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1 **Light-struck taste in white wine: reaction mechanisms, preventive strategies and**
2 **future perspectives to preserve wine quality**

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11 **Abstract**

12 *Background*

13 The light-dependent reactions involving riboflavin (RF) and methionine (Met) as substrates
14 are responsible for the light-struck taste (LST). This fault is associated to cabbage-like
15 odors due to the formation of methanethiol and dimethyl disulfide impacting negatively on
16 the sensory properties of white wine. The reaction can occur for a relatively short period of
17 white wine bottled in clear glass under both natural and artificial lights.

18 *Scope and Approach*

19 This review aimed to point out the aspects related to the mechanisms of light-dependent
20 reactions and the oenological strategies applicable to counteract the appearance of this
21 detrimental fault.

22 *Key Findings and Conclusions*

23 LST can be prevented through the proper choice of the fermenting yeast, the addition of
24 certain adjuvants being able to remove RF, and additives with a protective effect, such as
25 hydrolysable tannins. As the use of these oenological tools plays an important role in
26 limiting the detrimental change, they represent the strategies applicable in productive
27 approaches. In this context, the more recent findings are summarized also to update the
28 knowledge about the complex reaction mechanisms allowing to overcome the formation of
29 this fault and supporting the wine industry.

30 **Keywords:** light exposure; riboflavin; methionine; sulfur compounds; off-flavors; storage.

31

32 1. Introduction

33 The quality maintenance of wine during its storage is a fundamental aspect for both wine
34 producers and consumers. This purpose can be achieved controlling certain environmental
35 factors, such as light exposure and temperature, which increase can be responsible for
36 faster oxidative reactions and quicker aroma decay. Nowadays, more attention has been
37 given to the light exposure that can cause detrimental changes in wine where the light-
38 induced off-flavours are associated to the light-struck taste (LST) or “*Goût de Lumière*”
39 (Dozon & Noble, 1989). This fault is mainly due to photochemical oxidation processes in
40 which riboflavin (RF), a highly photosensitive vitamin, plays an important role. The
41 photosensitisation process of RF proceeds with photo-oxidative degradation of methionine
42 (Met) generating methanethiol (MeSH) and dimethyl disulphide (DMDS) (Maujean &
43 Seguin, 1983a). Both volatile sulfur compounds (VOCs) give unpleasant cabbage and
44 onion-like odours that make wine undrinkable.

45 The prevention of LST appearance is crucial for the winemakers as the wine quality needs
46 to be ensured and maintained. In order to understand the impact of LST, a national survey
47 was carried out (<https://www.surveio.com/survey/d/K6Y3T0W6C5S5Z1G2J>) and 231
48 responses from Italian wineries were collected. The results showed that LST occurred
49 1011 times which makes 4.4 incidents per winery, and the wine was recalled from the
50 market in 15 wineries (6.5%), with consequent loss of income. Many producers utilized flint
51 bottles for their white and rosé wines (even 80% of the total production). Moreover, we
52 asked the technological procedures and treatments the winemakers usually apply to
53 prevent LST. Most of the winemakers (50%) use bentonite as a prevention tool; other
54 treatments include the addition of polyvinylpyrrolidone (PVPP) which is ineffective in
55 RF removal as a recent research showed (Fracassetti et al., 2017).

56 Beside white wine, the light exposure also affects the sensory characteristics of other
57 foods, such as milk (Patton, 1954) and beer. Particularly in the latter, the formation of 3-
58 methyl-2-butene-1-thiol induces a unique “skunky” odour and taste (Cardoso et al., 2012).
59 Riboflavin is the photosensitizer that causes the photolysis of iso- α -acids leading to the
60 beer spoilage in the presence of sulfur-containing amino acids (Gunst & Verzele, 1978;
61 Cardoso et al., 2012).

62 In order to clarify and point out LST-related aspects, this review focuses on (i) the reaction
63 mechanisms responsible for the defect formation, (ii) the light-induced faults in wine and
64 (iii) the other light-dependant effects. The (iv) oenological strategies are also examined
65 considering both microbiological and technological approaches.

66

67 **2. Reaction mechanisms involved in light-dependent changes**

68 LST is a wine fault recognizable as a distinctive, unpleasant sulfide-like aroma resembling
69 onion and cooked cabbage; it appears after light exposure with emission spectra within
70 UV-Vis, particularly between 370 and 450 nm. The photodegradative reactions may occur
71 within minutes or days. This spoilage concerns white wines, both still and sparkling,
72 usually bottled in flint glass which is ineffective in shielding the harmful wavelengths. Since
73 1970, the new marketing approaches have led to an increased use of clear bottles to show
74 the wine colour to the customers, because it is considered as an important feature of wine
75 quality (i.e., its oxidative status). Moreover, wine has begun to be increasingly available at
76 the large-scale retail trade or grocery stores where the protection against the light
77 exposure could hardly be ensured (Dozon & Noble, 1989).

78 RF, or vitamin B₂, is characterized by a bright, yellow colour and it is sensitive to UV-Vis
79 light radiation. Chemically it is composed of tricyclic heterocycle isoalloxazine, involved in
80 redox reactions, and ribitol, an alcohol responsible for protein binding. RF is a constituent

81 of prosthetic groups, flavin mononucleotide (FMN) and flavin adenine dinucleotide (FAD),
82 which play essential roles in oxidoreductase enzymes like dehydrogenases, oxidases, or
83 electron transferase (Choe et al., 2005). They take part in redox reactions due to their
84 ability to transfer single electrons and hydrogen atoms.

85 RF shows the highest light absorption at 225, 275, 370 and 450 nm at pH 7 (Drössler et
86 al., 2003; Abbas & Sibirny, 2011). Once RF is exposed to blue or UV-A light, it acts as a
87 photosensitizer. A photosensitizer is a species that reaches a high energy state when
88 exposed to light at specific wavelengths inducing chemical reactions or physical changes
89 in a target substrate. Specifically, when RF is exposed to light, it reaches the excited triplet
90 state, a bi-radical with powerful oxidant effect ($E^0 \sim +1,7 \text{ V}$) inducing the direct oxidation of
91 many biomolecules (Cardoso et al., 2012). Photo-oxidation can occur in two possible
92 pathways. In Type I mechanism, the triplet sensitizer reacts directly with compounds able
93 to donate electrons, such as phenols and amino acids (Figure 1). In this pathway, RF acts
94 as electron or hydrogen acceptor, leading to produce either free radicals or free radical
95 ions. The reaction between triplet RF and a substrate can occur through three different
96 mechanisms: electron transfer (ET), hydrogen atom transfer (HAT) and proton-coupled
97 electron transfer (PCET) (Cardoso et al., 2012). The proceeding of reaction depends on
98 the thermodynamic properties of both excited triplet RF and substrates. For ET, one-
99 electron oxidation potential below 1.8 V for the reducing substrate is the limiting
100 thermodynamic property, whereas for HAT mechanism, bond dissociation energy is the
101 limiting factor, which should be of less than 300 kJ. PCET is an intermediate mechanism
102 depending on both electron oxidation potential and dissociation energy. The formation of
103 free radicals initiates free-radical chain reactions by attracting hydrogen or electrons from
104 other compounds. As a consequence, oxygen may be reduced to peroxy radical which
105 generates hydrogen peroxide and therefore hydroxyl radical (Min & Boff, 2002; Cardoso et
106 al., 2012) triggering the possible further oxidation processes in wine. In direct reaction

