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Review

Grapevine, esca complex, and environment: the disease triangle

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Abstract. This review compiles the available knowledge on the triple impact of host-pathogens-environment in the progress of the esca disease complex of grapevine. The perennial crop grapevine encounters different biotic and abiotic factors responsible for numerous changes at the various growth stages. This review provides increased understanding of the esca disease complex, with emphasis on (1) the nature of esca-associated fungi as endophytes or pathogens in grapevine, (2) the importance of grapevine genotype and age in relation to resistance or susceptibility to the pathogens, (3) the significant effects of climatic changes, especially drought, on pathogen development and symptomatology, and (4) the physio-biochemical changes in the grapevines arising from the biotic and abiotic interactions. Drought often provides conditions favouring disease development in plants. Physiological and biochemical changes in plants play critical roles in this topic. The constantly increasing economic impacts of esca disease in many grape-producing countries, and the broad lack of knowledge so far, require precise studies on the transcriptional responses to biotic and abiotic factors in grapevines, as effects of "climate change" develop. On the viticultural side, improved management of water and adjusted nutrition balance in vineyards may become useful strategies to mitigate the widespread damage caused by grapevine wood pathogens.

Keywords. Climate change, esca disease complex, grapevine, water stress.

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INTRODUCTION

Viticulture, like other fields of agriculture, is deeply affected by a wide variety of biotic and abiotic factors. For the past three decades, the economic burden of trunk diseases such as esca has become a limiting factor for grapevine production in many countries (Larignon and Dubos, 1997; Mugnai *et al.*, 1999; Dubos *et al.*, 2002; Bertsch *et al.*, 2009; Úrbez-Torres, 2011; Bruez *et al.*, 2013; Mohammadi *et al.*, 2013; De la Fuente *et al.*, 2016). Advances in control of grapevine leaf strip disease (GLSD), the main disease in esca complex, have only recently been made with the introduction of *Trichoderma* as a biological treatment for wound protection, and with the possibility to reduce symptom expression by applications of mixtures of foliar fertilizers (Di Marco *et al*., 2004; Calzarano *et al*., 2014; Calzarano and Di Marco, 2018).

Esca is a disease complex, generally characterized by the development of typical inner necrosis in grapevine wood tissues and external symptoms known as "tiger-striped" leaves or black measles on the berries, assigned to infection by pathogenic fungi that invade the perennial plants and their vascular systems (Larignon and Dubos, 1997; Mugnai *et al*., 1999; Graniti *et al*., 2000). Petri disease, as part of the esca complex (Surico, 2001; Gramaje and Armengol, 2011) is caused by several fungi in the genera *Phaeomoniella* and *Phaeoacremonium* (Kubátová *et al*., 2004; Mostert *et al*., 2006; Essakhi *et al*., 2008; Gramaje *et al*., 2009; Gramaje and Armengol, 2011). Mature vineyards (10 years or more) are also affected by white rot linked with Basidiomycete taxa such as *Fomitiporia mediterranea* and related species (Fischer, 2002; Fischer and Kassemeyer, 2003; Fischer and Binder, 2004; Fischer *et al*., 2005; Fischer, 2006; Péros *et al*., 2008; Luque *et al*., 2009; Cloete, 2015; Fischer and González García, 2015).

In recent years there has been progressive evolution in the concept of esca and the diseases that are included within this complex (for example see Mugnai *et al*., 1999; Calzarano *et al*., 2001, 2014; Edwards *et al*., 2001; Larignon *et al*., 2001, 2009; Surico *et al*., 2008; Surico, 2009; Lecomte *et al*., 2012; Bertsch *et al*. 2013; Fontaine *et al*., 2016). Following the suggestion of Surico (2009), GLSD (previously known as "young esca") is considered the most important and widespread disease within the esca complex. Other diseases that are discussed within esca include brown wood streaking, Petri disease (black goo or slow dieback), and esca proper (including white rot). Co-existence of GLSD and esca proper is a common feature in mature vineyards. However, all of the above diseases may overlap, as they also do with canker agents such as those caused by members of the Botryosphaeriaceae or Diatrypaceae (Rolshausen *et al*., 2010; Gramaje *et al*., 2018; Moyo *et al*., 2018).

The above picture is not adopted throughout the community of pathologists and others with interests in esca, and differing views are taken, for instance, by Lecomte *et al*. (2012) or Larignon and collaborators (Larignon *et al*., 2001; 2009). Other, and less specific, designations have also been commonly used, including "manifest and hidden esca" (Marchi *et al*., 2006), "grapevine dieback disease" (Amponsah *et al*., 2011), "esca decline" (Lecomte *et al*., 2008, 2011) or "esca dieback foliar expression" (Guérin-Dubrana *et al*., 2012).

