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Review

Grapevine trunk disease fungi: their roles as latent pathogens and stress factors that favour disease development and symptom expression

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Summary. Grapevine trunk diseases (GTDs) are major biotic factors reducing yields and limiting vineyard economic life spans. Fungi in the GTD complex cause a range of symptoms in host plants, although these pathogens are slow wood colonizers and potentially latent pathogens. Understanding has recently increased on the possible roles that GTD fungi may play as latent pathogens, and how this can be translated into disease management. This paper summarizes evidence for the latent nature of infections by these fungi in grapevines and other hosts. Abiotic and biotic stressors have been associated with symptom expression in many hosts, but limited information is available regarding their roles in symptom development in grapevines. Based on research conducted in other pathosystems, this review discusses how abiotic and/or biotic stress factors may influence the transition from the endophytic to the pathogenic phases for GTD fungi. Potential methods for stress mitigation are also outlined as alternative GTD control strategies to minimize the economic impacts that that these diseases have on grape production.

Keywords. Abiotic and biotic stresses, black foot disease, Botryosphaeria dieback, endophyte, Esca, Eutypa dieback, Petri disease, Phomopsis dieback.

INTRODUCTION

Grapevine trunk diseases (GTDs) are major threats to the economic sustainability of viticulture; they cause significant economic losses due to reduced yields, increased crop management costs and shortened life spans for vineyards (Wicks and Davies, 1999; Siebert, 2001; Bertsch *et al.*, 2013; Kaplan *et al.*, 2016; Gramaje *et al.*, 2018). The GTD complex includes Black foot disease, Botryosphaeria dieback, Esca, Eutypa dieback, Petri disease, and Phomopsis dieback (Gramaje and Armengol, 2011; Úrbez-Torres, 2011; Agustí-Brisach and Armengol, 2013; Bertsch *et al.*, 2013; Gramaje *et al.*, 2018; Mondello *et al.*, 2018). These diseases are primarily caused by taxonomically unrelated Ascomycete fungi, and to lesser extent by several Basidiomycetes which are primarily associated with the Esca complex (Gramaje *et al.*, 2018). Black foot disease and Petri disease typically occur in grapevines aged 5 years or younger, while Botryosphaeria dieback, Esca, Eutypa dieback, and Phomopsis dieback are usually seen in older vineyards, although these diseases may also occur in young grapevines (Gramaje and Armengol, 2011; Úrbez-Torres *et al.*, 2008; Agustí-Brisach and Armengol, 2013; Bertsch *et al.*, 2013). Pruning wounds serve as major routes of infection by these pathogens in established vineyards. The discharge of spores from fruiting bodies and airborne transmission of these spores from plant to plant have primarily been associated with rainfall, with the exception of black foot pathogens, which are known to be soil-borne (Agustí-Brisach and Armengol, 2013; Agustí-Brisach *et al.*, 2014; Eskalen and Gubler, 2001; Rooney-Latham *et al.*, 2005; Trese, 1980; Úrbez-Torres *et al.*, 2010a; Úrbez-Torres *et al.*, 2010b).

Grapevine trunk diseases are caused by xylem-colonizing fungi, and are categorized as slow-progression diseases with symptoms sometimes taking several years to appear after infection. In addition, GTD symptoms are known to be expressed inconsistently from year to year on individual grapevines (Bertsch *et al.*, 2013; Calzarano *et al.*, 2018; Songy *et al.*, 2019). General symptoms of GTDs include delayed bud-break, leaf chlorosis, reduced vigour, stunted growth, wood necroses, canker formation, dieback, and eventual death of affected grapevine plants (Gramaje and Armengol, 2011; Úrbez-Torres, 2011; Agustí-Brisach and Armengol, 2013; Bertsch *et al.*, 2013; Gramaje *et al.*, 2018; Mondello *et al.*, 2018; Billones-Baaijens and Savocchia, 2019; Reis *et al.*, 2019; Songy *et al.*, 2019). Due to the inconsistent symptom expression from year to year for some GTDs, and the reported isolation of GTD fungi from asymptomatic tissues, it has been proposed that some of these fungi may act as latent pathogens (Úrbez-Torres, 2011; Gramaje *et al.*, 2018). The presence of GTD fungi in asymptomatic tissues can be very problematic for growers and propagators, as infections can spread unnoticed in the field or in nurseries. Asymptomatic infections in rootstock and scion mother plants can provide possible sources of infection in nurseries (Fourie and Halleen, 2004; Mondello *et al.*, 2018). In addition, abiotic and biotic stresses are likely to play important roles in GTD symptom development (Úrbez-Torres, 2011; Gramaje *et al.*, 2018; Reis *et al.*, 2019; Songy *et al.*, 2019).

Endophytes and latent pathogens: from endophytic to pathogenic phases

Endophytes are organisms found in the internal tissues of plants, including in roots, xylem, phloem, and/or leaves, and these organisms may act as saprobes, mutualists, or latent pathogens (Wilson, 1995; Hyde and Soytong, 2008; Rodriguez *et al.*, 2009). The definition of endophyte has changed several times; however, for this review, the definition of Petrini (1991) is followed, as *"all organisms inhabiting plant organs that at some time in their life, can colonize internal plant tissues without causing apparent harm to their host."* This definition includes latent pathogens during their asymptomatic phases (Stone *et al.*, 2000; Wilson, 2000; Wilson, 1995; Sieber, 2007). The term "endophyte" is used here for the endophytic phase of an organism's life cycle, the life cycle of which may include several other phases that may be transitory and/or pathogenic (Wilson, 1995; Stone *et al.*, 2000; Wilson, 2000).

Most fungal endophytes are in Ascomycota R.H. Whittaker, although some are in Basidiomycota Whittaker ex R.T. Moore, or Oomycota Arx (Hyde and Soytong, 2008; Petrini, 1986). Fungal endophytes can also be classified into two broad categories, as clavicipitalean endophytes, which live in the internal tissues of grasses and have been thoroughly researched, and non-clavicipatalean endophytes, which live in a wide range of hosts including woody perennials and non-vascular plants (Sieber, 2007; Hyde and Soytong, 2008; Rodriguez *et al.*, 2009). Rodriguez *et al.* (2009) suggested an endophyte classification system with four classes. This included Class 1 as clavicipitaceous endophytes which are grass endophytes. Classes 2 to 4 are non-clavicipitaceous endophytes. Class 2 edophytes are distinguished from the rest by their colonization of roots, stems, and leaves, and their transmission via seed coats and rhizomes. Class 3 endophytes have diverse plant host ranges, including woody perennials, and these endopytes live in the inner bark, wood, fruit, or flowers of their hosts, and can reproduce via sporulation on dead plant tissues. Class 3 endophytes include xylem-colonizing endophytes. Class 4 endophytes are only found in host roots, where they form melanised structures.

The focus of the present review is on xylem-colonizing Class 3 endophytes, which make up a distinct guild of xylem-inhabiting endophytes (Stone *et al.*, 2000). These include species in the order *Hypocreales* Lindau and in the genus *Hypoxylon* Bull, and to a lesser extent some Basidiomycetes. Survival strategies of many xylem-inhabiting endophytes consists of initial infection of host plants, followed by indeterminate periods of interrupted growth allowing for further invasion and exploitation of the substrates upon occurrence of favourable conditions, such as host stress (Stone *et al.*, 2000). These xylem-colonizing endophytes typically disperse through horizontal transmission, with drop-splash from rainfall for spore dispersal. Wind and/or other vectors such as animals or insects may also facilitate transmission of these fungi (Petrini, 1991; Wilson, 2000). Endophytes can either have wide host ranges, or as suggested by Petrini (1991), they may have coevolved with their host plants, allowing the endophytes to infect their hosts without activating host defense mechanisms.

There are three hypotheses for the causes of the transition from endophytic to pathogenic phases. The first is that some event occurs which increases host susceptibility, facilitating the transition. These events are most likely to be abiotic and/or biotic stressors, including drought, poor host nutrient supply, and/or host wounding (Petrini, 1991; Stone, *et al*., 2000). The second hypothesis includes endophyte changes, including single point mutations, the transfer of virulence genes, and/or virus infections causing change to a pathogenic state (Sieber, 2007). The third hypothesis is the threshold model developed by Sieber (2007) for conifer needle endophytes, and this could be relevant to other types of endophytes. This model suggests that endophytes live in needle tissues, which senesce once a colonization threshold has been reached. This threshold is only reached under normal circumstances during the natural senescence of the needles; however, under stress conditions, the colonization threshold is reached sooner, leading to premature death (Sieber, 2007). All these scenarios could be applied to GTD fungi thought to have endophytic phases before becoming pathogenic. Most GTD fungi are slow wood colonizers causing slow-developing diseases (Bradshaw *et al.,* 2005; Agusti-Brisach *et al.,* 2019). In healthy grapevines, fungal growth is characteristically slow. When vines become stressed, however, fungal growth is accelerated and colonization thresholds are reached sooner than under non-stress conditions. Additionally, this threshold could be reached sooner when multiple GTD fungi are present within a grapevine (Figure 1).

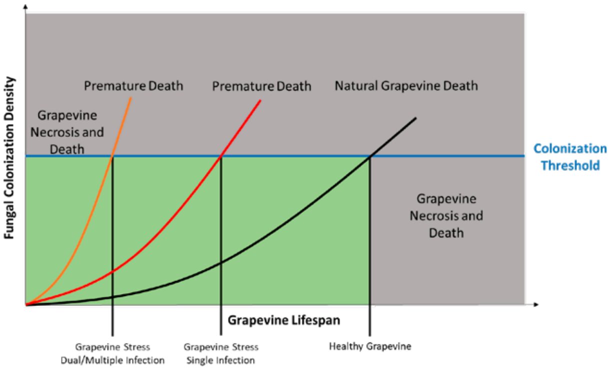

Figure 1. Illustration of the Threshold Model in grapevines, showing the relationship between the grapevine age and GTD fungal colonization density. Under normal conditions, fungal growth is slow, only reaching the colonization threshold in old grapevines during natural senescence. Under stress conditions, fungal growth is accelerated, and this threshold is reached rapidly in the grapevine lifespan, leading to disease progression and premature host death. This threshold is hypothesized to be reached sooner when multiple GTD fungi are present than when few fungi occur (adapted with permission from Sieber, 2007).

Endophytes in grapevines

Characterization of bacterial and fungal endophytes of grapevines has been a major focus of research, to identify potential biocontrol agents against pathogens (Bruisson *et al*., 2019). Endophytes colonize above- and below-ground plant organs, including, in grapevines, flowers, berries, xylem, roots, and seeds (Compant *et al*., 2011; Bruisson *et al*., 2019). Bacterial endophyte richness is greater than fungal endophyte richness in grapevines, and *Proteobacteria* Garrity et al., and Ascomycota species, respectively are the most abundant bacteria and fungi in grapevines (Deyett and Rolshausen, 2020). In *Vitis vinifera* L., Ascomycota endophytes are primarily Class 3 xylem-colonizing endophytes in the *Hypocreales*, *Pleosporales* Luttrell ex M.E. Barr, and *Xylariales* Nannf., which is consistent with other woody perennial hosts (Petrini, 1986; Hyde and Soytong, 2008; González and Tello, 2011).

