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Identifying the pedoclimatic conditions most critical in the susceptibility of a grapevine cultivar to esca disease

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ABSTRACT

Esca, one of the most destructive grapevine trunk diseases, is still poorly understood. As grapevine cultivars vary widely in their susceptibility to esca, we designed a four-year experiment to identify the environmental factors that influence the expression of the disease in a susceptible cultivar. We collected epidemiological and physiological data once a year for four consecutive years in 19 vineyard plots located in four wine-growing regions of Western Switzerland. We compared these data with climatic data obtained from weather stations for these same plots for four years and over the long term. We also estimated the soil water holding capacity of each plot. Confounding factors were minimal because all vineyards were planted in 2003 with the same cultivar and all plants grafted in the same nursery with genetically homogeneous grafting material. Principal component and regression analyses of combined epidemiological, biotic and pedoclimatic data identified a positive correlation between soil water retention capacity and plant mortality due to esca. These analyses also showed that leaf disease symptoms and apoplexy are more frequent when cold and wet periods are followed–or alternate with–hot and dry periods, and that apoplexy occurs more frequently when weather conditions change abruptly (a cold and wet May followed by a hot June) and deviate significantly from long-term climatic conditions. Regression analyses show that the soil water holding capacity impacts less the disease expression when the climate is warm and dry, both at the regional and year-specific levels. Having identified the most important environmental factors towards the expression of esca, this study allows recommendations to be given to the winegrowers for the cultivar studied but can also be used as a model to identify the environmental factors that influence the expression of fungal diseases in other grapevine cultivars and other grapevine trunk diseases.

KEYWORDS: grapevine trunk diseases, Gamaret grapevine cultivar, soil water holding capacity, nitrogen accessibility, rootstock 3309C

INTRODUCTION

Grapevine plants, with a lifespan of 30 years or more, are subject to a variety of biotic and abiotic stresses (Songy *et al.*, 2019; Suzuki *et al.*, 2014). Since the early 1980s in Europe, an increase in plant and crop losses in mature vineyards has begun to be reported (Gramaje *et al.*, 2018; Larignon & Dubos, 1997; Mugnai *et al.*, 1999). Plant decline was attributed to grapevine trunk diseases (GTDs), caused by fungal species repeatedly isolated from symptomatic wood (Bertsch *et al.*, 2013). GTDs pose a real threat to the viability and sustainability of viticulture (Bertsch *et al.*, 2009; Kenfaoui *et al.*, 2022). The most damaging GTD in Europe is esca (Bortolami & Gambetta, 2021a) although Dewasme *et al.* (2022) have recently suggested that the impact of this disease on yield, vine quality and plant mortality may be overestimated.

Numerous studies have attempted to understand the impact of soil type, particularly its ability to retain water, and/or climate on esca disease expression (Bortolami & Gambetta, 2021a; Calzarano *et al.*, 2018b; Dubos *et al.*, 2002; Fischer & Peighami-Ashnaei, 2019; Guérin-Dubrana *et al.*, 2013; Marchi *et al.*, 2006; Surico *et al.*, 2000). However, such studies have been conducted in different regions, countries, or continents, often on different grape varieties with different disease susceptibility (Andreini *et al.*, 2014), with plants of different ages, grown and pruned in different ways (Gramaje *et al.*, 2018). The disparity of these studies has made it difficult to generalise the results obtained and to precisely identify the role of the pedoclimatic and biotic factors responsible for the variability in the incidence of esca observed in different regions and for different grape varieties (Bertsch *et al.*, 2009).

The incidence and severity of esca typical leaf stripes symptoms (Surico *et al.*, 2009) were reported to vary from year to year (Andreini *et al.*, 2014; Calzarano *et al.*, 2007; Calzarano *et al.*, 2014; Del Frari *et al.*, 2022; Marchi *et al.*, 2006; Moret *et al.*, 2021; Ouadi *et al.*, 2019), independently of the rate of wood deterioration by fungi (Calzarano *et al.*, 2007). Moreover, plant mortality appeared higher for plants that had expressed foliar symptoms the previous year (Dewasme *et al.*, 2022; Guérin-Dubrana *et al.*, 2013; Serra *et al.*, 2021). Environmental constraints seem though to play a key role as they impact grapevine physiological behaviour by influencing host–microbiome interactions (Delmas, 2021), triggering the transition from a fungal endophyte state to a pathogenic state (Porras-Alfaro & Bayman, 2011; Saikkonen *et al.*, 2003) and/or accelerate the translocation of metabolic compounds throughout the plant via sap flow (Claverie *et al.,* 2020). Soils with high water holding capacity (deep, clayey soils) and climatic variations during the summer are factors reported to increase the risk of sap flow disruption (Surico *et al.*, 2006). Vines with even mild foliar symptoms already suffer from hydraulic failure, a decrease in conductance in petioles and shoots, compared to healthy plants (Ouadi *et al.*, 2019). Other important factors influencing disease expression appear to be linked to the plant physiology including the plant water status during growth periods, vigour (leaf area), carbon:nitrogen ratio in plant tissues (Berger *et al.*, 2007), functioning of the vascular system (Andreini *et al.*, 2009; Edwards *et al.*, 2007) and macro and micro-element content (Calzarano *et al.*, 2021; Calzarano *et al.*, 2023). Two main hypotheses have been put forward to explain conductance failure: gas embolism (Canny, 1997) and/or occlusions (Sun *et al.*, 2007), the latter either related or not with fungal pathogens. A recent study has shown that occlusions by tyloses and gels, probably induced remotely by phytotoxins produced by esca-associated fungi, lead to hydraulic failure in veins of esca-symptomatic leaves (Bortolami *et al.*, 2019). However, the role of esca-associated fungi in the expression of foliar symptoms is still under investigation. Removal of dead wood from vines showing foliar symptoms of esca has proved effective in enabling plants affected by the disease to recover for several years (Lecomte *et al.*, 2022). Another study recently tested the effect of drought on grapevines under controlled conditions (Bortolami & Farolfi, 2021b) and found that it prevents the expression of esca symptoms, while rain in spring and early summer tends to increase esca symptoms expression (Marchi *et al.*, 2006, Calzarano *et al.*, 2018b). Bortolami and Gambetta (2021a) also showed that, although esca had no long-term impact on plant sensitivity to drought, the two stresses, drought and esca vascular occlusions, could jointly contribute to plant mortality. While differences in esca susceptibility between cultivars are relatively well documented (Bruez *et al.*, 2013; Chacón-Vozmediano *et al.*, 2021; Guérin-Dubrana *et al.*, 2019; Marchi, 2001; Serra *et al.*, 2021), variation in esca susceptibility of a single grape variety across multiple viticultural regions has rarely been tracked in long-term epidemiological studies (Dewasme *et al.*, 2022; Guérin-Dubrana *et al.*, 2013; Surico *et al.*, 2000) and never, to our knowledge, by combining epidemiological data not only with climatic conditions but also with soil characteristics and plant physiological data.

To determine the impact of soil, climate and biotic factors on esca expression, we reduced the effects of confounding factors by using a network of vineyards and studied for esca expression since planting in 2003. In this network, 19 plots of an esca susceptible cultivar (Gamaret) were selected, with all plants grafted with homogeneous scion and rootstock material in the same nursery and managed under uniform cultural practices. Such a network of vineyards can serve as a model to study the relationship between esca disease expression and soil and climatic regional and microclimatic conditions. Since climatic demand and soil characteristics vary within this network, this creates optimal conditions to study the influence of pedoclimatic factors on the prevalence of esca. This experimental design allowed us i) to examine the variability of esca incidence in vineyards located in different geographical areas, independently of plant age, cultivar and vineyard cultural practices; ii) to explore the relationship (independence or correlation) between esca expression, pedoclimatic factors and vine physiological factors in different vine-growing regions iii) to identify which factor(s) could be a good candidate(s) to predict esca expression.

MATERIALS AND METHODS

1. Study sites, esca epidemiology and plant material

The study was carried out in 19 vineyards in Western Switzerland (Figure 1). These plots were all planted in 2003 with *Vitis vinifera* L. cv Gamaret, a Swiss red variety developed from a cross between Gamay × Reichensteiner. This vine variety is well established in Switzerland with circa 500 ha (representing 3 % of the Swiss vineyard area). Vine plants were all grafted onto 3309C rootstock (*V. riparia x V. rupestris*) with the same plant/genetic material coming from the same nursery stock. All vines were trained in the single Guyot system (vertical shoot-positioned foliage) with an average planting density of 7500 ± 500 vines ha^{-1}. All the vineyards were pruned with comparable techniques. The soil management included a natural cover cropping between the rows for all the plots implanted in Vaud (15 plots, Figure 1A). On the Valais plots (Figure 1A), chemical weed control was carried out.

