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Review

Impact of industrial yeast derivative products on the modification of wine aroma compounds and sensorial profile. A review

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1. Introduction

Wine is a complex matrix comprised of hundreds of volatile aroma compounds that originate from grapes or develop as yeast metabolism products during alcoholic fermentation. Wine aroma complexity can vary depending on the geographic origin of the grapes and the associated pedo-climatic conditions (also called terroir), viticultural practices, wine-making processes and the type of bottling and ageing. In addition, aroma compounds can interact with one another or with other molecules in wine such as oxygen, proteins, polyphenols, and polysaccharides, thus seeing their sensorial impact modified. The unfolding of this wide variety of volatile compounds in the complex wine matrix defines wine quality. A controlled management of the different techniques or conditions of wine making can help enhancing the genesis of pleasant aroma compounds, while reducing the formation of unpleasant aroma compounds due to stuck fermentation, microbial contamination or oxidation phenomena, thus improving wine quality.

For several years now, yeast derivative products (YDPs) have found widespread use in the winemaking process for fermentation management and wine stabilization. These products were used either to supply assimilable nitrogen or to stimulate yeast and lactic bacteria growth and prevent stuck fermentations, but also for the role played by yeast mannoproteins in increasing wine colloidal stability (Ángeles Pozo-Bayón, Andújar-Ortiz, & Moreno-Arribas, 2009; Comuzzo et al., 2011; Morata, Palomero, Loira, & Suárez-Lepe, 2018). More recently, YDPs have been widely used to improve either the technological process or protect the chromatic and sensory characteristics of wines (Andújar-Ortiz, Chaya, Martín-Álvarez, Moreno-Arribas, & Pozo-Bayón, 2014; Charpentier & Feuillat, 1992; Feuillat & Charpentier, 1982; Lubbers, Voilley, Feuillat, & Charpentier, 1994; Pozo-Bayón, Andújar-Ortiz, & Moreno-Arribas, 2009). The application of yeast protein extract for wine fining was allowed by the International Organization of Vine and Wine (OIV) (resolution OIV-OENO 417–2011). This practice reduces wine turbidity, preserves the intensity of the color and the structure of wines, eliminates the excess of tannins and improves wine filterability. More recently, wine treatment using inactivated yeasts with guaranteed glutathione levels was accepted by OIV (resolution OIV-OENO 533–2017) to limit the oxidation of certain varietal aromatic compounds revealed by yeast metabolism, particularly thiols. The enological applications of these yeast derivative products were reviewed by Ángeles Pozo-Bayón et al. (2009). However, our knowledge of the mechanisms of action of these products on wine organoleptic characteristics is often empirical and these mechanisms are not very well understood.

In the late 90′s-early 2000′s, scientific studies started to report the ability of yeast walls and purified yeast macromolecules to bind volatile compounds in model wines (i.e. aqueous solutions with ethanol, organic acids and salt at pH 3.5), thus affecting wine sensory perception (Bautista, Fernández, & Falqué, 2007; Lubbers, Charpentier, Feuillat, & Voilley, 1994; Lubbers, Voilley et al., 1994; Vasserot, Steinmetz, & Jeandet, 2003). Later, new studies reported not only the binding ability of YDPs and purified yeast macromolecules, but also the release into model wines of the volatile compounds originally present in the additives, as a consequence of thermal and/or oxidative degradation of lipids, sugars, amino acids and thiamin during YDPs manufacturing (Comuzzo, Tat, Tonizzo, & Battistutta, 2006; Pozo-Bayón et al., 2009). More recent studies have also reported the impact of YDPs in red and white wines.

However, these studies were performed with YDPs at different doses and from different providers, so their composition may have varied depending on the yeast strain used, on yeast culture conditions and on the conditions of the manufacturing process. In addition, the grape variety and aroma compounds of interest were not always identical, which makes it difficult to compare these results. Therefore, this paper aims at reviewing and compiling the different experimental conditions and data obtained in the different studies and to highlight the impact of YDPs on the wine aroma compounds and wine sensory characteristics, taking into account the nature of YDP, the physico-chemical characteristics of the

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aroma compounds and the wine matrix. The following sections will first present the different YDPs that can be found in oenology, then the genesis of aroma compounds during the wine making process and their impact on the wine sensory profile and lastly, the impact of YDPs on the evolution of aroma compounds and sensorial profile of model and real wines.

2. Industrial yeast derivative and their use in winemaking

2.1. Yeats derivative products

Yeast derivative products (YDPs) are inactivated yeast preparations obtained from *Saccharomyces* and/or non-*Saccharomyces* yeasts through different industrial processes (heat treatment, enzymatic hydrolysis, physical disruption, fractionation, …). In the field of oenology, these products have experienced in recent years a significant expansion, as well as a great diversification. Industrial production of yeast fractions to improve wine quality is the result of the interest in ageing on lees (dead yeasts and organic residues) for the quality of wines and at the same time of its drawbacks under oenological conditions.

2.1.1. Wine ageing on lees

Traditionally, ageing on lees consists of keeping the ageing wine in contact with yeasts and organic residues resulting from the fermentation step. During this prolonged contact, there are three simultaneous phenomena: i) an enzymatic self-degradation of dead yeast (autolysis), leading to the release of cytoplasmic (proteins, peptides, amino acids, fatty acids, nucleotides) and parietal (mannoproteins, glucans, oligosaccharides) components into wine (Charpentier & Freyssinet, 1989; Feuillat & Charpentier, 1982); ii) an adsorption of wine constituents onto yeast cell walls (Caridi, 2006; Mazauric & Salmon, 2006; Palomero et al., 2009); (iii) a consumption of dissolved oxygen by yeast, attributed to plasma membranes and glutathione (Salmon, Fornairon-Bonnefond, & Mazauric, 2002). This material transfer is accompanied by a modification in wine composition and properties. Various positive effects of ageing on lees on wine characteristics have been mentioned, including: improvement of mouthfeel, colloidal (tartaric and protein) and colour stability, aromatic profile, and preservation of wines against oxidation (Charpentier & Feuillat, 1992; Feuillat & Charpentier, 1998; Lubbers, Charpentier et al., 1994). All of these parameters are mainly influenced by the addition of parietal polysaccharides and intracellular nitrogen compounds made soluble by a post-fermentation lysis phase. In practice, in order to promote these reactions, enzymes targeted at yeast parietal envelopes have been developed in recent years (described in the International Oenological Codex), and lee resuspension phases have been optimized (Vivas, Nedjma, & Vivas De Gaulejac, 2016). However, complete lysis, and therefore lees contribution to wine, is not always achieved and the results obtained are thus irregular (Vivas et al., 2016). In particular, the temperature criterion represents a limiting factor for lysis, which depends on endothermic enzymatic reactions. On the other hand, in red wines, the inhibiting effect of tannins on endogenous or added enzymes leads to increased irregularity in the results. Finally, in the case of high pH (above 3.7), risks of contamination from the natural lees cannot be excluded (Fornairon-bonnefond, Salmon, Camarasa, & Moutounet, 2001; Vivas et al., 2016).

2.1.2. Emergence of industrial inactivated yeast preparations

Under these conditions, research and development of an oenological preparation composed of partially lysed yeasts may be of interest. The main advantages would be: lysis regularity and intensity, the possibility of modulating the impact on wines by adapting the treatment to the type of wine, the speed of action and the elimination of constraints linked to temperature, polyphenols inhibition and risks of contamination (Vivas et al., 2016). This is why, in recent years, we have seen the emergence of products derived from industrially produced yeasts for different applications from vine to wine. Fig. 1 shows the main classes of products derived from industrially processed yeasts. In the context of oenology, the Organization of Vine and Wine (OIV) only authorizes the use of some of them only -inactivated yeast, inactivated yeast with guaranteed level of glutathione, autolysate, yeast protein extract, yeast walls and mannoproteins- and for very specific applications. In the following section, we will talk in more detail about these different products, their

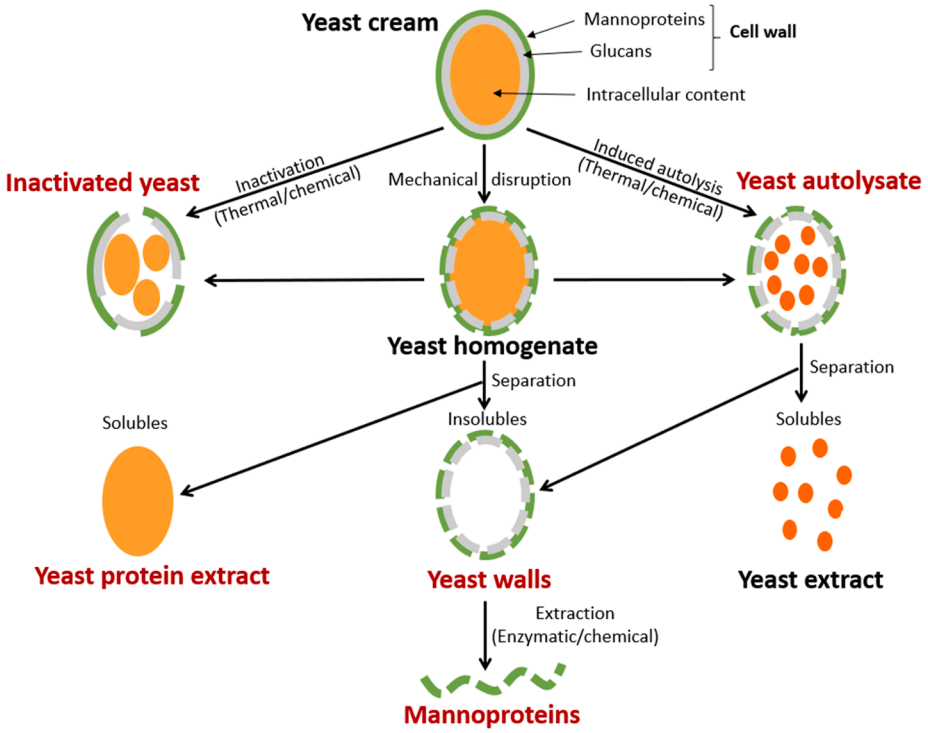

Fig. 1. Main classes of products derived from industrially produced yeasts. The names in red are yeast derivatives authorized and defined by OIV.

production process and their applications in oenology.