Among these Ascomycetes, species in the *Hypocreales* and *Pleosporales* were the most abundant endophytes found across multiple grapevine cultivars in a study in Spain (González and Tello, 2011). However, the cultivars were colonized by different endophyte populations, showing that grapevines cannot be viewed as a homogeneous group of hosts, but cultivars must be studied individually. For example, González and Tello (2011) found ‘Tempranillo’ and ‘Merlot’ cultivars harboured high levels of *Eurotiales* G.W. Martin ex Benny & Kimbr., while ‘Cabernet Sauvignon’ harboured the least variable endophyte diversity. This study also showed high prevalence of the GTD pathogen *Diaporthe ampelina* (Berkeley & M.A. Curtis) R.R. Gomes, C. Glienke & Crous, (syn. *Phomopsis viticola* Sacc.) in asymptomatic and symptomatic grapevines (González and Tello, 2011). Other GTD pathogens found less widely in asymptomatic vines include *Phaeomoniella chlamydospora* (W. Gams, Crous, M.J. Wingf. & Mugnai) Crous & W. Gams, *Phaeoacremonium minimum* (Tul. & C. Tul.) D. Gramaje, L. Mostert & Crous, and *Phaeoacremonium inflatipes* W. Gams, Crous & M.J. Wingf. (involved in Petri disease and Esca), *Ilyonectria destructans* (Zinssm.) Rossman, L. Lombard & Crous (associated with Black foot disease), and species in the *Botryosphaeriaceae* Theiss. & P. Syd. [causing Botryosphaeria dieback (Gonzalez and Tello, 2011)]. These results, along with other reports of GTD fungi isolated from asymptomatic grapevines (Halleen and Petrini, 2003; Zanzotto *et al.*, 2007; Kaliterna *et al.*, 2009; Aroca *et al.*, 2010; Carlucci *et al.*, 2017), support the hypothesis that some of these fungi may have roles as latent pathogens in grapevines (González and Tello, 2011; Gramaje and Armengol, 2011; Úrbez-Torres, 2011; Gramaje *et al.*, 2018).

The objectives of this review are to provide up-to-date information indicating that GTD fungi may function as latent grapevine pathogens, to develop a synthesis of current knowledge available on the different abiotic and biotic stress factors that may influence the transition from endophytic to pathogenic phases, and to indicate future research directions for advancing understanding and management of these complex diseases.

GRAPEVINE TRUNK DISEASE FUNGI AS LATENT PATHOGENS

Most knowledge on the potential of GTD fungi to act as latent pathogens comes from studies in two main groups of Ascomycetes: *Botryosphaeriaceae* and *Ilyonectria* P. Chaverri & C. Salgado (“*Cylindrocarpon*” Wollenw.) spp., on grapevines as well as other woody perennials (Fourie and Halleen, 2004; Slippers and Wingfield, 2007; Úrbez-Torres, 2011). This paper also reviews the endophytic-pathogenic continuum of *Phaeomoniella chlamydospora*, *Diatrypaceae* and species of *Phaeoacremonium* and *Diaporthe* on grapevines.

Botryosphaeriaceae

Botryosphaeriaceae includes morphologically diverse fungi which have been found in gymnosperms and angiosperms in every climatic region except the polar regions (Phillips *et al.*, 2013; Slippers and Wingfield, 2007). Not all fungi in the *Botryosphaeriaceae* produce disease symptoms, and some species may be true endophytes, which never produce disease symptoms (Slippers and Wingfield, 2007). Some *Botryosphaeriaceae* have been shown to be important pathogens and have become problems in economically important agricultural crops, with several different species found to be associated with decline symptoms in apple trees (Brown-Rytlewski and McManus, 2000; Úrbez-Torres *et al.*, 2016), Eucalyptus (Burgess *et al.*, 2005), dwarf cashew (Cardoso *et al.*, 2006), hickory (Dai *et al.*, 2017), macadamia (Jeff-Ego and Akinsanmi, 2019), bay laurel (Lawrence *et al.*, 2017), almond, dried plum, pistachio, walnut (Luo *et al.*, 2019), peach, pear, blueberry (Sessa *et al.*, 2018), black currant (Singer and Cox, 2010), olive (Úrbez-Torres *et al.*, 2013b), and grapevine (Úrbez-Torres, 2011). However, even in the most severe diseases caused by *Botryosphaeriaceae* in some hosts, virulence is probably favoured by abiotic and/or biotic stresses suffered by host plants (Slippers and Wingfield, 2007). Fungi in the *Botryosphaeriaceae* have been found in several hosts which were asymptomatic and symptomatic (Brown-Rytlewski and McManus, 2000; Tennakoon *et al.*, 2018; Panahandeh *et al.*, 2019; Scala *et al.*, 2019). *Botryosphaeriaceae* isolated from asymptomatic hosts have been found to be pathogenic in pathogenicity trials conducted under controlled greenhouse conditions (Manzanos *et al.*, 2017; Steinrucken *et al.*, 2017). The *Botryosphaeriaceae* have gone through extensive taxonomic changes and revisions since first introduced in 1918, and have primarily been considered to be saprophytes (Phillips *et al.*, 2013). Only in the last two decades have detailed studies on the *Botryosphaeriaceae,* supported by the use of molecular techniques, revealed the widespread presence of these fungi in asymptomatic hosts, which has led to further investigations of the hypothesis that some of *Botryosphaeriaceae* species may act as latent pathogens.

In grapevines, up to 26 species of *Botryosphaeriaceae* have been identified as pathogens responsible for symptoms associated with the GTD Botryosphaeria dieback. These symptoms include leaf chlorosis, bud and wood necrosis, weak spring growth, and vascular cankers primarily in the shape of wedges (Úrbez-Torres, 2011; Gramaje *et al.*, 2018; Billones-Baaijens and Savocchia, 2019) (Figure 2). Among all species known to be associated with Botryosphaeria dieback, *Botryosphaeria dothidea* (Moug. ex Fr.) Ces. & De Not. has been described as a latent pathogen of global importance in woody perennials (Marsberg *et al.*, 2017). Several other *Botryosphaeriaceae* species have been described as latent pathogens in other woody hosts, but have not been confirmed in grapevines (Slippers and Wingfield, 2007; Carlucci *et al.*, 2015; Marsberg *et al.*, 2017; Billones-Baaijens and Savocchia, 2019). Lecomte and Bailey (2011) found *Botryosphaeriaceae* species, primarily *Diplodia seriata* De Not., in wounded host tissues, which was attributed to presence of these fungi in the bark prior to wounding, suggesting that the fungi may act as latent pathogens in grapevines. This is important for grape production, as Botryosphaeria dieback is one of the most prevalent diseases of grapevines, and the causal pathogens may not be detected due to their latent nature (Marsberg *et al.*,

Figure 2. Botryosphaeria dieback, Eutypa, Phomopsis dieback, and Esca symptoms. Botryosphaeria dieback symptoms on wine (**A**) and table grapevines (**B**) are characterized by dead spurs and cordons with no spring growth. Characteristic foliar symptoms of Eutypa dieback are shoots with short internodes and chlorotic and cupped leaves (**C** and **D**). Phomopsis dieback symptoms resemble those of Botryosphaeria dieback, with dead spurs and lack of spring growth (**E**). Vines affected by Botryosphaeria, Eutypa and/or Phomopsis dieback have perennial cankers in spurs, cordons and trunks, often with wedge shapes (**F**). Tiger-striped leaves (**G**) and characteristic soft yellowish wood rot (**H**) caused by Basidiomycete fungi are commonly associated with Esca disease.

2017; Agusti-Brisach *et al.*, 2019; Billones-Baaijens and Savocchia, 2019). *Neofusiccocum parvum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips remained latent in 'Cabernet Sauvignon' grapevines, with limited pathogen spread or lesion growth for 1.5 months after inoculation; thereafter, lesion lengths increased (Czemmel *et al.*, 2015). However, no cause for the transition from endophyte to pathogen was investigated, and more research should be conducted to determine whether this is the normal latency period of *N. parvum*, and/or if some external factors played roles in the transition, such as abiotic or biotic stress.

Some GTD fungi can be detected in asymptomatic host tissues far beyond necrotic or cankered wood. For example, *B. dothidea* colonizes asymptomatic tissues beyond canker margins in many different hosts, which supports the hypothesis of its endophytic nature (Wene, 1979; Schoeneweiss, 1981). Similarly, *Botryosphaeriaceae* known to be pathogenic in grapevines have been found in asymptomatic and symptomatic grapevines (Halleen and Petrini, 2003; Aroca *et al.*, 2010; Abreo *et al.*, 2013; Úrbez-Torres *et al.*, 2015). Other *Botryosphaeriaceae* have also been shown to infect asymptomatic tissues beyond lesions in grapevines (Amponsah *et al.*, 2011; Billones-Baaijens *et al.*, 2013a). As in other hosts, the relationship between symptomatic tissue and/or hosts in grapevines has also become an area of interest, with particular emphasis on the role that drought stress may play on symptom expression and disease development.

Ilyonectria

Species of *Ilyonectria* are cosmopolitan soil-borne fungi, and the fungi are weak and/or opportunistic pathogens associated with root rot diseases in several economically important hosts, including apple (Manici *et al.*, 2013), avocado (Parkinson *et al.*, 2017), banana (Booth and Stover, 1974), Mexican blue palm, Guadalupe palm, Kentia palm (Aiello *et al.*, 2014), clover (Barbetti *et al.*, 2007), ginseng (Rahman and Punja, 2005), hazelnut (Guerrero *et al.*, 2014), kiwifruit (Erper *et al.*, 2013), loquat (Agustí-Brisach *et al.*, 2016), olive (Úrbez-Torres *et al.*, 2012), strawberry (Ceja-Torres *et al.*, 2008), and other fruit trees and nut producing hosts (Lawrence et al. 2019). In addition, several *Ilyonectria* species and closely related *Campylocarpon* Halleen, Schroers & Crous, *Cylindrocladiella* Boesew., *Dactylonectria* L. Lombard & Crous, *Neonectria* Wollenw., and *Thelonectria* P. Chaverri & C. Salgado, are known to cause black foot of grapevines (Agusti-Brisach *et al.,* 2013). Black foot pathogens have been isolated from asymptomatic and symptomatic rootstock mother-plants, rootstock cuttings, and young grafted grapevines, in nurseries and young vineyards, as well as from other hosts, which has led to the hypothesis that Black foot pathogens act as latent and/or weak pathogens in grapevines (Agustí-Brisach and Armengol, 2013; Carlucci *et al.*, 2017; Dubrovsky and Fabritius, 2007; Dumroese *et al.*, 2002; Halleen and Petrini, 2003; Úrbez-Torres *et al.*, 2015).

