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Grapevine vigour: A critical factor associated with trunk disease symptom expression

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ABSTRACT

Grapevine trunk diseases (GTDs), especially Esca and *Botryosphaeria* dieback, cause mortality and production decline in vineyards worldwide. As they are thought to be complex diseases, unravelling the different factors that determine symptom expression is crucial in mitigating the impact on growers. While cultivar, climate, age, and pruning system are known contributors, they do not fully explain the variability in GTD incidence. This study investigates the role of grapevine vigour as a determinant factor in GTD foliar symptom expression.

Three vineyard networks were monitored in 2022 and 2023, each consisting of approximately 30 commercial vineyard plots of Grenache noir, uniform in age. To minimise climate variation, the selected vineyards were located within small geographical areas. We evaluated grapevine vigour and its primary drivers including water and nitrogen status, weed cover, production, and vegetation biomass—and correlated them with GTD incidence over the two seasons.

Results show that current season vigour is positively correlated with the GTD incidence rate in most of the network*year scenarios. The relationship shape suggests that, while low to moderate vigour is consistently associated with reduced symptom expression, high vigour can be correlated with either high or low expression which implies the involvement of additional factors. In one instance, previous year water stress indicators were the ones most correlated with current year GTD incidence, though vigour was also influential. For the plots where GTD expression was greatest, the previous year's water stress was combined with the current year's substantial spring vigour. While these results need to be confirmed over a longer period, in more regions and with other cultivars, they open new perspectives of applications for growers. As correlation with vigour is recurrent but not exclusive, it suggests a wider implication of grapevine physiology.

KEYWORDS: grapevine, Esca, *Botryosphaeria* dieback, vigour, physiology, Grenache N, decline

INTRODUCTION

Trunk diseases are a major cause of grapevine dieback worldwide (Gramaje *et al.,* 2018; Guérin Dubrana *et al.,* 2019; La Fuente *et al.,* 2016). In France, it causes a heavy economic burden for wineries and grape growers, especially for the last 20 years since an increase in trunk disease expression has been observed in many wine-growing regions.

Among all grapevine trunk diseases (GTDs), Esca disease as well as *Botryosphaeria* dieback, *Eutypa* dieback and to a lesser degree Phomopsis dieback are the most widespread in Europe (Guérin Dubrana *et al.,* 2019). A recent study conducted in France showed the average prevalence of Esca and *Eutypa* dieback were 74 % and 41 % of the surveyed plots respectively. These diseases cause internal necroses in grapevine trunks and cordons and/or foliar symptoms on leaves, shoots and grapes which can eventually result in a complete drying and wilting of the vine, culminating in the death of the vine, generally within a few years. These symptoms result in yield losses and death of parts or entire vines (Dewasme *et al.,* 2022), feeding the vineyard decline process and thus impeding productivity. Apart from trunk necroses, a typical foliar symptom of Esca is the "tiger stripe-like" pattern on leaves, showing discoloured and sometimes dried parts between leaf veins (Larignon & Dubos, 1997; Lecomte *et al.,* 2012; Mugnai *et al.,* 1999) whereas *Botryosphaeria* dieback is most often reported worldwide causing reduced vigour, lack of spring growth and spur death on affected vines (Úrbez-Torres, 2011). For some authors though, *Botryosphaeria* dieback also leads to tiger-stripe leaf phenotypes, usually observed in early summer, generating controversy and making it difficult to state between Esca and *Botryosphaeria* dieback on a mere foliar symptom point of view (Larignon *et al.,* 2001; Lecomte *et al.,* 2012; Moret *et al.,* 2024; Surico *et al.,* 2006; Úrbez-Torres, 2011; van Niekerk *et al.,* 2006).

GTDs are thought to be due to a complex of different fungi that enter the vine through wounds, mainly during winter pruning or shoot thinning in the springtime and develop inside the wood causing necrosis and decay. For Esca and *Botryosphaeria* dieback, foliar symptoms can be irregular in time, as a vine plant can show foliar symptoms a given year but not the following one; fungal pathogens are scarcely retrieved from leaves of symptomatic vines and very few attempts to reproduce the typical foliar symptoms from fungal inoculations have been successful. For all these reasons, GTDs are considered to be multi-factorial complex diseases that still remain only partially understood (for reviews see: Bertsch *et al.,* 2013; Claverie *et al.,* 2020; Larignon *et al.,* 2009; Mugnai *et al.,* 1999; Surico *et al.,* 2006; Wagschal *et al.,* 2008).

The incidence of GTD foliar symptoms in vineyards is highly variable (Fernandez *et al.,* 2024), depending on the year, the cultivar, the age of the vineyard (Bruez *et al.,* 2013; Dewasme *et al.,* 2024; Etienne *et al.,* 2024), the pruning type and training management (Dal *et al.,* 2008; Kraus *et al.,* 2022; Lecomte *et al.,* 2019; Travadon *et al.,* 2016), and the climate (Bortolami *et al.,* 2021; Calzarano *et al.,* 2018; Dewasme *et al.,* 2024; Larignon, 2009; Larignon, 2020; Lecomte *et al.,* 2023; Marchi *et al.,* 2006; Surico *et al.,* 2000). There is a big challenge in understanding what determines disease symptom expression, which can be critical in mitigating the impact of these diseases on growers. But even in the same region, in the same year, and with the same cultivar and age, there are still big potential differences between vineyard plots (Dewasme *et al.,* 2022; Etienne *et al.,* 2024; Gastou *et al.,* 2024; Monod *et al.,* 2025; Li *et al.,* 2017). This incited us to explore why and to set our work at an even smaller scale than the previously mentioned studies, *i.e*., local networks of a few km wide. At such a scale, climate is supposed to show little variation, and these were conducive conditions to test the hypothesis of an influence of the vigour in the plot.

'Vigour' is a word that, at least for grapevine, encompasses many things: the vigour of a plant characterises its ability to grow and produce vegetative biomass, from leaves to grapes, roots and wood. For grapevine, Champagnol (1984) states that vigour is the indicator of intense metabolic activity of the growing plant that depends on external factors (mainly the environment) and grapevine factors (grapevine genetics, bud load and quality of sap flow, amount of reserve material, etc). To quote: Reynier (2011), "*A vigorous grapevine has an active growth, shoots with long internodes, numerous lateral shoots, an elevated number of bunches*." However, Champagnol restricts the use of the word 'vigour' to the mean biomass of one shoot or cane, *i.e*., the total vegetative biomass per number of shoots. Vigour can sometimes be also applied to the potential of the environment, proper functioning and fertility of the soil and its ability to feed the vine and produce biomass. In this work, we considered 'vigour' as the expression of the total vegetative biomass of a grapevine plant. As grapevine vigour is closely related to many components of the environment, like climate (rain, temperature, vapour pressure deficit…), soil characteristics, genetic profile of the grapevine itself (cultivar, rootstock and clone), competition with other vines (planting density) or other plants (weeds in particular) and cultural practices (fertilisation, irrigation, soil management…), we can be tempted to consider the system as a whole, including vine vigour and its determinants.