The vineyard plots (Figure 1B) were monitored for esca mortality from their planting in 2003 until the beginning of this study in 2018. Cumulated plant mortality data gathered before the experiment (2003–2017) appeared highly variable (Figure 1B), ranging from 0 % to 48 % depending on the vineyard plots. Consequently, the Gamaret cultivar was selected as a good candidate to study the influence of biotic and abiotic factors on the incidence of esca.

For four consecutive experimental years (2018–2021), when esca symptoms were most visible in late August or early September, about 300 vines in each of the studied vineyard plots were examined for the presence of esca symptoms (5700 plants on the whole network). For the epidemiological monitoring, we classified symptoms into five categories: 1) apparently healthy plants (plants exhibiting no discernible symptoms); 2) weak foliar symptoms (a single symptomatic shoot); 3) medium foliar symptoms (more than one symptomatic shoot); 4) strong foliar symptoms (shoots all displaying symptoms); 5) apoplectic symptoms on the entire plant. The proportion of affected plants per plot, from year to year, was inferred based on the number of plants originally planted in 2003 and still present in 2021.

2. Climatic data

Meteorological data were collected from the Data portal for teaching and research (IDAweb; https://www.meteoswiss.admin.ch/services-and-publications/service/weather-and-climate-products/data-portal-for-teaching-and-research.html) of the Federal Office of Meteorology and Climatology MeteoSwiss. Climatic data were collected from meteorologic stations for locations representative of each of the four wine-growing regions under study (Figure 1A): Lake of Geneva (Pully), Lake of Neuchâtel (Method), Chablais (Aigle) and Valais (Sion). We collected weather data for the four years of the experiment (2018–2021) as well as for previous years (1990–2017) to derive a climate norm for comparison. Meteorological norms (min, max, quartiles and median) were then computed for these four stations.

To increase the accuracy of meteorological data, automatic stations in the Agrometeo (http://www.agrometeo.ch) were chosen according to their proximity to the network plots. Those stations were thus not suitable for the computations of climatic norms but were used for the measurements during the experiment (2018–2021). We gathered from Agrometeo the precipitation, temperature and evapotranspiration measurements for 11 c stations. Secondary variables were computed from the raw data. From the precipitation data, we created nine secondary variables (Table 2): monthly precipitation; number of days per month with rainfall; number of days per month with ≥ 0.1 mm, > 0.3 mm, > 10 mm, > 100 mm; absolute deviation from monthly median sum; deviation of the number of days per month with precipitation from the monthly average; number of days per month superior and inferior to the median. From the temperature data, we created four secondary variables: number of days per month above and below the median; number of days per month with > 25 °C; number of unusually hot days (maximum temperature ≥ 30 °C) per month, deviation from

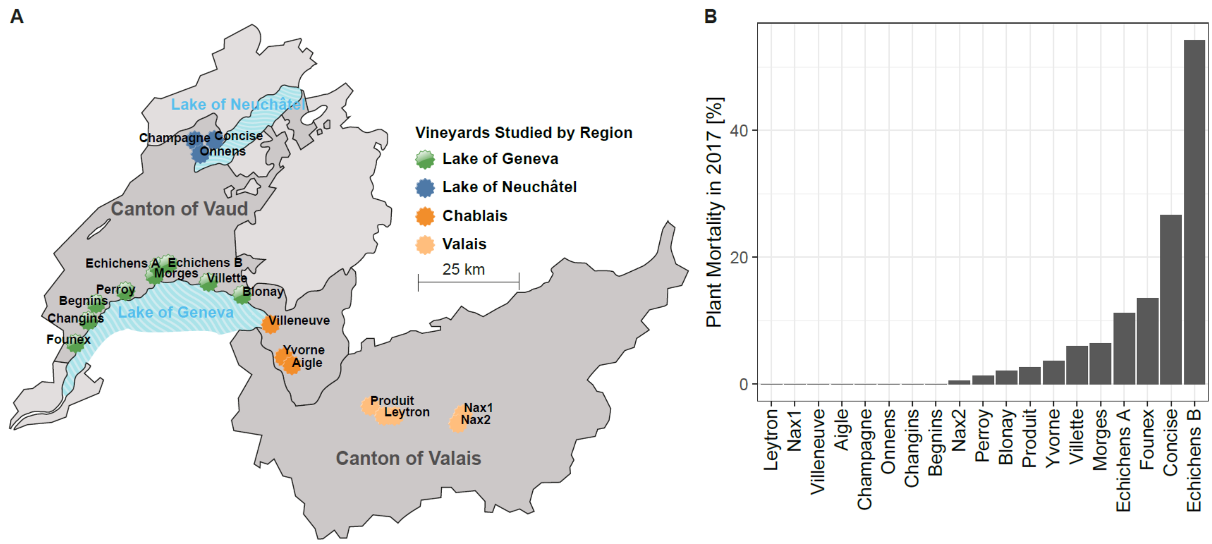

FIGURE 1. A) Map of the Gamaret vineyards monitored across western Switzerland. B) Cumulative replacement rate [% of plants] from vineyard plantation in 2003 through 2017 across the study plot network.

TABLE 1. Biotic and abiotic variables were considered to establish Pearson and Xicor correlation coefficients with esca epidemiological monitoring data on the entire plot network.

Variables name	Variable description
Total_acidity	See "Material and methods"
Brix	
K	
Mg	
P	
N_Assim	
N_tester	
N_tot	
Delta13C	
Berries_weight	
Pruning_weight	
SWHC	
Cover_cropping	
ColderDays_Apr	Days colder than the norm (1990–2017) per month
ColderDays_Aug	
ColderDays_Jul	
ColderDays_Jun	
ColderDays_Mar	
ColderDays_May	
diffRainfallNorm_Apr	Difference to norm (1991–2017) amount of rainfall per month
diffRainfallNorm_Aug	
diffRainfallNorm_Jul	
diffRainfallNorm_Jun	
diffRainfallNorm_Mar	
diffRainfallNorm_May	
diffRainyDaysNorm_Apr	Difference to the norm (1991–2017) nb. Rainy days per month
diffRainyDaysNorm_Aug	
diffRainyDaysNorm_Jul	
diffRainyDaysNorm_Jun	
diffRainyDaysNorm_Mar	
diffRainyDaysNorm_May	
WarmerDays_Apr	Difference to norm temperature per month
WarmerDays_Aug	
WarmerDays_Jul	
WarmerDays_Jun	
WarmerDays_Mar	
WarmerDays_May	

Variables name	Variable description
EPT_Apr	Evapotranspiration per month
EPT_Aug	
EPT_Jul	
EPT_Jun	
EPT_Mar	
EPT_May	
NbDay01_Apr	Nb days with rain >1 mm per month
NbDay01_Aug	
NbDay01_Jul	
NbDay01_Jun	
NbDay01_Mar	
NbDay01_May	
NbDay03_Apr	Nb days with rain >3 mm per month
NbDay03_Aug	
NbDay03_Jul	
NbDay03_Jun	
NbDay03_Mar	
NbDay03_May	
NbDay10_Apr	Nb days with rain >10 mm per month
NbDay10_Aug	
NbDay10_Jul	
NbDay10_Jun	
NbDay10_Mar	
NbDay10_May	
Rainfall_Apr	Precipitations [mm] per monthw
Rainfall_Aug	
Rainfall_Jul	
Rainfall_Jun	
Rainfall_Mar	
Rainfall_May	
SummerDays_Aug	Nb days with >25 °C per month
SummerDays_Jul	
SummerDays_Jun	

average (1991–2020 norm). We consider only meteorological data from April to September, the period most likely to influence the incidence of esca foliar symptoms and plant mortality.

3. Soil types and soil water holding capacity (SWHC)

Around 80 % of the vineyard plots studied are alpine moraines. Moraines can be classified into three types (Letessier & Fermond, 2004): bottom moraines with few stones (< 30 % coarse elements), stony moraines (30–60 % coarse elements) and gravely moraines (> 60 % large elements and stones).

For most of the plots (15), a hole of 1.5 m deep × 1 m wide was dug between two rows of vines. For four plots, the hole was dug to a depth of 2 m because the roots were deeper, and the bedrock was not reached. The SWHC was calculated according to (Letessier & Fermond, 2004). A cultural coefficient was applied for each of the soil textures (Baize & Jabiol, 2011).

