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REVIEW

The status of Botryosphaeriaceae species infecting grapevines

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Summary. Species in the Botryosphaeriaceae have a cosmopolitan distribution, and occur on a wide range of annual and perennial hosts including grapevines. To date, morphological and taxonomic studies, as well as analyses of nucleotide sequences of multiple genes, have allowed the identification of at least 21 different species in the Botryosphaeriaceae occurring in grapevines worldwide. Grapevine disease symptoms caused by members of this family include leaf spots, fruit rots, shoot dieback, bud necrosis, vascular discoloration of the wood, and perennial cankers, and their current status as pathogens is reviewed. Additionally, the disease name Botryosphaeria dieback is proposed here to describe the different grapevine trunk disease symptoms caused by species of Botryosphaeriaceae. Much has been written during the last decade about the association between species in the Botryosphaeriaceae and grapevine trunk diseases, which has contributed to a better understanding of the role that these fungal taxa play in grapevine diseases. Although virulence has been shown to vary between species and isolates of the same species in different countries, these fungi have become well-recognized as important grapevine pathogens worldwide. Latest and novel findings from studies conducted in different countries, on disease etiology and species distribution, epidemiology and biology are discussed. Much progress has been achieved in the development and implementation of novel diagnostic and detection techniques.Vineyard sanitation techniques, as well as chemical, biological, and cultural control strategies available at the present time to reduce the infection caused by botryosphaeriaceous fungi, are presented in this review.

Key words: black dead arm, black rot, Botryosphaeria canker, Botryosphaeria dieback, excoriose, Macrophoma rot.

Introduction

Species in the Botryosphaeriaceae Theiss. & P. Syd. 1918 occur in most parts of the world under various ecological niches, and are found as endophytes, parasites and saprophytes on a vast number of both annual and perennial plants (Barr, 1972; Punithalingam, 1980; von Arx, 1987; Slippers and Wingfield, 2007). Several species of this family are significant plant pathogens causing leaf spots, fruit rots, dieback, perennial cankers, and eventual death in economically important woody perennial crops and ornamental plants as well as both in native and introduced forest tree species (Farr and Rossman, 2011). Additionally, some species in the Botryosphaeriaceae have been recognized as opportunistic human pathogens causing subcutaneous, ocular and/or internal organ infections (Rebell and Forster, 1976; Maslen *et al*., 1996; Summerbell *et al*., 2004; Tan *et al*., 2008; Woo *et al*., 2008).

Although it is currently well-accepted that *Botryosphaeria* Cesari & De Notaris. is a member of the Botryosphaeriales in the family Botryosphaeriaceae (Hawksworth *et al*., 1995; Crous *et al*., 2006; Cannon and Kirk, 2007), the taxonomic his-

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tory of *Botryosphaeria* is complex, and the genus has been subjected to numerous taxonomic rearrangements in the systematic position of both the family and the genera included (Denman *et al*., 2000). Since the introduction of *Botryosphaeria* for nine species, over 250 different *Botryosphaeria* spp. have now been recorded including varieties and *formae specialies* (Robert *et al*., 2005). Although many of these species have been either transferred to other genera or considered synonyms over the years, there were still 143 different species comprised in the genus *Botryosphaeria* by 2000 (Denman *et al*., 2000). However, species identification in *Botryosphaeria* has been complicated due to the lack of sufficient diversity among teleomorph features of species within this genus. Additionally, the difficulty of finding teleomorphs in nature or obtaining them under laboratory conditions, has forced the identification of these fungi to be primarily based on anamorphic characters (Jacobs and Rehner, 1998; Denman *et al*., 2000; Phillips, 2002). Consequently, many different anamorph genera have been linked to *Botryosphaeria*. However, because anamorph genera of *Botryosphaeria* were not well-defined when first described, different species names were given to similar fungi adding more controversy to the genus (Crous and Palm, 1999; Phillips, 2002). Therefore, species differentiation based only on anamorphic characters has not been simplified due to the fact that different species within the same genera often have overlapping morphological features (Slippers *et al*., 2004; Pavlic *et al*., 2009). As a consequence, characterization of *Botryosphaeria* to species level has not always been accurate, which has, for many years, raised even more confusion regarding their association and pathogenicity on many hosts, including grapevines. Revising the taxonomy of *Botryosphaeria* and its current status is beyond the scope of this review and thus, it will not be addressed here. More detailed overviews on the taxonomic history of *Botryosphaeria* have been published by Crous and Palm (1999), Denman *et al*. (2000), Phillips (2000a), Phillips (2002), Crous *et al*. (2006), and Phillips *et al*. (2008).

During the late 1990s and early 2000s, the implementation of DNA-based identification techniques and phylogenetic analyses of nucleotide sequences helped to resolve some of the taxonomic conflicts previously existing in *Botryosphaeria* (Jacobs and Rehner, 1998; Denman *et al*., 2000; Smith and Stanosz, 2001; Zhou and Stanosz, 2001). As consequence of some of these studies, *Botryosphaeria* was suggested to be monophyletic and the different taxa identified within this teleomorphic genus were placed under the well-differentiated anamorphic genera *Fusicoccum* Corda (hyaline and thin-walled conidia) or *Diplodia* Fr. (pigmented and thick-walled conidia). However, these studies could not resolve the taxonomic status of *Lasiodiplodia* Ellis & Everh., another anamorphic genus with grapevine pathogens described, and suggested that it should be included as a synonym of *Diplodia* (Denman *et al*., 2000). An additional problem arising from these studies was that the accepted classification was in discordance with the logical state that only a single anamorph genus can be associated with a single teleomorph genus (Seifert *et al*., 2000). This debate continued until 2006, when a phylogenetic study based on 28S rDNA sequences showed *Botryosphaeria* to be polyphyletic comprising several phylogenetic lineages (Crous *et al*., 2006). Since then, *Botryosphaeria* was restricted to species with *Fusicoccum* anamorphs, which currently include *Botryosphaeria dothidea* (Mough. :Fr.) Ces. & De Not (anamorph: *Fusicoccum aesculi* Corda), *Botryosphaeria corticis* (Demaree & M.S. Wilcox) Arx & E. Müll. (anamorph: *Fusicoccum* sp.), *Fusicoccum ramosum* (Pavlic, Burgess, M.J. Wingfield), and *Fusicoccum atrovirens* (J.W.M. Mehl & B. Slippers). However, the study could not fully resolve the status of the *Diplodia*/*Lasiodiplodia* group. Two years later, Phillips *et al*. (2008) partially solved the *Diplodia*/*Lasiodiplodia* conflict based on a multigene phylogenetic analysis, which introduced four genera into this group revising the taxonomic status of numerous dematiaceous Botryosphaeriaceae, including some that infect grapevines. As a consequence of this and other studies (Pavlic *et al*., 2004; Abdollahzadeh *et al*., 2010), it is currently well-accepted that *Lasiodiplodia* is a distinct lineage in the Botryosphaeriaceae. Based on these recent findings and until completion of novel taxonomic studies in Botryosphaeriaceae, the nomenclature proposed by both Crous *et al*. (2006) and Phillips *et al*. (2008) should be followed in order to avoid adding more confusion within this family. There-

fore, this review has adopted to use the existing anamorph generic names for many of the taxa to refer to species in the Botryosphaeriaceae infecting grapevines.

Among all agricultural commodities affected by Botryosphaeriaceae, grapevines are currently of significant relevance. Grapevine disease symptoms caused by botryosphaeriaceous fungi include leaf spots, fruit rots, shoot dieback, bud necrosis, vascular discoloration of the wood, and perennial cankers. Whereas grapevine fruit rot symptoms caused by species in the Botryosphaeriaceae have been known and studied over the years (Clayton, 1975; Ferrin and Ramsdell, 1977; Milholland, 1991; Kummuang *et al*., 1996; Wilcox, 2003), the status of Botryosphaeriaceae species as grapevine trunk disease pathogens has remained overlooked until recently. The reasons for this omission may be due to the fact that species in the Botryosphaeriaceae have been largely considered saprophytes, secondary colonizers or weak pathogens in grapevine wood (Phillips, 2002). In addition, vascular and foliar symptoms caused by Botryosphaeriaceae in grapevines have probably been unnoticed due to the difficulty to differentiate them from those caused by other grapevine trunk disease pathogens such as *Eutypa lata* (Pers. : Fr.) Tul. & C. Tul. (Leavitt, 1990), *Phomopsis viticola* Sacc. (Phillips, 1998; Castillo-Pando *et al*., 2001), *Phaeomoniella chlamydospora* Crous & W. Gams and *Phaeoacremonium aleophilum* W. Gams, Crous, M.J. Wingfield & L. Mugnai (Phillips, 2002; Surico *et al*., 2006). Moreover, grapevine trunk diseases such as Eutypa dieback and esca have been the main and sometimes the only focus of study for most researchers throughout the past century, which has not helped to exactly clarify the role that Botryosphaeriaceae played on grapevine diseases.

Although previous studies showed the presence of the conidial states of some Botryosphaeriaceae species on *Vitis* spp. (Stevens, 1926; Luttrel, 1948; Shoemaker, 1964), it was not until 1964 that Chamberlain *et al*. (1964) reported *Diplodia mutila* (Fr.) Mont. (as *Sphaeropsis malorum* Berk.) to be isolated in about equal proportions, either alone or together with *P. viticola* from lesions on trunks and stubs. Additionally, the same study confirmed that spores of *D. mutila* could infect freshly cut grapevine stubs and be reisolated from the resulting lesions, for what can be considered the first evidence of a Botryosphaeriaceae species as a grapevine trunk pathogen. Several studies on Botryosphaeriaceae infecting grapevine wood followed from 1970 to 2000. El-Goorani and El Meleigi (1972) showed that *Lasiodiplodia theobromae* (Pat.) Griff. & Maubl. (as *Botryodiplodia theobromae* Pat.) was the causal agent of grapevine dieback in Egypt. Two years later, Lehoczky (1974a, 1974b) associated *D. mutila* with a grapevine dieback which he called black dead arm, observed both in mature vines in the field and nursery grafts. Cristinzio (1978) reported for the first time the association of *Diplodia seriata* De Not. (as "*Botryosphaeria*" *obtusa* Schwein. Shoemaker) with grapevine dieback in Italy. In the 1980s, *B. dothidea*, *D. mutila* and *L. theobromae* were shown to cause grapevine cankers and dieback in Chile (Latorre *et al*., 1986), Italy (Rovesti and Montermini, 1987) and California (Leavitt, 1990), respectively. In the following decade, Filho *et al*. (1995) associated *B. dothidea* with trunk canker of grapevines in Brazil. A few years later, Phillips (1998) isolated *B. dothidea*, *D. mutila* and *D. seriata* from grapevines showing symptoms of excoriose and dieback in Portugal. During the same period, Larignon and Dubos (1997) reported *D. seriata* from grapevines showing characteristic symptoms of esca in France, while Pascoe (1998) confirmed the presence of *L. theobromae*, *D. seriata* and *D. mutila* from wedge-shaped wood symptoms in Australia, in which *E. lata* was not present. Based on these studies, it was apparent that species of Botryosphaeriaceae were gaining importance as grapevine pathogens. Nevertheless, it has not been until the last decade when research conducted in different countries has finally recognized the status of these fungi as significant grapevine trunk disease pathogens (Phillips, 2002; van Niekerk *et al*., 2004; Taylor *et al*., 2005; van Niekerk *et al*., 2006; Úrbez-Torres *et al*., 2008; Úrbez-Torres and Gubler, 2009a; Pitt *et al*., 2010).

The epidemiology of *Guignardia bidwellii* (Ellis) Viala & Ravaz and *B. dothidea*, Botryosphaeriaceae species responsible for causing the grape fruit rot diseases black rot and Macrophoma rot, respectively, has been widely studied over the years (Ferrin and Ramsdell, 1977; 1978; Clayton, 1975; Spotts, 1977, 1980; Milholland,

1991; Becker and Pearson, 1996; Kummuang *et al*., 1996; Jermini and Gessler, 1996; Hoffman *et al*., 2002). This has allowed both development and implementation of effective disease management strategies (Clayton 1975; Milholland 1991; Wilcox, 2003; Bordelon *et al*., 2011; Sutton and Burrack, 2011; Wilcox, 2011; Cline and Burrack, 2011). In the same way, many studies have been reported on Botryosphaeriaceae species causing fruit rot, dieback and cankers on perennial woody crops such as apple, peach and pistachio (Holmes and Rich 1970; Sutton, 1981; Brown and Britton, 1986; Arauz and Sutton, 1989; Pusey, 1989a,1989b; Sutton and Arauz, 1991; Michailides, 1991; Pusey and Bertrand, 1993; Ahimera *et al*., 2004; Copes and Hendrix, 2004). On the other hand, and probably as a consequence of the delay in recognizing species of Botryosphaeriaceae as important grapevine pathogens, there has been a lack of information on the epidemiology of these fungal taxa associated with grapevine trunk diseases. Early studies suggested that species of Botryosphaeriaceae overwinter as pycnidia and/or perithecia on diseased woody parts of vines, and the spores are probably discharged under wet and humid conditions. Infection of grapevines is either through natural openings, or mainly through pruning wounds (Chamberlain *et al*. 1964; Hewitt 1988; Lehoczky, 1988; Leavitt 1990), or through the graft unions between rootstocks and scions (Lehoczky, 1974b). However, only recently have studies been focusing on the epidemiology and biology of Botryosphaeriaceae spp. associated with grapevine trunk diseases been conducted to elucidate some of those hypotheses (van Niekerk *et al*., 2007; Serra *et al*., 2008; Amponsah *et al*., 2009a; Kuntzmann *et al*., 2009; Úrbez-Torres *et al*., 2010a; Úrbez-Torres *et al*., 2010d; van Niekerk *et al*., 2010a; Úrbez-Torres and Gubler, 2011).

The lack of knowledge regarding the importance of botryosphaeriaceous taxa as grapevine trunk disease pathogens, along with the lack of epidemiological studies, has limited the development and implementation of successful control methods. No chemical control has ever been specifically available to treat Botryosphaeriaceae infected vines. In France sodium arsenite was registered to effectively control other grapevine trunk diseases, in particular esca diseased vines but some authors suggested it may have some side effects on diseases caused by botryosphaeriaceous fungi (Larignon and Dubos, 2001). However, sodium arsenite was removed from the market in 2001 due to both environmental and public health concerns (Decoin, 2001), leaving the wine industry with remedial surgery as one of the only management strategies to combat grapevine trunk diseases (Creaser and Wicks, 2004; Sosnowski *et al*., 2010b). Consequently, the evaluation of novel active ingredients as well as of cultural practices that effectively could be used to reduce infection caused by grapevine trunk disease pathogens has been the main priority for industry and researchers during the last decade.

To date, 21 species in the Botryosphaeriaceae, in the anamorphic genera *Diplodia*, *Dothiorella* Sacc., *Fusicoccum*, *Guignardia* Viala & Ravaz, *Lasiodiplodia*, *Neofusicoccum* Crous, Slippers & A.J.L. Phillips, and *Phaeobotryosphaeria* Speg. have been recognized to be pathogenic on grapes (Table 1). The purpose of this review is to update the status of the different grapevine diseases caused by Botryosphaeriaceae species, as well as to compile the research results published during the last decade on the distribution, diagnosis, pathogenicity, epidemiology, biology, and control of Botryosphaeriaceae species infecting grapevines.

Grapevine diseases attributed to Botryosphaeriaceae species: fruit rot diseases

Black rot

Black rot does not affect the framework of vines (spur positions, cordons and trunk), but it can cause up to 100% fruit losses in regions with warm and humid climates (Ferrin and Ramsdell, 1977). Although all young green vine tissues (young leaves, petioles, shoots, tendrils, pedicels, and peduncles) are susceptible to infection throughout the growing season, infection of the fruit is a major concern among growers. Leaves are highly susceptible to the disease when they emerge becoming more resistant as they fully expand (Wilcox, 2003). Infection on the leaves appear as small circular lesions of a light-brown color in the center which are bordered by dark

Table 1. Species of Botryosphaeriaceae currently known to infect grapevines.