Phaeomoniella chlamydospora *and* Phaeoacremonium *species*

Petri disease is mainly caused by *P. chlamydospora* and *Phaeoacremonium* spp. in young grapevines, while Esca is thought to be caused by the same species of fungi along with colonization of various Basidiomycetes in older grapevines (Gramaje *et al.*, 2018). While Petri disease and Esca are different, for the purpose of this review these two diseases are considered together (Figure 3). *Phaeomoniella chlamydospora* and *Phaeoacremonium* spp. have been isolated from asymptomatic and symptomatic wood from grapevines and other hosts (Halleen and Petrini, 2003; Edwards and Pascoe, 2004; Zanzotto *et al.*, 2007; Abreo *et al.*, 2011; Panahandeh *et al.*, 2019). Some grapevines infected with Esca pathogens have displayed symptoms one year but not in the next, which has been proposed to correspond to differences in environmental conditions, primarily temperature and rainfall (Surico *et al.*, 2000; Marchi *et al.*, 2006; Péros *et al.*, 2008; Calzarano *et al.*, 2018). In addition, *P. chlamydospora* and *Phaeoacremonium* spp. have been found to widely occur in grapevines in several regions such as in Australia and British Columbia (Canada). However, Esca foliar symptoms are rarely observed in these regions in comparison with Europe, where these symptoms are common (M. Sosnowski, Personal Communication; Úrbez-Torres *et al.*, 2014a). Though not yet studied, the lack of Esca symptom expression in Australia and/or Canada may result from the lack of Basidiomycete species associated with Esca symptoms in Europe, primarily those in *Fomitiporia* Murrill (Fischer, 2002; Fischer and Kassemeyer, 2003). On the other hand, other studies have tended to exclude a direct role of *Fomitiporia* in Esca leaf symptom expression (Calzarano and Di Marco, 2007). In a study in Australia, *P. chlamydospora* was widely found in south-eastern Australia, less commonly in western Australia, and absent from the northern region, indicating that host range may be mainly influenced by climatic factors (Edwards and Pascoe, 2004). Nevertheless, these observations suggest that Esca internal symptoms are not necessarily indicative of external symptoms, and that foliar symptom expression may rely also on external abiotic or biotic stress fac-

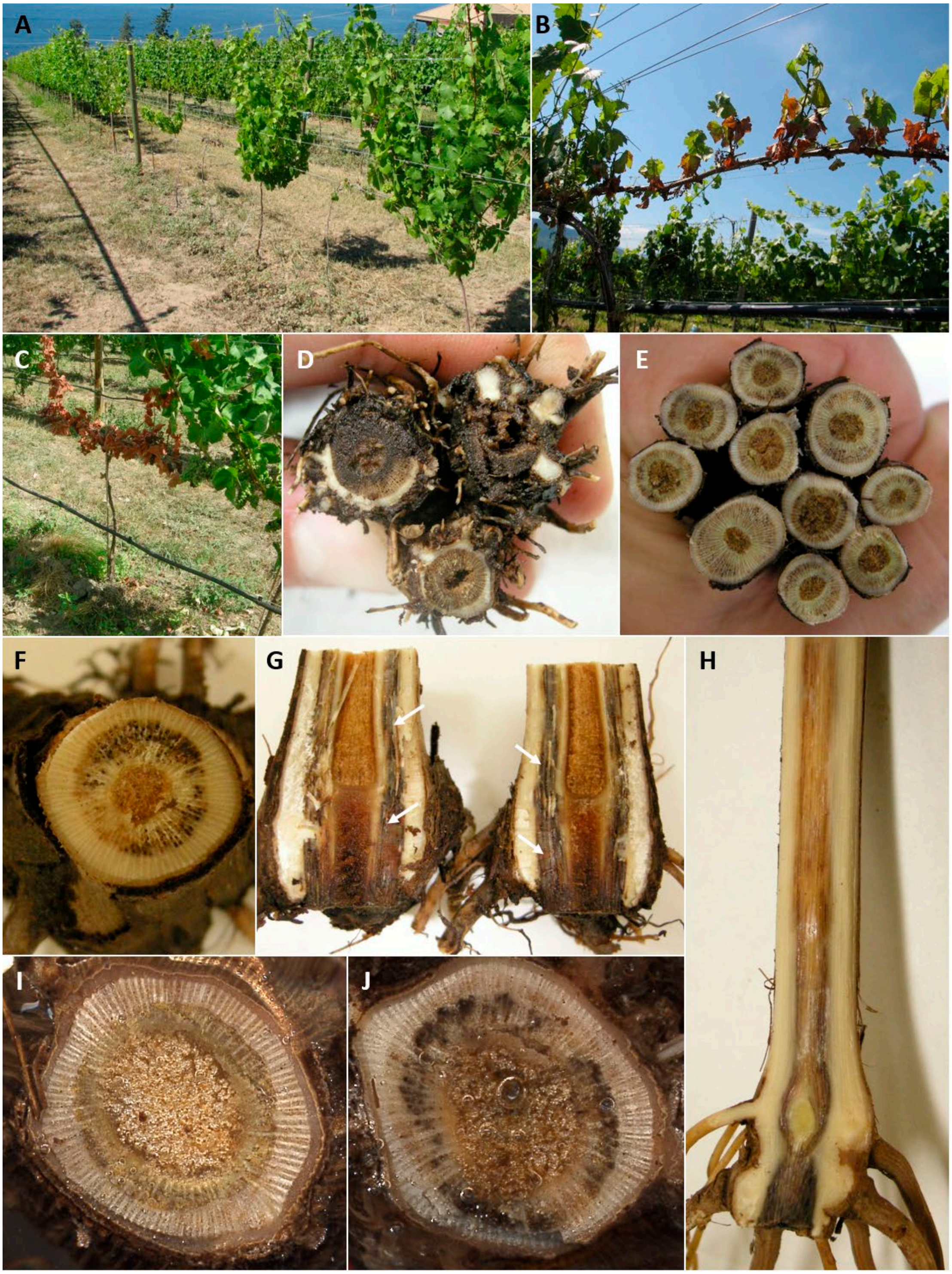

Figure 3. Decline of young vines caused by Petri disease and/or black foot. Overall symptoms in the field include poor vigour, leaf chlorosis, short internodes (**A** and **B**) and eventual or sudden collapse (**C**) during the growing season. Internal wood necrosis observed at the basal end of the rootstock (**D**) commonly associated with black foot. Tylosis plugged xylem vessels and necrosis observed at a graft union (**E**) and trunk base, usually associated with Petri disease in young vines (**F**). Longitudinal section of a ready-to-plant nursery vine showing vascular necrosis originating from the basal end of the rootstock (**G** and **H**). *Phaeomoniella chlamydospora*, *Phaeoacremonium* spp., *Ilyonectria* spp., and some *Botryosphaeriaceae* spp. can be isolated from asymptomatic (**I**) and symptomatic (**J**) wood tissues from nursery propagated material, which reveals their potential latent phases in grapevines.

tors (Surico *et al.*, 2000; Zanzotto *et al.*, 2007; Calzarano and Di Marco, 2018). Lack of correlation between extent of vascular alteration and foliar symptom expression in Esca may indicate a latent phase (Calzarano and Di Marco, 2007). In addition, rainfall has been suggested to be involved in foliar symptom expression regardless of the extent of fungal colonization (Calzarano *et al.*, 2018).

Diatrypaceae

The causal organism for Eutypa dieback is the diatrypaceous fungus *Eutypa lata* (Pers.) Tul. & C. Tul. Although other 23 species in the Diatrypaceae Nitschke have been isolated from grapevine cankers, only *E. lata* has been proven to cause the foliar symptoms associated with Eutypa dieback (Trouillas and Gubler, 2010; Gramaje *et al.*, 2018). These symptoms include internal wood wedge-shaped necroses, cordon dieback, leaf chlorosis, and stunted shoots (Rolshausen *et al.*, 2015) (Figure 2). These symptoms mainly appear on grapevines that are 7 years or older, and foliar symptoms typically do not appear for 3 to 8 years post-infection (Rolshausen *et al.*, 2015). Symptoms have also been observed to be inconsistent from year to year, with individual grapevines displaying symptoms one year, while appearing asymptomatic the next (Sosnowski *et al.*, 2007b; Bertsch *et al.*, 2013; Mundy and McLachlan, 2016). Several hypotheses have been proposed to explain why symptoms do not appear for extended periods, including the influence of environmental factors. Bruez *et al.* (2016) found *E. lata* among other GTD pathogens in asymptomatic grapevines aged 40 years or older and suggested that there was a balance between beneficial organisms and pathogenic fungi, which prevented the pathogens from developing further in grapevines. *Eutypa lata* and other *Diatrypaceae* have been isolated from asymptomatic or healthy tissues several centimeters ahead of disease margins, indicating pathogen latency (Pitt *et al.*, 2013). Other hypotheses, including the threshold model (above), could also explain these observations.

Diaporthe

The main causal agent of Phomopsis dieback is *D. ampelina*, which has recently been added to the list of pathogens in the GTD complex (Úrbez-Torres *et al.*, 2013a). Symptoms of Phomopsis dieback are similar to those observed in Botryosphaeria dieback, and include perennial cankers, lack of or delayed bud break and leaf chlorosis (Úrbez-Torres *et al.*, 2013a) (Figure 2). Fungi in *Diaporthe* Nitschke are diverse, inhabiting many different hosts including grapevines, as pathogens, true endophytes, or saprobes (Gomes *et al.*, 2013; Úrbez-Torres *et al.*, 2013a). In grapevines, a diversity of *Diaporthe* species, including *D. ampelina*, have been found in asymptomatic and symptomatic grapevine tissues from mature vines and especially from nursery propagated plants, leading to the suggestion that some Phomopsis dieback pathogens may have endophytic phases. However, research into this is limited (Mostert *et al.*, 2000; Kaliterna *et al.*, 2009; Król, 2012; Guarnaccia *et al.*, 2018;).

