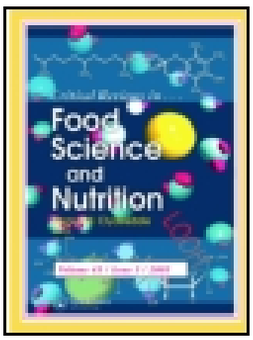

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Critical Reviews in Food Science and Nutrition

ISSN: 1040-8398 (Print) 1549-7852 (Online) Journal homepage: http://www.tandfonline.com/loi/bfsn20

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To cite this article: Mr Richard Gawel, Dr Paul A. Smith, Dr Sara Cicerale & Russell Keast (2017): The Mouthfeel of White Wine, Critical Reviews in Food Science and Nutrition, DOI: 10.1080/10408398.2017.1346584

To link to this article: http://dx.doi.org/10.1080/10408398.2017.1346584

Accepted author version posted online: 05 Jul 2017.

The Mouthfeel of White Wine

Mr Richard Gawel[1,a]. Dr Paul A. Smith[1,b], Dr Sara Cicerale[2,c], Russell Keast[2,d]

[1]Australian Wine Research Institute, Paratoo Road, Urrbrae, 5064 Australia

[2]Deakin University Faculty of Health, School of Exercise and Nutrition Sciences, Burwood, 3125 Australia

[a]Corresponding Author : Email: richard.gawel@awri.com.au

[b]Corresponding Author : Email: paul.smith@awri.com.au

[c]Corresponding Author : Email: sara.cicerale@deakin.edu.au

[d]Corresponding Author : Email: russell.keast@deakin.edu.au

Abstract

White wine mouthfeel which encompasses the tactile, chemosensory and taste attributes of perceived viscosity, astringency, hotness and bitterness is increasingly being recognised as an important component of overall white wine quality. This review summarises the physiological basis for the perception of white wine mouthfeel and the direct and interactive effects of white wine composition, specifically those of low molecular weight phenolic compounds, polysaccharides, pH, ethanol, glycerol, dissolved carbon dioxide and peptides. Ethyl alcohol concentration and pH play a direct role in determining most aspects of mouthfeel perception, and provide an overall framework on which the other minor wine components can interact to influence white wine mouthfeel. Phenolic compounds broadly impact on the mouthfeel by contributing to its viscosity, astringency, hotness and bitterness. Their breadth of influence likely

results from their structural diversity which would allow them to activate multiple sensory mechanisms involved in mouthfeel perception. Conversely, polysaccharides have a small modulating effect on astringency and hotness perception, and glycerol does not affect perceived viscosity within the narrow concentration range found in white wine. Many of the major sensory attributes that contribute to the overall impression of mouthfeel are elicited by more than one class compound suggesting that different physiological mechanisms may be involved in the construct of mouthfeel percepts.

Keywords

white wine, mouthfeel, texture, phenolics, polysaccharides, alcohol, acidity

Introduction

Many of the recognised great white wines of the world display a textural profile or 'mouthfeel' that typifies the grape cultivars from which they were made and the methods used to vinify them. As examples, highly respected examples of wines made from the cultivars Viognier and Pinot Gris are as much defined by their oily mouthfeel as by varietal flavours, and winemakers worldwide invest in high cost processes to create the creamy texture that defines barrel fermented Chardonnay wines (Robinson, 1999).

White wine elicits tactile sensations of viscosity and astringency/dryness, and the chemosensory sensations of warmth, pricking and spritz (Jackson, 2014; Oberholster, et al., 2009; Pickering and DeMiglio, 2008). Other mouthfeel attributes such as metallic (Jones et al., 2008) and pungency (Gawel et al., 2013) that likely incorporate aspects of bitter taste have also been reported. Mouthfeel has been defined as 'the group of sensations characterised by a tactile response in the mouth' (Pickering and DeMiglio, 2008). However, considering recent findings that chemically induced irritation and thermal sensations also contribute to white wine mouthfeel, we propose a broader definition that wine mouth-feel comprises 'the tactile, irritant and thermal sensations resulting from the activation of chemosensory and somatosensory receptors within the oral cavity by wine chemical stimuli'.

The compositional factors mostly cited as those contributing to the mouthfeel of white wine are low molecular weight phenolic compounds, ethanol, glycerol, organic acids, polysaccharides and dissolved carbon dioxide. The review will discuss 1) how these compounds individually and through interaction affect the mouthfeel of white wine and 2) the physiological basis for mouth-feel perception in white wine. The review is scoped by studies specifically related to non-volatile

compounds found in dry white wine that have been shown to, or could potentially influence white wine mouthfeel. Specifically, only reports of the influence of low molecular weight phenolic compounds, and polysaccharides relevant to white wine are reviewed, and the effects of compounds at concentrations typical of those found in dry white wine are emphasised. While it is acknowledged that bitterness is a taste rather than a texture, it has been included for discussion on the presumption that bitterness is likely to modulate the perception of mouthfeel characters in white wine.

Physiology of the Mouth Related to Mouthfeel

The oral mucosa is the tissue membrane that lines the oral cavity. Among its varied functions, it provides physical and immunological protection, as well as enabling the sensations of touch, temperature and taste. The oral mucosa is structurally heterogeneous as it must necessarily accommodate many physical functions. The mucosa of the inside lips, cheek, tongue, and soft palate need to be elastic and moveable as otherwise phonation would be impossible. Conversely the gum and hard palate mucosa are significantly more rigid as they are routinely subjected to considerable mechanical forces encountered when chewing food. The gum and hard palate mucosa are more rigid because they are relatively thinner and are embedded with a dense layer of keratin. In contrast, the thicker and more elastic mucosa of the inner lips, cheek and soft palate are keratinised to a significantly lesser degree (Squier and Kremer, 2001).

Trigeminal (5^{th} cranial nerve) free nerve endings that extend into the middle and upper layers of the oral epithelium are found throughout most of the oral cavity. Transient receptor potential (TRP) channels that respond to combinations of heat, cold and other chemical stimuli such as ethanol are located on these nerve endings (Clapham, 2003). As the receptive elements for these

chemical stimuli are located on the intracellular domain of the TRP channel, the substance must firstly pass through a lipid bilayer before the receptor can be activated (Furlan et al., 2014). Other receptors found on fast conducting afferent nerve fibres that innervate the basal cells of the epithelium function as mechanoreceptors (Watanabe, 2004). These receptors respond exclusively to tactile stimuli such as providing information as to the velocity and position of the food bolus necessary for swallowing, but logically may also signal stretching and 'sticking' sensations between oral surfaces experienced during wine consumption.

The oral mucosa is covered by a thin layer of adsorbed salivary proteins called the acquired pellicle and on top of that, a significantly thicker film of bulk saliva. Together, they play an important role in lubricating the soft tissues in the oral cavity, but when disrupted by tasting wine may also influence the perception of some aspects of mouthfeel. Details of the sources and composition of the salivary proteins that are likely to interact with wine components and therefore influence mouthfeel have been reviewed elsewhere (Gawel, 1998). Model studies using both hydrophilic and hydrophobic surfaces (modelling the keratinised and non-keratinised mouth surfaces respectively) suggest that salivary proteins rapidly form a thin boundary layer which is capable of lubricating surfaces (Maheshwari and Dhathathreyan, 2006; Vitkov et al., 2004). Two mechanisms for pellicle formation have been proposed: 1) the smaller salivary proteins excreted from the parotid gland, PRP-1, statherin and histadin crosslink to form a pellicle which is then scaffolded by adsorbed mucins excreted from the submandibular and sublingual glands (Proctor et al., 2005; Yao et al., 2003; Berg et al., 2003), and 2) the smaller parotid proteins cross-link and stabilise a previously established mucin layer hydrophobically bound to the epithelia (Svendsen et al., 2006; Iontcheva et al., 2000). In either case, a thin lubricative proteinaceous layer is

formed as under both proposed scenarios, the oligosaccharide side chains of the attached mucins can form outward facing 'molecular brushes' that can repel opposing similar surfaces by osmotic pressure or steric effects (Cardenas et al., 2007; Schwender et al., 2005). However, the salivary film covering the oral epithelium at between 18 and 50μm (Lee et al., 2002) is sufficiently thick to suggest that mouth lubrication by saliva consists of a mixed form of hydrodynamic lubrication resulting primarily from unattached mucins operating between opposing mouth surfaces (Szabo et al., 2000; Gong and Osada, 1998) and thin film lubrication by the pellicle at the oral surface.

Physiological Basis for Mouthfeel and Bitterness

Astringency

The dominant paradigm is that astringency is the perception of increased friction between oral surfaces resulting from reduced salivary lubrication following an interaction between salivary proteins and polyphenols (Gawel, 1998). The interaction mostly involves both hydrogen bonding between amino acid carbonyl groups and the hydroxyl groups on the polyphenol, and hydrophobic stacking of the benzoic ring with the apolar face of amino acid residues on the protein (Baxter et al., 1997; Haslam and Lilley, 1988; Luck et al., 1994; Spencer et al., 1988). Proline rich proteins (PRP's) have mostly been the focus of the studies as they are 1) the dominant class of proteins secreted by the parotid gland and submandibular glands which provide the greatest volume of saliva (Walz et al., 2006; Kauffman et al., 1991), and 2) have a strong binding affinity with wine polyphenols due to their open and flexible structure that promotes hydrogen bonding (Bacon and Rhodes, 2000; Luck et al., 1994). However, a causal link between interactions of wine polyphenols and PRP's found in the bulk saliva leading to

changes to its rheology and therefore astringency perception is yet to be established. Fundamentally, the oral lubrication paradigm of astringency is contingent upon mechanoreceptors of somatosensory nerves being activated during oral exposure to astringents. To our knowledge, direct evidence of such activation is yet to be shown. However, deactivation of the branch of the trigeminal nerve V that innervates oral mechanoreceptors and chemoreceptors has been shown to result in a loss of astringency perception (Schobel et al., 2014) suggesting that mechanoreception could play a role in the perception of astringency.

