



Review

Flor yeasts of *Saccharomyces cerevisiae*—Their ecology, genetics and metabolism



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ABSTRACT

The aging of certain white wines is dependent on the presence of yeast strains that develop a biofilm on the wine surface after the alcoholic fermentation. These strains belong to the genus *Saccharomyces* and are called flor yeasts. These strains possess distinctive characteristics compared with *Saccharomyces cerevisiae* fermenting strain. The most important one is their capacity to form a biofilm on the air–liquid interface of the wine. The major gene involved in this phenotype is *FLO11*, however other genes are also involved in velum formation by these yeast and will be detailed. Other striking features presented in this review are their aneuploidy, and their mitochondrial DNA polymorphism which seems to reflect adaptive evolution of the yeast to a stressful environment where acetaldehyde and ethanol are present at elevated concentration. The biofilm assures access to oxygen and therefore permits continued growth on non-fermentable ethanol. This specific metabolism explains the peculiar organoleptic profile of these wines, especially their content in acetaldehyde and sotolon. This review deals with these different specificities of flor yeasts and will also underline the existing gaps regarding these astonishing yeasts.

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1. Introduction

Several types of wines are characterized by the development of a film of yeast at the surface; this is known as flor velum yeast or “Flor yeast”. Sherry is the most well-known of this group of wines and its production process has been explained in detail by Pozo-Bayón and Moreno-Arribas (2011) and Benitez et al. (2011). After fermentation of Palomino fino grapes, the fermented wine is fortified with wine alcohol to 15% (v/v), clarified by natural sedimentation and transferred into oak casks for storage. The storage period is minimum two years and can last more than 10 years and, during this time, a yeast velum (Flor

yeasts) develops naturally on the surface of the wine which is in contact with air. The production of French flor sherry wine (*Vin Jaune*) in the Jura region of France, where film-forming yeast (Flor yeast) develops on the surface of the wine, is similar to the process used to produce Fino Sherry in the Xeres and Montilla-Moriles regions in Spain (Charpentier et al., 2002) except that wines are not fortified after the end of alcoholic fermentation and do not undergo sherry wine aging system. Film-forming yeast strains can be present on the surface of aging dry and sweet Szamorodni wines (belonging to the well known Tokay wine group). *Vernaccia di Oristano* is a Sardinian wine undergoing biological aging which unlike sherry wines is not fortified and which does not undergo the “Solera” system. Aging with flor yeasts to produce wines similar to flor sherry is a method also used in areas such as South Africa, Armenia, California and southern Australia.

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In all of these wines, a buoyant yeast biofilm develops at the surface during aging, and protects the wine from oxidation. The oxidative metabolism of the flor yeasts facilitates changes in the characteristics of the wine as the biofilm assures access to oxygen allowing their growth on non-fermentable ethanol. Film-forming and oxidative metabolism is adaptive mechanisms which allow cells to survive under such conditions. Flor yeasts have recently been reviewed (Pozo-Bayón and Moreno-Arribas, 2011; Benitez et al., 2011). However, the first study mainly focuses on sherry wine with different aspects such as sherry wine process and chemical composition. The second study also deals with sherry wines and especially with the aging method, the physiological characteristics of both fermentation and aging yeasts. The authors give an in-depth overview regarding the role of *FLO11* in velum forming. In this review the involvement of other genes is also discussed. The aim of the present study is not to review the process but to describe in details the specificity of flor yeasts encountered not only in sherry wines as described previously but also in Vernaccia di Oristano or “Vin Jaune”. Here, we provide an updated review as to what is known and unknown about this unusual type of yeast, with a focus on their ecology, and specific aspects of their genetics and metabolic activities.

2. Flor yeast ecology

During aging of flor sherry wines, a yeast biofilm (Fig. 1) develops under harsh conditions: low oxygen concentration, high ethanol concentration (from 14%v/v to 16%v/v), low pH and the presence of sulphites (around 30 mg/L total SO₂). Few microorganisms can survive in such conditions. Consequently, more than 95% of the flor may be composed of *Saccharomyces cerevisiae* as this is the most adapted yeast to grow in this environment (Pozo-Bayón and Moreno-Arribas, 2011). Although the velum (Flor) is mainly composed of *Saccharomyces*, other yeast and bacteria can also be present.

Analysis of 54 yeast strains isolated from the velum of French flor sherry (*Vin Jaune*) has shown that all the strains belong to *S. cerevisiae* (Charpentier et al., 2009). Other species such as *Pichia*, *Candida* and *Hansenula* have also been found in velum (Suarez-Lepez and Inigo-Leal, 2004). The presence of the spoilage yeast *Brettanomyces* has been shown to be responsible for increased volatile acidity in wine during biological aging (Ibeas et al., 1996). A physiological study by Martinez et al. (1995) reported that there are four main races of yeast involved in the formation of velum: *Saccharomyces beticus*, *Saccharomyces cheresiensis*, *Saccharomyces montuliensis* and *Saccharomyces rouxii* (also known as *Zygosaccharomyces rouxii*). This classification was based on the ability of yeasts to ferment different sugars (galactose, dextrose, lactose, maltose, melibiose, raffinose and sucrose). Other studies confirm the presence of different yeasts in sherry flor (Mesa et al., 2000) as well as in *Vin Jaune* flor (Charpentier et al., 2009). However, *S. beticus* and *S. cheresiensis* are no longer considered as races or subspecies of *S. cerevisiae* according to the last taxonomic study (Kurtzman et al., 2011). Indeed, all these previously named races or subspecies are now considered as *S. cerevisiae* synonyms based on nuclear DNA

