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Abstract: Grape production worldwide is increasingly threatened by grapevine trunk diseases (GTDs). No grapevine cultivar is known to be entirely resistant to GTDs, but susceptibility varies greatly. To quantify these differences, four Hungarian grape germplasm collections containing 305 different cultivars were surveyed to determine the ratios of GTDs based on symptom expression and mortality rate. The cultivars of monophyletic *Vitis vinifera* L. origin were amongst the most sensitive ones, and their sensitivity was significantly ($p<0.01$) higher than that of the interspecific (hybrid) cultivars assessed, which are defined by the presence of *Vitis* species other than *V. vinifera* (e.g. *V. labrusca* L., *V. rupestris* Scheele, *V. amurensis* Rupr.) in their pedigree. We conclude that ancestral diversity of the grape confers higher degrees of resilience against GTDs.

Keywords: interspecific cultivars; *Vitis vinifera*; *Vitis amurensis*; *Vitis rupestris*; *Vitis labrusca*; grape germplasm collection; GTDs

1. Introduction

Grapevine trunk diseases (GTDs) are amongst the most important diseases of grapevines with estimated losses of 1.5 billions of USD worldwide while the average GTD incidences were reported to be between 10 % (Spain) to 22 % (Italy) in European vineyards [1,2,3,4]. Moreover, the increases in disease incidence has been recognized in several grape growing countries such as Spain, Italy, Canada [5,6,7,8]. GTD fungal pathogens colonize the woody part of the plant, producing different toxins and enzymes, and resulting leaf symptoms (tiger stripes) stunted growth, reduced quantity and quality of grape, and dieback of the plant [2]. GTDs are complex diseases, including esca, eutypa dieback, black foot, botryosphaeria and Petri diseases, and are affected by several biotic and abiotic factors [2,4,9,10,11,12,]. More than 100 fungal species have been recognized as GTD pathogens, characterized by different taxonomic status, disease cycle, fungicide sensitivity and host range [13].

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Moreover, infections usually do not manifest rapidly and can linger on for years. Factors and circumstances that turn the latent infection into an active one giving rise to mild (e.g., foliar symptoms) or serious symptoms (partial or whole plant dieback) are not fully understood. Wounds, environmental stress (frost, drought, flood), and increased age of the vineyards appear to correlate with increased disease incidence of GTDs [4,14,15,16,17]. Chronic symptom expression does not necessarily lead to significant yield or quality loss of the fruit, or plant loss within a few years [4,18]; conversely, apoplexy of the trunk leads to plant loss and results in irreversible economic loss in the plantation. Replenishing vineyards with young, healthy vines is challenging and often unsuccessful.

Tolerant plant cultivars are widely in use as they are one of the most effective means to control plant disease, providing economic and environmentally friendly plant protection technology while reducing pesticide usage and dependency [19]. Disease-resistant cultivars would also provide solutions when effective protection by chemical pesticides is not available, like in the case of GTDs [20,21,22].

Due to the susceptibility of traditional European grape varieties to different pathogens, an interspecific hybrid breeding program was started in France in the early fourties of the 19th century , by crossing *Vitis* vinifera varieties from France with American species, which resulted in more resistant, high-quality hybrids that exhibit partial resistance toward the fungal pathogens [23]. The hybrid offspring were subsequently used in the resistance breeding programs in Hungary as 'Seibel' and 'Seyve-Villard' varieties [24]. However, with the propagating plants, the phylloxera (*Daktulosphaira vitifoliae* Fitch) insect pest was also introduced, which resulted in dramatic loss of plants in the European vineyards. It also has become common practice to graft American rootstock, resistant to phylloxera, to preserve susceptible cultivated European varieties, and grape breeding programs were initiated to control phylloxera, powdery mildew (*Erysiphe necator* Schwein.) and downy mildew (*Plasmopara viticola* (Berk. et Curt.) Berl. et De Toni) [23,25,26,27,28].

Vitis amurensis Rupr., native to China, has several beneficial properties, such as cold resistance and resistance against several phytopathogens causing diseases, like grape crown gall (*Allorhizobium vitis*), white rot (*Coniella diplodiella* (Speg.) Petr. et Syd.), downy mildew and anthracnose of grapes (*Elsinoe ampelina* Shear). Therefore, it is often used as rootstock or in breeding interspecific hybrids [29,30,31,32,33,34,35,36]. Introduction of American and Asian grape species to the breeding programs increases genetic diversity, and compensates the bottleneck effect (when the size of a population is severely reduced), that developed historically as the consequence of the domestication of *V. vinifera* [37,38].

There are no *V. vinifera* cultivars known to be completely resistant to GTD pathogens, however considerable differences in sensitivity have been recognized during *in planta* tests and in field surveys (Table 1). There were differences observed between the tolerance to different GTD pathogen fungi in one cultivar, which may due to the various climate conditions and/or grape-producing technologies. In the case of eutypa dieback, Dubos [39] categorized Aligote, Grolleau, Merlot, Semillion and Sylvaner cultivars as resistant, and later Carter [40] reported possible resistance against *Eutypa lata* (Pers.) Tul. & C. Tul in some French cultivars. Borgo et al. [41] and Murolo-Romanazzi [42] classified the degree of GTD expression for six and 86 varieties, distinguishing between red and white grape varieties. Sosnowski et al. [43] ranked 118 varieties based on plant death and foliar symptoms. These and other studies have shown that, among internationally recognized and cultivated varieties, Cabernet Sauvignon, Cabernet Franc and Sauvignon Blanc are particularly susceptible to GTDs, while the Merlot is much more resilient.