Astringency perception may also involve chemothesis, whereby oral free nerve endings with transient receptor potential channels V1 (TRPV1) are activated by chemical or physical stimuli responsible for perceived irritation, hotness and coolness. Kurogi et al. (2015) found that dimeric flavanols in tea activated TRPV1 channels in sensory neurons. Consistent with the concept that astringency perception has a chemosensory component, monomeric and polymeric phenolic compounds also activate trigeminal ganglion neurons within a time frame consistent with the onset of astringency perception (Schobel et al., 2014). Related to this is the observation that ethanol, which elicits a drying mouth-feel (Jones et al., 2008) also perturbs the lipid layer of oral epithelial cells in a similar fashion to polyphenols (Furlan et al., 2015).

Astringency can be perceived even when oral surfaces have been stripped of bulk saliva (Nayak and Carpenter, 2008) which suggests that astringency perception may also involve interactions between polyphenols and the proteins that comprise the acquired pellicle, or other connective epithelial or membrane bound proteins (Coles et al., 2010; Malone et al., 2003). Wine tannins are capable of binding directly to oral epithelial cells (Payne et al., 2009) with an efficacy related to their degree of polymerisation (Soares et al., 2016).

Similarly, the perceived astringency of whey proteins and the polysaccharide chitosan also correlate with their ability to bind with oral epithelial cells (Ye et al., 2012; Malone et al., 2003). The exact mechanism of cell binding, or of which receptor channels would relay information about the presence of astringent compounds under these circumstances is unknown.

Anecdotally, astringency can be clearly perceived in a stationary mouth whereby there is no movement between opposing oral surfaces. While this does not rule out the influence of mechanoreception, as constriction of oral surfaces may be involved (Verhagen and Engelen, 2006), it does strengthen the argument that astringency is most likely the result of multimodal actions involving interactions with the bulk saliva, acquired pellicle and oral epithelial cells leading to a general somatosensory response most likely involving both chemoreception and mechanoreception.

Bitterness

Bitter taste is elicited by taste receptor cells located in taste buds that are embedded in the epithelium of papillae on the tongue and soft palate. These taste receptor cells contain sub-sets of the 25 member family of G protein-coupled receptors known as T2Rs (Chandrashekar et al., 2000, Adler et al., 2000). The sub-structure of these receptors has not been fully defined, but if they are heterodimeric like those of sweetness and umami receptors, then there could be up to 325 functional bitterness receptors in humans (DuBois, 2011).

Bitterness is unique amongst the tastes in that bitter tasting compounds display a high level of structural diversity. This can be explained at a receptor level by 1) different expression patterns of the 25 T2Rs across receptor cells (Chandrashekar et al., 2000) which like the olfactory system

may provide a mechanism for perceptual discrimination between bitter compounds and 2) most of the T2Rs are broadly tuned i.e. individual T2R's can be activated by multiple structurally different bitterants, and alternatively, the same bitterant can activate multiple receptor types (Meyerhof et al., 2010). Broad tuning of T2R bitter receptors to white wine phenolic compounds has recently been demonstrated (Soares et al., 2013). Furthermore, it is known that post-receptor (cell level) transduction mechanisms are also involved in eliciting bitterness, which in the case of white wine, may also include the direct activation of secondary messenger systems following the passing of bitter hydrophobic compounds through receptor cell membranes (Furlan et al., 2015).

Hotness and Perceived Viscosity

The perceived oral warmth/hotness, bitterness and dryness of white wine are influenced by its ethanol content (Jones et al., 2008; Gawel et al., 2007). The physiological basis for these effects is evidenced by the existence of the thermally responsive TRPV1 noiceptors embedded within the oral mucosa and the bitter responsive T2R38 receptors located in the circumvallate papillae at back of the tongue robustly respond to the presence of ethanol (Allen et al., 2014; Trevisani et al., 2002).

The perceived viscosity of Newtonian fluids with low physical viscosity, i.e. white wine has been defined as "an appraisal of the ease with which the liquid flows between the upper surfaces of the tongue and the palate" (Van Vliet et al., 2009). While the physical viscosities encountered in dry white wine are narrow (estimated by Kosmerl et al., 2000 at 0.15 mPa/s), tasters are able to perceive changes in the oral viscosity of commercial white wines at around $1/5^{th}$ (0.027 mPa/s) of that physical range, and viscous mouthfeel and physical viscosity were significantly correlated (Runnebaum et al., 2011) suggesting that perceived viscosity is related to physical

viscosity in white wine. However, it is notable that higher pH (Gawel et al., 2013, 2014a), or higher lactate (Runnebaum et al., 2011; Skogerson et al., 2009) which is a proxy for higher pH in white wine has been shown to be strongly associated with higher perceived viscosity. As pH is unlikely to affect physical viscosity, these results suggest that physical viscosity of the wine is likely not solely responsible for the perception of oral viscosity in white wine.

Compositional Factors Affecting White Wine Mouthfeel

Phenolic compounds

The phenolic compounds in white wine comprise a broad family of compounds that in their basic form possess one or more benzenoid rings substituted by at least one hydroxyl group. White wine phenolics can be categorised as either 1) non-flavonoids or 2) flavonoids according to their benzoic ring structure. The structures, reported concentration ranges and sensory thresholds of the phenolic compounds in white wine are given in Figure 1, and Tables 1 and 2 respectively.

The major non-flavonoids in white wine are the hydroxycinnamic and hydroxybenzoic acids and their derivatives. Hydroxybenzoic acids comprise of a single benzenoid ring and hydroxyl group but are characterised by a further substitution with a carboxylic acid group. The hydroxycinnamic acids are characterised by an ethylene group between the benzene ring and the carboxylic acid group.

The flavonoids are more complex comprising a C15 skeleton with an aromatic (A) and benzodihydropyran (C) ring bearing another aromatic ring (B) in position 2. The flavonoid sub-groups are classified by the oxidation state of the C ring and individual compounds within each group are differentiated by the number and location of either hydroxyl or methoxyl groups, and

glycosylation on the B ring. Flavonols and flavan-3-ols are most significant classes of flavonoids in white wine in terms of concentration, but others such as flavanonols and flavanones have consistently been found to be present.

Non-flavonoids: The hydroxycinnamic acids in white wine occur mainly in the form of tartaric acid esters, particularly those of caffeic (caftaric), p-coumaric (coutaric) and ferulic (fertaric) acids. Free forms and ethyl and methyl esters are also formed in lower concentrations by hydrolysis and pectinase catalysed esterification. Caftaric acid is also the most abundant phenolic compound found in white juice (Ong and Nagel, 1978). When the juice is subjected to oxidative must handling practices e.g. polyphenol oxidase hyperoxidation, the caftaric acid quinone reacts with the grape peptide glutathione under the action of polyphenol oxidase to form 2-S-glutathionyl caftaric acid (Grape Reaction Product or GRP) (Cheynier et al., 1986; Singleton et al., 1985). Other similar conjugates of p-coutaric acid and caffeic acid with cysteine and glutamine are also formed in smaller amounts by the same mechanism (Cejudo-Bastante et al., 2010; Cheynier et al., 1986).

The most prevalent hydroxybenzoic acids in white wine are gallic, gentisic, p-hydroxybenzoic, syringic and salicylic acids (Monagas et al., 2005). They are mostly found in their free form but ethyl, methyl and glucose esters have been reported in Riesling wines (Baderschneider and Winterhalter, 2001).

Flavonoids: Flavonols are mostly confined to the epidermal skin tissues of the grape (Rodríguez Montealegre et al., 2006). Their concentration in white grapes have been shown to increase disproportionately to other skin phenolics following sun exposure (Friedel et al., 2015) suggesting that they may play a protective role against grape tissue damage by UV light. The

dominant flavonols in white and wine are the 3-O-glycosides of quercetin particularly the glycosidic and glucuronic forms (Castillo-Muñoz et al., 2010) but myricetin, kaempferol and isorhamnetin glycosides are also present (Di Lecce et al., 2014; Vilanova et al., 2009).

Flavanols are mostly found in the hypodermal layers of the skins and the parenchyma of seeds and in conventional winemaking are extracted during a brief (0.5-24 hr) period between grape crushing and draining when the skins and seeds are in contact the juice prior to fermentation (Di Lecce et al., 2014). (+)-catechin and its distereoisomer (–)-epicatechin are the dominant flavanols in white wine. They are dihyroxylated on the C-3' and C-4' positions on the B ring. The trihydroxylated form, (-)-epigallocatechin which is localised in skin, and those esterified with gallic acid notably (-)-epigallocatechin gallate and (–)-epicatechin-3-O-gallate which are localised in seeds are also present in white wine (Oszmianski and Sapis, 1989). Flavanol dimers and trimers are also present in white wine but in lower concentrations (Ricardo da Silva, et al., 1993; Lea, et al., 1979). They consist mainly of (+)-catechin and (-)-epicatechin units linked by C4-C8 and/or C4-C6 bonds (Foo and Porter, 1980) but other dimers containing gallocatechin and epigallocatechin units (de Pascual-Teresa et al., 2000; Fulcrand et al., 1999) and gallic acid units have also been detected in white wine (Ricardo da Silva et al., 1993).