In the past decades of research on grapevine trunk diseases, there is not much scientific data about the relationship between grapevine vigour and GTDs: vigour is not mentioned as a determinant factor in most of the reviews on GTDs (Bertsch *et al.,* 2013; Gramaje *et al.,* 2018; Mondello *et al.,* 2018; Mugnai *et al.,* 1999). However, the influence of some environmental factors on GTDs has been studied and documented much more, particularly heat and water stress (Bortolami *et al.,* 2021; Calvo-Garrido *et al.,* 2021; Fischer & Kassemeyer, 2012; Fischer & Peighami-Ashnaei, 2019; Songy *et al.,* 2019; van Niekerk *et al.,* 2011). The influence of GTDs on grapevine physiology has also been documented, as reviewed by Fontaine *et al*. (2016). Nevertheless, in the field, some

empirical evidence of the influence of vigour sometimes emerges: vine growers or field advisors occasionally mention a positive vigour effect on GTDs or mortality, generally on plots showing a gradient of vigour, for example due to the effect of a slope or the competition with a border of nearby trees (as also reported by: Surico *et al*. (2000)). In that case, vines located in the higher competition zone are less vigorous and show less symptoms of GTDs.

Apart from empirical observations, some scientific references on the influence of vigour exist: between 2004 and 2006; Destrac-Irvine *et al*. (2007) monitored a network composed of 22 vineyard plots located in different sub-regions of Bordeaux. They observed that, besides an overall decrease in GTD expression in the driest year (2005), the incidence of GTDs in a given year was higher in plots with a higher water holding capacity, comfortable nitrogen status and yield. In addition, in a long-term trial comparing different ground vegetation cover and N fertilisation combinations in the Cognac region of France, Dumot (2022) assessed mortality rates after 20 years of study. Treatments consisted of vineyard blocks with different doses of fertilisers combined or not with levels of ground vegetation cover. Mortality, caused mainly by GTDs, was highest in the treatment with higher fertilisation (60 N unit per ha) and no ground vegetation cover and was lowest in the non-fertilised block with ground vegetation cover. Kuntzmann *et al*. (2013) investigated the role of a set of cultural factors in explaining the expression of Esca or *Botryosphaeria* dieback on a network of plots of different cultivars and ages monitored between 2003 and 2011 in the Alsace region of France. Among the different significant factors that were pointed out, these authors mentioned vigour and yield were frequently associated with higher expressions of GTDs, even if they also point out discrepancies with other studies and years where higher GTD expression was associated with lower vigour. Lately, as part of a more recent study of the GTD network in the Alsace area, higher incidence rates have been associated with plots showing lower soil water holding capacities (Abidon *et al.,* 2019). Finally, three recent studies included vigour and their related variables among the factors tested for their influence on GTD expression: Monod *et al*. (2025) showed that on a network of plots of the same cultivar (Gamaret), age and planting material origin, set among 4 Swiss wine producing regions, the variables most correlated to GTD incidence were climatic variables (especially rainfall in May and June) and soil water holding capacity; vine vigour being not significant, though showing a slight correlation with GTD symptom expression and vine mortality, more pronounced in certain years. In the study conducted by Gastou *et al*. (2024), consisting of 46 cultivars in one vineyard plot in Bordeaux in which monitoring was done on epidemiological and biotic variables (vine vigour, nitrogen and δC13 indices, phenology), water use efficiency of the cultivar, and to a lesser extent vigour, proved to be both positively correlated to Esca incidence and mortality. Finally, Dell'Acqua *et* al. (2024) showed that a decrease in Esca foliar symptom incidence was associated with a low level of nitrogen fertilisation compared to a medium level, whereas a high level did not significantly increase disease expression on potted Sauvignon blanc uprooted from two Esca-affected vineyards in the Bordeaux region, monitored during three years.

	Network-B	Network-G	Network-V
	43.6537°N, 5.2624°E	44.1028°N, 4.6578°E	44.2687°N, 5.1252°E
Number of plots	n = 30	n = 25	n = 25
Grapevine cultivar	Grenache N		
Rootstocks	Unknown (25 %), 110R and 140Ru (63 % and 27 %, respectively, of the known rootstocks)		
Vine planting year	1998–2004 (mean = 19.6 y/old)	1998–2004 (mean = 19.6 y/old)	1996–2006 (mean = 19.9 y/old)
Altitude	170–370 m	30–200 m	260–450 m
Climate type	Mediterranean (average Huglin index over the last decade: 2400–2600 °C; average wetness soil index between 2017 and 2023: –100 to –180mm)		
Soil types	Mostly clayey calcareous soils (*calcosols*) and loamy and sandy soils from colluvial deposits (*colluviosols*) A few particular soil types like chromic soils (*fersialsols*) and cambisols (*brunisols*)		
Training system	Mainly spur-pruned double cordon		
Planting densities	3500–4500 vines/ha (mainly 4000)		
Irrigation	14 to 16/30 plots	3/25 plots	No irrigation
N fertilisation	Unknown (10 %) 20 ± 10 U N/ha/year	Unknown (17 %) 26 ± 9 U N/ha/year	Unknown (40 %) 20 ± 10 U N/ha/year
Soil management	Tillage (26/30) Permanent cover (4/30)	Tillage (7/25) Permanent cover (18/25)	Tillage (18/25) Permanent cover (7/25)
Yield target	~60 hl/ha	~40–50 hl/ha	

TABLE 1. Agronomical characteristics of the 3 networks.

N fertilisation information was given by growers as mean amounts of N supplied per ha and per year.

In this study, we intended to test if vine vigour, in relation to its main drivers, could be related to GTD symptom expression during a 2-year course of monitoring. We worked on 3 small local networks of commercial vineyard plots of the same vine cultivar Grenache N with similar ages and no or little climatic variation between plots in the same year.

MATERIALS AND METHODS

1. Three geographical networks each composed of ~30 vineyard plots

This work was conducted in the south-eastern Mediterranean wine regions of France (regions *Sud* and *Occitanie*) in 3 different areas: in the Bouches-du-Rhône, Gard and Vaucluse departments. For each area, about 30 commercial vineyard plots were selected within a small geographical area of a few kilometres in diameter, corresponding to a group of 3 to 6 nearby towns. These groups of plots are thereby denominated "networks": Network-B, Network-G and Network-V, respectively.

All plots are planted with the same cultivar, Grenache noir. For each network, the selection of the vineyard plots monitored in 2022 and 2023 is a subsample deriving from a larger 100-plot network where a preliminary GTD incidence evaluation was conducted in 2021. The selection criteria were chosen to (1) keep all the plots showing maximum and minimum incidence of GTDs in 2021, as well as intermediate levels, (2) tighten vine ages around 20 years old (which has shown to be the age of maximum GTD incidence) to minimise a bias effect of age and (3) ensure the selected subsample properly reflects the diversity of agronomical situations in the area (in terms of irrigation and soil management in particular) so that vigour can show a wide range of values.

Even if cultivar, vine age and climate were chosen to vary as little as possible, as the plots are commercial vineyards set in natural conditions and conducted by different growers, they can show different characteristics from one to another in terms of rootstock, soil, training system and agricultural practices. The main characteristics of the 3 networks are displayed in Table 1.

Even if the plots can occasionally be affected by other dieback diseases than GTDs, such as fan leaf virus or root rot due to *Armillaria (*'Yellows' phytoplasma diseases remaining scarce), GTDs are the main cause of dieback in most of the plots selected in this study.