4. Physiological and agronomical monitoring of the vineyard plots

To determine the vine water status, two approaches were used: the measurement of predawn leaf water potential (Ψ_{PD}) and the analysis of the carbon isotope composition ($\delta^{13}C$) in berries at harvest. Predawn leaf water potentials (Ψ_{PD}) were measured using a pressure chamber (Scholander *et al.*, 1965) between 2 and 5 a.m., in complete darkness, on eight mature, undamaged, and non-senescent leaves centrally placed in the foliage on each location when evapotranspiration was at the minimum. The mean values of eight leaves per plot were used as predawn water potential variables. The level of water stress of each plot was assigned according to (van Leeuwen *et al.*, 2009). Predawn water potentials were measured at the veraison (BBCH 83-85) stage once a year in August. The stable carbon isotope ($\delta^{13}C$) composition of the must sugars (200 berries sample by plot) was determined at harvest at the Stable Isotopes Laboratory of the University of Lausanne by elemental analysis-isotope ratio mass spectrometry (EA-IRMS) using a Carlo Erba 1108 elemental analyzer connected to a Thermo Fischer Scientific (Bremen, Germany) DeltaV mass spectrometer. The stable isotope composition was reported as $\delta^{13}C$ values per mille (‰), with deviations of the isotope ratio relative to known standards as follows: \delta = $[(R_{\text{sample}} - R_{\text{standard}})\,/\,R_{\text{standard}}] \times 1000$, where is the ratio of heavy to light isotopes ($^{13}C/^{12}C$). The R_{standard} value for $\delta^{13}C$ in Vienna Pee Dee Belemnite limestone is 0.0112372 (Deléens *et al.*, 1994).

At veraison, a foliar analysis was performed to determine the levels of leaf nitrogen, potassium, phosphorous, calcium and magnesium. The samples consisted of 30 leaves gathered in the cluster zone. Leaves with petioles were washed, over-dried, ground and analysed by Sol Conseils (Gland, Switzerland). Leaf chlorophyll index was measured using an N-tester device (Yara, Nanterre, France) on adult leaves situated in the middle of shoots. In early winter, the total weight of the pruned vine shoots was recorded (30 shoots per vineyard). The second or last shoot of the fruiting cane was chosen for the measurement. Thirty shoots per plot (one per plant) were sampled and cut to a length of 1 meter and individual shoot weights were determined (g/linear meter).

At harvest, 200 berries per vineyard were randomly selected and weighted. After weighing the berries, the juices extracted from the individual berries were analysed by the Oenology Laboratory of Agroscope to establish their sugar, pH, malic and tartaric acid contents, and their assimilable nitrogen content Using WinScan® infrared spectroscopy (FOSS NIRSystems, USA).

5. Statistical analyses

We used principal component analyses (PCA) to see if meteorological and physiological parameters could influence annual esca incidence and test if these variables could be used to predict disease incidence. These analyses also feature collinearity between meteorological and physiological variables. Three variables reporting for esca incidence were created: the number of apoplectic plants over the four years of the experiment, the sum of all types of foliar symptoms, and the overall symptoms (all types of foliar symptoms plus apoplexy).

We then used two distinct methods to assess the strength of the relationships between our variables (Table 1). We first considered Pearson's correlation coefficient and a recently developed correlation-coefficient index $\xi-$correlation coefficient (Chatterjee, 2019) that considers any kind of functional relationship with the property of being equal to zero if and only if there is independence. It has been implemented in R in the package xicor (Holmes & Chatterjee, 2021). To screen the explanatory variables that might influence the esca incidence, we fixed some thresholds and considered the variables whose correlation with the variables of incidence was higher (in absolute value for the correlation).

RESULTS

1. Esca epidemiological data across the four-year experiment

Looking at the percentage of plant apoplexy and foliar symptoms in the different regions from 2018 to 2021 (Figure 2) the plots located on the shores of Lake of Geneva, and to a lesser extent the plots located on the shores of Lake of Neuchâtel, expressed more esca symptoms of both types than the other two regions studied, consistently over the years under study. In Valais, annual symptoms (apoplexy and foliar symptoms) were close to zero, while in Chablais they were slightly higher but always inferior to 1 %. However, apoplexy and foliar symptoms showed a different evolution during the four years of experimentation. The years 2019 and 2021 were the worst for apoplexy in three of the regions (Lake of Geneva, Lake of Neuchâtel and Chablais; Figure 2), as were the leaf symptoms of Esca, but only in Lake of Neuchâtel. In 2020 and 2021, more than 4 % of the vines in the Lake of Geneva plots expressed foliar symptoms, compared to just over 2 % in 2018 and 2019. Foliar symptoms were generally slightly increasing from year to year in all regions except Valais. Of the four regions studied, Lake of Geneva is clearly the most susceptible to Esca, while Valais and Chablais seem much less susceptible.

A closer examination of the epidemiological data, looking at individual plots rather than wine-growing regions (Figure 3), showed that Morges was the plot with the highest cumulative esca symptoms in the Lake of Geneva region (21 % in 2018 to 56 % in 2021), followed by Begnins (17–40 %), Echichens A (18–27 %) and Villette (7–18 %), but never exceeded 10 % in Blonay during the four years of the experiment. In the Lake of Neuchâtel region, Champagne and Concise showed more symptoms (8–12 % and 10–25 %, respectively) than Onnens (4–11 %) from 2018 to 2020. This situation reversed in 2021, with Onnens and Champagne both expressing a cumulative incidence of esca symptoms more than twice as high (> 20 %) than Concise (10 %). In the Chablais region, the plot with the highest rate of esca was Yvorne (with a peak of 14 % in 2019), while the disease incidence in plots in Villeneuve and Aigle has never exceeded 5 %, except in Villeneuve in 2021 (9 %). In Valais, Produit was the plot with

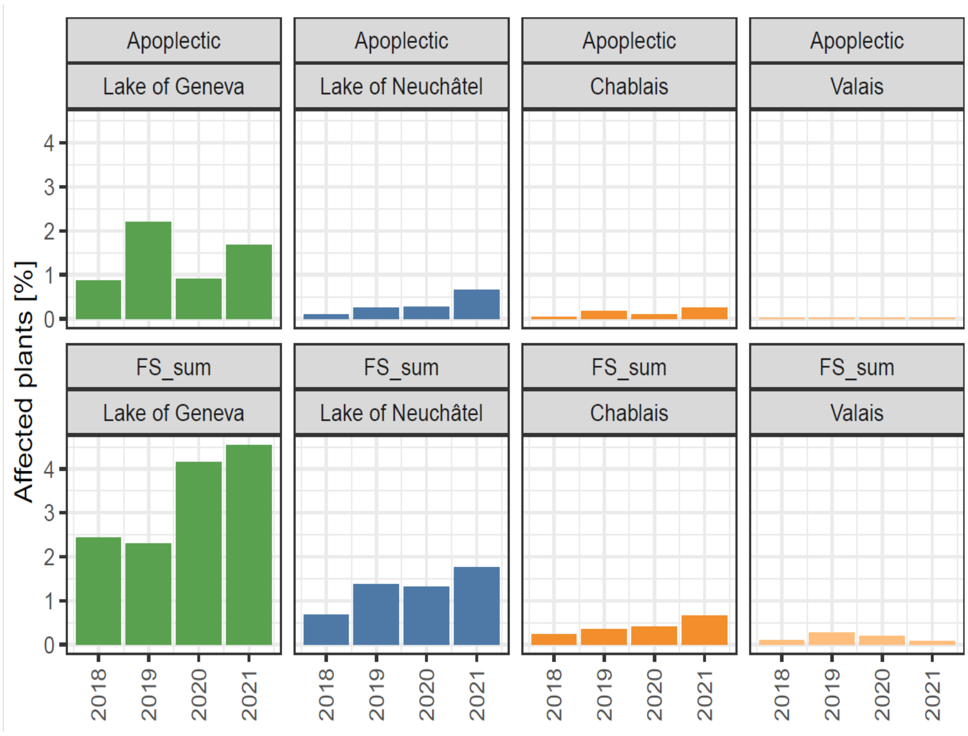

FIGURE 2. Sum of plants [%] affected by apoplectic symptoms and by the sum of foliar symptoms (FS_sum) for the four monitored vintages (2018–2021) by wine-growing region.

the highest incidence of symptoms (4–8 %), followed by Nax 2 (6 % in 2019 and 5 % in 2020). In Leytron and Nax 1, the incidence of esca was almost zero in all four years. These results show that the incidence of esca symptoms varies from year to year and plot to plot, whatever the region considered.

2. Climatic characterisation of the survey period

The four-year survey period was marked by precipitation regimes often deviating from the long-term norm (Figure 4). While 2018 was drier than the norm, except in the Lake of Neuchâtel region from May to July (Figure 1A), 2019 and 2020 were characterised by alternate drier or wetter months than the long-term norm during the six months of grapevine vegetative period considered.

The year 2021 was very wet from May to July, preceded and followed by drier-than-normal months, with the exception of June in Valais. Precipitation differences to the long-term norms were observed in all four wine-growing regions (Figure 4), however, they were more pronounced in Lake of Geneva, Lake of Neuchâtel and Chablais than in Valais, where except in 2021 in May and July, the precipitation regime remained closer to the norm than in the three other regions.

