Interreg
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VITES QUALITAS

SUSTAINABILITY AND COMPETITIVENESS OF VITICULTURE IN THE POCTEFA TERRITORY

INCREASING VINE LONGEVITY AND HEALTH THROUGH THE EVALUATION AND TRANSFER OF PLANT PRODUCTION AND PRUNING PRACTICES

EFA324/19

State of the art: Fungal grapevine trunk diseases. Importance of grafting and pruning in disease development

Activities 3.2 and 4.3

09/03/2021

European Regional Development Fund (ERDF)

Report title	State of the art: Fungal grapevine trunk diseases. Importance of grafting and pruning in disease development
Version	V1
Responsible for deliverable	ICVV-CSIC
Activity	Activities 3.2 and 4.3
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Contributor(s)	UPNA
Reference	EFA324/19
Programme	Interreg V-A Spain-France-Andorra programme (POCTEFA 2014-2020)
Project start date	01/12/2019
Duration	36 months
Project coordinator	UNIVERSIDAD PÚBLICA DE NAVARRA

The project has been 65% cofinanced by the European Regional Development Fund (ERDF) through the Interreg V-A Spain-France-Andorra programme (POCTEFA 2014-2020). POCTEFA aims to reinforce the economic and social integration of the French–Spanish–Andorran border. Its support is focused on developing economic, social and environmental cross-border activities through joint strategies favouring sustainable territorial development.

SUMMARY

Grapevine trunk diseases (GTD) decrease both quality and yield of grapevines all over the world. Grafting is a critical stage in the grapevine propagation process and necessitates making wounds that are inherently vulnerable to contamination with trunk pathogens. In mature vineyards, GTD fungi primarily infect grapes through pruning wounds, subsequently colonizing the vascular tissues. Recent studies indicated that training systems and pruning techniques can influence the level of GTD foliar symptoms. Therefore, there is an urgent need (i) to evaluate the impact of different grafting types on fungal infection, (ii) to investigate the efficacy of sustainable products to protect pruning wounds under natural infections in the vineyard and (iii) to scientifically assess the variables associated with different pruning systems in order to corroborate the GTD foliar symptoms being reported in the vineyard.

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1. INTRODUCTION

The term 'grapevine trunk disease' (GTD) is relatively new and was established in late 1990s to include several symptoms observed in both foliage and vascular tissue of grapevines, which were thought to be caused by a group of fungi that primarily infect grapes through pruning wounds, subsequently colonizing the vascular tissues (Mugnai 2011). However, symptoms of what we today call GTD as well as fungi associated with them are long known. It has even been suggested that the disease currently known as esca may be as old as vine cultivation (Mugnai et al. 1999).

Although GTD have been known since the end of the 19th century (Ravaz, 1898), their significance and impact on plant health have only been recognized recently. The recent increase of GTD incidence worldwide is believed to be the consequence of several factors, including changes in production practices, loss of effective chemicals, predominance of susceptible cultivars and ageing of vineyards. Accordingly, it is well-accepted that GTD represent one of the major threats to the future economic sustainability of viticulture, causing significant economic losses due to reduced yields, increased crop management costs for cultural and chemical preventive measures, and shortened life span of vineyards (Bertsch et al. 2013; Kaplan et al. 2016).

To date, up to 133 fungal species belonging to 34 genera have been associated with GTD worldwide, although Koch's postulates have not been completed for all of them. Nonetheless, GTD fungi account for the largest group of pathogens known to infect grapes (Gramaje et al. 2018). GTD are primarily caused by ascomyceteous fungi but some basidiomiceteous taxa are also thought to play an important role in this disease complex (Fischer 2002; Cloete et al. 2015). Petri disease and black foot affect young grapevines whilst the diseases Eutypa and Phomopsis dieback, and esca affect mature grapevines. Botryosphaeriae dieback can affect both young and mature grapevines (Table 1).

