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# Esca of grapevine: a disease complex or a complex of diseases?

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**Summary.** Over the last few years research on esca has led to considerable progress in our understanding of the aetiology, epidemiology and physiology of the disease and revealed its complexity. On the basis of the available information, esca can be considered: 1. a disease complex, in the sense that several interacting factors and micro-organisms concur to produce the overall syndrome; 2. a complex of at least two distinct diseases: 'white rot' caused by *Fomitiporia punctata* or other wood-rotting fungi, and brown wood-streaking and gummosis, caused by one or more species of *Phaeoacremonium* infecting the woody tissue; 3. a real hadromycosis induced by one or more species of *Phaeoacremonium* or related genera, which in mature or old grapevines is further complicated by the white rot caused by *F. punctata*. Research has also shown that different syndromes are produced depending on the origin of the infections, the prevalence of the associated fungi and the order in which they become active, and environmental factors. Five syndromes can be distinguished: 1. "brown wood streaking" (Petri, 1912). This affects rooted cuttings, rootstocks, and grafted or mother plants and is caused by species of *Phaeoacremonium* or related genera, often without external symptoms; 2. "Petri grapevine decline". This name has been proposed to designate a decline of young grapevines known under various local names ('black goo', 'slow dieback', 'Phaeoacremonium grapevine decline'), which occurs when propagation material or young grapevines are infected, again by species of *Phaeoacremonium* or related genera; 3. "young esca". This syndrome, which Petri thought would evolve in 'esca proper', is characterised by black or brown wood-streaking and xylem gummosis in actively growing grapevines, with or without external symptoms. It is also caused by species of *Phaeoacremonium* or related genera, like the brown wood-streaking of point 1 above; 4. "white rot". When infection is through wounds and solely or mainly by *F. punctata* or other wood-rotting basidiomycetes, it is characterised by wood rot, which may or may not be accompanied by external (leaf and fruit) symptoms; 5. "esca proper". This occurs when white rot develops in the trunks of mature or old vines together with, or after, the development of brown wood-streaking. This, the full-fledged esca syndrome, is caused by the combined or successive action of one or more species of *Phaeoacremonium*, occasionally accompanied by other fungi, and *F. punctata*.

**Key words:** grapevine, esca, *Fomitiporia punctata*, *Phaeoacremonium chlamydosporum*, *P. aleophilum*.

## Introduction

In two recent reviews on esca (Mugnai *et al*., 1999; Graniti *et al*., 1999), hypotheses were put forward about the nature, origin and fungi involved in the grapevine disease known as "esca" or by other common names ("apoplexy", "black measles").

For about a century, esca was considered a simple disease of old vines associated with wounds and white rot of the trunk and the main branches. It could be kept under control by sanitary practices such as the removal of rotted wood and the surface protection of large pruning wounds, and by arsenite sprays in winter, before sprouting. A dramatic upsurge in the disease has occurred in the last 10-15 years, however, coinciding with the extensive establishment of new vineyards, especially in southern Europe. This intensification of the dis-

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ease has been placed in relation with several factors, such as changes in vineyard management and cultural practices, reduced sanitary care of rootstocks and vine propagation material, poor protection of pruning wounds due to the increasing cost of labour, and the replacement of arsenite treatments, which have been banned in several countries, with less efficient fungicides.

The subsequent increase in studies on the disease has led to the conviction that esca is a complex disease whose symptoms are caused by varied structural and physiological changes that cannot be reduced to one simple scheme of cause and effect. In esca, symptoms that look alike may have different causes.

**Aetiology and pathogenicity of associated fungi**

The aetiology of esca itself remained undefined for a long time and even today cannot be said to be completely understood. Several lignicolous fungi have been found associated with esca-affected grapevines. They include wood-rotting basidiomycetes such as *Fomitiporia punctata* (Fr.) Murrill and a few ascomycetes, and also certain mitosporic fungi (hyphomycetes) such as *Phaeoacremonium chlamydosporum* W. Gams *et al.* ([1]), *P. aleophilum* W. Gams *et al.* and, to a lesser extent, *P. inflatipes* W. Gams *et al.* and *P. angustius* W. Gams *et al.* (see, for Italy, Mugnai *et al.*, 1996a, 1997, 1999; Graniti *et al.*, 1999; Serra, 1999; for France, Larignon and Dubos, 1997; for USA, Australia, South Africa and other countries, Morton, 1999). All these species are isolated with high frequency from the discoloured woody tissue of esca-affected vines, especially from the brown or black longitudinal streaks, where marked gummosis of the xylem elements also occurs.

