

Fungal community of grapevine trunk diseases: a continuum of symptoms?

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The fungal community of grapevines affected with trunk diseases was studied in different grape growing regions of Uruguay. Plants with symptoms were sampled and fungi were isolated from diseased tissues for morphological identification. Following surface disinfection, wood fragments were placed on Petri dishes containing PDA for fungal isolation. Identified species were classified in their corresponding genera, and the relative density of each genus was calculated. Correspondence analyses to assess the associations of genera with symptoms and with geographic region were carried out. Black-foot symptom was separated from the symptoms affecting the aerial portions of the trunk: phaeotracheomycosis, esca and dead-arm. These latter symptoms shared a group of pathogenic fungal species which were not specific to any of them and therefore a continuum of species became evident. Geographical distribution of genera was homogenous throughout the country, with only *Greeneria uvicola* and *Eutypella vitis* being specific for the warmer or cooler regions, respectively.

Key words: esca, black-foot, dead-arm, Bot. canker, eutypiose, Petri, Uruguay, *Vitis*.

Trunk diseases of grapevines have been observed for centuries, and their study have had different waves and intensities (Surico 2009). These diseases have been better delimited according to recently described genera and species whose pathogenicity has been demonstrated (Moller and Kasimatis 1978; Mugnai 1999; Crous & Gams 2000; Halleen *et al.* 2004, 2007; Mostert *et al.* 2006; Úrbez-Torres & Gubler 2009). Brown wood streaking, Petri disease and grapevine leaf stripe disease (formerly young esca) caused by *Phaeo-monniella chlamydospora* (W. Gams, Crous, M. J. Wingf. & Mugnai) Crous & W. Gams and *Phaeoacremonium aleophilum* W. Gams, Crous, M. J. Wingf. & Mugnai have been grouped under the term phaeotracheomycosis to emphasize the fact that the three of them are caused by the same species. The esca or esca proper designation is retained to name the simultaneous though erratic occurrence of the tiger striped leaves caused by the former species together with the white rot of trunks caused by Basidiomycetes, that is, the traditional definition of esca (Surico 2009). This definition accommodates the historical accepted view of esca as the rotten grapevine wood accompa-

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nied by tiger striped leaves. However both symptoms are not related and the tiger striped leaves may be the consequence of toxic metabolite production by the phaeotracheomycosis fungi (Mugnai 1999). Similarly, within the dead-arm general designation, *Eutypa* die-back or eutypiose caused by *Eutypa lata* (Pers.) Tul. & C. Tul. has been separated from the apparently more frequent black dead-arm or Bot. canker produced by *Botryosphaeria* species (Úrbez-Torres *et al.* 2006). Whereas internal symptoms in the wood are undistinguishable, external symptoms might differ. *Eutypa* die-back symptoms are expressed as shoots that exhibit stunted growth with typical cup-shaped leaves. In black dead arm, stunted growth is occasional (Castillo-Pando *et al.* 2001), and controversy exists about the foliar symptoms described by Larignon *et al.* (2003) due to their similarity with the foliar symptoms assigned to esca (Lecomte *et al.* 2005, Surico *et al.* 2006). Recently, Navarrete *et al.* (2009, 2011) have suggested that *Greeneria uvicola* (Berk. & M.A. Curtis) Punith. should be considered an additional pathogenic species associated with the black dead-arm disease. Comparing external and internal symptoms with associated fungal species, Luque *et al.* (2009) concluded that internal symptoms of two or even three trunk diseases coexisted in the same plant and that internal symptoms did not always correlate with external symptoms which usually were misleading.

Black-foot is also regarded as a trunk disease of grapevines. *Cylindrocarpon*-like species have been shown to produce black discolorations at the base of the trunk and extending into the roots (Sweetingham 1983). External symptoms include delayed budburst in spring, poor vegetation and death of the whole plant. *Cylindrocarpon liriodendri* J. D. MacDon. & E. E. Butler, *Cylindrocarpon macrodidymum* Schroers, Halleen & Crous, *Campylocarpon fasciculare* Schroers, Halleen & Crous and *Campylocarpon pseudofasciculare* Halleen, Schroers & Crous have been considered the most pathogenic species (Halleen *et al.* 2004, 2006; Alaniz *et al.* 2009).