107 between excited triplet RF and various substrates, reduced RF radical or anionic RF
108 radical are formed (Figure 1). These RF radicals can be oxidized by oxygen, regenerating
109 ground state RF, and forming superoxide anion radical. The latter may then form hydrogen
110 peroxide, a strong oxidising species, by dismutation that causes depletion of antioxidants
111 present in wine, including sulfur dioxide and polyphenols. Furthermore, the reaction
112 between hydrogen peroxide and superoxide anion (Haber-Weiss reaction) may occur,
113 leading to hydroxyl radical formation (Choe et al., 2005). Moreover, hydrogen peroxide
114 may undergo Fenton reaction catalysed by iron (II) ions, leading to hydroxyl radical
115 formation as well. Hydroxyl radical with a reduction potential of + 2.3 V is one of the
116 strongest oxidizing species, that may induce the oxidation of wine and the appearance of
117 sensory fault. It has been demonstrated that in Type I pathway the excited triplet RF may
118 also react directly with triplet oxygen, transferring an electron to form superoxide anion.
119 However, only less than 1% of the reaction of triplet sensitizer and triplet oxygen produces
120 superoxide anion (Kepka & Grosswiener, 1972). Such reaction causes the conversion of
121 triplet oxygen to singlet oxygen ($^1\text{O}_2$) and ground state RF (Type II pathway) (Figure 1).
122 Singlet oxygen directly and rapidly gives rise to non-radical reactions with electron rich
123 compounds (e.g., with double bonds) that result oxidised (Min & Boff, 2002).
124 Singlet oxygen can find different substrates in wine, such as amino acids or phenolic
125 compounds (Thomas & Foote, 1978; DeRosa & Crutchley, 2002). Regarding amino acids,
126 singlet oxygen primarily reacts with tryptophan, histidine, tyrosine, Met and cysteine at
127 significant rates, forming peroxides (Min & Boff, 2002; Huvaere & Skibsted, 2015).
128 Tryptophan, histidine and tyrosine contain double bonds in their structure, which make
129 them promptly attacked by singlet oxygen. Methionine and cysteine contain a sulfur atom
130 with four nonbonding electrons which are rapidly attracted by electrophilic singlet oxygen.
131 Remucal and McNeill (2011) demonstrated that in aqueous solution at pH 7.4 tyrosine,
132 tryptophan, Met and histidine react with singlet oxygen at similar rates, but the amount of

133 amino acid degradation which can be attributed to single oxygen reaction varies from 10%
134 for tyrosine and tryptophan up to 100% for histidine. In the presence of RF, singlet oxygen
135 is responsible for about 33% of Met degradation (Remucal & McNeill, 2011). One of known
136 compounds arising from the reaction between Met and singlet oxygen is methionine
137 sulfoxide (Fracassetti et al., 2020), a stable compound which does not undergo further
138 oxidation or degradation processes (Barata-Vallejo et al., 2010).

139 Singlet oxygen can react with certain di-phenols (e.g., catechol) firstly generating
140 hydroquinones as well as benzoquinones as secondary oxidation product (Briviba et al.,
141 1993).

142 Flavonoids present in wine can interact with singlet oxygen through both chemical and
143 physical processes. The latter pathway prevails with increasing abundance of phenolic
144 functions as well as, with the presence of catechol and pyrogallol rings (Huvaere &
145 Skibsted, 2015). Chemical quenching leads to the transfer of energy from a molecule in
146 high-energy state to another molecule, the latter can be oxidized or its spin is modified.
147 When chemical quenching occurs, the generated quinones can trigger oxidation chain
148 reactions. Consequently, quinones can bind to other phenols producing brown dimers or
149 polymers which may precipitate when high molecular weight is reached (Ribéreau-Gayon
150 et al., 2006). Furthermore, xanthylum derivatives can be produced thus inducing the
151 browning of white wine (Li et al., 2008).

152 The occurrence of the two photo-oxidative mechanisms depends on the concentration of
153 oxygen in the reaction environment. In anoxic conditions only Type I occurs, whereas in
154 the presence of oxygen, both mechanisms may take place to a different extent (Min & Boff,
155 2002; Grant-Preece et al., 2017b). Compounds that are easily oxidised, like certain
156 phenolics or amino acids, promote Type I pathway, while species not prone to oxidising
157 like alkenes, favour Type II. In any case, the factor mainly influencing the reaction
158 mechanism is the presence or absence of oxygen, as some compounds degraded via

159 Type I at low oxygen concentrations may be degraded via Type II when the oxygen
160 concentration increases (Min & Boff, 2002).

161

162 **3. The light-induced faults in wine**

163 RF and Met are the two factors mainly affecting LST formation. RF concentration in grape
164 and must seldom exceeds a few tens micrograms per liter (Riberau-Gayon et al., 2006),
165 but its content can rise to 110-250 µg/L during alcoholic fermentation (Mattivi et al., 2000;
166 Fracassetti et al., 2017), due to the activity of *Saccharomyces cerevisiae*. RF amount can
167 be further increased to 160-318 µg/L when wine remains in contact with yeast lees once
168 the alcoholic fermentation is completed (Andrés-Lacueva et al., 1998). A concentration of
169 RF lower than 50-80 µg/L greatly decreases the risk of developing the LST (Pichler, 1996;
170 Mattivi et al., 2000; Fracassetti et al., 2019a). Therefore, the measurement of RF
171 concentration in finished wine may be a suitable chemical marker for the susceptibility of
172 wine to develop LST (Andrés-Lacueva et al., 1998; Mattivi et al., 2000). In the study
173 carried out by Mattivi et al. (2000), sensory evaluation of 85 white wines from Italy,
174 Slovenia and Spain was performed. Each wine was prepared in double, with and without
175 the addition of RF (1 mg/L), then both samples were exposed to light for 48 h. After that,
176 trained panelists rated the intensity of the off-flavour aroma. Results showed that the
177 intensity of the defect was significantly higher in the samples with the RF added,
178 confirming that RF is a crucial factor for the appearance of this off-flavour. RF
179 concentration in wine and sensory values of the LST were positively correlated, but the low
180 correlation coefficient ($r = 0.3544$) indicated that RF concentration did not allow to predict
181 the intensity of the off-flavour formed. Noteworthy, there were also some samples with a
182 high concentration of RF which did not develop the off-flavour, as well as some wines that
183 did get spoiled despite their low concentration of RF. These results evidenced that there

184 are some other wine features that can affect the stability to light and that the occurrence of
185 LST is due to complex mechanisms that cannot be fully explained only considering the
186 presence of RF. In fact, other factors can affect the light stability of wine including the
187 transition metals, as they are involved in redox reactions, polyphenols, precursors of the
188 off-flavour, sulfur-containing amino acids, sulfur dioxide (Mattivi et al., 2000). The latter
189 plays an important role on the rate of light-induced radical reaction chains (Fracassetti et
190 al., 2020).