In general, knowledge of the role that species in the *Diaporthaceae* Höhn. ex Wehm. may have as latent pathogens comes from hosts other than grapevines. For example, *Diaporthe toxica* P.M. Will., Highet, W. Gams & Sivasith., the cause of Phomopsis stem blight in *Lupinus albus* L., has been suggested as a latent pathogen, due to a prolonged latent period under which no visible symptoms occur (Cowley *et al.*, 2012). Tongsri *et al.* (2016) also suggested an endophytic phase for *Diaporthe* pathogens in durian leaves and flowers, with symptoms typically occurring 32 d after infection. Similarly, lupins infected with *Phomopsis leptostromiformis* (J.G. Kühn) Bubák, exhibited a 20 d asymptomatic period after infection (Williamson *et al.*, 1991). Furthermore, symptom expression from *D. toxica* and *P. leptostromiformis* infections in lupins has typically been associated with host senescence (Cowling *et al.*, 1984; Williamson and Sivasithamparam, 1994). Mature durian leaves also contained a higher density of *Diaporthe* pathogens than immature leaves (Tongsri *et al.*, 2016). This evidence indicates that these pathogens reach their thresholds for transition from endophytic to pathogenic phase during natural senescence in mature leaves and/or hosts, as suggested by Sieber (2007). However, further research is required to confirm these observations, particularly in grapevines, to determine if Phomopsis dieback pathogens act similarly across different host plants.

YOUNG VINE DECLINE AND GRAPEVINE NURSERY STOCK

As outlined above, some of the pathogens responsible for Botryosphaeria dieback, Black foot and Petri disease in grapevines have been isolated from ready-to-plant nursery material and from plants in young vineyards, either separately or together and either from symptomatic or asymptomatic tissues. Accordingly, some of these pathogens may often be latent or weak pathogens, remaining in asymptomatic grapevines for indeterminate periods, and being widespread in vineyards (Rumbos and Rumbou, 2001; Halleen and Petrini, 2003; Giménez-Jaime *et al.*, 2006; Dubrovsky and Fabritius, 2007; Halleen *et al.*, 2007a; Gramaje and Armengol, 2011; Agustí-Brisach and Armengol, 2013; Úrbez-Torres *et al.*, 2014a, 2014b; Carlucci *et al.*, 2017).

Black foot pathogens are soil-borne and can be present and ready to infect young grapevines when new vineyards are established (Halleen and Petrini, 2003; Carlucci *et al.*, 2017; Agusti-Brisach *et al.*, 2019;). However, serious infections and disease outbreaks by these pathogens have been found shortly after grapevines were planted (Úrbez-Torres *et al.*, 2014b). This rapid disease development has been suggested to result from: i) exposure to abiotic and/or biotic stress factors during planting in material that is already contaminated with *Ilyonectria* spp. (Halleen *et al.*, 2006); or ii) greater than normal infection thresholds that host plants cannot withstand (Úrbez-Torres *et al.*, 2014b; Gramaje *et al.*, 2018). In addition, Black foot pathogens have been found in soil in rootstock mother fields and young plant nurseries (Cardoso *et al.*, 2013; Whitelaw-Weckert *et al.*, 2013; Agustí-Brisach *et al.*, 2014).

These pathogens are prevalent in asymptomatic inner tissues of nursery stock, as shown in 15 nurseries in Northern Spain (Berlanas *et al.*, 2020). A total 1,427 isolates of Black foot pathogens were found, including species of *Dactylonectria, Ilyonectria, Neonectria,* and *Thelonectria* from 3,426 ready-to-plant grafted grapevines. Of these pathogens, *Dactylonectria torresensis* (A. Cabral, Rego & Crous) L. Lombard & Crous made up 75% of all isolates. Further research should be conducted in other regions on the incidence of Black foot and Petri disease pathogens in nurseries and young vineyards to better determine the scale of this problem. In particular, species of *Cadophora* Lagerb. & Melin have come to attention, since they have been found in grapevines in many regions, including Africa, Europe, North America, and South America (Halleen *et al.*, 2007b; Casieri *et al.*, 2009; Úrbez-Torres *et al.*, 2014a; Travadon *et al.*, 2015). *Cadophora* species have also been shown to be occur in nursery material in Northern Spain (Maldonado-Gonzalez *et al.*, 2020), with *Cadophora luteo-olivacea* (J.F.H. Beyma) T.C. Harr. & McNew found in 27% of 'Tempranillo'/'110R' dormant grapevines.

Recent studies have also identified species in *Fusarium* Link to occur in high numbers in nursery material and vineyards in Canada (Úrbez-Torres *et al.*, 2017). Pathogenicity studies have shown some *Fusarium* species to be capable of causing necrosis in grapevines to the same extent as *Ilyonectria* spp. under favourable conditions. This indicates that *Fusarium* species potentially act as weak or latent pathogens in grapevines, transitioning from endophytic to pathogenic phases under stress conditions, thus playing roles in young vine decline symptom development (Úrbez-Torres *et al.*, 2017). The suggestion that *Fusarium* is involved in grapevine decline is not new, and had been proposed by Highet and Nair (1995), when a clear association between *Fusarium oxysporum* Schlecht. emend. Snyder & Hansen and vine decline was found in vineyards in New South Wales, Australia. However, the roles of *Cadophora* and *Fusarium* in nursery material and young vineyards, and any interactions of these fungi with Petri disease and Black foot pathogens is not well-understood, although the high incidence of these fungi in nursery material warrants further investigation of them as potentially relevant to young vine decline. In addition, the roles of different types of stress, and the effects of intermittent *versus* prolonged stress on young grapevines remains unknown. Research on the roles of *Cadophora* and *Fusarium* spp. in association with Black foot and Petri disease pathogens should be further investigated.

Infection during the grapevine propagation

Several Black foot pathogens have also been discovered in nurseries on grapevine scion cuttings, cutting tools, in water from hydration tanks, and in callusing medium, indicating that infections can occur at several steps in the propagation process, and in the field (Gramaje and Armengol, 2011; Cardoso *et al.*, 2013). The presence of pathogens during several steps of nursery processes has also been observed with several *Botryosphaeriaceae* species associated with Botryosphaeria dieback in New Zealand. In a study of three commercial nurseries, 33 to 100% of canes contained detectable amounts of *Botryosphaeriaceae* on the surfaces of the canes, and 15 to 68% of canes were internally infected with these fungi (Billones-Baaijens *et al.*, 2013b). In a separate study in New Zealand, three of ten apparently healthy '3309' mother grapevines and two out of ten '101-14' grapevines were internally infected with *Botryosphaeriaceae* in nursery mother blocks. External infection rates in plant bark were also high, with the bark in one out of three shoots infected in one grapevine. Therefore, it was suggested that these *Botryosphaeriaceae* remained latent in the bark of dormant cuttings, which may be a potential route of infection and spread during nursery propagation (Billones-Baaijens *et al.*, 2015). These results also indicate that disease control should begin in mother blocks from which scion and rootstock material is obtained, and precautions should also be taken during the propagation processes, in which there are several possible avenues of spread of these pathogens.

Current best practices for the prevention of transmission have been outlined (Gramaje and Armengol, 2011; Waite *et al*., 2018). In addition to adopting these best practices, rootstocks are a promising avenue to reduce transmission. Berlanas *et al*., (2019) found that '161-49C', '140 Ru', '1103P', and '110R'had lower abundance of "*Cylindrocarpon*"-like asexual morphs, compared to '41B' rootstocks.

Rootstock and scion resistance to GTD fungi

In grapevines infected with Botryosphaeria dieback pathogens, it has been shown that some scion varieties are more susceptible than others to these pathogens (Úrbez-Torres and Gubler, 2009). Studies in New Zealand vineyards showed 'Sauvignon Blanc', with 83% incidence of infection, was more susceptible to species of *Botryosphaeriaceae* compared to 'Pinot noir', which had 42% incidence (Baskarathevan *et al*., 2012). Similarly, 'Shiraz' and 'Sauvignon Blanc' had greater susceptibility to *D. seriata* (pathogen recovery 12 to 21 mm from inoculation sites, while 'Green Veltliner' and 'Muscadelle' were less susceptible (pathogen recovery 8 to 17 mm from inoculation sites (Sosnowski *et al*., 2017c). Pintos *et al*., (2018) showed that 'Savagnin' grafted plants had greater Botryosphaeria dieback pathogen infections (66%) than other cultivars.

Rootstock susceptibility to Black foot has also been evaluated, and among the screened rootstocks, a majority were found to be susceptible, in particular '110R'. This rootstock was the most susceptible to infection by *Ilyonectria liriodendri* (Halleen, Rego & Crous) Chaverri & C. Salgado and *Ilyonectria macrodidyma* (Halleen, Schroers & Crous) P. Chaverri & C. Salgado, which are considered the main pathogens of Black foot. These results were similar to those for susceptibility of '110R' to *P. chlamydospora* (Zanzotto *et al*., 2008; Alaniz *et al*., 2010; Nguyen, 2013). 'SO4', 'Freedom', and 'Riparia Glorie' were also susceptible to *I. liriodendri* and *I. macrodidyma*, while '44-53' and 'St. George' were more tolerant to these fungi (Nguyen, 2013). Susceptibility of different rootstocks to co-infection of Black foot pathogens and those causing either Petri disease or Botryosphaeria dieback should be studied further, along with the impacts of nematode damage on rootstocks infected by GTD pathogens.

Symptom expression of grapevines infected with Esca and/or Petri disease pathogens may be influenced by scion variety, with 'Merlot' found to be very tolerant to Esca disease (1.5 to 3.6% incidence), while 'Cabernet Sauvignon' was less resistant (20.2 to 27.8% incidence) (Christen *et al*., 2007). Andreini *et al*., (2009) showed that 'Trebbiano' and 'Sangiovese' grapevines were found to have lower disease incidence than 'Cabernet Sauvignon', which is probably one of the most affected cultivars. Several other studies have noted varying degrees of susceptibility between rootstocks and scions; however, the factors influencing scion and rootstock susceptibility remain unknown (Edwards and Pascoe, 2004; Edwards *et al*., 2007a, 2007b). A detached cane assay study conducted by Martinez-Diz *et al*. (2019) found variations in colonization of xylem tissues among 20 cultivars, varying from 3 to 34 mm when infected with *P. chlamydospora* and 9 to 48 mm when infected with *P. minimum*. Gramaje *et al*. (2010) showed that 1-year-old rootstocks of '110R' and '140Ru' were very susceptible to *P. chlamydospora, Phaeoacremonium* spp., and *Cadophora* spp., while '161-49C' was the most tolerant rootstock to these pathogens. 'Fiano' and 'Sauvignon Blanc' scions grafted onto 'SO4' rootstock, which is intolerant to drought stress, displayed increased disease incidence compared to when grafted onto '1103P' rootstock, which is more drought tolerant (Murolo and Romanazzi, 2014). These results are similar to those of Cardoso *et al*. (2006), in that scion and/or rootstock resistance to abiotic or biotic stress factors may influence disease susceptibility. This requires further investigation, however.