The diseases included in the esca complex are often cryptic and symptoms usually take several years to develop, in some of the diseases discontinuously (Surico *et al*., 2000, 2006; Christen *et al*., 2007; Calzarano *et al*., 2018). A potentially important group of pathogens are endophytic fungi (Petrini, 1986), which may be pathogenic or mutualistic, depending on the circumstances (Schulz and Boyle, 2005; Alvarez-Loayza *et al*., 2011). In the endophytic phase they asymptomatically colonize their hosts to form latent infections, but may modify their behaviour and become invasive when the plant gets stressed (Verhoeff, 1974; Gubler *et al*., 2005; Aroca *et al*., 2006; Surico *et al*., 2006; Slippers and Wingfield, 2007; Sakalidis *et al*., 2011; Hofstetter *et al*., 2012). There has been considerable debate during the past two decades whether, and to what extent, environmental factors influence fungal development in vineyards and the expression of symptoms (Calzarano *et al*., 2018). Several biotic and abiotic factors (Cramer *et al*., 2007; McDowell *et al*., 2008; Deluc *et al*., 2009; Andreini *et al*., 2014; Kovacs *et al*., 2017) naturally affect the physio-biochemical processes of grapevines, and subsequently their responses to pathogens, as in the case of GLSD phytoalexin patterns during leaf symptom development (Calzarano *et al*., 2016; 2017a; 2017b).

It is well known that exposure of plants to different stresses generally induces the expression of various genes. As a result, various enzymes and plant hormones (Vanholme *et al*., 2008; Vogt, 2010) with multiple biological functions are produced in response to different environmental stimuli. In this way, the variable virulence of potential pathogens, the host defense responses, and environmental conditions constitute the disease triangle (Agrios, 2005).

This eventually leads to an even more diffused picture of esca and the related diseases, making it challenging to clearly separate between diseases and fungal endophytes/pathogens and stress related symptomatology. In the case of grapevine and esca, whenever possible we refer to the specific designations of the diseases.

In this review, we refer to a large amount of literature, most of which is original research papers. In addition, we cite several review articles, which provide useful summaries of certain aspects of the "plant and stress" topic. A considerable proportion of the references refers to plants other than grapevine. While we particularly emphasize grapevine and the esca complex, numerous entries in Tables 1 and 2 also refer to other groups of plants. First, this underlines the overall significance of the subject, i.e. interrelations between stress factors and host plants. Secondly, data generated for non-grapevine hosts may assist understanding of esca and related disease phenomena.

ESCA-ASSOCIATED FUNGI: ENDOPHYTES OR PATHOGENS?

Some vascular-inhabiting fungi isolated from declining vines (Ferreira *et al.*, 1999) or other hosts have been considered as latent opportunistic pathogens, and cause diseases when their hosts are subjected to abiotic stresses (Pearce, 1996; Slippers and Wingfield, 2007; Jactel *et al.*, 2012).

One of the main features of GLSD is the variability in external symptom expression, whereby symptoms on leaves and berries may be obvious one year but are not apparent in another. The significant increase in foliar symptoms in 20-year-old potted vines induced by excessive watering (Surico *et al.*, 2010), and the relationship between growing season rainfall (particularly in July) and leaf symptoms expression (Calzarano *et al.*, 2018) have confirmed the role of rainy seasons and water in the soil in GLSD symptom development (Surico *et al.*, 2000; Marchi *et al.*, 2006). Factors extraneous to the plant-pathogen interactions (e.g. light, soil type, nutrients, and water availability) have been hypothesized to play roles in the erratic nature of the foliar symptoms of esca (Mugnai *et al.*, 1999; Calzarano *et al.*, 2007; 2009; 2014). The observed rates of mortality of vines are not necessarily, or not always, in accordance with the incidence of external symptoms (Andreini *et al.*, 2014). However, Calzarano and collaborators (2018) observed greater mortality of GLSD affected vines that showed severe leaf symptoms at the first appearance, compared to vines with low symptom severity.

Although several studies have dealt with various aspects of esca related pathogens, the causes of foliar symptom development still remain elusive (Surico *et al.*, 2006; Larignon *et al.*, 2009; Camps *et al.*, 2010). It was hypothesized that toxic metabolites produced by fungi in colonized wood reach leaves through the xylem vessels, triggering defense responses that result in the development of leaf symptoms (Evidente *et al.*, 2000; Tabacchi *et al.*, 2000; Andolfi *et al.*, 2011; Bertsch *et al.*, 2013). These plant responses include the formation of necrotic lesions on leaves as a hypersensitive reaction. In GLSD symptomatic vines, phytoalexins increased with increasing severity of leaf symptoms, confirming that these substances are synthesized as a reaction to lesions occurring on leaves, usually followed by formation of antimicrobial compounds such as stilbene derivatives (Heath, 2000; Calzarano *et al.*, 2016; 2017a; 2017b).

No strict correlation has been found between the occurrence of symptoms and the extent of pathogen colonization or wood necrosis (Calzarano and Di Marco, 2007; Liminana *et al.*, 2009; Fischer and Kassemeyer, 2012). In contrast, Lecomte *et al.* (2008) showed that vines exhibiting leaf symptoms had, on average, greater proportions of necrotic wood than asymptomatic plants. The degree of wood necrosis may also be positively correlated with the mortality of vines (Liminana *et al.*, 2009).

No significant difference was observed between the fungal communities that inhabit apparently healthy and visibly diseased individual plants (Hofstetter *et al.*, 2012). Both *Phaeomoniella chlamydospora* and *Phaeoacremonium* spp. have been isolated from asymptomatic tissue (Mugnai *et al.*, 1999; Bruez *et al.*, 2014; Elena *et al.*, 2018), supporting the concept of latent phases for these pathogens. Furthermore, the time delay between infection and symptom expression (Di Marco and Osti, 2008) may reinforce the role of other factors in esca disease development. A possible explanation for this situation may be the different environmental factors prevailing. The varying interactions between such factors and symptom expression caused by vascular pathogens has been extensively reviewed by Mundy and Manning (2011). Characterizing the impacts of abiotic factors in grapevine responses may be a key step towards obtaining complete knowledge of physicochemical changes in plants that lead to disease development and the appearance of symptoms.