191 LST in wine was first described by Maujean et al. (1978), who focused their study on the
192 effect of light on Champagne. They found that the molecules responsible for the fault
193 formation were sulfur-containing amino acids, as Met and cysteine, and RF as a
194 photosensitizer. According to these authors, the addition of RF, Met and cysteine to
195 Champagne, increased the off-flavour formation after exposure to light in anoxic
196 conditions. The proposed mechanism of the light-dependent reaction concerns the
197 formation of triplet state RF (Maujean & Seguin, 1983a). This species is characterized by
198 having high energy, unstable electronic distribution, weaker bonds and high capacity to
199 accept electrons making triplet state RF more reactive compared to its equivalent ground
200 state (Wardle, 2009). Met is among the wine components able to donate electrons. Met is
201 firstly decarboxylated and it loses a hydrogen atom generating an imine. In this way, RF is
202 fully reduced by acquiring two electron-equivalents and two hydrogen atoms (Figure 2).
203 The imine is not stable and easily hydrolyses to methional. The latter is also chemically
204 unstable, photosensitive and, through a retro Michael reaction, decomposes to MeSH and
205 acrolein. Two molecules of MeSH can yield dimethyl disulfide (DMDS) (Maujean & Seguin,
206 1983a). Both these sulfur compounds are highly volatile and have a low perception
207 threshold, as 0,3 µg/L in model solution and 2-10 µg/L in wine for MeSH and 20-45 µg/L in
208 wine for DMDS (Mestres et al., 2000; Pripis-Nicolau et al., 2004; Fracassetti & Vigentini,
209 2018). MeSH is characterized by rotten egg or cabbage-like olfactory notes, whereas

210 DMDS gives cooked cabbage and onion-like odour. These two molecules are responsible
211 for the LST.

212 Met concentration also affects LST formation. Fracassetti et al. (2019a) found that in
213 model wine solution with a constant concentration of Met (3 mg/L) and increasing
214 concentration of RF (0-300 µg/L), the amount of degraded Met rose in parallel after light
215 exposure. On the other hand, when RF concentration was constant (200 µg/L) and Met
216 concentration increased (0–13 mg/L), Met degraded to a much greater extent. The
217 average content of Met in wine is about 3-5 mg/L (Amerine & Ough, 1980; Riberau-Gayon
218 et al., 2006; Grant-Preece et al., 2017; Sartor et al., 2021), nonetheless it can vary
219 depending on different factors such as grape cultivar, vineyard treatments, winemaking
220 conditions, yeast performing the alcoholic fermentation and its autolysis, and it can reach
221 about 15 mg/L (Soufleros et al., 2003; Fiechter & Mayer, 2011). The molar ratio of
222 degraded Met/degraded RF ranged between 2 and 35, which disagrees with the 1:1 ratio
223 previously thought to occur between these two substrates (Maujean & Seguin, 1983b).
224 This could be explained by the formation of other products originating from Met in photo-
225 degradative reactions (Barata-Vallejo et al., 2010). Additionally, the concentrations of
226 DMDS and dimethyl trisulfide (DMTS), product of the reaction between MeSH and DMDS,
227 were about ten times higher in the samples where Met concentration increased, compared
228 to samples where RF concentration increased. These results are in agreement with the
229 sensory evaluation performed by the expert panelists who perceived cooked cabbage
230 odour with higher intensity in the set of samples with increasing Met concentration. This
231 study clearly shows that LST formation in terms of concentration of VOCs and perception
232 of this defect, linearly increased as Met concentration grew indicating that this amino acid
233 can be more detrimental than RF. Therefore, besides RF, the level of Met in white wine
234 needs to be considered for preventing LST.

235 The mechanism of LST formation is very complex and certain aspects of the reactions
236 occurring in wine matrix need further clarification. Recently, a new possible pathway of
237 MeSH formation was described by using the proton-transfer-reaction mass spectrometry
238 (PTR-MS) technique (Asaduzzaman et al., 2020). In the experimental conditions adopted
239 (Met 75 mg/L, RF 1.7 mg/L pH 8.0, light exposure at wavelengths 405-640 nm with
240 maximum at 430, 550 and 640 nm for six hours), MeSH was the first compound appearing
241 just after only 2.3 min under light, and it rapidly increased. DMDS was found, after 3.5 min
242 of light exposure. These results confirm that two molecules of MeSH yield to DMDS. The
243 third detected compound was methional (at 5.30 min) that is surprising and disagrees to
244 the light-dependent mechanism previously proposed by Maujean and Seguin (1983a).
245 Other coproducts of MeSH formation *via* methional, such as formic acid and 2-propenal,
246 occurred only after 29 and 22.5 min of light exposure, respectively. A further proof that
247 MeSH can be directly formed from Met under light exposure conditions was obtained when
248 an aldehyde group blocker (sodium cyanoborohydride) was added prior to light exposure.
249 In this case MeSH increased rapidly, similarly to the previous conditions without aldehyde
250 blocker (Asaduzzaman et al., 2020). According to Asaduzzaman et al. (2020), during the
251 early steps of photo-oxidation, MeSH can be generated by an alternative and fast pathway
252 that does not include methional and involves a direct cleavage of Met side chain.
253 However, no data related the occurrence of sulfur compounds in model wine or wine was
254 reported which acidic pH can influence RF behaviour under light (Sheraz et al., 2014).
255 Besides Met, Maujean and Seguin (1983a) investigated also another sulfur amino acid,
256 cysteine, which may also take part in the off-flavour development. Hydrogen sulfide may
257 also have a role in unpleasant odour perception (Haye et al., 1977; Maujean et al., 1978;
258 Maujean & Seguin 1983a).

259 As previously stated, the photodegradation reactions of RF can occur in two possible
260 pathways depending mainly on the oxygen concentration. In bottled wine, the

261 concentration of oxygen ranges between 1 mg/L and 9 mg/L (Ugliano et al., 2013). The
262 oxygen-free environment is rapidly obtained in bottled wines especially if the bottling is
263 carried out using inert gases and the wine is added with SO₂. That is why in wine Type I
264 mechanism is favoured, where excited triplet RF reacts with electron rich compounds like
265 Met, leading to unpleasant sulfur compounds formation. Besides Met, RF can also react
266 with other electron-rich amino acids like tyrosine, tryptophan, histidine or cysteine (Choe et
267 al., 2005; Huvaere & Skibsted, 2015). RF quenching leads to the formation of substrate
268 radicals, which fate in wine is not fully understood yet (Cardoso et al., 2012).
269 Among wine components phenolic compounds are also efficient quenchers of triplet RF
270 (Huvaere & Skibsted, 2015). The reaction between phenols and flavins is a chemical type
271 of quenching, resulting in oxidative degradation of phenols (Cardoso et al., 2012). In
272 particular, flavonoids with a catechol-like B ring have high quenching rates, probably due
273 to the stabilisation of *o*-hydroxy phenoxyl radical anion. Deactivation of excited triplet RF
274 by flavonoids results in their consumption with generation of dimeric compounds and other
275 oxidised species. These may affect the colour and antioxidant capacity of wines.