Temperatures (Figure 5) were overall higher than the long-term norm during the first three years of the survey period (2018–2020) in the four wine-growing regions, except for May in 2019, which was particularly cold everywhere, and June which was a bit colder than usually in all regions except in Valais. The year 2021 was very peculiar regarding temperatures and highly similar in the four wine-growing regions. This year was characterised by an alternance of cold and hot months in all regions. While April and particularly May were colder than the long-term temperature norm, June appeared hotter than the norm, July and August cooler and September hotter. The month of May appeared the most singular month in 2019 and 2021, with very cold temperatures compared to the long-term norm in all four regions. Moreover, during the four years of the survey period, temperatures were more homogenous across regions (Figure 5) than the precipitations (Figure 4) and Valais appeared no different than the other three wine-growing regions regarding temperature fluctuations.

3. Soil types and soil water holding capacity (SWHC)

The sites studied were roughly grouped by category of SWHC (Table 1). The SWHC was calculated on each plot by taking into account the amount of stones, texture, root colonisation and rooting depth (Letessier and Fermond, 2004). The SWHC corresponds to the maximum amount of water in the soil that the vine can extract (Baize and Jabiol, 2011). A quarter of the plots have a SWHC ≤ 100 mm (low), another quarter of the plots have a SWHC between 100 and 150 mm (medium), and half of the plots have a SWHC > 150 mm (high).

4. Physiological and agronomical monitoring of the vineyard plot

Comparing the different record years, none of the plant physiological indices (Ψ_{PD}, $\delta^{13}C$, assimilable nitrogen, chlorophyll content of the leaves, weight of the pruning and of the berries) remained stable across the four years experiment (Figure 6). Apart from water potential (Ψ_{PD}), which increased in 2020 for plots with an average SWHC, remained stable for plots with a high SWHC and decreased

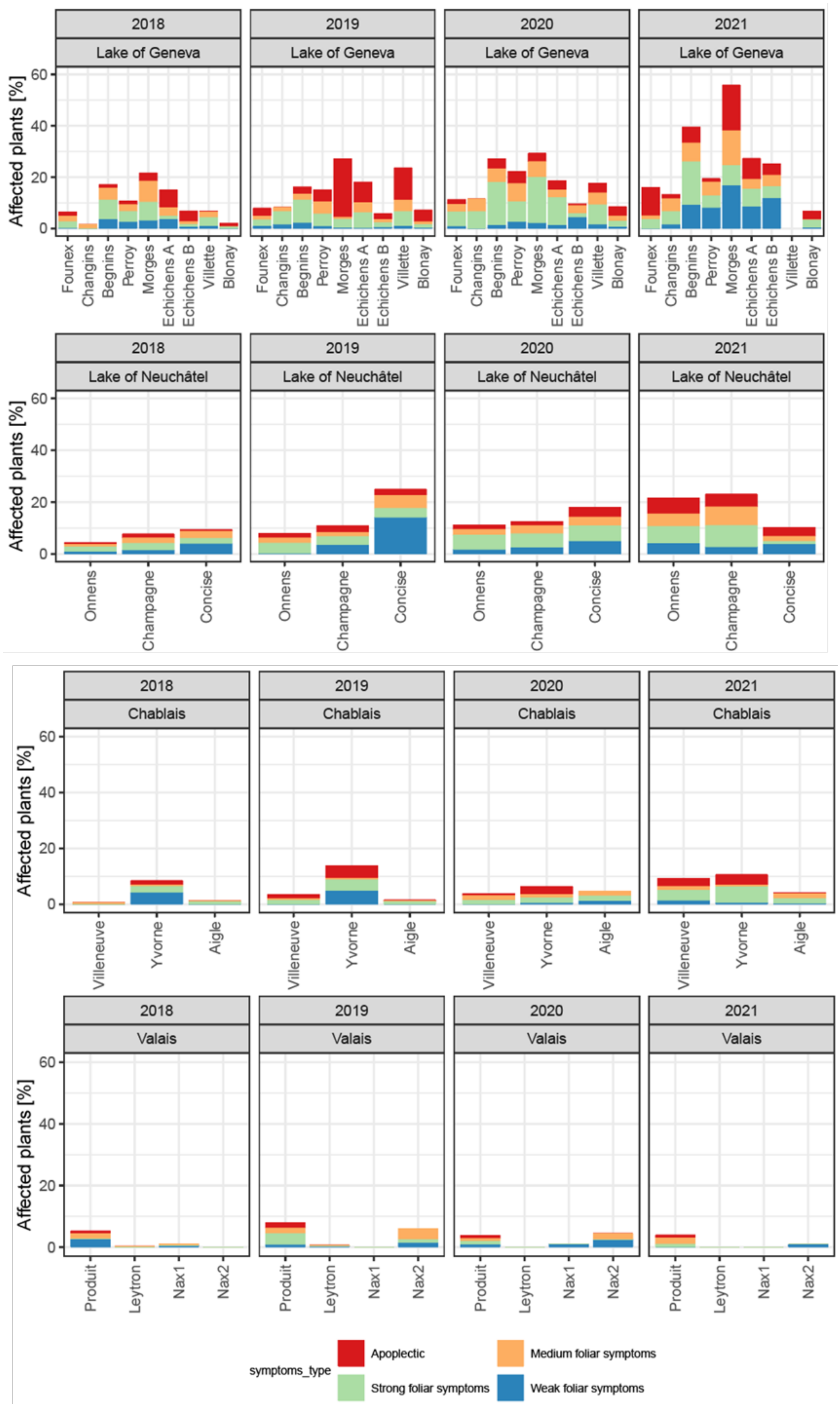

FIGURE 3. Annual rate of esca symptomatic plants by vineyard plots and by region for weak, medium, and strong foliar symptoms and apoplectic plants (2018–2020).

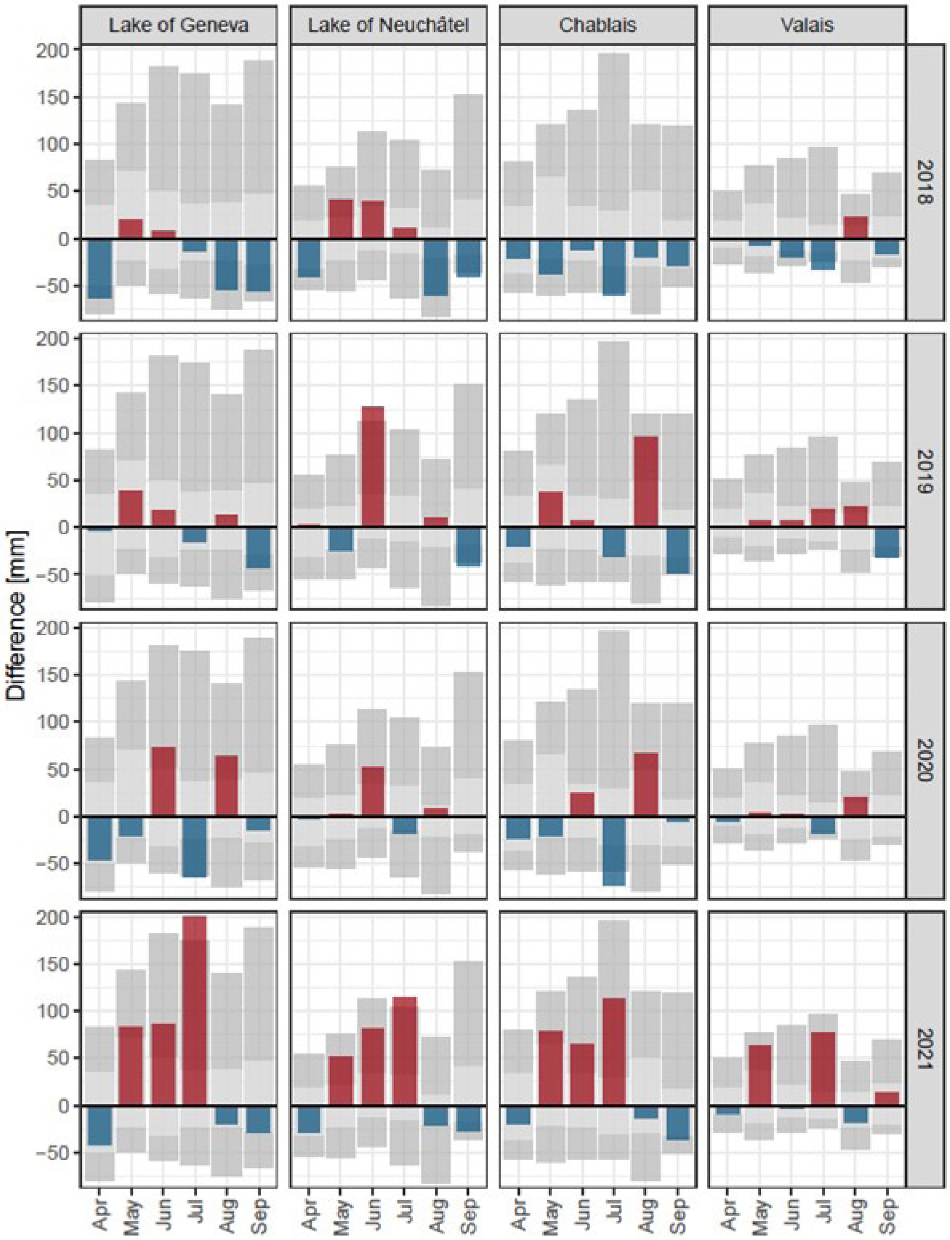

FIGURE 4. Positive (red) or negative (blue) differences to the long-term median (1990–2017) in monthly spring and summer precipitations (mm) in four wine-growing regions of Western Switzerland from 2018 to 2021. The background rectangles are the minimum and maximum (dark grey) and the 25 % and 75 % percentile (light grey) of the same data over the period 1990–2017.