It is generally accepted that stress conditions predispose grapevines to the development of trunk diseases. Being lianas, the xylem vessels of grapevines are wider than those of trees and remain active for more years to compensate for the smaller diameter of trunks and the necessity to transport water efficiently to the climbing shoot tips. The wider vessels are more sensitive to cavitation and fungal infections and the loss of a vessel implies a more significant risk for grapevines than for trees (Ewers 1985).

In Uruguay, grapevines are grown in a range of soils, and are subjected to different climate conditions. Average annual rains account for 1200 mm distributed throughout the year, with occasional drought periods that can extend for several months, stressing the plants and thus affecting their growth. Whereas most of the vineyards are located in the southern territories within 30 km from the sea with maximum temperature of the warmest month between 28 °C and 29 °C, some vineyards are located in the central and northern territories, which have a rather continental climate with maximum temperature of the warmest month between 30 °C and 32 °C (Ferrer *et al.* 2007). The origin of plants is also diverse; grafted grapevines have been pro-

duced locally, or they have been imported from France, South Africa and other countries as well. As in most countries, local certification programs for grapevines do not take into account the presence of vascular fungi and imported plantlets are not analyzed for their presence either. The most abundant *Vitis vinifera* L. cultivars are Tannat, Muscat d'Hambourg, Merlot, Cabernet Sauvignon, Ugni Blanc, Chardonnay, Sauvignon Blanc, and to a lesser extent Marselan, Pinot Noir and others (Instituto Nacional de Vitivinicultura <http://www.inavi.com.uy/>). These cultivars are mostly grafted on rootstock SO4, and less frequently on 3309C and 101-14. Grapevines are usually trained in vertical shoot positioning (VSP) and Lyre systems, and young vigorous plants start bearing fruit in their third growth season and sometimes earlier in their second growth season, when stress by over cropping might easily be enhanced by periods of drought and heat spells.

Several fungal species usually associated with trunk diseases have been identified in Uruguay: *Cadophora luteo-olivacea* (J. F. H. Beyma) T. C. Harr. & McNew, *Eutypella vitis* (Schwein.) Ellis & Everh., *Inocutis jamaicensis* (Murrill) A. M. Gottlieb, J. E. Wright & Moncalvo (Abreo *et al.* 2008), *Phaeomoniliella chlamydospora*, *Phaeoacremonium aleophilum*, *Pm. australiense* L. Mostert, Summerb. & Crous (Abreo *et al.* 2008, 2011), *Greeneria uvicola* (Navarrete *et al.* 2009, 2011), *Cylindrocarpon liriodendri*, *C. macrodidymum*, *C. olidum* (Wollenw.) Wollenw., *C. pauciseptatum* Schroers & Crous, *Campylo-carpon pseudofasciculare* (Abreo *et al.* 2009, 2010), *Botryosphaeria parva* Pennycook & Samuels, *B. lutea* A. J. L. Phillips, *B. dothidea* (Moug.) Ces. & De Not. and *B. obtusa* (Schwein.) Shoemaker. (Martínez *et al.* 2009).

The main aim of this work was to analyze the composition and the variations of the community of pathogenic fungi associated with diseased tissues of grapevines affected with phaeotracheomycosis, esca proper, dead-arm and black-foot in different grape growing regions of Uruguay. A model of the successive pathogenic activities of fungal species that matches the composition of the fungal community in diseased tissues is suggested.

Materials and methods

Sampling of grapevines with symptoms

Grapevines with external symptoms of phaeotracheomycosis, esca proper and dead-arm were sampled from all grape-growing regions of Uruguay. Samples comprised a portion of the trunk extending 10 cm above and below the graft union in the case of phaeotracheomycosis, and the portion of the arm or trunk that contained diseased tissues in the case of esca or dead-arm. Grapevines suffering from black-foot were sampled only from vineyards in the southern regions, and samples consisted of roots of 0.5–1.0 cm diameter from next to the trunk base.

