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Supranutritional doses of vitamin E to improve lamb meat quality

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24 1. Introduction

25 Lamb is defined as a high quality product and it is considered a delicacy in
26 Mediterranean countries (Karabagias, Badeka, & Kontominas, 2011; Vieira, &
27 Fernández, 2014). Visual appearance is the most important sensory property of lamb
28 because consumer purchasing decisions rely on meat appearance (Faustman et al.,
29 2010). Consumers associate a bright red colour with freshness and superior meat
30 quality. Therefore, fresh lamb for retail display is commonly packaged in oxygen-
31 enriched atmospheres to satisfy consumers demand for fresh, tender and tasty meat with
32 an attractive appearance (Bellés, Alonso, Roncalés, & Beltrán, 2017). High
33 concentrations of oxygen in the gas mixture have been demonstrated to result in
34 optimum colour in red meats by promoting oxymyoglobin formation. However, the high
35 level of oxygen in the package enhances oxidative reactions, which lead to
36 discoloration, development of off flavours, formation of toxic compounds, nutrient and
37 drip losses, and can also have a negative impact on texture, compromising meat quality.
38 Oxidation is one of the main causes of lamb deterioration, which explains the great
39 efforts that have been taken to solve this problem (Bellés et al. 2017). The addition of
40 compounds having antioxidant activity in the feed or in the package has emerged as a
41 promising strategy to inhibit oxidative reactions and therefore, to offer a product with a
42 higher quality and extended shelf life.

43 Vitamin E is the main fat soluble antioxidant preventing damage in live animals, and its
44 antioxidant effects are also present post mortem. A large number of studies have
45 observed that the administration of supranutritional doses of vitamin E before slaughter
46 favours the deposition of tocopherol in the muscle, increasing the stability of meat
47 against oxidation (Álvarez et al., 2008; Bellés et al., 2018; de la Fuente et al., 2007;
48 Jose, Jacob, Pethick, & Gardner, 2016; Kasapidou et al., 2012; Kerry, O'Sullivan,

49 Buckley, Lynch, & Morrissey, 2000; Ponnampalam, Burnett, Norng, Warner, & Jacobs,
50 2012a; Ponnampalam et al. 2017). Dietary vitamin E has been shown to have great
51 potential to reduce the negative effect of oxidative reactions on lamb quality, making it
52 vital to optimize its feeding strategy in order to obtain maximum benefit. The present
53 review focuses on vitamin E chemistry, biochemistry, factors effecting its accumulation
54 in muscle, and summarizes recommendations to producers and retailers for its
55 supplementation to maintain lamb quality.

56 **2. Chemistry and biochemistry**

57 **2.1 Chemical structure**

58 The generic term vitamin E includes several compounds having a similar antioxidant
59 activity (Jensen, & Lauridsen, 2007). These compounds comprise both tocopherols and
60 tocotrienols, which are characterised by possessing a hydroquinone nucleus and an
61 isoprenoid side chain. The chemical difference between them is located in the
62 isoprenoid side chain; tocopherols have a saturated side chain while tocotrienols have an
63 unsaturated side chain containing three double bonds. Moreover, four different
64 tocopherols (α , β , γ , δ) and four tocotrienols (α , β , γ , δ) are differentiated depending on
65 the position of methyl ($-\text{CH}_3$) groups at positions 5, 7 or 8 of the chroman ring
66 (Colombo, 2010). Table 1 shows the chemical structure of vitamin E-like compounds.

67 Among all of them, α -tocopherol shows the highest biological activity (Jensen,
68 Nørgaard, & Lauridsen, 2006). Alpha-tocopherol is a chiral molecule, which means that
69 it is non-superposable on its mirror image. Each one of the mirror images of a chiral
70 molecule is called enantiomer or optical isomer. Chirality is often produced due to the
71 presence of an asymmetric carbon centre. Indeed, α -tocopherol presents three chiral
72 centres at positions 2C, 4C and 8C of the phytyl tail. At each chiral centre two

73 configurations are possible, which are named R or S, so there are eight different
74 stereoisomers of α -tocopherol (Dersjant-Li, & Peisker, 2010; Jensen, & Lauridsen,
75 2007). Figure 1 presents the chemical structure of α -tocopherol stereoisomers. Alpha-
76 tocopherol obtained from natural sources consists of a single stereoisomer presenting a
77 RRR configuration, which means that it presents a configuration of R at the three
78 positions (2C, 4C and 8C). In contrast, chemically synthesised vitamin E comprises an
79 equimolar mixture of the eight different α -tocopherol stereoisomers (RRR, RRS, RSS,
80 RSR, SRR, SSR, SRS, and SSS) (Dersjant-Li & Peisker, 2010). According to IUPAC
81 recommendations (1982), vitamin E obtained from natural sources is called RRR- α -
82 tocopherol while that which is chemically synthesised is named all-rac- α -tocopherol in
83 order to describe the differences in chemical composition between both sources.