for plots with a low SWHC (Figure 6A), all the other biotic factors (Figure 6B–F) followed the same pattern depending on the vintage and independently of the SWHC. Grapevine plants grown on soils having a low SWHC exhibit lower pre-dawn water potential and pruning weight but a higher rate of assimilable nitrogen and chlorophyll than vineyards planted in soils with medium and high SWHC. For these latter plots, assimilable nitrogen in harvested berries (Figure 6C) was generally low in 2018 and 2021 (with average values between 60 and 80 mg N/litre), tendency less pronounced for plots with low SWHC, and reflecting a marked nitrogen deficiency in grapes during the first and last year of the experiment. Pruning weight (Figure 6E) was particularly low in 2020 but only for plots having a low SWHC. Berry weight was high in 2019, independently of SWHC (Figure 6F). Consequently, the biotic factors associated with the vineyard plots seem to vary more from one vintage to another than according to the SWHC category.

5. Multivariate analyses including abiotic and biotic factors

Collinearity between measured abiotic parameters and incidence of the disease with the main pattern of variation (Figure 7) were summarised with a principal component analysis (PCA). The first PCA axis explains between 43.8 % and 54.8 % of the variance depending on vintages and is mainly driven by nitrogen indices, esca incidence indices, cover cropping and SWHC. The second PCA axis explains

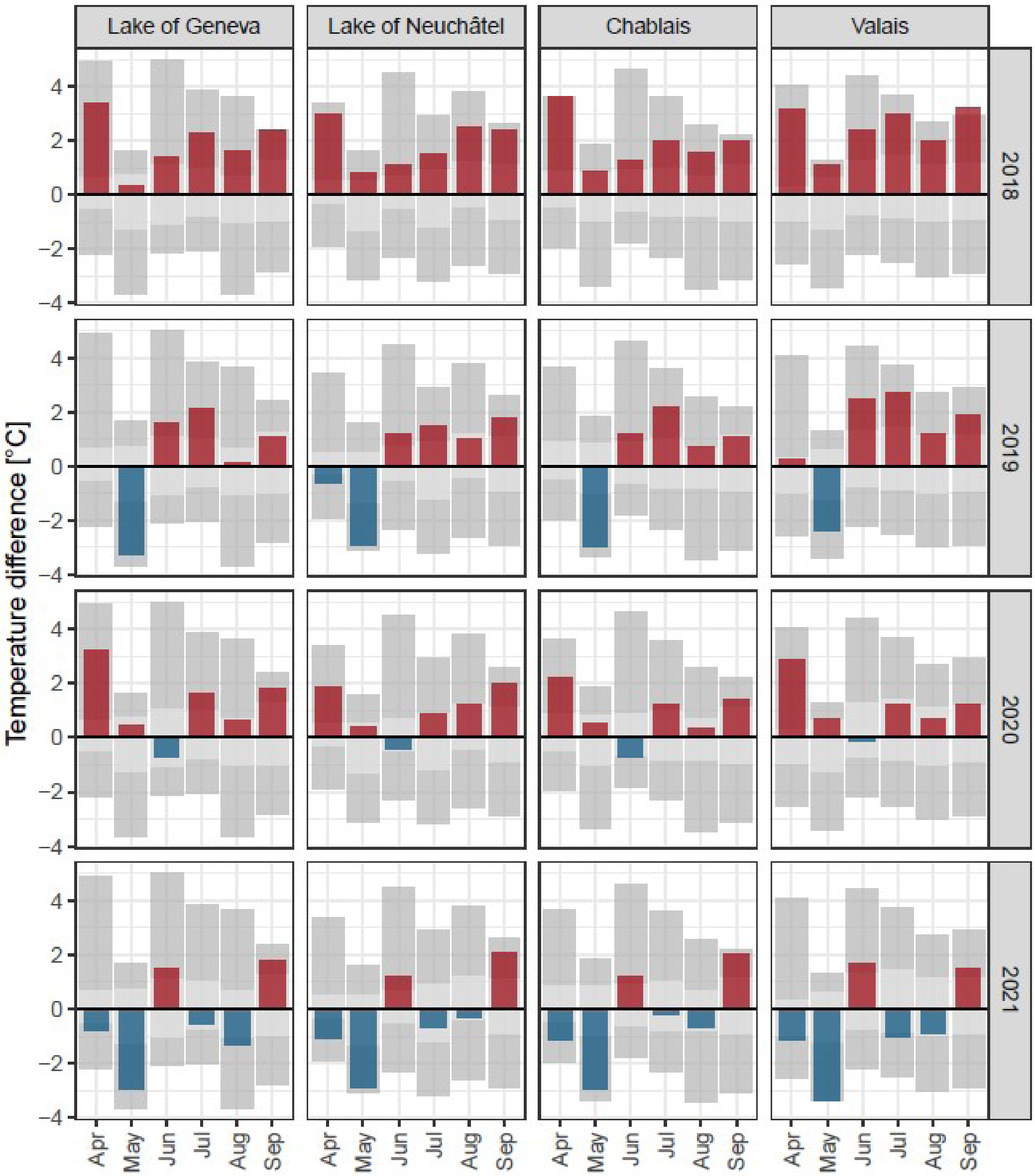

FIGURE 5. Positive (red) or negative (blue) differences to the long-term median (1990–2017) in monthly spring and summer temperatures (°C) in four wine-growing regions of Western Switzerland from 2018 to 2021. The background rectangles are the minimum and maximum (dark grey) and the 25 % and 75 % percentile (light grey) of the same data over the period 1990–2017.

between 12.9 to 24.9 % of the variance and is mainly driven by wood and berries weight and, however to a lower rate, by water stress indices (Delta13C and Base_pot) depending on the vintages.

According to PCA results, SWHC is correlated with the cumulated incidence of esca over the years. (arrows point in the same direction). SWHC arrow is closer to plant mortality in 2019 and 2021 and with the sum of foliar symptoms in 2018 and 2020. PCA also highlights a consistent directional coherence among variables tied to cover cropping, berry weight, and wood weight. Notably, this alignment is more pronounced in comparison to other biotic factors and closely mirrors the direction of esca incidence indices, underscoring their substantial correlation. This is more pronounced in 2019 and 2021. Plots located in Valais (Leytron, Nax1, Nax2 and Produit) are clearly discriminated by PCA for the four observed years and are more correlated with nitrogen and water stress indices. These indices were well correlated, especially in 2019 and 2021. These plots are also the least affected by esca (according to annual symptom incidence; Figure 2). Plots most affected by esca are usually characterised by high SWHC and cover cropping indices. Vigour indices (wood and berry weight) tend to be negatively correlated with high nitrogen indices (more strongly detected in 2019, 2020 and 2021). Cover cropping is always negatively correlated with nitrogen indices.

As SWHC appeared well correlated with plant mortality, the relationship between the total mortality rate since the vines were planted (2003) and the SWHC was tested for the 19 studied vineyard plots. Linear regression (Figure 8) inferred

TABLE 2. Experimental sites in four wine-growing regions (Switzerland), with their soil type managements (% soil cover cropping) and their soil water holding capacity (SWHC).

Sites	Region	Soil types	% Cover cropping	SWHC (mm)	SWHC category
Founex	Lake of Geneva	Gravelly moraines	70	155	Medium
Changins	Lake of Geneva	Bottom moraines	70	110	Medium
Begnins	Lake of Geneva	Bottom moraines	70	130	Medium
Perroy	Lake of Geneva	Bottom moraines	70	155	High
Morges	Lake of Geneva	Bottom moraines	70	240	High
Echichens A	Lake of Geneva	Bottom moraines	70	230	High
Echichens B	Lake of Geneva	Bottom moraines	70	230	High
Villette	Lake of Geneva	Marly sandstones	70	250	High
Blonay	Lake of Geneva	Marly sandstones	70	200	High
Onnens	Lake of Neuchâtel	Jurassic sandy stones	70	120	Medium
Champagne	Lake of Neuchâtel	Jurassic sandy stones	60	95	Low
Concise	Lake of Neuchâtel	Jurassic sandy stones	70	180	High
Villeneuve	Chablais	Gravelly moraines	70	90	Low
Yvorne	Chablais	Gravelly moraines	50	100	Low
Aigle	Chablais	Gravelly moraines	50	80	Low
Produit	Valais	Clay schists	0	160	High
Leytron	Valais	Stony moraines	0	100	Low
Nax1	Valais	Stony moraines	0	90	Low
Nax2	Valais	Colluvial/stony moraines	0	140	Medium

a positive correlation ($R^2 = 0.6$ [$P < 0.001$]) between plant mortality and SWHC. However, while such a correlation is clearly inferred for most of the plots (13 out of 19), SWHC does not explain the plant mortality for six plots, especially for Echichens B, Concise and Villette. However, for the latter, this is probably due to the absence of epidemiological data in 2021, as this vineyard was uprooted in 2020. Nevertheless, the correlation between plant mortality and SWHC suggests that soil water storage capacity is one of the main factors explaining the incidence of esca mortality for the Gamaret cultivar.