Botryosphaeriaceae species and authority	Culture	Anamorph - Teleomorph connection[a]	Hosts No.[b]	Reference
Botryosphaeria dothidea (Moug. ex Fr.) Ces. & De Not.	CMW8000[ee]	*Fusicoccum aesculi*	338	Cesati and De Notaris, 1863; Slippers *et al*., 2004b
Diplodia corticola A.J.L. Phillips, A. Alves & J. Luque	CBS 112549	"*Botryosphaeria*" *corticola*	8	Alves *et al*., 2004
Diplodia mutila (Fr.) Mont.	CBS 112553[ee]	"*Botryosphaeria*" *stevensii*	26	Montagne, 1834; Shoemaker, 1964; Alves *et al*., 2004
Diplodia seriata De Not.	CBS 112555[ee]	"*Botryosphaeria*" *obtusa*	59	De Notaris, 1845; Phillips *et al*., 2007
Dothiorella iberica A.J.L. Phillips, J. Luque & A. Alves	CBS 115035[et]	"*Botryosphaeria*" *iberica*	5	Phillips *et al*., 2005
Dothiorella americana J.R. Úrbez-Torres, F. Peduto & W.D. Gubler	CBS128309[et]	Unknown	2	Úrbez-Torres *et al*., 2011
Guignardia bidwellii (Ellis) Viala & Ravaz	IMI 207141[et]	Unknown	19	Viala and Ravaz, 1892
Lasiodiplodia crassispora T.I. Burgess & Barber	CBS11874[et]	Unknown	6	Burguess *et al*., 2006
Lasiodiplodia missouriana J.R. Úrbez-Torres, F. Peduto & W.D. Gubler	CBS128311[et]	Unknown	2	Úrbez-Torres *et al*., 2011
Lasiodiplodia theobromae (Pat.) Griff. & Maubl.	K(M)118158[h]	"*Botryosphaeria*" *rhodina*	442	Griffon and Maublanc, 1909; Punithalingam, 1976
Lasiodiplodia viticola J.R. Úrbez-Torres, F. Peduto & W.D. Gubler	CBS128313[et]	Unknown	2	Úrbez-Torres *et al*., 2011
Neofusicoccum australe (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips	CMW6838[et]	"*Botryosphaeria*" *australe*	30	Slippers *et al*., 2004b; Crous *et al*., 2006
Neofusicoccum luteum (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips	CBS 110299[et]	"*Botryosphaeria*" *lutea*	16	Pennycook and Samuels, 1985; Phillips *et al*., 2002; Crous *et al*., 2006
Neofusicoccum macroclavatum (T.I. Burgess, Barber & Hardy) T.I. Burgess, Barber & Hardy	CBS 118223[et]	Unknown	3	Burguess *et al*., 2005; Crous *et al*., 2006
Neofusicoccum mediterraneum Crous, M.J. Wingf. & A.J.L. Phillips	CBS 121718[et]	Unknown	13	Crous *et al*., 2007
Neofusicoccum parvum (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips	CMW9081[et]	"*Botryosphaeria*" *parva*	34	Pennycook and Samuels, 1985; Crous *et al*., 2006
Neofusicoccum ribis (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips	CMW7772[et]	Unknown	242	Slippers *et al*., 2004; Crous *et al*., 2006
Neofusicoccum viticlavatum (Van Niekerk & Crous) Crous, Slippers & A.J.L. Phillips	CBS 112878[et]	Unknown	1	Van Niekerk *et al*., 2004; Crous *et al*., 2006
Neofusicoccum vitifusiforme (Van Niekerk & Crous) Crous, Slippers & A.J.L. Phillips	CBS 110887[et]	Unknown	1	Van Niekerk *et al*., 2004; Crous *et al*., 2006
Phaeobotryosphaeria porosa (Van Niekerk & Crous) Crous & A.J.L. Phillips	CBS 110496[et]	Unknown	1	Van Niekerk *et al*., 2004; Phillips *et al*., 2008
Spencermartinsia viticola (A.J.L. Phillips & J. Luque) A.J.L. Phillips, A. Alves & Crous	CBS 117009[et]	*Dothiorella viticola*	4	Luque *et al*., 2005; Phillips *et al*., 2008

[a] Robert *et al*., 2005.
[b] Number of different plant hosts, including *Vitis* spp., described for each Botryosphaeriaceae species Retrieved from Farr and Rossman, July 2011: http://nt.ars-grin.gov/fungaldatabases/fungushost/fungushost.cfm Acronyms of cultures collections: CMW: Culture Collection Forestry and Agricultural Biotechnology Institute, University of Pretoria, South Africa; WAC: Department of Agriculture Western Australia, Plant Pathogen Collection; CBS: Centraalbureau Schimmelcultures, Utrecht, Netherlands; IMI: CABI Filamentous Fungi Database (Formerly IMI), Egham, United Kingdom.
[ee] Ex-epitype
[et] Ex-type
[h] Holotype

brown bands (Figure 1a). Pycnidia develop within a few days in the center of the lesions and appear as minuscule black spheres (Figure 1b). Petioles show black elongated lesions that can eventually girdle these organs causing wilt and death of the affected leaves. Shoot infections appear as black cankers which may vary in length and cause wilt and/or eventual death of these organs by both breakage and/or girdling. Pycnidia can also be observed on the surfaces of these lesions (Ramsdell and Milholland, 1988; Wilcox, 2003). Infections of the fruit have been suggested to start developing either from lenticels or from existing lesions on the pedicels, and first appear light in color gradually becoming dark brown (Figure 1c). Berries eventually shrivel becoming black raisin-like masses known as "mummies", which are covered with pycnidia of the fungus (Figure 1d) (Ramsdell and Milholland, 1988; Wilcox, 2003).

Black rot is caused by *Guignardia bidwellii* and was the first grapevine disease attributed to a botryosphaeriaceous fungus. Although symptoms of black rot were probably observed in earlier years, an accurate description of the disease was first given by Scribner and Viala (1888). Black rot was described for the first time in eastern Unites States where it is considered an important disease of grapevines. However, it also causes significant economic losses in grape-growing areas of Asia, Europe and South America (Jermini and Gessler, 1996; Wilcox, 2003). The disease is particularly severe in all *Vitis vinifera* L. cultivars, whereas native American *Vitis* spp. and interspecific hybrids show a wide variation in susceptibility (Jeffry *et al*., 1985; Martin, 2010). A distinct race of the fungus, *G. bidwellii* (Ellis) Viala & Ravaz f. *muscadinii* Luttrell, is responsible for causing disease on Muscadine grapes (*Vitis rotundifolia* Michx.). Black rot on Muscadine grapes is considered to be of little importance with regard to yield losses but it can significantly affect fruit quality (Kummuang *et al*., 1996).

Macrophoma rot

Although Macrophoma rot can be observed in cultivars of both *V. vinifera* and *V. labrusca*, it is a much more important disease of muscadine grapes (*V. rotundifolia*) (Milholland, 1988). Muscadine grapes are native to the southeastern USA where they have been cultivated for over 400 years (Olien, 1990). Although muscadine grape production has not reached its full economic potential for wine, there is significant interest in cultivating this grape for use in functional foods or nutraceuticals due to its high antioxidant and polyphenolic content (Olien, 1990; Pastrana-Bonilla *et al*., 2003). Macrophoma rot symptoms appear when berries reach full size and increase in prevalence as they ripen. At first, lesions appear as one or more dark circular spots with a tan color in the centre and may be associated with rachis blight. Lesions are flat or slightly sunken and can vary from 1 to 4 mm in diameter (Figure 1e). Pycnidia can be observed embedded in the center of each lesion. As the disease progresses, a brown soft rot covers the berries spreading throughout the whole cluster (Figure 1f). Consequently, infected berries shrivel and drop off the pedicels. Over time, abundant pycnidia can be observed on the surface of the dry berries on the vineyard floor (Clayton, 1975; Milholland, 1991).

Macrophoma rot is caused by *B. dothidea*, and although this fungus has been reported to be present in most grape-growing regions throughout the world, the disease appears to be restricted to muscadine vineyards in the southeastern USA where it can cause up to 30% losses of ripening berries (Milholland, 1991). To date, *B. dothidea* is the only species associated with Macrophoma rot. However, this species name has been used throughout the past century in a broad sense not taking into account that it was indeed a complex of species (Phillips, 2002; Slippers *et al*., 2004). Therefore, it would be reasonable to speculate that species in the Botryosphaeriaceae other than *B. dothidea* may also be involved in causing Macrophoma rot, and thus, further studies to reassess the etiology of this disease are needed

Other fruit rots associated with Botryosphaeriaceae spp.

In the early 1960s, a fruit rot was observed in the southern San Joaquin and Coachella Valleys of California, USA, primarily on table grapes var. Thompson Seedless. The disease was named summer bunch rot and at first it was thought to be caused by *Phomopsis viticola* (as *Diplodia viticola* Desm.) (Hewitt *et al*., 1962). Summer bunch rot affects berries, which at first appear slightly water-soaked. As the rot progresses the skin of

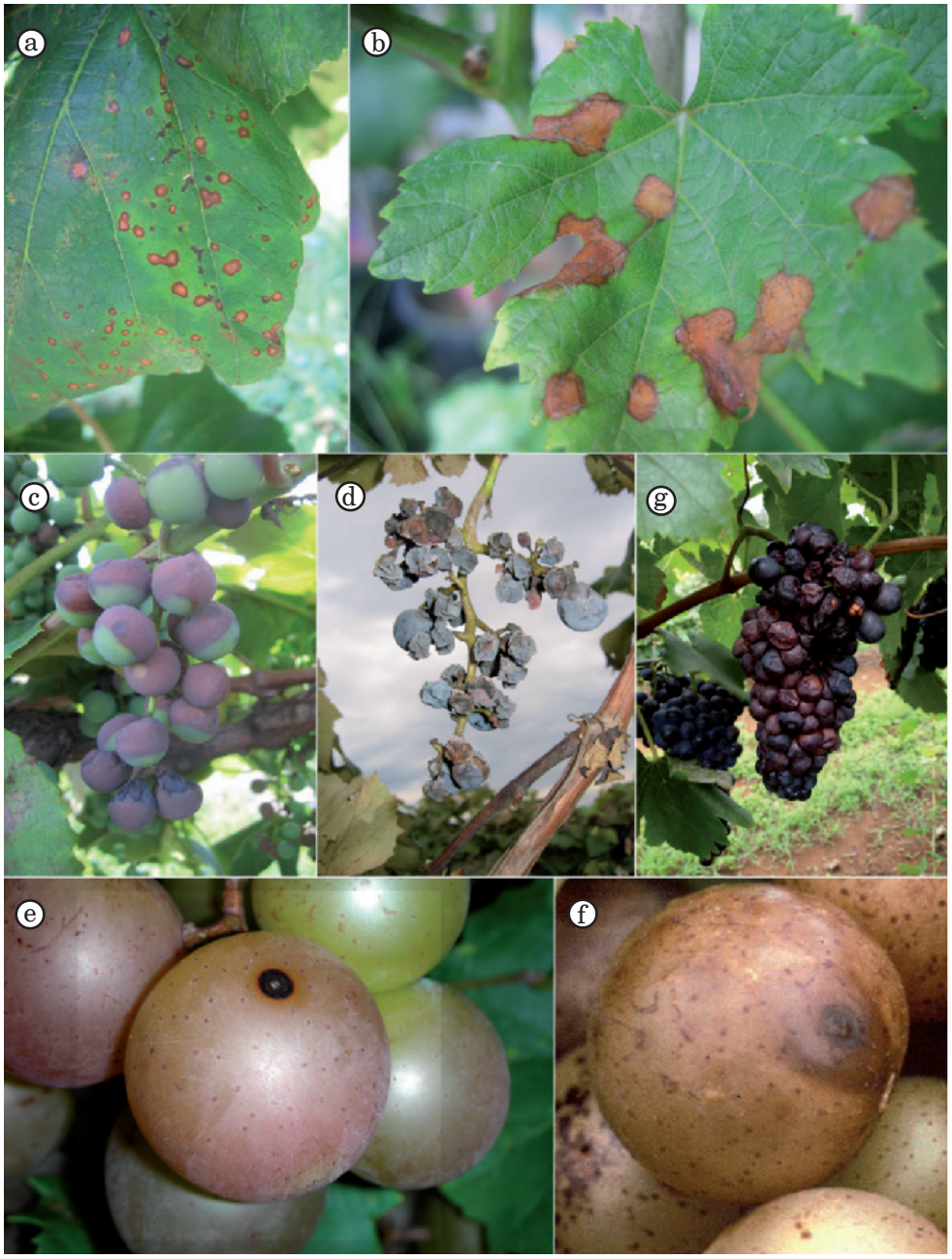

Figure 1. a–d. Black rot. a. Infections caused by *Guignardia bidwellii* on leaves start as small circular lesions. b. As infection progresses lesions expand and pycnidia develop in the center of the lesions. c. Infection of the fruit first appears light in color. d. As fruit infection progresses, berries turn dark in color and eventually shrivel becoming raising-like body masses named "mummies" and covered with pycnidia. (Pictures courtesy of Dr. M. Sosnowski, South Australian Research and Development Institute, Adelaide, Australia). e–f. Macrophoma rot. e. Infections caused by Botryosphaera dothidea first appear as single flat or slighted sunken dark areas. f. As disease progresses, a brown soft rot covers the berry spreading through the whole cluster. (Pictures courtesy of Dr. T.B. Sutton, Department of Plant Pathology, North Carolina State University, Raleigh, North Carolina, USA). g. Bunch rot associated with Botryosphaeriaceae spp. on Shiraz in southeastern Australia (Picture courtesy of N. Wunderlich, Charles Sturt University, Wagga Wagga, Australia).

the berry cracks dripping juice, which produces a sour vinegar odor that attracts numerous fruit flies (*Drosophila melanogaster* Meigen) and from which up to 35 different microorganisms primarily *Aspergillus niger* Tiegh. and an *Acetobacter* sp. could be isolated (Hewitt, 1979). The disease was reported to cause losses exceeding 30% in some vineyards. However, because most of the fruit rot was observed in vineyards showing a tip blight symptom caused by *L. theobromae* (as *Diplodia natalensis* Desm.), the disease was reassessed as Diplodia bunch rot and attributed to this fungus (Hewitt, 1979; Hewitt, 1988). Nevertheless, symptoms of Diplodia bunch rot were only reproducible when clusters were first inoculated with *L. theobromae* spores, enclosing them in high humidity chambers infested with fruit flies and finally inoculating them with different organism including several yeasts (Hewitt, 1979). Although the symptoms were never successfully reproduced in the field, it was concluded that *L. theobromae* initiated the disease. Nowadays, researchers agree that the symptoms first described as summer bunch rot are indeed what are currently known as non-*Botrytis* bunch rot and/or sour rot, an emergent problem primarily on table-grapes. Significant research on these fruit rots has been conducted in the last decade and many different organisms have been reported to be involved (Latorre *et al*., 2002; Morgan and Michailides, 2004; Steel *et al*., 2007; Rooney-Latham *et al*., 2008). However, all studies failed to associate *L. theobromae* with this disorder, primarily because the fungus was never isolated from the affected berries. Although *L. theobromae* is known to be associated with wood decay in vineyards of southern California (Leavitt 1990; Úrbez-Torres *et al*., 2006a) and thus, it would be reasonable to think that spores of the fungus could potentially be found on berries, all recent studies have shown enough evidences to reject the fact that this fungus initiates either sour rot or other types of bunch rot in California. Consequently, Diplodia bunch rot etiology as described by Hewitt (1988) should be considered obsolete.

More recently, Botryosphaeriaceae species commonly isolated from grapevine trunk disease symptoms have been associated with a bunch rot of Chardonnay and Shiraz grapes in southeastern Australia (Wunderlich *et al*., 2009). *Diplodia seriata*, *Neofusicoccum parvum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips and *B. dothidea* were isolated from berries at harvest with or without bunch rot symptoms. *In vitro* pathogenicity assays on berries under favorable conditions showed that these species cause similar symptoms to those observed in the field. However, bunch rot symptoms have still not been reproduced under field conditions by inoculating solely with Botryosphaeriaceae species. Furthermore, botryosphaeriaceous fungi were isolated from berries along with fungal species associated with both non-*Botrytis* and *Botrytis* bunch rot including, *Alternaria* sp., *Botrytis cinerea* Pers., *Cladosporium* sp., *Colletotrichum acutatum* J.H. Simmonds, *Epicoccum* sp., *Fusarium* sp., *Greeneria uvicola* (Berk. & M.A. Curtis) Punith., *Penicillum* sp., and *Pestalotiopsis* sp. (Steel *et al*., 2007; Wunderlich *et al*., 2009), raising the question as to whether these Botryosphaeriaceae species are able to initiate bunch rot by themselves or they just contribute to the bunch rot disease complex. Therefore, it is obvious at the present time that further studies are required to clarify the role that these Botryosphaeriaceae species play in bunch rot disease of grapes.

Additionally, *D. mutila* and *Neofusicoccum ribis* (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips have been associated with berry wilt and rot of grapes in South Africa (Verwoerd and Dippenaar, 1930) and Taiwan (Kuo *et al*., 1989), respectively. However, the lack of literature and follow-up studies on both fruit rots make it difficult to draw conclusions on the etiology and epidemiology of these diseases at the present time.