Table 1. The tolerance of *V. vinifera cultivars* to different grapevine trunk diseases. Adopted from Songy et al. [17].

	Cultivars[1]	GTDs		Inoculation test/Disease incidence survey[3]	References
		Tolerance	Disease[2]		
White	Chardonnay	high	BD, Eutypa	Test	[44]
		medium	BD	Survey	[43]
		medium	Esca	Survey	[41]
	Pinot Gris	high	BD, Eutypa	Survey	[43]
		medium	Esca	Survey	[10]
	Riesling	high	Eutypa	Survey	[43]

		medium	BD	Test	[45]
		medium/low	Esca	Test	[44]
	Sauvignon Blanc	high	BD	Test	[45]
		medium	Eutypa	Test and Survey	[43]
		low	BD	Test and Survey	[43]
		low	Esca	Survey	[42,46]
	Semillon	high	BD, Eutypa	Test and Survey	[43]
		low	Esca	Survey	[10]
	Thompson seedless	high	Esca	Test	[47,44]
		medium/low	Eutypa	Test	[44]
		low	BD, Eutypa	Test	[47,44]
	Ugni Blanc	medium/high	BD	Survey	[43]
		low	Eutypa	Test	[48]
		low	Esca, Eutypa	Test	[49]
				Survey	[41,43]
	Welshriesling	high	BD, Eutypa	Test and Survey	[43]
				Survey	[41]
		low	Esca	Survey	[7]
Red	Cabernet Franc	medium/high	Eutypa	Test	[44]
		medium	BD	Test	[44]
		low	Esca	Test and Survey	[43]
	Cabernet Sauvignon	high	BD	Test	[45]
		low	Eutypa	Test	[48]
		low	Esca, Eutypa	Survey	[41,46,50
			BD	Survey	[43]
	Grenache	high	Esca, Eutypa	Survey	[43]
		high	Esca	Test	[47]
		BD	medium/high	Survey	[43]
	Merlot	high	Eutypa	Test	[44,48]
		medium/high	BD	Test	[44]
		medium	Esca	Survey	[42,50]
	Pinot Noir	high	Esca	Survey	[41]
			Eutypa, Esca	Test and Survey	[43]
		medium	BD	Test and Survey	[43]
	Sangiovese	high	BD, Esca, Eutypa	Test and Survey	[43]
		medium	Esca	Survey	[41]
	Syrah	high	Esca	Survey	[41]
		low	BD, Eutypa	Test	[21,44
				Test and Survey	[43]
Hybrid (V.	Concord (*Vitis labrusca* hybrid)	high	BD, Esca, Eutypa	Test	[44]

[1]Cultivar primer names from VIVC database [51]. [2]BD: Botryosphaeria dieback; Eutypa: Eutypa dieback. [3]Test: Inoculation of cuttings; Survey: in field survey of disease incidence.

Both GTD chronic symptom expression and apoplexy combined with subsequent loss of plants were monitored in four Hungarian grape germplasm collections containing a total of 305 different cultivars. Disease incidence (DI) was calculated to compare (i) the degree of GTD sensitivity of the most important international and national grape cultivars (ii) the severity of GTD symptoms in cultivars with monophyletic *V. vinifera* origin and interspecific (hybrid) cultivars with various American or Asian *Vitis* species in their pedigree. These data may provide important information for extended and future grape breeding programmes.

2. Results

Four grapevine germplasm collections with 537 cultivars were surveyed. GTD symptoms were categorized as new symptoms during the annual vegetative period (leaf stripes with white or brown

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rot, and dieback) (Figure 1 a-d) or as dead and missing (removed) plants from previous dieback events in past years (Figure 1 e-f).

The total disease incidence (DI %) was over 25 % in each of the survey sites (Table 2), therefore, the conditions for a meaningful survey of symptom expression rates were considered adequate for further analysis. The average ratio of dead plants and total disease incidence (i.e., all symptoms) was similar in each germplasm collection. Altogether, these results, with previous records of dieback symptoms of currently dead and removed (dead) plants validated the connection between missing plants and previous dieback.

Table 2. Total disease incidence (DI) of grapevine trunk diseases (GTDs) (mean±SE) and the ratio of dead plants (mean±SE) within GTD symptoms in the different germplasm collections. Small letters show significant differences based on Mann-Whitney U-test ($p<0.05$).

Location	No. Cultivars	GTDs	
		Total DI % (±SE)	Ratio of dead plants (% ±SE)
Badacsonytomaj	90	44.58(±2.62) c	74.63(±3.14) a
Kecskemét	130	28.05(±2.19) a	76.49(±3.11) a
Pallag	166	37.05(±2.16) b	73.78(±3.10) a
Pécs	151	28.41(±1.92) a	69.94(±3.23) a
Total	537	33.70(±1.13)	73.56(±1.59)

Figure 1. GTDs symptoms: a, d: leaf stripes; b: partial dieback; c: esca symptoms with white rot and leaf stripe; e: dead plant from previous dieback (indicated by arrow), and new (annual) symptomatic plants (middle and right side); f: dead plant from previous vintage.

The total DI of the most important cultivars with only *V. vinifera* ancestors were compared (Figure 2). Sauvignon Blanc and Cabernet Sauvignon were the most susceptible cultivars, while Merlot and Syrah were the less susceptible ones (Figure 2, Table 1). There were both white and red grapes among the most and the less sensitive cultivars within the analyzed genuine *V. vinifera* cultivars. The susceptibility of Furmint, one of the most important Hungarian white cultivars was similar to that of Veltliner Gruen and Muscat Lunel, while another indigenous white cultivar, Juhfark, was less susceptible, more similar to that of Blauburger and Pinot Blanc. The indigenous table grape, Csaba Gyoengye, was less susceptible than Furmint, showing similar DI to those of Welschriesling,

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Cabernet Franc and Muscat Ottonel. Blaufraenkish, a grapevine variety with regional importance was amongst the less susceptible cultivars, like e.g., Pinot Blanc and Pinot Noir.