276

277 **3.1 Other consequences of light exposure of wine**

278 After light exposure modifications of wines composition other than the sulfur compounds-
279 related off-flavours can occur. Dozon and Noble (1989) conducted a sensory analysis of
280 still and sparkling white wines, exposed to 40-watt fluorescent light bulbs with spectrum
281 similar to that of sunlight. The results of descriptive analysis of wines kept under light for
282 24 and 72 hours showed that after longer light exposure, not only the perception of cooked
283 cabbage and wet dog odours increased, but also citrus and honey aroma perception was
284 significantly lower. This could be due to either the masking effect of LST appearance or
285 the chemical changes in the composition of other aroma, such as esters or terpenes,

286 undergoing to degradation or hydrolysis (Benítez et al., 2003; D'Auria et al., 2009). Indeed,
287 the exposure to UV light of Champagne for 24 hours completely changed the esters
288 profile. The content of certain esters decreased, like ethyl acetate, ethyl butanoate, 3-
289 methyl-1-butanol acetate, ethyl hexanoate, or disappeared like ethyl decanoate. In order to
290 clarify the possible influence of RF on depletion of these molecules, ethyl hexanoate (14
291 mg) was irradiated in the presence of RF (2 mg) for one hour. At the end of illumination,
292 the concentration of the ester was measured, and it showed a decrease up to 9%. This
293 observation proved that the photo-oxidation of RF can induce changes in concentrations of
294 other aromas, including esters (D'Auria et al., 2003). Since the sensory analysis was not
295 carried out, we cannot state if such a difference had a relevant impact on the overall
296 flavour perception.

297 Light exposure can also induce the formation of other undesirable aroma compounds such
298 as acetaldehyde, which is considered one of the main markers of oxidative reactions
299 (Danilewicz, 2003; Han et al., 2019). Dias and co-authors (2013) found that the dominating
300 descriptor identified in Chardonnay wine stored under light for 18 days was acetaldehyde
301 which increase was significant after 10 days of exposure. This compound was also present
302 in model wine samples left outdoor during Australian summer. On the contrary,
303 acetaldehyde was not detected in the samples kept in the dark neither at room
304 temperature nor at 45°C (Clark et al., 2007). The light exposure was crucial for the
305 formation of acetaldehyde and it had a greater affect than temperature. Similarly, in
306 different Spanish white wines saturated with oxygen and left one week in the dark, there
307 was not a significant change in acetaldehyde concentration (Escudero et al., 2002). These
308 results highlight the light exposure is required for the formation of acetaldehyde at least in
309 terms of triggering the oxidation processes in short periods of time. As the light exposure
310 promotes also the formation of radicals, other wine compounds, e.g. tartaric acid, amino
311 acids other than Met, phenolics, can be also oxidized.

312 Tartaric acid (TA) is among the most abundant compounds of wine (Clark et al., 2007;
313 Riberau-Gayon et al., 2006). Its oxidation leads first to the formation of dihydroxyfumaric
314 acid. By its further oxidation and decarboxylation, glyoxal and glyoxylic acid (GA) are
315 formed (Clark, 2008). Both these molecules can bind two flavanol units such as (+)-
316 catechin or (-)-epicatechin, forming a dimer with the units bound through a carboxymethine
317 bridge. Afterwards, the dimer undergoes a dehydration and an oxidation leading to a
318 formation of yellow pigments, known as xanthylum ions (Li et al., 2008). These
319 compounds contribute to the oxidative browning spoilage of wine. The oxidative
320 degradation of TA is favoured in the presence of iron ions. Iron (III) forms complexes with
321 α -hydroxy carboxylic acids, such as TA, which are relatively stable when stored in
322 darkness, but are photodegraded once exposed to light (Grant-Preece et al., 2017a;
323 Grant-Preece et al., 2017b). The mechanism of photochemical degradation of α -hydroxy
324 acids includes their oxidative decarboxylation in the presence of iron (III) acting as
325 catalyzer of oxidation (Balzani & Carassiti, 1970). According to this pathway, TA degrades
326 to 2-hydroxy-3-oxo-propanoic acid and its possible tautomers, 2,3-dihydroxypropenoic acid
327 and hydroxypyruvic acid. These compounds can react with hydrogen peroxide present in
328 the solution due to Fenton reaction, leading to GA formation among other degradation
329 compounds (Figure 3). Moreover, in the irradiated TA solution, the dissolved oxygen
330 consumption accelerates (Grant-Preece et al., 2017a). This is because transition metal
331 ions in their reduced forms can reduce oxygen to radical species. The superoxide radical
332 anion in acidic condition forms hydroperoxyl radical, which in turn yields hydrogen
333 peroxide. The latter can be further reduced by iron (II) generating hydroxyl radical that is a
334 very powerful oxidant and even at low concentrations can readily oxidise TA. In this
335 pathway, known as Fenton reaction, TA forms a radical which is then oxidised by
336 molecular oxygen or iron (III) to dihydroxymaleic acid which is in equilibrium with its
337 tautomers, hydroxyoxaloacetic acid and dihydroxyfumaric acid (Clark & Scollary, 2003).

338 These compounds can be further oxidised and decarboxylated to glyoxylic and other
339 acids. The light exposure may increase the browning potential of white wines. The
340 oxidation of TA probably proceeds through both photodegradation of iron (III) tartrate and
341 Fenton reaction. GA formation requires the light exposure as well as the presence of
342 oxygen and iron which plays a major role as initiator of both photodegradation and Fenton
343 reaction (Clark et al., 2007). As for LST, the protection of wine against the light can
344 prevent the oxidation of TA and the consequent browning of wine. Nonetheless, a lower
345 content of iron, being the catalyser of Fenton reaction, can also limit the TA-related
346 oxidative pathways. Iron can derive from grape and it can be introduced in wine through
347 the adsorption from winemaking equipment as well as the treatment with fining agents,
348 such as bentonite (Hopfer et al., 2015; Bekker et al., 2019). It is among the metal ions that
349 may change during winemaking as a consequence of processes (e.g., filtering, pH
350 adjustments, yeast hull addition and bentonite fining) (Castineira Gomez et al., 2004;
351 Nicolini et al., 2004). Some operations in winemaking process including the treatment with
352 polyvinylpyrrolidone or chelating resin (Loubser & Sanderson, 1985), ion exchange
353 technique (Benítez et al., 2002) as well as the use of bentonite, the proper filtration system
354 and the yeast lees (Bekker et al., 2019) can allow to keep lower the concentration of iron
355 and slow down the oxidative rate of Fenton reaction.

356 357 **4. Oenological strategies preventing the light-struck taste**

358 **4.1 Microbiological approaches: lowering riboflavin and methionine levels**

359 Microbiological strategies suitable for limiting the concentration of compounds involved in
360 LTS defect are not available, yet. Fracassetti and collaborators (2017) observed that some
361 commercial strains of *S. cerevisiae* released different amount of RF in wine, revealing that
362 is probably a strain-dependent character. This evidence paves the way for the

363 development of new approaches that exploit the natural biodiversity of the strains in terms
364 of RF and Met production. To this purpose, a better understanding of RF and Met
365 pathways under oenological conditions is advised. This section illustrates the metabolism
366 of LTS-associated molecules in *S. cerevisiae* with particular attention to the involved
367 genes and enzymatic reactions. Besides *S. cerevisiae*, non-*Saccharomyces* yeasts are
368 gaining interest due to their positive impact on aromatic profiles of certain wines. For this
369 reason, sequential inoculum or co-inoculum schemes can be carried out. A focus on non-
370 *Saccharomyces* yeasts is presented as well as the possible role of lactic acid bacteria on
371 RF and Met production and release.