Plants with a field diagnosis of phaeotracheomycosis were identified within recently planted blocks of otherwise healthy looking plants younger than three years old. Plants with poor vegetative growth, wilting, or that had

failed to burst in spring were considered as affected by phaeotracheomycosis. Plants showing chronic and acute esca symptoms were found in blocks of adult plants. Poor vegetative vigor and reddish leaves were considered a symptom of chronic esca, whereas wilted shoots still holding grape bunches and new water-shoots growing from the healthy base of the trunk were considered symptoms of acute esca. When present, the basidioma of *Inocutis jamaicensis* was taken as a confirmation of white rot of esca. Grapevines showing the dead-arm symptom (either *Eutypa* die-back or black dead-arm) were found in adult blocks. The observation of stunted shoots, dead spurs and arms with an internal V-shaped necrosis were considered as part of the dead-arm symptom. Grapevines suffering from black-foot were identified in blocks of young and adult grapevines. Late and uneven budburst in spring and the presence of necrotic regions in roots sampled from near the trunk base were considered for the field diagnosis of black-foot.

Isolation of fungi

The bark of the trunk segments was removed, and segments were surface disinfected by immersion in 70 % ethanol for 1 min, 4 % NaOCl for 2 min and washed in sterile distilled water. The disinfected trunk segments were longitudinally cut opened with heat sterilized pruning shears. Fragments of 3 × 1 mm of the exposed xylem with black streaks or lesions were aseptically removed and placed on Petri dishes containing potato dextrose agar (PDA, Oxoid, Hampshire, UK) and incubated at room temperature during four weeks. Fragments which initially did not show fungal growth were systematically transferred to fresh Petri dishes with PDA to avoid their masking by rapid growing fungi. Identification of isolates was done on colonies growing on PDA.

Data analysis

One isolate of each fungal species per sample was determined, and species were grouped in their respective genera for subsequent analysis. To study the relationship between symptoms and genera, the relative density of each genus in each symptom was calculated as the number of isolates of each genus/total number of isolates × 100. Correspondence analysis to establish the probable relation between symptoms and genera was performed with PAST (Hammer *et al.* 2001). Similarly, the relationship between viticultural region and genera was described with a correspondence analysis but excluding black-foot and other fungi that were surveyed only in vineyards in the south of the country.

Results

The relative density of genera associated with the symptoms is presented in Tab. 1 and in different regions of Uruguay in Tab. 2. The ordination of symptoms according to the relative density of genera by means of the correspondence analysis is presented in Fig. 1. The three first axes accumulated

Tab. 1. Relative density of genera associated with symptoms of grapevine trunk diseases.

Genus	Code	Dead-arm	Esca	Phaeotra- cheomycosis	Black-foot
<i>Acremonium</i>	1	0.019	0.000	0.017	0.000
<i>Alternaria</i>	2	0.000	0.000	0.051	0.000
<i>Aureobasidium</i>	3	0.000	0.000	0.034	0.000
<i>Botryosphaeria</i>	4	0.302	0.222	0.102	0.000
<i>Cadophora</i>	5	0.019	0.000	0.068	0.000
<i>Cladosporium</i>	6	0.019	0.000	0.000	0.100
<i>Crinipellis</i>	7	0.000	0.000	0.000	0.100
<i>Cylindrocarpon/Campylocarpon</i>	8	0.000	0.000	0.017	0.300
<i>Eupenicillium</i>	9	0.000	0.000	0.017	0.100
<i>Eutypella</i>	10	0.038	0.000	0.000	0.000
<i>Fusarium</i>	11	0.019	0.037	0.085	0.300
<i>Gliocladium</i>	12	0.000	0.000	0.017	0.000
<i>Greeneria</i>	13	0.057	0.037	0.034	0.000
<i>Inocutis</i>	14	0.132	0.074	0.017	0.000
<i>Microsphaeropsis</i>	15	0.000	0.037	0.017	0.000
<i>Penicillium</i>	16	0.000	0.074	0.017	0.000
<i>Periconia</i>	17	0.000	0.000	0.000	0.100
<i>Pestalotiopsis</i>	18	0.019	0.000	0.017	0.000
<i>Phaeoacremonium</i>	19	0.113	0.148	0.136	0.000
<i>Phaeomoniella</i>	20	0.170	0.222	0.288	0.000
<i>Phoma</i>	21	0.000	0.037	0.000	0.000
<i>Phomopsis</i>	22	0.057	0.074	0.034	0.000
<i>Trichoderma</i>	23	0.019	0.037	0.017	0.000
<i>Verticillium</i>	24	0.019	0.000	0.000	0.000