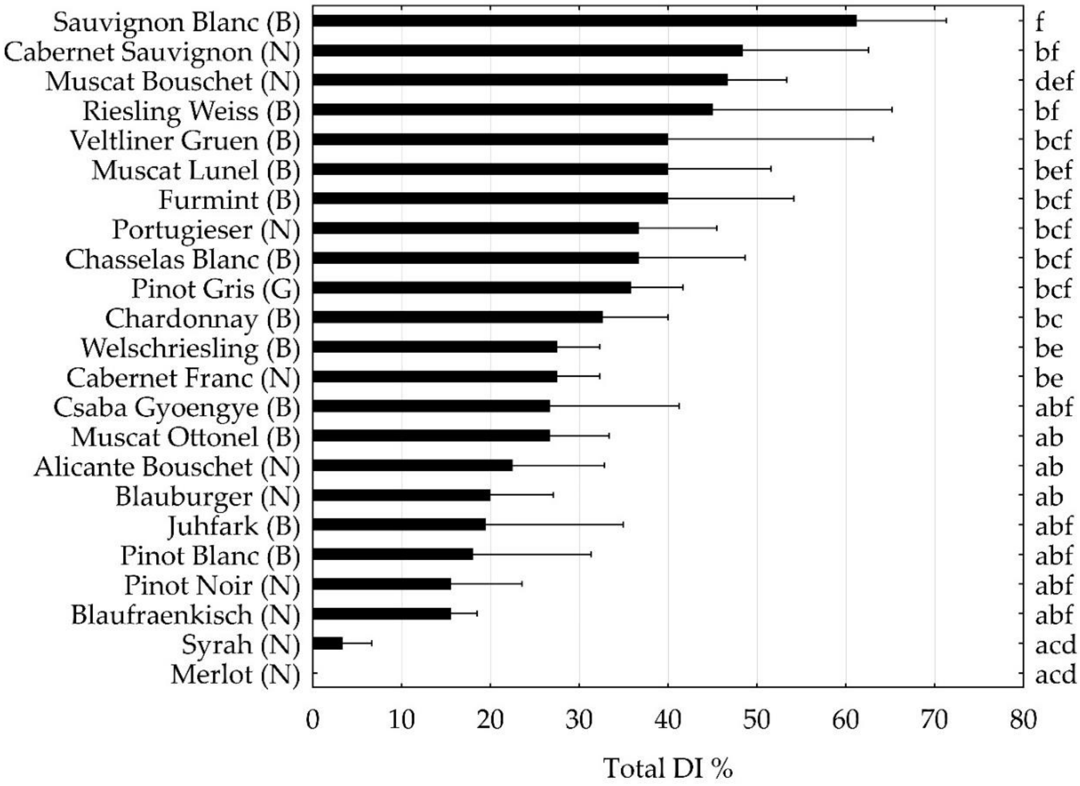

Figure 2. Total disease incidence (DI) of grapevine trunk diseases of the most important international and national grape cultivars, surveyed in 3 or 4 Hungarian germplasm collections. The capital letters between brackets indicate the berry skin color: (N): noir, (B): blanc, (G): gris as defined in the VIVC database [51]. Small letters show significant differences based on Mann-Whitney U-test ($p<0.05$).

Severity of disease expression categories were defined to separate cultivars. When a cultivar has a tendency to not demonstrate GTD symptoms *in situ*, it is defined as unsusceptible. When only annual developed (usually mild) GTD symptoms are displayed, the cultivar is listed as resilient. Sensitive cultivars demonstrated tendency of developing dieback symptoms eventually resulting in plant loss in parallel with other GTD symptoms in other individuals, while exclusively plant loss of infected specimen was detected in vulnerable cultivars that are highly sensitive. The majority of the cultivars with only *V. vinifera* ancestors in their pedigree were categorized as highly sensitive or sensitive to GTDs with exclusively plant loss or high plant demise concurrent with non-lethal symptoms (Figure 3). The level of resistence to GTD pathogens was generally better or much better in the case of interspecific hybrid *Vitis* cultivars, with a considerably higher ratio of unsusceptible or resilient cultivars, than encountered amongst monophyletic *V. vinifera* ones (Figure 3).