2.2. Yeast derived products in oenology

2.2.1. Inactivated yeast

Inactivated yeast corresponds to killed yeast, deprived of fermenting capacity, and having undergone neither extraction nor addition" (JOCE, n°C5, January 8, 1975). The general process for manufacturing inactivated yeasts in the oenological context consists in inactivating a *Saccharomyces* yeast cream by heat and/or by a pH change; yeast cells may have undergone natural autolysis under the action of endogenous enzymes (Resolution OIV-OENO 459–2013). Inactivated yeast still includes the yeast cell content although cell integrity is not maintained because cell wall membranes have been disrupted. The cellular constituents are more soluble and of lower molecular weight if autolysis has taken place. Yeasts treated in this way are generally spray-dried. If some autolysis occurs, it must be moderate to meet OIV specifications that stipulate that the insoluble fraction must be greater than or equal to 60% w/w of dry matter (Resolution OIV-OENO 459–2013). The total nitrogen content must be less than 10% of dry matter. The ammonia nitrogen content must be less than 0.5% of dry matter. The content of free and soluble amino acids and small peptides in glycine equivalent must be less than 10% of dry matter (Resolution OIV-OENO 459–2013).

Inactivated yeasts are used as yeast nutrients at the beginning of and during alcoholic fermentation and also to promote the rehydration of active dry yeasts. They can help reducing ochratoxin A (a mycotoxin produced by several microscopic fungi) level during wine maturation and clarification. Recently, inactivated yeasts rich in glutathione have been authorized to limit oxidation phenomena in musts and wines (Resolution OIV-OENO 603–2018). Reduced glutathione (GSH) can be accompanied by its precursors, cysteine and, in particular, gamma-glutamyl-cysteine. Their addition increases the level of glutathione produced by living yeasts during fermentation for a better preservation of wine against oxidation. Like classic inactivated dry yeasts, they also provide nutrients to yeasts during fermentation. They can reduce ochratoxin A level, at both stages of maturation and clarification of wines (resolution OIV-OENO 459–2013). They are derived from *Saccharomyces* and/or non-*Saccharomyces spp* biomasses, the production of which is directed in such a way as to increase the natural production of glutathione in reduced form (GSH).

2.2.2. Yeast autolysate

Yeast autolysate is defined as a concentrated hydrolysate obtained following the autolysis of a yeast biomass, possibly combined with heat treatments and/or pH modifications. Autolysis is defined as the self-digestion of proteins and other cellular constituents by enzymes contained in yeast cells (Resolution OIV-OENO 496–2013). The autolysate has not undergone any extraction and contains both soluble and insoluble cellular constituents. In conventional industrial autolysis processes, yeast is diluted with water to a specified solids content before autolysis (Alexandre, 2011). Salt may be added to the resulting slurry to aid in cell membrane rupture (plasmolysis). Yeast components (proteins, nucleic acids, lipids, cell wall polysaccharides) are solubilized and hydrolyzed during the autolysis process. Cells are then heated (30 to 60 °C), encouraging further cell breakdown (Alexandre & Guilloux-Benatier, 2006; Alexandre, 2011). The addition of external enzymes to yeast is not allowed in the field of oenology. Upon completion of the autolytic process, no extraction is performed, but the slurry is concentrated and dried or used in liquid form. Yeast autolysate is highly soluble in water, although the soluble part of dry matter present in the autolysate in dry or liquid form must be less than 80% (Resolution OIV-OENO 496–2013). Yeast autolysates are used as nutrients for the rehydration of active dry yeasts and also as nutrients during alcoholic fermentation. The total nitrogen content must be less than 12% of dry matter. The ammonia nitrogen content must be less than 0.5% of dry matter. The amino acid content, in glycine equivalent, must be between 10% and 20% of dry matter (Resolution OIV-OENO 496–2013).

2.2.3. Yeast walls

Yeast cell wall as described in research data represents between 15 and 30% of the dry weight of the yeast *Saccharomyces cerevisiae* (Aguilar-Uscanga & Francois, 2003; Orlean, 2012). It is a structural component that confers to the yeast cell its shape and rigidity. It is a 110–200 nm wide network, mainly composed (on a dry matter basis) of β-1,3-glucans (50%), β-1,6-glucans (10%), mannoproteins (40%), and chitin (1–3%) (Lipke & Ovalle, 1998). Schematically, they can be described as two-layered structures: an inner microfibrillar layer mainly composed of β-glucans (cross-linked or not to chitin) and an outer brush-like layer that mostly consists of mannoproteins (Kapteyn, Van Den Ende, & Klis, 1999; Klis, Mol, Hellingwerf, & Brul, 2002; Orlean, 2012). According to the OIV description, yeast walls preparations can be a co-product of the production of yeast extract. After the autolysis phase, the insoluble fraction is separated by centrifugation from the soluble yeast extract. Yeast walls can also be obtained by physical processes (mechanical disruption). Whatever the case, the method of production must respect the surface and therefore the sorption capacity. The product is usually spray dried. The composition of yeast wall preparations can be close to that of the native yeast cell wall if the separation by centrifugation is done without any contamination by the cytoplasm. According to the OIV description, yeast walls preparations must contain more than 40% carbohydrates, of which at least 60% are mannans and glucans (Resolution OIV-OENO 459–2013). Yeast envelopes must be practically insoluble, the soluble fraction being less than 10% of the dry mass. The use of yeast cell envelopes is subject to a dosage limit (40 g/hL). They are used in oenology to prevent or cope with stuck fermentation. They have the property of fixing certain fatty acids (octanoic and decanoic acids) that are toxic for yeasts and bacteria during fermentations.

2.2.4. Mannoprotein

S. cerevisiae mannoproteins are mainly located in the outer layer of the cell wall. They are composed on average of 85 to 90% glycans, mainly D-mannose, linked by α(1,2), α(1,3) and α(1,6) bonds, and of 10 to 15% protein (Nakajima and Ballou, 1975; Orlean, 2012). According to OIV, mannoproteins must be extracted from the cell walls of *S. cerevisiae* by physico-chemical or enzymatic methods (Resolution Codex OIV-OENO 26–2004). Depending on the extraction method, mannoproteins may have different structures in terms of molecular mass, degree and type of glycosylation, and charge. Several studies have demonstrated the positive impact of mannoproteins on the sensory quality of wines: improvement of the perception in the mouth, reduction of astringency, addition of complexity and aromatic persistence, increase in sweetness and roundness (Del Barrio-Galan, Ortega-Heras, Sanchez-Iglesias, & Perez-Magarino, 2012; Del Barrio-galán et al., 2014; Del Barrio-Galán, Perez-Magarino, Ortega-Heras, Williams, & Doco, 2011a, 2011b; Vidal, Françis, et al., 2004; Vidal, Courcoux, et al., 2004). However, we note that, presently, mannoproteins are only authorized for their tartaric and/or protein stabilization activities in wines.

2.2.5. Yeast protein extract

Yeast protein extract is mainly the cytoplasm of *Saccharomyces spp* cells (Resolution OIV-OENO 452–2012). The cytoplasm of yeast cells is composed of cellular organelles (mitochondria, ribosomes, vesicles, endoplasmic reticulum, peroxisomes, Golgi apparatus, vacuoles, nucleus) and soluble molecules dispersed in the cytosol (Martins, Sakomura, Souza, Filho, Gomes, & Vasconcellos, 2014). The soluble molecules in the yeast cytosol are mainly proteins and nucleic acids (RNA), medium-sized molecules such as sugars, lipids, amino acids, nucleotides, various metabolites and very small molecules such as inorganic ions, divalent cations and dissolved gases (Martins et al., 2014). Beyond the presence of proteins, yeast protein extract therefore appears as a very complex mixture. According to OIV recommendations, the extract is obtained by applying physical methods after an extraction

process that limits protein hydrolysis (Resolution OIV-OENO 452–2012). Proteins in yeast protein extracts have variable molecular weights and electrical charges depending on how they were obtained. Yeast proteins have flocculating properties allowing musts and wines clarification and colloidal stabilization and yeast protein extract is thus authorized for fining operations in musts and wines. It is generally in powder form and must be water- but not ethanol- soluble. The total protein content of yeast protein extract must be greater than 50% of the dry product. At least 50% of the total proteins must have molecular weights higher than 15 kDa (Resolution OIV-OENO 452–2012). The amino nitrogen content expressed as glycine should represent 10 to 20% maximum of the dry product. As for yeast walls, there's a maximal legal dosage limit: 60 g/hL for red wines, 30 g/hL for musts, white and rosé wines.

Ultimately, as the definition of each product by OIV is very broad, the composition of these products can greatly vary from one producer to another.

2.2.6. Wine aroma

Wine bouquet is the main character that can best define wine quality and it can be seen as all the direct and retronasal olfactory - sensations a wine can procure. These sensations result from the combined effect of hundreds of volatile compounds in the complex wine matrix.

Wine aroma origin is classified into 3 categories, as reported in Table 2:

2.3. Varietal aroma compounds

The varietal aroma compounds originate from the vine either in a free form or bound to flavorless aroma precursors that are then released during the fermentation process. The most powerful varietal aromas are terpenoids, varietal thiols and methoxypyrazines.

2.3.1. Terpenoid compounds

Terpenoids compounds, also called isoprenoids, represent the largest class of natural products with different isomers and enantiomers (Ruiz, Kiene, Belda, Fracassetti, Marquina, Navascués, Calderón, & Benito, 2019). Among this family of compounds, wine contains mainly monoterpenes (C10 compounds), but also non negligible quantities of sesquiterpenes (C15 compounds) and C13-norisoprenoids.