2. FUNGAL TRUNK PATHOGENS IN THE GRAPEVINE PROPAGATION PROCESS

Planting material used in young vineyards is already infected by black-foot and Petri diseases pathogens, and Botryosphaeriaceae spp., either systemically from infected mother vines or by contamination during the propagation process. There are many opportunities for infection by trunk disease pathogens during nursery stages. Wounds are made in the tissue at every stage of production from collection and disbudding of cuttings to bench grafting and lifting and trimming of finished vines. Improperly healed graft unions are also vulnerable to infection in the nursery, and if the vines survive, after planting in the vineyard.

Grafting is a critical stage in the grapevine propagation process and necessitates making wounds that are inherently vulnerable to contamination with trunk pathogens (Gramaje and Armengol, 2011). Contaminated wounds and poorly matched graft unions fail to heal properly, remain open to fungal infection, and create structural weaknesses in the finished vines (Stamp, 2001). Viable propagules of black foot and Petri disease pathogens have been detected from washed omega grafting machines (Gramaje and Armengol, 2011; Agustí-Brisach et al. 2013; Cardoso et al. 2013). Recenlty, Mary et al. (2017) observed higher esca foliar symptoms in vines mechanically grafted (omega graft or whip and tongue graft) compared with vines grafted in the field (full cleft graft). These authors concluded that the spread of mechanical graft over the last 25 years could be one of the factors explaining the increasing incidence of esca in vineyard.

Table 1. Fungal trunk diseases in young and mature vineyards.

Disease name	Age of the vineyard[a]	Causal agents	Most prevalent species
Black-foot disease	Young	25 *Cylindrocarpon*-like asexual morphs belonging to the genera *Campylocarpon, Cylindrocladiella, Dactylonectria, Ilyonectria, Neonectria, Thelonectria* and *Pleiocarpon*	*Dactylonectria torresensis* *Dactylonectria macrodidyma* *Ilyonectria liriodendri*
Botryosphaeria dieback	Young / Mature	26 fungal species in the *Botryosphaeriaceae* family	*Neofusicoccum parvum* *Diplodia seriata*
Esca	Mature	*Phaeomoniella chlamydospora, Phaeoacremonium spp.* and *basidiomycetous fungi*	*Phaeomoniella chlamydospora* *Phaeoacremonium minimum* *Fomitiporia mediterranea*
Eutypa dieback	Mature	24 species in the *Diatrypaceae* family	*Eutypa lata*
Petri disease	Young	*Phaeomoniella chlamydospora,* 26 species of *Phaeoacremonium, Pleurostoma richardsiae* and 6 species of *Cadophora*	*Phaeomoniella chlamydospora* *Phaeoacremonium minimum* *Cadophora luteo-olivacea*
Phomopsis dieback	Young / Mature	7 species of *Diaporthe*	*Diaporthe ampelina*