Cultivar variety may affect symptom expression in grapevines infected with *E. lata*, with studies showing that different cultivars were more resistant or susceptible than others to Eutypa dieback (Baumgartner *et al*., 2019; Cardot *et al*., 2019). 'Merlot' was the most resistant to Eutypa dieback (38% plants asymptomatic), while 'Ugni Blanc' was very susceptible (87% of plants with symptoms) (Cardot *et al*., 2019). Péros and Berger (1994) assessed different cultivars for foliar symptoms 5- and 10-weeks post-inoculation. 'Cabernet Sauvignon' was the most susceptible (90% of plants displaying foliar symptoms), followed by 'Ugni Blanc', while 'Sauvignon' was the least susceptible.

Research is being instigated on rootstock tolerance to GTD pathogens under abiotic or biotic stress conditions. However, further studies are required on the tolerance of different rootstock and cultivars to Esca disease while under stress (Sosnowski *et al*., 2017a; Sosnowski *et al*., 2017b). In a field grapevine study, trunk disease severity was greater in red than white cultivars when infected with *E. lata*. 'Petit Verdot' had the least trunk symptom severity while 'Odola' had the greatest for red cultivars, while 'Traminer', 'Petit Meslier', 'Muscadelle', and 'Green Veltliner' displayed no trunk symptoms. Among white cultivars infected with *E. lata* 'Sauvignon Blanc' had the greatest trunk symptom severity (Sosnowski *et al*., 2017c). In a follow-up detached cane assay (Sosnowski *et* *al.*, 2017c), *E. lata* was recovered 20 to 23 mm from inoculation sites in 'Shiraz' and 'Sauvignon Blanc' compared to 4 to 14 mm in 'Petit Meslier', 'Petit Verdot', and 'Muscadelle' grapevines, confirming the field assessments. A later field inoculation experiment (Sosnowski *et al.*, 2017c) also showed that 'Petit Verdot' and 'Muscadelle' had increased resistance to pathogen colonization. Clonal susceptibility for 'Shiraz' varied between clones aged 21 to 34 years, for 'Sauvignon Blanc' clones between 20 to 44 years, and 'Chardonnay' clones between 18 to 45 years, with less symptom severity in younger than older grapevines. Plant age and resistance to environmental stresses in relation to pathogen resistance should be further explored, to determine how resistance varies as grapevines age.

Rootstock and scion varieties present a promising avenue for tolerance to GTD infection. However, further research is required on this subject, including host tolerance to infection under abiotic and biotic stress conditions. Research has been conducted on rootstock performance in varying growing condition, but the roles that abiotic and biotic stress factors play for grapevine latent infections by GTD pathogens in rootstocks, particularly during the first few years after planting, have not been explored (Fort *et al.*, 2017; Cuneo *et al.*, 2020). In particular, rootstock and scion tolerance to stress and symptom expression should be assessed at the regional levels, to determine the best rootstock selections, and which ones are best suited for unique stress factors encountered in each region.

ABIOTIC STRESS FACTORS AND GTD SYMPTOM EXPRESSION

Botryosphaeriaceae

Many members of the *Botryosphaeriaceae* are not host specific, but rather the environment probably plays a major role in host affinity (Slippers and Wingfield, 2007; Ibrahim *et al.*, 2017). Symptom expression in many different hosts has been found to coincide with periods of drought or other extreme weather events (Brown-Rytlewski and McManus, 2000; Ma *et al.*, 2001; Slippers and Wingfield, 2007; Golzar and Burgess, 2011; Bendixsen *et al.*, 2015; Crous *et al.*, 2017; Acimovic *et al.*, 2018; Jeff-Ego and Akinsanmi, 2019). Direct evidence for stress induced symptom expression includes the research of Old *et al.* (1990), which showed that *Neofusicoccum ribis* (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips, caused larger cankers in Eucalyptus when trees were defoliated or attacked by insects, than where insect attack was absent.

Drought stress is probably the most important factor in symptom expression, and has been the most extensively researched out of all potential stress factors (Brown-Rytlewski and McManus, 2000; Slippers and Wingfield, 2007; Scala *et al.*, 2019). Similarly, water stress which reduced leaf water potentials increased the symptoms caused by *B. dothidea*. Plants remained resistant to *B. dothidea* infection until a water potential threshold of -12 to -13 MPa was reached (Wene, 1979; Schoeneweiss, 1981). However, it was necessary to sustain stem water potentials at less than -12 MPa for at least 3 d to allow for predisposition to *B. dothidea*, and that under field conditions, the effects were reversible if drought was not sustained. Similarly, Ma *et al.*, (2001) in a greenhouse study showed that old pistachio trees could not recover from the combined effects of drought stress and *B. dothidea* infection, while young trees were more resilient. This may be explained by the ability of *B. dothidea* to grow rapidly when pistachio tree stem water potentials were decreased from 0 MPa to -2 MPa (Ma *et al.*, 2001). Pusey (1989) also found that drought conditions resulting in leaf water potential of -3.0 MPa increased lesion length in peach trees. These results indicate that symptom expression is a combination of reduced host resistance due to stress and increased pathogen colonization due to optimal growth conditions. Similarly, Cardoso *et al.* (2006) hypothesized that resistance in a dwarf cashew clone to *Lasiodiplodia theobromae* (Pat.) Griff. & Maubl. was due to indirect mechanisms related to the drought tolerance of the clone. In grapevines, under drought conditions, 'Cabernet Sauvignon' grapevines infected with *N. parvum* had larger lesions than plants provided with adequate water; however, grapevines infected with *Neofusiccocum luteum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips had larger lesions when grown at high soil moisture levels, indicating physiological conditions induced by low moisture content may affect wood symptom expression, but other factors may be involved that influence lesion length (Galarneau *et al.*, 2019). Qiu *et al.* (2016) reported similar results, where 'Chardonnay' grapevines infected with *N. parvum*, *B. dothidea*, *L. theobromae*, and *D. seriata* produced larger necrotic wood lesions in water stressed grapevines than in unstressed vines. Van Niekerk *et al.* (2011a) also showed that 'Shiraz' grapevines infected with *Neofusiccocum australe* (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips, *N. parvum, L. theobromae*, and *D. seriata* developed larger lesions and reduced shoot mass when water stressed compared with unstressed plants.

Other host stress factors, including freezing damage, root damage from transplanting, pathogenic nematode infestations, and suboptimal environmental conditions for growth (nutrient-poor or high-salt soils, excessive cold or heat) have also been associated with GTD symptom expression in multiple hosts. In addition to these associations, some research has been completed on freezing stress, showing similar effects to drought stress in *Cornus sericea* L. Localized cold exposure of this host to -30°C produced no visible signs of freeze damage, but colonization by *B. dothidea* occurred solely in the cold exposed areas and did not extend significantly beyond the margins. Similar results were also found in *Sorbus aucuparia* L. infected with *B. dothidea* (Wene, 1979; Schoeneweiss and Wene, 1980;). Manawasinghe *et al.* (2018) also suggested that *B. dothidea* outbreaks in China were associated with other stress factors, such as increased temperature and pest pressure.

Ilyonectria

Several factors have been shown to affect symptom expression in hosts infected with *Ilyonectria* spp. In apple and ginseng, root age affects lesion severity, with young roots developing more severe lesions compared to older roots, which displayed shallow lesions (Rahman and Punja, 2005; Manici *et al.*, 2018). Abiotic and biotic factors also probably affect symptom expression, including root damage, acidic soils, temperature, and drought. (Rahman and Punja, 2005; Barbetti *et al.*, 2007; Ruiz-Gómez *et al.*, 2019).

Black foot symptom expression on grapevines has been associated with three categories of stress factor: (1) nursery-related factors such as cold storage, grapevine defects, and low light and other conditions leading to low carbohydrate levels in the plants; (2) vineyard conditions and plant establishment stress factors, including nutrient deficient soils, poor soil drainage leading to low oxygen levels, drought, soil compaction, J-rooting, and other factors contributing to poor root development and temperature extremes; and (3) biotic factors, including fungal pathogens, pathogenic nematodes, and insect pests (Stamp, 2001; Rahman and Punja, 2005; Halleen *et al.*, 2006; Barbetti *et al.*, 2007; Gramaje and Armengol, 2011; Nguyen, 2013; Agusti-Brisach *et al.*, 2019; Ruiz-Gómez *et al.*, 2019) (Figure 4). Moreno-Sanz *et al.* (2013) suggested that symptom expression primarily occurs when grapevines are under stress, as defined by hindering of normal growth and development and photosynthesis, and causing physiological responses, e.g. increased stress hormones that lead to numerous responses that enhance plant survival at the expense of crop performance. As *Ilyonectria* spp. are likely weak or opportunistic pathogens, they probably only invade weakened or dead roots (Scheck *et al.*, 1998; Halleen *et al.*, 2006; Jankowiak *et al.*, 2016;). These conclusions were further supported by Probst *et al.* (2012), who found that increased cold storage time correlated with increased disease incidence and severity for several Black foot pathogens. Partial defoliation also decreased root dry weight and increased disease severity resulting in increased canker development in young grapevines infected with *I. destructans*, which was probably due to reduced carbohydrate levels (Brown *et al.*, 2012). This is similar to the results of Old *et al.* (1990) stated above.

Phaeomoniella chlamydospora *and* Phaeoacremonium species

Several stress factors have been associated with, or are thought to influence, symptom expression from Esca and Petri disease pathogens, including biological factors such as nematode or other fungal pathogens, and abiotic factors such as cold exposure, and those associated with poor soil quality including low water and nutrient supply, extreme pH, and excess salt (Stamp, 2001; Corino *et al.*, 2004; Oliveira *et al.*, 2009; Oliveira *et al.*, 2013; Fischer and Ashnaei, 2019). Drought has received the most attention. In young grapevines, wood symptom expression, plant growth, and likely survival of grapevines infected with Esca and/or Petri disease pathogens depends on sufficient water supply to avoid stress (Fischer and Kassemeyer, 2012). In two separate studies conducted in Australia, 'Cabernet Sauvignon' and 'Zinfandel' grapevines were infected with *P. chlamydospora* and subjected to either an irrigation regime that resulted in no measurable water stress, 50% irrigation, or 25% irrigation. While stomatal conductance and leaf water potentials were both progressively reduced in the 50% and 25% irrigation regimes, for both non-infected and *P. chlamydospora* infected grapevines, in each irrigation treatment the infected grapevines displayed greater stomatal conductance and less leaf water potential compared to non-infected grapevines. Furthermore, 'Chardonnay' grapevines displayed grater leaf water potentials than 'Cabernet Sauvignon' and 'Zinfandel', which may indicate 'Chardonnay' is more tolerant of *P. chlamydospora* infection (Edwards *et al.*, 2007a, 2007b). On potato dextrose agar (PDA) amended with either potassium chloride or sucrose to generate osmotic water potentials between -0.3 and -8.3 MPa, two out of three isolates of *P. chlamydospora* grew at down to -8.3 MPa (Whiting *et al.*, 2001), indicating that the the fungus could grow in severely water-stressed plant tissues. Results by Lima *et al.* (2017) indicated that a combination of water stress and Esca infection increased xylem sap nutrient concen-