Tab. 2. Relative density of genera associated with symptoms of grapevine trunk diseases in different regions of Uruguay.

Genus	Code	Artigas	Canelones	Colonia	Durazno	Maldonado	Paysandú
<i>Botryosphaeria</i>	1	0.385	0.130	0.190	0.429	0.200	0.235
<i>Cadophora</i>	2	0.000	0.043	0.048	0.143	0.200	0.059
<i>Eutypella</i>	3	0.000	0.087	0.000	0.000	0.000	0.000
<i>Fusarium</i>	4	0.000	0.087	0.143	0.000	0.200	0.059
<i>Greeneria</i>	5	0.231	0.000	0.000	0.000	0.000	0.118
<i>Inocutis</i>	6	0.000	0.043	0.048	0.286	0.000	0.176
<i>Phaeoacremonium</i>	7	0.154	0.130	0.238	0.000	0.100	0.176
<i>Phaeomoniella</i>	8	0.231	0.435	0.238	0.143	0.300	0.000
<i>Phomopsis</i>	9	0.000	0.043	0.095	0.000	0.000	0.176

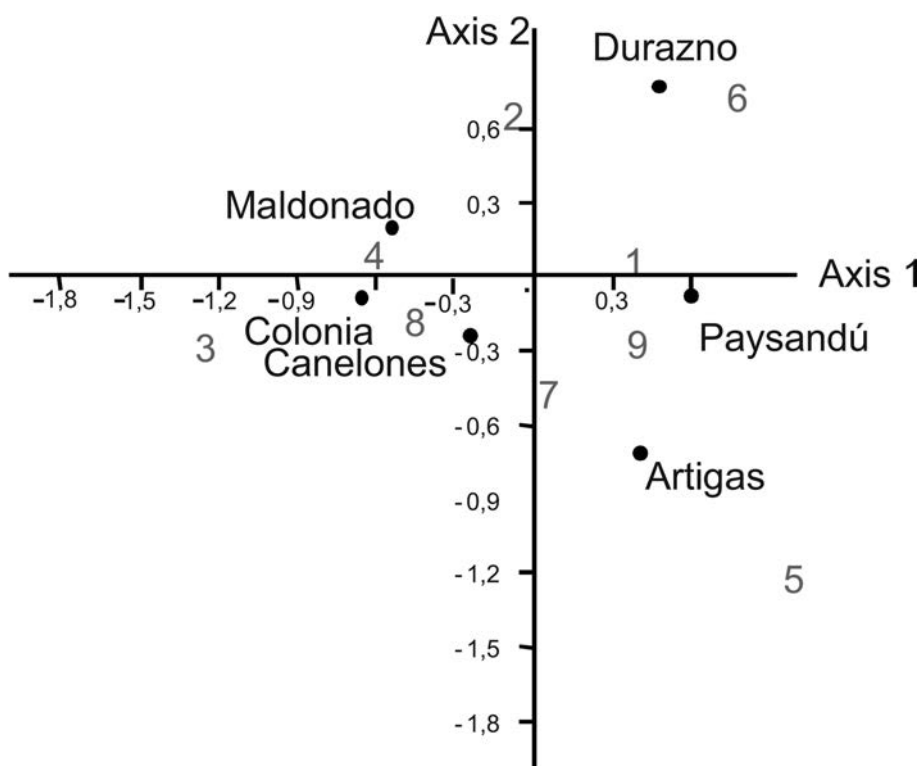


Fig. 2. Correspondence analysis. Ordination of sites on the two first axes. Variables are the relative isolation densities of genera. Numbers indicate the genera: 1 *Botryosphaeria*, 2 *Cadophora*, 3 *Eutypella*, 4 *Fusarium*, 5 *Greeneria*, 6 *Inocutis*, 7 *Phaeoacremonium*, 8 *Phaeoconiella*, 9 *Phomopsis*.

