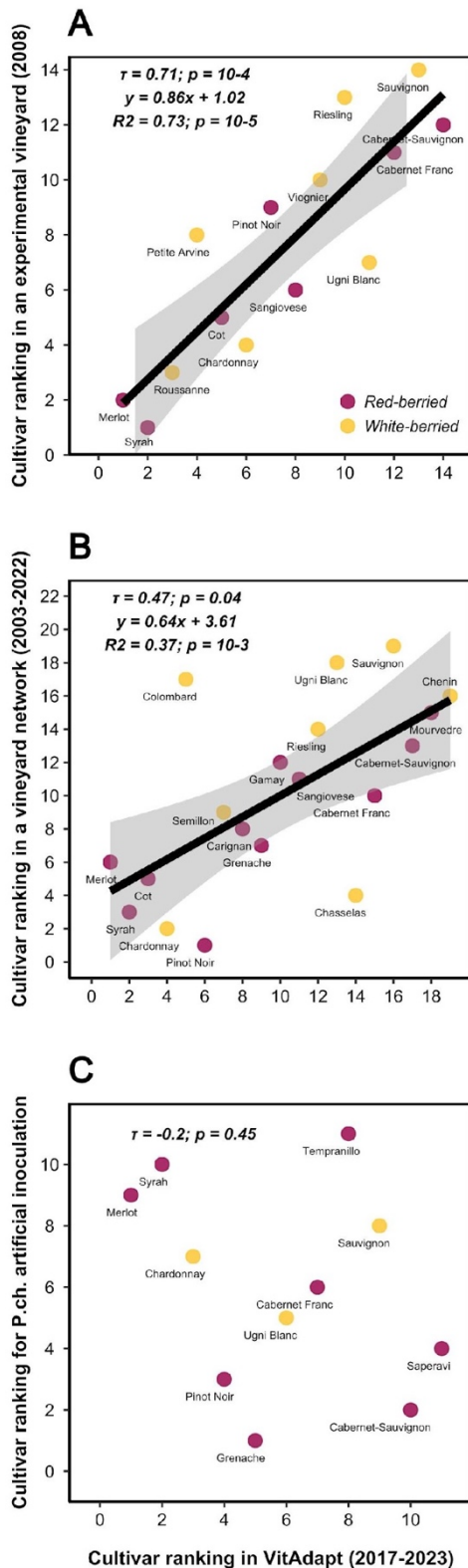
**Figure 8. Scatterplots showing the relationships between cultivar ranks for susceptibility to esca as assessed in this work and reported in previous publications.**

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.

35

## Acknowledgements

## Competing Interests statement

685    The authors have no competing interests to declare.

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