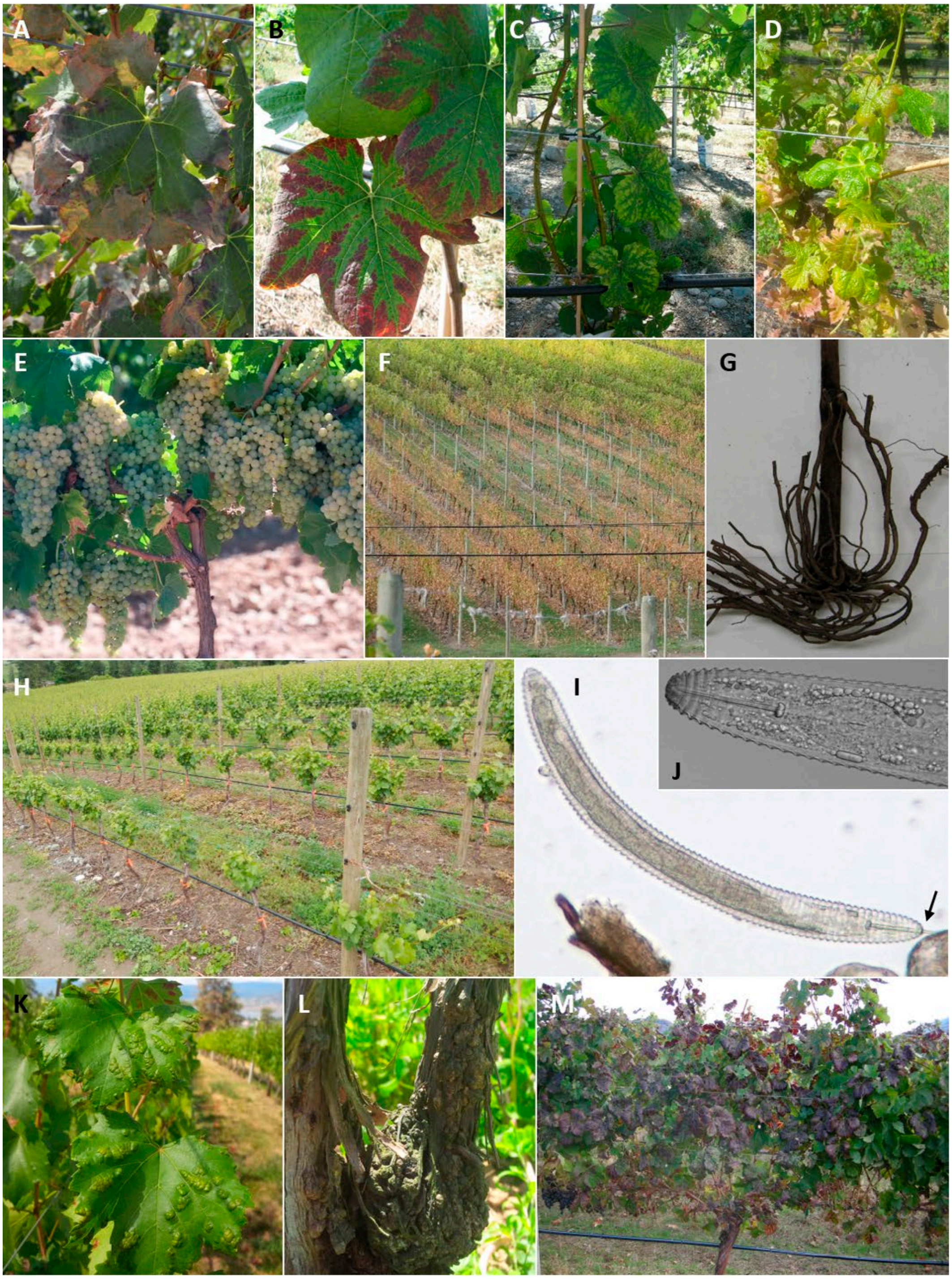

Figure 4. Abiotic and biotic stress factors hypothezised to contribute to grapevine trunk disease fungal development and symptom expression. **A.** Leaf scorching as a result of severe vine water stress. **B** and **C**. Leaves of young vines showing nutrient deficiency. **D.** Leaf deformities caused by herbicide damage. **E.** Severe over-cropping during the first years of vineyard establishment (courtesy of D. Gramaje, ICVV, Logroño, Spain). **F.** Winter damage and/or spring frost may favor disease development. **G.** J-rooting as a result of poor planting conditions. **H.** Low vigour vines caused by a nematode infestation. **I.** Ring nematode (*Mesocriconema xenoplax*) feeding on a root by introducing the stylet (black arrow). **J.** Close up of the ring nematode head. **K.** Leaf galls caused by erineum mite (*Colomerus vitis*). High levels of insect damage could increase vine stress. **L.** Grapevine crown gall caused by *Agrobacterium vitis*. **M.** Grapevine showing grapevine leaf roll symptoms caused by *Grapevine leafroll-associated virus 3*. Grapevines affected by biotic stress factors (fungal, bacterial or virus diseases) may favour GTD fungal infections, wood colonization and symptom expression.

trations, allowing for increased growth of the pathogens. In contrast, heavy rainfall from fruit set until veraison were associated with increasing Esca foliar symptoms, reducing grape quality (Calzarano and Di Marco, 2018). These results show that water stress may not be the only water status condition in grapevines that favour Esca development.

Diatrypaceae

It is well known that precipitation plays a role in *E. lata* distribution and frequency of occurrence. However, the effects of environmental conditions on symptom expression are not well understood. In a survey in France, the incidence and frequency of Eutypa dieback varied among different regions, indicating that climatic conditions, particularly temperature regimes which varied among regions, were major causes of differences in Eutypa occurrence (Guérin-Dubrana *et al.*, 2013). Magarey and Carter (1986) also found *E. lata* to be restricted to geographical locations where annual rainfall exceeded 350 mm, or in vineyards subject to overhead watering systems, indicating that precipitation affects *E. lata* distribution. Likewise, winter precipitation may be an additional requirement for the full development of *E. lata* in particular regions (Petzoldt *et al.*, 1983; van Niekerk *et al.*, 2011b; Úrbez-Torres *et al.*, 2019).

Guérin-Dubrana *et al.* (2013) and Sosnowski *et al.* (2007a) found that symptom expression and severity were influenced by climactic conditions in different regions. In Australia, *E. lata* isolates obtained from regions with intermediate climate had greater effects on symptom expression in a shadehouse experiment (Sosnowski *et al.*, 2007a). These isolates may have had greater virulence due to more favourable climactic conditions in the shade-house compared to the field. In a separate study in Australia, grapevines grown in extreme temperature and moisture conditions had increased foliar symptoms, but internal wood staining was not related to disease severity (Sosnowski *et al.*, 2007a; Sosnowski *et al.*, 2011). This is consistent with other reports on *Botryosphaeriaceae*, that indicate wood staining does not relate to colonization rates or correspond to foliar symptoms, but may be a consequence of wounding (Travadon *et al.*, 2013). Grapevines infected with *E. lata* also displayed decreased leaf water potential compared with non-infected grapevines when exposed to moisture deficits, suggesting that the pathogen increased sensitivity to water stress which may facilitate symptom development (Sosnowski *et al.*, 2011). Decreased leaf water potentials may be due to Eutypa dieback pathogens occluding the xylem vessels, but this needs to be confirmed (Sosnowski *et al.*, 2011).

Diaporthe

Host stress may also affect the transition from the endophytic to pathogenic phase. Hulke *et al.* (2019) found a correlation between increased disease incidence of Phomopsis stem blight of sunflowers and climate data over two decades. *Diaporthe citri* F.A. Wolf, J. Agric. also has been suggested to cause increased symptom expression in yuzu trees (*Citrus ichangensis* × *Citrus reticulata* var. *austera*) under adverse weather conditions (Kim *et al.*, 2015). However, investigations into the effects of stress on *Diaporthe* symptom expression are recent and limited, especially with grapevines.

ROLES OF BIOTIC STRESS FACTORS ON GTD SYMPTOM EXPRESSION

Though still limited, the number of studies investigating the roles that abiotic stress factors play in GTD symptom expression and disease progression is far greater than those investigating effects of biotic factors. Among the few studies available, two biotic factors have been identified: nematodes and other fungal pathogen interactions. In addition, few studies have primarily focused on the roles of biotic factors on GTD caused by *Ilyonectria* fungi.

Parasitic nematodes affecting Ilyonectria *symptom expression*

Plant parasitic nematodes have been shown to affect disease development and symptom expression across a range of pathosystems (Powelson and Rowe, 1993; LaMondia, 2003; Cao *et al.*, 2006), but data are scarce on their interactions with *Ilyonectria* spp. (Hastings and Bosher, 1938; Booth and Stover, 1974; Sutherland, 1977; Rahman and Punja, 2005).

While not involving *Ilyonectria*, bacterial canker of *Prunus* species fruit and nut trees provides an example of how nematodes can influence development and severity of a disease of woody perennials. Ring nematode infestation of roots has been shown to increase lesion length of bacterial canker in peach, caused by *Pseudomonas syringae* van Hall, (Cao *et al.*, 2005; Cao *et al.*, 2006). Ring nematode infestations lead to nitrogen deficiency in peach trees, which was suggested as the mechanism for nematodes increasing susceptibility to infection (Cao *et al.*, 2011). The effects of nitrogen deficiency on disease severity, measured by lesion length are mixed, however, with Cao *et al.* (2011) finding no association between host nitrogen levels and lesion length in peach, while in a separate study, Cao *et al.* (2013) showed that nitrogen fertilization led to significantly decreased lesion lengths in almond trees. The mechanisms for nitrogen fertilization effects were not determined, but it was suggested that the nitrogen may decrease nematode populations in the soil or by indirect effects such as increased host vigour.

Hastings and Bosher (1938) showed that growth of seedlings of several hosts was inhibited by a combined treatment of root lesion nematodes (*Pratylenchus pratensis)* (de Man) Filipjev and *I. destructans* to a greater extent than either pathogen or nematode alone. Rahman and Punja (2005) also found that development of root rot in ginseng was contingent on minor wounds, which could occur from nematode damage. This was also shown for root rot in clovers, where increased stress symptoms occurred when root systems were damaged (Barbetti *et al.*, 2007). Sutherland (1977) inoculated Douglas fir seedlings with dagger nematodes (*Xiphinema bakeri* Williams) and *I. destructans*, separately or in combination, and showed that while the nematode caused corky root symptoms on its own, the combined inoculation did not give a synergistic interaction.