The most important terpenoids in wine are mono-oxygenated monoterpenes such as linalool (citrus blossom; flowery), (E)-hotrienol (faintly flowery; elder flower), citronellol (green citrus), geraniol (rose-like; geranium), nerol (rose-like; citrus blossom), (−)-*cis*-rose oxide (geranium oil, floral green), and α-terpineol (floral, woody). The *cis*-rose oxide, linalool and citronellol have the lowest odor threshold, respectively 0.5 μg/L, 15 μg/L, 18 μg/L, α-terpineol and nerol the highest (400 μg/L) while Geraniol and (E)-hotrienol have an intermediate perception threshold of 130 and 110 μg/L respectively. Linalool, citronellol, geraniol and α-terpineol are the terpenes present at the highest concentration in Muscat varieties and they contribute to the floral, fruity and citrus aroma of the corresponding wines (Ruiz et al., 2019). However, they also contribute to the aroma of non-Muscat varieties such as Sylvaner, Weisser, Riesling, and Gewürztraminer (Marais, 2017). Monoterpenes are also present in other varieties such as Cabernet Sauvignon, Carignan, Chardonnay, Merlot, Sauvignon Blanc, and Shiraz but at a concentration below their odor detection threshold. Monoterpenes can be found in grapes and musts as free aroma compounds but, depending on the grape variety, they can be present in much higher concentration (90% in Muscat varieties), being linked to sugar moieties, the so-called terpene glycosidic non-volatile precursors (Gunata, Bayonove, Baumes, & Cordonnier, 1985). Conversion of these compounds into terpenes is mainly carried out through enzymatic hydrolysis, for example by β-glucosidases (from grapes or micro-organisms) during alcoholic and malolactic fermentation processes and, to a lesser extent, by acidic hydrolysis in musts (Charoenchai, Fleet, Henschke, & Todd, 1997; Günata, Bayonove, Tapiero, & Cordonnier, 1990; Ugliano, Bartowsky, McCarthy, Moio, & Henschke, 2006). During wine storage and under acidic, oxidative or high temperature conditions, monoterpenes can be transformed into different compounds that may be more or less aroma-intensive and may disrupt the original character of the wine (Marais, 2017; Ruiz et al., 2019). For example, linalool can be easily oxidized via an epoxyde to four oxides, namely cis- and trans- furan linalool oxide and cis/ trans pyran linalool oxide. Furthermore, geraniol is transformed into α-terpineol and nerol and the isomer of geraniol may react similarly (Marais, 2017).

C15 sesquiterpenes had been poorly studied since they were considered as less active aroma compounds due to their lower volatility in comparison to monoterpenes (Black, Parker, Siebert, Capone, & Francis, 2015; Li, Howell, Fang, & Zhang, 2020). Nevertheless, rotundone was first identified in Australian Shiraz red wines as a very potent sesquiterpene that imparts black pepper attributes, and this discovery has generated a growing interest in grape sesquiterpenes. Most sesquiterpenes identified in wines are reported to impart mainly balsamic, woody, and spicy notes. It was demonstrated that these compounds, including rotundone, derive from the farnesyl diphosphate precursor (FPP) and accumulate in the grape berry exocarp (Black et al., 2015; Li et al., 2020).

C13-norisoprenoids are secondary metabolites of grapes formed mainly by the biodegradation of the carotenoids β-carotene and neoxanthin. Carotenoids accumulate in berries prior to veraison and are generally found at a two to three times higher concentration in skins than in pulp (Mendes-Pinto, 2009). As berries mature, carotenoids concentration decreases as a result of an enzymatic cleavage with a carotenoid cleavage dioxygenase (CCD), resulting in C13 subunits (Walter and Strack 2011; Black et al., 2015). The norisoprenoid compounds identified in wine with very important sensory characteristics are β-ionone (violet, raspberry and rose), β-damascenone (rose, cooked apple, honey), 1,1,6-Trimethyl-1,2-dihydronaphthalene (TDN) (petrol or kerosene), vitispirane (flowery, fruity, earthy, woody depending on the isomer), actinidiol (camphoraceus, woody) (Black et al., 2015; Mendes-Pinto, 2009). It was reported that higher concentrations of C13-norisoprenoids were positively correlated with red fruit aromas and a higher quality rating by wine consumers (Sáenz-Navajas et al., 2015).

2.3.2. Varietal thiols

Varietal thiol compounds include those sulfur-containing wine compounds identified as key molecules for their positive contribution to the aroma of young wines elaborated with many varieties (Roland, Schneider, Razungles, & Cavelier, 2011). Among all the varietal thiols identified, three were found to be strong contributors to the aroma of white wines made from Sauvignon blanc, Macabeo, Gewürztraminer, Riesling, Verdejo, Merlot, and Cabernet Sauvignon: 4-methyl-mercapto-pentan-2-one (4MMP) that exhibits aromas of box tree and blackcurrant bud, 3 mercapto-hexyl acetate (3MHA) and 3 mercapto-hexanol (3MH) that both exhibit aromas of grape fruit, passion fruit, citrus zest and guava (Rigou, Triay, & Razungles, 2014; Roland et al., 2011; Ruiz et al., 2019). Although they are found in wines at very low concentrations (ng/L), they exhibit a very low odor perception threshold (0.4 ng/L; 4.2 ng/L and 60 ng/L respectively), which make them very powerful aroma compounds. Thiols are extremely reactive compounds, very prone to oxidation: their chemical oxidation generally occurs in fermenting grape must and in ageing wines and they can be transformed into disulfides and/or consumed by oxidized phenolic compounds. As volatile thiols are nucleophiles, they can add to electrophilic sites such as o-quinones through a Michael-type reaction, which leads to the formation of adducts (Nikolantonaki et al., 2010, 2012). Thiols nucleophilicity is mainly modulated by their steric hindrance, primary thiols being more reactive than tertiary thiols (Nikolantonaki et al., 2010, 2012). Thiols are not expressed in grape must but develop during the fermentation process from glutathionylated and cysteinylated precursors present in grapes. Yeast cells can take up these thiol precursors from grape juice and then

cleave the conjugated precursors, releasing the corresponding free thiols. Yeast then acetylates a fraction of 3MH to yield 3MHA (Roland et al., 2011).

2.3.3. Methoxypyrazines

3-alkyl-2 methoxypyrazines are very powerful odorants present in some grape varieties, particularly Sauvignon Blanc and Cabernet-Sauvignon, imparting a herbaceous (vegetative) character to wines (Lei, Xie, Guan, Song, Zhang, & Meng, 2018; Ruiz et al., 2019; Ryan, Watkins, Smith, Allen, & Marriott, 2005; Ryona, Pan, Intrigliolo, Lakso, & Sacks, 2008). The chemical structures of pyrazines all share a nitrogen heterocyclic ring ($C_4N_2H_4$) with different side chains, which make them very stable hydrophobic volatile compounds difficult to remove or reduce in wines (Lei et al., 2018). The side chains and their steric and electrostatic effects are responsible for their unique aromatic properties. The methoxypyrazine considered to be the most relevant to wine flavor is 3-isobutyl-2-methoxypyrazine (IBMP), that is very well correlated to the bell pepper aroma character in wines, whereas 3-*sec*-Butyl-2-methoxypyrazine (sBMP) and 3-isopropyl-2-methoxypyrazine (IPMP) are present at lower concentrations in wine grapes. One important characteristic of methoxypyrazines is their very low sensory threshold (between 1 and 10 ng/L) and therefore, their presence in wine at very low concentrations requires the development of very sensitive analytical methods for their detection. At low concentrations, the presence of methoxypyrazines can positively contribute to wine varietal aroma, but, in excessive amounts, they can be overpowering and detrimental to wine, imparting unpleasant green and herbaceous characters that common cellar practices such as bentonite fining, oak contact, pectinases and microoxygenation are not able to remove. It was demonstrated that the level of methoxypyrazines in grapes depends on the grape variety as well as environmental and viticultural factors such as climatic temperature, vine vigor, irrigation and light exposure (Dunlevy, Soole, Perkins, & Boss, 2010; Ruiz et al., 2019). The methoxypyrazines content of berries is a balance between their biosynthesis and their metabolism or degradation during berries development and maturation. However, little work has been done in elucidating the biosynthesis pathway of methoxypyrazines in grapes.

2.4. Fermentative aroma compounds

The aroma complexity of wine increases during alcoholic fermentation, mostly as a result of the synthesis of important volatile compounds through *Saccharomyces* and non-*Saccharomyces* yeast metabolism (Molina, Swiegers, Varela, Pretorius, & Agosin, 2007). These volatile compounds, also called fermentative aromas, are mainly constituted of volatile higher alcohols, acetate and ethyl esters, medium- and long-chain volatile acids, aldehydes, sulfur compounds (Molina et al., 2007). The production of these compounds depends on several factors such as must nitrogen content, fermentation temperature, yeast species and strain (Jeromel, Korenika, & Tomaz, 2019; Molina et al., 2007). It combines biochemical assimilation of nutrients by yeast and is governed by a dihydrogenase enzyme. This production has been mainly studied in *S. cerevisiae*, but new studies are being extended to other non-*Saccharomyces* yeasts (Jeromel et al., 2019).

Higher or fusel alcohols with more than two carbons are one of the most significant groups of volatile compounds produced by yeast. They are derivatives of amino acids and their biosynthesis occurs via the Ehrlich pathway, which includes different transamination, decarboxylation, and oxido-reduction reactions catalyzed by at least three aminotransferases, five decarboxylases, and six dehydrogenases (Jeromel et al., 2019). Higher alcohols are considered to be the aromatic compounds with the strongest effect on wine overall aroma but the literature is not unanimous on whether they have a positive or negative contribution. Although there is evidence of a negative effect, it was reported that this effect depends on the specific aromatic context, and that the role played by the type and concentration of the different alcohols in wine is still not completely understood (Ferreira, 2016). For example, amyl and isoamyl alcohols were reported to impart an aroma reminiscent of marzipan, and phenyl ethanol to be a potential contributor to the floral character of wines attributed to its rose-like aroma (Ruiz et al., 2019). However, Ferreira *et al.* 2016 demonstrated that, in a wine context where aroma nuances are clearly perceived, isoamyl alcohol, together with isobutanol, suppress pleasant odor notes such as strawberry/lactic/red fruit, coconut/wood/vanilla and unpleasant humidity/Trichloroanisole (TCA) off-flavors, although they did not affect leathery/animal/ink notes (Ferreira, 2016). Similarly, Cameleyre *et al.* (2015) reported a masking effect of higher alcohols on the overall fruity aroma in fruity model wine mixtures.

