Sift Desk Research Page SDRP Journal of Food Science & Technology 2016
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Review

Is wine savory? Umami taste in wine

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Received date: 30-01-2015; **Accepted date:** 13-02-2016; **Published date:** 10-03-2016

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ABSTRACT
Umami is an important taste element in natural products like wine. The umami taste has distinctive properties that differentiate it from other tastes, including a taste-enhancing synergism between two umami compounds, L-glutamate and 5'-ribonulceotides, and a prolonged aftertaste. In human taste cells, taste buds transduce the chemicals that elicit the umami tastes into membrane depolarization, which triggers release of transmitter to activate gustatory afferent nerve fibers. Umami taste stimuli are primarily received by type II receptor cells which contain the T1R and T2R families of G protein-coupled taste receptors. The taste sensation of umami requires protein hydrolysis which renders free glutamic acid. The main components of the nitrogen fraction of musts and wines are amino acids, peptides, proteins and ammonium ion. Their presence in wine is from amino acids of grapes, enzymatic degradation of grape proteins, excretion by living yeasts at the end of fermentation and to proteolysis during yeast autolysis. Thus, amino acids are important contributors of the wine savory taste and flavor.

KEYWORDS: Grape and wine amino acids, L-glutamate, 5'–ribonucleotides, savory compounds, umami taste perception, sensorial properties.

INTRODUCTION

Our sense of taste has evolved to detect key components in food which are important for healthy development and those which we need to avoid. There are six distinct, basic tastes that are universal and cannot be created by a combination of other tastes (Table 1).

Table 1 – Six basic tastes, taste stimulus and detection levels (%).

BASIC TASTES	INDICATES	TASTE STIMULUS	DETECTION LEVEL (%)
SWEET	Energy source	Sucrose	0.5
SOUR	Organic acids	Tartaric acid; Acetic acid	0.010; 0.012
SALTY	Minerals essential for fluid balance	Sodium chloride (salt)	0.2
BITTER	Harmful/toxins	Quinine	0.00005
UMAMI	Protein, amino acids	Glutamate/Monosodium glutamate	0.03
FAT TASTE*	Energy-dense foods	Non-esterified fatty acids	?

*Keast and Costanzo (2015); Running et al. (2015)

The fifth taste, referred to by the Japanese word umami, evokes savory, full-bodied, and meaty flavor sensations (Baylis and Rolls, 1991). Until the 20thcentury, umami was not thoroughly understood in Western societies; however, it has been unknowingly appreciated for years in stocks, broths, aged cheeses, protein-rich foods, tomato products, dried mushrooms, and kelp, among others.

The official discovery of umami was done by a Chemistry Professor, Dr. Kikunae Ikeda, at the Imperial University of Tokyo, in 1908. Dr. Ikeda proposed umami as a distinct taste recognizable in *dashi* which is Japanese stock flavored with kelp and dried bonito flakes. In research work identified glutamate as an amino acid prevalent in the broth ingredients and contributing of this different taste. The term "umami" was invented from the Japanese adjective for delicious (*umai*). It designates a pleasant taste sensation which is qualitatively different from sweet, salty, sour and bitter (Ikeda, 1909). Although research on umami in foods continued throughout the 20th century, it was not until the discovery made by Chaudhari et al. (2000) of a unique taste receptor, that umami was firmly established as the fifth basic taste. In fact, multidimensional scaling methods in humans have shown that the taste of glutamate - as its sodium salt monosodium glutamate (MSG) - cannot be reduced to any of the other four basic tastes (Yamaguchi and Kimizuka, 1979). Umami is a dominant taste of food containing L-glutamate, like chicken-broth, meat extracts and ageing cheese. The somewhat common amino acid L-glutamate thus guides the intake of peptides and proteins, from which it is released by proteolysis (curing and decay). Characteristic taste-enhancing effects arise from the presence of purine 5`-ribonucleotides such as disodium inosinate (IMP) and disodium guanylate (GMP), which are also present in decaying biological tissues (Lindemann, 2001).