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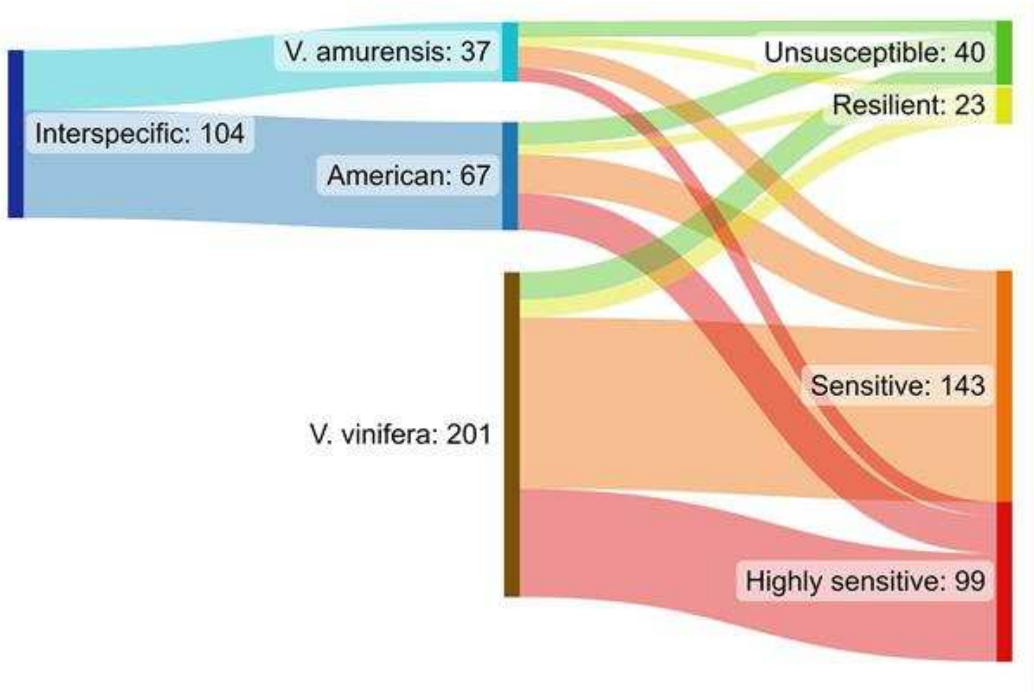

Figure 3. Distribution of the studied cultivars regarding their *Vitis* pure or mixed ancestry, and the GTD pathogens sensitivity groups. Diagram created by SankeyMATIC [52].

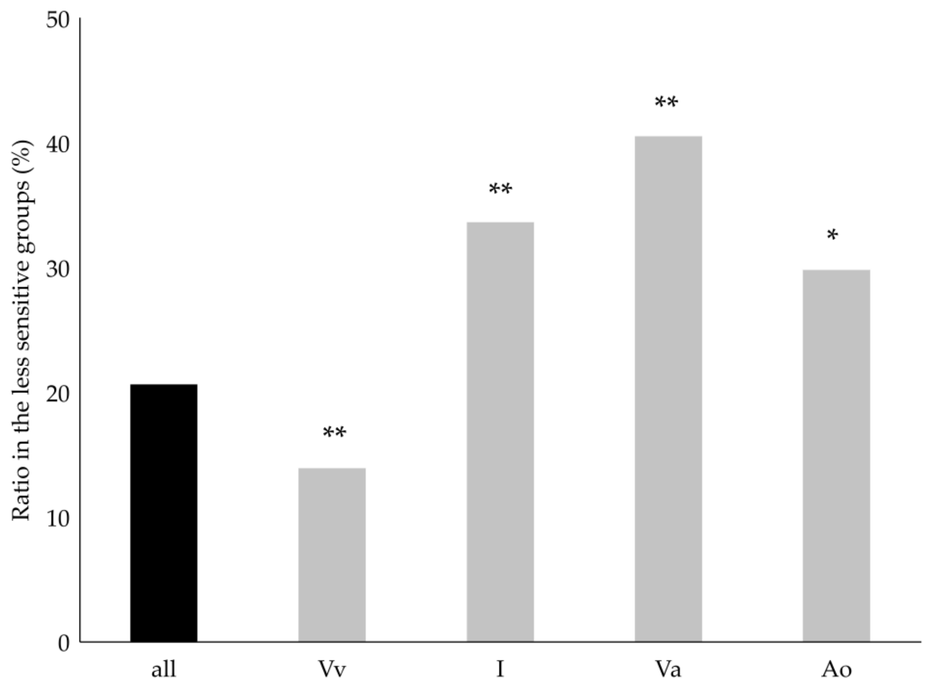

Figure 4. The ratio of the cultivars categorized in the less GTD pathogens sensitive group within monophyletic *V. vinifea* cultivars (Vv), and those in all interspecific cultivars combined (I), or with the interspecific cultivars with those with Asian (*V. amurensis*) (Va) or American species (*V. labrusca, V. riparia or V. rupestris*) (Va) ancestors treated separately. Results of the binomial probability test, indicating the difference between the examined group and the averages of all cultivars: * = $p<0.05$; ** = $p<0.01$.

The tendency of the cultivars with different origins for plant loss, was compared in binomial test. The ratio of the monophyletic *V. vinifera* cultivars was lower in the less sensitive groups (unsusceptible and resilient), than expected based that of all tested cultivars (Figure 4a). This indicates, that monophyletic *V. vinifera* cultivars have a higher tendency to display serious GTD symptoms including plant loss, than the average of all examined cultivars (overall samples). On the

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contrary, the ratio of cultivars without plant loss (less sensitive groups) was significantly higher for the group of the interspecific hybrids. Similarly, when the hybrids with American (*V. labrusca, V. riparia or V. rupestris*) or Asian (*V. amurensis*) ancestors were split and compared separately, the ratio of the cultivars in both groups were higher in the less susceptible categories compared to all cultivars studied (Figure 4b).