The pathogenicity of these fungi and their particular role in the development of esca have long been debated.

That wood-decaying fungi cause white rot in grapevine has been demonstrated both in the laboratory on small wood blocks, and by inoculation tests on standing vines. Evidence has been produced that *F. punctata,* penetrated through wounds, can rot the wood tissue of otherwise healthy grapevines without the help of any other fungi (Sparapano *et al.*, this issue). The rotting process is usually slow when in the trunks of old vines (Chiarappa, 1997), but in the branches of actively growing vines or the stems of young vines it can be brought about in less than two years (Mugnai *et al.*, 1996b, 1999; Sparapano *et al.*, this issue). So far however, esca cannot be attributed to *F. punctata* alone because it has never been possible to reproduce the whole syndrome of the disease, including foliar and fruit symptoms, experimentally with that fungus.

As regards brown or black wood-streaking and pink, reddish or brown discoloration of the woody portions of grapevine, field and greenhouse inoculation experiments indicate that *P. chlamydosporum* and *P. aleophilum* also colonise the wood of apparently healthy grapevines. Within one year after these fungi were inoculated in the woody tissue, well-developed discoloured wood columns and long brown streaks had extended in both directions from the inoculum dowel (Sparapano *et al.*, this issue). The inoculated fungi were readily reisolated from the brown discoloured xylem, which also showed tylosis and gummosis (Mugnai *et al.*, 1996b, 1997, 1999; Larignon and Dubos, 1997). Admittedly most inoculation experiments with these fungi on the trunks and branches of adult grapevines initially failed to reproduce also the foliar symptoms of esca. More recently, however, chlorotic and necrotic spots have also been produced, albeit not consistently, on the leaves of stem-inoculated grapevines in the greenhouse, and branch-inoculated grapevines in the field within six months of their inoculation with either *P. chlamydosporum* or *P. aleophilum* (Sparapano *et al.*, 1998 and this issue).

But the mitosporic fungi thus associated with brown wood-streaking of esca-affected grapevines also cause a decline of young grapevines that has been reported from several grape-growing areas of the world, where this condition is known under a variety of local names, “black goo”, “slow dieback”, “slow decline”, and “Phaeoacremonium grapevine decline” (Scheck *et al.*, 1998, Morton, 1999).

This particular decline was first reported in Italy by Petri (1912) on young grafted vines and mother plants. Petri succeeded in reproducing the symptom of brown wood-streaking in standing vines by injecting three mitosporic fungi isolated from diseased vines into the xylem of healthy-looking plants through wounds. Two of these fungi can now be identified as *P. chlamydosporum* and *P. aleophilum*.

In recent years, the occurrence of these fungi in

the wood of mother vines, as well as in rootstocks, cuttings and scions has been reported from a number of countries. In California, the four species of *Phaeoacremonium* mentioned have been shown to be pathogenic to young vines (Scheck *et al.*, 1998).

These and other fungi have also been isolated from asymptomatic vines, however, and there is evidence to suggest that they can live as endophyte-like organisms in grapevine xylem (Esseln and Weltzien, 1997; Bertelli *et al*., 1998).

The question then arises whether the mitosporic fungi associated with esca, and in particular the dominant species of *Phaeoacremonium* that colonise the woody tissues of grapevine, are endophytes, latent pathogens, weak pathogens or true vascular pathogens.

Endophytism is a way of life, not merely an ecological adaptation for some specialised groups of fungi. Most plant species are known to harbour fungi inside their aerial organs without visible signs of disease (Carroll, 1986). And indeed, endophytes are sometimes parasitic, but more often mutualistic, the host plant deriving advantage from the association, as happens for example with fungal endophytes in grasses and the leaves of woody plants (Siegal *et al.*, 1987; Redlin and Carris, 1996). Pathogenic fungi, including latent pathogens living without symptoms in plant tissue, are therefore generally excluded from the fungal endophytes (Sinclair and Cerkauskas, 1996), although an extension of the term has been proposed (Petrini, 1991) so that this group will comprise all organisms that, at any time in their life cycle, live asymptomatically within plant tissues.