A taste receptor for L-glutamate might possibly be related to one of the glutamate receptors well known from neuronal synapses (Lindemann, 2001). Glutamate mediates fast excitatory synaptic transmission by activating ionotropic receptors in the central nervous system. This neurotransmitter can also activate G protein-coupled receptors (GPCR) wish constitute a vast protein family that encompasses a wide range of functions, including various autocrine, paracrine and endocrine processes. Such as metabotropic glutamate receptors so called mGluRs (mGluR1 – 4) (Anwyl, 1999; Kinnamon, 2009). These receptors display differential expression on pre- and postsynaptic membranes and modulate the fast excitatory glutamatergic neurotransmission (Ramos et al., 2012).

Although brain mGluR4 has a rather large NTD (short amino-terminal domain), the taste variant has a shortened NTD wish seems to adapt the receptor to the high glutamate concentrations occurring in food (Chaudhari et al., 2000). Synergism with ribonucleotides (5`-ribonucleotides), a highlight of umami taste, was established (Delay et al., 2000).

Later, in 2002, Nelson and coworkers identified an amino acid receptor - T1R1 + T1R3. This receptor identified from mice showed synergism between 5'-inosinate and not only glutamate but also many other amino acids. Nevertheless, in human, the synergism is seen between 5'-inosinate and only glutamate. The behavior of this receptor is consistent with psychophysical data in human and then, T1R1 + T1R3 was established to be the human umami receptor (Kurihara, 2015), Figure 1.

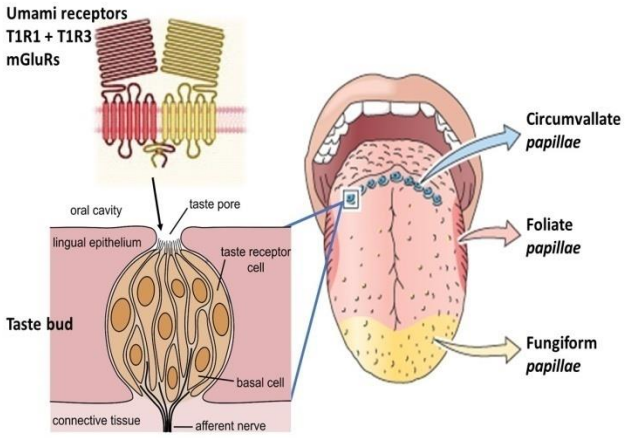

Figure 1 - Humans detect only six main tastes—salty, sour, sweet, bitter, fat (oleogustus – Running et al., 2015) and umami—using taste receptor cells located in structures called taste buds. Taste cells extend fine filaments into the taste pore of each bud, where tastants (chemical substances) come into contact with them. The taste buds are situated on small projections from the surface of the tongue called *papillae*. Umami taste is perceived by specialized receptor molecules belonging to mGluRs (metabotropic glutamate receptors) and the T1R1-T1R3 receptors families, which are coupled to G proteins.

Disodium 5'-ribonucleotides, are flavor enhancers which show synergistic with glutamates in creating the taste of umami. It is a mixture of disodium inosinate (IMP) and disodium guanylate (GMP) and is often used where a food already contains natural glutamates (as in meat extract) or added monosodium glutamate (MSG). Several amino acids and 5'–ribonucleotides, are found in wine in sufficient concentration to play an essential role in forming the taste and flavor profile and intensity of quality wines (Peynaud, 1981). Research shows sufficient levels of naturally occurring umami taste substances in both wine grapes and wine. Glutamic acid, a natural compound found in wine grapes and a precursor to glutamate taste substances, and 5' -ribonucleotides, which are associated with yeast fermentation and the enzymatic decomposition of ribonucleic acid from yeast cells give the wines their umami taste / flavor (Roubelakis - Angelakis, 2001), Figure 2.