Esters are another important class of yeast volatile compounds that contribute to wine fruity notes. The main esters can be divided into i) acetate esters such as isobutyl acetate (fruity aroma), amyl acetate, isoamyl acetate (banana aroma), hexyl acetate, and 2-phenylethyl acetate (rose-like aroma) and ii) ethyl fatty acids esters such as ethyl hexanoate (banana like aroma), ethyl octanoate (pineapple aroma), and ethyl decanoate (fruity and floral aroma). Branched-chain esters (ethyl 2-methylpropanoate, ethyl-2-methylbutanoate, and ethyl-3-methylbutanoate) that have very low odor threshold values are normally present in much lower concentrations in wines (Jeromel et al., 2019). Ester acetate compounds are produced by condensation of a higher alcohol and a coenzyme-A-activated acid (acetyl-CoA) through the action of alcohol acetyl transferases. The majority of ethyl fatty acid esters are considered to be formed through enzymatic esterification of activated fatty acids (acyl-CoA) (Jeromel et al., 2019; Molina et al., 2007; Saerens, Delvaux, Verstrepen, & Thevelein, 2010). Esters are normally present in wine at high concentrations, from one to a hundred ppm, well above their perception thresholds (ranging from 0.02 to 32 ppm) and they contribute to the fruity and floral aroma of wines, especially those made from cultivars with neutral flavor (Jeromel et al., 2019; Ruiz et al., 2019). Nevertheless, it is important to maintain low esters concentrations in order to preserve the varietal characteristics of the grapes. Indeed, it was demonstrated that, when present at high concentrations, esters can impart negative notes of varnish and/or nail polish to wine or, in the case of ethyl acetate, even inhibit wine fruity and floral aromas (Lytra, Tempere, Le Floch, De Revel, & Barbe, 2013; Ruiz et al., 2019).

Volatile fatty acids produced by yeast are responsible for wine volatile acidity. Acetic acid represents 90% of this volatile acidity, the rest of the acids being principally medium straight-chain fatty acids such as butyric, hexanoic, octanoic and decanoic acids and medium branched-chained fatty acids such as 2-methyl propanoic, 2-methyl butanoic, and 3-methyl butanoic acid. The fatty acids production pathway involves the conversion of acetyl-CoA into malonyl-CoA, which is utilized by the fatty acid synthetase complex that carries out repetitive condensation between enzyme-bound acetyl-CoA and malonyl-CoA for the synthesis of saturated fatty acids and for chain elongation (Pretorius, 2016; Swiegers, Bartowsky, Henschke, & Pretorius, 2005). However, acetic acid is produced by yeast as an intermediate in the pyruvate dehydrogenase (PDH) bypass, a pathway responsible for pyruvate conversion to acetyl-CoA through a series of reactions catalyzed by pyruvate decarboxylase (PDC), acetaldehyde dehydrogenase and acetyl- CoA synthase (Swiegers et al., 2005). At concentrations above 0.8 g/L, acetic acid can have a detrimental vinegar effect on wine aroma. However, it can contribute to a warm sensation on the palate at concentrations lower than the perception threshold. The total amount and proportion of the various medium-chain fatty acids released into the fermentation medium will depend on the yeast strain used, the composition of the medium, and on fermentation conditions such as pH, temperature, and degree of aeration during fermentation. These fatty acids were described as reminiscent of rancid, pungent, fatty, or cheese-like aromas, which makes them generally undesirable compounds in wine (Pretorius, 2016; Ruiz et al., 2019). One strategy to reduce final fatty acid concentration is the use of combined fermentations involving non– *Saccharomyces*

species such as *D. hansenii*, *C. zeylanoides*, *M. pulcherrima*, *T. delbrueckii*, *L. thermotolerans*, and *Z. bailii* (Escribano et al., 2018; Ruiz et al., 2019).

3. Impact of yeast derivative products on wine aroma compounds and wine aroma character.

Wine is a dynamic product that undergoes a period of maturation and ageing either in bottles or in oak barrels. Wine ageing generally causes the loss of some characteristic varietal and fermentative aroma compounds, and the generation of either new aroma compounds characteristic of older wines or atypical aromas associated with wine deterioration (Ruiz et al., 2019; Styger, Prior, & Bauer, 2011). These modifications in wine sensorial profile are a result of oxidation reactions, contact with lees, presence of oak wood, and wine deterioration. Oxygen accumulation in wine during the various handling operations can lead to oxidation of sensitive aroma compounds and the production of new ones, most specifically aliphatic aldehydes. Among these, acetaldehyde is the major aliphatic aldehyde that tends to accumulate with ageing time as a result of ethanol oxidation. Furthermore, it was observed that wines stored at high temperatures and supplemented with high levels of dissolved oxygen suffered a rapid and pronounced oxidative spoilage aroma, which was related to the presence of methional, responsible for boiled-potato odor notes, phenylacetaldehyde, with honey-like odor notes, sotolon with nutty and spicy odor notes and 1,1,6-trimethyl-1,2-dihydronaphthalene (TDN), responsible for the kerosene odor in aged Riesling (Oliveira, Ferreira, De Freitas, & Silva, 2011). The formation of new compounds during ageing can be directly linked to the oxidation of alcohols present in wine or due to either the Strecker degradation of the corresponding amino acids or Maillard reactions between sugars and amino acids (Escudero, Cacho, & Ferreira, 2000; Marchand et al., 2000, 2002; Oliveira et al., 2011; Silva Ferreira, De Pinho, Rodrigues, & Hogg, 2002).

When considering the presence of industrial preparation of yeast derivative products during the wine making process, other volatile compounds may be released in addition to the macromolecules previously cited, as a consequence of the physico-chemical conditions applied to yeast during the industrial processes. Several studies report the impact of commercial YDP preparations on the chemical and sensorial modifications of the overall wine aroma. However, this impact was investigated either in model wines or on a specific grape variety, as well as under different oenological conditions (temperature, time of ageing, YDP preparation and doses), which makes it complicated to reveal a clear tendency on the effect of such a process.

3.1. Aroma compounds released from industrial yeast derived products

Aroma compounds released in wine supplemented with YDPs can originate from yeast biosynthesis or be products of lipids thermal or oxidative degradation. However, the majority of volatile compounds are produced by the action of heat on sugars, amino-acids and thiamin during YDP industrial production (Morata et al., 2018; Münch & Schieberle, 1998; Münch, Hofmann, & Schieberle, 1997).

It was demonstrated that industrial inactivated dry yeast powders can contain up to 164 volatile compounds, but this number can vary depending on the strain and industrial process (Comuzzo et al., 2011; Kotseridis & Baumes, 2000; Pozo-Bayón et al., 2009).

Long-chain fatty acids and their ethyl esters are the major compounds that were found after solvent/ solid phase micro extraction from yeast powders (Comuzzo et al., 2006; Pozo-Bayón et al., 2009). Carboxylic acids (C8-C16) that result from the thermal degradation of fats can be present at a high concentration in YDPs, and can confer to wine a rancid, pungent, cheese-like aroma (Comuzzo et al., 2006; Pozo-Bayón et al., 2009). The corresponding ethyl esters formed by esterification of the long chain fatty acids are normally present in wine at a concentration lower than their perception threshold; however, their synergic effect with other aroma compounds can enhance the fruity aroma of young wines.

Aldehydes such as 2 methyl-propanal, 2–3-methyl butanal, pentanal, hexanal, octanal, and nonanal, form another class of compounds found in YDPs (Pozo-Bayón et al., 2009). The linear aldehydes pentanal, hexanal, octanal, and nonanal can be produced following fatty acids oxidation and the non– linear 2-methyl-propanal, and 2–3 methyl butanal are products of the Strecker degradation of amino-acids. The elongated aldehydes can participate in the increase in oily and fatty notes whilst the Strecker aldehydes can impart a malty flavor.

Nitrogen-containing heterocycles molecules were reported in yeast extracts as being Strecker degradation products of amino acids or formed by the Maillard reaction of 1,2-dicarbonyl compounds with α-amino acids. The most abundant nitrogen-containing heterocycles molecules found in dry yeast extracts are alkylpyrazines such as 2,3 and 2,5-Dimethylpyrazine, 2-Ethyl-3,5-methylpyrazine, 2,3,5,6-Tetramethylpyrazine (Comuzzo et al., 2006; Izzo & Ho, 1991; Pozo-Bayón et al., 2009). Among these pyrazines, 2-ethyl-3,5-methylpyrazine was found in relatively large amounts in a dry yeast extract (Izzo & Ho, 1991; Pozo-Bayón et al., 2009). These compounds normally have a nutty, roasted aroma or an earthy, potato-like aroma, but in wine, they are normally found at concentrations below their perception threshold. Higher carbon-substituted pyrazines such as methylpentylpyrazine and dimethylpentylpyrazine, were also found in autolyzed yeast extracts, probably as a result of aldehyde addition to metastable dihydropyrazine (Izzo & Ho, 1991; Pozo-Bayón et al., 2009).

Pyrrole derivatives were reported in yeast extracts in much lower amounts than pyrazine. These compounds, which are known to impart stale popcorn, and bakery notes, are most likely formed by the reaction of dicarbonyls with amino acids and a final aminocarbonyl cyclization (Izzo & Ho, 1991).

Lastly, sulfur-containing volatile compounds such as di- and trimethyl disulfides, methylthiazole, and benzothiazole, were found in yeast extracts and autolysates (Comuzzo et al., 2006; Kotseridis & Baumes, 2000; Pozo-Bayón et al., 2009; Zhang, Song, Li, Yao, & Xiong, 2017). Alkyl sulfides originate from the thermal degradation of sulfur-bearing amino acids such as methionine whilst thiazole compounds might be produced by the Maillard reaction of cysteine with reducing sugars (Izzo & Ho, 1991; Pozo-Bayón et al., 2009; Zhang et al., 2017). These compounds are associated with cabbage and rubber-like off-flavors.

Interestingly, both 3-mercaptohexanol and 4-mercapto-4-methylpentan2one were found in dry active *S. cerevisiae* wine yeasts (Kotseridis & Baumes, 2000). These thiol compounds normally originate from non-volatile cysteinylated and gluthathionylated precursors present in grapes and are released during the fermentation due to yeast β-lyase activity. Nevertheless, it was demonstrated in model wines that sulfur compounds can covalently bind to the free –SH functions of yeast mannoproteins (Vasserot et al., 2003).