2. Climate in 2021, 2022 and 2023 on the 3 networks

The data used to characterise climate during the monitoring period derived from Antilope and Arome models provided by *Météo France* using a 1-km grid of the territory. These spatialised data are calculated by integrating different data sources (real weather stations, satellite images and RADARs). Climate estimations can be done on any location using the 4 nearest points of the grid.

Temperature and rainfall data for the 3 monitored years are shown in supplementary Figure 1. 2021 and 2023 had well-watered spring times but with a water shortage in June and July in 2021, more markedly visible in Network-B. 2022 was characterised by spring and summer drought, particularly strong in Network-G with a total of 60 mm for the 3-month period from April to June, when Network-B and Network-V received about 100 and 130 mm of rainfall, respectively. This corresponds to one-half to one-third of the 2021 rainfall amount in the same period. 2022 average temperatures (and evapotranspiration, *not shown*) are also higher. 2023 was characterised by a return of rainfall to higher amounts, over 200 mm for the April–June period similar to 2021, but with a discontinuous regime between a dry winter and April (not shown) followed by comfortable rainfall in May and June.

3. Monitored variables during 2021, 2022 and 2023

Besides GTD incidence, variables monitored in this study are water uptake, nitrogen status and grapevine vigour, as well as ground vegetation cover. Grapevine yield and vegetation were also estimated. The different variables and indicators used are shown in Table 2.

Phenological period	Pre-flowering	Berry growth	Veraison	Harvest	Winter
Water status: apex index	2023	2022–2023	2022–2023	2022–2023	
Water status: δC13				2022*	
Nitrogen status: chlorophyll index	2023		2022–2023		
Ground vegetation cover: (total vs living, row vs inter-row) visual evaluation	2023	2022–2023	2022–2023	2022–2023	
Harvest score of grapevine yield/vegetative biomass/water status/nitrogen status: visual evaluation				2022–2023	
%GTD incidence				2021–2022–2023	
Vine vigour: pruning weight proxy (CN*SA)					2022*–2023

TABLE 2. Variables and indicators monitored between 2021 and 2023 during the different grapevine phenological stages.

* Not controlled on all vineyard plots in 2022.

3.1. Variables and indicators related to vigour

Two indicators describe the water uptake and status of the vine**:** (1) Visual observation of the slowing down of shoot growth using the "apex method" (Pichon *et al.,* 2022). At

each measurement date, 50 apical meristems are assessed depending on their growth profile (1 = full growth; 0.5 = moderate growth and 0 = stopped growth). The IC growth index is then calculated (ICapex) using the following formula:

$$ICapex = \%\ full\ growth + 0.5 * \%moderate\ growth \quad (1)$$

where % full growth is the number of apexes in full growth out of the 50 apexes assessed. As we can see from the formula, the higher the value of Icapex, the less the water stress. Assessment is made at 2 or 3 different stages during the summer between berry growth and ripening, generally around late June (berry growth), late July (early veraison) and late August (ripening). To integrate the 3 dates into one indicator, the Area Under the Curve (AUC) of ICapex (AUC_{Icapex}) was calculated as follows:

$$AUC_{Icapex} = \sum_{k=i}^{n} \frac{Icapex_{\,i} + Icapex_{\,(i+1)}}{2} * (t_{\,i+1} - t_i) \quad (2)$$

where t_i is the Julian day of the measure i. As for ICapex, the higher the value of AUC_{Icapex}, the less the water stress. (2) Carbon isotope discrimination analysis (δC13) (Gaudillère *et al.,* 2001) was done in 2022 on only half of the plots using a 200-berry sample that was randomly picked at harvest time. On the same day, a rapid visual assessment of the water status of the vine at harvest was done using grades: 0 if shoot growth is still active, 1 if growth has ceased and 2 if drought symptoms were present (basal leaves yellowing, drying and fall).

The chlorophyll index is used to account for the nitrogen status of the vine. The N-Tester (Yara, Oslo, Norway) or SPAD 502 (Konica Minolta, Nieuwegein, Netherlands) devices were used depending on the network. On each plot, the chlorophyll index is given after 30 measurements (pinching of the leaves in the fruit zone) distributed up and down along 2 rows. The measurement was performed at veraison time, except for Network-G in 2022 (pre-harvest time). In 2023, an additional measurement was performed in May at the pre-flowering time (*i.e.*, stage BBCH 57 for Network-G, Network-V and BBCH 60-65 for Network-B), to characterise spring vigour. As a probable bias of the phenological stage (between BBCH 57 and 65) was visible on the chlorophyll index (higher average values in Network-B measured at flowering than on the other 2 networks measured before flowering, not shown), we used the normalised values per network. At harvest time, in addition to the visual assessment of the water status of the vine, a rapid visual assessment of the nitrogen status of the canopy was done as well, based on aspects of the canopy (intensity of green colour and size and density of the leaves): 0 if nitrogen deficiency (typical pale light green canopy), 1 if moderate green colour and 2 if dark green and/or large basal leaves indicating high nitrogen nutrition.

The ground vegetation cover evaluation was done visually, using a 4-grade scale based on the percentage of the ground surface covered by weeds or crops (from 0 = no ground vegetation to 3 = entire surface covered by ground vegetation), and discriminating the row from the inter-rows (whether tilled or not), as well as discriminating the green living part (considered as the active weed cover part) from the total covered area. The ground cover was assessed at the same dates as the apex growth. Different indexes can then be used to characterise a plot depending on those different criteria and the date of the measurement. As these indexes are strongly inter-correlated within the same year, only the average annual score on (row + inter-row) has been kept in this article.

Grape production and vegetative biomass are assessed at harvest time using visual scoring. The assessment of production is based on the achievement of the yield objective for the considered network: 1 if production is far under the objective, 2 if production is under the objective, 3 if production reaches the objective and 4 if it is beyond. For vegetative biomass, a subjective expert note was used, based on the volume and density of the canopy, from 1 (very small) to 4 (big vegetation). Two operators proceed and compare their scores. These scoring methods have been used because of their good (time-consuming/robustness) ratio observed in previous studies.

Vigour assessment was done in winter, by counting the number of canes (CN) on 20 vines per plot and measuring cane basal diameter (d) on about 30 to 40 canes per plot to calculate the section area (SA) of the canes. Cane diameter was measured using an electronic calliper (precision 0.1mm), on all canes of one spur per vine on half of the 20 vines, between inter-node 2 and 4 at the base of the cane. In 2022, vigour assessment has only been done on part of the plots (23 out of 30, 15 out of 25 and 13 out of 25, respectively, in Network-B, Network-G and Network-V). On 13 out of 23 plots of Network-B, the plots had been previously pruned by the growers. In that case, diameter measurement was done on canes collected on the ground (entire canes *i.e.* including the first inter-node) and cane number by counting the number of spurs left on the vine and applying a correction factor of 2.6, which corresponds to the average number of canes per spur counted on the remaining unpruned plots. In this article, "CN*SA" is frequently called a "vigour" proxy even if it is *sensu stricto* a proxy of the total vegetative biomass of the vine. We chose CN*SA vigour proxy instead of traditional total cane weight measurement mainly because it remains valid after grapevine is pre-pruned (which is a very common practice in our networks) and also because it is less time-consuming.