GRAPEVINE GENOTYPE AND AGE

Genotype

Genotype relationships with possible tolerance of *Vitis* spp. to biotic and abiotic stresses has been the focus of many studies. Scion cultivars and the rootstocks may differ in their responses to stress. Rootstocks provide benefits, such as drought stress tolerance (Alsina *et al.*, 2007; Koundouras *et al.*, 2008; Gambetta *et al.*, 2012). However, information is scarce on the genetic backgrounds of these benefits, and specific responses to environmental factors.

Grapevine rootstocks have been shown to play important roles in adaptation to water deficit (Soar *et al.*, 2006; Marguerit *et al.*, 2012; Parker *et al.*, 2013), while scion transpiration rates and their acclimation to water deficit are, through different genetic architecture, controlled genetically by rootstocks (Marguerit *et al.*, 2012). Alsina *et al.* (2011) showed that scion stomatal conductance was more strongly down-regulated with drought-sensitive rootstocks (*V. riparia* × *V. rupestris* cv. 101-14Mgt) than with drought-tolerant ones (*V. berlandieri* × *V. rupestris* cv. Paulsen 1103).

Rootstock impacts may be mediated by chemical (Soar *et al*., 2006; Alsina *et al*., 2011), hormonal (particularly abscisic acid: ABA) and hydraulic signaling in responses to water deficit (Soar *et al*., 2006; Vandeleur *et al*., 2009; Marguerit *et al*., 2012). At the hydraulic level in roots, radial water movement mediated by aquaporins was shown to have a significant potential contribution to drought stress adaption (Vandeleur *et al*., 2009; Lovisolo *et al*., 2010). Aquaporins also affect root hydraulic conductance (Perrone *et al*., 2012), water uptake by fine roots (Koundouras *et al*., 2008, 2009; Gambetta *et al*., 2012) and, consequentially, vine growth (Pouzoulet *et al*., 2014). Selection of appropriate rootstocks may increase tolerance to extended drought stress periods, and even resistance to pathogens.

Rootstock genotype may affect the frequency of external symptoms (Marchi, 2001; Murolo and Romanazzi, 2014). However, leaf symptoms are not necessarily related to alterations observed in wood (Eskalen *et al*., 2001; Feliciano *et al*., 2004; Calzarano and di Marco, 2007; Romanazzi *et al*., 2009; Andreini *et al*., 2013; Murolo and Romanazzi, 2014).

The comparative transcriptome analysis in Pinot Noir grapevine highlighted rootstock-dependent differences in the response of genes involved in the jasmonic acid (JA) metabolism and pathogenesis-related (PR) proteins (Berdeja *et al*., 2014). JA is a well known regulator of wound responses against pathogens, and plays a role in water stress perception and regulation and, subsequently, in expression of several related genes (Bell and Mullet, 1991; Zhang and Memelink, 2009; see Table 1 for more information on gene expression induced by environmental factors in different plants). In grapevine, production of PR proteins is the most frequent defense reaction to fungal infection (Derckel *et al*., 1999); they accumulate in leaves and berries after pathogen infection and contribute to grapevine resistance (Giannakis *et al*., 1998). Berdeja *et al*. (2014) indicated that, under drought stress, the transcript abundance of some specific PR genes, e.g. PR1 and PR4, differed between rootstock cultivars. This indicates a link between JAs and ABA in water-stressed grapevines (Suhita *et al*., 2004).

As for scion cultivars, *V. vinifera* Chardonnay and Merlot have been classified as less susceptible to esca than Cabernet Sauvignon, which is considered as susceptible due to the high proportions of symptomatic vines observed in different climatic conditions (Christen *et al*., 2007; Andreini *et al*., 2009; Bruez *et al*., 2013; Murolo and Romanazzi, 2014). Varieties with small xylem vessels are considered less likely to express foliar symptoms because of a limited drought-induced xylem cavitation (Pouzoulet *et al*., 2014). Furthermore, own rooted vines sometimes show lower incidence of esca disease than grafted vines (Andreini *et al*., 2014), possibly because they avoid contamination by fungal spores on wounds at graft unions during propagation processes (Halleen *et al*., 2003; Hofstetter *et al*., 2012). In contrast, vines grafted on SO4, with low drought resistance, and those grafted on 1103P, conferring high drought resistance, had very similar amounts of apoplexy, while the rate in own-rooted vines, also with high drought resistance, was much higher (Marchi, 2001).

With other combinations of cultivar and rootstock, the rootstocks may be less important than other factors, both internal and external. This suggests that the susceptibility of vine genotypes to esca depends on environment and genotype factors (Marchi, 2001). The complexity of esca, and the effects of several environmental factors in appearance of symptoms, make evaluation of cultivar susceptibility very difficult. In-depth and broad genetic studies of varieties in response to biotic and abiotic stresses are necessary.