372

373 4.1.1 Riboflavin

374 RF is one of the essential vitamins for the growth of animals, being involved as a
375 coenzyme in a great variety of metabolic reactions. In particular, FAD and FMN, the two
376 RF active forms, act as cofactors for oxidoreductases and as prosthetic groups for
377 enzymes in the β -oxidation pathway (Massey, 2000). Since mammals have lost the ability
378 to produce RF, it assumed a great commercial value; thus, lower organisms such as
379 yeasts have been exploited in the industrial processes to produce this vitamin (Garcia-
380 Ramírez et al., 1995). Some microorganisms and all animal cells are capable of uptake
381 riboflavin, while riboflavin overproducers have distinct systems for riboflavin excretion
382 (Abbas et al., 2011). Partly for this reason, yeast metabolism determines a significant
383 contribution to RF concentration in wine and to study if the RF production is dependent on
384 the used yeast strain become relevant in the LST occurrence (Fracassetti et al., 2017). RF
385 biosynthetic pathway has been widely studied in *S. cerevisiae* both for academic and
386 biotechnological interests. RF precursors are GTP and ribulose 5-phosphate and in the
387 first step of the pathway, GTP is converted by GTP cyclohydrolase II, (Rib1) to 2,5-

388 diamino-6-(ribosylamino)-4-(3H)-pyrimidinone 5'-phosphate (DRAP); then, it is reduced by
389 Rib7p to 2,5-diamino-6-(ribitylamino)-4-(3H)-pyrimidinone 5'-phosphate (Gudipati et al.
390 2014). Afterwards, a deamination occurs to obtain the 5-amino-6-ribitylamino-2,4-(1H,3H)-
391 pyrimidinedione-5'-phosphate catalysed by Rib2p (Urban et al., 2003). The two following
392 steps consist of a dephosphorylation through an unidentified phosphatase and of a
393 condensation with ribulose 5-phosphate, obtaining the 3,4-dihydroxy-2-butanone-4-
394 phosphate (DHAB) by the DHBP synthase (RIB3). The latter step is catalysed by lumazine
395 synthase (RIB4) and provides the formation of the 6,7-dimethyl-8-(1-D-ribityl) lumazine (Jin
396 et al., 2003; García-Ramírez et al., 1995). Finally, the last reaction uses two molecules of
397 6,7-dimethyl-8-(1-D-ribityl)-lumazine and the riboflavin synthase (RIB5) catalyses the
398 generation of one molecule of riboflavin (Santos et al. 1995) (Figure 4). Hence, starting
399 from RF, FMN and FAD are synthesized by riboflavin kinase (Fmn1p) and FAD synthetase
400 (Fad1p), respectively (Santos et al. 2000; Wu et al. 1995). The characterization of the *S.*
401 *cerevisiae* biosynthetic pathway was carried out studying the deletion mutants for all the
402 interesting genes: *RIB1*, *RIB2* and *RIB7* (Oltmanns et al., 1972), *RIB3* (Bacher et al.,
403 1977), *RIB4* (Garcia-Ramirez et al., 1995) and *RIB5* (Santos et al., 1995). All the obtained
404 mutants revealed an auxotrophic behaviour for RF, suggesting that *S. cerevisiae* strains
405 could be genetically modified to get strains not RF producers. Since it is not currently
406 acceptable to propose genetically modified organisms (GMOs) in oenology, these mutants
407 could be used to obtain yeast extracts suitable as nutrients during the winemaking process
408 or as an additive to prevent the anti-fermentative activity of medium-chain fatty acids, as
409 described in Ribéreau-Gayon et al. (2006). In 2017, Fracassetti and collaborators
410 evaluated the impact of several conventional oenological nutrients derived from yeast,
411 usually containing vitamins, on RF concentration during vinification. Results revealed a
412 higher RF level in wine samples added with the nutrients (76 and 72 µg/L, for yeast extract
413 and yeast lysate, respectively) in comparison to the unfortified ones (55 µg/L); in particular,

414 RF increase of 21 µg/L detected in the presence of yeast extract can be ascribed to the
415 RF found in the tested additive (70 µg/g) (Fracassetti et al., 2017).

416 Spontaneous fermentations are characterized by a succession of several non-
417 *Saccharomyces* yeasts resulting from their natural presence on grapes as well as
418 promoted by oenological practices, technology and cellar hygiene (Jolly et al., 2014).
419 Despite these findings, non-*Saccharomyces* yeasts usually disappear during the early
420 stages of fermentation (Fleet et al., 1984; Henick-Kling et al., 1998) because of their slow
421 growth and inhibition due to SO₂, high ethanol and low oxygen concentrations (Jolly et al.,
422 2014). Though no evidence is reported in literature, it may be hypothesized that the lysis
423 of non-*Saccharomyces* cells can contribute to the release of RF, even during the early
424 stage of the fermentation process.

425 Concerning the wine-related lactic acid bacteria (LAB), the genera *Oenococcus* and
426 *Lactobacillus* were compared by Terrade and co-authors (2009) to determine their
427 vitamins requirements for growth conditions. The authors discovered that the tested
428 *Lactobacillus* strains were auxotroph for RF as opposed to the *O. oeni* strains, revealing
429 the ability of the latter species to synthesize vitamin B₂.

430

431 4.1.2 Methionine

432 In grape and must 28-39% of the total nitrogen is represented by free amino acids (Rapp
433 & Versini, 1991). Nitrogen content increases during grape maturation and at grapevine
434 harvest it corresponds to 70% of the organic nitrogen. Amino acids are the main part of
435 nitrogen source for yeasts during the alcoholic fermentation and for lactic bacteria in
436 malolactic fermentation. Moreover, they can be a source of undesirable compounds in
437 wines, such as ethyl carbamate, biogenic amines, and β-carbolines (Herraiz & Ough,
438 1993). In addition, free amino acids are a source of assimilable sulfur, essential for yeast

439 growth and relevant in winemaking, since sulfur metabolism can generate unpleasant
440 compounds, such as hydrogen sulphide and mercaptans (Rauhut, 1993).

441 For all these reasons the free amino acids concentration must be taken into account,
442 especially at the end of the alcoholic fermentation since the autolysis of the yeast cells
443 leads to their discharge (Moreno-Arribas et al., 2009).

444 Particularly, Met, a sulfur-containing amino acid, plays several roles in yeast metabolism
445 (Henschke & Jiranek, 1991) and in wine off-flavour (Fracassetti et al., 2019). Its catabolism
446 in yeasts has been especially studied in *S. cerevisiae*. The enzyme 5-methyl-
447 tetrahydropteroyltriglutamate-homocysteine S-methyltransferase (Met6) catalyses the
448 transformation of a molecule of 5-methyltetrahydropteroyltriglutamate and one of L-
449 homocysteine to Met and tetrahydropteroyltriglutamate (Ugliano & Henschke, 2009).