3.2. GTD foliar symptom

The foliar symptoms observed on Grenache N in our study are shown in Figure S2: "tiger-stripe-like" mild form of symptoms on the leaves can be present (Figure S2A to S2F), frequently associated with more severe symptoms, *i.e.*, leaf drying and falling, sometimes affecting only a few leaves on a shoot, but more frequently entire shoots or vines (Figure S2B to S2C). Sometimes shoots are completely defoliated, therefore showing more or less green vs. dried dead portions more likely affecting the apical part of the shoot (see Figure S2B, top of the shoots). However, apoplexy form can also

be regularly seen (Figure S2G); it corresponds to a sudden wilting and drying of the entire vegetation (sometimes only half a vine but always affecting more than a shoot) with a homogeneous aspect between leaves and shoots (resembling as if the vine trunk had been ploughed off).

According to some authors (Lecomte *et al.,* 2012), these symptoms are clearly attributable to Esca disease, although according to others descriptions, they are caused by *Botryosphaeria* dieback (Larignon *et al.,* 2001; Moret *et al.,* 2024). For that confounding reason, and because the assessment of GTD incidence was done only on foliar symptom expression (neither necrose identification nor fungal isolation were performed), we decided to consider them all together as GTD symptoms in this study, as they can correspond to Esca, *Botryosphaeria* dieback or a mix of both. *Eutypa* dieback was scarcely found and, therefore, was not recorded nor considered in this study.

Prior to harvest (*i.e.*, from the end of August to mid-September), well-trained operators counted the number of GTD symptomatic vines on 200 to 600 living vines per plot (average 350–400 depending on the network), in at least 4 rows per plot, to represent the total surface of the plot using the same fixed row numbers over the three years. Incidence is therefore calculated as the number of vines showing foliar symptoms to the total number of living vines ratio.

4. Statistical analysis

We used principal component analysis (PCA) to explore and summarise the relationships among the different indicators belonging to the monitored grapevine variable set as well as with GTD expression. We chose to represent both years on the same PCA to compare them. We also included GTD incidences as supplementary variables so that the projection of these response variables on the first 2 axes of the PCA would be independent of the construction of the components and thus reflect the correlation between GTDs and grapevine variables. On that PCA, δC13 and CN*SA in 2022 were deliberately withdrawn because of the many missing values. We ran R software with the *FactoMineR* library.

We also built the Pearson correlation matrix after reintegrating δC13 and CN*SA in 2022, using *ggplot2* and *corrplot* libraries on R software. The matrix indicates the R correlation coefficient only for significant correlations, *i.e.*, p-values below 0.10. We chose to use 0.10 as a threshold for p-values in order not to be too restrictive on the relationships to be observed. For missing values, we used the pairwise suppression option.

We finally represented the bivariate scatter plots between the drivers best correlated to GTD variables. We added the linear regression model on each plot and indicated the R^2 determination coefficient and the p-value of the correlation. We also analysed the data in R using the *ggplot2* library.

RESULTS

1. Differential expression of GTD symptoms per network over the 3-year period

The values of GTD incidence for each network and year are shown in Figure 1. Mean incidence per year ranges between 1.9 % and 6.4 % between networks and years, and an important deviation is observed inside each network*year, which was expected. Symptom expression shows some significant differences between networks and years: Network-G in 2021 with the greatest incidence and Network-G and Network-V in 2022 showing the least. For Network-B, no year effect is visible whereas for Network-V and G, the 2022 expression is reduced by a factor of 2 and 3, respectively compared to 2021.

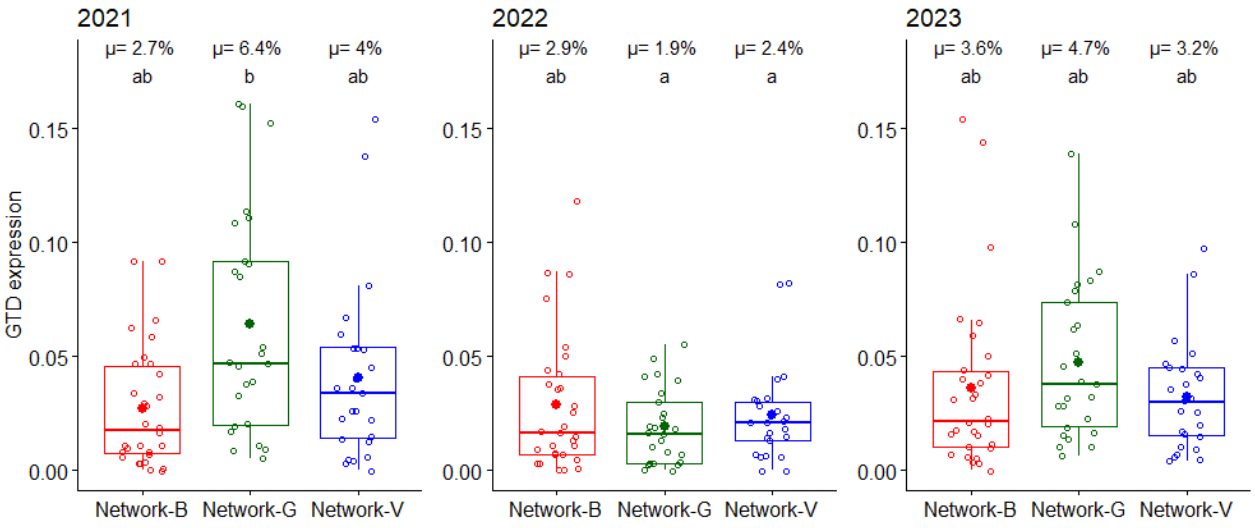


FIGURE 1. GTD foliar symptom incidence per year (2021, 2022 and 2023) for each Network-B, Network-V and Network-G.

Boxplot horizontal bars display 1st quartile, median value and 3rd quartile thresholds. For each network, open dots stand for individual vineyard plots. The filled dot is the mean value, with label ('μ') on top and label letters below as Kruskal–Wallis test groups.

2. Multivariate analyses including plant and GTD factors

A PCA was done per network to represent the inter-relations between all the variables monitored in the study (except δC13 and vigour proxy CN*SA in 2022 because of too many missing data) and for the 2 years 2022 and 2023 taken together (Figure 2).

Axis 1 summarises most of the information, as, depending on the network, it accounts for 43 to 52 % and axis 2 for 11 to 16 % of the total variance of the data set. Axis 1 is driven, for all 3 networks, by AUC_{ICapex}, chlorophyll index, yield, vegetation and nitrogen scores at harvest, and vigour proxy CN*SA as opposed to total weed cover to a lesser degree. These indicators are strongly correlated to one another. Axis 1 can thus be interpreted for all 3 networks as a "grapevine vigour" information axis. Network-B is the one showing most of the indicators correlated to axis 1 whereas for Network-G, more variables are projected on axis 2: chlorophyll index in 2023 and water score at harvest in 2022 and 2023 are mainly driving axis 2.

In this context, GTD expression is best projected on axis 1 for Networks B and V for both 2022 and 2023. GTD expression for network G in contrast, is correlated to both axes in 2022 but only to axis 2 in 2023.

PCA shows that GTD incidence is mainly driven by indicators related to vigour with a positive relationship but with a slight difference for Network-G in 2023, where it is best related to axis 2 and indicators related to vigour and to water status, in an opposite way to vigour for the latter.