The association of each sampling site with the different fungal genera was visualized by means of the respective correspondence analysis (Fig. 2). The main three axes explained 84 % of the total variation. The first axis (36 % of variation) separates the sampling sites located in the southern territories (Canelones, Colonia, Maldonado), from the sampling sites located in the central and northern territories (Artigas, Paysandú, Durazno). Along the second axis (28 % of variation) a gradient within this last group could be established, being Paysandú in an intermediate position. The warmest sites in the central and north of the country were mostly characterized by the presence of *Inocutis jamaicensis*, *Botryosphaeria* spp., and *Greeneria uvicola*, whereas the sampling sites in the south of the country were mostly characterized by *Eutypella vitis* and *Fusarium* spp. *Greeneria uvicola* was exclusively isolated from vineyards in the warmest regions of Artigas and Paysandú, whereas *Eutypella vitis* was isolated – only twice – in a vineyard affected with dead arm in the cooler region of Canelones. *Phaeoconiella chlamydospora* and *Phaeoacremonium aleophilum* were indistinctly isolated from warmer or cooler regions.

Discussion

Symptoms of the aerial parts of the trunk were poorly separated as most of the genera were isolated from all plants analyzed, and therefore a continuum between them was evident. *Inocutis jamaicensis*, the basidiomycete associated with “hoja de malvón” in Argentina (Lupo *et al.* 2006) and the white rot of esca in Uruguay (Abreo *et al.* 2008) was also isolated from dead-arm affected grapevines, in which it possibly produced the observed softening of some of the otherwise hard V-shaped cankers typical of the dead-arm. Similarly, *Phaeomoniella chlamydospora* and *Phaeoacremonium aleophilum* were isolated from plants suffering from phaeotracheomycosis and esca, but also from dead-arm symptomatic tissues, where they might have acted as pioneer fungi before the growth of other species like *Botryosphaeria* spp. (Pascoe 1998). It is known that *Pa. chlamydospora* infection interferes with the water relations of the grapevine, consistently reducing the water potential of leaves particularly under conditions of water deficits (Edwards *et al.* 2007). Disease expression for *Botryosphaeria* species, which is almost exclusively associated with different forms of plant stress (Slippers & Wingfield 2007), could be favored directly and indirectly by early *Phaeomoniella chlamydospora* infections. The initial presence and pathogenic activity of *Phaeomoniella chlamydospora* and *Phaeoacremonium aleophilum* could produce favorable conditions for the growth of *Botryosphaeria* spp. and could help explain their co-occurrence in necrotic tissues obtained from dead-arms.

Other species associated with the dead-arm symptom were mostly *Neofusicoccum parvum*, *N. luteum*, *Fusicoccum aesculi*, *Diplodia seriata*, *Greeneria uvicola* and *Eutypella vitis* (Abreo *et al.* 2008, Martínez *et al.* 2009). Remarkably, *Eutypa lata* – the species after which the original *Eutypa* dieback or eutypiose was named – could not be isolated from any plant affected by dead-arm in any of the sampled viticultural regions. Only *Eutypella vitis*, with similar cultural characteristics to *Eutypa lata* was isolated twice from a Cabernet Sauvignon plant affected by dead-arm. Therefore, according to our results, the dead-arm symptom observed in Uruguay corresponds mostly to Bot. canker or black dead-arm and not *Eutypa* die-back.