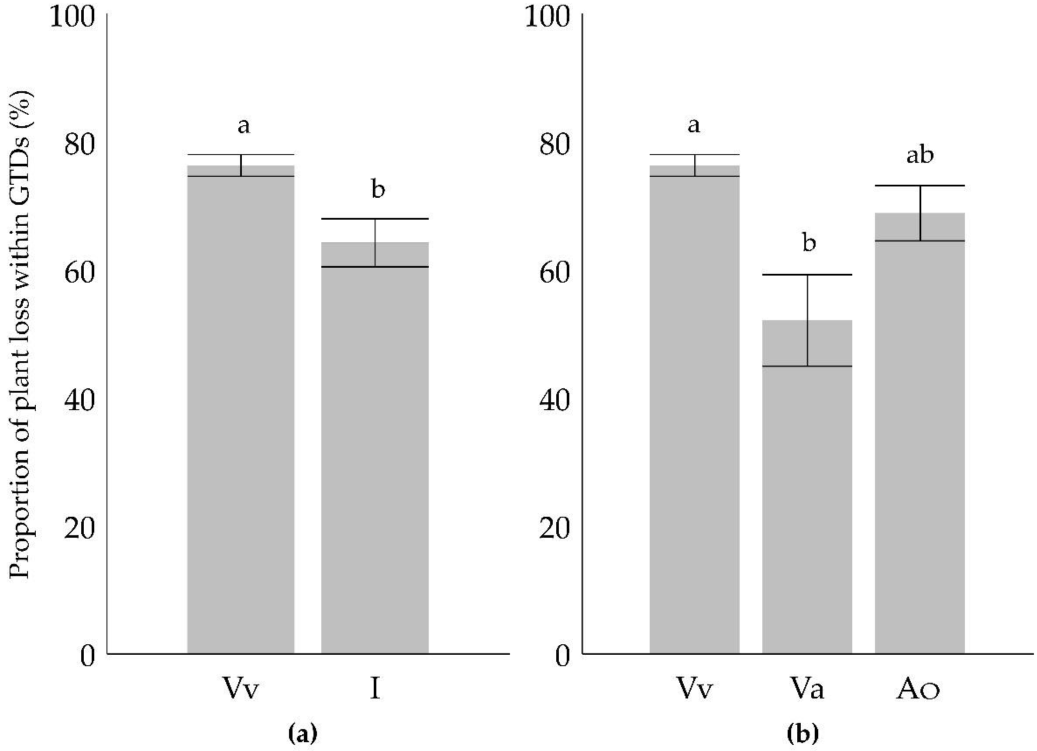

Figure 5. Proportion of plant loss within all recorded GTD symptoms (a) comparing the average of these cultivars with that in exclusively *V. vinifera* (Vv) ancestors, and with that in all the interspecific hybrids (I) and (b) the same comparison with Vv but now with hybrids with *V. amurensis* (Va) in their pedigree or those with American(Ao) (*V. labrusca*, *V. riparia* or *V. rupestris*) ancestry, separatedly. Small letters indicate significant differences between datasets based on Mann-Whitney U-test (p<0.01).

The susceptibility of the cultivars with different species ancestry (i.e., exclusively *V. vinifera* or interspecific hybrids) was compared regarding the cultivar specimen mortality from GTDs as part of the total GTD disease incidence (i.e., all symptoms). Plant death as a consequence of GTD expression was more likely in cultivars with monophyletic *V. vinifera* origin, than in the interspecific *Vitis* cultivars. Separating the group of the interspecific cultivars into cultivars with Asian and American origins, the ratio of dead plants within the displayed GTD symptoms was meaningfully lower exclusively for cultivars with *V. amurensis* ancestry , than the ones with monophyletic *V. vinifera* cultivars (Figure 5). Thus, the calculated difference was not significant for the group of cultivars with *V. labrusca*, *V. riparia* or *V. rupestris* (American species) in their pedigree.

3. Discussion

There are differences in sensitivity to GTDs displayed by the *V. vinifera* cultivars, however, no completely resistant has been identified. The physiological and genetic background of these differences in sensitivity or resistance against GTD-causing pathogens is not understood [53,54]. In accordance with previous results, Sauvignon Blanc and Cabernet Sauvignon showed the highest DI in the surveyed Hungarian germplasm collections, all four with their own climate and soil characteristics, while Furmint, Chardonnay and Cabernet Franc were found less GTD susceptible [12,42,43,46,55]. Blaufraenkisch (also referred to as Limberger), again confirmed by our current results, constistently one of the lowest DI [42,43, 46,55], while Merlot and Pinot Noir usually were also found less susceptible to most of GTDs in general [12,42,46,55,56].

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Comparing the sensitivity of different grapevine cultivars to esca, significant differences were found between those with red and those with white berries, and their respective xylem vessel diameter and density [46]. The average vessel diameter of the white cultivars was larger with higher densities, compared to the red grapevines. A similar trend was observed for overall disease incidence, where the mean disease incidence was higher for white-berry cultivars than for red-berry cultivars. Foliar symptom symptoms are hypothesized to result from fungal toxins translocated to leaves from primary infection sites [53,57,58]. Higher rates of leaf symptoms were explained by the larger vessel diameters, since it provides space for more intensive xylem cavitation, which can assist toxin translocation to the green plant parts [46]. Moreover, Pouzoulet et al. [59] stated, that the esca pathogens may escape compartmentalization more efficiently when the vessels are wider, and the more gel and tyloses in the vessels, the more substrate is provided for wood pathogens [59].

No GTDs symptom expression was detected in the Hungarian germplasm collections on the extant Merlot cultivars, whose outstanding tolerance was reported in several previous studies in other countries [21,39,44,42,50,60,61]. The lignin content of Merlot was found to be significantly higher than in Cabernet Sauvignon, a cultivar to be considerably more susceptible to GTDs [41,43,46,50]. Other cultivars identified as less sensitive to GTD had in general smaller vessel diameter and higher lignin content than the most sensitive grapevine varieties [62,63]. The results of Rolshausen et al. [62] highlighted the potential importance of lignin in the *E. lata*-grapevine interaction. The costumary defence response of grapevines to infection is compartmentalization, where the plant attempts to contain the invading agent by depositing suberin and lignin which impedes the spread of the pathogens throughout the xylem. A higher lignin content was detected in the infected grape tissues, which indicates that lignin deposition is initiated in response to the fungal infection [62].