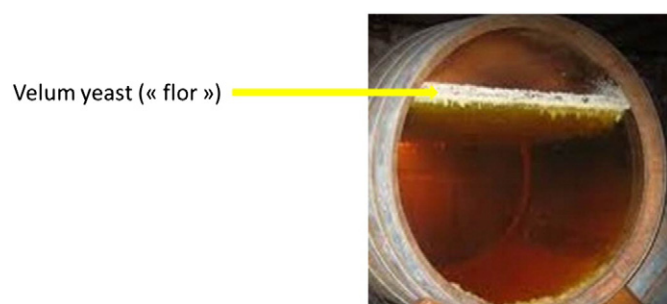


Fig. 1. Velum yeast on French flor sherry wine *Vin Jaune*.

relatedness. Regarding *S. montuliensis*, it is now considered as *Torul-asporea delbrueckii*. Molecular analysis tools have been developed to identify these yeasts (Esteve-Zarzoso et al., 2001). RFLP analysis of the 5.8S rRNA gene and the 5.8S-ITS region allows *S. cerevisiae* velum yeast to be differentiated from other *S. cerevisiae* (Fernandez-Espinar et al., 2000) as velum yeast is generally characterized by a 24 bp deletion in the ITS1 (Internal Transcribed Spacer) (Esteve-Zarzoso et al., 2004). *S. cerevisiae* from *Vin Jaune* has no 24 bp deletion in the ITS1 region (Charpentier et al., 2009) but has an additional C residue resulting in the creation of a *HaeIII* site in this sequence (Fig. 2). An additional 370 bp sequence in this region was revealed by RFLP analysis using *CfoI* (Charpentier et al., 2009). The 24 bp deletion has been proposed to be related to a nuclear gene involved in ethanol tolerance (Fernandez-Espinar et al., 2000). Thus, the difference between yeasts associated with *Vin Jaune* and Spanish flor could be due to differences in alcohol content although Charpentier et al. (2009) suggest that the differences between these yeasts are more likely to be linked to their phylogenetic origin.

Two yeast groups have been identified in a biodiversity study on *Vin Jaune* velum yeast. These groups, isolated from geographically separate areas, were shown by interdelta sequence typing to have different genetic structures (Charpentier et al., 2009); the velum aspect appears to be correlated with the interdelta profile. Yeasts characterized by the production of a thin velum have similar interdelta profile, which are different to that of yeasts producing a thick velum.

The origin of these yeasts is unclear; we do not know if they are present on grapes or found in the cellar. In *Vin Jaune* it is still to be determined whether the yeasts responsible for alcoholic fermentation are the same as those present in the velum. For sherry wines, one study has followed the population dynamics of yeasts during alcoholic fermentation and biological aging (Esteve-Zarzoso et al., 2001). Sherry wines are fortified (the addition of alcohol) after the initial fermentation and it is only after fortification that flor yeasts were detected in the medium. These yeasts were not found during alcoholic fermentation, probably because their cell concentration is too low. During aging it is mainly flor yeasts belonging to *S. cerevisiae* species that were present, although these are sometimes found together with *Brettanomyces* (previously shown by Ibeas et al. (1996)). The study concludes that yeasts responsible for alcoholic fermentation are different from velum yeast. However, the must in this study was inoculated with commercial yeast (Esteve-Zarzoso et al., 2001) which could have influenced the development of indigenous yeast. Further studies are required, particularly for *Vin Jaune* and *Vernaccia* wines where there are currently no data available. As the aging process is different from sherry wine, there may also be differences between the biological aging processes.

Contradictory results have been reported regarding the dynamics of yeast populations during biological aging. Martinez et al. (1997b) have shown that different yeasts succeed during aging: *S. cerevisiae beticus* (now *S. cerevisiae*) is faster at forming velum and predominates in younger wines, whereas *S. cerevisiae montuliensis* (now *T. delbrueckii*) produces and resists higher acetaldehyde concentrations and so appears later. However, Ibeas et al. (1997) reported that in different wine cellars, different flor yeasts dominate and persist during aging and this was confirmed by Esteve-Zarzoso et al. (2001). In view of the latest yeast taxonomy it is important to underline that there are no more races (Kurtzman et al., 2011).

3. Distinctive genetic features of velum yeast

Some authors suggest that velum yeast possesses distinct genetic features that are different to that of other wine yeasts (for example, low chromosomal polymorphism (Martinez et al., 1995; Ibeas and Jimenez, 1996)). Elevated ethanol concentration found in wines aged under yeast velum may be responsible for such genetic differences (Ibeas et al., 1997; Martinez et al., 1998; Mesa et al., 1999, 2000). Genetic heterogeneity could be associated with adaptation to a wine medium

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