Glycosylated flavanonols have been identified in the skin and stems, with the 3-O rhamnosides of dihydroquercetin (astilbin) and dihydrokaempferol (engeletin) being the most significant in white wine (Masa et al., 2007; Singleton and Trousdale, 1983). Flavanonol concentrations in 94 commercial white wines were found to range between 1 and 13 mg/L (Vitrac et al., 2002).

Other phenolic compounds: Tyrosol is formed from tyrosine by yeast during fermentation and as such its concentration depends on yeast strain and on the initial concentration of sugars and

tyrosine in the must (Peña-Neira et al., 2000). The contribution of tyrosol to total white wine phenolic concentration is unclear. Some have reported that tyrosol dominates the profile (Peña-Neira et al., 2000), while others estimate that tyrosol comprises between 3% (Gawel et al. 2014a) and 10% (Myers and Singleton, 1979) of the total phenolic content of white wine.

Polysaccharides

Polysaccharides in white wine arise from both grape and yeast activity during and after fermentation. They are classified as macromolecules that range from 5 to 200 kDa, making them as a group, the highest molecular weight compounds found in white wine (Jones et al., 2008). The major classes of polysaccharides in white wine have been defined by a combination of their monosaccharide composition and their probable oenological source. 1) Mannoproteins are either released from yeast cell walls during fermentation, and during the autolysis stage whereby non-active 'spent' yeast cells (yeast lees) contact the wine during the maturation phase (Escot et al., 2001). They are characterised by a high content of mannose relative to other monosaccharides (Gonçalves et al., 2002), but constitute a broad molecular weight distribution which suggests that several populations of mannnoproteins exist depending on their source. 2) Arabinogalactan proteins (AGP's) are characterised by a high proportion of arabinose and galactose residues and associated with a protein core comprising a high proportion of hydroxyproline (Fincher and Stone, 1983). AGP's exist in the grape vacuole intracellular spaces and are therefore easily extracted during juicing and during the early stages of fermentation (Guadalupe and Ayestarán, 2007), and 3) Rhamnogalacturonan polysaccharides are released from pectins embedded within the grape cell wall and are characterised by their low MW (<20kDa), a relatively high proportion of galacturonic

acid and rhamnose residues, and by the presence of the diagnostic sugars fucose and apiose (Pellerin et al., 1996).

Influence of white wine composition on mouthfeel

Phenolic compounds

General Discussion: The traditional paradigm of astringency i.e. decreased oral lubrication following exposure to polyphenols depends on the polyphenol being capable of binding with a salivary protein at different positions and aggregating multiple salivary proteins (Baxter et al., 1997). The question as to whether the monomeric and dimeric polyphenols that make up the majority of the phenolic profile of white wines have sufficient numbers of hydrogen bonding sites and/or hydrophobic surfaces to interact with salivary proteins has only recently been addressed. Recent studies have shown that the basic proline rich protein (PRPb) amino acid probes IB-5 (Canon et al., 2011) and IB9-37 (Canon et al., 2013; Cala et al., 2012) are able to bind to and aggregate epicatechin gallate and epigallocatechin gallate (Pascal et al., 2009) molecules. Flavanol dimers with extended structures have also been shown to act as bidentate ligands for IB7-14 (Cala et al., 2010). Other monomeric non-flavanols such as naringenin, apigenin and quercetin rhamnoside and rutinoside also have affinities for IB14 and entire PRPb (Plet et al., 2015). These studies show that many monomeric and dimeric polyphenols found in white wine can form complexes with basic proline rich proteins, and therefore have the potential to elicit astringency under the tactile model.

With respect to the alternative paradigms for astringency perception, Soares et al. (2016) found that in vivo, low molecular weight polyphenol fractions comprising monomers and dimers did

not bind well to oral epithelial cells regardless of the simultaneous presence of salivary proteins, which under the epithelial binding model of astringency would suggest that low molecular weight polyphenols do not contribute to astringency. However, it should be noted that the influence of a salivary pellicle, and epithelial bound salivary proteins typical of an oral surface were not modelled in their experiment.

There is conflicting evidence as to whether monomers can elicit astringency under the chemesthetic model. TRPV1 channels were not activated in response to a variety of flavanol monomers (Kurogi et al., 2015; Carpenter, 2013), galloylated flavanol monomers have been shown to stimulate trigeminal neurons suggesting that they at least can elicit astringency (Schobel et al., 2014). In conclusion, these differences may be due to the widely different methods used to determine oral physiological response to the phenolic stimulus.

Total Phenolics: White wine phenolics are mostly monomeric and comprise over 80 compounds spanning a range of phenolic classes defined by their ring structures, and within each class they take on different forms based on their patterns of hydroxylation, glycosylation, esterification or conjugation with amino acids. Despite this diversity, the summed concentration of the phenolic species in white wine is relatively low compared to those in red wines where polymeric flavanols derived from fermentation on skins and seeds dominate their phenolic profile. However, as the sensory response to mixtures of non-volatiles that elicit tastes and astringency are known to be at least partially additive (Ferrer-Gallego et al., 2014; Keast et al., 2003), it is prudent to also consider the effects of combined total of phenolic compounds on mouthfeel in white wines.

The first study of its type in white wine used both conventional, and unconventional winemaking methods more akin to those used in red winemaking to create extremes in total phenolic

concentration (Singleton et al., 1975). They found that white wine bitterness was unrelated to total phenolic concentration which would suggest that either 1) other (non-phenolic) compounds contribute to bitterness, or 2) that the winemaking methods influenced the relative contribution of bitter phenolic compounds (e.g. epicatechin and naringin) over non-bitter phenolic compounds (e.g. caftaric acid and GRP) within the total pool of phenolics present in the wines. In a broader study, Gawel et al. (2014a) found that a six-fold difference in total wine phenolic concentration obtained by applying conventional winemaking techniques increased bitterness only slightly, but the increases were strongly correlated with total phenolic concentration.

The perceived viscosity of white wine has been associated with its total phenolic concentration (Gawel et al., 2013; Okuda et al. 2007). In contrast, lower phenolic concentration white wines made from hyperoxidised free run juice were not lower in 'body' than the control wines (Cejudo-Bastante 2011a,b). The differences in conclusions may be explained by the expected differences in the range of total phenolics, and from variations in other compositional factors such as pH and residual sugar resulting from the different winemaking methods that were applied. To overcome the limitations of correlative studies, addition studies have also been conducted. White wines fortified with the total phenolic pool extracted from each of three different varietal wines were consistently perceived to be more viscous, astringent and bitter (Gawel et al., 2013). Total phenolics were also shown to enhance the perceived hotness and astringency of model white wine, but only of those that were initially low in hotness (i.e. low alcohol), and low in the astringent/drying character (i.e. high pH).

Non-Flavonoids: Benzoic acid derivatives when presented at two orders of magnitude higher than that found in white wine elicit complex oral sensations of sourness, bitterness, astringency

and a ‘prickling’ (Peleg and Noble, 1995). The substitution pattern was found to affect mouthfeel, with those substituted in the ortho position (salicylic and gentisic acids) being astringent, and those with a greater number of hydroxyl groups more ‘prickling’ (Peleg and Noble, 1995). It is unclear if these results are relevant to white wine, however as gentisic acid has also been reported to be astringent when tasted at white wine like concentrations (Dadic and Belleau, 1973) it is possible that it and other benzoic acids found in white wine may affect mouthfeel.

Many hydroxycinnamic acids and their ethyl and tartaric acid esters have been reported to be astringent and bitter at concentrations higher than those observed in white wine (Hufnagel and Hofmann, 2008). However, as the hydroxycinnamic acid concentrations found in white wine are typically below their detection thresholds (Okamura and Watanabe, 1981; Maga and Lorenz, 1973) it would suggest that they do not impact on the taste or mouthfeel of white wine. Indeed, fortifying white (Vérette et al., 1988) and red (Sáenz-Navajas et al., 2012) wines with realistic levels of caftaric acid did not produce perceptible changes to their taste or mouthfeel. However, when in model wine, wine-realistic levels of caftaric acid has been found to impact on acidity (Vérette et al., 1988), and astringency (Gawel et al., 2014b). Similarly, wine realistic concentrations of grape reaction product did not affect the palate properties when added to a real white wine (Vérette et al., 1988), but GRP was found to increase the intensity of oily mouthfeel and a burning aftertaste unrelated to ethanol when added to model white wine (Gawel et al., 2014b).

Flavonoids: A rutinoside (di-glycoside) of quercetin has been suggested by (Scharbert et al., (2004) to be a powerful astringent at concentrations well below those of white wine. The

possible mouthfeel and taste impact of flavonol monoglycosides were demonstrated when quercetin 3-O-glucoside, albeit at higher concentrations than found in white wine, elicited astringency and bitterness (Ferrer-Gallego et al., 2016). A 3-O-rhamnoside of quercetin has also been reported to be bitter and astringent at white wine like concentrations (Dadic and Belleau, 1973).

More studies have been conducted on the taste and mouth-feel properties of flavanols than any other phenolic class due to their occurrence in many different beverages including wine, green and black tea, and cider. However, all studies to date have used concentrations far higher than those observed in white wine (i.e. > 500 mg/L). Therefore, the results of the studies should be considered only indicative of possible sensory outcomes in white wine.

Catechin and its stereoisomer (-)-epicatechin are reported to be astringent and bitter (Peleg et al., 1999; Thorngate and Noble, 1995; Robichaud and Noble, 1990) with epicatechin being more astringent and bitter than catechin (Ferrer-Gallego et al., 2014). However, perceptual mapping of these simple monomers against recognised bitter and astringent compounds suggests that they are more bitter than they are astringent (Kielhorn and Thorngate, 1999).