To specify the significant indicators correlated with GTD incidence, we performed a Pearson correlation matrix between all the variables monitored per network (Figure S3), δC13 and CN*SA 2022 being reincluded in the matrix. For Network-B, we can check that the indicators best correlated with GTD expression in 2022 and 2023 are vine age, yield or vegetation scores, chlorophyll index and CN*SA vigour proxy. For Network-V, vegetation and yield scores, as well as vigour proxy CN*SA are best correlated to GTD expression in 2022 and 2023. For Network-G, GTD expression in 2022 is mostly correlated to vegetation score and vigour proxy CN*SA, as well as opposed to weed cover, but in 2023 as we could tell from the PCA, the strongest correlations to emerge are met with indicators AUC_{ICapex} and δC13 in 2022. Vigour proxies CN*SA in 2023 and chlorophyll index at flowering in 2023 are also correlated, though with a higher p-value (0.09).

3. Focus on relationships between GTD expression and its main correlated proxies

3.1. Focus on relationship with vigour proxy CN*SA

As vigour proxy CN*SA is significantly correlated to GTD incidence in most of the network*year situations (Figure 2 and Figure S3), we performed bivariate correlation plots to investigate the shape of the relationship (Figure 3).

We can see that the relationship between vigour proxy and GTD incidence recurrently shows the same type of shape, with a decreasing variance among GTD incidence rates as grapevine vigour decreases: Network-B and Network-V in 2023 best account for that, where Network-G in 2023 does not.

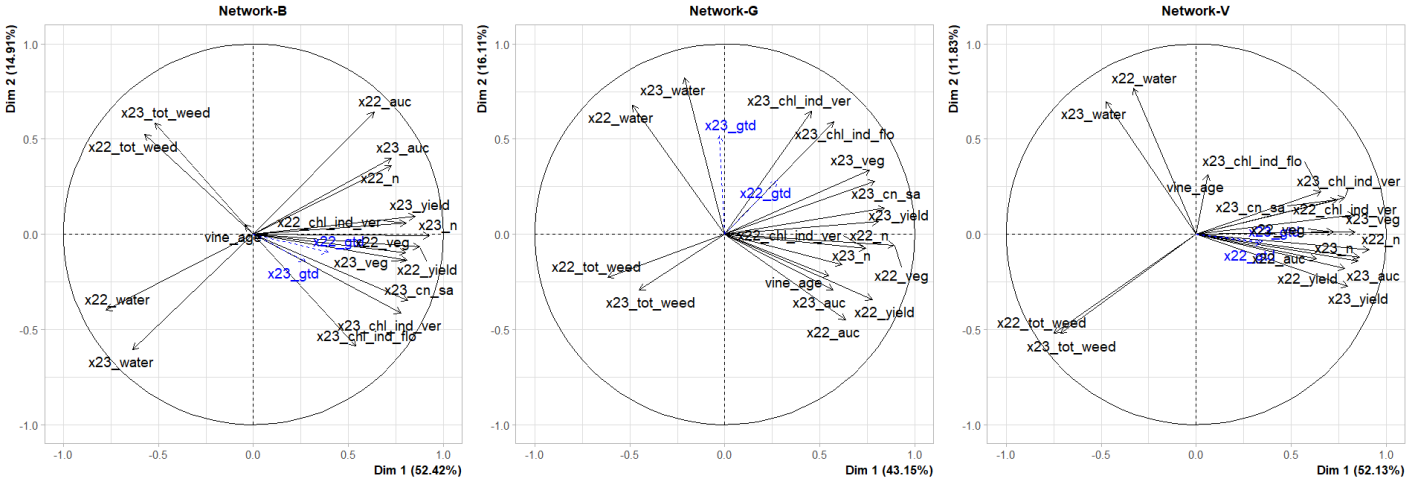


FIGURE 2. PCA performed on the matrix of the plant indicators (water and nitrogen status, ground cover, production and vegetation score at harvest and vigour), featuring GTD expression in 2022 and 2023 as supplementary variables.

The main variables are in black solid arrows, while the supplementary variables are in blue dotted arrows. Legend for variable labels: x_year_variable acronym. Example: *x22_gtd* = GTD incidence in 2022. Acronyms for variables: *auc* = AUC_{ICapex}, *tot_weed* = ground vegetation cover average annual score on (row + inter-row), *yield* = yield score at harvest, *veg* = vegetation biomass score at harvest, *water* = grapevine water status score at harvest, *n* = Nitrogen score at harvest, *chl_ind_flo / chlo_ind_ver* = chlorophyll index at flowering/veraison, *cn_sa* = cane number per section area (CN*SA) vigour proxy, *gtd* = GTD incidence and *vine_age* = age of the plot in 2021.