Age

Age of plants is a key factor governing the interaction between responses to the biotic and abiotic stresses, and whether plants are tolerant or susceptible to stress factors; the overall effect of stress combination on plants largely depends on their age (Pandey *et al*., 2015). Age of vines also affects disease incidence, resulting in greater incidence of diseased plants in old vineyards. Older plants experience more infection cycles than young plants, through wounds they have received (McCutcheon *et al*., 1993; Mugnai *et al*., 1999; Zabalgogeazcoa, 2008; Amponsah *et al*., 2011; Kovacs *et al*., 2017). As a result, there are positive correlations between vine age and trunk disease incidence, and, on a global scale, the disease remains the greatest limitation to maintaining optimum yields (Brown *et al*., 2016).

CLIMATIC AND ENVIRONMENTAL CHANGES AS ABIOTIC FACTORS

Climatic and edaphic factors have been reported to influence the incidence of esca and other grapevine trunk diseases (Graniti *et al*., 2000; van Niekerk *et al*., 2011; Sosnowski *et al*., 2011; Calzarano *et al*., 2018). This indicates that the pathogens are not the only agents responsible for the disease symptoms. Changes in environmental conditions are known to exacerbate disease symptoms in plants (Boyer, 1995). In latent vine infections, the presence of pathogens does not necessar-

Table 1. Gene expression in response to genotype and various environmental factors and the putative action in different plants.

Gene Expression	Plant species (as cited in respective research papers)	Environmental factors	Putative action	Reference
Pathogenesis-related proteins	*Vitis* ssp. *V. vinifera* *V. vinifera*	Pathogen infection; Genotype	Defense genes against pathogens	Giannakis *et al*., 1998 Derckel *et al*., 1999 Letousey *et al*., 2010
Phenylalanine ammonia lyase (PAL)	*Vitis* sp. *V. vinifera* *V. vinifera* *V. vinifera*	Pathogen infection; Water stress	Related to synthesis of the phytoalexin in grapevine and general responses against biotic and abiotic stresses	Melchior and Kindl, 1991 Grimplet *et al*., 2007 Deluc *et al*., 2009 Letousey *et al*., 2010
Abscisic acid (ABA)	*Zea mays* *Glycine max* *Z. mays* *V. vinifera* *Arabidopsis thaliana* *V. vinifera* *A. thaliana* *Solanum lycopersicum* *V. vinifera* *Vitis* spp. *Pinus taeda*	Water stress; Rootstock genotype	Stomatal closure; Regulation of transpiration and root hydraulic traits; Affecting SA-, JA and ET-related defense genes; Suppressing PAL activity and ROS production	Zhang and Davies, 1990 McDonald and Cahill, 1999 Kizis and Peges, 2002 Soar *et al*., 2004 Kariola *et al*., 2006 Soar *et al*., 2006 Adie *et al*., 2007 Asselbergh *et al*., 2008 Vandeleur *et al*., 2009 Lovisolo *et al*., 2010 Lorenz *et al*., 2011
Cytokinins	*S. lycopersicum* *Z. mays*	Water stress	Influencing shoot responses	Kudoyarova *et al*., 2007 Alvarez *et al*., 2008
Sugars	*V. vinifera* *Prunus persica* *V. vinifera* *V. vinifera* *V. vinifera* *P. persica* *P. persica*	Water stress; Genotype	Sugar accumulation in fruit	Freeman and Kliewer, 1983 Golding *et al*., 2006 Castellarin *et al*., 2007 Deluc *et al*., 2009 Koundouras *et al*., 2009 Lopresti *et al*., 2014 Cirilli *et al*., 2016
Amino acids	*Ocimum* sp. *V. vinifera* *V. vinifera*	Water stress; Rootstock genotype	Adjusting the osmotic potential in cytoplasm; Affecting berry composition	Khalid, 2006 Deluc *et al*., 2009 Berdeja *et al*., 2014
Polyamines (PAs)	*Oryza sativa* *Z. mays*	Saline stress; Pathogen infection	Involved in many physiological processes, such as cell growth and response to stress tolerance	Krishnamurthy and Bhagwat, 1989 Rodriguez-Kessler *et al*., 2008
Anthocyanins	*Pisum sativum*	UV-B radiation; Water stress	Developing a light red color in leaves and playing a primary role in photosynthesis;	Noguees *et al*., 1998
	V. vinifera		Playing a major role in wine quality, including colour, flavor and bitterness	Berdeja *et al*., 2014
Lignin	*Z. mays*	Water stress	Important in plant defense	Alvarez *et al*., 2008
Stilbenes	*Sorghum bicolor* *V. vinifera*	Pathogen infection; Water stress	Protection against environmental challenges	Yu *et al*., 2005 Grimplet *et al*., 2007
Flavonoids	*P. sativum* *Hordeum vulgare*	UV-B radiation; Water stress; Saline stress	Decreasing the auxin level in plant tissues and causing growth retardation	Noguees *et al*., 1998 Ali and Abbas, 2003

ily result in the immediate appearance of symptoms (Di Marco and Osti, 2008), as abiotic factors affect the appearance and the severity of the disease (Lecomte *et al.*, 2011). As a result, incidence and symptom profiles of diseases associated with the different esca pathogens may vary between different climatic areas (van Niekerk *et al.*, 2011). Climate changes will not occur uniformly in different regions, particularly for host and pathogen exposure to drought (Schultz, 2016).