[a] Young vineyard: <8-year-old; Mature vineyard: >8-year-old

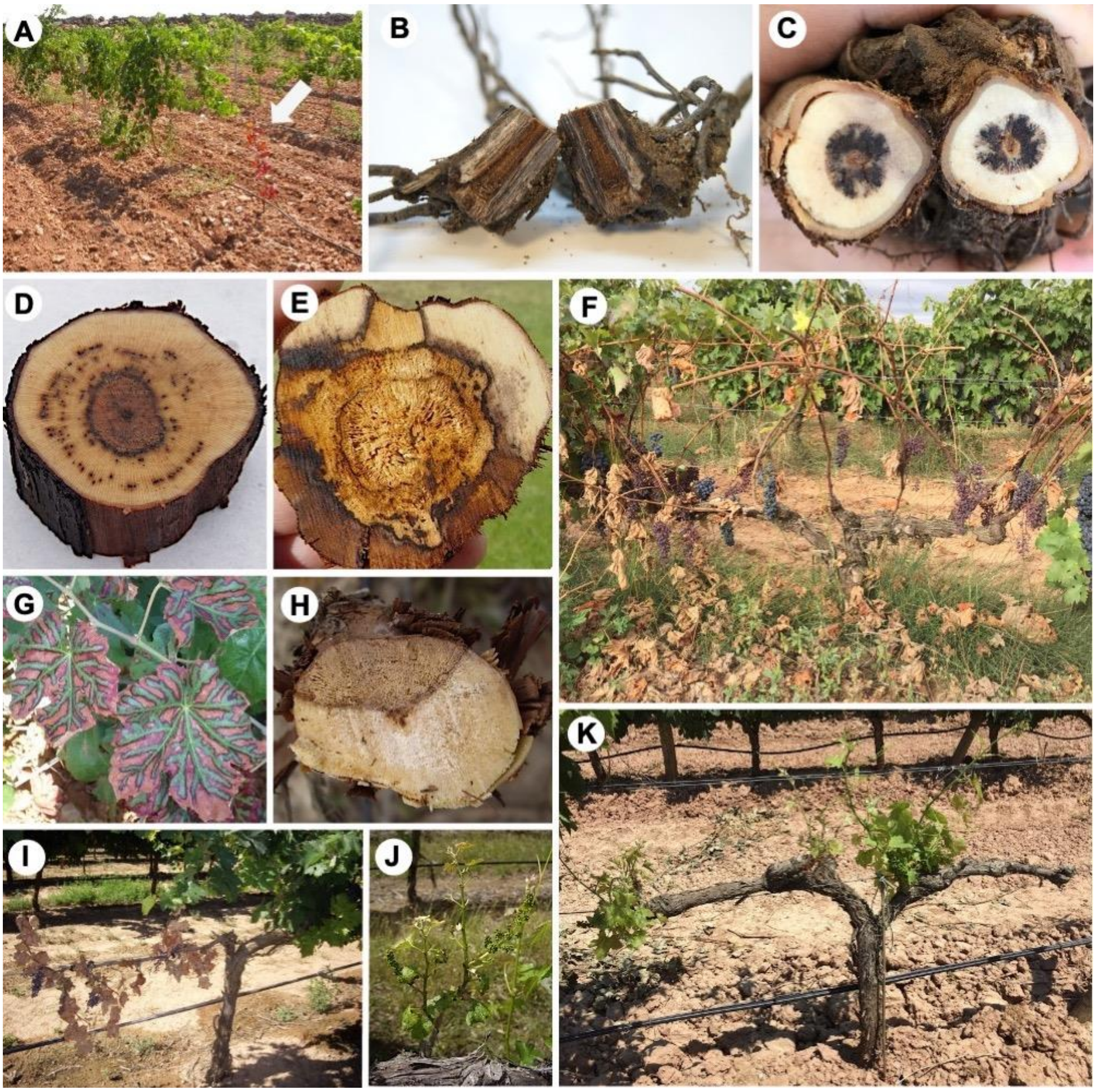

Figure 1. A, Symptoms of severe leaf wilting and dieback (plant indicated by arrow). B, Black discoloration and necrosis of wood tissue which develops from the base of the rootstock characteristic of black-foot disease. C, Rootstock cross sections showing a ring of necrotic xylem vessels surrounding the pith, characteristic of Petri disease. Cross-section showing black-spots (D) and a central white rot surrounded by a sectorial necrosis (E) of an esca infected vine. F, esca acute or apoplectic form is characterized by a sudden wilting of the entire plant. G, 'tiger-stripe' symptoms on leaves of a red cultivar characteristic of esca. H, canker and internal, necrotic, wedge-shaped staining in the cross-section of a cordon characteristic of Botryosphaeria, Eutypa and Phomopsis diebacks. I, cordon dieback along with lack of spring growth can be observed in vines affected by Botryosphaeria dieback. J and K, foliar symptoms of Eutypa dieback include shoots with chlorotic leaves often cupped and with necrotic margins.