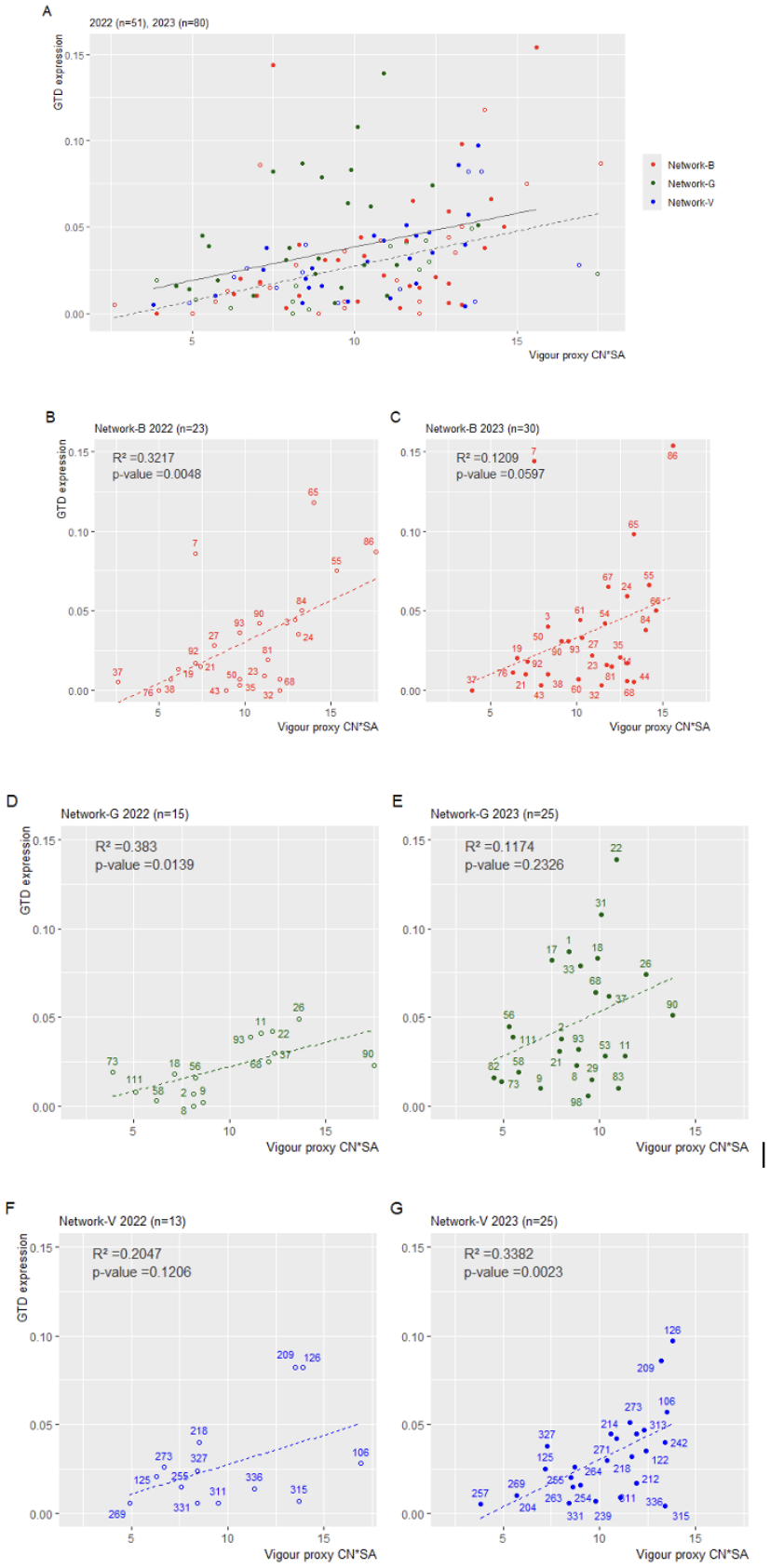


FIGURE 3. Bivariate relationships between vigour proxy CN*SA and GTD incidence for all plots and years together (A) and per year and each local Network-B (B and C), Network-G (D and E) and Network-V (F and G) separately. A: open circles and dotted linear model trend line = 2022 and filled circles and solid linear model trend line = 2023. B to G: 2022 on left graphs and open circles, 2023 on right graphs and filled circles. Linear regression model trend line (dotted line) and associated R^2 determination coefficient and p-value. Labels = vineyard plot identification number.

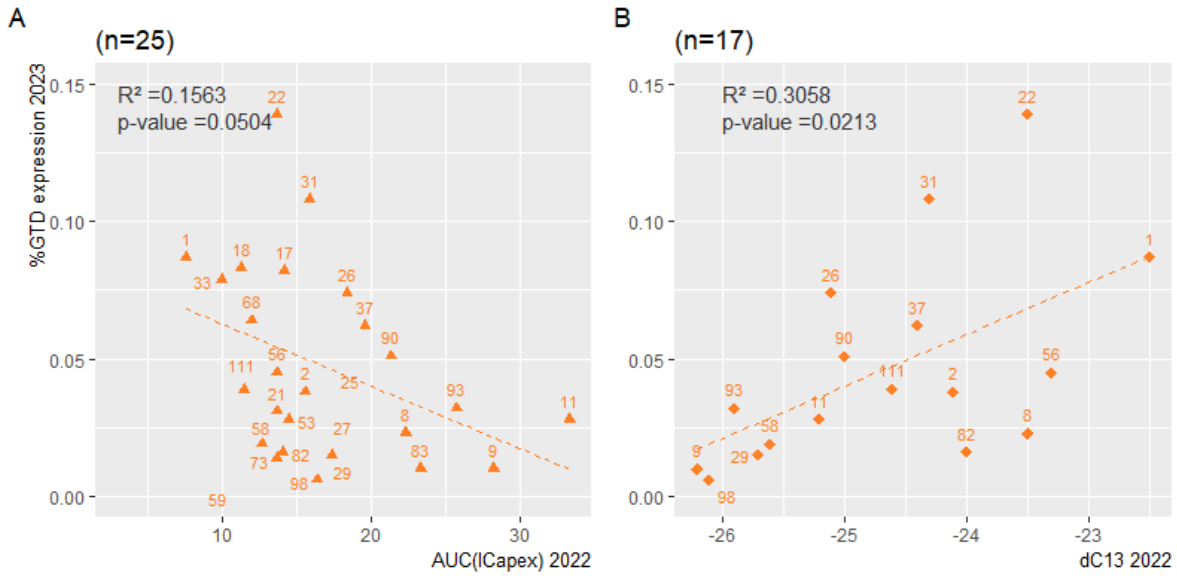


FIGURE 4. Bivariate relationships between GTD incidence in 2023 in Network-G and 2 indicators related to water status in 2022 (A, AUC_{ICapex} and B, $\delta C13$).

Labels = vineyard plot identification number.

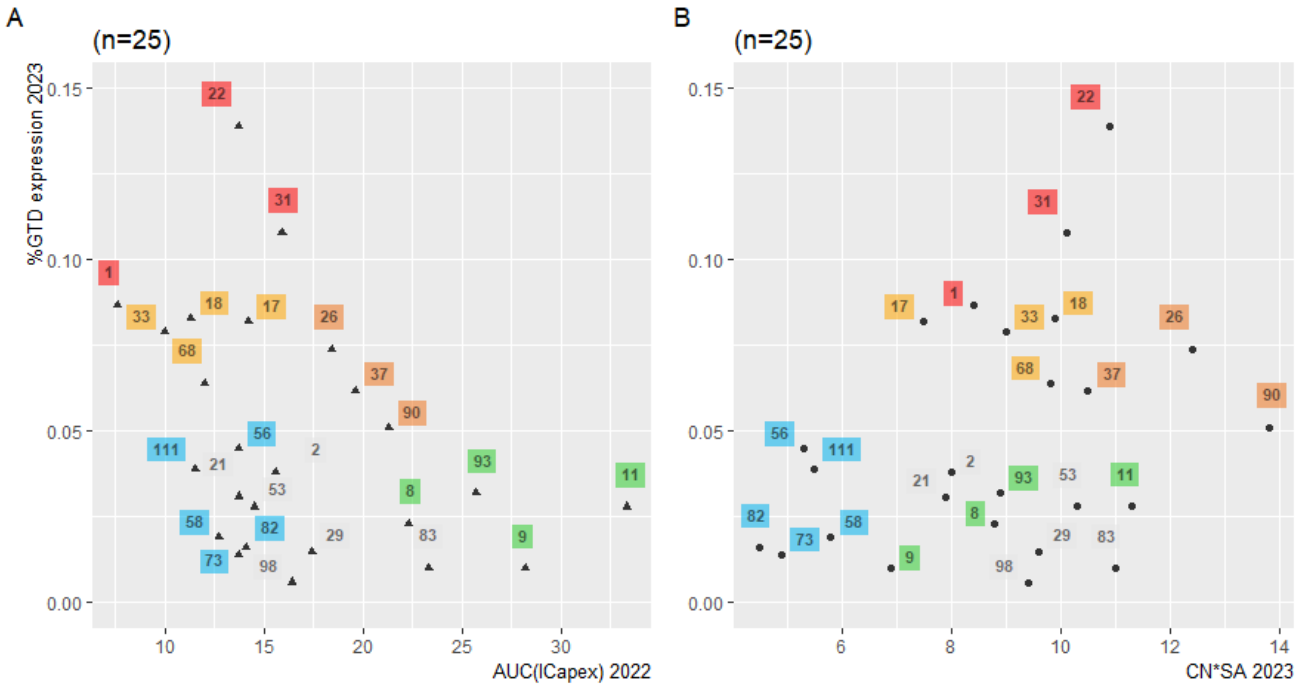


FIGURE 5. Bivariate relationships between GTD incidence in 2023 in Network-G and A, AUC_{ICapex} indicator related to water status in 2022 and B, vigour indicator CN*SA in 2023 illustrating specific groups of plots described in the discussion to help reading and understanding.