Dihydroxylated and trihdroxylated flavanols esterified with gallic acid e.g. epicatechin gallate and epigallocatechin gallate have also been deemed to be bitter and astringent in taste tests on tea (Yu et al., 2014; Narukawa et al., 2010), with bitterness being later confirmed physiologically by the observation that they activated the human bitter taste receptor hTAS2R14 (Yamazaki et al., 2013).

Schobel et al. (2014) proposed that 3 hydroxyl groups on the B ring (galloylation) is a necessary condition for robustly stimulating an oral chemosensory response indicative of astringency. This

would indicate that the dehydroxylated flavanols catechin and epicatechin cannot elicit astringency. However, this conclusion is contingent on the assumption that chemesthesis is the only astringency mechanism at play. Galloylation also appears to favour astringency perception under the salivary protein interaction model of astringency as trihydroxylation of the B-ring results in increased interactions with poly-L-proteins (Poncet-Legrand et al., 2006), salivary mucins (Peleg et al., 1999) and basic PRP's (Cala et al., 2010). Glycosylated PRP's which are considered important in salivary lubrication are also precipitated by epigallocatechin gallate (Pascal et al., 2008). In contrast, Ferrer-Gallego et al. (2015) noted that galloylated forms were less astringent than dihydroxylated forms which they attribute to the ability of basic PRP's to simultaneously interact with fewer galloylated flavanol molecules.

Epigallocatechin gallate has been reported as being more astringent than other flavanols monomers (Rossetti et al., 2009) and is the main contributor to astringency in green tea (Yu et al., 2014). EGCG has been shown to increase the friction coefficient of whole saliva while epicatechin had no effect, suggesting that esterification with gallic acid and trihydroxylation of the B-ring may enhance the production of astringency (Rossetti et al., 2009).

Compared to red wines, the flavanols in white wines have a low degree of polymerisation (dP), typically ranging from monomers to trimers. It is now well understood that the first stage of astringency perception under the tactile model involves complex formation between proteins and flavanols, and this complexation increases with the flavanols' degree of polymerisation (Baxter et al., 1997). White wine flavanols (dP 1-3) have been shown to be astringent (Peleg et al., 1999) with their astringency increasing with dP. Consistent with this, flavanol dimers have been shown to form soluble complexes with salivary proteins (Sarni-Manchado and Cheynier, 2002), and that

they can also activate TRPV1 channels associated with chemosensory perception (Kurogi et al., 2015).

Other Phenolic Compounds: The 'tannin taste' of Riesling wines from the same juice with different levels of must solids correlated strongly with their tyrosol concentration, while being poorly correlated with hydroxycinnamic acid and flavan-3-ol concentration (Konitz et al., 2003). A flavanone, naringin has recently been tentatively identified in white wine (Gawel et al., 2014a). While flavanones are only likely to be present in white wine at very low concentrations a possible effect on white wine bitterness cannot be ruled out some flavanone glycosides are intensely bitter when glycosylated in specific forms (Horowitz and Gentili, 1969).

Other Considerations: The perceived intensity of mixtures of similar tasting compounds including those that are bitter, are known to be additive or sub-additive (Keast et al., 2003), and in the case of some white wine phenolics, their effect on mouthfeel may even be hyperadditive (Ferrer-Gallego et al., 2014). Therefore, even if the concentrations of individual phenolic species are insufficient to induce a sensation in white wine, they may do so in combination. Caftaric acid and its derivative GRP have been shown to be mutually antagonistic with respect to astringency and burning after-taste, and were also found to be able to suppress the astringent/drying sensation produced by the wine matrix (Gawel et al., 2014b), showing the potential for phenolic compounds to interact in complex ways with each other and other major components found in wine.

Polysaccharides

Mixtures of mannoproteins and AGP's at wine like concentrations have been shown to enhance the perception of viscosity in model white wine (Gawel et al., 2016; Vidal et al., 2004a). However, the effect of these polysaccharides on viscosity was shown depend on pH, with the increase in perceived viscosity only occurring in higher pH wines (Gawel et al., 2016). Possible reasons of this pH effect include charge effects on acidic polysaccharides, or changes to the ordering of bulk water in the environment surrounding the polysaccharide – both of which could alter its hydration state and therefore viscosity. The possible effect of polysaccharides on perceived viscosity has also been demonstrated in real white wine as the 'thickness' of white Koshu wines was shown to associate with the concentration of neutral polysaccharides (Okuda et al., 2007). However, it was shown that doubling the total polysaccharide concentration of white wine had a small but statistically insignificant effect on perceived viscosity (Gawel et al., 2016).

The hotness of white wine was also reduced by realistic levels of white wine polysaccharides, mostly attributed to medium molecular weight mannoproteins and AGP's in the 13-93 kDa MW range (Gawel et al., 2016). The physiological mechanism for the suppression of alcohol hotness by polysaccharides is unknown but worthy of further investigation given that increased flavour in white wine can be obtained by picking grapes when riper, but this can incur an expense in wine quality as doing so may result in excessive levels of palate hotness.

Wine polysaccharides may also influence astringency perception as they have been shown to disrupt the interaction and aggregation between salivary proteins and polymerised flavanols (Carvalho et al., 2006). This effect could be due to either solubilisation following formation of ternary complexes between the protein, polyphenol and polysaccharide, or by competition between the polysaccharide and protein for the polyphenol (Luck et al., 1994). Such possible disruption has

been shown in a red wine context with lower perceived astringency of model wine containing polymerised grape seed flavanols following addition of Rhamnogalacturonan-II (Vidal et al., 2004b), and correlations between mannoprotein and AGP concentrations with the astringency of Tempranillo red wines (Quijada-Morín et al., 2014).

However, studies using white wines have found little evidence that polysaccharides influence their astringency. Additions of whole white wine polysaccharides at wine realistic concentrations did not influence the astringent/drying character of white wine (Gawel et al., 2016), and the astringency of white wines made using a broad spectrum of white winemaking methods and grape cultivars were found to be unrelated to their total polysaccharide concentration (Gawel et al., 2014a). The differences in the observed effects of polysaccharides on astringency across studies could be due to the difference in the pH of the wines that were used which could alter the charge properties of the polysaccharides (Verhnet et al., 1996) and salivary proteins (McArthur et al., 1995) and therefore their interaction with wine polyphenols, or to differences in the relative concentrations of phenolic compounds to polysaccharides which could also determine the type of interaction i.e. whether it be competitive or associative (Soares et al., 2009).

The effect of polysaccharides on white wine bitterness and (presumably) related characters such as metallic and pungency is unclear. In model systems, the bitterness of polymerised grape seed tannin was reduced by a mixture of mannoproteins and arabinogalactan-proteins (Vidal et al., 2004b) and whole polysaccharides from white wine reduced the metallic character of a complex model white wine which included ethanol, flavour compounds, glycerol, and white wine proteins (Jones et al., 2008). However, others found that white wine polysaccharides did not affect the

bitterness of a high phenolic white wine, nor the bitterness elicited by ethanol in a simple model white wine (Gawel et al., 2016). Further addition studies utilising real white wine are clearly required to properly address the effect of polysaccharides on white wine bitterness.

Glycerol

Glycerol is the third most abundant compound in white wine after water and ethanol. Glycerol is a product of yeast fermentation, and ranges between 5-10 g/L depending on yeast strain and fermentation conditions (Nieuwoudt et al., 2002). In its pure form, glycerol is clearly viscous suggesting that it may influence white wine viscosity. However, the estimated viscosity difference threshold of glycerol in white wine is 26 g/L which suggests that it does not influence the perception of viscosity (Noble and Bursick, 1984). Increasing glycerol by 5g/L in white wine (Gawel et al., 2007) and model white wine (Jones et al., 2008) resulted in small increases in perceived viscosity. However, in both these studies there was the possibility that the perception of perceived viscosity was confounded with the inherent sweetness of glycerol. When the sweet taste of glycerol was neutralised by blocking sweet taste receptors using the anti-saccharin agent gymnemic acid, or was equalised by the addition of a non-viscous artificial sweetener, then glycerol was found to have no effect on perceived viscosity (Gawel and Waters, 2008). The sweetness of glycerol may also be a factor in the reduced bitterness via mixture suppression as observed by Jones et al. (2008) in model white wine.

Ethanol

Increased hotness in white wine due to ethanol can be perceived even within the relatively narrow range of concentrations typically encountered in white wine (Gawel et al., 2007). Higher

ethanol white wines are also perceived to be slightly higher in body/density (Nurgel and Pickering, 2005).

The intensity of astringent sensation declines in the presence of increasing amounts of ethanol (DeMiglio and Pickering, 2008; Lea and Arnold 1978). Increasing ethanol concentration results in reduced precipitation (Rinaldi et al., 2012) and interaction strength (McRae et al., 2015) between salivary proteins and polymerised tannins. The reduced impact of polyphenols on salivary proteins in the presence of ethanol has been postulated to be due to the ability of ethanol to interfere with interactions between protein H-acceptor sites and polyphenol hydroxyl groups, and by disrupting hydrophobic interactions due to its influence on water cohesion (Pascal et al., 2008). Ethanol may contribute directly to the observed reduction in astringency as it has been shown to reduce the astringency of model wine devoid of phenolics (Fontoin et al., 2008) which suggests that it may be able to modulate the drying sensation elicited by organic acids. However, it is noteworthy that others have found ethanol to increase dryness under similar conditions (Symoneaux et al., 2015; Jones et al., 2008). Increased ethanol concentration may also improve the ‘quality’ of the astringent sensation as it has shown to enhanced the production of sub-qualities 'velvety', and 'mouth-coat' (DeMiglio et al., 2002), and reductions in other possibly less desirable characters of 'puckery', 'coarse' (Vidal et al., 2004b) and ‘grippy/adhesive’ (DeMiglio and Pickering, 2008).