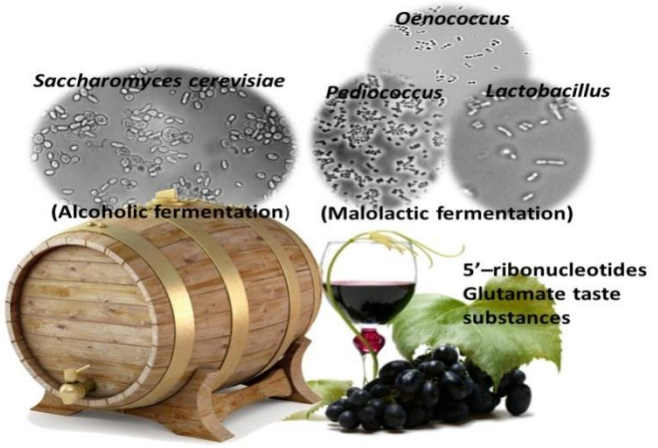

Figure 2 - Glutamic acid, a precursor to glutamate taste substances, and 5' -ribonucleotides associated with yeast fermentation and the enzymatic decomposition of ribonucleic acid from yeast cells are the responsible for naturally occurring umami taste in both wine grapes and wine.

Synergized by 5'-ribonucleotides, lesser amounts of glutamic acid would contribute significantly to the taste and flavor of wine. Alanine, proline, glycine and arginine have been found to contribute to the sweet taste in various foods and are associated with the "sweet" taste of crab and other seafood (Konosu, 2009). These amino acids are found in significant levels in wine grapes and wine. Therefore, understanding the importance of the umami wine taste is essential, in order to implement winemaking practices that will generate higher concentrations of the appropriate precursors.

Umami taste transduction mechanism

Taste buds transduce the chemicals that elicit the sweet, bitter, salty, sour, fat-taste and umami tastes into membrane depolarization, which triggers release of transmitter to activate gustatory afferent nerve fibers. Type II cells, also called 'receptor' cells, contain the T1R and T2R families of G protein-coupled taste receptors for bitter, sweet, and umami taste stimuli (Kinnamon, 2013)(Figure 3). Both T1R (for sweet and umami) and T2R (for bitter) receptors activate similar transduction cascades in different subsets of Type II cells. These involve G protein activation of a signaling complex that elicits release of Ca^{2+} from intracellular stores and subsequent activation of a transduction channel that depolarizes the membrane to cause transmitter release and the activation of gustatory nerve fibers (Chaudhari and Roper, 2010). The taste sensation of umami requires protein hydrolysis which renders free glutamic acid. Although some foods naturally contain free glutamic acid, common food processing techniques such as dehydration, fermentation, aging, and ripening assist in breaking down proteins into smaller peptides and individual amino acids. This results in protein hydrolysis and liberation of free glutamic acid (Krasnow et al., 2012).

The transduction mechanism is complex — one variant involves the sustained closure of an unspecific cation conductance, presumably causing hyperpolarization, even though transient inward currents, which would cause depolarization, were also observed (Bigiani et al., 1997; Lin and Kinnamon, 1999).

The ion channel pannexin 1 is expressed in all Type II taste cells and its expression appears to be restricted to taste buds with little or no expression in surrounding non-gustatory epithelia. When isolated single Type II cells are exposed to bitter and sweet stimuli, biosensor cells respond with a Ca^{2+} signal that is inhibited by low concentrations of carbenoxolone, a pharmacological agent reportedly specific for pannexin-based ATP release channels (Huang et al., 2007). Additionally, Huang and Roper (2010) studies have shown that taste-evoked ATP release is dependent on intracellular Ca^{2+} and the transduction channel TrpM5, and that ATP released from single Type II taste cells (measured by luciferin/luciferase assay) is directly proportional to the number of action potentials evoked by taste stimulation (Murata et al., 2010). Collectively, these data suggest a model in which Type II cells are activated by taste stimuli, causing release of Ca^{2+} from intracellular stores, which activates TrpM5, resulting in depolarization and activation of voltage-gated Na^{+} channels, which trigger opening of the voltage- and Ca^{2+}dependent pannexin 1 ATP-release channel (Figure 3).