Labels = vineyard plot identification number. Label colour fill = groups of interpretation.

This relationship shape can be read as (1) under a "CN*SA" proxy value of approximately 8, GTD expression is low to even absent. (2) Rising from 8, the area described by the plots enlarges as vigour increases in such a way that for higher values of vigour, incidence can be either high or not. For example, in 2023, for Network-B and "CN*SA" scoring over 13, plots 65 and 86 show high levels of GTDs, whereas plots 11, 44 and 68 do not. In Network-V, plots 126 and 209 show high levels of GTDs in 2023 whereas plot 315 does not.

Very low values of vigour are associated with no (or very little) GTD expression, and this is visible on plots coming from all 3 networks: plots 37, 76, 19 or 21 in Network-B, plots 82 and 73 in Network-G, plots 269 and 257 in Network-V. These plots all have in common a high level

of ground vegetation cover that is generally long-term permanent cover. Agronomically, these plots show low N status, little vegetative biomass, and very low yield. Plot 7 of Network-B seems to be an odd value, but not an outlier: despite a moderate vigour, GTD expression in all 3 years is high.

As both (1) low vigour is associated with little GTD symptom and (2) higher rates of symptoms are only seen for higher values of vigour (except for 2023 Network-G), we can conclude that vigour is associated with GTD expression. However, the fact that higher values of vigour can also be associated with low values of GTDs shows that other factors are also influential on GTD expression.

3.2. The case of Network-G in 2023

According to Figure 2 and Figure S3, the case of Network-G in 2023 is slightly different from the others. Only four indicators are correlated to 2023 GTD expression under a 0.1 p-value threshold. The best correlation is shown with water status indicators (AUC_{ICapex} and δC13) the year before, and in an opposite way from the one it would have had with vigour (Figure 4).

Nevertheless, there is a correlation trend with vigour proxies 2023 CN*SA and chlorophyll index, showing a p-value close to the threshold of respectively 0.094 and 0.095. Because of this possible interesting dual action of vigour and previous year water stress indicators, we analysed the GTD expression using the interaction of the two (2022 AUC_{ICapex} and 2023 CN*SA, Figure 5).

The analysis of the respective position of the vineyard plots on either 2023 CN*SA or 2022 AUC_{ICapex} plots shows that there is a decoupling between both indicators showing distinct combinations depending on the vineyard plot:

- Some plots that showed a high vigour in 2023, may have suffered either low water stress in 2022 (see orange labelled plots 26-37-90, GTD expression is 5 to 8 % in 2023) or higher water stress in 2022 (see red labelled plots 31, 22 and 1, %GTDs 8 to 14 % in 2023);
- On the contrary, plots with moderate vigour in 2023 (especially in spring, not shown) may have suffered water stress (see yellow labelled plots 17-18-33-68, %GTDs 8 %) or not (see green labelled irrigated plots 8-9-11 or non-irrigated 93 one, %GTDs 1–3 %) in 2022.
- Finally, blue-labelled plots show the lowest level of vigour on the 2023 CN*SA indicator, even if they suffered water stress in 2022.

The worst situation for GTD incidence (8–14 %) seems to occur when the plot suffered higher water stress in 2022 and still shows substantial vigour in 2023 (red labelled group), especially in the spring (not shown). These 3 plots are all located on the sites of a former pine forest with clayey soils that are probably fertile in the springtime (due to high levels of organic matter) but dry out quickly in the summer. It would be interesting to confirm if this could also be the case of plot 7 from Network-B.

Plots 90 and 26 are very fertile. They had no water stress in 2022 and had high GTD expression in 2023 (6–8 %) but still less than the red group of plots that experienced water stress in 2022.

We can notice that, as long as the vigour is very low (blue labelled plots), GTD incidence rates seem to be low as well, whatever the water stress in 2022.

Here again, the same scatter plot type of shape is noticeable for both variables (vigour and water stress) indicating that apart from those 2 variables, there are still some additional hidden factors acting on GTD expression. Plots 98, 2 and 17, for instance, showed similar moderate vigour in 2023 and similar low to moderate water stress in 2022 but still displayed distinct levels of GTDs in 2023 (< 1 %, 4 % and 8 %, respectively). The case of plot 83 is also interesting because it is a rather vigorous plot with no water stress in 2022 and very low GTD expression.

DISCUSSION

The cases of the three networks studied over two contrasting years offer a diverse range of viticultural practices influencing grapevine vigour (such as rootstocks, irrigation, permanent ground vegetation cover and production goals) as well as environmental conditions, in particular, climate: the 2022 season was dry, while 2023 showed a dry spring followed by rainy May and June. These were conducive conditions to test the "grapevine vigour" hypothesis in different contexts.

This study shows that GTD expression in 2022 and 2023 was significantly correlated to a set of grapevine indicators belonging to water, nitrogen status, yield and vegetation biomass as well as cane pruning weight that altogether suggest a correlation with grapevine vigour. Indeed there is a rich long-term pre-existing knowledge on the intricate relationship between grapevine vigour and water and nitrogen status (Chone *et al.,* 2017; Deloire *et al.,* 2016; Verdenal *et al.,* 2021), as well as ground cover (Celette & Gary, 2013; Delpuech & Metay, 2018). Our results show that when the vigour is very low, there is only little to no GTD expression and that the highest rates of GTD incidence were always associated with high vigour, even if high vigorous plots can also show little GTD incidence.

These results of the positive effect of vigour on GTD symptoms are in accordance with Dumot (2022) in the French Cognac region and Gastou *et al*. (2024) who in addition, highlighted the same kind of relationship with both pruning weight and water use efficiency. Monod *et al*. (2025) observed a positive relationship between GTD incidence and soil water holding capacity, which is also consistent with a positive influence of 'vigour.' However, in that study, the correlation with the pruning weight vigour proxy itself was weaker. In our study too, we observe that the best-correlated variable is generally vigour but, depending on the network and year, it can turn out to be N status or yield or vegetation biomass indicators.

This study also showed that in one case out of six, the one of Network-G in 2023, the primary factors driving GTD expression were not vigour and related variables, even if current season vigour was still influential. The best correlations in these specific plot conditions implicated the apex growth index and δC13 indicators of water stress in the previous year. Even if in this study, there was no physiological indicator of grapevine water stress such as predawn water potential for instance, those 2 indicators, along with water status visual scoring at harvest, can reasonably be assumed to properly reflect vine water stress, as AUC_{ICapex} values below 15 were frequently associated with defoliation symptoms (visual water scores > 1.5) or values of δC13 indicating moderate to severe water stress. Given that, our results suggest that the water stress in 2022 positively influenced GTD expression in 2023 and the plots that displayed the highest levels of symptoms in 2023 were the ones that suffered the highest water stress in 2022 but still showed rather high levels of spring vigour in 2023. However, as this latter observation was only made on some plots of a single network and year, we consider it a preliminary result at this stage that would need to be reinforced by additional similar results. Yet it is interesting to note that the network in which we found the putative influence of water stress was Network-G, the one characterised by lesser rain amounts in 2022 and the highest permanent ground vegetation cover rates. In 2022, we observed in distinct south-eastern Mediterranean situations that the vineyards that first began to suffer from water stress in early June were the ones showing substantial and competitive ground vegetation cover. Consequently, it is plausible that highly competitive weed cover significantly burdened grapevine physiology in the particularly dry year 2022 in our Mediterranean region.