84 Both natural and synthesised vitamin E free forms can be easily degraded during the
85 processing, manufacturing and storage of feeds, which make it difficult to use vitamin E
86 as an additive in feedstuffs. To overcome these problems more stable forms have been
87 developed. Since esters are less susceptible to oxidation, the phenol group of α -
88 tocopherol is commonly converted to an ester by using acetic or succinic acid, so
89 vitamin E is commercialised as α -tocopheryl-acetate or α -tocopheryl-succinate. These
90 forms are very stable to in vitro oxidation but they need to be hydrolysed in the animal
91 gut to show antioxidant activity (Vagni, Saccone, Pinotti, & Baldi, 2011). The all-rac α -
92 tocopheryl acetate is the form of vitamin E most used to supplement animal feeds due to
93 its high stability and lower cost.

94 **2.2 Bioavailability and biopotency**

95 Bioavailability and biopotency are close-knit concepts. The first one is defined as the
96 absorbed proportion of a substance after its administration while biopotency refers to
97 the ability of a compound to exert an effect in a biological system (Dersjant-Li &

98 Peisker, 2010). It is obvious that a substance needs to be absorbed prior to **acting** in an
99 organism. Therefore, knowing the mechanism of absorption of vitamin E is the key to
100 maximize its benefits in meat quality, even more in ruminants whose digestive anatomy
101 and physiology is markedly different and more complex than that of monogastric
102 animals. Several studies have been carried out to assess the effect of ruminal microbiota
103 and fermentations on vitamin E absorption. Weiss, Smith, Hogan and Steiner (1995)
104 observed that vitamin E was not degraded during *in vitro* ruminal fermentation. In
105 agreement, Hymøller and Jensen (2010) noted neither *in vitro* nor *in vivo* hydrolysis of
106 α -tocopherol in the rumen. Taking into account that α -tocopherol esters need to be
107 hydrolysed before their absorption, little if any absorption of vitamin E in the rumen
108 should be expected.

109 In contrast, tocopherol esters are largely hydrolysed in the intestinal lumen, where they
110 are then absorbed in combination with lipid micelles. Once in the enterocytes, vitamin E
111 is packed into chylomicrons and delivered **to the liver in the form of chylomicron**
112 **remnants** (Lauridsen, & Jensen, 2012). In the liver, the hepatic α -tocopherol transfer
113 protein, α -TTP, binds to the vitamin E to facilitate its incorporation into nascent VLDL
114 and its secretion from hepatocytes. This lipoprotein has a central role in vitamin E
115 metabolism as it regulates the body-wide levels of α -tocopherol (Rigotti, 2007).
116 Furthermore, the α -TTP seems to be a major cause of the differences found among the
117 bioavailability of the different vitamin E-like compounds. Both tocopherols and
118 tocotrienols **are transported via chylomicron remnants to the liver, but at this point, the**
119 α -TTP exerts a selective transport. Hosomi et al. (1997) demonstrated *in vitro*
120 differences in the affinity of α -TTP to the different types of tocopherols and
121 tocotrienols. Relative affinities (RRR- α -tocopherol = 100%) were as follows: RRR- β -
122 tocopherol, 38%; RRR- γ -tocopherol, 9%; RRR- δ -tocopherol, 2%; α -tocopherol acetate,