450 Met catabolism proceeds by the conversion of methionine to α -keto- γ -(methylthio)butyrate
451 (KMBA). KMBA is then decarboxylated to methional, that is subsequently reduced to
452 methionol (Perpète et al., 2006). Moreover, Met can be transformed to methanethiol by a
453 demethylase and then esterified to methanethioacetate (Ugliano & Henschke, 2009).

454 Usually, around 3-4 mg/L of methionine is found in wine and it derives from yeast cells
455 lysis (Riberau-Gayon et al., 2006, Fracassetti et al., 2017). Met is stable in RF-free
456 conditions, while RF presence induces Met degradation to form MeSH and DMDS
457 (Maujean et al., 1978; Maujean and Seguin, 1983b; Andrés-Lacueva et al., 1998).

458 Also non-*Saccharomyces* yeasts could contribute to increase Met concentration in wine
459 during the winemaking process with similar release mechanisms, even though this aspect
460 was not previously described for non-*Saccharomyces* yeasts.

461 Specific attention has to be given to *O. oeni*, because this species contributes to wine
462 sensorial properties producing VOCs deriving from Met degradation in significant
463 quantities, such as methanethiol and dimethyl disulfide (Pripis-Nicolau et al., 2004; Vallet

464 et al., 2007). It is probable that also cell lysis of LAB could discharge significant amount of
465 Met and its derivatives at the end of the malolactic fermentation.

466

467 **4.2 Technological approaches**

468 The prevention of LST can be achieved by applying some oenological procedures in
469 winery once the alcoholic fermentation is completed. Several approaches have been
470 investigated with the aim either to reduce the RF concentration, or to add compounds that
471 could act as a triplet RF quencher and/or as a Met competitor for the reaction with the
472 excited triplet RF, thus reducing the formation of Met-derived spoilage molecules. In any
473 case, the technologies applied in wine production should not take part in the formation of
474 LST and, in general, in any wine fault. In this context, attention is required in case of using
475 UV-C light. UV radiation is widely used in food processing due to its antimicrobial effect
476 (Bintsis et al., 2000). Even if the treatment is not approved by the International
477 Organization of Vine and Wine (OIV), it was successfully applied for decreasing the
478 microbial population in must (Fredericks et al., 2011; Falguera et al., 2013; Fracassetti et
479 al., 2019) and wine (Matias et al., 2016; Mijowska et al., 2017). The UV radiation of wine
480 containing RF can cause its photo-degradation and the formation of VOCs leading to the
481 detrimental change of the sensory property.

482

483 *4.2.1 Riboflavin removal*

484 Because RF is one of triggering factor of LST formation, its depletion should reduce wine
485 defect. A level of RF lower than 80-100 $\mu\text{g/L}$ decrease the risk of LST appearance
486 (Pichler, 1996; Mattivi et al., 2000). RF removal from wine can be attained by the use of
487 fining agents, such as bentonite. Bentonite is a montmorillonite clay that assumes negative
488 charge at wine pH and is commonly used in winemaking process as a clarifying agent. Its

489 main task in winemaking is the adsorption of wine proteins that are positively charged, in
490 order to avoid the formation of protein-related haziness. Its usual dosage ranges between
491 2 g/L and 8 g/L that should be specifically calculated for each wine (Riberau-Gayon et al.,
492 2006).

493 Bentonite shows the capacity to adsorb RF, but its action is not specific, thus the amount
494 of clay necessary for an adequate RF depletion is high (Pichler, 1996). In the study of
495 Pichler (1996), 2 g/L of bentonite were needed for the removal of 95 $\mu\text{g/L}$ of RF. However,
496 such bentonite dosage can lead to a significant depletion of wine aromas, thus the
497 reduction of its overall quality (Riberau-Gayon et al., 2006).

498 More recently Fracassetti et al. (2017) investigated the effectiveness of different fining
499 agents (bentonite, zeolite, polyvinylpolypyrrolidone [PVPP], kaolin, colloidal suspension of
500 pure silica, egg albumin charcoal) in terms of RF removal from model wine solution and
501 white wine. In a model wine solution RF was added up to 350 $\mu\text{g/L}$. The results pointed out
502 that the RF depletion was proportional to the increased concentrations of bentonite added
503 and at the highest concentration of bentonite (1 g/L), 35% of RF was removed. Another
504 effective adjuvant was zeolite even if its use is not approved by OIV. An addition of 1 g/L
505 zeolite decreased the RF concentration by 40%; this adjuvant was tested because it
506 represents a possible replacement of bentonite to improve protein and tartrate stability
507 (Mercurio et al., 2010). Large pore-sized charcoal was able to adsorb 70% and 94% of RF
508 at the concentration of 5 mg/L and 10 mg/L, respectively. Doses higher than 10 mg/L
509 completely removed RF in model solution. The small pore-sized charcoal was less active,
510 it removed 50% of RF. PVPP, silica, kaolin and egg white were not effective in RF
511 depletion. Bentonite, charcoal and zeolite were then evaluated in Chardonnay wine
512 containing 350 $\mu\text{g/L}$ of RF. Their capacity to remove RF resulted lower compared to that in
513 a model wine solution, with RF removed corresponding to 10% for zeolite, 25% for
514 bentonite and 70% for charcoal. This could be due to the role played by other wine

515 components such as proteins, phenols, lipids, polysaccharides that can be adsorbed by
516 the clarifying agents which active sites are less available to adsorb RF (Ribéreau-Gayon et
517 al., 2006). The adsorption mechanism is not RF-specific, that is why the compounds
518 present at higher concentrations in wine compete with RF for the active sites of charcoal,
519 preventing the vitamin from being adsorbed. Moreover, both charcoal and high doses of
520 bentonite, can adsorb flavouring compounds, thus making the wine poorer in terms of
521 aroma complexity and sensory characteristics. With the usually applied doses the amount
522 of RF removed is not high enough to ensure the total prevention of LST.

523

524 *4.2.2 The use of antioxidants in LST prevention*

525 Some antioxidants are present in wine, those originated from yeast metabolism, such as
526 glutathione (GSH), or added during the winemaking procedures, such as sulfur dioxide
527 (SO₂), and phenolics. Among the latter, flavan-3-ols showed the ability to inhibit the light-
528 induced fault. Specifically, the addition of (+)-catechin and (-)-epicatechin monomers and
529 dimers slowed down the formation of LST (Maujean & Seguin, 1983b). These authors
530 suggested that flavan-3-ols and maybe the condensed tannins, which building blocks are
531 represented by flavan-3-ols, can shield RF from light. Additionally, phenolic compounds
532 demonstrate the capacity to quench triplet RF in model beer solutions (Grant-Preece et al.,
533 2017). The use of phenols, both condensed and hydrolysable tannins, is a promising way
534 to limit the appearance of LST thanks to their antioxidant properties as well as to their
535 ability in quenching the singlet oxygen (Briviba et al., 1993; DeRosa & Crutchley, 2002).
536 Nevertheless, the phenolics need to be adequately chosen because of their bitter taste
537 and astringency, and also woody texture in case of hydrolysable tannins (Vivas et al.,
538 2003). Therefore, their addition to white wine should be thoroughly evaluated in order not
539 to alter the sensory properties of wine.