According to our correlation test among 70 variables (Table 1) with our esca incidence indexes, the variables most correlated are variables accounting for monthly precipitation regimes in May and June, SWHC, cover cropping and chlorophyll content for Pearson's correlation coefficient [PCC] (Figure 10). The highest PCC obtained (0.58) describes a positive relation between the sum of symptoms and the rainfall in June (Figure 9A). PCC also underscores a positive correlation for the precipitation regime observed in June and May between the amount of rainfall and the number of days with rain > 10 mm in May and June and the difference of precipitation compared to the norm (1991–2017) in June and our esca incidence indices (Figure 9A). SWHC is also positively correlated with all the esca incidence indices but more strongly with apoplexy. Chlorophyll content was negatively correlated with our esca incidence. This negative relationship between nitrogen and esca incidence was also underscored by the PCA (Figure 8). The variables most linked with esca incidence indices according to ξ-correlation (XCC) are June rainfall and, to a lesser extent, July rainfall but only for apoplexy. Cover cropping and SWHC are also retained as not independent from our esca incidence indices (Figure 9B).

DISCUSSION

Our study was carried out in 19 vineyards planted in 2003 with a single grape variety (Gamaret) over a period of four consecutive years. In the years preceding this study, this cultivar had shown a very high variability in susceptibility to esca (Figure 1). Our main objective was to investigate the potential associations of a series of pedoclimatic factors with the prevalence of esca disease in different viticultural regions, to identify those that might explain Gamaret's highly variable susceptibility to this disease. To this end, we carried out annual epidemiological measurements (esca leaf symptoms and apoplexy) and closely monitored various physiological indicators, including berry and wood weights, δ13C values and the chemical composition of grape musts and leaves in all the vineyard plots studied. We also considered soil characteristics and collected extensive data on climatic conditions.

1. Esca incidence of a single grapevine cultivar varies annually and regionally

Over the four years of monitoring the winegrowing network studied, we observed annual variations in the incidence of esca within the same winegrowing region. For example, in

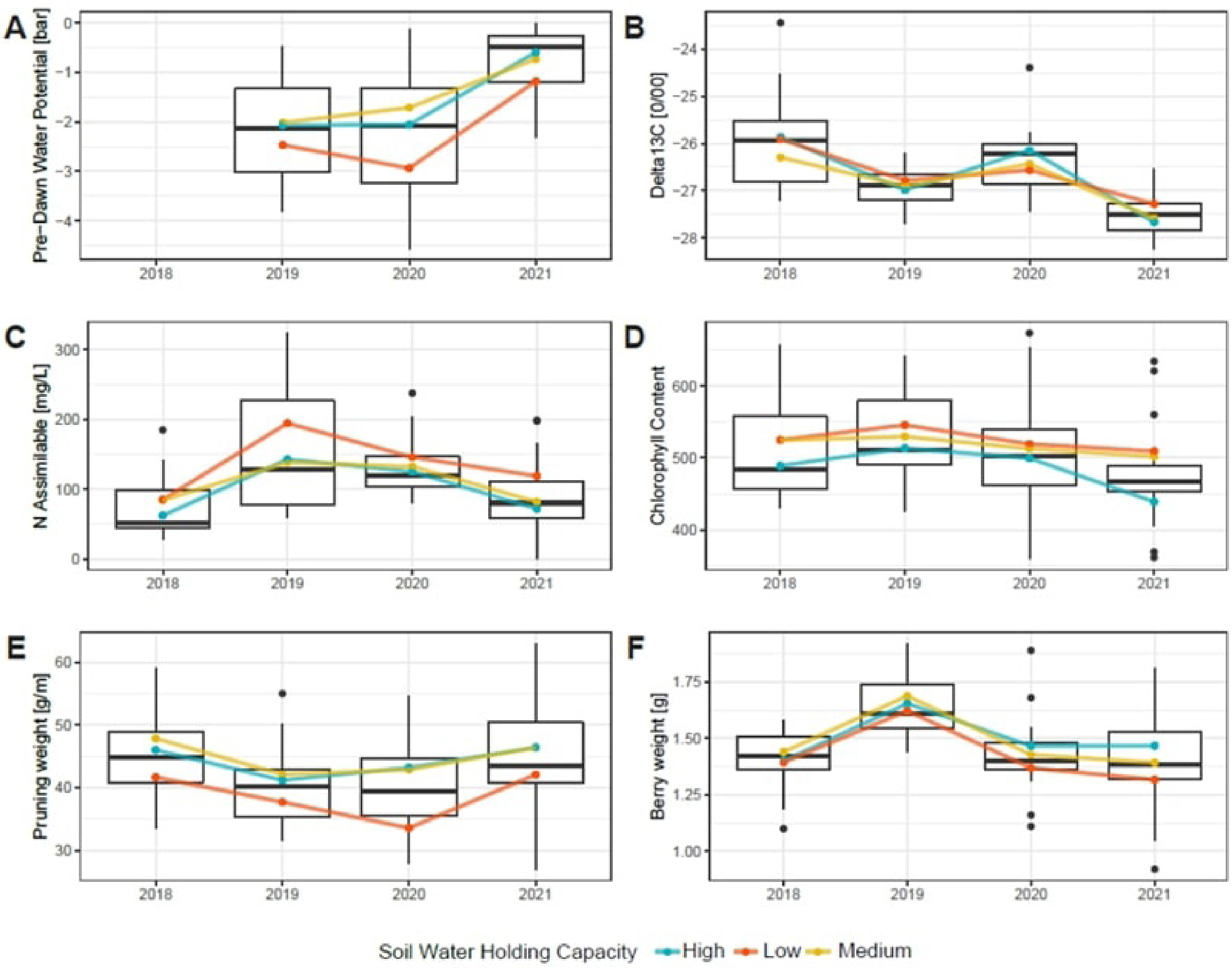

FIGURE 6. Mean values of measured physiological indexes of plots categorised by SWHC (< 100 low [orange], > 100–150 medium [yellow], > 150 high [blue]) across four consecutive years (2018–2021) A) pre-dawn leaf water potential (Ψ_{PD}), B) δ13C, C) Assimilable nitrogen, D) Chlorophyll content index (N-tester), E) Pruning weight, F) Berries weight.

the Lake of Geneva region, the incidence of esca in Morges rose from 21 % to 56 % over the four years of epidemiological monitoring (Figures 2 and 3). Variations in esca incidence were also observed between plots in the same wine-growing region with similar weather conditions. For example, in the Chablais region, the incidence of esca was higher in Yvorne than in other plots in the same region throughout the four years of epidemiological monitoring. The same observation was made in Valais for the Produit plot. Such variability has been also observed inter-regionally. Esca incidence was the highest in the Lake of Geneva region, while almost null in Valais (Figures 2 and 3). Such intra- and interregional variability in disease expression in a single grapevine variety strongly suggested that specific environmental conditions influence esca incidence, as advanced by several authors (Fischer & Peighami-Ashnaei, 2019; Marchi *et al.*, 2006; Mugnai *et al.*, 1999; Surico *et al.*, 2000; Surico *et al.*, 2010), and this primarily due to the time lag (often several years) between pathogenic fungal infection of esca and symptom expression (Di Marco & Osti, 2008). Consequently, we tried to determine which pedoclimatic factors could influence the incidence and severity of esca symptoms.