123 2%; α -tocopherol quinone, 2%; SRR- α -tocopherol, 11%; α -tocotrienol, 12%.
124 Therefore, α -TPP not only has a higher affinity for tocopherols but it is also able to sort
125 out among isomers. The different **affinities** of α -TPP to α -tocopherol stereoisomers
126 seems to be the major cause of their differences in activity. RRR- α -tocopherol is
127 generally accepted to have the highest bioactivity but the equivalence of the different
128 isomers is still a point of concern. The first study about this topic assigned a value of 1
129 IU mg⁻¹ for 2-ambo- α -tocopheryl acetate (a mixture of RRR-and SRR- α -tocopherol)
130 while a value of 1.36 IUmg⁻¹ was proposed for RRR- α -tocopheryl acetate (Harris &
131 Ludwig, 1949). This ratio was later corroborated by Weiser and Vecchi (1982), who
132 also associated a relative biopotency to each α -tocopherol stereoisomer. The results
133 obtained were: RRR = 1, RRS = 0.9, RSS = 0.73, SSS = 0.6, RSR = 0.57, SRS = 0.37,
134 SRR = 0.31 and SSR = 0.2. Despite both studies used clinical endpoints based on the
135 physiological activity of vitamin E during the gestation on rats to determine the
136 bioequivalence (RRR- α -tocopheryl acetate = 1.36 IUmg⁻¹), it was accepted by the
137 United States Pharmacopeia (USP) and widely used as the conversion factor either for
138 human or livestock.

139 Nevertheless, an intense debate about the adequacy of this ratio for livestock is growing
140 among researchers. Jensen and Lauridsen (2003) observed that cows have a higher
141 selectivity than rats to utilise the different stereoisomers; so, while cows mostly
142 preferred the RRR form, rats were able to utilize all 2R forms. Moreover, it has been
143 noted that vitamin E bioavailability is also influenced by dietary dosage, feeding period,
144 age and tissue (Dersjant-Li & Peisker, 2010; Jensen et al., 2006; Jensen, & Lauridsen,
145 2007). All these data support the need of calculating the equivalence between
146 stereoisomers more accurately, taking into account both species and age. Equivalences
147 in large animals cannot be determined with clinical endpoint markers due to ethical and

148 practical aspects, so they are calculated by bioavailability studies. It has been
149 demonstrated a higher bioavailability of RRR- α -tocopherol in cattle (Meglia, Jensen,
150 Lauridsen, & Waller, 2006; Weiss, Hogan, & Wyatt, 2009), dairy cows (Weiss et al.,
151 2009), sows (Lauridsen, Engel, Jensen, Craig, & Traber, 2002), piglets (Lauridsen et al.,
152 2002) and finishing swine (Yang et al., 2009). Table 2 shows some ratios for livestock.
153 Unfortunately, there is a lack of studies about this topic in lambs.

154 **2.3 Antioxidant activity**

155 As it has been stated above, vitamin E encompasses several compounds that show
156 antioxidant activity. Nevertheless, the isomers of vitamin E possess a different
157 antioxidant power and exert non-redundant biological functions. α -tocopherol presents
158 the highest antioxidant effect *in vivo*. It acts as a chain-breaking antioxidant by donating
159 a hydrogen atom to a peroxy radical, thus converting it to a hydroperoxide, which is
160 unable to propagate the oxidative process. Besides the lipid antioxidant action, α -
161 tocopherol has been associated to different physiological functions by taking part in
162 cellular signalling, modulating the expression of some proteins involved in
163 atherogenesis and regulating arachidonic acid cascade pathway (Brigelius-Flohe and
164 Traber, 1999; Schneider, 2005).

165 Similarly, γ and δ -tocopherol isomers show a chain-breaking mechanism of action. γ -
166 tocopherol transfers a hydrogen atom to a peroxy radical, resulting in a stabilized γ -
167 tocopheroxy radical. This molecule can further follow two different ways: it can react
168 with a new peroxy radical to form the covalent adducts, 8 α -(alkyl-dioxy)- γ -
169 tocopherones or with each other to form 5-(γ -tocopheroxy-5- γ)- γ -tocopherol and 5- γ -
170 tocopheroxy)- γ -tocopherol (Yamauchi, 1997). Moreover, γ -tocopherol is a powerful
171 nucleophile that traps electrophilic mutagens in lipophilic compartments, thereby

172 protecting lipids, DNA, and proteins from peroxy nitrite damage (Brigelius-Flohe and
173 Traber, 1999).

174 Regarding tocotrienols, they have been described to exert a higher antioxidant activity
175 in membranes than tocopherols, but their bioavailability after oral ingestion is less than
176 that of α -tocopherol. Tocotrienols are also chain-breaking antioxidants by scavenging
177 free radicals (Packer, Weber, & Rimbach, 2001). Apart from their antioxidant
178 properties, tocotrienols may present anticancer and neuroprotection functions (Sen,
179 Khanna, Rink, & Roy, 2007).