Grapevine diseases attributed to Botryosphaeriaceae species: trunk diseases

Black dead arm

Black dead arm (BDA) was first described in the Tokaj grape-growing region of Hungary in 1974, and was associated with *D. mutila* (Lehoczky, 1974a). The original description did not associate any characteristic symptomatology on the grapevine green parts and/or clusters with the disease other than a diffuse chlorosis followed by leaf wilting. However, the fungus was repeatedly

isolated from the wood of mature vines showing the dead arm-like symptoms previously associated with *P. viticola* in North America (Reddick, 1914; Coleman 1928; Pine 1958; Chamberlain *et al*., 1964) and Hungary (Lehoczky, 1972). Lehoczky (1974a) observed that buds from affected vines sometimes did not burst and eventually died. Additionally, the bark tissue of the diseased parts (cordons and/or trunks) collapsed at the sites of infection, becoming discolored to dark-brown, a characteristic symptom which gave BDA its name. After colonization of the xylem by the fungus the wood became black and this discoloration spread downwards and upwards in a narrow straight stripe (Lehoczky, 1974a). In 1978, similar symptoms were described on grapevines in the Italian province of Isernia, although they were associated with *D. seriata* (Cristinzio, 1978). Cristinzio (1978), on the other hand, associated foliar symptoms with the disease, characterized by reddening and scorching of the leaves. The leaves of affected vines showed a dramatic loss of turgor with death of the plant within 2 years. However, neither of these studies completed Koch's postulates to confirm that the symptoms observed were indeed caused by those fungi. A few years later, Rovesti and Montermini (1987) isolated *D. mutila* from necrotic wood of grapevines in the Reggio Emilia province in Italy, which had similar symptoms to those previously described by Cristinzio (1978). However, Rovesti and Montermini (1987) associated the symptoms with esca disease of grapevines and not with black dead arm. Pathogenicity tests confirmed that the necrosis observed in the xylem of affected vines was caused by *D. mutila* (Rovesti and Montermini, 1987). No more reports could be found in the literature until the early 2000s, when Larignon and Dubos (2001) and Larignon *et al*. (2001) reported BDA on grapevines in the French region of Bordeaux, and associated the disease with *B. dothidea* and *D. seriata*. Contrary to the original description of the disease, Larignon *et al*. (2001) associated BDA with particular foliar symptoms characterized by two different phases of the disease described as mild and severe forms. The mild form was characterized by dark-red and yellowish-orange patches of the leaves in red and white grape cultivars, respectively. These patches first appear at the margin of the leaves and/or blades and gradually expand between the veins (Figure 2a). Consequently, leaves lose their turgor and the affected tissue between the veins eventually dries out (Figure 2b). The severe form was characterized by a rapid drying and fall of the leaves from the shoots of affected vines (Figure 3c) (Larignon and Dubos, 2001; Larignon *et al*., 2001). Symptoms in the wood were characterized by light-brown streaks under the bark which extended from the base of the infected shoots to the graft unions, and even to the rootstock (Figure 3d) (Larignon *et al*., 2001). Additionally, yellowish-orange areas at the edges of the streaks were also recorded in France, which differed from the original description of BDA. Furthermore, a wedge-shape canker symptom was added to the disease symptoms (Larignon and Dubos, 2001). Larignon *et al*. (2001) completed pathogenicity tests and though they showed that both *B. dothidea* and *D. seriata* cause dark streaking of the wood in 1-year-old detached canes, the characteristic foliar and wood symptoms associated with BDA were not reproduced. Annual losses in the Bordeaux region associated with BDA were estimated to be up to 20%. In the following years, *D. seriata* was reported to be the cause of BDA on table grapes in Chile (Auger *et al*., 2004), and on both table and wine grapes in Lebanon (Choueiri *et al*., 2006) showing similar symptoms as those described by Larignon and Dubos (2001).

Both mild and severe forms of BDA described by Larignon *et al*. (2001) have been the subject of debate because of their resemblance to the "tiger-stripe" patterns and apoplexy symptoms that are characteristic of esca infected vines (Mugnai *et al*., 1999). However, Larignon *et al*. (2001) stated that "It is not difficult to differentiate this disease from esca when symptoms first appear". They further reported that foliar symptoms of BDA appear earlier in the season, leaves never show esca-like yellow spots and light-brown streaking is not observed in esca infected vines. Nevertheless, it is well-documented that esca infected vines can display a broad range of symptoms from one growing season to another, which can consequently make it difficult to distinguish them from those associated with BDA (Lecomte *et al*., 2005; Surico *et al*., 2006). Moreover, earlier reports already showed the light-brown discoloration of the wood under the bark to occur on vines

Figure 2. Symptoms attributed to black dead arm by Larignon and Dubos (2001) and Larignon *et al*., (2001). a–b. Symptoms on the leaves are dark-red patches that extend causing eventual dry out of the tissues between the veins and the margin of the leaf. c. Severe form of the disease causing a quick dry out and fall of the leaves in the entire vine. d. Light-brown streak under the bark extending from spur position. Based on studies conducted by Lecomte *et al*., (2005) and Surico *et al*., (2006), it is currently well accepted that these symptoms correspond with esca disease of grapevines and not with Black dead arm. (Pictures courtesy of P. Lecomte, UMR Santé Végétale INRA-ENITAB, Villenave d'Ornon, France).

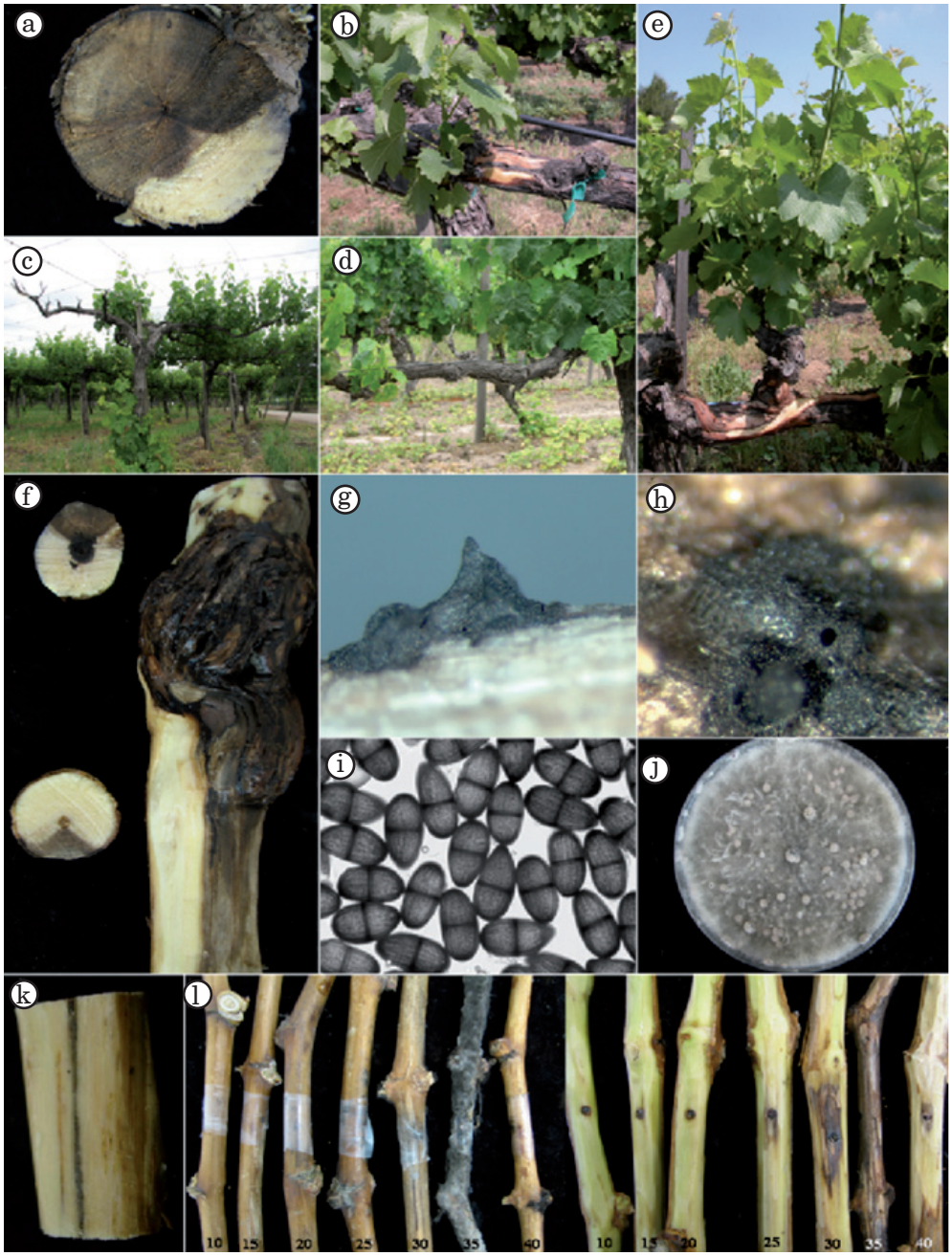

Figure 3. Botryosphaeria canker. a. Perennial canker (wedge-shape) in the trunk. b. Cankers generally develop from pruning wounds. c and d. Lack of spring growth is commonly observed in vines affected by Botryosphaeria canker. e. Normal and healthy growth can also be observed in vines affected by the disease. f. Infections can occur at the graft union causing wedge-shape cankers in both scion and rootstock. g–k. *Lasiodiplodia theobromae*, one out of the 19 botryosphaeriaceous fungi isolated from cankers. g. Pycnidia erupting through the bark. h. Aerial view of pycnidium showing the ostiole from which conidiospores are released. i. Conidiospores of *L. theobromae*. j. Characteristic colony morphology of *L. theobromae* on potato dextrose agar. k. Several species such as *Botryosphaeria dothidea*, *Diplodia mutila*, and *Neofusicoccum parvum* also cause dark streaking of the wood. l. Effect of seven different temperatures (°C) on the length of vascular discoloration caused by *L. theobromae*.

infected with esca (Galet, 1977). A more detailed description of similarities between esca and BDA foliar symptoms has been published recently by Surico *et al*. (2006). Interestingly, the foliar symptoms described by Larignon *et al*. (2001) in France were either never recorded or were randomly associated with Botryosphaeriaceae species during large-scale field surveys conducted in different grape-growing regions worldwide (van Niekerk *et al*., 2004; Úrbez-Torres *et al*., 2006a; Úrbez-Torres *et al*., 2008; Pitt *et al*., 2010). Furthermore, a recent survey conducted in northeast Spain showed the impossibility of differentiating BDA foliar symptoms *per se* as they commonly occurred along with both Eutypa dieback and esca symptoms in the same plant (Luque *et al*., 2009). Mugnai *et al*. (1999) reported *B. dothidea* and *D. seriata* to commonly occur on esca infected vines. These observations, along with the fact that both BDA foliar and vascular symptoms have not been reproduced by artificial inoculation with any of the botryosphaeriaceous fungi involved in the disease, raise doubts about whether or not BDA should be considered a distinct disease, caused only by species in the Botryosphaeriaceae, or it may be the result of a complex combination of several fungi including those causing esca in a specific stage of the vines. Based on the latest research and findings there is a common consensus among most researchers that BDA foliar symptoms are probably one of the many manifestations of esca (Surico *et al*., 2006). However, these symptoms may also result from unknown causes still to be determined. Therefore, and until further investigations clarify the status of BDA, researchers should be cautious when reporting this disease from vineyards in order to avoid further confusion.

Botryosphaeria canker

Grapevine cankers caused *B. dothidea* were first reported in Chile on table grapes cv. Flame Seedless (Latorre *et al*., 1986). Nevertheless, the disease known as Botryosphaeria canker of grapevines was first named by Leavitt (1990) to describe particular symptoms caused by *L. theobromae*, observed in vineyards in southern California. The disease was characterized by the presence of wedged- or pie-shape perennial cankers in spurs, cordons and/or trunks, which were indistinguishable from those caused by *E. lata* (Figure 3a). Cankers were shown to start developing primarily from pruning wounds but also from cracks and natural openings on the framework of vines as well as from big cuts left after re-training vines (Figure 3b). However, Leavitt observed that vines showing perennial cankers in this geographical region failed to manifest the distinctive foliar symptoms caused by *E. lata* (small cupped and chlorotic leaves, short internodes and stunted chlorotic spring growth) during the years following infection, which was corroborated a few years later by Pascoe (1998) in Australia. Grapevines affected by Botryosphaeria canker on the other hand showed either a total absence of spring growth or normal and healthy development of shoots (Figure 3c–e). Additionally, lack of spring growth in one or more spur positions and normal and healthy growth in others could be observed in the same cordon of individual vines. *Lasiodiplodia theobromae* was reported to be the most prevalent, and in many vineyards, the only fungus isolated from those cankers (Figures 3g–j). Disease incidence in the southern California region of Coachella Valley was reported to be as great as 100% in vineyards 10 years old and older, with several cankers per vine. Although it is known that Botryosphaeria canker is more prevalent in mature vineyards, cankers caused by *L. theobromae* along with lack of spring growth in spur positions have been reported in vines younger than 5 years old (Leavitt 1990; Úrbez-Torres *et al*., 2008). Leavitt (1990) completed Koch's postulates and reproduced the symptoms observed in the field. Since then, *L. theobromae* has been considered an endemic pathogen of grapes in the southern San Joaquin and Coachella Valleys of California, Arizona and in the Hermosillo province of Mexico, where the disease has been known locally as "Bot canker".

Extensive research has been conducted on Botryosphaeria canker during the last decade in California, where it is currently recognized as one of the most prevalent diseases in the State limiting both vineyard longevity and productivity (Úrbez-Torres *et al*., 2006a; Úrbez-Torres and Gubler, 2009a). The importance of this disease is also reflected by a recent study in which the overall loss for the California wine industry caused by both Botryosphaeria canker and Eutypa dieback

was estimated to be over $US260 million per year (Siebert, 2001). Furthermore, research conducted in the United States has shown that Botryosphaeria canker is not solely caused by *L. theobromae* and that several Botryosphaeriaceae species are involved in the disease. These include: *B. dothidea*, *Diplodia corticola* A.J.L. Phillips, A. Alves & J. Luque, *D. mutila*, *D. seriata*, *Dothiorella iberica* A.J.L. Phillips, J. Luque & A. Alves, *Dothiorella americana* J.R. Úbez-Torres, F. Peduto & W.D. Gubler, *Lasiodiplodia crassispora* T.I. Burgess & Barber, *Lasiodiplodia missouriana*, J.R. Úrbez-Torres, F. Peduto & W.D. Gubler, *Lasiodiplodia viticola* J.R. Úrbez-Torres, F. Peduto & W.D. Gubler, *Neofusicoccum australe* (Slippers, Crous & M.J. Wingf.) Crous, Slippers & A.J.L. Phillips, *Neofusicoccum luteum* (Pennycook & Samuels) Crous, Slippers & A.J.L. Phillips, *Neofusicoccum macroclavatum* (T.I. Burgess, Barber & Hardy) T.I. Burgess, Barber & Hardy, *Neofusicoccum mediterraneum* Crous, M.J. Wingf. & A.J.L. Phillips, *N. parvum*, *N. ribis*, *Neofusicoccum viticlavatum* (Van Niekerk & Crous) Crous, Slippers & A.J.L. Phillips, *Neofusicoccum vitifusiforme* (Van Niekerk & Crous) Crous, Slippers & A.J.L. Phillips, and *Spencermartinsia viticola* (A.J.L. Phillips & J. Luque) A.J.L. Phillips, A. Alves & Crous (van Niekerk *et al*., 2004; Taylor *et al*., 2005; Wood and Wood, 2005; Úrbez-Torres *et al*., 2006a; Úrbez-Torres *et al*., 2007a; Úrbez-Torres *et al*., 2009; Úrbez-Torres *et al*., 20010b; Úrbez-Torres *et al*., 2010c; Billones *et al*., 2010; Úrbez-Torres *et al*., 2011). To date, cankers caused by Botryosphaeriaceae species have been confirmed to occur in vineyards in 16 different States in the USA (Úrbez-Torres *et al*., 2007b; Rolshausen and Wilcox, 2009) as well as in grape-growing areas of Africa, Asia, Australia, Central America, Europe, and South America (Table 2).