Ethanol is inherently bitter (Mattes and DiMeglio, 2001) and is known to stimulate the bitter taste receptor TAS2R (Allen et al., 2014). Indeed, the difference in ethanol concentrations encountered in white wine at around 4% contributed more to the bitterness of model white wine

than the flavanol catechin at concentrations the high end of the range found in red wine (Fischer and Noble, 1994).

Organic acids/pH

White wines can vary in pH from between 3.1 to 4.0, but typically are within the range of 3.3 to 3.5. The total acidity of white wine is mostly the combination of tartaric and malic acid from the grape, and lactic acid in the case of wines that have undergone malolactic fermentation. The fermentation product succinic acid which has been described as salty and acidic (Kubícková and Grosch, 1998) and umami like (Rotzoll et al., 2006; Kaneko et al., 2006) is also found in reasonable concentrations in white wine.

Organic acids including those in white wine have been shown in model studies to elicit mouth drying sensations (Hartwig and McDaniel, 1995). These sensations have been attributed to hydrogen ion concentration rather than the total acidity or the anion species involved (Sowalski and Noble, 1998; Lawless et al., 1996). Consistent with these model studies, the astringency/dryness of white wines made using a broad set of commercial juice extraction and handling methods consistently increased with decreasing pH, but astringency was unrelated to total phenolic concentration (Gawel et al., 2014a).

The increases in perceived astringency/dryness with decreasing pH may be explained by reduced salivary viscosity (Veerman et al., 1989; Nordbo et al., 1984) possibly resulting from greater interaction after charged salivary proteins neutralise at pH's closer to their isoelectric point. Alternative explanations could be an increased binding of astringent compounds to oral epithelial cells which has been observed with both phenolic (Payne et al., 2009) and non-phenolic

compounds (Ye et al., 2012), or that H^+ ions which are strong disruptors of water structure may change the hydration environment surrounding the solvated proteins embedded within salivary pellicle, possibly leading to a feeling of palate dryness.

Carbon Dioxide

Most bottled white wines contain some dissolved carbon dioxide as part of their bottling specification with concentrations typically in the range 0.5 to 1 g/L. Dissolved CO_2 can create a mouthfeel character often described as 'spritz', which in the case of still white wine is considered a negative quality attribute. To our knowledge, no studies have been conducted on the effect of dissolved CO_2 at white wine concentrations on the perception of spritz or other mouthfeel characters. However, in a closely analogous situation to white wine, 5 g/L of dissolved CO_2 (a level typical of semi sparkling wine) increased the perceived astringency of model apple cider containing polyphenols (Symoneaux et al., 2015). Similar enhancing effects on the astringency of model solutions by saturated solutions of CO_2 have been observed (Hewson et al., 2009). The increased astringency may be due to lower pH levels resulting from the presence of carbonic acid formed by the dissociation of CO_2 in solution, but given that both the perception of dissolved CO_2 and astringency may be of somatosensory origin, a direct effect of dissolved CO_2 on perceived astringency is possible.

Amino Acids and Peptides

It has been known for some time that many amino acids and peptides are bitter (Solms, 1969). The common structural features of bitter amino acids are that they have an L configuration and a hydrophobic side chain. The bitterness of peptides can similarly be equated to the average

hydrophobicity of their amino acid components (Maga, 1990). White wine contains several hydrophobic peptides that are bitter (Desportes et al., 2001). However, it is unknown if they are found in white wine in sufficient concentrations to produce a bitter sensation either individually or in combination. Peptides may impact on the fullness of white wine. Using an untargeted approach Skogerson et al. (2009) found that the concentration of amino acids in white wine (both individually and in total) were good predictors of whether a white wine was low, medium or high in body.

Practical Implications and Future Directions

This review aimed to identify the aspects of white wine composition that directly, or by interaction influence white wine mouthfeel, and to elucidate the possible mechanisms that underpin mouthfeel perception in white wine. Alcohol, pH and phenolics were found to influence most aspects of white wine mouthfeel while the role of polysaccharides in white wine appeared to be mostly confined to moderating the negative quality attribute of perceived hotness. and the effect of glycerol concentration on mouthfeel perception of dry white wine appears to be negligible.

These conclusions have significant implications for winemaking practice. The pH and alcohol level of white wine are mostly determined by the maturity of the grape at harvest, but are routinely modified by winemakers primarily to ensure that the wine is microbiologically and chemically stable and that it has a balanced taste that meets expectations of the consumer. The literature suggests that modulating ethanol content and (particularly) pH are the front-line tools that can be used by winemakers to creating wines with specific mouthfeel attributes.

The knowledge that glycerol which is the third most abundant compound in white wine cannot be varied sufficiently by traditional winemaking practice to influence mouthfeel suggests that no further work be conducted. However, in response to consumer demands for 'fruit forward' wines from riper grapes but with a lower alcohol content, new technologies have emerged whereby carbon metabolism of the yeast *Saccharomyces cerevisiae* has been directed away from ethanol in favour of glycerol production (reviewed in Goold et al., 2017), which if translated to commercial practice could potentially increase the glycerol concentration of some white wines.

The conventional wisdom amongst many white wine makers has been that low phenolic concentration in wine equates to greater purity of varietal character and lower bitterness and 'coarseness' (Singleton et al., 1975). More recently though, winemakers have considered incorporating phenolics into their wines to add complexity by the way of mouthfeel (McLean, 2005). The review suggests that phenolics have an overarching effect on all major aspects of white wine mouthfeel, affecting the perception of astringency, viscosity, oiliness, hotness and bitterness. However, while most winemakers know how to influence total phenolic concentration in their wines, and some are also aware of how they can influence the phenolic makeup of their wines by their production decisions, knowledge as to how they can influence mouthfeel via phenolic management is lacking. Such knowledge would present a powerful tool as it would allow winemakers to better construct wines with desirable mouthfeels and modulate their overall style.

Looking ahead, a worthy goal of further research would be to provide theoretically based mixture models that can be applied in practical situations to predict the mouthfeel profiles of white wine from knowledge of their composition. A prerequisite for the construction of mixture

models in other modalities such as olfaction and taste has been requisite on a knowledge of the psychophysical functions of each of the components that make up the 'mixture' that is white wine. Developing these models will be challenging. Apart from the practical difficulties of obtaining sufficient pure material for large scale sensory studies, the sensory assessment of all combinations of compounds that could possibly impact on mouthfeel is unfeasible. So how could any such mixture model be simplified inasmuch that it is practical but also theoretically valid? Research in the taste modality provides some guidance in this matter. In that modality, similar tasting substances are known to be additive (Keast et al., 2003; Bartoshuk, 1975) and that in circumstances whereby compound concentrations are correlated (as is the case with phenolics), then they add along an averaged psychophysical function (Frijters and DeGraaf, 1987). If this were shown to be true of phenolic compounds and their relationship to mouthfeel, then the summed concentrations of phenolic compounds with similar mouthfeel attributes could be modelled rather than the impractically larger number of individual compounds, and that a single indicative compound could be used to quantify the combined effect of multiple members of the same class of compounds. However, a further question arises as to which phenolics have the same mouthfeel attributes. Small changes to the substitution pattern of phenolics i.e. hydroxylation, esterification, glycosylation, and derivitisation with glutathione can significantly alter the mouthfeel of phenolic compounds indicating that classifying phenolic compounds based on their ring structure is likely to be inadequate. Therefore, a broad set of structure-function relationship studies of phenolic compounds is needed to derive a general set of rules which could be used to create a general classification of phenolic compounds based on their sensory properties.

The overall perception of mouthfeel in white wine is a response to the chemosensory, tactile and taste systems. A large body of work in the related field of gustation which also involve interactions between different sensory modalities suggest that the overall percepts of flavour and taste cannot be understood by simply investigating its contributing parts. Prescott (1999) proposed that flavour might be considered as a functionally distinct modality cognitively constructed from the integration of the distinct physiological sensory systems of olfaction and taste, the latter of which is itself may be considered an integrated construct of sensory systems in the mouth (Green, 2002). It has been known for some time that the non-volatiles food (Delwiche 2004), and in white wine (Lubbers et al. 1994, 2001) can influence flavour perception. A few studies have also demonstrated the reverse case of retronasally perceived volatile compounds influencing mouthfeel perception (Oladokun et al., 2017; Symoneaux et al. 2015; Sáenz-Navajas et al., 2010; Jones et al. 2008). Further work needs to be conducted to establish whether the interaction between volatile and non-volatile components in white wine is of a symmetric or asymmetric nature. Forty years ago, Van Bursick and Erickson (1977) proposed that the trigeminal system acts to bind the physiologically distinct olfactory and gustatory systems into a single perceptual system known as flavour. Under a similar integrated interpretation, mouthfeel in white wine should also be considered as a multidimensional sensory construct and future research be conducted accordingly.

The measurement of mouthfeel provides unique challenges due to the heterogeneity but physical proximity of the receptive systems involved and that the physiological mechanisms that govern perception of mouthfeel attributes are unclear. Astringency is a case in point. For over a half a

century the dominant paradigm for astringency has been that of polyphenol-salivary tannin interaction leading the changes to salivary rheology that are detected by oral mechanoreceptors. Yet while a substantial body of work has identified the basic mechanisms of salivary protein and wine polyphenol binding (some) leading to a change to salivary rheology, it is yet to be demonstrated how these changes in the bulk phase of saliva translate to astringency perception. More recent findings using in-vitro receptor based studies indicate that astringency is a chemoreceptive process which must therefore necessarily involve binding of astringent molecules to the oral mucosa. However, the issue of possible interaction between polyphenols and salivary proteins in the bulk saliva or salivary pellicle preceding the binding have not been adequately addressed in these studies. Therefore, a more comprehensive and integrated approach involving investigation of interaction of astringent substances with the salivary phase, mucosal binding mechanisms, and crucially, which receptive fields are innervated resulting from changes to salivary rheology and/or mucosal binding is required if astringency perception is to be fully understood.