3.2. Aroma compounds released in wine added with YDPs

Among the thousands of compounds identified in yeast derivatives, only part of them were found in model wines and wines aged with the product. The nature of the compounds released into wine depends on the nature of YDPs (e.g. solubility in wine) and on the ageing process conditions (e.g. the amount of YDPs used, the ageing time and the oxydo-reduction conditions in the medium). In addition, these compounds can evolve in wine along ageing time because of the presence of ethanol or oxygen in the medium. Most studies reporting the impact of YDPs on the evolution of the aromatic profile of model and real wines have shown an increase in alcohols, fatty acids and long chain fatty esters contents (Andújar-Ortiz et al., 2014; Bautista et al., 2007; Comuzzo et al., 2006; Gabrielli, Aleixandre-Tudo, Kilmartin, Sieczkowski, & du Toit, 2017). Such changes correspond to the aromatic compounds present in YDPs. However, the balance between alcohols, acids and esters can be disrupted due to the esterification of fatty acids in the presence of

ethanol, or to the hydrolysis of esters in presence of water. For example, it was demonstrated, in a Sauvignon Blanc aged for 2 months with or without addition of commercial YDPs, that ethyl esters of straight chain fatty acids (ethyl decanoate, ethyl dodecanoate) and higher alcohol acetate concentration decreased because of a hydrolysis phenomenon. Hydrolysis was faster for ethyl esters with increasing chain length due to the lower activation energy required. Nevertheless, octyl acetate, which has a similar carbon chain to ethyl octanoate, was hydrolyzed more rapidly (Šuklje et al., 2016). The decrease in straight chain ethyl esters and higher alcohols acetate was lower in the presence of YDPs than in an untreated control wine. Also, the esterification of branched amino acids into the corresponding ethyl esters in presence of ethanol, was lower in wines supplemented with YDPs (Šuklje et al., 2016). These results demonstrate that YDPs addition to wine can slow down the kinetics of hydrolysis and esterification processes. The compounds with antioxidant activity such as sulfur-containing compounds, for instance Glutathione (GSH), and small peptides containing tyrosine, tryptophan or methionine, released at a higher concentration in certain YDPs, may be indirectly involved in this last phenomenon by reducing the impact of oxygen on potential catalysts of esters hydrolysis and fatty acids esterification (Šuklje et al., 2016). Similarly, Rodríguez-Bencomo, Andújar-Ortiz, Moreno-Arribas, Simó, González, Chana, and Pozo-Bayón (2014) demonstrated that the use of YDPs preparations with or without GSH reduces the oxidation of certain terpenes during accelerated ageing of model wine.

The increase in 3-mercaptohexanol and 3-mercaptohexyl acetate concentrations in a Sauvignon Blanc wine aged with inactive *S. cerevisiae* product (LalVigne™ Aroma, Lallemand Inc.), in comparison with the untreated control, was demonstrated by Šuklje et al. (2016). However, this increase did not occur in the presence of a YDP enriched in GSH. It was suggested that the release from YDPs of certain amino acids in the medium may have influenced the production of volatile thiols (Pinu et al., 2014; Šuklje et al., 2016). Other studies reported similar increase in the same thiols when an inactivated yeast preparation rich in reduced glutathione was added to must before fermentation (Gabrielli et al., 2017; Pinu et al., 2014).

The presence of alkyl pyrazine originating from YDPs was only reported in model wine aged with inactive *Saccharomyces cerevisiae* product (Lallemand Inc.) at 400 mg/L. In this case, the mass spectrometry signal of four targeted masses corresponding to 2,5-dimethylpyrazine, trimethylpyrazine, methylbutylpyrazine and 2-ethyl-3,5-dimethylpyrazine increased in the synthetic wines after a 13-day contact with YDP (Pozo-Bayón et al., 2009). So far, these alkyl pyrazines have never been reported in real wines; however, it should be noted that such compounds have a very low detection threshold and yet could have a strong impact on the wine aromatic profile.

3.3. Interactions of aroma compounds with YDPs

During wine ageing on lees, colloids concentrations in wine increase, especially for glucans and mannans released from yeast cell walls. The removal of a large part of these colloids following clarification processes was found to have a deleterious effect on wine aromatic quality, especially for aged wines (Vigne & Du, 1987; Voilley, Lamer, Dubois, & Feuillat, 1990). The binding of volatile compounds with colloids subsequently eliminated by clarification was therefore presumed (Lubbers, Voilley et al., 1994; Vigne & Du, 1987; Voilley et al., 1990). Consequently, YDP influence on the volatility of aroma compounds was studied in wines, and Table 1 reports a compilation of the results obtained on certain aroma compounds. It clearly appears that the interactions between YDPs and aroma compounds depend on the physico-chemical characteristics of the latter, on the nature of the YDPs, but also on the wine matrix considered and the duration of the ageing process.

3.3.1. Effect of physico-chemical characteristics of the aroma compounds

Results reported in Table 1 show that the retention of the aroma compounds varies depending on their chemical nature and physico-chemical characteristics. Lubbers, Voilley et al. (1994) reported that hydrophobic and lipophilic compounds with low vapor pressure are more strongly retained by YDPs and the compiled data in Table 1 confirms such a tendency. Indeed, the norisoprenoid β-ionone and the esters ethyl hexanoate and ethyl octanoate, which are the most hydrophobic compounds with high volatility, are subjected to the highest variations in model wines supplemented with YDPs. When in contact with yeast walls or purified mannoproteins, β-ionone concentration in model wine can experience a decrease as large as 50 or 70% and ethyl hexanoate concentration can decrease by 27 or 44% (Chalier, Angot, Delteil, Doco, & Gunata, 2007; Lubbers, Charpentier et al., 1994). Ethyl octanoate can also be retained at 50% when in contact with yeast walls and parietal polysaccharides (Del Barrio-Galán, Ortega-Heras, Sánchez-Iglesias, & Pérez-Magariño, 2012; Lubbers, Charpentier et al., 1994). However, Del Barrio-Galan et al. (2012) reported an increase in β-ionone concentration when in contact for 15 days with a yeast autolysate enriched with polysaccharides, followed by a decrease at 30 days of ageing. Between 30 and 60 days of contact, the level of β-ionone increases again to reach a concentration 30% higher than the initial concentration. After 60 days of ageing, ethyl hexanoate and ethyl octanoate concentrations also increased. These increases were not explained, but it was suggested by other authors that the presence of simple sugars released from YDPs can reduce the stability of the volatile molecules in solution by sequestering a part of their solvation water, rendering them more accessible and easier to extract (salting out effect) (Comuzzo et al., 2011). Therefore, one could presume a competitive effect between retention and salting out from the different macromolecules (sugars, proteins, lipids) released from the autolysate over time, and the reversibility of such interactions after a longer ageing duration.

Higher alcohols such as 1-hexanol, isoamyl alcohol and 2-phenylethanol, tended to interact with most YDPs-treated wines, but to a lesser extent than ethyl esters and norisoprenoids (Chalier et al., 2007; Comuzzo et al., 2011; Del Barrio-Galán, Pérez-Magariño, Ortega-Heras, Guadalupe, & Ayestarán, 2012; Lubbers, Charpentier et al., 1994; Lubbers, Voilley et al., 1994). Regarding 1-hexanol, its concentration decreased in all cases. However, after 60 days of ageing, the difference with the control wine was not significant any more. It was suggested that 1-hexanol could have been adsorbed onto lees, but that this adsorption became reversible after one month of ageing (Del Barrio-Galán, Ortega-Heras et al., 2012).

The terpene linalool concentration tends to increase in most cases, such an increase being more pronounced (50% increase) after longer ageing duration (Del Barrio-Galán, Ortega-Heras et al., 2012). As previously mentioned, this increase can result from a salting-out effect in presence of simple sugars. However, in another study, linalool concentration was found to slightly decrease (4–8%) or to present no significant changes in presence of a yeast autolysate (Comuzzo et al., 2011). In the first study (Del Barrio-Galán, Ortega-Heras et al., 2012), linalool was in solution with 9 other compounds, whilst in the other study (Comuzzo et al., 2011), it was in solution with only 4 other compounds. Therefore, competition for binding sites may have occurred in presence of numerous other aroma compounds, thus reducing linalool retention and favoring the salting-out effect. In addition, the concentration of aroma compounds in solution was reported to be an important factor that can modify their retention due to competition for binding sites (Comuzzo et al., 2011). But, generally, for a short ageing duration, linalool volatility seems to be little affected by YDPs presence.

The volatile phenol 4-ethylphenol was retained in all cases, and yeast wall products exhibited retention capacities up to 50% (Del Barrio-Galán et al., 2012; Pradelles, Alexandre, Ortiz-Julien, & Chassagne, 2008). Pradelles et al. (2008) established that cell wall mannoproteins play an important positive role in the sorption of 4-ethylphenol and that the mechanism of adsorption would be a balance between hydrophobic electron acceptors and electrostatic interactions. Because volatile phenols produced after contamination by *Brettanomyces* yeasts can impart to

Table 1
Compilation of data reported in the literature regarding the evolution of aroma compounds in model wines and real wines added with different types of yeast derivative products. nsd: not statistically different.