GTDs are complex diseases, resulting serious economic loss by reduced grape productivity, and characterized by remarkable differences in the disease severity and manifestation [2]. Infection with GTD fungal pathogens may result in latency, accidental or repeated annual disease expression, and serious partial or whole plant dieback [64]. The most serious disease symptom is plant loss resulting irreversible economic damage. Previously, only foliar or chronic and dead cordon or apoplexic (partial and whole plant) individual disease expressions were differentiated amongst GTD symptoms [43,46,55]. This traditional categorization or subsequent merging different symptom manifestations and calculating disease incidence indicates only the susceptibility of a cultivar, and does not take into account the severity of the infection and the plant's responses. Cultivars that are able to survive infection for a longer period of time - specimens of which are more likely to express the milder foliar symptoms and partial dieback rather than whole plant apoplexy and death - are considered more resistant to the fungal GTD pathogens in our present survey and analysis.

The survey and analysis of four Hungarian germplasm collections concluded that the interspecific hybrid cultivars, in particular the ones with Asian *V. amurensis* ancestry are generally less susceptible to GTDs, expressing no or milder symptoms, than monophyletic cultivars with only *V. vinifera* ancestors. In these hybrid cultivars with some level of East-Asian ancestry, infection by GTD fungal pathogens resulted in less plant losses, which is the most serious, and irreversible consequence of GTD infection. One of the possible backgrounds of this lower sensitivity (or higher resistance) may concur with the xylem vessel diameter, as *V. amurensis* had the smallest vessel diameter amongst different grape species [65,66]. By contrast, the vessel diameter of the American species *V. labrusca* was reported to be rather large [65]. In a more recent study, there was no substantial difference in xylem vessel diameter recorded between *V. vinifera* and American interspecific hybrid called Noiret, with *V. labrusca* ancestry [63].

Since most of the GTD pathogens are wound-colonizing fungi, frost cracks of the wood parts of the plant could facilitate the prevalence of the GTD disease complex in grapevine [67,68]. Compared to *V. vinifera* and *V. labrusca* species, *V. amurensis* is extraordinarily cold-resistant and can survive long and cold winters as a result of its relatively low respiratory intensity, a lower level of active metabolism and a longer dormancy period [32]. *V. amurensis* is cultivated as a cold-resistant grape in the colder regions of China [32,69,70,71]. Wang et al. [72] identified 17 genes possibly involved in this increased cold hardiness. Accumulation of several amino acids (valine, isoleucine and proline) was reported to be higher in *V. amurensis* than in *V. vinifera* cultivars, the level of which was subject to abiotic stress [73]. This property together with the accumulation of other bioactive compounds (polyphenols, tannin, and the stilbene phytoalexin resveratrol) can protect plants from long-term cold damage [32,74].

The induction of stilbene biosynthesis was found correlated with basal immunity against the downy mildew and eutypa dieback [48,75]. American *Vitis* species are also employed in breeding more cold-hardy cultivars [76]. Increased stilbene biosynthesis has relevance in increased resistance to different fungal diseases [77], and may have importance in GTD tolerance, as grapevine rootstock transformed with grapevine stilbene synthase gene expressed from a pathogen-inducible promoter showed increased resistance against *E. lata* [48].

V. amurensis is not only cold-tolerant, but also resistant to white rot, grape anthracnose and grape bitter rot (*Greeneria uvicola* (Berk. & M.A. Curtis) Punith) fungal diseases, and has a high resistance to downy mildew, caused by the Oomycete *P. viticola* [29,31,32,33,74,78,79,80]. The resistance of grapevine against the bacterial trunk pathogen *A. vitis* was introgressed from *V. amurensis* upon interspecific breeding [30]. Hybrids with *V. amurensis* ancestry were unambiguously less sensitive to GTD pathogens in our survey, illustrated by the considerably higher ratio of resilient and tolerant hybrid cultivars to Botryosphaeria dieback (BD) and esca diseases.

Pretorius and Høj [81] assumed that the product of a single gene or its pyramid (stacking multiple genes into a single genotype to combine desirable traits) is effective only against a narrowly related group of pathogens within the GTD complex. These authors differentiated the tolerance toward various GTD pathogens in numerous monophyletic American *Vitis* cultivars and hybrids. The resistance loci Rda1 and Rda2 originating from *Vitis cinerea* (Engelm.) Engelm. ex Millard B9, a native American grape, and the interspecific Horizon cultivar, respectively, largely prevented the development of Phomopsis dieback symptoms [82]. Concord, an interspecific cultivar with parental varieties Catawba and *V. labrusca* showed a reduced sensitivity to *Neofusicoccum parvum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips, in inoculation assays. On the other hand, the American *Vitis* spp. were found to be more susceptible against Eutypa dieback, than *V. vinifera* [44]. Co-evolution of *V. vinifera* and *E. lata* in a natural habitat, could have increased the resistance of the plants prior to domestication [44].

One of the main goals of breeding programs nowadays is to pyramid extant, independent biotic and abiotic resistance genes from different lineages of American or Asian grapes and to attain additive accumulation of broad resistance against or tolerance to phytopathogens into one parent which can be crossed with European *V. vinifera* [84]. The domestication bottleneck effect, the result of thousands of years of vegetative propagation without meiosis and recombination, and the continuous incrossings of the high-quality cultivar resulted in low genetic diversity across domesticated *V. vinifera* grapes [37,38]. Engaging American and Asian *Vitis* species in breeding has the potential to enhance biotic and abiotic vine stress tolerance lost over the course of domestication [29,30,31,32,33, 34,35,36,69,70,71], which is relevant to GTD symptom expression and disease severity in grape cultivars.