Remarks on black dead arm and Botryosphaeria canker disease names

Since BDA was described, much controversy and debate have followed regarding the cause, and consequently the name, of this disease. Although BDA was originally described as been caused by only one botyosphaeriaceous fungus (*D. mutila*), there are currently three species associated with the disease (*B. dothidea*, *D. mutila*, *D. seriata*), which are currently known to be associated with different grapevine symptoms worldwide (Milholland, 1988; Phillips, 2002; Taylor *et al*., 2005; Urbez-Torres *et al*., 2006a). Furthermore, symptoms such as wedge-shape cankers, light-brown discoloration of the wood and foliar symptoms have not only been added erroneously through the years to BDA (Surico *et al*., 2006) but they have not yet been reproduced by inoculating healthy vines with the different botryosphaeriaceous taxa associated with the disease. Additionally, the same Botryosphaeriaceae species, including those linked to BDA, have been reported to cause different grapevine dieback symptoms in different countries and even between different grape-growing regions within the same country (van Niekerk *et al*., 2004). Therefore, it is clear that the name BDA is being applied erroneously to one or multiple diseases, and thus, the use of the name should be restricted only to cases that coincide exactly with the original concept of the disease (diffuse chlorosis of the leaves followed by wilting, black streaking of the wood in the xylem, and caused by *D. mutila*). Moreover, BDA should not to be applied to any of the modifications to the symptoms of the disease such as sectorial necrosis, light-brown discoloration of the wood and the "tiger-stripe" like patterns on the leaves.

Likewise, although Botryosphaeria canker was originally thought to be caused only by *L. theobromae* in the USA, multiple Botryosphaeriaceae species are currently known to cause not only perennial cankers but other grapevine dieback symptoms worldwide. Moreover, symptoms associated with Botryosphaeria canker such as wedge-shaped canker, dark streaking of the wood and/or bud failure coincide with symptoms already used to describe BDA. It could therefore be concluded that BDA and Botryosphaeria canker may be different names to often refer to the same symptoms. The use of two different names, BDA and Botryosphaeria canker, to often describe the same symptoms has created much of the confusion on the etiology of these diseases over the past years. Additionally, different Botryosphaeriaceae species can be isolated from the same vascular symptom in grapevines showing diverse foliar symptoms, either alone or along with other grapevine trunk disease pathogens (Úrbez-Torres *et al*. 2006a; Luque *et al*., 2009; Úrbez-Torres *et al*., 2011). To date, there are up to 21 Botryospha-

Table 2. Grapevine symptoms from which Botryosphaeriaceae species have been isolated in different grape-growing regions worldwide.

Species	Grapevine symptoms and countries from which Botryosphaeriaceae species have been isolated													
	WSC[a]	DSW[b]	FR[c]	BLS[d]	LBSW[e]	BC[f]	CN[g]	RN[h]	BN[i]	PN[j]	AW[k]	GPM[l]	PD[m]	GF[n]
B. dothidea	AUS[1,2], BRA[3], CAN[4], CHL[5], CHN[6], ESP[7,8], NZL[9], USA[10,11,12]	ESP[7,13], USA[10,11]	AUS[14] USA[15]	PRT[16]	FRA[17]	PRT[16]	ESP[13]		PRT[16]	NZL[9]		ESP[18]		PRT[19]
D. corticola	MEX[20], USA[11,21]													
D. mutila	AUS[2,22], CAN[23] NZL[9], USA[8]	HUN[24], PRT[19]				AUS[2], PRT[16]		AUS[25]	AUS[2], PRT[19]	NZL[9]				HUN[24], NZL[9]
D. seriata	AUS[2,22], CAN[4,26], ESP[7,8,13], FRA[17], LBN[27] MEX[28], NZL[9], USA[10,11,12], ZAF[29]	AUS[30], ESP[7,11] ITA[31], PRT[19]	AUS[14]	PRT[16]	CHL[32], FRA[17] ITA[31], LBN[27]	AUS[30], PRT[16]	ESP[13] LBN[27]		AUS[30], USA[33]	NZL[9]	ZAF[34]	ESP[18]		PRT[19]
Do. iberica	AUS[2], USA[35]													
Do. americana	USA[12]													
G. bidwellii			USA[36]											
L. crassispora	USA[37], ZAF[38]													
L. missouriana	USA[12]													
L. theobromae	AUS[2,22,39], BOL[40], CHN[41], EGY[42], ITA[43] MEX[28], USA[10,11], ZAF[29]	ITA[43]				AUS[39]		USA[33]			ZAF[34]	ESP[44]		
L. viticola	USA[12]													
N. australe	AUS[2,22], MEX[20], USA[10], ZAF[29]					AUS[2]					ZAF[34]			
N. luteum	AUS[1], ESP[13], NZL[45], USA[10]		AUS[14]			NZL[9], PRT[19]			NZL[9]		ZAF[34]			NZL[9]
N. macroclavatum	NZL[46]										NZL[46]			
N. mediterraneum	USA[36]													
N. parvum	AUS[2], CAN[4], ESP[8,13], NZL[9], PRT[19],USA[10,11], ZAF[29]	ESP[13], PRT[19] USA[10,11]	AUS[14]			PRT[19]	ESP[13]	USA[33]	NZL[9], PRT[19]		ZAF[34]	ESP[18]		NZL[9], PRT[19]
N. ribis	USA[12]		AUS[47] TW[48]											
N. viticlavatum											ZAF[34]			
N. vitifusiforme	ESP[13], MEX[20], USA[12]	ZAF[29]												
P. porosa													ZAF[29]	
S. viticola	AUS[2], ESP[13], USA[35]												ESP[49]	

Symptom abbreviations: [a]Wedge-Shaped Canker, [b]dark streaking of the wood, [c]fruit rot, [d]elongated black lesions on the shoots, [e]light-brown streaking of the wood, [f]bleached cane, [g]central necrosis, [h]root necrosis, [i]bud necrosis, [j]pith necrosis, [k]asymptomatic wood, [l]Grapevine planting material (scion, graft-union and/or rootstock), [m]Pruning debris, and [n]graft failure.
Country abbreviations: AUS = Australia, BOL = Bolivia, BRA = Brazil, CAN = Canada, CHL = Chile, CHN = China, EGY = Egypt, ESP = Spain, FRA = France, HUN = Hungary, ITA = Italy, LBN = Lebanon, MEX = Mexico, PRT = Portugal, USA = United States of America, and ZAF = South Africa.
References: [1]Savocchia *et al*., 2007; [2]Pitt *et al*., 2010; [3]Filho *et al*., 1995; [4]O'Gorman *et al*., 2010; [5]Latorre *et al*., 1986; [6]Li *et al*., 2010; [7]Armengol *et al*., 2001; [8]Úrbez-Torres *et al*., 2006b; [9]Bonfiglioli and McGregor, 2006; [10]Úrbez-Torres *et al*., 2006a; [11]Úrbez-Torres *et al*., 2009; [12]Úrbez-Torres *et al*., 2011; [13]Luque *et al*., 2009; [14]Wunderlich *et al*. 2009; [15]Milholland 1991; [16]Phillips 1998; [17]Larignon *et al*., 2001; [18]Aroca *et al*. 2006; [19]Phillips 2002; [20]Candolfi-Arballo *et al*., 2010; [21]Úrbez-Torres *et al*., 2010b; [22]Taylor *et al*., 2005; [23]Chamberlain *et al*., 1964; [24]Lehoczky 1974a; [25]Whitelaw-Weckert *et al*., 2006; [26]Shoemaker 1964; [27]Choueiri *et al*. 2006; [28]Úrbez-Torres *et al*., 2008; [29]van Niekerk *et al*. 2004; [30]Castillo-Pando *et al*., 2001; [31]Cristinzio 1978; [32]Auger *et al*., 2004; [33]Úrbez-Torres J.R. (unpublished), [34]Halleen *et al*., 2005; [35]Úrbez-Torres *et al*., 2007a; [36]Úrbez-Torres *et al*., 2010c; [37]Úrbez-Torres *et al*., 2010c; [38]van Niekerk *et al*., 2010b; [39]Wood and Wood, 2005; [40]Kaiser *et al*., 2009; [41]Yan *et al*. 2011; [42]El-Goorani and El Meleigi, 1972; [43]Burruano *et al*., 2008; [44]Aroca *et al*., 2008; [45]Amponsah *et al*., 2009b; [46]Billones *et al*., 2010; [47]Pascoe 1998; [48]Kuo *et al*., 1989; [49]Luque *et al*., 2005.

eriaceae species causing multiple grapevine disease symptoms worldwide and thus, the use of a unique name for a unique disease with characteristic symptoms does not appear to be appropriate.

With some particular differences, most of the disease symptoms associated with Botryosphaeriaceae species on grapevines (wedge-shaped cankers, necrosis of the wood, progressive budbreak failure, and plant dieback) resemble those associated with Eutypa dieback. Consequently, the name Botryosphaeria dieback is proposed here to describe these types of symptoms caused by Botryosphaeriaceae species The use of Botryosphaeria dieback appears more appropriate than BDA or Botryosphaeria canker to describe the broad number of different grapevine trunk disease symptoms that Botryosphaeriaceae species cause on grapevine wood.

Excoriose

The name excoriose was introduced by Ravaz and Verge (1925) to describe a characteristic disease observed throughout several grapevine-growing regions in France. According to these authors, symptoms of the disease were characterized by elongated black lesions that developed on the internodes of affected vines early in the growing season. Later on, affected shoots may collapse or die-back. Another characteristic symptom of the disease can be observed after harvest when the black areas on the canes turn white and/or light-grey giving them a bleached appearance. Spotted black fruiting bodies of the fungus can be observed embedded in the host tissue (Ravaz and Verge, 1925; Phillips 1998). Ravaz and Verge (1925) reported *Phoma flaccida* Viala & Ravaz as the causal agent of excoriose in France. Thereafter, descriptions of the disease under the name of *Macrophoma flaccida* (Viala & Ravaz) Cavara followed in South Africa (Doidge *et al*., 1953), France (Gaudineau, 1961), Greece (Pantidou, 1973), and Portugal (Dias and Lucas, 1980; Tomaz and Rego, 1990). While *M. flaccida* was thought to be the cause of excoriose in Europe (European excoriose), *P. viticola* was attributed to cause the disease in the USA (American excoriose) (Bugaret, 1987; Hewitt and Pearson, 1988). Afterward, the disease was named Phomopsis cane and leaf spot in the USA, and attributed solely to *P. viticola* (Hewitt and Pearson, 1988). Since *M. flaccida* was never inoculated onto host plants to complete Koch's postulates, the pathogenic ability of this species was placed in doubt following the reports of *P. viticola* in Germany in the mid 1960s (Claus, 1965; Thate, 1965). Consequently, many authors concluded that excoriose in Europe was not caused by *M. flaccida* (Branas, 1967; Bugaret, 1987) but by *P. viticola* (Dias, 1980). Tomaz and Rego (1990) on the other hand, reported *M. flaccida* to be commonly found and widespread on grapevines showing excoriose symptoms in Portugal. A review of the current status of both excoriose and the pathogens associated with the disease was published by Phillips (2000b).

In 1997, *M. flaccida* was shown to be a synonym of *F. aesculi*, the anamorph of *B. dothidea* (Phillips and Lucas, 1997). A field survey conducted throughout several grape-growing regions in Portugal revealed *B. dothidea* as the most prevalent species isolated from excoriose symptoms (Figure 4), followed, among others, by *P. viticola*, *D. seriata* and *D. mutila* (Phillips, 1998). Completion of pathogenicity tests showed both *B. dothidea* and *P. viticola* to be pathogenic both on wounded and unwounded grape shoots. Moreover, excoriose symptoms were reproduced on both wounded and unwounded shoots when canes were inoculated with *B. dothidea* isolates (Phillips, 1998). Although *D. mutila* and *D. seriata* caused smaller lesions than *B. dothidea* and *P. viticola* in the wounded treatments, they failed to cause any symptom on unwounded shoots (Phillips, 1998). This study provided strong evidence that *B. dothidea* does indeed cause excoriose, confirming earlier reports, in which the cause of excoriose was attributed to *M. flaccida*. Based on these studies (Phillips and Lucas 1997; Phillips 1998; Phillips, 2000b), it should be broadly accepted that excoriose is caused by *B. dothidea* and not by *P. viticola*, which is the cause of Phomopsis cane and leaf spot, a different disease as stated by Hewitt and Pearson (1988). Because these studies were conducted before the concept of *B. dothidea* was clarified, it is currently clear that *N. parvum*, and not *B. dothidea*, is the pathogen causing excoriose of grapevines (Phillips, personal communication).

Disease symptoms attributed to Botryosphaeriaceae and their geographical distribution

Although species of Botryosphaeriaceae have been primarily isolated from perennial cankers

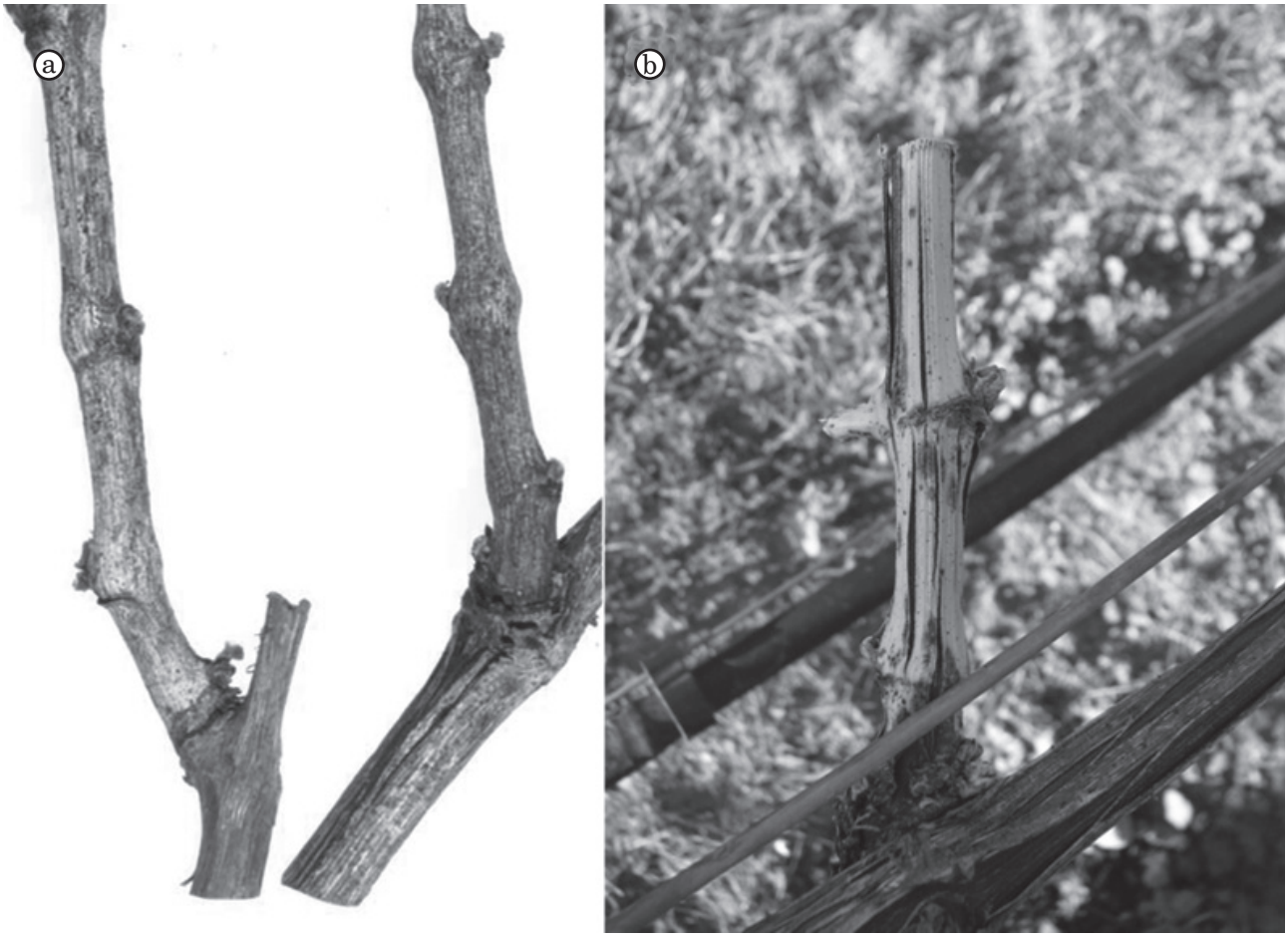

Figure 4. a–b. Grapevine canes with bleached appearance characteristic of excoriose symptoms. (Picture a courtesy of A.J.L. Phillips, Faculdade de Ciências e Tecnologia, Universidade Nova de Lisboa, Quinta da Torre, Caparica, Portugal).

worldwide, these fungi have been also reported during the last decade from a wide variety of wood decay symptoms, including dark streaking of the wood, elongated black lesions on the shoots, light-brown streaking of the wood, cane bleaching, shoot dieback, graft failure, bud death, and central, bud, pith, and root necrosis. Botryosphaeriaceae species and symptoms from which they have been isolated in different grape-growing regions worldwide are summarized in Table 2.