Aroma compounds			Hexanol	Isoamyl alcohol	Acetate isoamyl	Ethyl hexanoate	Ethyl octanoate	2-phenylethanol	B-ionone	linalool	4-ethyl phenol	Octanoic Acid
Solubility in water g/L (at 25°C)			6	26.7	2	0.3	0.07	22	0.17	1.6	6.15	0.79
Log P			2.03	1.16	2.26	2.823	3.94	1.36	3.995	2.97	2.58	3.05
Vapor Pressure mmHg (at 25°C)			0.947	2.37	5.6	1.67	0.15	0.087	0.017	0.016	0.04	0.022
Model wines	**Doses of YDP (mg/L)**	**Time of ageing**	**Variation of aroma compounds in the wine or in the headspace of the wine**									
Yeast autolysate (Comuzzo et al., 2011)	450	7 days					-	-	-	-		-
Aroma dosage in the wine							(14-22%)	(2-5%)	(7-12%)	(3.6-8.5%)		(4-8%)
Yeast autolysate enriched in polysaccharides (Del Barrio-Galán et al., 2012)	400	15 days	-		nsd	nsd	nsd		+	+	-	
Aroma dosage in the wine			15%						15%	15%		
		30 days	-		nsd	nsd	-		nsd	+	-	
			11%				10%			12%		
		60 days	nsd		+	+	nsd		+	+	-	
					33%	31%			33%	50%		
Yeast autolysate enriched in polysaccharides and with β-glucanase activity (Del Barrio-Galán et al., 2012)	400	15 days	-		+	+	+		+	+	-	
Aroma dosage in the wine			15%		16%	20%	8%		43%	44%		
		30 days	-		nsd	-	-		nsd	nsd	-	
			11%			-15%	21%					
		60 days	nsd		nsd	+	nsd		+	+	-	
						22%			35%	44%		
Yeast cell walls (Pradelles et al., 2008)	50000 of yeast biomass										-	
Aroma dosage in the wine											(20-50%)	
Yeast cellular walls rich in mannoproteins and nucleotides. Mannoproteins with a molecular weight medium (150 kDa.) (Del Barrio-Galán et al., 2012)	400	15 days	nsd		nsd	nsd	-		nsd	nsd	-	
Aroma dosage in the wine							10%					
		30 days	-		nsd	nsd	nsd		-	nsd	-	
			11%						15%			
		60 days	nsd		nsd	nsd	nsd		nsd	+	-	
										20%		
Yeast cellular walls rich in mannoproteins and nucleotides (Del Barrio-Galán et al., 2012)	400	15 days	nsd		nsd	nsd	-		nsd	+	nsd	
Aroma dosage in the wine							11%			11%		
		30 days	nsd		nsd	nsd	nsd		-	nsd	nsd	
									15%			
		60 days	nsd		+	+	nsd		-	+	+	
					10%	9%			21%	11%		
Colloids extracted from yeast (Comuzzo et al., 2011)	450	7 days					nsd	-	-	nsd		-
Aroma dosage in the headspace								16-24%	12-23%)			15-22%
Purified mannoproteins released from yeast (Lubbers et al., 1994)	1000	12h		+		-	+		-			
Aroma dosage in the headspace				6%		8%	19%		(4-17.5%)			
Purified whole mannoproteins (Chalier et al., 2007)	150	24h	-		nsd	-			-			
Aroma dosage in the headspace			(16-17%)			(32-44%)			(40-54%)			

(*continued on next page*)

Table 1 (*continued*)

Aroma compounds			Hexanol	Isoamyl alcohol	Acetate isoamyl	Ethyl hexanoate	Ethyl octanoate	2-phenylethanol	B-ionone	linalool	4-ethyl phenol	Octanoic Acid
Parietal polysaccharides extracted enzymatically of the selected yeast walls (Del Barrio-Galán et al., 2012)	400	15 days	-		nsd	nsd	-		+	+	nsd	
Aroma dosage in the wine			16%				23%		15%	32%		
		30 days	-		nsd	nsd	-		-	+	-	
			9%				48%		20%%	10%		
		60 days	nsd		+	+	+		nsd	+	-	
					28%	24%	44%			48%		
Polysaccharides from the yeast cell wall. It contains 25% of free highly soluble mannoproteíns (Del Barrio-Galán et al., 2012)	400	15 days	nsd		nsd	nsd	-		nsd	+	nsd	
Aroma dosage in the wine							26%			11%		
		30 days	nsd		nsd	nsd	-		-	nsd	-	
							26%		18%			
		60 days	nsd		+	+	nsd		nsd	+	-	
					19%	16%				34%		
Peptide fraction found in the yeast which has sweeter power (Del Barrio-Galán et al., 2012)	400	15 days	-		nsd	nsd	-		nsd	+	nsd	
Aroma dosage in the wine			11%				10%			15%		
		30 days	-		nsd	nsd	-		-	+	-	
			22%				8%		11%	37%		
		60 days	nsd		nsd	nsd	nsd		nsd	+	-	
										20%		
Inactivated dry yeast- Fraction < 3kDa (Rodríguez-Bencomo et al., 2014)	100									-		
Aroma dosage in the headspace										20%		
Glutathione-enriched Inactivated dry yeast- Fraction < 3kDa (Rodríguez-Bencomo et al., 2014)	100									-		
Aroma dosage in the headspace										25%		
Real wines		**Time of ageing**	**Hexanol**	**Isoamyl alcohol**	**Acetate isoamyl**	**Ethyl hexanoate**	**Ethyl octanoate**	**2-phenylethanol**	**B-ionone**	**linalool**	**4-ethylphenol**	**Octanoic Acid**
Galician white variety (Bautista et al., 2007)												
Commercial yeast product compared to control wine (Bautista et al., 2007)	Not mentioned	2 month	+	-	+	+	+	+		+		+
Aroma dosage in the wine			**37%**	**14%**	**60%**	**64%**	**35%**	**20%**		**56%**		**79%**
		7 month	nsd	-	+	-	nsd	-		+		-
				5%	**149%**	**6%**		**3%**		**17%**		**11%**
White Italian wine (11% alcohol, pH 3.2) (Comuzzo et al., 2011)												
Yeast autolysate (Comuzzo et al., 2011)	450	7 days					nsd	+				+
Aroma dosage in the headspace												
Tempranillo red wine (Rodríguez-Bencomo et al., 2010)												
Commercial Yeast derivative (Rodríguez-Bencomo et al., 2010)	300	35 days	nsd	nsd	nsd	nsd	nsd	nsd			- 9%	nsd
Aroma dosage in the wine		6 month	nsd	nsd	nsd	nsd	nsd	nsd			- 10%	nsd
Tempranillo red wine (Del Barrio-Galán et al., 2012)			**Hexanol**	**Isoamyl alcohol**	**Acetate isoamyl**	**Ethyl hexanoate**	**Ethyl octanoate**	**2-phenylethanol**	**B-ionone**	**linalool**	**4-ethylphenol**	**Octanoic Acid**
Yeast autolysate enriched in polysaccharides (Del Barrio-Galán et al., 2012)	400	60 days	nsd	nsd	nsd	nsd	nsd	nsd		nsd	-	nsd
Aroma dosage in the wine											7%	

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Table 1 (*continued*)

Aroma compounds			Hexanol	Isoamyl alcohol	Acetate isoamyl	Ethyl hexanoate	Ethyl octanoate	2-phenylethanol	B-ionone	linalool	4-ethyl phenol	Octanoic Acid
Yeast autolysate enriched in polysaccharides and with β-glucanase activity (Del Barrio-Galán et al., 2012)	400	60 days	nsd	nsd	nsd	nsd	nsd	nsd		nsd	-	nsd
Aroma dosage in the wine											5%	
Parietal polysaccharides extracted enzymatically of the selected yeasts walls (Del Barrio-Galán et al., 2012)	400	60 days	+	nsd	+	nsd	+	nsd		nsd	-	nsd
Aroma dosage in the wine			6%		20%		10%				7%	
Peptide fraction found in the yeast which has sweeter power (Del Barrio-Galán et al., 2012)	400	60 days	+	nsd	nsd	nsd	+	nsd		nsd	-	nsd
Aroma dosage in the wine			6%				10%				8%	
Polysaccharides from the yeast cell wall. It contains 25% of free highly soluble mannoproteíns (Del Barrio-Galán et al., 2012)	400	60 days	+	nsd	+	+	nsd	nsd		+	-	-
Aroma dosage in the wine			4%		24%	30%				3%	7%	**8%**
Yeast cellular walls rich in mannoproteins and nucleotides. Mannoproteins with a molecular weight medium (150 kDa.) (Del Barrio-Galán et al., 2012)	400	60 days	nsd	nsd	nsd	nsd	+	nsd		nsd	-	nsd
Aroma dosage in the wine							12%				5%	

the wine a horsy, medicinal and spicy character, their retention by YDPs during wine ageing should be favorable to the overall wine aroma (Chassagne, Guilloux-Benatier, Alexandre, & Voilley, 2005; Pérez-Serradilla & de Castro, 2008; Pradelles et al., 2008).

The effect of YDPs on the volatility of octanoic acid in model wine was reported by Comuzzo et al. (2011). They described a slight retention of this fatty acid by yeast autolysate, this retention effect being even more pronounced in presence of purified colloids, suggesting interactions between macromolecules and this fatty acid (Comuzzo et al., 2011).

Liberation of sulphur compounds occurs during the traditional on-lees maturation of wines, but lees are also able to remove some of these compounds from wines. Lavigne and Dubourdieu (1996) reported that yeast lees had the capability to adsorb certain volatile thiols. They also demonstrated that yeast walls prepared by mechanical disruption of whole cells in the presence of a reducing agent were also able to adsorb the same thiols. However, yeast walls deprived of mannoproteins through hydrolysis by a β-glucanase preparation lost their adsorption capacity (Lavigne & Dubourdieu, 1996). These results suggest that thiol consumption by yeast lees is mediated by the establishment of disulphide bridges between thiols and the cysteinyl residues of yeast cell wall mannoproteins according to the following mechanism:

Mannoprotein–SH + CH_3–SH + O_2 → mannoprotein—S—S—CH_3 + H_2O

However, Vasserot et al. (2003) did not agree with such a mechanism. They demonstrated that the consumption of thiols did not require molecular oxygen and that ethylene diamine tetraacetic acid (EDTA) was able to inhibit this consumption. Consequently, they suggested that metallic cations were involved in the establishment of disulphide bridges between thiols and mannoproteins (Vasserot et al., 2003).

3.3.2. *Effect of the nature of YDPs*

YDPs are classified in Table 1 from the least purified products (yeast autolysate, yeast walls) to the most purified macromolecule fractions (whole macromolecules extracted from yeast cell, parietal and yeast wall polysaccharides, purified mannoproteins, peptides).

Studies reported that YDP degree of purification can affect the interactions with aroma compounds (Chalier et al., 2007; Del Barrio-Galan et al., 2012). In Table 1, we can see that colloids isolated from a yeast autolysate retained 5 times more 2-phenylethanol and 2 times more β-ionone than the whole yeast autolysate. Also, Chalier et al. (2007) demonstrated that 1-hexanol was 3 times more retained in purified fractions of mannoproteins than in a whole mannoproteins extract. This fact was explained by a possible modification in binding sites accessibility after purification (Chalier et al., 2007). In the same study, the retention of ethyl hexanoate was found stronger (40%) in the richest mannoprotein fraction in glucose units than in the richest one in proteins (20%), presuming a better compound affinity for the glycosidic part of the mannoproteins than for the protein part. Lubbers, Charpentier et al. (1994), Lubbers, Voilley et al. (1994) found similar results for ethyl hexanoate that was only retained by the richest fraction in proteins and glucose.