It is possible that the isolation of certain plant pathogenic fungi such as *Phomopsis viticola* (Sacc.) Sacc., *Eutypa lata* (Pers. : Fr.) Tul. & C. Tul. and *Botryosphaeria obtusa* (Schwein.) Shoemaker from the wood of esca-affected vines indicates that the diseases caused by these organisms are already present in the vines, though still only in latent form. There is evidence that species or strains of *Phaeoacremonium,* too, cause overt syndromes in young grapevines when the functioning xylem is directly invaded by them. It seems likely therefore that the species or strains of *Phaeoacremonium* which colonise the inner tissues of grapevines are all more or less pathogenic, but that the actual expression of symptoms will depend upon a number of other factors, such as the age and susceptibility of the infected cultivars, the mode of infection, the age and functionality of the annual rings invaded, the reaction of the host tissues, and such environmental factors as nutrients, water supply, temperature, etc. As soon as these fungi become established in the woody tissue, they begin to cause changes in the host's structures and functions. When the deterioration of the substrate becomes sufficiently great, with an evident host reaction and the formation of harmful by-products, the affected tissue becomes symptomatic. It is our view that external symptoms are mostly produced by metabolites — toxins and enzymes — which spread through the wood parenchyma and eventually reach the aerial organs via the transpiration stream in the functioning xylem (Sparapano *et al.*, 1998; Sparapano *et al.* this issue). Under particular stress conditions, a slow wilt of shoots and grape clusters or a sudden collapse of the whole vine — called apoplexy — may result.

Based on the information and experimental data currently available, and considering only the few fungal species most likely to be involved in the disease (see also the questions posed by Pascoe, 1999), the following scenarios for esca and related syndromes can be hypothesised:

**Nature of the disease**

- Esca is a disease complex, i.e. its syndrome cannot be attributed to the action of a single pathogen. Several factors and microorganisms, acting in association or in succession, must concur to produce the overall syndrome, which, moreover, becomes fully expressed only under optimal environmental conditions.
- Esca is a complex of at least two distinct diseases: white rot, caused by *F. punctata* or other wood-rotting basidiomycetes, and brown wood-streaking and gummosis, caused by one or more species of *Phaeoacremonium* or related genera ([1]) infecting the woody tissue. The relative prevalence of either of these fungi, also in relation to the age of the host, accounts for the variability of the symptoms, which is a characteristic of esca.
- Esca is a real hadromycosis induced by one or more species of *Phaeoacremonium* or related genera ([1]), and which in mature or old grape-

vines is further complicated by the wood rot caused by *F. punctata*.

**Specific syndromes**

In relation to the origin of the infections and to plant age:

- *Brown wood-streaking*. The infection of rooted cuttings, rootstocks, grafted and mother plants by *P. chlamydosporum* and other species of *Phaeoacremonium* or related genera ([1]) causes brown wood-streaking (Petri, 1912), commonly without external symptoms.
- *Petri grapevine decline*. This name has been proposed (Mugnai *et al*., 1999) for the decline of young grapevines already known under local names ("black goo", "slow dieback", "Phaeoacremonium grapevine decline"), and which is caused by early infection of propagation material or young grapevines by species of *Phaeoacremonium* or related genera.
- *Young esca*. When *Phaeoacremonium* infects actively growing (up to 8-10 year old) grapevines through grafting or pruning wounds, it produces black or brown wood-streaking and vascular gummosis deep inside the trunk and branches, with or without foliar symptoms. As Petri supposed, this condition may evolve into "esca proper" as defined below, and consequently can be called "young esca".
- *White rot*. When infection through wounds is solely or mainly by *F. punctata* or other wood-rotting basidiomycetes with or without external symptoms, a spongy wood decay (white rot) results, which may or may not be accompanied by leaf and fruit symptoms.
- *Esca proper*. White rot develops in the trunk of mature or old vines together with, or after, the development of brown wood-streaking. This full-scale syndrome is caused by the combined or successive action of one or more species of *Phaeoacremonium* or related genera ([1]) (occasionally together other fungi) and *F. punctata*.

Further research will have to determine which of these scenarios is correct, and whether the species of fungi associated with esca really do produce different syndromes according to their prevalence and interaction, way of infection, host reaction and environmental factors; in other words, whether esca is a disease complex or a complex of two or more diseases.

([1]) This species has been redisposed in the new genus *Phaeomoniella* Crous & W. Gams as *P. chlamydospora* (W. Gams *et al.*) Crous & W. Gams. See Crous and Gams in this issue.

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