Diagnosis and detection

Research has shown that different Botryosphaeriaceae species are isolated from the same vascular symptoms from grapevines showing diverse foliar symptoms. Additionally, these fungi can often be isolated along with other grapevine trunk disease pathogens from the same symptom or from different symptoms in the same vine (Úrbez-Torres *et al*., 2006a; Luque *et al*., 2009; Úrbez-Torres *et al*., 2011). Consequently, diagnosis of grapevine diseases caused by Botryosphaeriaceae can be difficult based merely on observations both of vascular and external symptoms, and thus, accurate diagnosis by means of isolations and/or molecular techniques is required to confirm the presence of these species. Accurate identification of species in the Botryosphaeriaceae has become significantly relevant due to the high variability in virulence observed among the different species infecting grapes (van Niekerk *et al*., 2004; Taylor *et al*., 2005; Úrbez-Torres and Gubler, 2009a). As

occurred with the rest of fungal taxa prior to the introduction of DNA-PCR-based techniques, identification and characterization of species in the Botryosphaeriaceae were solely based on morphology (Stevens, 1926; Luttrel, 1948; Chamberlain *et al*., 1964; Shoemaker, 1964; Leavitt, 1990; Phillips, 1998; Phillips, 2002). However, the fact that morphological characters in the Botryosphaeriaceae can often overlap among different species resulted in continuous misidentifications, which may have contributed to the confusion created on the etiology of some grapevine diseases caused by this taxonomic group. The most significant example of this misidentification has probably occurred with *B. dothidea*, which has been constantly reported as the causal agent of wood decays and fruit rots in many different perennial plants since it was described (Farr and Rossman, 2011). Although some researchers have viewed *B. dothidea* and *B. ribis* as distinct species (Punithalingam and Holliday, 1973; Morgan-Jones and White, 1987; Smith and Stanoz, 2001), many authors have largely treated them as synonymous over the years (Witcher and Clayton, 1963; Barr, 1972; Pennycook and Samuels, 1985; Brown and Britton, 1986; Smith *et al*., 1994). Phylogenetic studies conducted by Jacobs and Rehner (1998), Denman *et al*. (2000), Zhou *et al*. (2001), and Zhou and Stanosz (2001) showed *B. dothidea* to form two separate clades representing *B. dothidea* and *B. ribis*, which raised questions regarding their synonymy. Following these findings, multigene phylogenetic analyses along with morphological studies were able to differentiate several Bo-tryosphaeriaceae species previously identified as *B. dothidea* (Slippers *et al*., 2004a). Smith *et al*. (2001) showed that a different *Fusicoccum* sp. was present within *B. dothidea* isolates from Pistachio when compared by random amplified polymorphic DNA (RAPD) markers, nuclear rDNA internal transcribed spacer (ITS) region sequences, and conidium morphology. Thereafter, Phillips *et al*. (2002) described the novel species "*Botryo-sphaeria*" *lutea* within the *B. dothidea* complex. Afterwards, Slippers *et al*. (2004a) clearly distinguished "*Botryosphaeria*" *parva* and "*Botryosphaeria*" *ribis* from *B. dothidea*. Recently, Crous *et al*. (2007) described *N. mediterraneum* on leaves of a *Eucalytus* sp. and showed that this species was previously misidentified as *B. dothidea* by some researchers.

Similarly, the use of several molecular techniques, including random amplified polymorphic DNA markers (RAPDs), inter simple or short sequence repeat fingerprinting (ISSR), microsatellite loci, sequences of the ITS1-5.8S-ITS2 region, and protein coding genes allowed clear differentiation of two populations (designated A and B) within *Diplodia pinea* (Desm.) (as *Sphaeropsis sapinea* (Fr.) Dyko & B. Sutton), which was otherwise unfeasible based only on morphology. Furthermore it led to the recognition that the group B is a distinct species, which was subsequently named *Diplodia scrobiculata* J. de Wet, Slippers & M.J. Wingf. (Smith and Stanosz, 1995; Stanosz *et al*., 1999; de Wet *et al*., 2003; Smith and Stanosz, 2006).

Although species identification using single-locus sequence data alone is known to be much more accurate, reliable and faster than previous morphology-based methods, it has not always resolved all taxonomic issues in Botryosphaeriaceae. *Neofusicoccum ribis* and *N. parvum*, often misidentified with *B. dothidea*, are closely related species forming what has been known as the *N. parvum*/N. *ribis* complex. These species have been reported to be very difficult to differentiate due to their similarity among morphological characters and alike or identical ITS sequences (Zhou *et al*., 2001). ISSR fingerprinting developed by Zhou *et al*. (2001) clearly separated isolates of *B. dothidea* from those of *N. ribis* and support the differentiation of *N. luteum*, *N. parvum* and *N. ribis* within the *N. parvum*/N. *ribis* complex. Additionally, ISSR fingerprint revealed a much greater interspecific variation when compared to ITS sequences and RAPD markers, which were previously shown to not clearly separate these species (Smith and Stanosz, 2001; Zhou and Stanosz, 2001). Microsatellite loci were later successfully used to characterize *L. theobromae* isolates from different hosts and geographical locations (Burgess *et al*., 2003). Slippers *et al*. (2004a, 2004b) showed that combined multi-allelic DNA sequence analyses from the rDNA (ITS1-5.8S-ITS2), β-tubulin (TUB) and EF1-α genes were very helpful in distinguishing species in the Botryosphaeriaceae, especially *N. parvum* from *N. ribis* when β-tubulin and EF1-α genealogies were combined. Hence, multi-locus analyses are being routinely incorporated in all research stud-

ies dealing with separation and identification of species in the Botryosphaeriaceae from different hosts, including grapevines. To date, up to eight different gene coding regions have been used either in single- or multi-locus gene studies in the Botryosphaeriaceae, including the 18S small subunit (SSU), 5.8S (ITS), 28S large subunit (LSU), β-tubulin, EF1-α, RNA polymerase II subunit (RPB2), glyceraldehyde-3-phosphate dehydrogenase (GPD), heat shock protein (HSP), and histone-3 (HIS) (Slippers *et al*., 2004a, 2004b; Crous *et al*., 2006; Phillips *et al*., 2008; Úrbez-Torres *et al*., 2008; Pavlic *et al*., 2009; Inderbitzin *et al*., 2010). Although, combined analyses of ITS and EF1-α sequences are probably the most widely used for phylogenetics in Botryosphaeriaceae, Inderbitzin *et al*. (2010) demonstrated that the combined analyses of six loci (ITS, TUB, EF1-α,GPD, HSP, and HIS) resulted in the highest phylogenetic resolution to discriminate among species in the Botryosphaeriaceae. Moreover, the fact that EF1-α shows the highest number of parsimony informative characters among all these coding regions, makes this gene the most appropriated to use in single-locus phylogenetic analyses in the Botryosphaeriaceae. In recent studies, nucleotide sequence data from multiple genes have been used to reveal cryptic species within both single species (Alves *et al*., 2008) and species complexes (Pavlic *et al*., 2009) in the Botryosphaeriaceae, including those infecting grapevines (Úrbez-Torres *et al*., 2011). PCR-based techniques such as amplified ribosomal DNA restriction analysis (ARDRA), microsatellite-primed polymerase chain reaction (MSP-PCR) and repetitive-sequence-based polymerase chain reaction (rep-PCR) have been shown not only to be very efficient in discriminating up to 27 species in the Botryosphaeriaceae but to be an inexpensive and simple alternative to sequencing, which could be specially useful in population studies when working with large sets of isolates (Alves *et al*., 2005; Alves *et al*., 2007).

Isolations from symptomatic tissue and traditional plating along with single- and/or multi-locus phylogenetic studies have proven useful to both differentiate existing Botryosphaeriaceae species and identify novel ones. However, these culture-dependent identification techniques are time-consuming and restricted in terms of detection (Spagnolo *et al*., 2011). Hence, the recent implementation of molecular techniques based on the development of species-specific primers tested in a nested-PCR has shown broad potential for detection of species in the Botryosphaeriaceae, as shown by Flowers *et al*. (2003) who developed a nested-PCR protocol for the detection of *S. sapinea* latent infections in *Pinus nigra* shoots. More recently, Spagnolo *et al*. (2011) showed two ITS-RDNA-based nested-PCR protocols to be efficient, sensible and reliable in detecting the presence of at least six different species in the Botryosphaeriaceae from naturally infected tissue from both mature standing vines and dormant grafted rooted cuttings. Although further research is needed to improve and refine this method, nested-PCR techniques have been shown to offer significant advantages over traditional-plating and sequencing in terms of time (positive identification within 1 day versus 2–3 weeks), costs and reproducibility. Furthermore, the possibility of detecting low levels of fungal DNA in symptomatic and asymptomatic tissues makes this technique very helpful in future epidemiological studies. PCR-based techniques used for DNA detection, on the other hand, do not allow for pathogen viability assessment, which should be taken into account depending on the relevant research objective.

Pathogenicity and virulence

Pathogenicity of Botryosphaeriaceae species on grapevines has been widely debated. Although some of the reasons for this debate have been explained in the introduction of this review, one of the main causes of this discussion is probably a response to the lack of studies in which pathogenicity was tested. Between 1964 and 2003, most of the studies simply described the association of one or more Botryosphaeriaceae species with a grapevine dieback symptom without completing pathogenicity tests. During those years, only six studies fulfilled Koch's postulates (El-Goorani and El Meleigi, 1972; Rovesti and Montermini, 1987; Leavitt, 1990; Phillips 1998; Larignon *et al*., 2001; Castillo-Pando *et al*., 2001). As a result of these studies *B. dothidea*, *D. mutila*, *D. seriata*, and *L. theobromae* were shown to cause dark vascular discoloration, perennial cankers, elongated black regions on the shoots, and

bud mortality in grapevines. However, the vascular symptoms observed in the original declining vines in the field were not always successfully reproduced, which was probably because most of the pathogenicity tests were conducted on either excised young wood, including green shoots, or young rooted cuttings, and not on mature wood of standing vines. Additionally, most pathogenicity tests were conducted for short periods of time, which probably did not allow the infections to develop, and thus resemble those observed in the field. By the end of 2003 the pathogenicity of *B. dothidea* and *L. theobromae* on grapevines was confirmed, but the pathogenic status of *D. mutila* and *D. seriata* was still unclear (Phillips, 2002).

The first attempt to clarify the pathogenicity of some Botryosphaeriaceae species associated with grapevines was conducted by van Niekerk *et al*. (2004). This study showed the pathogenicity of 12 Botryosphaeriaceae species based on both *in vitro* and *in vivo* pathogenicity assays. Whereas *in vitro* assays conducted on excised grapevine green shoots showed *N. australe* and *N. parvum*, and *D. seriata* and *Phaeobotryosphaeria porosa* to be the most and least virulent species, respectively; *in vitro* assays conducted on mature excised canes showed *N. ribis* and *N. australe* to be the most virulent species, and *N. luteum* and *L. theobromae* to be the least virulent. On the other hand, when inoculations were done both on canes attached to the vine and on mature wood, the species that caused the most severe lesions were *L. theobromae*, *N. australe*, *N. parvum*, and *P. porosa*. The symptoms recorded both in mature canes and wood were primarily dark streaking of the wood, which was similar to symptoms observed in the field (van Niekerk *et al*., 2004). These results obviously indicated that the role of Botryosphaeriaceae species in grapevine diseases was more important than originally thought, and thus needed to be more carefully considered. Results from this study showed virulence of Bo-tryosphaeriaceae species to vary depending on the type of inoculated tissue. However, results from the *in vitro* assays should be carefully interpreted since the incubation conditions (continuous darkness, high relative humidity and high temperature) favored the growth of the fungi and did not accurately resemble those occurring in the field. Moreover, no final conclusions regarding the pathogenicity and virulence of the Botryosphaeriaceae species tested in the *in vivo* assay could be made, since multiple isolates for each species were not tested. Shortly after, Auger *et al*. (2004) showed that 20 weeks after artificially inoculating Red Globe grapevine cuttings with *D. seriata* they exhibited light-brown streaks in the wood identical to symptoms observed in naturally infected vines in Chile. Between 2004 and 2007, Koch's postulates confirmed the pathogenicity of several Botryosphaeriaceae species on grapevines in Australia, reporting *L. theobromae*, *N. australe* and *N. luteum* as the most virulent species causing both vascular discoloration and perennial cankers in the wood (Taylor *et al*., 2005; Wood and Wood, 2005; Savocchia *et al*., 2007). Several isolates of each Botryosphaeriaceae species were tested in these studies showing a high variability in virulence within isolates of the same species. Thereafter, Úrbez-Torres *et al*. (2008) were able to reproduce the wedge-shape canker symptom observed in symptomatic vines in Mexico by inoculating rooted grapevine cuttings with *D. seriata* and *L. theobromae*. Moreover, this study showed *L. theobromae* isolates from Mexico to be capable of killing both Chardonnay and Thompson Seedless rooted cuttings 8 weeks after inoculation, and thus demonstrated the high virulence of this species on grapevines. Isolates of *D. seriata* were shown on the other hand to be less virulent. Additionally, virulence among isolates of both species varied depending on the inoculated tissue (mature canes vs. green-shoot) or grapevine cultivar (Úrbez-Torres *et al*., 2008). Later pathogenicity studies corroborated the high virulence of *L. theobromae* isolates obtained from mature vines in Italy (Burruano *et al*., 2008) and from mother rootstock plants in Spain (Aroca *et al*., 2008). Although these studies presented enough evidence to confirm the role of Botryosphaeriaceae species as grapevine wood colonizers, the fact that the same botryosphaeriaceous fungi were associated with different vascular symptoms along with discrepancies in virulence among Botryosphaeriaceae species reported from different countries, still created confusion among researchers.

Discrepancies in virulence among Botryosphaeriaceae species from different countries probably relate to differences in isolate origin, type of inoculated tissue, short incubation periods,

type of inoculum used, age of the host, or differences in cultivar susceptibility, among other possible factors. New attempts have been made recently in the USA to clarify the pathogenicity and virulence of Botryosphaeriaceae species on grapevines. Úrbez-Torres and Gubler (2009a) conducted a pathogenicity study in which a total of 72 isolates representing nine different Botryosphaeriaceae species were tested in five different pathogenicity tests, which included inoculation of five different types of wood tissue from different *V. vinifera* cultivars using either mycelium or spore suspension inoculum. Additionally, incubation periods varied from 6 to 24 months. Overall, this study showed all nine Botryosphaeriaceae species tested were able to infect both young and mature tissues as well as green shoots of the new vegetative growth, causing cankers, vascular discoloration, or otherwise dark streaking of the wood. Virulence was shown to vary between species and among isolates within the same species. *Lasiodiplodia theobromae* was confirmed as the most virulent species followed by *N. luteum*, *N. parvum*, and *N. australe*, all categorized as highly virulent. *Botryosphaeria dothidea*, *D. mutila* and *D. seriata* were considered intermediately virulent while *D. iberica*, and *S. viticola* were shown to be weakly virulent. Moreover, inoculation of mature wood showed that wood colonization by *L. theobromae*, *N. australe*, *N. parvum*, and *N. luteum* occurred up to three times faster when compare to the well-known wood pathogen *E. lata*. Luque *et al*. (2009) confirmed some of the pathogenicity results reported in California, showing *N. parvum* and *N. luteum* as highly virulent species, *B. dothidea* as moderately virulent, and *D. seriata* as the least virulent species in a study conducted in Spain. Subsequent studies confirmed the high virulence of *L. theobromae* and *N. parvum* on grapevines in the USA and added *D. corticola*, *L. crassispora*, *L. missouriana*, *L. viticola*, *N. mediterraneum*, and *N. ribis* as important grapevine pathogens in that country (Úrbez-Torres *et al*., 2009; Úrbez-Torres *et al*., 2010b; Úrbez-Torres *et al*., 2010c; Úrbez-Torres *et al*., 2011). As a result of all these studies, the importance of Botryosphaeriaceae as grapevine trunk disease pathogens was finally accepted. Consequently, it was suggested that species of Botryosphaeriaceae infecting grapevines could be divided into three different virulence rankings including, highly virulent species (*Lasiodiplodia* spp. and *Neofusicoccum* spp.), moderately virulent (*B. dothidea* and *Diplodia* spp.) and slightly virulent (*Dothiorella* spp. and *S. viticola*).