Del Barrio-Galán et al. (2012) investigated the retention of ethyl hexanoate when in contact with seven different YDPs in model wines and observed a strong retention after 15 days of contact with autolysed yeast enriched in polysacharides and with β-glucanase activity. This result can strengthen the important role of yeast polysacharides in the interaction mechanisms and the hypothesis that a change in conformation of the sugar moitie, due to β-glucanase activity, may have favored these interactions. However, this retention effect was not significant after 60 days of contact, showing the reversibility of the interactions (Del Barrio-Galán, Ortega-Heras et al., 2012).

Chalier et al. (2007) found that the purified mannoproteins fraction with the highest molecular weight and mainly composed of *N*-glycans mannoproteins was the fraction that exhibited the strongest interactions with β-ionone (80%) when compared to the other fractions (40–50%).

Table 2
Names, chemical classes, origin in the wine, structure, and odor impact of most aroma compounds cited in the manuscript.

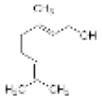
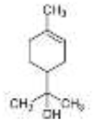
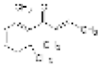
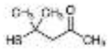
Chemical Class	Origin	Aroma	Structure
VARIETAL AROMA COMPOUNDS			
TERPENOIDS			
Monoterperns			
Linalool	Terpene glycosylated precursors from the grapes	Citrus blossom, Flowery	
Citronellol	Terpene glycosylated precursors from the grapes	Green Citrus	
Geraniol	Terpene glycosylated precursors from the grapes	Rose-like, geranium	
Alpha Terpineol	Terpene glycosylated precursors from the grapes	Floral, woody	
Sesquiterpens			
Rotondone	Farnesyl diphosphate precursor from the grapes	Black pepper	
C13-Norisoprenoids			
B-ionone	Carotenoids from the grapes	violet raspberry and rose	
B -damascenone	Carotenoids from the grapes	rose, cooked apple, honey	
1,1,6-Trimethyl-1,2-dihydronaphthalene (TDN)	Carotenoids from the grapes	petrol or kerosene	
Vitispirane	Carotenoids from the grapes	flowery, fruity, earthy, woody	
THIOLS			
4-methyl-mercapto-pentan-2-one (4MMP)	Glutathionylated and cysteinylated precursors present in grapes	box tree and blackcurrant bud	

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Table 2 (*continued*)

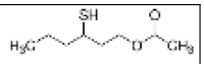
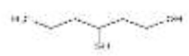
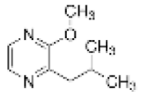
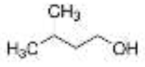
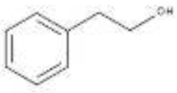
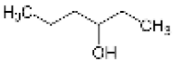
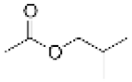
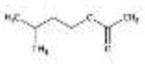
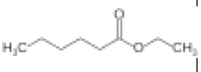
3 mercapto-hexyl acetate (3MHA)	Glutathionylated and cysteinylated precursors present in grapes	grape fruit, passion fruit, citrus zest and guava	
3 mercapto-hexanol (3MH)	Glutathionylated and cysteinylated precursors present in grapes	grape fruit, passion fruit, citrus zest and guava	
METHOXYPYRAZINE			
3-isobutyl-2-methoxypyrazine (IBMP)	Grapes	pepper	
FERMENTATIVE AROMA COMPOUNDS			
Higher Alcohols			
isoamyl alcohol	Yeast metabolism-Amino acids catabolism	Marpizan	
2-phenyl ethanol	Yeast metabolism- Amino acids catabolism	Rose-like	
Hexanol	Yeast metabolism- Amino acids catabolism	Herbaceous, grass, woody	
Esters			
isobutyl acetate	Yeast metabolism- Condensation of a higher alcohol and acetyl-CoA	Fruity	
isoamyl acetate	Yeast metabolism- Condensation of a higher alcohol and acetyl-CoA	Banana	
2-phenylethyl acetate	Yeast metabolism- Condensation of a higher alcohol and acetyl-CoA	Rose	
ethyl hexanoate	Yeast metabolism- esterification of activated fatty acids in ethanol	Fruity, green apple, banana	

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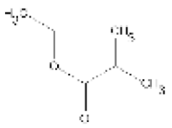
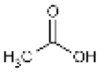
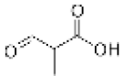
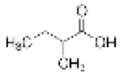
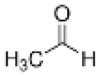
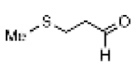
Table 2 (*continued*)

ethyl octanoate	Yeast metabolism- esterification of activated fatty acids in ethanol	Pineapple	
ethyl 2-methylpropanoate	Yeast metabolism- esterification of activated fatty acids in ethanol	Fruity	
SHORT CHAIN ACIDS			
Acetic acid	Yeast metabolism of Pyruvate	Vinegar	
Butyric acid	Yeast metabolism- Conversion of Acetyl-CoA	Rancid Cheese, sweet	
Hexanoic acid	Yeast metabolism- Conversion of Acetyl-CoA	Cheese	
Octanoic acid	Yeast metabolism- Conversion of Acetyl-CoA	Sweet, cheesy	
2-methyl propanoic acid	Yeast metabolism- Conversion of Acetyl-CoA	Rancid, butter, Cheese	
2-methyl butanoic acid	Yeast metabolism- Conversion of Acetyl-CoA	Fermented, Cheese, Acid	
AGEING AROMA			
AlDEHYDES			
Acetaldehyde	Yeast metabolism- Pyruvate conversion. Fenton oxidation of ethanol	Rotten apples	
Methional	Peroxydation of methionol	boiled-potato	
Phenylacetaldehyde	Peroxydation of 2-phenyl ethanol	honey	

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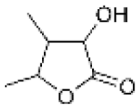
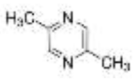
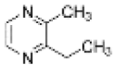
LACTONE			
Sotolon	Unknown	nutty and spicy	
AROMA FROM YDPs			
LONG CHAIN FATTY ACIDS			
C8-C16 acid	YDP	Sweet, Cheesy, waxy, fatty	
LONG CHAIN ETHYL ESTERS			
C8-C16 ethyl esters	YDP	Fruity aroma enhancer	
ALDEHYDES			
Pentanal	YDP	Fermented, bready, coca, chocolate	
Hexanal	YDP	Grassy, Green	
Nonanal	YDP	Fatty, citrus	
Octanal		Waxy, Green	
2-methyl-propanal	YDP	Fresh, herbal, green, malty	
2-3 methyl butanal	YDP	Fruity, peach-like, chocolate	
ALKYLPYRAZINES			
2,3-Dimethylpyrazine	YDP	Musty, cocoa, nuts, roasted	
2,5-Dimethylpyrazine	YDP	Musty, cocoa, nuts, roasted	
2-Ethyl-3,5-methylpyrazine	YDP	Earthy, green, pepper	

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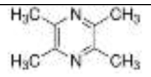
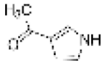
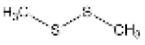
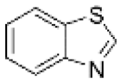
Table 2 (*continued*)

2,3,5,6-Tetramethylpyrazine	YDP	Nutty, musty, coca, vanilla	
PYRROLE			
Pyrrole	YDP	Nutty	
2-methylpyrrole	YDP	Not determined	
2-acetylpyrrole	YDP	Musty, nutty, coumarinic	
SULFUR dimethyl disulfides	YDP	Vegetable, cabbage, onion	
thiazole	YDP	Fishy, nutty, meaty	
benzothiazole	YDP	Sulfurus, rubbery, vegetable	

Among all the products tested by Del Barrio-Galán et al. (2012), only the purified products and the insoluble yeast walls richest in mannoproteins were able to retain β-ionone. Again, these results clearly confirm the role played by mannoproteins in aroma compounds retention during the wine ageing process, and the impact of products solubility and purification on binding sites accessibility (Del Barrio-Galán, Ortega-Heras et al., 2012; Lubbers, Charpentier et al., 1994).

However, mannoproteins may not be the only macromolecules responsible for the retention of ethyl hexanoate and β-ionone. Indeed, Lubbers, Charpentier et al. (1994), Lubbers, Voilley et al. (1994) reported that the retention of these compounds was lower when in contact with lipid-free yeast walls compared with lipid-containing yeast walls (18% and 28% respectively), demonstrating the implication of yeast wall lipids in the interactions, most specifically in the case of the most lipophilic compounds. In the same study, they demonstrated that the product retention capacities were higher when their concentration increased from 1 to 10 g/L because of a change in macromolecules conformation at high concentrations and the possible formation of aggregates able to trap aroma compounds.

It was reported by Pradelles et al. (2008) that the sorption capacities of yeast derivatise products depend not only on the nature of the yeast product but also on the yeast strain and the industrial process applied. They demonstrated that the macromolecules composition of yeast wall products obtained from different strains can vary, resulting in yeast wall products with different hydrophobicity, electron donor character and zeta potential. They observed that their retention capacity towards 4-ethyl phenol was greater when surface hydrophobicity was higher, but this capacity decreased with the greater electron donor character of the product. The industrial process -such as a heat treatment- used to obtain the product can also cause significant changes in yeast parietal structure with changes in the glucan microstructure and properties, denaturation of proteins and enzymes that may affect the retention capacities. These findings may therefore explain the differing results obtained by Comuzzo et al. (2011) and Del Barrio-Galan et al. (2012) for aroma compounds in contact with yeast autolysate products. Indeed, Comuzzo et al. (2011) reported the retention of linalool and β-ionone after contact with a yeast autolysate, whilst Del Barrio-Galan et al. (2012) found a salting-out effect on the same aroma compounds for two different yeast autolysates. Autolysate differences in original strains and/or manufacturing process may explain these discrepancies.

YDPs retention capacity will therefore depends on its nature and concentration in relation to the composition and the conformation of the macromolecules and their ability to create hydrophobic interactions with the aroma compounds. It is clear that mannoproteins play an important role in the interactions of aroma compounds with YDPs products. However, mannoproteins are not the only chemicals involved in volatility changes and the mechanism of adsorption involves a balance between different kinds of interactions (hydrophobic, electrostatic van der Waals) (Pradelles et al., 2008).