Environmental changes may affect the nature of host responses to the pathogens. Firstly, plants adjust to environmental challenges by tightly and differentially regulating their transcriptomes (Baker *et al.*, 1997; Chen *et al.*, 2002; Yamaguchi and Shinozaki, 2006). These alterations, often found associated with duration and severity of stresses, determine a plant's ability to respond to internal and external signals, and to adjust to changing conditions (Eastburn *et al.*, 2011; Pandey *et al.*, 2015). Plant responses to environmental changes, e.g. development of thicker wax layers on leaves or changes in stomatal densities, could impact the processes of infection and expression of symptoms (Campbell and Madden, 1990). Abiotic stresses have impacts on the defense-growth trade-off that plants face whenever there is a pathogen attack (Huang *et al.* 2008; Leakey *et al.* 2009; Kontunen-Soppela *et al.*, 2010), causing resistance or susceptibility to the pathogens (Kuldau and Yates, 2000; Amtmann *et al.*, 2008; Mittler and Blumwald, 2010). Environmental changes can also have direct effects on the pathogens. With esca, as indicated above, climatic conditions influence not only the distribution of pathogens but also the disease symptoms they cause (Surico *et al.*, 2000; Marchi *et al.*, 2006; van Niekerk *et al.*, 2011; Calzarano *et al.*, 2018).

Climatic changes have the potential to alter the incidence and severity of plant disease epidemics, as well as to reshape the co-evolutionary relationships between pathogens and host plants (Burdon *et al.*, 2006; Ziska and Runion, 2007; Crowl *et al.*, 2008). Drought and temperature, as the most influential factors, affect pathogens by altering growth rates, propagule germination, and the rates of inoculum production (Huber and Gillespie, 1992). Eventually, increased colonization of plants by pathogens may occur in the presence of abiotic stresses (Koga *et al.*, 2004).

Drought

With the background of "climate change", the frequencies and intensities of drought periods are increasing worldwide. Increased drought leads to enhanced plant respiration, resulting in carbon (C) losses at the plant level (Schultz, 2000; Moriondo *et al.*, 2011), and plant death due to C starvation (Martinez-Vilalta *et al.*, 2002; Breda *et al.*, 2006; McDowell *et al.*, 2008; Adams *et al.*, 2013; see Table 2 for additional information on the effect of water stress on different plants).

Low soil water content and resulting water deficit have been considered as causes of stress on grapevines (Lovisolo and Schubert, 1998; Lovisolo *et al.*, 2010; Lanari and Silvestroni, 2015). Among different stress combinations that occur in vineyards, the influential interaction between esca and drought has often been considered (Surico *et al.*, 2000, 2006, 2010; Edwards *et al.*, 2007b, c; Luque *et al.*, 2010; Fischer and Kassemeyer, 2012; Bostock *et al.*, 2014; Ramegowda and Senthil-Kumar, 2015).

Analysis of *V. vinifera* plants subjected to individual drought stress and/or pathogen infection revealed down-regulation of transcripts involved in photosynthesis, nutrient assimilation, and cellular homeostasis (Choi *et al.*, 2013). Two mechanisms have been suggested to illustrate how water deficit increases the susceptibility of grapevine to pathogen attack: first, limitation of photosynthesis (Flexas *et al.*, 1999; Escalona *et al.*, 1999) eliminates the plant's ability to produce defensive compounds, and, second, plant growth is reduced in the presence of the pathogen, allowing further progression of the pathogen and eventually expression of symptoms.

Drought-induced plant death under pathogen attack is influenced by the type of interaction between pathogen and host (Oliva *et al.*, 2014). Studies reviewed by Boyer (1995) showed that predisposition to disease is often observed in host plants experiencing soil water deficits, and, among other cases, this has been illustrated in increases of bacterial leaf scorch symptoms (in *Parthenocissus*: McElrone *et al.*, 2001,), and esca-related wood symptoms (caused by *P. chlamydospora* in *Vitis*: Fischer and Kassemeyer, 2012). Conversely, it was shown that resistance is typically restored when water stress is remediated (in *Pinus*: Johnson *et al.*, 1997).

The pathogen may act: i) simultaneously with drought, as an opportunistic agent taking advantage of the effects of water stress on the host; or ii) prior to drought events (Oliva *et al.*, 2014). Drought occurring during infection may have greater impact than previous drought episodes (Croise *et al.*, 2001). For example, vascular wilt pathogens can accelerate drought-induced mortality by damaging the xylem vascular system, causing phloem impairment and foliage wilting (Oliva *et al.*, 2014). These conditions tend to increase evapotranspiration, producing favourable conditions for the development of xylem embolism, as is also observed in esca (Pouzoulet *et al.*, 2014).

Table 2. Different plant species and their adaptive changes in response to water stress.