Phaeobotryosphaeria porosa was found either highly or slightly virulent on grapevines depending on the tissue that was inoculated (van Niekerk *et al*., 2004). These results along with the lack of further studies on the pathogenicity of this species make it difficult to add *P. porosa* to any of the virulence rankings at the present time.

Phytotoxic metabolites

While pathogenicity studies have resolved the status of Botryosphaeriaceae species as grapevine pathogens and have been able to establish a firm correlation between the different wood symptoms observed and the different Botryosphaeriaceae species isolated from them, the relationship between the botryosphaeriaceous fungi found in the diseased wood and the foliar symptoms observed in some declining vines is still not well understood. Several studies have shown bio-active toxic metabolites to be not only produced by different grapevine trunk disease pathogens but to be also the cause of disease symptoms, including the expression of foliar symptoms (Tabacchi *et al*., 2000; Mahoney *et al*., 2005; Rolshausen *et al*., 2008). Although extensive research has been done in identifying some exopolysaccharides (EPS) secreted by the botryosphaeriaceous fungi *L. theobromae* and *D. seriata* from non-grapevine isolates (Venkatasubbaiah and Chilton, 1990; Venkatasubbaiah *et al*., 1991; Barbosa *et al*., 2003; Crognale *et al*., 2003; Selbmann *et al*., 2003; Corradi da Silva *et al*., 2005), whether or not Botryosphaeriaceae species on grapevines produce toxic substances and their role in disease development was completely unknown. Recently, Martos *et al*. (2008) showed for the first time that five Botryosphaeriaceae species (*B. dothidea*, *D. seriata*, *N. luteum*, *N. parvum*, and *S. viticola*) involved in decline of grapevines, were capable of producing hydrophilic high-molecular weight compounds with phytotoxic properties, which were thought to be EPS. Further analyses of the EPS produced by *N. parvum* showed these substances to be composed mainly of glucose, mannose and galactose (Martos *et al*., 2008). This study also showed that

whereas *N. luteum* and *N. parvum* had the highest phytotoxic activity, *B. dothidea*, *D. seriata* and *S. viticola* showed low phytotoxicity levels, which shows some correlation with the results obtained from previous pathogenicity assays. Additionally, both *N. luteum* and *N. parvum* produced lipophilic, acid, low-molecular weight phytotoxins (Martos *et al*., 2008). Moreover, withering of the leaves and the appearance of necrotic and discoloured spots were shown when grapevine leaves were immersed in *N. parvum* culture filtrate. However, identification of the chemical structures of the phytotoxic compounds produced by the different Botryosphaeriaceae species was not assessed in this study. More recently, some of those lipophilic, low-molecular weight phytotoxins were identified and characterized for first time to be produced by one isolate of *N. parvum* from grapevines, and included (3R,4R)-(-)-4-hydroxymellein, (3R,4S)-(-)-4-hydroxymellein, isosclerone, and tyrosol (Evidente *et al*., 2010). All four metabolites produced leaf wilting when tested on tomato plants, with (3R,4S)-(-)-4-hydroxymellein and isosclerone causing the most severe wilting. Additionally, a different study identified four toxic compounds, mellein, 4-hydroxymellein, 7-hydroxymellein, and 4,7-dihydroxymellein from a grapevine isolate of *D. seriata* (Djoukeng *et al*., 2009). Although all of these compounds possessed a similar level of toxicity, 4,7-dihydroxymellein caused full grape leaf necrosis. As speculated by the authors in all these studies, it is possible that the production of these compounds may induce phytotoxic effects on Botryosphaeriaceae-infected grapevines. However, further investigations need to be conducted, such as *in vivo* inoculations as well as detection of these phytotoxic compounds in grapevines infected by Botryosphaeriaceae species, to better understand the role that these and other toxic compounds could play on disease symptom expression.

Botryosphaeriaceae as grapevine endophytes

Since species of Botryosphaeriaceae were first described, research has been mainly focused in studying their role as plant pathogens. However, the potential role of Botryosphaeriaceae species as plant endophytes has also been considered. Nevertheless, the importance of botryosphaeriaceous fungi both as endophytes and latent pathogens was not fully recognized until the 1990s, when several species within this family were shown to be commonly found in asymptomatic xylem tissue of different native and introduced forest trees as well as woody perennial crop plants (Johnson *et al*., 1992; Fisher *et al*., 1993; Smith *et al*., 1996; Stanoz *et al*., 1997). Nowadays, it is well-known that several species within this family are common endophytes, which in some cases are found to dominate the endophytic community of several hosts (Smith *et al*., 1996; Burgess *et al*., 2005). A detailed review on the diversity, ecology and impact of Botryosphaeriaceae species as endophytes and latent pathogens of woody plants has been published recently by Slippers and Wingfield (2007).

Although the endophytic phase of some fungi involved on grapevine trunk diseases is well-recognized (Mugnai *et al*., 1999; Mostert *et al*., 2000), the status of Botryosphaeriaceae species as endophytes on grapevines is still not clear. Nevertheless, several studies conducted in the past decade have produced evidence that suggests an endophytic role of these fungi during the infection process on grapevines. Wood and Wood (2005) reported the isolation of *L. theobromae* from tissue within 2 cm of pruning wounds of 1-year-old spur positions with total absence of both external and internal discoloration. Furthermore, researchers in South Africa, Spain and Switzerland routinely isolated several Botryosphaeriaceae species from apparently healthy tissue in the graft union areas, wood of both scions and rootstocks, pruning wounds, pith, and in the basal ends of grapevine cuttings in nurseries (Halleen *et al*., 2005; Aroca *et al*., 2006; Giménez-Jaime *et al*., 2006; Casieri *et al*., 2009). Furthermore, Casieri *et al*. (2009) found a *Fusicoccum* sp. to be one of the most prevalent fungi isolated from asymptomatic planting material in Switzerland. Recently, a study conducted in central Spain to identify the endophytic mycota associated with grapevines showed *D. seriata*, *D. mutila* and *N. parvum* to be isolated from asymptomatic tissue of both of young and mature plants (González and Tello, 2011). However, contrary to what Casieri *et al*. (2009) reported, these botryosphaeriaceous fungi were shown to be among the least frequent fungi

isolated from apparently healthy tissue.

Based on these studies, it is reasonable to speculate that some Botryosphaeriaceae species could infect grapevines either in the field or during propagation in nurseries, and then persist as endophytes or latent pathogens in grapevine tissues. Mostert *et al*. (2000) described the term *true endophytes* as "fungi whose colonization never results in disease symptoms". To date, all Botryosphaeriaceae species thought to act as endophytes in grapevines have been either isolated from symptomatic vascular tissue or cause vascular discoloration when inoculated into grapevines. Therefore, the term *latent pathogen* (Mostert *et al*., 2000; Slippers and Wingfield, 2007) seems to better fit the role that has been described for some botryosphaeriaceous fungi on grapevines.

It has been shown that stress factors, especially water stress, can contribute to either activate disease development by latent pathogens or to exacerbate the severity of the symptoms caused by Botryosphaeriaceae in several hosts (Madar *et al*., 1989; Pusey, 1989a; Mullen *et al*., 1991; Ma *et al*., 2000). Recently, Luque *et al*. (2010) showed water stress to increase the length of necrosis in grapevines inoculated with *E. lata* and *N. parvum*. Similarly, Sosnowski *et al*. (2010a) showed that vines under severe stress in Australia (water and high temperature) were more susceptible to infection by *E. lata*. However, it is still not well understood which abiotic and/or biotic stress factors could be responsible for the potential transition from latent pathogen to pathogen in these fungi on grapevines. Therefore, it is clear at this point that further research will be necessary to elucidate the endophytic and/or latent pathogen status of Botryosphaeriaceae on grapevines.

Epidemiology

Much has been written in the subject of epidemiology of Botryosphaeriaceae species causing black rot (Spotts, 1977, 1980; Ferrin and Ramsdell, 1977, 1978; Becker and Pearson, 1996; Jermini and Gessler, 1996; Hoffman *et al*., 2002) and Macrophoma rot (Clayton, 1975; Milholland, 1991; Kummuang *et al*., 1996) of grapevines, so this will not be addressed in this review. Epidemiology of diseases caused by these fungi in perennial hosts other than grapevines has also been well studied (Pusey, 1989b; Michailides, 1991; Michailides and Morgan, 1993; Pusey and Bertrand, 1993). Under humid conditions, pycnidia of Botryosphaeriaceae species produce pycnidiospores that are generally exuded in gelatinous matrices forming cirrhi, which are ribbon-like masses of spores (Michailides and Morgan, 1993; Phillips, 2002). Spores are then disseminated during rainfall by the impact of water droplets on the fruiting structures. In order for infection to occur, spores must land on susceptible pruning wounds and then germinate. On the other hand, the large numbers of botryosphaeriaceous taxa involved in grapevine decline, along with the wide range of climatic conditions under which they are found, have complicated the elaboration of epidemiological studies of grapevine trunk diseases caused by these fungi (van Niekerk *et al*., 2006). However, some progress has been recently achieved elucidating their epidemiology thanks to research conducted in determining potential sources of inoculum, conditions that favour spore release, seasonal spore release patterns, seasonal susceptibility of pruning wounds, and factors that favour infection.

Sources of inoculum

Inoculum from grapevines

Pycnidia of Botryo-sphaeriaceae species are commonly found embedded in diseased woody parts of vines as well as in wood debris left in the vineyard after pruning (Lehoczky, 1974a, Leavitt, 1990, van Niekerk *et al*., 2004; Úrbez-Torres *et al*., 2006a). Additionally, because pycnidia and not perithecia are the main overwinter structures in Botryosphaeriaceae, dissemination of pycnidiospores is thought to be primarily water-splashed over relatively short distances (Ahimera *et al*., 2004; Baskarathevan *et al*., 2010; Úrbez-Torres *et al*., 2010a), and it is currently well-accepted that most of the inoculum leading to new infections is produced within vineyards. A recent study using endogenous molecular markers corroborated this hypothesis by showing that spore movement of *Neofusicoccum* spp. within a vineyard was detected up to a maximum of 2 m from the inoculum source in a single rainfall event (Baskarathevan *et al*., 2010). Although fruiting bodies on plant organs and pruning debris are considered to be one of the main sources of inoculum, infected propa-

gation material can also play an important role in the epidemic development. As described previously in this review, it is currently well-accepted that Bo-tryosphaeriaceae infections can take place during propagation in nurseries (Halleen *et al*., 2003; Giménez-Jaime *et al*., 2006). Giménez-Jaime *et al*. (2006) showed that whereas Botryosphaeriaceae species were not isolated from rootstock cuttings collected in winter and stored for 2 months (first step in the propagation process), these fungi (especially *D. seriata*) were frequently isolated from propagation material in all the following steps including, after storage and either before or after immersion in water, after grafting and callusing, and after being planted in nursery fields for rooting. This clearly demonstrated that infection can occur during the process. Also, the status of some Botryosphaeriaceae species as latent pathogens has been previously discussed. It has been shown that asymptomatic propagation material (rootstock and/or scion cuttings) from vineyards or mother plant fields already infected by botryosphaeriaceous fungi can enter into the nurseries and consequently into commercial vineyards (Fourie and Halleen, 2004a; Aroca *et al*., 2010). Recently, a study conducted by Aroca *et al*. (2010) to evaluate grapevine nursery propagation material as a potential source of inoculum of *Pa. chlamydospora* and *Phaeoacremonium* spp., revealed the botryosphaeriaceous taxa *D. seriata* and *N. parvum* to be the most prevalent fungi isolated from grapevine rootstock mother fields in Spain. The same study also found *B. dothidea*, *L. theobromae*, *N. mediterraneum*, and *N. vitifusiforme* in the propagation material, although only in nine out of the 140 plants surveyed. Consequently, these primary infections could remain latent in vineyards until conditions are favorable for disease development (biotic and/or abiotic stress), explaining the decline and even death of young vines caused by species in the Botryosphaeriaceae (van Niekerk *et al*., 2006).

Inoculum from non-grapevine hosts

Many Botryosphaeriaceae species, including some infecting grapevines, are known to be plurivorous occurring in many native or introduced flora as well as in a broad range of agricultural crops (Farr and Rossman, 2011) (Table 1). Many of these hosts are commonly found surrounding vineyards. The wide host range of this family could potentially provide an important source of primary inoculum in vineyards due to the numerous fruiting bodies produced on those hosts. This hypothesis has been proven to occur with infections caused by *E. lata* on grapevines, whose ascospores can be disseminated by wind over 100 miles from the source of inoculum (Ramos *et al*., 1975). Moreover, it was shown that *E. lata* isolates from different hosts were able to cause disease when inoculated into grapevines (Trouillas and Gubler, 2010). The widely accepted idea of Botryosphaeriaceae species as plurivorous fungi would support the cross-infection hypothesis between non-grapevine hosts and grapevines. However, only van Niekerk *et al*. (2004) has so far corroborated this theory, by proving that one isolate of *N. ribis* from *Ribes* sp. was very virulent when inoculated on grapevines. Additionally, the role that wind plays in conidium dissemination of Botryosphaeriaceae species, which may affect long distance dispersal, is currently unknown. Consequently, it is clear that based on the current information further research is needed to explain the role that inoculum from non-grapevine hosts surrounding vineyards has on the disease cycle.

Spore trapping studies

Spore trapping studies conducted during 2009 and 2010 in both Northern and Southern Hemisphere grape-growing regions have, to some extent, elucidated the climatic conditions that favour spore release by Botryosphaeriaceae species, and consequently have determined seasonal spore dispersal patterns (Amponsah *et al*., 2009a; Kuntzmann *et al*., 2009; Úrbez-Torres *et al*., 2010a; van Niekerk *et al*., 2010a). All four studies agreed in that conidia of these fungi are primarily released from fruiting bodies during rain events. Furthermore, Úrbez-Torres *et al*. (2010a) confirmed that in addition to rainfall, overhead sprinkler irrigation could trigger spore release in Californian vineyards. The seasonal spore dispersal patterns, on the other hand, varied among different locations. Kuntzmann *et al*. (2009) and Amponsah *et al*. (2009a) showed that spores of Botryosphaeriaceae were present throughout the year in France and New Zealand, respectively, but with the highest numbers of spores being de-

tected during the summer months. Úrbez-Torres *et al*. (2010a) showed that most Botryosphaeriaceae spores (60% of the total spores captured) were trapped following rain events during the winter months in California and that spore release was much lower in fall and early spring (22%), and very few or no spores were trapped in late spring and summer (3%). Van Niekerk *et al*. (2010a) also showed that spores of Botryosphaeriaceae are captured in high numbers during rain events in winter months in South Africa. However; spore trapping was only conducted from June to mid-September in South Africa ignoring possible spore release during spring, summer and fall of the Southern Hemisphere. Spore release of Botryosphaeriaceae species was detected during the occurrence of at least 0.2 mm of rain (Úrbez-Torres *et al*., 2010a; van Niekerk *et al*., 2010a). The seasonal spore release differences observed among these studies may be a consequence of variations in climatic conditions. Whereas in the Alsace region of France the main rainy season occurs from spring to fall, California weather conditions are marked by two distinct seasons, a rainy season (October to April) and a dry season. In New Zealand, although the highest precipitation during the time of the study was recorded during the winter months, the lower number of spores trapped compared to summer months was explained by the fact that after pruning there was a significant reduction of the inoculum present on the canes (Amponsah *et al*., 2009a).

Van Niekerk et al. (2010a) showed that spore release events and number of spores released were both dependant on high relative humidity (RH) and rainfall occurring before and during the period of spore release in South Africa. However, results of this study showed that in the absence of rainfall, spores of Botryosphaeriaceae were not captured even when RH was high. Similar results were reported by Úrbez-Torres *et al*. (2010a) in California, where spores of Botryosphaeriaceae were not usually trapped after 2 h after rainfall, even though RH was still high. High relative humidity can trigger spore release from pycnidia, but because spores of Botryosphaeriaceae appear to be less airborne than those for example of *E. lata*, the impact of water droplets from rain appears to be critical for spore dispersal to occur. Even though rainfall was recorded during the winter months in the Alsace region of France, Kunztmann *et al*. (2009) attributed the low capture of spores during some dates of that period to the low temperatures registered. On the other hand, authors have reported that a rise in temperature (max 9°C) accompanied by rains during the winter months resulted in large numbers of spores being captured. Amponsah *et al*. (2009a) also attributed the abundance of conidia during the summer months in New Zealand to an increase in temperatures. Úrbez-Torres *et al*. (2010a) showed, on the other hand, that spore release occurred in Californian vineyards during winter months when temperatures between 3 and 7°C were accompanied by rainfall, which was corroborate by van Niekerk *et al*. (2010a) in the study conducted in South Africa. *In vivo* studies conducted by Copes and Hendrix (2004) showed sporulation from pycnidia of *B. dothidea*, *D. seriata* and *L. theobromae* to occur at temperatures as low as 6°C. Consequently, it has been well-documented that Botryosphaeriaceae spore release can occur at low temperatures. On the other hand, temperatures close to or below 0°C may limit spore release from pycnidia in cool climate viticulture areas such as the Alsace region of France. However, the effect of freezing temperatures on spore release requires further investigation.