180 **3. Relationship between vitamin E requirements, breeding conditions** 181 **and their effect on production parameters**

182 Vitamin E is an essential nutrient which plays a significant role in many biological
183 functions like reproduction and immunity. A dosage of 20 mg vitamin E/kg feed has
184 been recommended for lambs for the normal function of the body (NRC, 2001). At
185 lower than this supplementation level, a decrease of livestock production performance
186 could be expected, besides the appearance of some diseases related to vitamin
187 deficiency. Nevertheless, there are some breeding conditions which may modify vitamin
188 E requirements.

189 A large number of studies (Berthelot, Broudiscou, & Schmidely, 2014; Lauzurica et al.,
190 2005; Liu, Ge, Luo, Yue, & Yan, 2013; Leal et al., 2018; Zhao et al., 2013) have
191 demonstrated that supranutritional intakes of tocopherol do not exert any effect on
192 average dairy gain, live weight, feed intake or feed efficiency. Moreover, neither carcass
193 conformation nor fatness are affected by dietary vitamin E. Therefore, no modifications
194 of growth performance and carcass characteristics would be expected in mature lambs
195 by increasing the content of tocopherol of the feed if the minimum requirements for

196 normal growth and health are already satisfied. By contrast, supra nutritional dosages of
197 vitamin E seems to improve productive parameters in young animals. Maiorano et al.
198 (2007) observed a higher average daily gain (ADG) in suckling lambs **receiving**
199 **intramuscular injections of 150 IU/wk** for eight weeks in comparison to those which
200 only **received** vitamin E from milk. A feasible explanation **for** these results could be the
201 key role of vitamin E in the development of the immune system of young animals.
202 Vitamin E concentration in milk mainly depends on diet, so the non-supplemented
203 lambs might have consumed very low levels of vitamin E. The lack of this vitamin may
204 impact the correct growth of these lambs.

205 Ambient conditions may increase the demands of vitamin E for normal function and
206 growth too. Heat stress is responsible for significant economic losses for the livestock
207 industry during the summer months and constitutes a growing concern due to climate
208 change (Bernabucci et al., 2010). Heat stress lessens oxidative defences by producing
209 excessive ROS, thereby exerting oxidative damage to many biological molecules which
210 may further compromise animal health and growth (Chauhan et al., 2014b). Therefore,
211 lambs **may have increased requirements for antioxidants under** adverse climatic
212 conditions. In this sense, Chauhan, Celi, Leury, Clarke and Dunshea (2014a)
213 demonstrated that the supplementation with vitamin E of lambs reared under heat stress
214 conditions ameliorate their physiological and oxidative **stress**. Moreover, Chauhan et al.
215 (2016) pointed out that the administration of supranutritional levels of vitamin E and Se
216 during the finishing period may avoid the decrease of average daily feed intake and
217 average daily gain of lambs exposed to heat stress. Thus, the administration of
218 supranutritional doses of vitamin E seems to be a strategy to mitigate production losses
219 during hot seasons.

220 The requirements of vitamin E also depend on animal lipid depots. Early maturing
221 breeds tend to deposit more fat in the body than late maturing breeds at the same age, so
222 the first ones need more vitamin E to maintain oxidative status for normal function and
223 growth (Brand, Van der Westhuizen, Van Der Merwe, & Hoffman, 2018). On the other
224 hand, early maturing lambs would present with a higher content of this vitamin
225 compared with leaner animals if enough vitamin E is administered in the diet, since
226 vitamin E accumulates in fat tissue. In this sense, Ponnampalam et al. (2014) observed
227 greater concentrations of vitamin E in faster growing lambs, which presented a higher
228 percentage of fat, than those of lighter body weight animals.

229 Both fattening and fat composition are also influenced by animal feed. It has been
230 demonstrated that animal fat composition can be modified to produce healthier meat by
231 changing feed composition. Generally, this strategy aims to increase the content of
232 PUFA and conjugated linoleic acid. In this sense, several studies have shown that
233 dietary *n*-6 and *n*-3 PUFA can be incorporated into adipose tissue and muscle of lambs
234 despite the biohydrogenation of dietary fatty acids in the rumen (Wood et al., 2008).
235 Moreover, differences in fat composition have been registered depending on the feeding
236 system. Nuernberg et al. (2005) observed a higher proportion of PUFA, SFA and *n*-3
237 fatty acids in grass-fed than in grain-fed lambs. Similarly, meat from alfalfa fed lambs
238 showed a greater PUFA *n*-3 content than their concentrate-fed counterparts (Álvarez-
239 Rodríguez et al., 2018). Nevertheless, increasing the unsaturated fatty acids in the
240 muscle cell membranes may result in reduced oxidative stability and therefore, in
241 increased vitamin E requirements (Monahan, Buckley, Morrissey, Lynch, & Gray,
242 1992). Grass fed animals would be able to correct this status by means of tocopherol,
243 carotenoids and many other antioxidants present in their diet, but increasing the PUFA