In addition to grapevines, *Inocutis jamaicensis* has been also isolated from *Eucalyptus* (Martínez 2005) and native bushes in Uruguay (Perez *et al.* 2008), where it produced white rot in trunks. Population studies have shown that there is only one population colonizing these hosts (Perez *et al.* 2008). Its presence not only in esca rotten tissues but also in dead arm affected grapevines in which a soft V-shaped rot was observed could be considered as the natural extension of its wood degrading activities. Similarly, *Fomitiporia mediterranea* M. Fisch., the lignicolous basidiomycete responsible for the white rot of the esca proper symptom in Europe (Fischer 2006), has been found in association with central or sectorial white rot (Kuntzmann *et al.* 2010) and V-shaped necrosis typical of *Eutypa* die-back and black dead-arm (Luque *et al.* 2009).

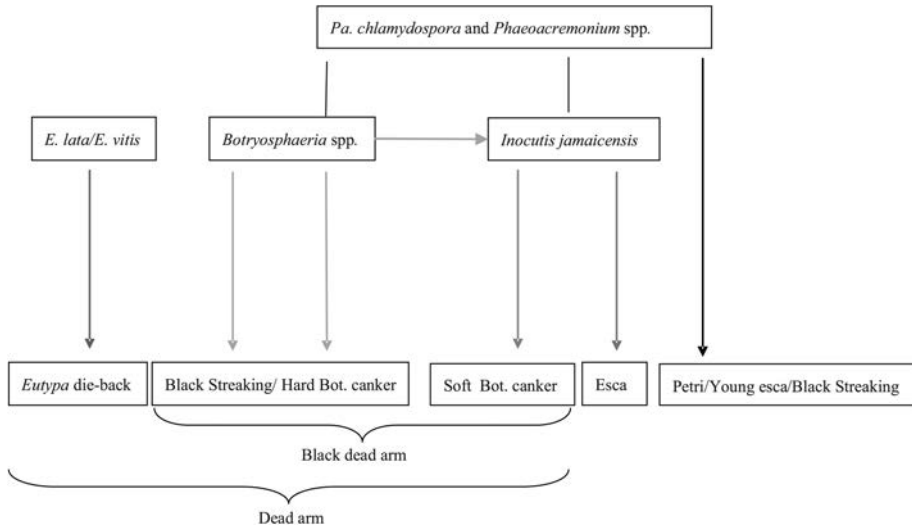


Fig. 3. Model of successive pathogenic activities that lead to the observed community composition associated to symptoms of the aerial parts of the trunk.

A model of alternative pathogenic activities of the main pathogens is presented to accommodate the results of the correspondence analysis of relative density of genera and symptoms (Fig. 3). In this model, a succession of the pathogenic activities of genera is suggested but not a succession of the genera or species, since for instance *Botryosphaeria* spp. could have been present before *Phaeoacremonium chlamydospora* but its pathogenic activity could not have started until after *Pa. chlamydospora* became active as a pathogen. According to the model, *Pa. chlamydospora* / *Phaeoacremonium* spp., *Botryosphaeria* or *E. lata* can initiate a disease process. A process which was started and finished solely by *Botryosphaeria* spp. would produce the hard Bot. canker symptom. Also, a process initiated by *Phaeoacremonium* and followed by *Botryosphaeria* would produce the same symptom. If the activity of *Botryosphaeria* was followed by *I. jamaicensis* activity, then the soft Bot. canker symptom would be produced. Hard and soft Bot. cankers constitute the black dead-arm symptom. *Eutypa lata* (not found in Uruguay) and *Eutypella vitis* would be responsible of the *Eutypa* die-back symptom, which together with Bot. canker compose the dead-arm symptom. If initial activity of *Pa. chlamydospora* / *Phaeoacremonium* was followed directly by *I. jamaicensis* activity, the final symptom would be esca proper. If only *Pa. chlamydospora* / *Phaeoacremonium* were active in a young plant the symptom produced might be that of Petri disease, black streaking and young esca (phaeotracheomyces). It would be necessary to investigate the nature of the interactions between fungal species leading to the particular expression of this continuum of symptoms.

Black-foot was associated with a different set of species namely *Cylindrocarpon* and *Campylocarpon*, and therefore it did not belong to this continuum. Differences between viticultural regions was not based on variations in the distribution of the main pathogens, but on the relative density of less known pathogens like *Eutypella vitis* and *Greeneria uvicola*.

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