Pruning of grapevines in both California and South Africa takes place during the major rainfall periods and consequently during the main spore release periods. Thus, highly susceptible infection sites are readily available to the botryosphaeriaceous fungi, making the dormant season the highest risk infection period in these grape-growing regions. On the other hand, further research is still needed to clarify the significance of high spore release numbers during the growing season, observed in areas such as France and New Zealand, to determine how these fungi infect during the period when pruning wounds appear to be much less susceptible. Therefore, the result reported by Phillips (1998), that *B. dothidea* was capable of causing disease symptoms on unwounded grapevine shoots, might be significant in those situations. All these studies have contributed to a better understanding of the climatic factors that favour Botryosphaeriaceae spore release. However, it is still evident that

due to the high variation in climatic conditions among countries and even within regions in the same country, further epidemiological studies are required to elucidate the different seasonal spore release patterns for each particular grape-growing region.

Pruning wound susceptibility

Species in the Botryosphaeriaceae infect grapevines mainly through openings and wounds located in the framework of vines. Consequently, and as shown with other grapevine trunk disease pathogens (Petzoldt *et al*., 1981; Chapuis *et al*., 1998; Eskalen *et al*., 2007a), knowledge of the duration of pruning wound susceptibility appears to be a critical factor in better understanding epidemiology, and thus control, of the diseases they cause. Van Niekerk *et al*. (2007) showed that pruning wounds were susceptibile to infection by *N. australe* for up to 21 days during winter months in South Africa. This study showed that pruning wound susceptibility was very high during the dormant season and that it did not decline over time. However, the study was conducted only during one dormant season, and susceptibility was assessed for only 21 days after pruning. Serra *et al*. (2008) published a more comprehensive study on the susceptibility of pruning wounds to infection by *D. seriata* in Italy. Their study was conducted during three consecutive dormant seasons and pruning wound susceptibility was assessed each week for up to 4 months after pruning in January, February and March. Although pruning wound susceptibility was shown to decline over time in two out of the three dormant seasons, overall results revealed that wound susceptibility remained high for up to 4 months after pruning, even in late spring when grapevines were bleeding. Furthermore, fresh wound susceptibility (wounds inoculated immediately after pruning) was shown to be greater in March than in January in two of the dormant seasons. Different results were reported from a 2 year study in California by Úrbez-Torres and Gubler (2011). Susceptibility of pruning wounds was evaluated in two different cultivars from November to March up to 84 days after pruning. Grapevine pruning wounds were susceptible to infection by *L. theobromae* and *N. parvum* throughout the dormant season in California, but susceptibility of pruning wounds was greatest when inoculations were done immediately after pruning, and decreased as the interval between pruning and inoculation increased. Furthermore, susceptibility of fresh pruning wounds was less when vines were pruned in early March compared to pruning in November, December, January or February in California. This study also showed a positive correlation between the increment of temperatures and decline of pruning wound susceptibility in January and February. Among many different environmental factors, it has been well-documented that decline in susceptibility of pruning wounds over time in perennial plants is strongly correlated with increases in temperature, which accelerates the wound-healing process (Bostock and Stermer, 1989). Moreover, and as previously reported with infections caused by *E. lata* (Chapuis *et al*., 1998), Úrbez-Torres and Gubler (2011) showed that pruning wound susceptibility to infection by species in the Botryosphaeriaceae did not differ between 1- and 2-year-old wood.

Parallel to what has been reported in spore trapping studies, some divergence among grape-growing regions has also been shown regarding pruning wound susceptibility to infection by Botryosphaeriaceae. All three studies evaluated pruning wound susceptibility using different Botryosphaeriaceae species on different grapevine cultivars and under completely different environmental conditions, all factors which could differently affect both biological and physiological wound responses. Also, the cited studies relied entirely on artificial inoculations of pruning wounds, and thus did not determine the minimum inoculum potential needed for the establishment of infections. Consequently, it could be speculated that an excessive "inoculum pressure" could overpass the natural healing of wounds and artificially extend pruning wound susceptibility periods. The lack of more studies in this area makes it difficult to determine other factors that could explain these discrepancies. Finally, whether or not pruning wounds remain susceptible to infection by Botryosphaeriaceae throughout the growing season has not been evaluated yet. This information could be valuable in areas where release of spores has been reported to be quite high throughout both late spring and summer. Eskalen *et al*. (2007a) reported fresh prun-

ing wounds to be susceptible to infection by *Pm. aleophilum* and *Pa. chlamydospora* regardless of the time of pruning from February to December in California.

Geographical distribution of Botryosphaeriaceae species

Although species of Botryosphaeriaceae occur in grape-growing regions worldwide (Table 2), recent studies have shown geographical differences in their distribution, mainly attributed to climatic conditions (Leavitt, 1990; Taylor *et al*., 2005; van Niekerk *et al*., 2006; Úrbez-Torres *et al*., 2006a; Úrbez-Torres *et al*., 2008; Pitt *et al*., 2010). Although there are currently 21 different Botryosphaeriaceae species known to infect grapevines, these geographical differences have been mainly attributed to *L. theobromae*. Leavitt (1990) reported two different *L. theobromae* biotypes in California, which he designated as low and high temperature tolerant, respectively. Whereas the low temperature tolerant biotype was shown to have optimal growth at 25–30°C and to be isolated mainly from grapevines in both northern California and the San Joaquin Valley, the high temperature tolerant biotype had optimal growth at 35–40°C. This biotype was not only the more prevalent in vineyards of southern San Joaquin Valley but was the only one reported to occur in the Coachella Valley, the warmest and driest grape-growing region in California. Although several years later Úrbez-Torres *et al*. (2006a) showed that the low temperature tolerant biotype was indeed *D. seriata*, Leavitt (1990) was the first investigator to propose that climate differences may influence the geographical distribution of some Botryosphaeriaceae species on grapevines. Recent studies conducted in Australia (Taylor *et al*., 2005; Pitt *et al*., 2010), Mexico (Úrbez-Torres *et al*., 2008), and in California (Úrbez-Torres *et al*., 2006a) and Arizona (Úrbez-Torres *et al*., 2007b) in the USA have corroborated Leavitt's observations, showing *L. theobromae* to be either the most prevalent or the only Botryosphaeriaceae species isolated from the warmest regions of those countries. *Lasiodiplodia theobromae* is known to be a pleomorphic and plurivorous Ascomycete occurring mostly in tropical and subtropical climate regions (Punithalingam, 1976). The possible association between climate and geographical distribution of *L. theobromae* is reinforced by the fact that *L. theobromae* has not been isolated from any field survey conducted in cool climate viticulture regions such us Canada (Chamberlain *et al*., 1964; O'Gorman *et al*., 2010) and northeastern USA vineyards (Úrbez-Torres *et al*., 2007b; Rolshausen and Wilcox, 2009), in which *B. dothidea* and *N. parvum* were the most prevalent species. In Europe, *L. theobromae* has been reported to occur only in the warm Mediterranean grape-growing regions of Spain (Aroca *et al*., 2008) and in Sicily, the south of Italy, again one of the warmest areas of that country (Burruano *et al*., 2008). Additionally, among all Botryosphaeriaceae species infecting grapevines, studies have shown *L. theobromae* to have both optimum mycelium growth and spore germination at the highest temperature (30–40°C). This supports the conclusions that climatic conditions are one of the possible causes of the geographical differences observed in *L. theobromae* (Leavitt, 1990; Copes and Hendrix, 2004; Úrbez-Torres *et al*., 2006a; Úrbez-Torres *et al*., 2008; Úrbez-Torres *et al*., 2010d).

Results from these studies also revealed that among all Botryosphaeriaceae species studied, conidia of *D. seriata* showed the greatest germination percentage and optimum mycelial growth under the widest range of temperatures (10–40°C), which may explain why this species is probably the most cosmopolitan botryosphaeriaceous fungus infecting grapevines. To date, *D. seriata* has been reported to be the only one of these fungi to occur in all grape-growing regions (Table 2). The fact that conidia of botryosphaeriaceous fungi are capable of germination under a broad range of temperatures, including those considered to be extreme, may explain the success of these species as grapevine pathogens throughout most of the grape-growing areas in both Northern and Southern Hemispheres. Another example of the specific geographical distribution of a botryosphaeriaceous fungus could be *G. bidwellii*, which only causes disease in grape-growing regions characterized by warm and humid conditions during summer.

Temperature might also affect the virulence of some species in the Botryosphaeriaceae. This has been observed by Úrbez-Torres and Gubler, (unpublished data), when Thompson Seedless

dormant cuttings were inoculated with different *L. theobromae* isolates from the desert regions of Mexico and California and incubated at different temperatures (10–40°C) (Figure 3l). Thirty days after inoculation, virulence of *L. theobromae* isolates varied dramatically depending on temperature. Whereas wood necrosis was barely observed at 10 and 15°C, virulence of *L. theobromae* isolates (measured as length of vascular discoloration) increased as temperature was raised from 20°C (mean discoloration length = 44.5 mm) to 35°C (mean length = 252.7 mm) (Figure 3l). Necrosis of the wood was also observed at 40°C (27.2 mm) (Figure 3l). These preliminary results may explain the high adaptability and infection success that *L. theobromae* possesses in desert-like grape production areas. There is insufficient evidence to reach a conclusion on this matter, so further research needs to be conducted, but these observations might add insights as to the main period in which wood colonization occurs by some species in the Botryosphaeriaceae. Although most of the infections have been shown to occur during the dormant season after pruning, colonization and consequent degradation of the grapevine wood might primarily occur during the growing season after an increase in temperature. Among several factors, temperature affects the activity of secondary metabolites in plant pathogenic fungi, including those related to degradation of wood cell walls, and thus probably determining their virulence (Wells and Boddy, 1995; Rolshausen *et al*., 2008; Alfonzo *et al*., 2009; Valtaud *et al*., 2009).

Control strategies

Control measures for grapevine diseases caused by species in the Botryosphaeriaceae currently include the use of both chemical and biological spray programs, vineyard sanitation and cultural practices. However, the strategies used to manage fruit rot diseases and grapevine trunk diseases caused by botryosphaeriaceous fungi differ considerably and thus, they are separately described here.

Black rot and Macrophoma rot diseases of grapevines affect all green parts of vines, and consequently, their control is mainly based on fungicide applications during the growing season. However, the success of any fungicide program has been shown to be greatly enhanced if combined both with sanitation and cultural practices designed to reduce the amount of inoculum in vineyards. This is critical in grape-growing regions where these diseases are a permanent problem (Milholland, 1991; Wilcox, 2003). Infected berries (mummies) left in vineyards, either attached to the canes or on the ground are the main source of inoculum for the infection in the next growth season. Removing all mummies when pruning during the dormant season, and cultivating beneath the vines near bud break to bury them, are probably the best sanitation practices to greatly reduce the number of spores released. *Guignardia bidwellii* has been shown to overwinter for at least 2 years within lesions of infected shoots (Wilcox, 2003). Therefore, severe pruning followed by either chopping up the shoots for incorporation into the soil, or shoot removal from the vineyard and elimination by means of burning or other methods, will significantly improve inoculum reduction. Moreover, implementation of cultural practices such as planting grapevines in areas with good air circulation and appropriate leaf removal during the growing season, will not only reduce disease severity by lowering the humidity and thus speeding up the drying of leaves and berries, but will also provide better spray penetration and coverage (Milholland, 1991; Wilcox, 2003). Most fungicides and spray schedules recommended for control of grapevine fruit rots, including Black rot and Macrophoma rot, arose from studies conducted by Clayton (1975) between 1966 and 1974 (Milholland, 1991). Currently, there are over 20 different commercial fungicides available for the control of black rot, from which at least 16 are highly effective (Bordelon *et al*., 2011). Spray programs for black rot start early in the growing season (bud break to 10 cm shoot stage) and protective fungicides must be applied routinely (10- to 14-day intervals) until grape berries start to become resistant to infection. This occurs when berries reach full size and sugar content starts to increase (veraison). Hence, sprays should not be needed after berries start to ripen (Bordelon *et al*., 2011). However, type of fungicide and frequency of application will especially depend on climatic conditions through the growing season, cultivar susceptibility and

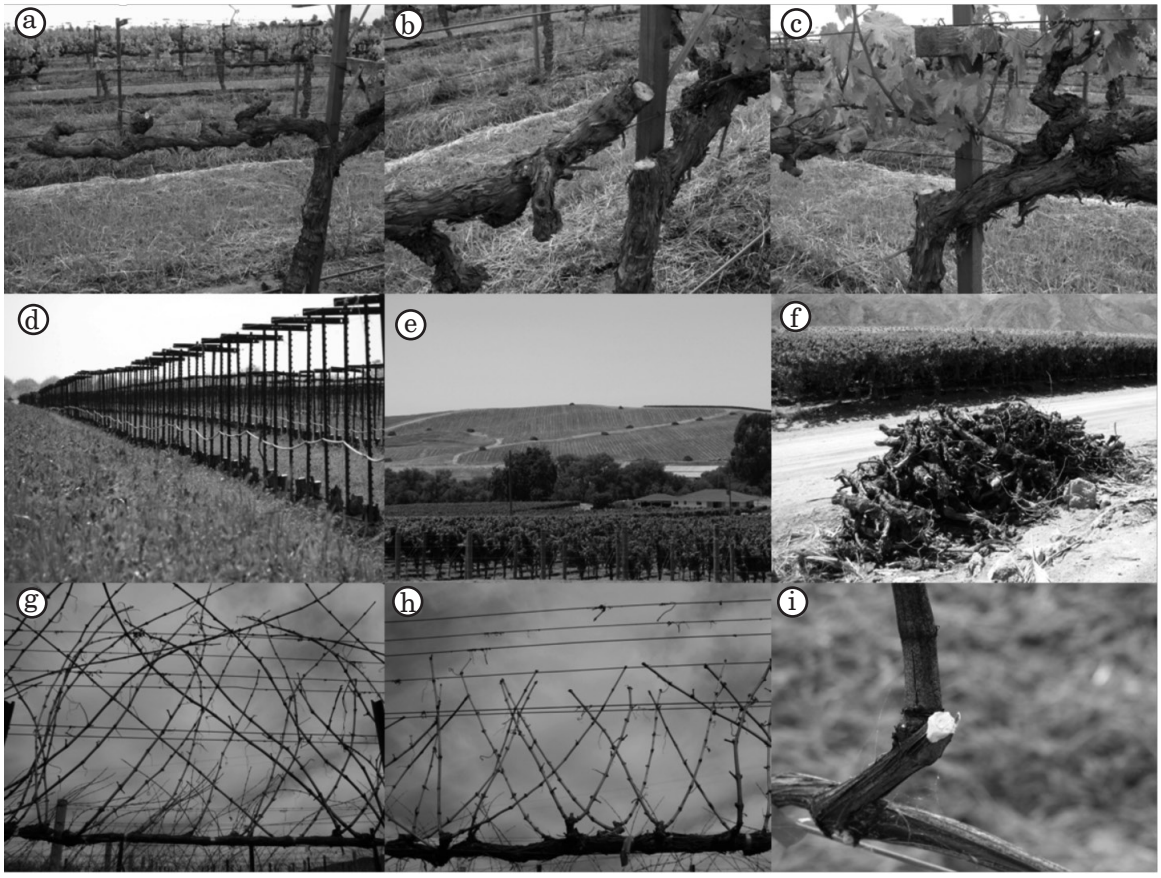

Figure 5. a–c. Remedial surgery. Pruned dead cordon and replacement by a healthy shoot located in the other healthy cordon. (Pictures courtesy of G.M. Leavitt, University of California Davis Cooperative Extension, Madera, USA). d. If infection reaches the trunk, re-training must be done from shoots from buds above the graft unions or from suckers if vines are own-rooted. e. Mature vineyards with high disease pressure make fruit production economically nonviable and consequently need to be eventually pulled out, which causes significant economic losses to the grapevine industry. f. All pruned debris must be eliminated from vineyards to avoid build up of inoculum. g–h. Double pruning of grapevines has been shown to reduce infections caused by Botryosphaeriaceae species in California. i. Fungicides incorporated into pruning wound sealant pastes are used to protect wounds from new infections.

amount of initial inoculum, which will determine disease severity. Consequently, different spray calendars may be necessary depending on the grape-growing region (Bordelon *et al*., 2011; Sutton and Burrack, 2011; Wilcox, 2011). While *V. vinifera* is very susceptible to black rot, *Vitis* spp. such as *V. rupestris*, *V. berlandieri*, *V. cordifolia*, *V. riparia*, and *V. candicans* are highly resistant (Ramsdell and Milholland, 1988). A complete spray program for black rot should help to prevent early Macrophoma rot infections. However, *B. dothidea* is still able to cause late infections on muscadine grapes, and hence, if conditions are favorable, Macrophoma rot symptoms will significantly increase as berries ripen. Fungicide applications in areas where the disease is prevalent must, therefore, continue through the fruit ripening period until harvest. Very efficient fungicides are currently available to control Macrophoma rot on muscadine grapes (Cline and Burrack, 2011). Additionally, resistant muscadine cultivars such as Hunt and Scuppernong are available (Milholland, 1991).