3. EPIDEMIOLOGY OF GRAPEVINE TRUNK DISEASES IN MATURE VINEYARDS

Grapevine pathogens responsible for Eutypa dieback, Botryosphaeria dieback, Phomopsis dieback, and esca are primarly spread through the dispersion of airborne spores. These spores are released from fruiting bodies embedded in the bark and/or on the surface of dead grapevine wood (Gramaje et al. 2018), and are released under favorable environmental conditions, which are primarily associated with rain events and/or high relative humidity along with temperatures above freezing, which also favor spore germination (van Niekerk et al. 2010). Spores are then spread from fruiting bodies by rain-droplets, wind or arthropods until they land on susceptible pruning wounds to germinate and start colonizing new xylem vessels and pith parenchyma cells (Gramaje et al. 2018).

It has been shown that spore release and hence, high risk infection periods throughout the growing season vary depending on the fungal pathogen and geographical location but primarily overlap with dormant pruning seasons in both the Northern and Southern Hemispheres. Susceptibility of grapevine pruning wounds to GTD fungi primarily depend on the pruning month and the time elapsed between pruning and possible infection events. Studies using artificial inoculations with spores indicate that grapevine pruning wound susceptibility is high when infections occur at the time of pruning but decreases as the interval between pruning and infection increases over the following weeks and months, with seasonal variation reported between regions, due mainly to climatic differences.

4. PRUNING WOUND PROTECTION

Based on the knowledge gained from the different epidemiological studies conducted in grape-growing regions around the world, reduction of new GTD infections in a vineyard can be effectively achieved by pruning management. No matter which GTD fungi are involved, spore release has generally been shown to correlate with rain events and moderate temperatures. Accordingly, pruning in wet weather should be avoided and conducted during periods when inoculum is less prominent.

Wound protection is the most effective strategy for controlling GTD when compared with remedial surgery (Sosnowski and McCarthy 2017), and especially if adopted early in the life of the vineyard (Kaplan et al. 2016). Many products have been evaluated, but in general, grafting mastic, paints and pastes are the most reliable wound protectant, particularly when they are supplemented with fungicides (Martínez-Diz et al. 2021). These not only provide a physical barrier to stop GTD pathogen spores from entering the wounds, but should the physical barrier be compromised by sap flow, rain or cracking when drying, the fungicide can then act on the pathogens. Paint and paste treatments are applied by hand with paint brush or specially designed applicators. This can be very costly, two to four times the cost of application with a tractor mounted sprayer (Sosnowski and McCarthy 2017) and so prohibitive. Hence there is a need for effective liquid formulation fungicides that can be applied with a sprayer. However, limited products are registered for use on grapevines, and only in some countries, with many species of the taxonomically variable pathogens yet to be evaluated. Successful biological control of GTDs with antagonistic microorganisms is practiced to a rather limited extent. Experimentally, biological control can be obtained against trunk disease pathogens, but most of the studies so far have been applied in one-year-old grafted vines under greenhouse conditions and field applications are still mostly ineffective.

5. FUTURE DIRECTION OF GTD RESEARCH ON GRAFTING AND PRUNING

One of the earliest nursery stages where infections by fungal trunk pathogens can occur is during grafting. The quality of graft can promote the development of pathogens in grapevine wood. There is an urgent need to evaluate the impact of different grafting types on fungal infection. Wound protection is the most effective strategy to prevent infection by GTD fungi. However, most of pruning wound protection trials significantly used higher 'GTD pressure' than that which might be expected to occur under natural conditions. The future direction of research needs to investigate the efficacy of pruning wound protectants under lower artificial GTD inoculum levels or natural infections in the vineyard.

It has been shown that training systems and pruning techniques can influence the level of Eutypa dieback (Gu et al. 2005; Dumot et al. 2012) and esca disease (Lecomte et al. 2012; Travadon et al. 2016) in vineyards. Recently, there has been greater emphasis placed on the importance of pruning systems for managing GTD (Lee 2016) so there is a need to scientifically evaluate the variables of different pruning systems, such as proximity of wounds to the trunk, wound surface area and blocking the flow of sap in vascular tissue, by wrapping too tightly on the wire or from natural desiccation extending from wounds, in order to corroborate the GTD foliar symptoms being reported in the vineyard.

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