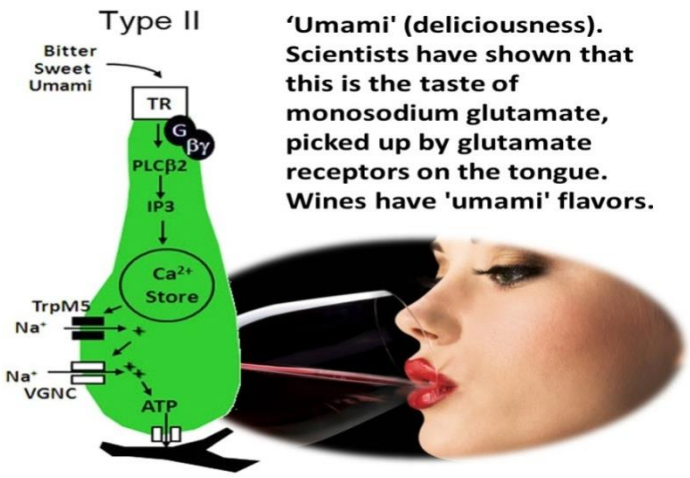

Figure 3 - Type II cells contain the G protein-coupled taste receptors (TR) for bitter, sweet, and umami taste stimuli. Although the receptors are expressed in different subsets of Type II cells, they all couple to the same downstream signaling cascade, which includes Gβγ activation of phospholipase C β2 (PLCβ2), causing release of Ca^{2+} from intracellular stores, Ca^{2+}-dependent activation of transient receptor potential cation subfamily M member 5 (TrpM5), membrane depolarization, and release of

ATP as a transmitter via an ATP-release channel. Adapted from Kinnamon (2009).

Grapes and wine compounds associated with umami taste

Umami taste is associated to nitrogenous compounds, such as amino acids, nucleic acids and peptides. The amount and composition of amino acids is highly influenced by the maturity of the grapes. The major free amino acids found in the most varieties of *Vitis vinifera* grapes are arginine, proline, alanine and glutamic acid. Usually the highest concentrations are found in the final phase of the ripeness of the grapes (Klosse, 2013). Regarding to the distribution of the amino acid in the berry, its predominance is verified in grape skin for *Vitis rotundifolia* grapes (Lamikanra and Kassa, 1999). For the same grape variety, Chardonnay, cultivated in two distinct countries Greece and Spain, high concentrations of the main amino acids were found in Greek wines, thus leading Soufleros et al. (2003) to attribute this difference, possibly to the climatic conditions in the regions/countries. These observations point to the conclusion that wine made from berries that were not fully mature due to climatic conditions or harvesting choices (i.e. harvested before full maturity is reached) have potentially fewer umami capabilities (Klosse, 2013).The amino acids that cause the umami taste, are synthesized by the grape vine and transported to the grape berry, so grape vine genetics combined with the terroir such as soil type and its nitrogen sources, as well as the degree of grape maturation and pre-fermentation operations influenced the umami taste (Moreno-Arribas and Polo, 2009). Amino acids in the grape must are generally present in concentrations ranging from 100 - 4000 mg/L, whereas in wine the total concentration may range from 3 - 3000 mg/L. The concentration of individual amino acids in grapes musts depends mainly on grape variety, viticulture and wine management, and environmental conditions (Feuillat, 1974; Ough and Tabacman, 1979; Etiévant et al., 1988; Jackson et al., 1993; Ribéreau-Gayon et al., 2006). The free amino acids present in wine may be from different sources such as those derived from grapes which are partially or totally metabolized by yeast during fermentation, and amino acids released by living yeast at the end of fermentation to proteolysis using their enzyme degradation of low molecular weight peptides releasing different amino acids to the medium or derived by proteolysis during yeast autolysis (Moreno-Arribas et al., 1998; Soufleros et al., 2003).Wines that undergo malolactic fermentation have a lower concentration of free amino acids, especially arginine, which is preferably metabolized by the lactic acid bacteria. However, the concentration of some amino acids such as leucine, methionine, tryptophan, aspartic acid and glutamic acid can significantly increase after this period (Soufleros et al., 2003). So, the amino acid content in wines varies with yeast strain, temperature, time of storage over yeast (Margheri et al., 1986), as well as by the technology used in wine making (Etiévant et al., 1988).Therefore, since the concentration of nitrogenous compounds is some wines is very low, umami taste in red and white wine is also associated to the nitrogen compounds obtained from the yeast autolyze and the malolactic fermentation.