Plant species (as cited in respective research papers)	Physio-biochemical changes	Reference
Acer platanoides, *Populus tremula*, etc.	Stomatal closure	Aasamaa *et al*., 2001
Juglans regiax×nigra		Cochard *et al*., 2002
Betula alleghaniensis, *B. davurica,* etc.		Gu and Rom, 2007
Vitis vinifera		Letousey *et al*., 2010
Zea mays	Changes in photosynthetic rate and Carbon reserves	Westgate and Boyer, 1985
V. vinifera		Christen *et al*., 2007
Arabidopsis thaliana		Hummel *et al*., 2010
Pinus edulis		Sevanto *et al*., 2014
V. vinifera	Enhanced respiration	Schultz, 2000
A. saccharum, *Thuja occidentalis*, etc.	Lower shoot hydraulic conductance and leaf specific conductivity	Tyree and Sperry, 1988
V. vinifera	Lower transectional areas in xylem vessels	Lovisolo and Schubert, 1998
Eucalyptus globulus	Impaired function of phloem	Pate and Arthur, 1998
Vitis sp.	Aquaporin gene expression	Galmes *et al*., 2007
V. vinifera	Growth reduction	Shellie and Brown, 2012
Melissa officinalis	Chlorophyll loss	Munne-Bosch and Alegre, 1999
Z. mays	Alteration in root structure and function	Zhang *et al*., 1995
V. berlandieri×V. rupestris		Dry *et al*., 2000
Lycopersicom esculentum		Mingo *et al*., 2004
Glycine max	ABA-responsive signaling pathway, e.g. the activation of JA-related defense genes, alteration in PAL activity, etc.	Ward *et al*., 1989
Z. mays		Zhang and Davies, 1990
G. max		McDonald and Cahill, 1999
L. esculentum		Audenaert *et al*., 2002
A. thaliana		Kariola *et al*., 2006
A. thaliana		Adie *et al*., 2007
V. vinifera		Grimplet *et al*., 2007
Solanum lycopersicum		Asselbergh *et al*., 2008
V. vinifera		Deluc *et al*., 2009
Vitis sp.		Lovisolo *et al*., 2010
S. lycopersicum	Cytokinin production	Kudoyarova *et al*., 2007
Z. mays		Alvarez *et al*., 2008
V. vinifera	Sugar accumulation	Castellarin *et al*., 2007
V. vinifera		Deluc *et al*., 2009
V. vinifera		Koundouras *et al*., 2009
Ocimum sp.	Accumulation of amino acids, *e.g.* proline	Khalid, 2006
V. vinifera		Deluc *et al*., 2009
V. vinifera		Berdeja *et al*., 2014
G. max	Reduction of isoflavone content	Gutierrez-Gonzalez *et al*., 2010
Z. mays	Changes in lignin content	Alvarez *et al*., 2008

Evidence of esca complex and drought interactions in grapevine

The effects of esca pathogens and water stress on grapevines have been intensively studied. Water stress exacerbated decline symptoms associated with *P. chlamydospora* in young plantations (Ferreira *et al*., 1999). In glasshouse experiments, leaf water potentials in vines subjected to water stress were reduced when the vines were infected by *P. chlamydospora*, indicating that infection altered host plant responses to water stress, making it difficult for vines to get water to their leaves (Edwards *et al*., 2007b; c). Pasquier *et al*. (2013) showed that foliar symptoms of esca proper may impact stress-related pathways in grapevines, e.g. sHSP (small heatshock protein) which is induced during water, salt, and oxidative stresses (Löw *et al*., 2000; Scharf *et al*., 2001). Christen *et al*. (2007), however, showed that foliar symptoms (in the case of GLSD) was not simply a water transport-deficit disease, but that xylem dysfunction due to pathogen spread partly explained the appearance of the foliar symptoms.

Intensity and timing of water deficit

Water supply plays an important role in plants under stress. Several studies have shown that water availability induces modifications of vessel diameter in different plants, including *V. vinifera* (Lovisolo and Schubert, 1998; Fichot *et al*., 2009; Bauerle *et al*., 2011). Annual changes in esca symptom expression may be partly due to differences in the size of new vessels formed under different water regimes (Pouzoulet *et al*., 2014).

Root systems that are able to maintain water uptake under low water availability may increase drought resistance (Passioura, 2002; Comas *et al*., 2013; Barrios-Masias and Jackson, 2014). Hydraulic conductivity and suberization of grapevine roots can change dramatically when they are subjected to water deficit, so irrigation management could be used to modify the water uptake capacity of root systems (Barrios-Masias *et al*., 2015). Moderate water deficit increases root growth of grapevine, as this is required for water uptake from deeper layers of soil, and maintains stomatal conductance under declining soil moisture (Alsina *et al*., 2007, 2011). Water use efficiency is consequentially optimized (Shellie and Brown, 2012).

Intensity and timing of water deficit may play critical roles in grapevine health and productivity, particularly in semi-arid regions. Schreiner and Lee (2014) suggested that there will be only small negative impacts of late-season water deficit in Pinot noir grapevines, from evidence with plants grown in pot-in-pot microplots.

Wine grapes are often intentionally grown under water deficit regimes to meet wine quality goals (Castellarin *et al*., 2007). In contrast, increased amounts of rainfall during summer and soils with high water reserves were shown to increase severity of GLSD and other diseases in the esca complex (Calzarano *et al*., 2016; 2017a, 2017b; Guérin-Dubrana *et al*., 2005, 2012; Marchi *et al*., 2006). Apoplectic symptoms are often correlated with excess of soil water combined with hot weather, leading to dramatic imbalance between foliar transpiration and root absorption (Surico *et al*., 2006).

OTHER ABIOTIC FACTORS

Adding plant nutrients (fertilizers) to soils, to promote plant growth, was reported to enhance esca disease expression. For esca proper, high availability of nutrients in a growing season increased the proportion of diseased vines with symptoms, and decreased the proportion of infected but symptomless vines (Calzarano and Di Marco, 2007; Calzarano *et al*., 2009).