2. Soil water holding capacity and Rainfall are positively correlated with esca incidence

Our principal component analysis (Figure 7) suggested a correlation between esca incidence, particularly plant mortality, and SWHC. The association between a higher SWHC and esca incidence was observed between vineyards located in similar climatic regions (i.e., the same temperature and amount of precipitation for a given year). In Valais, the geographical region the less impacted by esca incidence, the plot with the highest SWHC was Produit, exhibiting the highest esca incidence and mortality rate. Similar trends were observed between plots in the Lake of Neuchâtel region at Concise compared to the other vineyards. Fine-textured soils tend to maintain their hydraulic conductance for longer periods and at more negative water potentials compared to coarse-textured soils (McDowell *et al.*, 2008). To precise this relationship, we conducted a linear regression analysis to explore the association between overall plant mortality and

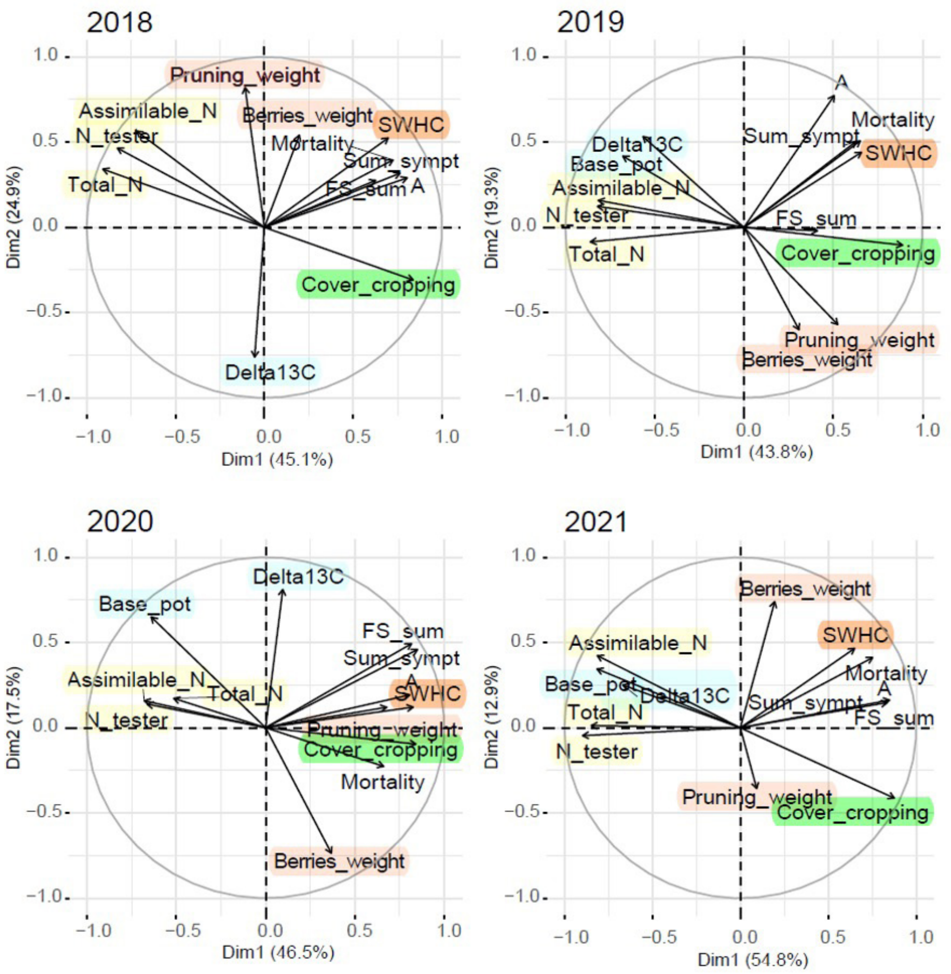

FIGURE 7. Principal Component Analysis (biplot PCA) based on abiotic and epidemiological variables by vintages 2018–2021 (left) taking into account the 19 plots (right). Colour code accounts for nitrogen content (yellow), vigour (pink), water stress index (blue), cover cropping (green), soil water holding capacity (orange) and epidemiological esca variables (no colour) with apoplexy (A), sum of foliar symptoms (FS_sum), all symptoms (A+FS_sum) and mortality.

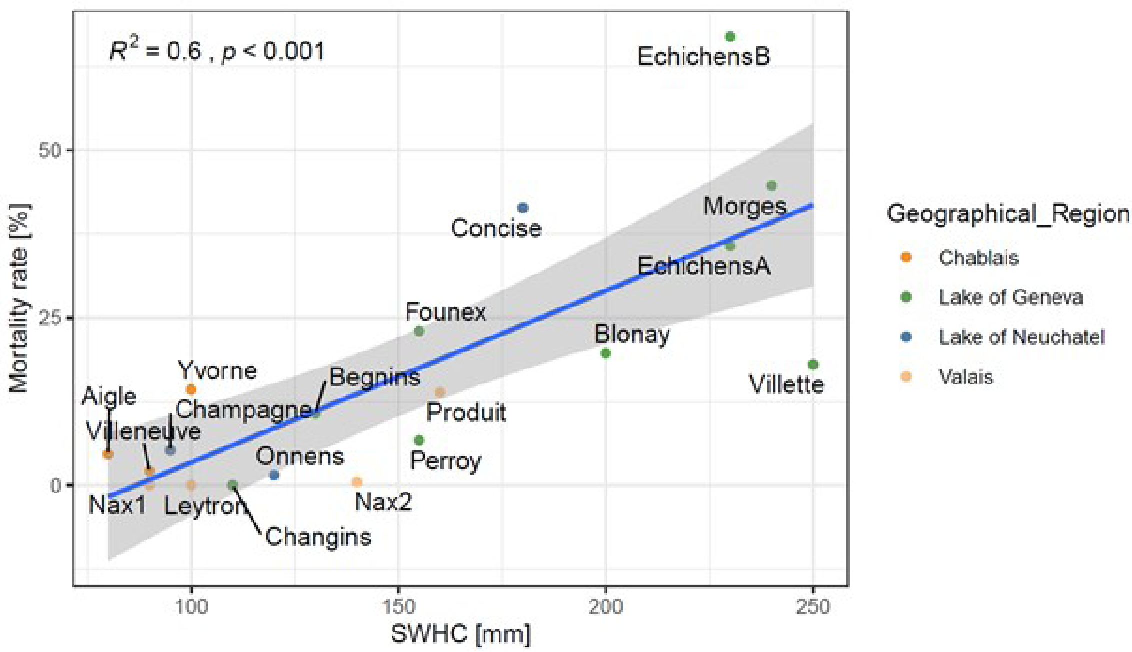

FIGURE 8. Linear regression between total mortality rate by vineyard plot (from 2003–2021) and soil water holding capacity (SWHC) index for each plot based on Pearson's correlation coefficient.

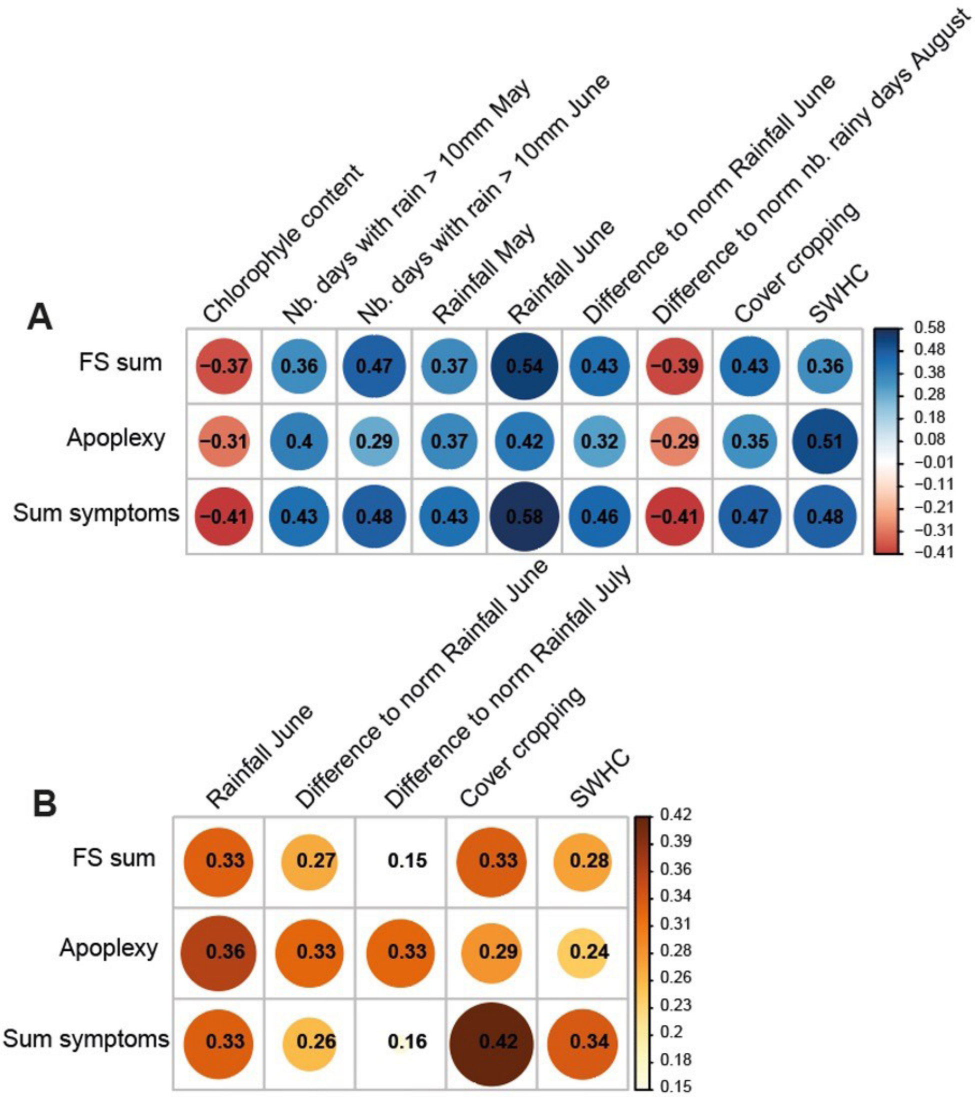

FIGURE 9. Correlation coefficient matrix with variables most correlated with the esca incidence indices: A) Variables with the highest correlation rate with the esca incidence indices according to the Pearson correlation coefficient (red corresponds to a negative relationship and blue to a positive relationship). B) Variables most correlated with the esca incidence indices according to the Xicor correlation coefficient. Abbreviations used: number of plants with foliar symptoms (FS_sum), number of plants with apoplectic symptoms (Apoplexy), number of plants affected by esca (FS_sum + Apoplexy). The size of the dot reflects the strength of the correlation.