540 The hydrolysable tannins are commonly used in winemaking in order to improve wine
541 stability and sensory characteristics (Vivas et al., 2003; Pascual et al., 2017; Vignault et
542 al., 2018). Hydrolysable tannins have also been assessed as a potential effective measure
543 to prevent LST, as proved by Fracassetti et al. (2019a) who investigated the influence of
544 the addition of chestnut, oak and nut gall tannins in model wine solution. Their capacity to
545 prevent LST was investigated at the concentration of 40 mg/L, since this amount of
546 tannins added to wine does not influence the astringency or bitterness perception
547 (Robichaud & Noble, 1990). The experiments were carried out both in oxic and anoxic
548 conditions. In the presence of oxygen, nut gall tannin was able to decrease Met
549 degradation (11% of degraded Met), compared to either the tannin-free conditions (18% of
550 degraded Met) or samples added with chestnut or oak tannins (18.1 and 21.5%,
551 respectively). The major Met protection with nut gall tannin compared to other tannins,
552 could be due to its two-fold higher total phenol index (TPI) and high concentration of gallic
553 acid. This phenolic acid is a singlet oxygen quencher (Lagunes & Trigos, 2015), therefore,
554 it can reduce singlet oxygen thus preventing Met degradation. In anoxic conditions, Met
555 degradation increased in all samples, but once again nut gall tannin showed a major
556 protective effect (20.2% of degraded Met in solution with nut gall tannin, compared to
557 28.5% degraded in control sample). In air-free conditions, Type I mechanism occurs,
558 where triplet excited RF reacts directly with Met. The authors suggested that nut gall
559 tannin can compete with Met for the reaction with RF, thus limiting its degradation. In
560 terms of VSCs formation, both MeSH and DMTS concentrations were six-folds higher in
561 anoxic conditions compared to oxic ones. DMDS concentration was even eighty-four folds
562 higher. These results are in agreement with the theoretical LST mechanism: in the
563 presence of oxygen, both Type I and II mechanisms can take place (Min & Boff, 2002;
564 Grant-Preece et al., 2017). Oxygen can quench triplet excited RF and can also react with
565 Met giving its stable oxidation products, including methionine sulfoxide (Fracassetti et al.,

566 2020). As a consequence, less VSC are formed in oxic conditions. In the presence of
567 oxygen, the addition of hydrolysable tannins hampered the DMTS formation, as this
568 compound was not found in the solution. DMDS production was significantly lower when
569 chestnut and oak tannins were added, while with nut gull tannin it was not detected at all.
570 The most significant differences in VSC formation were even more evident in anoxic
571 conditions, where lower concentrations of MeSH, DMDS and DMTS were found in the
572 presence of tannins in comparison to control sample. These differences were also
573 sensorially perceived and significantly lower scores were found in the presence of tannins,
574 accordingly to VSC content.

575 The possible mechanisms of LST prevention performed by tannins can be due to their
576 ability in RF quenching, thus protect Met from degradation, or they can react with singlet
577 oxygen forming quinones (DeRosa & Crutchley, 2002), electrophile molecules able to
578 react with amine group of Met or with free thiol group of MeSH protecting from DMDS and
579 DMTS formation.

580 As regard to the addition of tannins in white wine, the effectiveness of chestnut tannin was
581 investigated (Fracassetti et al., 2019b). A RF-enriched wine was exposed to light in
582 presence of chestnut tannin. After two hours of illumination and consequent twenty-four
583 months of storage in the dark the analysis showed that MeSH and DMDS were not
584 detected or found in concentrations lower than a perception threshold as the sensory
585 analysis did not reveal an olfactory defect.

586 Hydrolysable tannins showed to successfully limit both Met degradation and VSC
587 formation. They may not totally prevent LST, but their addition prior to bottling can limit the
588 risk of the formation of light-dependent spoilage. An important aspect to take into
589 consideration when applying this preventive method is the dosage of tannins in order not
590 to affect the taste of wine. It is noteworthy to mention that tannins at concentrations
591 studied (50 mg/L) did not lead to any colour alterations after light exposure (Fracassetti et

592 al., 2019b; Fracassetti et al., 2019c). Other antioxidants, including GSH and SO₂, were
593 tested individually or in combinations, together with chestnut tannin. In model wine, the
594 most effective condition preventing the appearance of LST was the addition of all three
595 antioxidants together, as only negligible amount of MeSH and DMTS were detected, while
596 no DMDS was detected. On the other hand, the results obtained in white wine slightly
597 differed from the model solution. In the presence of chestnut tannin and GSH alone or in
598 combination with SO₂, MeSH and DMDS were undetected or detected at concentrations
599 below their perception threshold. MeSH was present in concentrations over the perception
600 threshold in samples of white wine without any added antioxidant but with SO₂. These
601 results suggest that SO₂ could not be able to protect from LST during wine storage,
602 contrarily to what was observed in model wine solution. The formation of sulfonate
603 compounds was showed in white wine where SO₂ was added and in an environment
604 where oxygen is present (Arapitsas et al., 2016). The concentration of these compounds
605 increased for higher amounts of oxygen dissolved on bottling. We can assume SO₂
606 favoured the formation of VOCs in the experimental conditions adopted even because a
607 medium richer in radicals could be generated as a consequence of the photo-degradation
608 of RF. In fact, SO₂ showed to favour the oxidative pathways when an acidic solution
609 containing RF and Met is exposed to light (Figure 5). The photo-oxidation, monitored by
610 NMR, led to strong and fast increase of Met sulfoxide which formation was limited when
611 gallic acid was present instead of SO₂ (Fracassetti et al., 2020). This suggests the ability
612 of phenolics in the overall prevention of the light-dependent oxidations which have a
613 detrimental impact on desired sensory characteristics of wine.

614 To the best of our knowledge no data have been reported on RF and Met decay with
615 regards to the wood ageing and batonnage. Even if these winemaking practices are less
616 common for white wine than for red wine, the ageing in oak containers is becoming a
617 common practice in some winegrowing regions (González-Centeno et al., 2020) increasing

618 and improving the availability of white wines aged in wood in the market, adapting to the
619 demands of the international trade (Alañón et al., 2018). During the wood ageing, amino
620 acids can undergo through oxidative deamination generating higher alcohols (Câmara et
621 al., 2006; Carpena et al., 2020). However, no specific result was reported on Met and its
622 susceptibility to oxidative deamination in such winemaking condition.

623

624 **4.3 Packaging and storage approaches**

625 Glass bottle is a physical barrier shielding wine from light. Its choice is of crucial
626 importance when it comes to limiting the risk of LST. Consumers often prefer flint glass
627 bottles because the colour of wine, a marker of its oxidative status, is visible. Moreover,
628 the production and recycling costs are lower for clear bottles and they have a lower carbon
629 footprint (Hartley, 2008). In a survey carried out among 231 Italian wineries
630 (<https://www.surveio.com/survey/d/K6Y3T0W6C5S5Z1G2J>), up to 80% of total white wine
631 production *per* winery is bottled in clear glass. The protection from UV/Vis light offered by
632 clear glass is significantly lower compared to other commonly used bottle colours, such as
633 amber or green. Flint glass allows to pass about 90% of the harmful light (under 500 nm),
634 whereas green and amber bottles allow to pass 50% and 10% of light, respectively (Clark
635 et al., 2011).