This preliminary observation made in Network-G in 2023, outlining a correlation between GTD expression and occurrence of water stress the year before, is also consistent with testimonies collected from different French regions like Alsace, Jura or Beaujolais vineyards (*personal communication*). Interestingly, permanent ground vegetation cover is frequent in these vineyards, as it is in Network-G. It would be interesting to replicate similar monitoring across a broader range of viticultural situations, including years, regions and cultivar/rootstock genotypes to confirm the two putative profiles observed in our study.

In this study, two associated factors proved to be involved in GTD expression: vine vigour on one hand, and the previous year's water stress on the other, possibly acting together. Other studies have highlighted additional favourable factors, such as harvest date (Kuntzmann *et al.,* 2013), water stress (Calvo-Garrido *et al.,* 2021) or on the contrary, water availability (Bortolami *et al.,* 2021). Moreover, we observed, as previously discussed, that even when a positive effect of vigour on GTD expression is observed, the best proxy can differ from one study, region or year to another. All these arguments strongly suggest that, beyond these variables, there might be a more upstream factor in relation to the global vine physiology that could be the relevant latent variable explaining GTD symptom expression. To account for that, we can postulate that the latent variable could be related to grapevine carbon or nitrogen balance, and grapevine source:sink relationships: it is then possible to assume that, depending on the study, the best proxy variables will differ depending on the one that is most impacting C or N balance in each situation. This, along with the fact that they rely on different metrics and periods, can account for the only apparent discrepancies between the different studies cited above. From that C and N source: sink perspective, vigour on one hand, related to high vegetative biomass and grapes, is indeed a strong sink for C assimilates. Water stress the year before, on the other hand, can limit photosynthesis (and hence the source production) and consequently interfere with C allocations between organs (Gómez-del-Campo *et al.,* 2016). It can hamper the following year's reserve pool mainly because of re translocation of C from the perennial organs to the grapes during maturation (Rossouw *et al.,* 2017; Savi *et al.,* 2019). For vigorous plots for example, with deep fertile soils, or recurrent rainy springs, vigour and productivity are the main drivers impacting grapevine C balance. On the opposite side, fertile soils combined with rainy enough springs followed by summer drought with competitive ground cover for instance could severely impede C balance both in spring and in summer along with high vegetation and grape biomass and poor C restorage. Any other vineyard*year situation could then be placed among this wide range of situations. It could be assumed that, for Network-G, grapevine cropping conditions, especially the ones relative to soil and ground cover, would be critical to determine whether, for some years, plots would be on a vigorous mode only (like 2022) or be submitted to previous year water stress impact too (like 2023). Given the year-to-year climatic condition variations, such plots would swing from one mode to another depending on the impact of these environmental conditions on their C balance.

The link between the grapevine C balance hypothesis and GTD symptom expression can be assumed to originate from defence metabolites. These defence metabolites are often considered in plants to derive from C primary metabolism (Berger *et al.,* 2007; Bolton, 2009) and as a result, source:sink relationships may be highly influent (Pellegrino *et al.,* 2006). They might as well rely on starch and other C or N reserves, particularly the ones stored in the trunk in the vicinity of wood-inhabiting fungal agents of trunk diseases before or during the outburst of a symptomatic event. The allocation for defence metabolites might thus be favoured by an excess of C available, once the priority sinks have been supplied. This hypothesis is supported by the results of Dell'Acqua *et al*. (2024), who observed that decreases in Esca symptoms in the low N treatment are associated with an increase in phenylpropanoid secondary compounds in leaves in early summer, and this (along with a reduction in vine transpiration) is more likely to explain Esca incidence than a change in tissue composition or fungal communities in the healthy wood of the trunks. As for the time period of susceptibility, springtime has proven to be an important stage: Spagnolo *et al*. (2014) showed that flowering is a particularly susceptible stage when contaminating green

shoots with two *Botryosphaeriaceae* species. Moreover, climate analysis has also proven that the temperature and rainfall conditions during the 2 months preceding the symptomatic events, *i.e.*, in our conditions from April to May, are critical (Fréjaville *et al.,* 2022; Larignon, 2009). In this study, we observed that in 2023, when we measured the chlorophyll index both at the flowering and veraison times, the correlation with GTD expression was always slightly better with the measurement made at flowering (not shown). We can assume that springtime is a critical period that could be either triggering or predisposing the vine to the subsequent symptomatic event. This, along with the previous ones, are hypotheses that would be worth investigating in further research.

In this study, we thoroughly discussed the possibility that vigour could impact GTD expression through grapevine physiological mechanisms. This does not exclude other possible explanations, for example, vigour could indirectly promote necrosis amounts in wood because of additional and thicker diameter canes to be pruned in winter. Vigour could also act by enhancing xylem vessel diameters, which can lead to higher susceptibility to some vascular pathogens, as evidenced by some authors (Pouzoulet *et al.,* 2014; Pouzoulet *et al.,* 2017).

As for the other additional variables that are needed to account for vigorous and GTD symptom-less plots, this is not really surprising, as expected from these complex multi-factorial diseases. These variables must be strong enough to counteract the effect of vigour, or they might act priorly to vigour and be necessary (still not sufficient) to lead to high-level symptom expression. We could think of winter pruning as one of those influential variables, affecting the internal health of the wood relative to subsequent desiccation and necrosis amounts. In this regard, plots 83 and 98 from Network-G, which show particularly low GTD expression relative to their vigour and water stress levels, indeed use training systems respectful of sap flow pathways (respectively goblet and cordon with elongated branches) and this has been cited as an influent factor (Lecomte *et al.,* 2019). Nevertheless, as this same type of scatter plot shape is also observed by Gastou *et al*. (2024), but coming from a single vineyard plot, it can be questioned whether winter pruning is the only explaining factor, as we can postulate that pruning conditions in that plot might be similar for all cultivars. Anyway, assessing pruning quality and grapevine trunk necroses status in plots with similar vigour but different GTD expression levels could still provide valuable insights to explain at least part of the GTD incidence variance residuals.

In this study, we identified the implication of grapevine vigour and possibly more upstream physiological factors on GTD expression, and this opens new perspectives of applications for growers, like assessing whether vigour management could be a sustainable way to reduce trunk disease expression and mortality for the affected plots. For vigorous plots showing a high incidence of GTDs, it would be relevant to test growing cover crops during winter and spring, as well as managing N fertilisation, as those two practices are known to reduce vigour. On the other hand, questioning ground weed or crop cover optimisation (in time or space), especially on shallow soils and for dry climates would be useful, at least if further results happen to confirm the observations we made on Network-G in 2023. This raises several additional questions: what is the expected time frame for observing the response on GTD symptoms? As vigour reduction is frequently associated with yield decrease, is a trade-off achievable, *i.e.*, can we drive vigour reduction in a susceptible vineyard without too much yield inflexion relative to the growers' objectives? What about the subsequent grape and wine typicity in the current climate change context?

Further work is encouraged to address these questions relying both on research and field experiments, to better understand as well as provide control practices to growers.

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