3.3.3. *Effect of the matrix (wine, pH, temperature)*

A few studies have described the effect of YDPs on the volatility of aroma compounds in red and white wines. Table 1 reports the results obtained on the same aroma compounds as those studied in model wines and it clearly appears that YDP impact is different in model wine and in wine.

In red Tempranillo wines, the impact of YDPs is not significant for most of the aroma compounds reported in Table 1 and for most of the

products tested (Del Barrio-Galán, Ortega-Heras et al., 2012; Rodríguez-Bencomo, Ortega-Heras, & Pérez-Magariño, 2010). A stark difference concerns terpene linalool whose volatility is not significantly affected in red wine, whilst its concentration highly increased in all studies in model wines. However, the ageing of a red wine on products containing purified polysaccharides or peptide have resulted in a stronger salting out effect on isoamyl acetate, ethyl hexanoate and ethyl octanoate (Table 1) (Del Barrio-Galán, Ortega-Heras et al., 2012). As regards hexanol, whilst this compound was either retained or not significantly affected when in contact with purified polysacharides or peptides in model wine, its concentration increased when in contact with the same products in red wine. Lastly, 4-ethyl phenol concentration has the same tendency to decrease when in contact with YDPs in model wine and red wines.

In white Galician wine, the volatility of most of the aroma compounds reported in Table 1 was significantly affected when compared with a control wine (Bautista et al., 2007). After two months of ageing, the concentration of terpenes, ethyl esters and acetate, 2-phenylethanol and fatty acids increased in the wine treated with YDPs, when compared to the control. However, after 7 month of ageing, the concentration of these compounds tended to decrease more in treated wines than in the control, suggesting some aroma compounds retention with a longer ageing time (Bautista et al., 2007).

These differences between model and real wine matrices were explained by the competition of other volatile and non-volatile wine molecules for binding sites (Comuzzo et al., 2011; Del Barrio-Galán, Ortega-Heras et al., 2012). Most specifically, it was demonstrated that yeast derivative products can interact with phenolic compounds that compete with aroma compounds for binding sites (Del Barrio-Galán, Ortega-Heras et al., 2012; Del Barrio-Galán et al., 2011a, 2011b). Because phenolic compounds are present at a higher concentration in red wines than in white wines, they may qualify as the molecules responsible for the differences observed between white and red wines.

Wine pH is another factor that was reported to affect the retention of aroma compounds (Comuzzo et al., 2011). Comuzzo et al. (2011) demonstrated that the interactions of 2-phenylethanol, β-ionone, linalool, octanoic acid and ethyl octanoate in a model wine supplemented with yeast autolysate were higher at pH 3 than at pH 4. They explained this effect by a possible increase in polar and particle charge interactions, probably connected with the protein and polysaccharidic fractions of the cell walls added. They also demonstrated that an increase in temperature from 20 °C to 37 °C could more easily disrupt the interactions of 2-phenylethanol, β-ionone and octanoic acid with autolysate colloids in a model wine at pH 3 than at pH 4 (Comuzzo et al., 2011). This result suggests that the interaction is quantitatively higher at a more acidic pH, but seems to be qualitatively stronger at a higher pH (Comuzzo et al., 2011).

3.4. Impact of the YDPs on the sensorial profile of the wine

The impact of YDP on wine aromatic characteristics is a balance between the aroma compounds released in the medium from YDPs and the interactions between the aroma compounds and the macromolecules present in wine. This balance will depend on the type of wine but also on the characteristics and the quantity of the YDPs added and the duration of the ageing process (Bautista et al., 2007; Comuzzo et al., 2006; Del Barrio-Galán et al., 2011a, 2011b; Rodríguez-Bencomo et al., 2014).

The demonstration of the stabilizing role of YDPs towards volatile aromatics compounds, normally very prone to oxidation, and their ability to boost the production of certain varietal thiols, ethyl esters and fused alcohols can be correlated to the more intense floral, fruity, herbal and exotic notes attributed to white wines aged in presence of YDPs for a short time (Bautista et al., 2007; Bueno, Peinado, Medina, & Moreno, 2006; Comuzzo et al., 2006; Del Barrio-Galán, Pérez-Magariño, et al., 2012; Juega, Nunez, Carrascosa, & Martinez-Rodriguez, 2012; Loscos, Hernández-Orte, Cacho, & Ferreira, 2009; Šuklje et al., 2016). However, the amount of YDPs added to wine is an important factor to be considered. Indeed, it was demonstrated that a two-week ageing of a Chardonnay wine with 200 mg/L YDPs imparted flowery and fruity notes, not detected in the control wine, that were connected to higher levels of some esters, alcohols and terpenes. However, cheese-like and unpleasant notes newly appeared with increasing levels of YDPs from 500 mg/L to 1 g/L, which was correlated to an increasing release of some carboxylic acids, most particularly butanoic, hexanoic and decanoic acids (Comuzzo et al., 2006). Nevertheless, the authors mentioned that YDP solubility could modulate the release of such exogenous compounds and that a yeast autolysate with low solubility could be useful to reduce such a release, in comparison to a more soluble yeast extract (Comuzzo et al., 2006). In addition, Bautista et al. (2007) demonstrated that the pleasant floral and grassy nuances initially developed in a wine elaborated from a white Galician grape variety and aged in presence of yeast autolysate for two months were replaced with unpleasant caramel, sulfurous and woody aromas after 7 month of ageing. The same wines from white Galician grapes aged or not in presence of natural lees presented the same tendency, with a decrease in fruity or floral aromas after 7 month of ageing and an increase in sulfurous attributes (Bautista et al., 2007). A similar effect was reported for other white wines aged on yeast autolysates (Bueno et al., 2006; Juega, Carrascosa, & Martinez-Rodriguez, 2015; Loscos et al., 2009). However, Del Barrio-Galán et al. (2011a), Del Barrio-Galán et al. (2011b) reported that Verdejo (white) wines aged for 6 months on polysaccharides extracted from yeast walls revealed stronger varietal, fruity and floral notes, with higher olfactory intensity, in comparison to the same wines tested just after the treatment (Del Barrio-Galán et al., 2011a, 2011b). Enhancement of the fruity aroma of Verdejo and Gordillo sparkling wines aged for 9 months in presence of yeast autolysates enriched in polysaccharides and mannoproteins was also reported by Pérez-Magariño et al. (2015). Therefore, a shorter ageing time seems to better benefit wines, but this effect may depend on the type of yeast product used. Lastly, most of the studies that evaluated the sensorial impact of white wines aged on YDPs reported that this process benefits more neuter or least aromatic wines by improving aromatic complexity, but may not benefit wines with typical varietal aromas (Bautista et al., 2007; Bueno et al., 2006; Comuzzo et al., 2006).

There are only few studies reporting YDP impact on red wine aroma profiles. Indeed, most studies on red wine have focused on YDP impact on the phenolic compounds, wine color and wine organoleptic attributes such as astringency, bitterness, mouthfeel and balance. Nevertheless, two studies report that the ageing of Tempranillo red wine on yeast products for 1 to 3 months had no significant effect on wine aroma profile (Del Barrio-Galán, Pérez-Magariño, et al., 2012; Rodríguez-Bencomo et al., 2010). No significant effect either was reported by Pérez-Magariño et al. (2015) for Rosé sparkling wine aged on yeast autolysates enriched in polysaccharides and mannoproteins. These results are in agreement with previous ones obtained on YDP impact on wine aroma compounds composition.

4. Conclusion

The use of yeast derivatives has been widely extended within the oenological industry although there is a lack of scientific information about these products and their effects on wine quality. However, in the last few years, scientific studies have focused on the impact of YDPs on wine aroma compounds and wine aroma profile in model wines. It is now clearly demonstrated that the use of YDPs in the enological process affects the aroma compounds composition of model wines due to the release of exogenous volatile compounds, but that it also affects wine aroma solubility because of covalent and non-covalent interactions.

YDPs contain more than a thousand aroma compounds produced, in majority, by the action of heat on sugars, amino acids and thiamin during the industrial process. Alcohols, long-chain fatty acids and esters are the compounds released in wines at the highest concentration compared with aldehydes, alkyl pyrazines, pyroles derivatives and

sulfur compounds. The proportion of alcohols/fatty acids/fatty esters can vary with esterification and hydrolysis reactions occurring in the ethanolic medium and, indirectly, with the presence in the medium of glutathion or small peptides containing tyrosine, tryptophane or methionine and released from YDP at different concentrations.

YDPs also contain macromolecules that can be released in wine and interact with aroma compounds. Hydrophobic and lipophilic compounds with low vapor pressure such as β-ionone, ethyl hexanoate, ethyl octanoate, are the compounds most retained by YDPs. Volatile thiols can also be adsorbed by yeast wall mannoproteins through the establishment of disulfides bridges, and 4-ethyl phenol concentration can be reduced down to 50% in presence of YDPs. The decrease in this last compound produced after *Brettanomyces* contamination is favorable to the overall wine aroma.

The degree of interactions between aroma compounds and YDPs is modulated by the degree of purification of the fractions and by their chemical composition. Colloids isolated from yeast autolysate can retain aromas such as β-ionone, 1-hexanol, 2-phenyl ethanol 2 to 5 times more than the autolysate. Yeast wall mannoproteins are the macromolecules identified to be so far the most involved in hydrophobic interactions. Yeast wall lipids are also responsible for lipophilic compounds retention, but to a lesser extent. The retention capacity of those parietal macromolecule can vary among yeast strains, but mostly with the industrial treatment conditions applied that can cause significant changes in yeast parietal structure.

The impact of YDPs on the wine sensorial profile benefits more to wines made from poorly aromatic or neuter grape varieties, but may be detrimental to wines made from grapes with intense varietal aroma. In addition, this effect seems less pronounced in red wines, probably due to the competitive effect of polyphenols for the binding sites of yeast macromolecules. However, the data obtained on red wines are very scarce, maybe due to the inadequacy of the analytical methods available to study the evolution of aroma in presence of such a complex matrix.

But if the impact of the use of YDPs in wines is globally understood, the variability of such effect remains unclear and requires further investigation in order to better orient the use of YDPs according to the type of wine that is expected.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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