636 The importance of wine bottle colour in LST prevention is a well-known aspect needing a
637 further consideration. Dozon and Noble (1989) carried out a sensory study to evaluate the
638 effect of light on white wines, both sparkling and still, which were bottled in flint and green
639 bottles, and then exposed to light. Panel of trained judges determined the minimum time of
640 exposure necessary to produce a difference in aroma compared to a control kept in the
641 dark. The results showed that for samples in flint bottles, the time required to develop an
642 off-odour was significantly shorter than for samples kept in green bottles. For flint bottles it

643 was 3.4 and 3.3 hours for still and sparkling wine, respectively. In green bottles, an off-
644 odour appeared after 18 and 31.1 hours for still and sparkling wine, respectively. Green
645 bottles do not provide a total protection against LST, but they definitely increase the time
646 necessary for the fault perception, which resulted six- and ten-fold longer for still and
647 sparkling wines, respectively. It is noteworthy to mention that in this study wine samples
648 were kept 35 cm from the light source, while in the commercial retail conditions, wines
649 usually are placed farther from the light source. In real life conditions, time of light
650 exposure necessary to produce the olfactory defect, probably would have to be longer.

651 Differences between flint and green bottles in preventing LST were also investigated by
652 Arapitsas et al. (2020). In their study, wines were kept in a specially arranged room
653 simulating supermarket conditions, with windows with curtains, shelves, air conditioning
654 and lamps kept on 12 hours/day. Sensory analysis managed by an expert panel, who
655 evaluated wines within fifty days of light exposure, showed that most of flint bottles
656 developed LST after four weeks. The more intense perception of the defect was observed
657 for longer time of light exposure, proving this factor to be mainly causative to LST
658 occurrence. Moreover, all the wines bottled in flint glass developed LST, whereas the
659 wines bottled in green glass never exceeded four out of 10 point-scale in sensory analysis,
660 meaning that the spoilage was not clearly developed. These results confirm the previous
661 ones, regarding the capacity of green bottles to protect wines from LST better than flint
662 ones (Dozon & Noble, 1989). Moreover, wines in green bottles were resistant to LST
663 development up to 50 days of light exposure which confirms that in retailing conditions,
664 due to further wine positioning from the light source, LST needs more time to develop
665 (Arapitsas et al., 2020).

666 Another interesting outcome from this work is that LST is irreversible; the sensory
667 evaluation conducted after one year of wine storage in the dark showed the same results
668 as the analysis performed immediately after the light exposure (Arapitsas et al., 2020). The

669 light can be both absorbed by the glass and partially reflected. As a consequence, the
670 shape of the bottle and the direction of the light can also affect the occurrence of LST in
671 wine. It has been proved that long neck bottles with a shallow angle on the bottle shoulder
672 such as Rhenish bottles, show a better protection from light compared to short neck or
673 sharp shoulder angle bottles (Hartley, 2008).

674 Nonetheless, even if dark bottles can shield the light and prevent the appearance of LST,
675 the light exposure of white wine bottled in dark glasses (Antique Green and French Green)
676 can have an impact on its characteristics. In this condition, highest concentration of
677 xanthylum ions causing a major browning was found indicating a more evidenced
678 oxidation. This occurred as a consequence of the increase of temperature due to the dark
679 bottle (Maury et al., 2010). For this reason, taking into account the overall quality of white
680 wine, oenological approaches built up by means of technology, chemistry and
681 microbiology are crucial to counteract the detrimental light-dependent faults.

682 Nowadays, in order to protect the wine bottles in flint bottles, plastic or paper films are
683 used to cover the bottles. These devices are able to absorb the wavelengths that cause
684 LST, but they increase the cost of wine production in terms of necessary material and
685 labouring hours, since each bottle has to be wrapped individually. Moreover, the bottle
686 wine wrapping is associated with the waste disposal problems and the increase of plastic
687 material production.

688

689 **5. Conclusions**

690 Several factors are involved into the light-dependent spoilage of wine. LST depends
691 mainly on the concentration of RF and Met, but also to the chemical composition of wine
692 (i.e. iron, copper, phenolic compounds, antioxidants added). The type of light source in
693 terms of wavelengths emitted by the lamps, the duration of the light exposure during wine

694 storage, the distance of the lamp as well as the bottle shape and color need to be taken
695 into account. As many aspects can affect the occurrence of wine faults, it is clear that the
696 entire winemaking process, from the must production and alcoholic fermentation up to the
697 storage and selling conditions, are important aspects that have to be considered in order
698 to maintain and ensure the quality of the wine till the bottle opening.

699 In an oenological perspective, technological aspects including the use of specific
700 adjuvants having the ability of bind sulfur-containing off-flavors and quench excited RF or
701 oxidized Met as well as removing RF represent a challenge to counteract this wine fault.
702 As the same time, the use of yeast able to release low amounts of RF and Met can carry
703 out a protective effect. In this scenario, investigation on oenological tannins of different
704 origin will support the wine industry with affective tool against the detrimental effect of LST.
705 Contemporarily, the selection of low RF and Met producing yeast strains can also open up
706 new applications to positively tackle this problem of current oenology and a further
707 improvement of precision oenology.

708

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713 **Figures' Captions**

714 **Figure 1:** Riboflavin photosensitization by Type I or Type II mechanisms (Cardoso et al.,
715 2012).

716 **Figure 2:** Reaction scheme of methional formation due to light exposure (Maujean &
717 Seguin, 1983).

718 **Figure 3:** Scheme of the proposed tartaric acid degradation through the Fenton reaction
719 and under light exposure (Clark et al., 2007).

720 **Figure 4:** Riboflavin pathway in *Saccharomyces cerevisiae* (Gudipati et al. 2014).

721 **Figure 5:** Photo-catalytic cycle for the riboflavin-mediated oxidation of methionine in the
722 presence of gallic acid and sulfur dioxide through Type I and Type II mechanisms
723 (Fracassetti et al., 2020).

724

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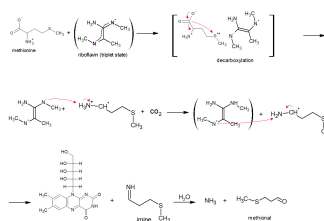
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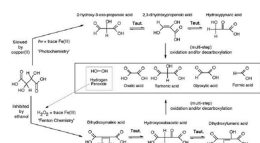
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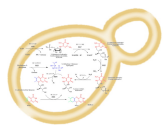
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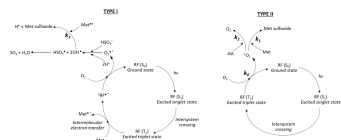
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Highlights

- Light-struck taste is detrimental for the sensory profile of white wine
- Sulfur compounds are produced from the reaction between riboflavin and methionine
- Fermenting yeast plays the major role on riboflavin content in wine
- Riboflavin depletion can be obtained with wine treatment with fining agents
- Tannins can represent an effective tool against the light-struck taste