In vineyards, several genera of plant parasitic nematodes are ubiquitous, including root-knot nematodes (*Meloidogyne* Goeldi), ring nematodes (*Mesocriconema xenoplax* Andrassy), root lesion nematodes (*Pratylenchus* Filipjev), and dagger nematodes (*Xiphinema* Cobb) (Storey *et al.*, 2017) (Figure 4). Recently research has begun to focus on nematode/pathogen relationships. Rahman *et al.*, (2014) assessed population densities of the ring nematode (*Mesocriconema xenoplax* (Raski) Loof & De Grisse) and the citrus nematode (*Tylenchulus semipenetrans* Cobb) under symptomatic and non-symptomatic vines infected with *Ilyonectria* spp. Nematode population densities did not differ between the symptomatic and asymptomatic vines. However, this study was conducted during a drought period, which is not considered conductive to the spread of *Ilyonectria* spp. or to the buildup of nematode populations, and was carried out with 'Ramsey' rootstock, which is resistant to ring nematodes. Similarly, co-infections of Black foot pathogens with other pathogenic fungi have also been associated with an increase in disease incidence and severity (Probst *et al.*, 2012).

Fungal pathogen interactions and infection thresholds

The interactions between *Ilyonectria* spp. and other fungal pathogens has been documented in apples. For apple replant disease (ARD), a combination of *I. macrodidyma* and *Pythium irregulare* Buisman reduced seedling growth when compared to single inoculations of each pathogen (Tewoldemedhin *et al.*, 2011). Braun (1991) also measured reductions in plant weight and size when apple trees were co-inoculated with *P. irregulare* and *Thelonectria lucida* (Höhn.) P. Chaverri & C. Salgado, which had previously been shown to be pathogenic to apple seedlings (Jaffee, 1982).

Research on effects of co-infections on expression of GTDs has recently increased. Young 'Chardonnay' grapevines infected with pathogens causing Botryosphaeria dieback and Black foot gave more severe decline compared to single pathogen inoculation, while 'Sauvignon Blanc' grafted onto '101-14' infected with Petri disease and Black foot pathogens also had increased disease incidence and severity than with single pathogen infections (Probst *et al.*, 2012; Whitelaw-Weckert *et al.*, 2013). This is important, because co-infections with Black foot and Botryosphaeria dieback pathogens, and especially with those causing Black foot and Petri disease, are common in nurseries and young vineyards (Halleen and Petrini, 2003; Halleen *et al.*, 2007a; Úrbez-Torres *et al.*, 2014a; 2014b).

Fungal interactions in infected grapevines probably affect disease development. Several Basidiomycetes, particularly *Fomitiporia* species, have been associated with Esca symptoms in old grapevines, and are commonly associated with *P. chlamydospora* and *Phaeoacremonium* spp. (Fischer, 2002; Fischer and Kassemeyer, 2003; White *et al.*, 2011; Cloete *et al.*, 2014;). Fischer and Kassemeyer (2003) isolated *F. mediterranea* M. Fisch., along with *P. chlamydospora* and *Phaeocremonium* spp. from symptomatic tissues. In addition to *F. mediterranea*, other species of *Hymenchaetales* Oberw, have been associated with Esca symptoms, including species in *Fomitiporella* Murrill, *Inocutis* Fiasson & Niemela, *Inonotus* P. Karst., and *Phellinus* Quél. (Cloete *et al.*, 2015a; Cloete *et al.*, 2015b). This has led to the hypothesis that some Basidiomycetes are involved in the development of Esca symptoms, but has yet to be confirmed (Gramaje *et al.*, 2018). Similar to *Ilyonectria* spp. co-infections with other GTD pathogens discussed above, the presence of Basidiomycetes may act as inciting factors in symptom expression. However, further research is required to demonstrate specific roles that Basidiomycetes play in Esca disease of grapevines.

While environmental and biotic triggering factors are likely to be important, threshold fungal concentrations within grapevines may also affect the switch from endophyte to pathogen. Inoculation of up to 10^4 conidia mL^{-1} suspensions of *N. luteum* increased lesion lengths, but greater inoculum concentrations decreased lesion lengths (Amponsah *et al.*, 2014). This contrasts with *B.*

dothidea, where spore concentrations up to 10^6 conidia mL^{-1} gave increasing lesion lengths in non-wounded peach bark (Pusey, 1989). Reduced lesion length may be due to competition in small inoculation sites, which was 3 mm diam. In this case, further research into effects of spore concentration on disease severity and grapevine mortality has been suggested (Amponsah *et al.*, 2014). Additionally, differences were observed in virulence among different isolates of individual species of *Botryosphaeriaceae* (Úrbez-Torres and Gubler, 2009). Secondary metabolites produced by different GTD fungi, such as Eutypines produced by *E. lata*, are known to be phytotoxic (Andolfi *et al.*, 2011). Other species producing secondary metabolites include *P. chlamydospora* and several *Botryosphaeriaceae* involved in Botryosphaeria dieback (Andolfi *et al.*, 2011). However, the roles these secondary metabolites play in symptom expression and differences in virulence, in particular among the other GTD fungi, are unclear. In addition, how secondary metabolites may respond in grapevines under either abiotic or biotic stress needs to be elucidated.

CLIMATE CHANGE AND VITICULTURE PRACTICES: IMPACTS ON ABIOTIC AND BIOTIC STRESS FACTORS AND GTD SYMPTOM EXPRESSION

The predicted effects of climate change vary from variations in average temperatures and precipitation, to extreme weather events such as flooding or droughts (Dixon, 2012; Ali, 2013). Several projections have predicted increasing global temperatures and variations in precipitation, as well as expressing concerns about these changes affecting global food security. Temperature increases associated with climate change are expected to increase occurrence of heat waves, agricultural droughts, and river floods, which will likely impact grape-growing regions (Arnell *et al.*, 2019). Environmental stress factors such as drought, temperature increases, and salinity are of concern for plant health, particularly relating to climate change (Ahuja *et al.*, 2010). Grapevines are sensitive to climate change, particularly temperature, which may put them at increased risk in major grape-growing regions such as the Mediterranean basin (Giorgi and Lionello, 2008; Biasi *et al.*, 2019). In addition to likely crop stress due to climate change, it is expected that these climate changes will lead to increased pathogen incidence in crops, due to improved survivability in milder winters, altering the geographic distribution of pathogens, and possible modifications in host resistance to pathogens and plant-pathogen relationships (Dixon, 2012). In particular, climate change may affect grapevines grown in optimal grape-growing regions such as California, where increasingly mild winters may prevent latent bud hardening and pests and pathogens reduced by cold winters may increase (Dixon, 2012). Similar effects have been observed for *Fusarium* infections in maize, where mild winters resulted in increased biomass of *Fusarium* in maize debris while frost-thaw cycles reduced biomass and reduced risks of infection (Lukas *et al.*, 2014). Extreme weather conditions such as drought may impact plant defenses, and increased temperatures may lead to plant stress in summers when temperatures peak. However, predictions on effects of climate change on plants are difficult to confirm, as experiments are typically carried out in controlled environments rather than in the field (Elad and Pertot, 2014).

Water deficit irrigation

Some viticulture practices employed to improve grape and wine quality may be stress factors with unintended consequences for GTD's. One example which requires further investigation is regulated deficit irrigation, which involves maintaining water deficits for particular seasonal development periods. For wine grapes, deficit irrigation is often employed from after fruit set until veraison, when normal irrigation recommences (Chaves *et al.*, 2010; Intrigliolo and Castel, 2010; Santesteban *et al.*, 2011). Deficit irrigation possibly increases grape and wine quality (Acevedo-Opazo *et al.*, 2010; Santesteban *et al.*, 2011), although there are conflicting reports on the effectiveness of regulated deficit irrigation for improved quality of grapes in all situations (Hepner *et al.*, 1985; Acevedo-Opazo *et al.*, 2010; Chaves *et al.*, 2010; Santesteban *et al.*, 2011; Lauer, 2012). Úrbez-Torres (personal communication) observed a difference in GTD incidence on mature 'Cabernet Sauvignon' vineyards grown for different wine quality in Chile. Vineyard blocks grown for premium quality wines at high elevation with poor soils and subjected to a severe water deficit irrigation to improve quality, showed a much greater incidence of Botryosphaeria dieback than other blocks cultivated for the production of bulk table wines grown in valleys on fertile soils and subjected to no water deficit irrigation. Although these observations require explanation, they are consistent with the hypothesis that water stress may enhance GTD development. In contrast, Sosnowski *et al.* (2016), studying 'Cabernet Sauvignon' in South Australia to assess effects of water stress on pruning wound susceptibility to *E. lata* and *D. seriata*, showed that water stress did not increased susceptibility to pruning wound infections. Their results indicated that drought and deficit irrigation practices were not likely to contribute to increased prevalence of GTD in vineyards. Regulated deficit irrigation for grapevines involves moderate water stress, but the effects of this stress on GTD symptom expression and disease development are unclear. These should be further investigated as a potential grapevine health concern for plants that may contain asymptomatic infections (Santesteban *et al.*, 2011; Tarara and Perez Peña, 2015).

Vine pruning and training practices

Travadon *et al.,* (2016), in a study in France assessed incidence of Esca on 'Syrah' 'Mourvèdre' vines grafted onto '140Ru' rootstocks, to assess effects of minimal pruning and spur pruning on a bilateral cordon system. Both cultivars displayed more symptomatic vines when spur pruned than those that had minimal pruning. Mean necrosis was likewise greater (35%) for spur pruned vines than those receiving minimal pruning (21%). Similar results were obtained in California, United States of America, in 'Cabernet Sauvignon' responses to Eutypa dieback symptoms, with minimal pruning in the summer producing less dieback than the pruning of dormant vines or using the Sylvoz system (Gu *et al.*, 2015). Lecomte *et al.* (2012) observed that vineyards with the Lyra training system had foliar symptoms in 56% of grapevines, but also had a low proportion of trunks affected. This indicated that the long cordons of the Lyra training system may have been one of the causes. In a follow-up study in France, it was confirmed that different training practices affected Esca foliar symptom severity. Grapevines with short cordons had more severe symptoms than grapevines with long cordons. In addition, plants which were pruned less had less severe symptoms than those that were heavily pruned (Lecomte *et al.*, 2018). These surveys only recorded foliar symptoms, but the results were similar to those of Travadon *et al.* (2016), who recorded decreased necrosis in minimally pruned grapevines. While these results are promising, further research is required for other GTD fungi, particularly for those causing Black foot, Botryosphaeria dieback, and Phomopsis. Furthermore, the effects of pruning and training practices require further investigation to determine if and/or how they influence wood necrosis. In addition, grapevines under different pruning regimes and training systems may respond differently to stress conditions, and thus may develop GTD symptoms differently. No studies have been reported on this subject, but these would likely provide greater understanding of these interactions, which would improve management of GTD under different pruning and training systems.