While much has been investigated in controlling grapevine fruit rots since the mid 20th century, no efficient control strategies of grapevine

trunk diseases caused by species in the Botryosphaeriaceae were available until recently, due to the very limited information on disease etiology and epidemiology. Although great progress has been made in developing and implementing novel control techniques against these diseases throughout the last decade, management is still extremely difficult due to the wide range of different species causing disease. Furthermore, the cosmopolitan distribution of Botryosphaeriaceae species causing grapevine trunk diseases means that efficient control strategies developed in one grape-growing region may not be effective in others, as a result of variability in climatic conditions and hence, possible differences in species occurrence and epidemiology. Management of grapevine wood diseases caused by species in the Botryosphaeriaceae has been traditionally achieved by remedial surgery, a control method widely used to prolong the life of grapevines infected by *E. lata* (Figures 5a-c) (Carter, 1991; Sosnowski *et al*., 2008; Sosnowski *et al*., 2010b). Remedial surgery includes pruning out all infected wood in cordons and/or trunk at least 10 cm below the visible vascular symptoms (canker and/or dark streaking of the wood). Vines need then to be re-trained from healthy shoots coming from buds located in either spur positions or trunk (above graft-unions) to replace those sections of the vine killed by the disease (Figure 5d). If the infected vines are own-rooted, the suckers coming from below the ground have been shown to be the best for re-training (Leavitt, 1990). Application of pruning wound protectants on big cuts left after surgery is highly recommended to extend the protection period against species in the Botryosphaeriaceae, if re-training is done when the highest inoculum concentration is present (i.e. dormant season in California). In these cases, it is recommended to conduct this strategy during the dry weather months of summer. Additionally, because numerous fruiting bodies (pycnidia) of several species in the Botryosphaeriaceae have been found on pruning debris left in vineyards (Úrbez-Torres *et al*., 2006a), removing and destroying all diseased wood is essential to reduce inoculum sources and avoid new infections (Figure 5f). If re-training is not possible, the best recommendation is to remove infected vines to avoid building up of inoculum (Figure 5e). Remedial surgery has been used to effectively control Botryosphaeria canker of grapevines in California since the disease was first observed (Leavitt, 1990), and is still used in high cash return mature vineyards, since this technique offers several advantages over replanting, including preservation of the original clones, fruit quality, faster return into production, and robustness as a result of a well-developed root systems (Creaser and Wicks, 2004). However, remedial surgery can be labor intensive, requires high-skilled workers and at the present time, is economically non-viable in many grape-growing regions worldwide. A recent study has shown that the cost of cutting vines 30 cm above the graft unions along with all vineyard operations required to train the new shoot was about $US 4.2 per vine or about $US 5,300 per ha in California (Epstein *et al*., 2008). Consequently, the development and implementation of novel chemical, cultural and organically efficient and cost-effective control methods for diseases caused by Botryosphaeriaceae have recently become the main focus of study. Double pruning, a cultural practice widely used to reduced infections caused by *E. lata* in California (Weber *et al*., 2007), was proven to also be very efficient in reducing infections caused by *L. theobromae* and *N. parvum* (Úrbez-Torres and Gubler, 2009b) (Figures 4g-h). Double pruning ensures that final wounds are made when pathogens are least likely to successfully colonize exposed tissue, either because their presence in the environment is limited or because of decreased pruning wound susceptibility. However, this technique is only economically viable if the first pruning pass is done mechanically, reducing its application to solely vertical shoot positioning (VSP) training system vineyards. Additionally, this technique may not be as effective as in California in grape-growing regions where both inoculum and wound susceptibility are still high by the end of the dormant season, as is the case in grape-growing regions of France (Kuntzmann *et al*., 2009) and New Zealand (Amponsah *et al*., 2009a).

Because species in the Botryosphaeriaceae infect grapevines primarily through wounds, most of the strategies developed to control these pathogens have been based on protection of pruning wounds (Figure 5i). Leavitt (1990) was the first to show success in reducing the incidence of in-

fection caused by *L. theobromae* by applications of benomyl, captan, iprodione, and penconazole fungicides as pruning paint protectants on fresh pruning wounds. This study showed, on the other hand, that latex paint alone, widely used by then because it was thought to protect pruning cuts in fruit trees, reduced infection to some extent but was not acceptable as a control method. However, application of a similar durable paint on big cuts left after surgery was shown to be effective in controlling infections caused by *D. seriata* (Epstein *et al*., 2008). Discrepancies in the results observed regarding the effectiveness of latex paints between these two studies may be a consequence of virulence differences between *L. theobromae* and *D. seriata*. However, factors such as material application procedures, differences in type of material applied, seasonal environmental conditions, and host susceptibility, among many others, may explain the differences observed between the two studies. Savochia *et al*. (2005), based on *in vitro* assays, found tebuconazole and fluazinam to be the most effective fungicides inhibiting mycelial growth of *D. seriata* and *N. luteum* isolates from Australia. Thereafter, Bester *et al*. (2007) evaluated ten different fungicides as potential grapevine pruning wound protectants against *D. seriata*, *L. theobromae*, *N. australe*, and *N. parvum* in South Africa. *In vitro* assays showed low concentrations of benomyl, tebuconazole, prochloraz manganese chloride (mc), and flusilazole to be very effective in inhibiting mycelial growth. Although glasshouse bioassays conducted on 1-year-old potted plants showed benomyl, tebuconazole and prochloraz mc as potential pruning wound protectants, the authors considered these results inconclusive due to the low and varied re-isolation incidences (Bester *et al*., 2007). Rolshausen *et al*. (2010) were the first to evaluate the efficacy of different fungicides as pruning wound protectants against species in the Botryosphaeriaceae in long-term experiments conducted in commercial vineyards in California. Among all the fungicides tested either as liquid or as paste solutions, thiophanate-methyl was the most efficeous chemical, achieving over 80% pruning wound protection against species in the Botryosphaeriaceae (Rolshausen *et al*., 2010). Thiophanate-methyl also gave very good protection against other grapevine trunk disease pathogens, including *E. lata*, *Pa. chlamydospora*, *Pm. parasiticum*, *Pm. aleophilum,* and *Pleurostomophora richardsiae* (Rolshausen *et al*., 2010). Active ingredients such as pyraclostrobin and cyproconazole plus iodocarb, as well as a boron-based paste, known to successfully reduce infections caused by *E. lata* (Rolshausen and Gubler, 2005), also gave some control of some of the Botryosphaeriaceae species tested (Rolshausen *et al*., 2010). A later study conducted in commercial vineyards in South Africa showed, on the other hand, that the fungicides flusilazole and benomyl, as well as several commercial *Trichoderma*- and *Bacillus*-based biological products, did not reduce Botryosphaeriaceae species infections compared to both inoculated and non-inoculated experimental controls (Halleen *et al*., 2010). In contrast, all these evaluated products performed very well in reducing infections caused by *E. lata*. Several chemical and biological products have been also shown to reduce infection caused by species in the Botryosphaeriaceae during the grapevine propagation process (Fourie and Halleen, 2006). Biological and chemical products tested to date against Botryosphaeriaceae sppecies as grapevine trunk disease pathogens are listed in Table 3. However, some of these fungicides are banned, or their use is restricted, in many countries. A clear example is benomyl, which has been withdrawn from use in all European Union countries and the USA.

Complete control of Botryosphaeriaceae and other grapevine trunk disease pathogens is virtually impossible at the present time due to the fact that single active ingredients are unlikely to control a wide spectrum of taxonomically different and sometimes unrelated fungi. Moreover, control is extremely difficult due to the high number of wounds made on individual vines each year and the long time that wounds remain susceptible (Rolshausen *et al*., 2010). Additionally, it is still not clear how long the pruning wounds can be protected by these treatments. Hence, the current high cost associated with hand application of pruning wound treatments, along with the possibility that more than one fungicide application is required to protect through the entire period of wound susceptibility, make these treatments economically non-viable in modern viticulture. Some growers

Table 3. Biological and chemical products tested against Botryosphaeriaceae species as grapevine trunk disease pathogens. Only active ingredients that have given positive effects in controlling botryosphaeriaceous taxa are included.

Active Ingredient	Formulation	Botryosphaeriaceae spp. tested	Reference
Bacillus subtilis[a]	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)
Benomyl[a]	Paste	*L. theobromae*	Leavitt (1990)
	Liquid	*D. seriata*, *L. theobromae*, *N. australe* and *N. parvum*	Bester *et al*. (2007)
	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)
Hydrogen peroxide[a]	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)
Boron[a]	Paste	*B. dothidea*, *D. seriata*, *L. theobromae* and *S. viticola*	Rolshausen *et al*. (2010)
Halogenated alcohols + water[a]	Liquid	Botryosphaeriaceae spp.[b]	Fourie and Halleen (2006)
Captan[a]	Paste	*L. theobromae*	Leavitt (1990)
	Liquid	Botryosphaeriaceae spp.[b]	Fourie and Halleen (2006)
Hydroxyquinoline sulphate[a]	Liquid	Botryosphaeriaceae spp.[b]	Fourie and Halleen (2006)
Cyproconazole + Iodocarb[a]	Paste	*B. dothidea*, *D. seriata*, *L. theobromae* and *S. viticola*	Rolshausen *et al*. (2010)
Fenbuconazole[a]	Liquid	*L. theobromae*	Herche and Gubler (2009)
Fenarimol	Liquid	*D. seriata*, *L. theobromae*, *N. australe* and *N. parvum*	Bester *et al*. (2007)
Fluazinam	n.a.	*D. seriata* and *N. luteum*	Savocchia *et al*. (2005)
Flusilazole[a]	n.a.	*D. seriata* and *N. luteum*	Savocchia *et al*. (2005)
	Liquid	*D. seriata*, *L. theobromae*, *N. australe* and *N. parvum*	Bester *et al*. (2007)
	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)
Myclobutanil[a]	Liquid	*L. theobromae*	Herche and Gubler (2009)
Penconazole	Paste	*L. theobromae*	Leavitt (1990)
Prochloraz manganese chloride[a]	Liquid	*D. seriata*, *L. theobromae*, *N. australe* and *N. parvum*	Bester *et al*. (2007)
Pyraclostrobin[a]	Liquid	*B. dothidea*, *D. seriata*, *L. theobromae* and *S. viticola*	Rolshausen *et al*. (2010)
Spiroxamine	n.a.	*D. seriata* and *N. luteum*	Savocchia *et al*. (2005)
Didecyldimethyl-amonium chloride[a]	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)
Tebuconazole[a]	n.a.	*D. seriata* and *N. luteum*	Savocchia *et al*. (2005)
	Liquid	*D. seriata*, *L. theobromae*, *N. australe* and *N. parvum*	Bester *et al*. (2007)
Thiophanate-methyl[a]	Liquid	*B. dothidea*, *D. seriata*, *L. theobromae* and *S. viticola*	Rolshausen *et al*. (2010)
	Liquid	*L. theobromae*	Herche and Gubler (2009)
Trichoderma harzianum[a]	Liquid / Paste	Botryosphaeriaceae spp.[b]	Fourie and Halleen (2006)
	Liquid	Botryosphaeriaceae spp.[b]	Halleen *et al*. (2010)

[a] Active ingredients also evaluated for grapevine trunk disease pathogens other than Botryosphaeriaceae spp.
[b] Species of Botryosphaeriaceae tested were not specified.
na, Not applicable.

have tried to reduce the cost associated of treatments by applying them only to older wounds. However, epidemiological studies showed that both 1- and 2-year-old wounds are susceptible to infection by species in the Botryosphaeriaceae, so pruning wound protection treatments should be applied to all wounds (Úrbez-Torres and Gubler, 2011). Pruning wound protection using tractor applied spray programmes, on the other hand, can reduce cost significantly and make it feasible to quickly treat large vineyards. Recent research conducted at the University of California Davis has evaluated different fungicides including, fenbuconazole, myclobutanil and thiophanate-methyl using spray applications directly onto pruning wounds (Herche and Gubler, 2010). Although promising results in controlling species in the Botryosphaeriaceae and other grapevine trunk disease pathogens resulted from a single directed fungicide spray, control was enhanced when the different fungicides were amended with an organosilicone surfactant applied to dormant pruning wounds (Herche and Gubler, 2010). Wound protection by fungicide sprays may complement late pruning by ensuring that inoculum present on vulnerable sites fails to colonize the host resulting in an extra protection periods.

Finally, the detection of Botryosphaeriaceae spp. in the wood of scion and rootstock mother plants used for propagation in nurseries (Halleen *et al*., 2003; Fourie and Halleen, 2004a; Aroca *et al*., 2010), in the graft unions both of mature and young vines (Lehoczky J., 1974b; Rumbos and Rumbou, 2001; Phillips, 2002), as well as the possibility of clean material being infected during the propagation process by these fungi (Giménez-Jaime *et al*., 2006), suggests that appropriate sanitation practices should be used in nurseries to reduce the viability of botryosphaeriaceous fungi. Chemical and hot water treatments have both been successfully used to reduce infection by *Cylindrocarpon* spp., as well as *Pa. chlamydospora* and *T. minina*, the causal agents of black-foot and Petri disease, respectively in grapevine propagating material (Fourie and Halleen, 2004b; Edwards *et al*., 2004; Eskalen *et al*., 2007b; Halleen *et al*., 2007; Gramaje *et al*., 2009; Gramaje and Armengol, 2011; Alaniz *et al*., 2011). Although no such studies have been reported for species in the Botryosphaeriaceae, chemical and hot water treatments may have potential to be used as a management strategy for reducing infection caused by these fungi during the nursery propagation, and thus, further research on these subjects needs to be accomplished.

Conclusions

For over 60 years there has been a general lack of publications reporting studies on species in the Botryosphaeriaceae causing grapevine diseases. However, much has been written in the last decade regarding the role that members of this family play in grapevine health. Consequently, several botryosphaeriaceous fungi are now well-recognized as important grapevine pathogens worldwide, causing leaf spots, fruit rots, shoot dieback, bud necrosis, wood necrosis, and perennial cankers. Furthermore, research conducted in different countries has contributed to greater understanding of the etiology of grapevine diseases caused by botryosphaeriaceous fungi, as well as elucidation, to some extent, of their pathogenicity, virulence, epidemiology, biology and management. Detailed morphological characters and numerous DNA sequences are currently available, which has greatly facilitated identification and discrimination among species in the Botryosphaeriaceae. Furthermore, exhaustive information has been provided regarding the pathogenicity and virulence of each species in this family, in different countries, highlighting which species may represent major threats to the grapevine industry. Additionally, the disease name Botryosphaeria dieback is proposed to describe the different symptoms caused by Botryo-sphaeriaceae species as grapevine trunk disease pathogens. Novel diagnostic methods have been implemented contributing to rapid, accurate and inexpensive detection of these fungi from symptomatic and asymptomatic grapevine tissues, which will enhance further studies on the biology of these pathogens and epidemiology of the diseases they cause on grapevine. Although completely effective control has yet to be achieved, different vineyard sanitation procedures, as well as several chemical, biological and cultural management strategies, have been developed and

implemented in different countries in efforts to reduce the risk of disease caused by these fungi. These control methods will prolong production from vineyards. However, the wide spectrum of different Botryosphaeriaceae species capable of infecting grapevines, along with the possibility that they can co-infect with taxonomically unrelated fungi, makes chemical control strategies extremely difficult. Consequently, further research is needed to address this issue. Additionally, grapevines symptoms caused by species in the Botryosphaeriaceae as well as species occurrence, virulence, biology, and epidemiology have been shown to vary from country to country and even from different grape-growing areas within the same country due particularly to differences in climatic conditions, grape cultivars and/or *Vitis* spp. grown and grapevine cultivation. Consequently, is probably that individual studies will be required in different geographical regions to determine all the biological and epidemiological factors that will result in the best possible and efficient control strategies for each location.

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