Acknowledgements

The work was funded by Australia's grapegrowers and winemakers through their investment body, Wine Australia, with matching funds from the Australian government.

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Table 1: Mean and concentration ranges of phenolic compounds in white wine

	Mean concentration (mg/L)	Concentration range (mg/L)	References
NON-FLAVONOIDS			
Hydroxybenzoic acids			
Gallic acid	3.3	0-8.4	Fernández-Pachón et al. (2006)
	3.4		de Villiers et al. (2005)
	4.9	0.7-18.5	Singleton and Truesdale (1983)
	1.0		Betés-Saura et al. (1996)
	1.2		Kallithraka et al. (2009)
	1.9	0.8-3.2	Cejudo-Bastante et al. (2011a,b)
	0.8	0.4-1.2	Gawel et al. (2014a)
Syringic acid	0.04	0-0.5	Fernández-Pachón et al. (2006)
	0.4		Betés-Saura et al. (1996)
	1.1	0.3-2.2	Gawel et al. (2014a)
Protocatechuic acid	1.2	0-4.7	Fernández-Pachón et al. (2006)
	1.3		de Villiers et al. (2005)
	1.2		Betés-Saura et al. (1996)
	0.3	0-0.4	Gawel et al. (2014a)
Hydroxybenzoic ethyl esters	0.9	0.3-1.8	Gawel et al. (2014a)
Hydroxycinnamic acids			
Caffeic	1.3	0-2.7	Fernández-Pachón et al. (2006)
	2.7		de Villiers et al. (2005)
	0.2	0-0.5	Nicolini et al. (1991)
	1.6		Betés-Saura et al. (1996)
	1.6	0.3-4.3	Korenika et al. (2014)
	0.6		Kallithraka et al. (2009)
	1.4	0-4.0	Cheynier et al. (1986)
	2.7	2.6-2.8	Cejudo-Bastante et al. (2011a,b)
Coumaric	0.8	0-3.0	Fernández-Pachón et al. (2006)
	1.3		de Villiers et al. (2005)
	0.2		Betés-Saura et al. (1996)
	0.8	0.1-2.8	Korenika et al. (2014)
	0.2		Kallithraka et al. (2009)
	0.3	0-0.8	Cejudo-Bastante et al. (2011a,b)
Ferulic	0.4		de Villiers et al. (2005)
	0.1		Betés-Saura et al. (1996)
	0.6	0.4-1.3	Korenika et al. (2014)
	0.3		Kallithraka et al. (2009)

	0.9	0.9-1.0	Cejudo-Bastante et al. (2011a,b)
Tartaric acid esters			
Caftaric acid	17.8	3.9-53.5	Fernández-Pachón et al. (2006)
	12.1		de Villiers et al. (2005)
	11.9	0-44.8	Singleton and Truesdale (1983)
	2.3	0.5-5.4	Nicolini et al. (1991)
	39.4		Herrick and Nagel (1985)
	43.7	12.8-109.5	Herrick and Nagel (1985)
	12.6		Betés-Saura et al. (1996)
	15.1	1.5-42.3	Korenika et al. (2014)
	29.6		Kallithraka et al. (2009)
	109.0	24-267	Herrick and Nagel (1985)
	10.6	0-39.6	Cheynier et al. (1986)
	41.3	12.7-70.7	Ricardo da Silva et al. (1993)
	3.7	1.77-8.36	Cejudo-Bastante et al. (2011a,b)
	7.8	0-31	Gawel et al. (2014a)
Coutaric acid	2.3		de Villiers et al. (2005)
	3.8	0.2-14.5	Singleton and Truesdale (1983)
	0.9	0.13-1.70	Nicolini et al. (1991)
	3.2		Herrick and Nagel (1985)
	5.9	1.1-12.4	Herrick and Nagel (1985)
	16.3		Betés-Saura et al. (1996)
	4.4		Kallithraka et al. (2009)
	11.5	3.2-22.6	Ricardo da Silva et al. (1993)
	3.6	0.40-8.64	Cejudo-Bastante et al. (2011a,b)
	3.4	0.5-10.9	Gawel et al. (2014a)
Fertaric acid	5.4		Herrick and Nagel (1985)
	2.5	0.6-4.2	Herrick and Nagel (1985)
	0.2		Betés-Saura et al. (1996)
	0.7	0-2.95	Korenika et al. (2014)
	2.0		Kallithraka et al. (2009)
	4.3	2.96-5.12	Cejudo-Bastante et al. (2011a,b)
	1.6	0.1-3.9	Gawel et al. (2014a)
Other hydroxycinnamic acid derivatives			
Glutathione (GRP)	3.4	0.5-11.0	Nicolini et al. (1991)
	3.2		Betés-Saura et al. (1996)
	16.3	0-49.2	Cheynier et al. (1986)
	9.7	3.2-20.4	Ricardo da Silva et al. (1993)
	12.2	8.2-19.4	Cejudo-Bastante et al. (2011a,b)
	6.2	1.0-13.4	Gawel et al. (2014a)
Other amino acid	3.6	0.3-7.3	Cheynier et al. (1986)

derivatives	1.3		Gawel et al. (2014a)
Ethyl esters	0.4	0.2-1.0	Gawel et al. (2014a)
	1.4	0-3.5	Fernández-Pachón et al. (2006)
Coutaric acid glycoside	5.4	0-32.9	Fernández-Pachón et al. (2006)
	0.7	0.1-1.2	Nicolini et al. (1991)
Total hydroxycinnamic acids	34.1		Betés-Saura et al. (1996)
	63.1	38.2-101	Cejudo-Bastante et al. (2011a,b)
	21.7	5.2-51.6	Gawel et al. (2014a)
Total non-flavonoids	91	66-112	Singleton et al. (1980)
FLAVONOIDS			
Flavan-3-ols			
Epicatechin	0.8	0-10.4	Fernández-Pachón et al. (2006)
	3.7		de Villiers et al. (2005)
	27.3	0-80.8	Singleton and Truesdale (1983)
	19.3		Oberholster et al. (2008)
	4.1		Betés-Saura et al. (1996)
	5.3		Carando et al. (1999a)
	25.5		Kallithraka et al. (2009)
	5.0	0-8.7	Cejudo-Bastante et al. (2011a,b)
	4.8	0-21.3	Gawel et al. (2014a)
	33.8	0.2-71.7	Vitrac et al. (2002)
	2.6		Gürbüz et al. (2007)
Catechin	0.9	0-11.1	Fernández-Pachón et al. (2006)
	7.2		de Villiers et al. (2005)
	37.0	3-123.9	Singleton and Truesdale (1983)
	9.1		Oberholster et al. (2008)
	2.5		Betés-Saura et al. (1996)
	9.8		Carando et al. (1999a)
	17.7		Kallithraka et al. (2009)
	4.4	1.7-9.8	Cejudo-Bastante et al. (2011a,b)
	2.7	0-9.0	Gawel et al. (2014a)
	28.3	2.3-28.7	Vitrac et al. (2002)
	10.1		Gürbüz et al. (2007)
Epicatechin gallate	2.4	0-8.0	Gawel et al. (2014a)
Epigallocatechin gallate	2.5	0-15.6	Fernández-Pachón et al. (2006)
	1.0	0-6.0	Gawel et al. (2014a)
Flavan-3-ol oligomers			
B1 dimer	1.2	0-8.6	Fernández-Pachón et al. (2006)
		0.8-1.4	Carando et al. (1999b)
	6.1	0.1-24.1	Ricardo da Silva et al. (1993)
B2 dimer	1.4		Betés-Saura et al. (1996)
	0.5	0-1.5	Ricardo da Silva et al. (1993)
B3 dimer		0.9-2.2	Carando et al. (1999b)
	1.2		Betés-Saura et al. (1996)
	0.5	0-2.1	Ricardo da Silva et al. (1993)
B4 dimer		0.3-0.5	Carando et al. (1999b)
	0.13	0-0.4	Ricardo da Silva et al. (1993)