Soil salinity also is important. High salinity causes damage to plants from water deficit due to osmotic stress and by ion toxicity from excessive sodium ions (Zhu, 2003; Munns and Tester, 2008; Hasegawa, 2013), and this may provide favourable conditions for esca-related pathogens. However, grapevine is adapted to semi-arid environments, where drought and salinity are prevalent growth restraints, and is considered moderately tolerant to salinity stress (Walker *et al*., 2002; Gil *et al*., 2013). Combined drought and salt stresses led to enhanced sodium accumulation in roots and shoots (Ahmed *et al*., 2013). Ma *et al*. (2015) characterized physiological and molecular responses of grapevine to short-term osmotic and sodium chloride stresses; a close relationship between drought and salinity may exist, leading to eventual impacts on plant physiological responses.

The duration and intensity of light may affect the life cycles of fungal pathogens, including those causing esca. Mittler *et al*. (1997) and Alvarez-Loayza *et al*. (2011) demonstrated that low light intensity favoured endosymbiotic development, while high light intensity triggered pathogenicity of the fungi. These authors also showed that mycelial melanin, correlated with increased production of reactive oxygen species (ROS) in pathogens and often associated with increased virulence to hosts, increased with light exposure, for instance caused by natural radiation. The rates of spore survival are also influenced by light conditions, mainly due to the UV-B portion of the spectrum, and to increased surface temperatures caused by radiation (Rotem *et al*., 1985; Stevenson and Pennypacker, 1988; Braga *et al*., 2015). However, no such studies, for instance with respect to colonization of pruning wounds, have been conducted with esca pathogens.

Pandey *et al*. (2015) reviewed enhanced damage caused by heat and drought stress combinations in plants. Both stress types share a number of physiological traits; their overall effects on plants are additive and aggravate both conditions. Sosnowski *et al*. (2007) reported that temperature and rainfall were related to the symptom development of Eutypiosis. Cool, rainy summers favoured GLSD or esca proper (chronic esca), and hot dry summers favoured apoplexy (acute esca) (Surico *et al*., 2000). Marchi *et al*. (2006) reported on the relationship between annual incidence of manifest esca (diseased plants with foliar symptoms), hidden esca (asymptomatic plants through a growing season) and rainfall. Other data show that rainfall and temperature in (Northern Hemisphere) May-July or only in July were, respectively, directly and inversely related with esca leaf symptoms (Calzarano *et al*., 2018). Incidence of *P. chlamydospora* and *Phaeoacremonium* spp. infections were greater in winter rainfall regions than in marginal and summer rainfall regions, and this was attributed to the climatic preferences of these fungi (van Niekerk *et al*., 2011). Expression of PR-10 protein was found to be dependent on climatic conditions; therefore, it is possible that yearly temperature differences could influence the appearance of foliar symptoms in esca proper (Pasquier *et al*., 2013).

PHYSIO-BIOCHEMICAL CHANGES IN GRAPEVINE IN ADAPTATION TO ENVIRONMENTAL CHANGES

Acclimation of plants to environmental factors leads to adaptive changes in root and shoot growth and physio-biochemical processes, which subsequently can alter molecular host-pathogen interactions. Beckman (1964) noted that physiological changes in plants, such as increased respiration and changes in water balance, result in wilting due to lack of water rather than toxins produced by vascular pathogens, such as *Phaeomoniella* or *Phaeoacremonium*.

Physiological changes

Advanced soil drying decreases the amount of nitrate taken up by plant roots, and this raises the xylem sap pH, increasing the sensitivity of stomata to the hormone ABA (Wilkinson and Davies, 1997; see also Woodall and Ward, 2002; Benjamin and Nielsen, 2006). The effects of stress on xylem sap were investigated by Agüero *et al*. (2008), who reported that sap from water stressed grapevines enhanced the *in vitro* growth of *P. chlamydospora* and *Phaeoacremonium* spp.

Xylem morphology

During developmental stages, xylem is responsive to environmental signals, and biotic and abiotic stresses may threaten xylem function (Pouzoulet *et al*., 2014). Grapevine xylem is very efficient for water transport and by the formation of tyloses and gels is particularly vulnerable to cavitation (Alsina *et al*., 2007). This results in possible dysfunction due to water stresses (Hacke *et al*., 2000; McDowell *et al*., 2008; Choat *et al*., 2012; Vilagrosa *et al*., 2012), and the presence of pathogens (Kuroda, 1991; Edwards *et al*., 2007a; Raimondo *et al*., 2010). Resistance to drought-induced cavitation is correlated with xylem vessel dimensions (Hacke *et al*., 2001; Jacobsen *et al*., 2005; Sperry *et al*., 2006), which are the function of the plant's genetic makeup (Fichot *et al*., 2009). Pouzoulet *et al*. (2014) documented that the grape varieties Cabernet Sauvignon and Thompson Seedless, both considered susceptible to esca, had wider and longer vessels than other varieties. Occlusion processes taking place in vessels of wide diameter, with loose clusters of tyloses, compared to smaller diameter vessels with more compact clusters, would create favourable environments for *P. chlamydospora* (Pouzoulet *et al*., 2017).