Endophytes as potential reducers of host stress

Endophytes may increase plant tolerance to abiotic and biotic stresses associated with climate change (Chakraborty and Newton, 2011). Endophytes possibly contribute several beneficial attributes to their hosts, including enhanced water use efficiency leading to improved survival during drought, increased nutrient uptake and recycling, reduced stress associated with temperature increases or decreases, and increased tolerance to soil salinity, alkalinity, and heavy metals (Lata *et al.*, 2018). In two varieties of rice plants not well adapted to high soil salinity or drought, class 2 fungal endophytes enhanced host water use efficiency, and increased growth rates, reproductive yield, and biomass under drought and high salinity in greenhouse experiments. Class 2 endophytes conferred cold tolerance to rice plants subjected to temperatures ranging from 5°C to 20°C, in a plant growth chamber (Redman *et al.*, 2011). Similarly, fungal endophytes increased grain yields and second-generation seed viability in wheat subject to drought and increased temperature (Hubbard *et al.*, 2014).

The use of *Pythium oligandrum* Drechsler is another example of reduction of disease progression caused by *P. chlamydospora.* In a 4-month greenhouse assay with 'Cabernet Sauvignon' canes infected with *P. chlamydospora,* colonization of roots by *P. oligandrum* resulted in up to 50% reduction of necrosis, compared to grapevines infected with *P. chlamydospora* without *P. oligandrum* (Yacoub, *et al.,* 2016). In addition, in 'Cabernet Sauvignon', expression of several genes associated with *P. chlamydospora* infection was greater in vines with *P. oligandrum* colonization of the roots than in vines without *P. oligandrum*, suggesting that *P. oligandrum* induced resistance in grapevines. In addition, *P. oligandrum* may also reduce biotic stress by the way of fungus-produced tryptamine, an auxin compound involved in plant growth (Floch *et al.,* 2003; Benhamou *et al.*, 2012). Further studies, in particular in other grapevine cultivars and during prolonged intervals are required to determine the efficacy of *P. oligandrum* as a potential biocontrol agent. Promotion of plant growth may aid reduction in the effects of abiotic and biotic plant stress, but this requires further confirmation to determine what, effects this endophyte may have on grapevines infected with GTDs.

In grapevines, *Pseudomonas fluorescens* Migula promoted high salinity tolerance via production of endogenous melatonin in host roots, and promoted plant growth (Ma *et al.*, 2016). Bacterial and fungal endophytes have been associated with grapevine tolerance to drought, high salinity, heavy metals, and high and low temperatures (Pacifico *et al*., 2019). These factors include associated biotic tolerance to some GTD pathogens such as *P. chlamydospora,* and *N. parvum*. The use of endophytes to reduce environmental stress should be further investigated in relation to GTD disease development, to determine the roles that bacterial and fungal endophytes may have.

Arbuscular mycorrhizal fungi as potential stress reducers

While not endophytes by definition, arbuscular mycorrhizal (AM) fungi (*Glomeromycota* Walker & A. Schüßler) colonize roots, and these organisms can reduce stress associated with high and low temperatures, as well as water stress, soil compaction, and salinity (Ellis *et al*., 1985; Charest *et al*., 1993; Harrier and Watson, 2003; Lu *et al*., 2007; Zhu *et al*., 2010). Suggested mechanisms for increased tolerance include improved plant nutrition, compensation for damaged roots, competition for infection sites, alterations in root anatomy or morphology, alterations in the mycorrhizosphere, and activation of plant defenses (Azcón-Aguilar and Barea, 1997).

In addition to increased environmental stress tolerance, some evidence suggests that AM fungi increase tolerance to pathogens, in particular root pathogens, although the mechanisms are as yet unclear (Whipps, 2004; Comby *et al*., 2017). AM fungi may also affect tolerance to airborne pathogens, and plants have been reported to have increased resistance to hemibiotrophic and necrotrophic fungal infection, although results have been varied and some have reported increased susceptibility to these pathogens (Comby *et al*., 2017). In grapevines, AM fungi were shown to increase root and shoot biomass in '110R' rootstocks infected with *Armillaria mellea* (Vahl) P. Kumm., compared to plants without AM fungi (Nogales *et al*., 2009).

In greenhouse studies, AM fungi have been shown to influence disease severity in hosts infected by GTD pathogens. Petit and Gubler (2006) inoculated *Vitis rupestris* Scheele with the AM fungus *Rhizophagus irregularis* (Błaszk., Wubet, Renker & Buscot) C. Walker & A. Schüßler and *I. macrodidyma*, a causal agent of Black foot, in a controlled greenhouse environment. While *I. macrodidyma* was recovered from both AM fungus-inoculated roots and the non-inoculated roots, grapevines inoculated with *R. irregularis* displayed decreased disease severity. Also, apple trees with roots inoculated with AM fungi had decreased symptom expression and increased survival when infected with *N. ribis* compared to experimental controls (Krishna *et al*., 2010).

However, research into the effects of AM fungi on disease severity has given mixed responses, and, in some cases, these fungi have been shown to be detrimental to the plant health. In 'Riparia gloire' rootstocks infected with *I. liriodendri*, colonization by *R. irregularis* increased abundance of the pathogen in the roots, and had no effect on plant growth (Holland *et al*., 2019). Likewise, in '101-14' rootstocks planted in soil inoculated with *I. liriodendri,* a positive linear relationship was demonstrated between AM fungus colonization of roots and proportions of necrosis was found (Vukicevich *et al*., 2018). These results indicate that the use of commercial AM fungi inoculants for *Vitis vinifera* should be further investigated to determine the impacts of these fungi on GTD development.

The use of AM fungi to reduce plant stress is a potential avenue of research, and should be considered for its potential to increase environmental stress and disease tolerances, and the mechanisms of these tolerances should be further investigated. This should particularly be in relation to the potential environmental stress and symptom expression relationships for many GTDs. Field studies are required to determine effects of AM fungi on health of GTD-infected grapevines in field conditions. Field inoculations with commercial AM fungi has also given inconsistent response, and inoculum may spread beyond the intended fields. Further research should therefore be conducted on the use of regionally-based AM fungi inoculants (Farmer *et al*., 2007; Kokkoris *et al*., 2019). This is of particular importance for *Vitis*, as AM fungal communities differ between grapevine rows and inter-row plants. This indicates that grapevines may select for particular AM fungal communities (Holland *et al*., 2014). Increasing the diversity of cover crops may increase the diversity of AM fungal communities, allowing greater chances of grapevine root colonization, and also reduce soil-borne pathogen populations (Holland *et al*., 2014; Vukicevich *et al*., 2016).

CONCLUSIONS AND FUTURE DIRECTIONS

Limited research has been conducted on endophytes in economically important crops, particularly on their roles as latent pathogens. This is an increasing area of interest particularly in grapevines, where many GTD fungi have been suggested to have endophytic phases. Many of the hypotheses addressing transition from the endophytic to the pathogenic phases remain to be tested, in particular, the threshold model developed by Sieber (2007).

GTD as latent pathogens

The roles of *Botryosphaeriaceae* as potential latent pathogens has been well-documented particularly in forest trees. However, research has just begun in grapevines. Several *Botryosphaeriaceae* have been discovered in the asymptomatic and symptomatic grapevine wood. Effects of abiotic and biotic stress factors on disease development are still largely unknown, and research has only recently begun on the effect of pathogen quantities on symptom expression.

Likewise, the role of *Ilyonectria* spp. has been examined for a number of hosts, with several factors influencing symptom expression. Research on *Ilyonectria* spp. in grapevines is limited, however, with the most studies conducted in nurseries and young vineyards where these pathogens are mostly found. Biotic factors affecting nematode infection of the roots and co-infections of GTD fungi are likely to be important and productive areas of research. Petri disease pathogens in grapevine nurseries and young vineyards have been associated with stress factors in young grapevines, while Esca has been associated with biotic factors including Basidiomycete co-infections. Several abiotic factors have been associated with Petri disease and Esca. Eutypa dieback has received more research attention than other GTDs, but knowledge is limited and associations between symptom expression and climatic factors have only recently been assessed. Phomopsis dieback as a GTD is a new area of research, and most investigations of this disease have been in other hosts. Several species of *Diaporthe* have been suggested as latent pathogens, and their discovery in asymptomatic and symptomatic grapevines indicates that they are also latent pathogens in grapevines.

Latent pathogens in young vineyards

The roles of latent pathogens, particularly those causing Black foot and Petri disease in mother blocks, nurseries and young vineyards, are of particular importance. Many of these pathogens are widespread, and conditions during nursery propagation processes are optimal for the latent transmission of these fungi. Young grapevines may also be more susceptible to disease development and less able to recover, compared with mature grapevines which display symptoms erratically. Further study of the stress factors which may induce disease development is required to determine the nature of these pathogens, and indicate potential treatment options, including best planting conditions to avoid stress and the potential transition from endophytic to pathogenic phases by these fungi. Further study is required of abiotic stress, particularly in nurseries. Research on biotic stress, particularly from pathogenic nematodes and fungal interactions will also be worthwhile. Recently, work has begun on fungal interactions in GTDs, with grapevine initially infected with *D. seriata* followed by infection by one of *N. parvum*, or *P. chlamydospora*. Initial results have shown reduced lesion lengths and changes in host physiology (Wallis *et al*., 2019). These indicate an urgent need for further research, particularly focusing on fungal interactions involving Black foot and Petri disease pathogens in young grapevines.

Methods for host stress reduction

Reducing stress on grapevines is an important first step, but not all stress in the field can be controlled. Therefore, bacterial and fungal endophytes and AM fungi known to enhance resistance of plants to some stress factors are likely to be productive research candidates. However, the effects of AM fungi on disease development are variable, and regional-based approaches to AM fungi are recommended for further study. Rootstock and scion variety is also likely to be a productive area of study, and research is required to show how resistance of rootstocks to abiotic and biotic stress factors affect GTD development in grapevines.

While GTD fungi potentially acting as latent pathogens has long been the subject of speculation, recent discoveries aided by molecular biology research tools have led to the resurrection of this hypothesis. Study on latent pathogens has recently commenced, and requires urgent focus given the growing impacts of GTDs in most grape production areas. Endophytic phases may lead to uncontrolled spread of potential pathogens throughout nurseries and vineyards, and may cause harm within young vineyards before grape growers can recoup capital investments in new plantings, or may shorten the economic lives of vineyards. Effects of climate change along with specific viticulture practices may further increase the incidence and severity of GTDs, causing increased economic losses. Understanding the effects of these stress factors and development of methods to minimize stress on grapevines in relation to GTD disease development, are crucial first steps to reducing the effects of future climate change, and increasing the economic lifespan of vineyards containing asymptomatically infected grapevines.

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