Trimers		0.6-1.7	Carando et al. (1999b)
	1.8	0-6.3	Ricardo da Silva et al. (1993)
Total dimers	5.3	0.3-2.2	Carando et al. (1999b)
Total trimers	1.6	0.6-1.7	Carando et al. (1999b)
Total flavan-3-ols	20.2	13.9-22.6	Cejudo-Bastante et al. (2011a,b)
	12.8	2.8-31.3	Gawel et al. (2014a)
	11.0	3.4-17.3	Konitz et al. (2003)
Flavonols			
Quercetin (Q)	1.4	0-3.4	Korenika et al. (2014)
	1.5	0.1-3.2	Cejudo-Bastante et al. (2011a,b)
	0.4	0-4.7	Gawel et al. (2014a)
	0.7	0-1.2	Simonetti et al. (1997)
Q glucoside	0.4		de Villiers et al. (2005)
	0.4	0-0.8	Korenika et al. (2014)
	0.8	0.4-1.2	Cejudo-Bastante et al. (2011a,b)
	3.4	0-30.3	Gawel et al. (2014a)
Q-glucuronide	0.3		Betés-Saura et al. (1996)
	1.5	1.1-1.9	Cejudo-Bastante et al. (2011a,b)
	3.3	0-44.4	Gawel et al. (2014a)
Q-rutinoside	0.4	0.2-0.9	Simonetti et al. (1997)
Kaempferol (K)	0.04	0-0.3	Korenika et al. (2014)
	0.40	0-0.9	Cejudo-Bastante et al. (2011a,b)
	0.1	0.1-0.1	Simonetti et al. (1997)
K-glucoside	0.3	0.2-0.4	Cejudo-Bastante et al. (2011a,b)
K-galactoside	0.1	0.1-0.14	Cejudo-Bastante et al. (2011a,b)
Isorhamnetin (I)	0.02	0-0.4	Korenika et al. (2014)
Myricetin	0.2	0.1-0.3	Simonetti et al. (1997)
I-glucoside	0.04	0.04-0.04	Cejudo-Bastante et al. (2011a,b)
Total Flavonols	51.7	39.5-80.0	Cejudo-Bastante et al. (2011a,b)
	9.0	0.5-56.8	Gawel et al. (2014a)
Other Phenolic compounds			
Tyrosol	2.5	0-11.9	Fernández-Pachón et al. (2006)
	11.6		Betés-Saura et al. (1996)
	2.8	2.2-3.6	Gawel et al. (2014a)
	13.3	6.3-22.7	Konitz et al. (2003)
Total flavonoids	168	128-222	Singleton et al. (1980)
Flavanonols			
Dihydroquercetin rhamnoside (astilbin)	1.1	0-10.3	Singleton and Truesdale (1983)
	2.4	0-21.1	Gawel et al. (2014a)
	2.2	0.6-4.4	Vitrac et al. (2002)
Dihydrokaempferol rhamnoside (engeletin)	0.5	0-3.3	Singleton and Truesdale (1983)
Dihydromyricetin-rhamnoside	3.0	1.8-6.0	Vitrac et al. (2002)
Flavanones	2.6	0.1-11.2	Gawel et al. (2014a)
Total Phenolics	251	164-316	Konitz et al. (2003)

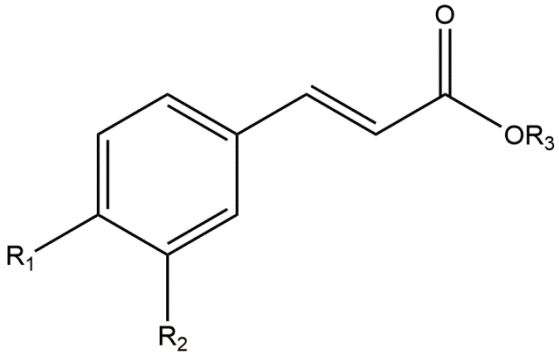
	258	224-328	Singleton et al. (1980)
	279		Kallithraka et al. (2009)
		168-404	Sokolowsky and Fischer (2012)
	201	152-281	Cejudo-Bastante et al. (2011a,b)

Table 2: Thresholds of Phenolic Compounds in White Wine

Compound	Threshold (mg/L)	Attribute	Medium	Method	Reference
Flavanols					
Catechin	119	astringency	water	staircase	Scharbert et al. (2004)
Catechin	290	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Catechin	20	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Catechin	46	detection	water	ascending limits	Delcour et al. (1984)
Dimer B1	139	astringency	water	staircase	Hufnagel and Hofmann (2008)
Dimer B1	231	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Dimer B2	110	astringency	water	staircase	Hufnagel and Hofmann (2008)
Dimer B2	280	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Dimer B3	116	astringency	water	staircase	Hufnagel and Hofmann (2008)
Dimer B3	17	astringency	water	ascending limits	Delcour et al. (1984)
Dimer B3	289	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Epicatechin	270	astringency	water	staircase	Scharbert et al. (2004)
Epicatechin	270	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Epicatechin	270	astringency	water	staircase	Hufnagel and Hofmann (2008)
Epicatechin gallate	110	astringency	water	staircase	Scharbert et al. (2004)
Epigallocatechin	169	astringency	water	staircase	Scharbert et al. (2004)
Epigallocatechin gallate	87	astringency	water	staircase	Scharbert et al. (2004)
Trimer C1	260	astringency	water	staircase	Hufnagel and Hofmann (2008)
Trimer C1	347	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Trimers+tetramers	4	detection	water	ascending limits	Delcour et al. (1984)
Hydroxybenzoic Acids					
Gallic acid	45	astringency	water	staircase	Glabasnia and Hofmann (2006)
Gallic acid	50	astringency	water	staircase	Hufnagel and Hofmann (2008)
Gallic acid	40	detection	water	ascending limits	Maga and Lorenz (1973)
Gallic acid	20	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Gallic acid	50	difference	beer	staircase	Dadic and Belleau (1973)
Protocatechuic acid	32	astringency	water	staircase	Hufnagel and Hofmann (2008)
Protocatechuic acid	30	detection	water	ascending limits	Maga and Lorenz (1973)
Protocatechuic acid	20	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Syringic acid	52	astringency	water	staircase	Hufnagel and Hofmann (2008)

Syringic acid	240	detection	water	ascending limits	Maga and Lorenz (1973)
Gallic acid ethyl ester	37	astringency	water	staircase	Hufnagel and Hofmann (2008)
Gallic acid ethyl ester	438	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Protocatechuic acid ethyl ester	9	astringency	water	staircase	Hufnagel and Hofmann (2008)
Protocatechuic acid ethyl ester	182	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Flavanonols					
Dihydroquercetin rhamnoside	1.7	detection	water	staircase	Hufnagel and Hofmann (2008)
Dihydrokaempferol rhamnoside	2.1	detection	water	staircase	Hufnagel and Hofmann (2008)
Hydroxycinnamic Acids					
Caffeic acid	13	astringency	water	staircase	Hufnagel and Hofmann (2008)
Caffeic acid	90	detection	water	ascending limits	Maga and Lorenz (1973)
Coumaric acid	23	astringency	water	staircase	Hufnagel and Hofmann (2008)
Coumaric acid	40	detection	water	ascending limits	Maga and Lorenz (1973)
Ferulic acid	13	astringency	water	staircase	Hufnagel and Hofmann (2008)
Ferulic acid	62	detection	water	E679-91	Work and Camire (1996)
Caffeic acid ethyl ester	69	astringency	water	staircase	Hufnagel and Hofmann (2008)
Caffeic acid ethyl ester	229	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Coumaric acid ethyl ester	27	astringency	water	staircase	Hufnagel and Hofmann (2008)
Coumaric acid ethyl ester	137	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Ferulic acid ethyl ester	15	astringency	water	staircase	Hufnagel and Hofmann (2008)
Ferulic acid ethyl ester	158	bitterness	water	triangle	Hufnagel and Hofmann (2008)
Caftaric acid	5	astringency	water	staircase	Hufnagel and Hofmann (2008)
Caftaric acid	<50	detection	water	yes/no	Okamura and Watanabe (1981)
Coutaric acid	<25	detection	water	yes/no	Okamura and Watanabe (1981)
Flavonols					
Quercetin	10	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Kaempferol	20	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Myricetin	10	detection	5% ethanol	staircase	Dadic and Belleau (1973)
Quercetin glucoside	1	astringency	water	staircase	Hufnagel and Hofmann (2008)
Quercetin rhamnoside	9	detection	water	staircase	Dadic and Belleau (1973)
Quercetin galactoside	0.2	astringency	water	staircase	Hufnagel and Hofmann (2008)
Other					
Naringin	17	bitter	water		Esaki et al. (1983)
Naringin	20	bitter	water		Guadagni et al. (1973)
Tyrosol	346	bitter	water	ascending limits	Takahashi et al. (1974)

Hydroxycinnamic acids and derivatives



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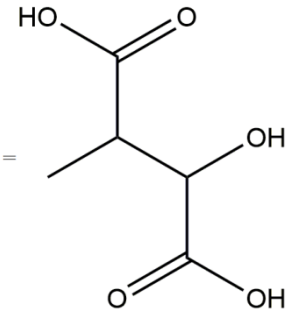
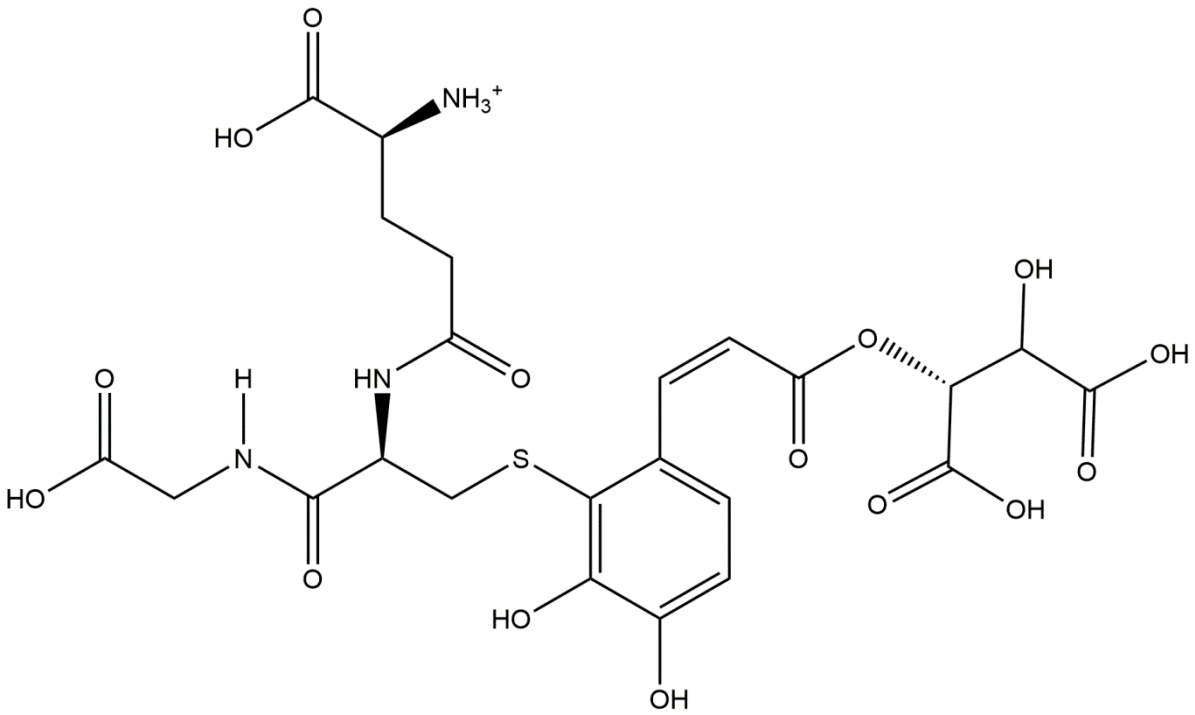