Several studies in different plant species have observed increases of vessel grouping (Tyree *et al*., 1994; Lopez *et al*., 2005; Robert *et al*., 2009; Lens *et al*., 2011; Carlquist, 2012), and fewer solitary vessels (Arx *et al*. 2013), with increasing water limitation. Vessel grouping improves hydraulic redundancy and reduces the potential loss of water transport capacity associated with cavitation (Pouzoulet *et al*., 2014). However, it was also hypothesized that the mechanism of tolerance towards esca is similar to that displayed by elms (*Ulmus* spp.) against Dutch elm disease, and therefore may not be correlated with vessel morphology (Venturas *et al*., 2013). Thorough evaluation of xylem structure in different grapevine varieties may offer increased understanding of xylem vulnerability to drought stress, and susceptibility to vascular pathogens.

BIOCHEMICAL CHANGES

Plant biochemical responses to biotic and abiotic factors are complex and based on a number of molecular factors.

Photosynthetic responses

Esca-affected and drought-stressed grapevines provided information on the distinct functional behaviour patterns of photosynthetic response for these two stress types. In a study by Christen *et al*. (2007), esca-infected plants showed greater fluorescence intensity than drought stressed plants. However, the pool size of electron carriers, the electron transport per cross section and the electron transport per active reaction centre increased in the drought stress plants, whereas they decreased in the esca-infected plants.

Defense-related metabolism

In response to biotic and abiotic factors, a "trade-off" exists between growth and defense-related metabolism in plants (Treutter, 2005). When defense compounds are produced, plant resources are used, including amino acids, carbohydrates and other nutrients. Plants with symptoms reduce their carbohydrate reserves during winter dormancy (Petit *et al*., 2006), and the lower pool of reserves may contribute to decreased plant development and vigour during the subsequent year (for grapevine, shown by Fontaine *et al*., 2016).

Vines infected with *P. chlamydospora* showed reduced carbohydrate reserves compared to the control vines during winter dormancy, and were characterized by an overall loss of plant vigour (Petit *et al*., 2006). Rudelle *et al*. (2005) suggested that high metabolic activity associated with secretory defense responses results from reduced starch storage. This associates with the first appearance of GLSD symptoms in a growing season in Trebbiano d'Abruzzo vineyards, at pre-bunch closure, and is when carbohydrate reserves in the wood are at their least. This condition could stimulate release of toxins by the pathogens in the vine wood, causing host leaf responses (Sumarah *et al*., 2005; Eaton *et al*., 2015). The reconstitution of these reserves between pre-bunch closure and veraison (Lebon *et al.,* 2008) was accompanied by reduced leaf symptom expression (Calzarano *et al*., 2016; 2017a; 2017b). In contrast, if a vine has already experienced water stress, and has allocated amino acids to proline production in order to maintain osmotic pressure (Keller, 2005; Deluc *et al*., 2009), less raw material will be available to produce plant defense compounds.

CONCLUSIONS

Considering the fact that grapevine culture and wine production are highly dependent on climatic conditions (van Leeuwen *et al*., 2004; Ollat *et al*., 2016), this review tried to provide new insights regarding biotic and abiotic factors in esca disease incidence.

Grapevines are economically important woody perennial fruit crops, with approx. 7.12 million ha cultivated and 74.5 million t of fruit harvested in 2014 (Gramaje *et al*., 2018). Viticulture is facing important environmental challenges that need to be addressed through coordinated research. To achieve this goal, it will be important to assess the effects of biotic and abiotic stressors on grapevine performance, since plant disease responses may change significantly under the influence of environmental parameters. Evidence for global climate change is generally accepted (Solomon *et al*., 2007; Bradley *et al*., 2012; Matyssek *et al*., 2012), and concomitant changes can lead to the disappearance or emergence of diseases in particular regions.

Water stress and the esca disease complex have been identified as the most important economic threats for viticulture (Luque *et al*., 2010; Sosnowski *et al*., 2011; van Niekerk *et al*., 2011). The worldwide economic cost for the replacement of dead grapevines is estimated to be in excess of 1.5 billion dollars per year (Hofstetter *et al*., 2012; see also De la Fuente *et al*., 2016). Since plant responses to environmental stressors are known to affect responses to pathogens, deciphering how grapevines adapt to drought conditions is an essential step to improving water use efficiency, and to adequately managing the linked pathogens. Understanding the role of xylem plasticity among grapevine varieties, and its consequences for xylem vulnerability to drought stress and susceptibility to vascular pathogens, are essential. Further research is needed to determine the physiological and molecular mechanisms underlying the plant-environment-pathogen triangle. Bio-informatic analyses may be useful for comparing the expression of various sets of biotic and abiotic stress-related genes involved in general plant responses to pathogen infection (Fontaine *et al*., 2016), and these analyses could improve understanding of the regulatory networks that control the plant responses to various stresses. To date, not enough information has been gathered on the effects of environmental stresses on the transcriptional responses of grapevine to the esca disease complex.

Long-term application of controlled conditions should be a priority, to increase understanding of the interactions between grapevine and the esca-related pathogens. The goal of this research should be to manipulate field growth conditions to favour vine hosts. Sustainable esca disease management will consist of a combination of appropriate grapevine cultivars and water regimes to mitigate the economic losses. Due to the extended periods of drought expected in the coming decades, the targeted use of protective endophytes, such as arbuscular mycorrhiza fungi, to improve plant nutrient uptake and osmotic stress tolerance, could provide improved drought tolerance (Schreiner, 2003; Schreiner and Linderman, 2005; Schreiner and Mihara, 2009; Trouvelot *et al*., 2015).

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