4. Materials and Methods

4.1. Survey sites and cultivars

The survey was conducted in 2022 involving four Hungarian germplasm collections (Figure 6) containing high number of cultivars with worldwide, Central-European, or Carpathian basin significance, and valuable parental lines for further breeding. The climatic and edaphic conditions differ considerably at the four locations, despite their geographical closeness (ranging from 60 to 330 km in distance). Pallag (University of Debrecen, Institutes for Agricultural Research and Educational Farm, Horticultural Experimental Plant of Pallag) and Kecskemét (Hungarian University of Agriculture and Life Sciences, Research Institute for Viticulture and Oenology) are in the eastern part of Hungary which has a continental climate with a relatively low annual precipitation (500-700 mm) [85]. These lowland sites in the Carpathian basin were established on phylloxera immune sandy soils, thus the plants growing at these locations are not grafted (Pallag) or in part growing on their own root (Kecskemét) [86].

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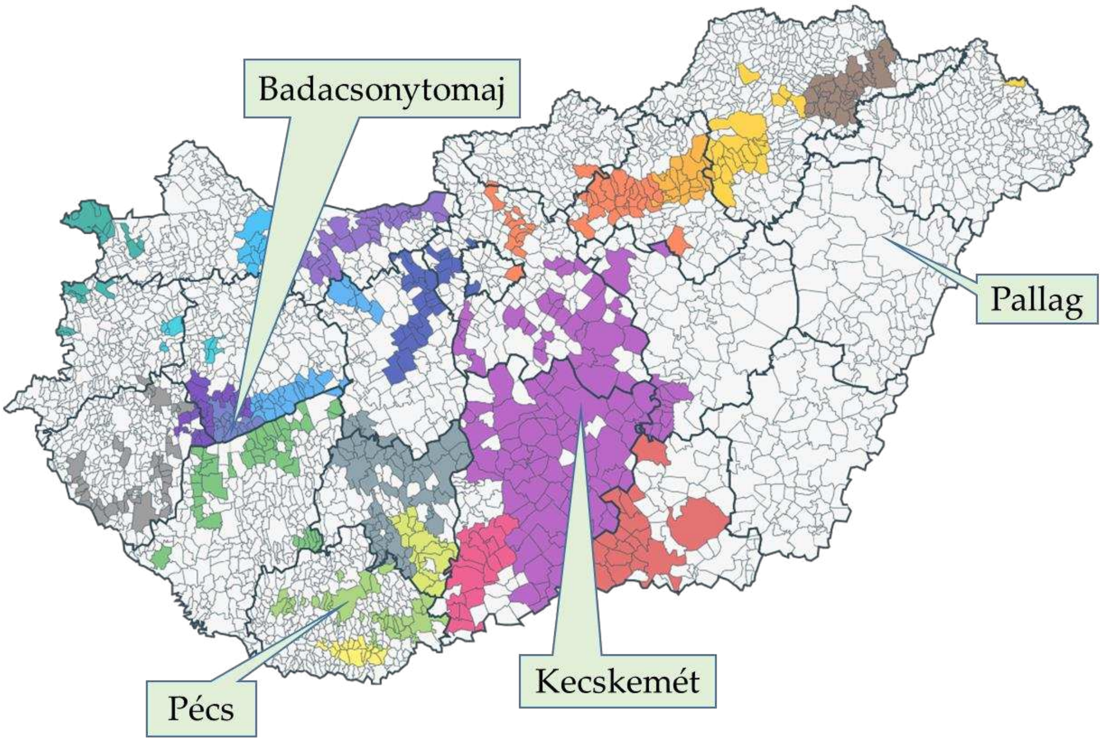

Figure 6. The location of the surveyed germplasm collections in Hungary. Different colors indicate the different Wine Regions [87].

Badacsonytomaj (Hungarian University of Agriculture and Life Sciences, Research Institute for Viticulture and Oenology) and Pécs (University of Pécs, Research Institute for Viticulture and Oenology) are in occidental part of the country, where the influence of the westerly winds associated with the more moderate oceanic climate is more pronounced. Both of these sites have mountain slope relief with terrace cultivation and a sub-Mediterranean climate with annual precipitation between 600-800 mm [85,88]. The soil type in Badacsonytomaj is volcanic erubase and eroded loess slope sediment and the region is heavily affected by the humidifying and moderating effect of the water body of the Lake Balaton [89]. The soil type in Pécs is Brown earth (Ramann's brown forest soil) overlying carbonate-rich red sandstone.

Table 6. Characteristics of germplasm collection locations.

	Badacsonytomaj	**Kecskemét**	**Pallag**	**Pécs**
Soil	erubase soil	sand	acidic sand	Brown earth
Relief	mountain slope (top-valley row direction, terrace cultivation)	lowland	lowland	mountain slope (terrace cultivation)
Cultivation type	grafted	own rooted	own rooted	grafted
Climate	submediterranean with dry, warm summer	continental	continental	submediterranean with dry, warm summer
Relative climate sector[1]	IIIc	Ib	Ia	IIIb
Average temperature fluctuation (°C)	21-22	23-24.5	23-24	21-22
Annual precipitation (mm)	600-800	500-550	550-700	600-800
Annual sunshine duration (h)	1950-2050	2000-2150	1900-2050	2000-2100

[1] Relative climate sector as taken from [85].