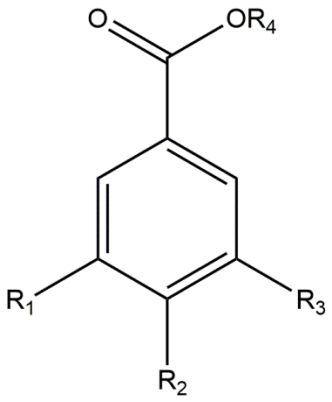
	R1	R2	R3
Caffeic acid	OH	OH	H
p-coumaric acid	OH	H	H
Ferulic acid	OH	OCH3	H
Caftaric acid	OH	OH	Tart
Coutaric acid	OH	H	Tart
Fertaric acid	OH	OCH3	Tart
Caffeic acid ethyl ester	OH	OH	C2CH3

Substitution table for figures 1a-b

2-S-glutathionyl caftaric acid (Grape Reaction Product, GRP)



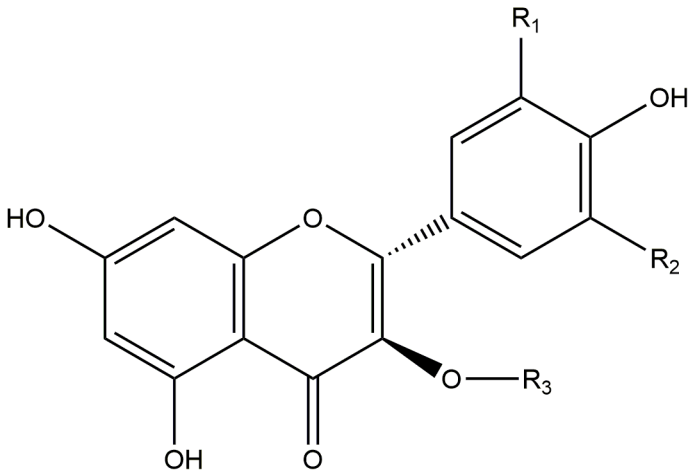
Hydroxybenzoic acids and derivatives



	R1	R2	R3	R4
Gallic acid	OH	OH	OH	H
Protocatechuic acid	H	OH	OH	H
Syringic acid	OCH3	OH	OCH3	H
Gallic acid ethyl ester	OH	OH	OH	CH2CH3

Substitution table for figures 1d

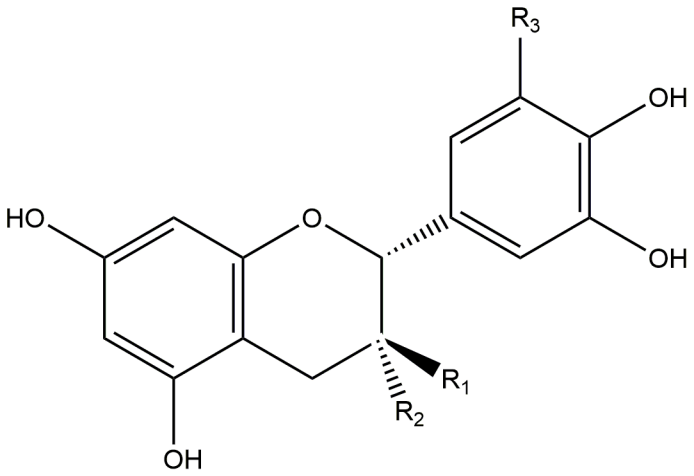
Flavonols and derivatives



				R3 Glycosides			
	R1	R2	R3	Glucuronic acid	Glucose	Galactose	Glucose-O-rhamnose
Quercetin	OH	H	H	*	*		*
Kaempferol	H	H	H		*	*	
Myricetin	OH	OH	H		*		
Isorhamnetin	OCH3	H	H		*		

Substitution table for Figures 1e

Flavanols and derivatives



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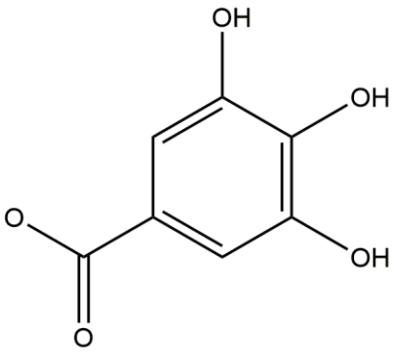
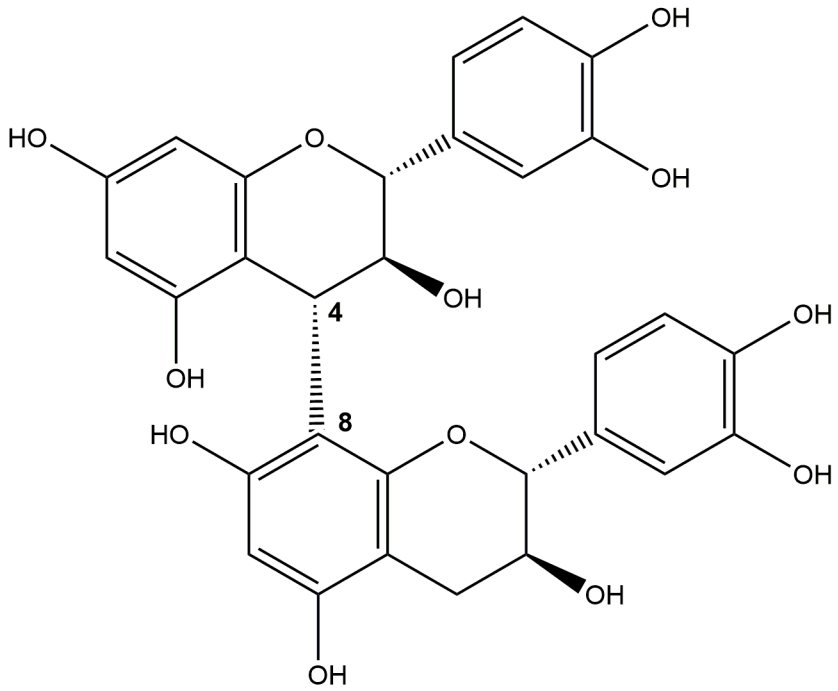


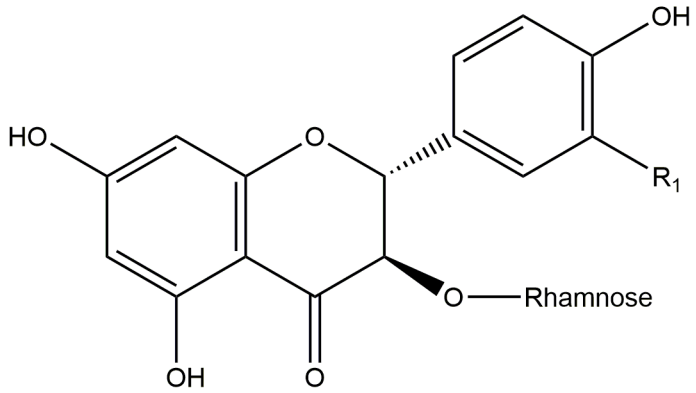
	R1	R2	R3
(+)- catechin	OH	H	H
(-)-epicatechin	H	OH	H
(-)-epicatechin-3-O-gallate	H	Gallate	H
(-)-epigallocatechin	H	OH	OH

Substitution table for Figures 1f-h

Flavanol dimer B3



Flavononols



	R1
Taxifolin 3-O rhamnoside (Astilbin)	OH
Dihydrokaempferol 3-O-rhamnoside (Engeletin)	H

Substitution table for Figures Figure 1i

Flavanones

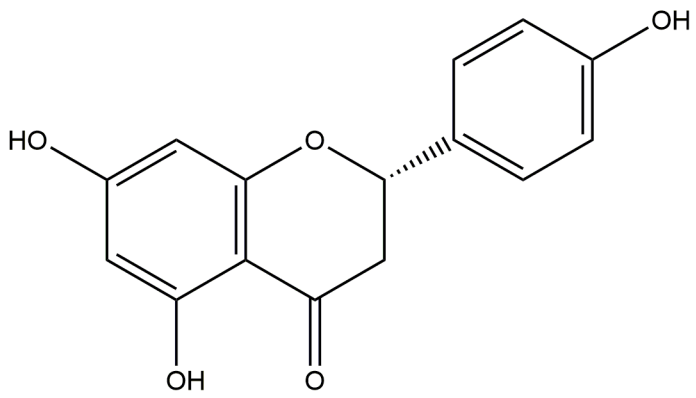


Figure 1: Structures of phenolic compounds reported in white wine