Nucleotides are important flavoring agents found in wine. These compounds have slight or no flavor or aroma but can improve the flavor of other compounds. *Saccharomyces cerevisiae* are source of nucleic acids for production of nucleotides due to their high nucleic acid content (Nagodawithana, 1992). Therefore, wines matured on yeast lees such as sparkling wines, flavor nucleotides may enhance the wine autolysis character (Courtis et al., 1998).

Winemaking techniques that enhance umami taste

Although the references of umami taste in wine are very scarce, this food product possesses a high potential to develop and reveal this basic taste during the vinification process and ageing (Klosse, 2013).

The glutamic acid, responsible for umami present in wine is derived from the grapes, and its concentration in wine may be influenced by the vinification techniques used, according to the type of wines produced and by the microorganisms involved in alcoholic and malolatic fermentations. Comparing red and white wines, red wines are likely to be richer in glutamic acid, due to the process of vinification that includes, in this type of wines, skin contact allowing a better extraction of the amino acid from the skins, thus enhancing the umami taste. Contrarily to the white wines, wines obtained only from the fermentation of juice separated from skins after the pressing of grapes. Extended maceration of red wines creates a flavor profile consistent with umami taste characteristics, and may explain the softening and reduced bitterness and astringency of red wines made with extended maceration. Late-harvest choices are likely to be beneficial to umami, potentiality in both white and red wines (Klosse, 2013).

For performing alcoholic fermentation yeasts use amino acids as a source of nitrogen, for their growth and transform them into higher alcohols, aldehydes, esters and ketonic acids thus, interfering in aroma/flavor of wines. According to Soufleros et al. (2003) after alcoholic fermentation, the same

amino acids are as abundant in wine as in grapes. As referred previously, arginine, alanine and glutamic acid are reported as being the primary free amino acids in wines and grapes. Due to the unpredictably of spontaneous fermentation, nowadays, most winemakers in the world, perform vinifications using specially selected starter cultures of *Saccharomyces cerevisiae* strains that may impart specific desirable characteristics to wines (Pretorius and Bauer, 2002). But, according to Klosse (2013) no specific references are made to the contribution of yeast in the development of glutamic acid, which led the author to propose adding this target to the already extensive list of the characteristics for starters cultures selection. Although, in a specific technique of vinification, called "batonnage", due to the extended contact with autolyzing yeast cells, such as during *sur lies* maturation or sparkling wine maturation, there is the release of nucleotides from the dead and dying cells. In this way, the enzymatic decomposition of ribonucleic acid from yeast cells during yeasts autolysis promotes the liberation of several nucleotides, giving the wines their umami taste/flavor (Courtis et al., 1998; Roubelakis-Angelakis, 2001).

A few studies have shown an increase in the content of glutamic acid after malolactic fermentation (Manca de Nadra et al., 1997; Fernandez and Manca de Nadra, 2006). These authors have observed a stimulation effect on proteolytic activity of the strains of lactic acid bacteria. Different strains of *Oenococcus oeni* and *Pediococcus pentosaceus*, responsible for malolactic fermentation, when grown together, promote an increase, in wine, of glutamic acid and other amino acids (Manca de Nadra et al., 1997; Fernandez and Manca de Nadra, 2006).

Special types of wines such as Madeira, Sherry and Port Wines, are characterized by much higher amino acid values than dry wines. This is due to the maturation of these wines for several years that concentrate the amino acids and thus may enhance umami taste/flavor (Klosse, 2013).

FINAL REMARKS

Several amino acids are found in significant levels in wine grapes and wine. Consequently, understanding the importance of the umami wine taste is vital to winemakers, in order to implement viticulture and winemaking practices that will led to higher concentrations of the appropriate precursors. These practices, when properly applied, will heighten the wine savory taste.

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