SWHC across our vineyards network (Figure 8). This analysis revealed a clear correlation between SWHC and esca plant mortality, both across regions and within regions. Our results are in accordance with previous studies which suggested that the capacity of the soil to retain water has an impact on esca incidence (Calvo-Garrido *et al.*, 2021; Calzarano & Di Marco, 2018a; Graniti *et al.*, 2000; Lecomte *et al.*, 2009; Sosnowski *et al.*, 2011; van Niekerk *et al.*, 2011).

We also tested the relationship between SWHC and some physiological indicators measured by grouping plots into three categories based on their SWHC (Table 1). Physiological indicators varied more with vintage than with the SWHC category (Figure 6) and are therefore not usable to evaluate the risk of esca incidence on a vineyard planted on a given soil type.

Esca incidence was correlated with precipitation, particularly in May and June by our regression analyses (Figure 9). Previous studies have mentioned that cool, rainy summers favour the expression of esca leaf symptoms (Surico *et al.*, 2000; Marchi *et al.*, 2006) and especially the rainfall pattern from May to July (Calzarano *et al.*, 2018b), which is consistent with our results. According to our observations, the years characterised by the highest rainfall are those in which the incidence of esca is the highest across the network of vineyards (years 2019 and 2021; Figures 4 and 5). Hot and dry summers are considered to favour apoplexy (Surico *et al.*, 2000; Marchi *et al.*, 2006). The appearance of apoplectic events was not linked with hot and dry weather in our observations. On the contrary, the year 2018 was particularly hot and dry during the summer and was the year with the lowest number of apoplectic events and foliar symptom rates (Figures 3 and 4). The year 2021 was the wettest year with the highest number of foliar symptoms and apoplectic events in three of the four viticultural regions monitored. Both years 2019 and 2021 were characterised by a particularly rainy and cold May, followed by a hot (2019) or rainy and hot (2021) summer. These observations align with earlier research, including Surico *et al.* (2000), which proposed a relation between apoplexy and alternating periods of dry, hot weather and wet, cool conditions. Such weather patterns promote vigorous leaf and canopy growth, leading to high evapotranspiration rates, and potentially disrupting sap flow (McDowell *et al.*, 2008). Bortolami *et al.* (2022) showed that occlusions lead to hydraulic misfunction in the veins of esca symptomatic leaves and that may be promoted by climatic conditions. Annual changes in the expression of esca symptoms may also be linked to the diameter of newly developed conductor vessels since their size can vary according to the water regime and vigour of the plants (Pouzoulet *et al.*, 2014). Moreover, our plants were all grafted onto 3309C rootstock, which enables the scions to maintain a higher stomatal conductance and water uptake under water-deficit conditions (De Souza *et al.*, 2022). Plants grafted to this rootstock showed the slowest increase in water deficit throughout the growing season which is thought to be due to its larger and deeper root system (De Souza *et al.*, 2022). In the *Catalogue des vignes cultivées en France* (http://plantgrape.plantnet-project.org), rootstock 3309C is described as particularly sensitive to water stress when it occurs suddenly during the growing season and as having a poor adaptation to excess water, particularly according to our results, when the soil has a high SWHC (Figure 8). This could also explain why apoplexy cases were more frequent in 2019 and 2021, years characterised by a sudden change in climatic conditions (between May and June in 2019) or by a particularly rainy summer accompanied by alternating cool and hot periods (2021). Our results oppose the prevailing notion that the combination of high temperatures and drought intensifies plant damage (Fernandez *et al.*, 2023; Fischer & Peighami-Ashnaei, 2019; Songy *et al.*, 2019; Pandey *et al.*, 2015; Murolo & Romanazzi, 2014). In regions characterised by arid conditions during June and July, the incidence of esca was virtually negligible in our monitored vineyards. Bortolami and Gambetta (2021a) showed that prolonged exposure to drought does not appear to significantly alter the susceptibility of a particular grape cultivar to esca, a hypothesis that our study confirmed, particularly in the dryer Valais region where the incidence of esca was the lowest. Our results also concur with previous studies (Bortolami & Farolfi, 2021b; Surico *et al.*, 2010), which demonstrated that vines subjected to water-stressed conditions do not show esca symptoms, whereas well-irrigated plants do. However, over the four years during which the vineyards were monitored, temperatures in each region for a given vintage were comparable, with the same monthly deviations from the long-term norm, and no correlation with the variability of esca incidence was observed. The influence of temperature on the incidence of esca was therefore not demonstrated by our data.

The correlation between esca incidence and rainfall variables may help explain the annual variability of esca incidence within the same plots and between vineyards located in different climatic regions. However, these correlations do not explain all the variability in the incidence of esca within a region sharing the same climatic conditions for a given season.

3. Physiological indicators showed no clear association with esca incidence

Correlation analyses indicate that chlorophyll content and cover cropping are negatively (chlorophyll content) or positively (cover cropping) correlated with the esca incidence (Figures 7 and 9). Chlorophyll content was higher in plots characterised by low SWHC (Figure 7) and correlated well with water stress indicators in our PCA (Figure 9). High chlorophyll levels could therefore be associated with vineyards with restricted access to water, indirectly confirming that vineyards in dry climates are less affected by the incidence of esca. For the cover cropping variable, we observe an opposite trend. Vineyards with cover cropping are those that do not suffer from water restriction and where competition for water between grass and vines is not an issue. It also suggests that vineyards where there are no water restrictions tend to have a higher incidence of esca.

The setup we analysed with a unique vine variety was particularly valuable as it helped mitigate potential confounding factors. It indicated that soil capacity to retain water and rainfall regime played a substantial role in influencing the expression of the disease. We have identified for the first time the water retention capacity of the soil as a factor limiting or aggravating the incidence and mortality due to esca (to be confirmed by studies on other susceptible grape varieties). These results enable us to formulate recommendations for winegrowers. An esca-susceptible cultivar such as Gamaret would be better suited on soils with low water retention capacity and rather dry climatic conditions. If these suggestions are followed, esca can be at least partially controlled in the case of a sensitive grape variety such as Gamaret, and probably in the case of other sensitive grape varieties. Several studies brought also attention to the potential role of soil water saturation caused by higher rainfall frequency and intensity contributing to tree decline (i.e., in oak decline in wet Atlantic forest (Rozas & García-González, 2012), in esca disease of grapevine (Marchi *et al.*, 2006; Guérin-Dubrana *et al.*, 2013), in Dutch elm disease (Solla & Gil, 2002), in olive tree affected by *Verticillium dahliae* (Jiménez-Díaz *et al.*, 2012). Excessive water levels have been found to influence the size and morphology of xylem vessels, which are responsive to environmental signals (Pouzoulet *et al.*, 2014). The characteristics of the xylem vessels seem to impact the susceptibility of perennial plants to vascular pathogens (Pouzoulet *et al.*, 2017; Solla & Gil, 2002). The morphology of the xylem influences the compartmentalisation resulting from the occlusion of vessels (tylosis formation), occlusions suggested to hinder the movement of pathogens in plant tissues (Pouzoulet *et al.*, 2014, 2017). According to these authors, large vessels are reported to be more sensitive to vascular pathogens with slower occlusion and therefore less pathogen restriction. Exploring the hypothesis of plasticity in xylem vessel morphology could provide valuable insights into the variability of esca symptom incidence within the same grapevine variety planted in different locations characterised by specific pedoclimatic properties. Although the role of water is increasingly established, the variability in the incidence of esca within a plot, with some plants being affected earlier than others, is not yet clear. The precise role of water availability or restriction in the expression of esca symptoms has yet to be clarified.

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