The germplasm collections are considered to be free from bacterial phytopathogens *A. vitis*, and *Rhizobium radiobacter*. Vineyard parts potentially affected by Flavescence dorée (*Ca. Phytoplasma vitis*) were consistently excluded from our survey. BD and esca symptoms were predominant at the surveyed sites but Eutypa-like symptoms [13] were encountered in few instances. The GTDs were

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visually diagnosed by the typical tiger-strip foliar symptoms (Figures 1a,d) while white and/or brown rot was detected on cross sections or debarked woody parts (Figure 1c) of the plants. The ensemble of BD, esca and Eutypa-like symptoms were counted as GTD symptoms. The new apoplectic symptoms (dead young shoots with leaves, Figure 1b) were considered as annual GTD symptoms. If there were no fresh sprouts in the vine specimen, the plant was considered as dead (Figures 1e-f). All evaluated cultivars were surveyed in over 10-years-old plants, therefore the chronic/milder (non-lethal) symptoms were evaluable [90,91].

Table 7. Categories of cultivars with multiple *Vitis* species ancestry.

Ancestors in parent or grandparent level	Categorization I.	Categorization II.
Vitis vinifera	*Vitis vinifera* (Vv)	*Vitis vinifera* (Vv)
Occurrence of American species [1]	Interspecific (I)	American origin (Ao)
Occurrence of *Vitis amurensis*	Interspecific (I)	*Vitis amurensis* origin (Va)

[1] V. labrusca, V. riparia or V. rupestris.

Many of the surveyed cultivars had non-*V. vinifera* ancestry. The different *Vitis* spp. in the pedigree of a cultivar was certified based on the data of the Vitis International Variety Catalogue (VIVC) [51]. The cultivars were grouped for the further analysis based on ancestry from different *Vitis* sp. (Table 7).

4.2. Data analysis

4.2.1. Susceptibility analysis

The total disease incidence (DI% - the ratio of plants showed fresh leaf symptoms and dieback, and whole plant apoplexy in previous years) was evaluated in the the cultivars of the surveyed germplasm collections. Since the overall disease incidence was over 25 % in every site and the spatial distribution of the symptom expressing plants was homogenous in all the vineyards, similar probabilities of infection were assumed for each cultivar. Given these conditions, the same the cultivars in the different surveyed sites could be considered as replicates in statistical analysis.

4.2.2. Sensitivity categories and analysis

The cultivars were categorized based on a new method to determine the disease expression severity (i.e., the severity of visible symptoms). Four categories were established to differentiate between (1) no symptom expression, (2) exclusively new (annual) symptoms, (3) both new symptoms and previous dieback resulting plant loss, and (4) exclusively previous dieback events all resulting in plant loss.

Four GTD sensitivity groups were created to catagorize the studied cultivars, based on the type (annual foliar symptoms and dieback, or apoplexy), and the frequency of the different symptoms. Highly sensitive (HS), where all symptomatic plants of the cultivar are dead; sensitive (S), where both dead plant (resulting from apoplexy of the trunk), and fresh GTD leaf and dieback symptoms are detected. The cultivar was considered resilient (R), if only foliar symptoms were present, while neither apoplexy nor annual GTD leaf and dieback symptoms were detected in unsusceptible (U) cultivars (Table 8).

Table 8. Categorization of cultivars according to the observed sensitivity toward grapevine trunk diseases (GTDs).

Sensitivity categories		GTDs symptoms	
Two groups	**Four groups**	**apoplexy (dead plant)**	**leaf symptoms and fresh dieback**
More sensitive	Highly sensitive (HS)	exclusively	-
	Sensitive (S)	present	present
Less sensitive	Resilient (R)	-	exclusively
	Unsusceptible (U)	-	-

To reveal potential differences in pathogen sensitivity amongst differences in the ancestry groups, the four original groups were re-appreciated, where the two more sensitive (HS and S) and the two less sensitive (R and U) categories were merged. The ratio of the lineage groups within each of these two re-defined sensitivity categories was compared to the theoretically expected distributions with the binominal test.

The tendency of GTD to kill the host plant was determined in parallel by calculating the proportion of individual plant losses within the total disease incidence of the lineage groups and compare the lineage groups in pairs. (1) Monophyletic European *V. vinifera* (Vv) cultivars against the interspecific (I) ones and hybrids with American (*V. rupestris*, *V. riparia*, *V. labrusca* - Ao) and Asian (*V. amurensis* – Va) species co-origin.

4.3. Statistical analysis and software background

The data sets did not fulfill the assumptions of parametric tests (i.e., normality and homogeneity of variances), that were analyzed with Q-Q plots and Levene test. During the analysis nonparametric Kruskal-Wallis test was used for comparison, which was backed up with Mann-Whitney U test as pairwise comparison with Statsoft Statistica 10 software.

The ratio of the sensitivity groups in different ancestral groups was compared with the binominal test executed using the online calculator of Stat Trek [92]. The Sankey diagram was generated by the Sankeymatic online diagram builder (https://sankeymatic.com).

5. Conclusions

Regarding the order in *V. vinifera* cultivar susceptibility based on total disease incidence, earlier data from the literature in other grape producing countries were confirmed and the main cultivars of the Carpathian basin were inserted in this ranking, where Juhfark proved to be more tolerant and Furmint more susceptible. Merlot did not show GTD symptoms in any of the Hungarian germplasm collections.

Interspecific *Vitis* cultivars had a lower tendency to plant loss following infection with GTD fungal pathogens Hybrid varieties with Asian *V. amurensis* ancestry have outstanding tolerance in our experimental set of more, than 300 cultivars. Engaging American and Asian *Vitis* species in breeding programs to enhance tolerance and resistence against GTDs has a great potential.

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