244 content of the concentrate-fed animals may require a higher level of vitamin E
245 supplementation (Ponnampalam et al., 2012b).

246 **4. Effect on meat quality**

247 **4.1 Muscle composition**

248 The deposition of vitamin E in muscle depends on the length and the level of
249 supplementation. Jose et al. (2016) measured the evolution of α -tocopherol
250 concentration in muscle using 6–8 month old lambs at different levels of
251 supplementation with synthetic vitamin E (30, 150, 275, 400 IU of all-rac tocopherol) or
252 on green pasture through the feeding period (up to 8 weeks), registering a continuous
253 increase with time in each treatment, except in that consist of 30 IU. This dosage
254 satisfactorily prevented lambs from nutrition related diseases, but it was not enough to
255 stimulate the deposition of tocopherol in muscle. The deposition rate of vitamin E
256 depended on the level of supplementation, the more dosage, the faster accumulation in
257 the muscle. In fact, the content of α -tocopherol in muscle after 6 weeks was 2 fold
258 higher in the lambs supplemented with 150 IU than in those receiving 30 IU, and it was
259 even 3 fold higher in the animals that were fed at the highest level of supplementation
260 (400 IU). Regarding the content of α -tocopherol of grass fed lambs, it was **similar to**
261 **those supplemented with** 275 IU of synthetic vitamin E. The deposition of tocopherol
262 through the feeding period showed a linear increase, the slope depending on the dosage;
263 however, a plateau was reached after 5 weeks at the highest level of supplementation
264 and after 4 weeks in the grass fed lambs, which suggests the existence of a saturation
265 point. At this time, the content of tocopherol in muscle was between 5 and 6 mg/kg
266 (Jose et al., 2016). In this sense, visual inspection of the published α -tocopherol
267 concentrations in muscle after slaughter (Figure 2) suggests a nonlinear relationship
268 between vitamin E consumption and the concentration of α -tocopherol in M.

269 *longissimus*: there is a point above which the rate of deposition of tocopherol in muscle
270 decreases.

271 A similar concentration of muscle tocopherol can be obtained with different
272 supplementation rates. Kasapidou et al. (2012) registered 3.73 mg α -tocopherol/kg
273 muscle by a moderate level of supplementation (500 mg all-rac α -tocopherol/kg) during
274 63 days. Increasing the level of supplementation to 1000 mg/kg allowed obtaining a
275 similar concentration of tocopherol in muscle with a reduced time of supplementation:
276 Álvarez et al. (2008) and De la Fuente et al. (2007) reached a muscle concentration of
277 3.57 mg α -tocopherol after 37 days while Bellés et al. (2018) quantified 3.91 mg even in
278 a shorter period of supplementation (14 d). On the other hand, Ponnampalam et al.
279 (2012a) quantified 3.2-5.6 mg α -tocopherol/kg meat in pasture fed animals (49 d) when
280 diets have 20-60 mg/kg DM, Turner, McClure, Weiss, Borton and Foster (2002)
281 registered up to 2.5 mg of α -tocopherol/kg meat in alfalfa-finished lambs (89 d) and
282 Álvarez-Rodríguez et al. (2018) reached 2.83 mg of α -tocopherol/kg meat by including
283 grazed alfalfa in the concentrate basis ration.

284 It is notorious that similar depositions of tocopherol, than that obtained with synthetic
285 vitamin E, have been obtained by lower concentrations of natural vitamin E in the diet.
286 A feasible explanation for this phenomenon may be the different efficacies of
287 conversion for vitamin E from forage diet and synthetic source to animal tissues.
288 Synthetic vitamin E is a racemic mixture containing the eight stereoisomers of α -
289 tocopherol, among which 2S stereoisomers present a low bioavailability. By contrast, α -
290 tocopherol appears naturally only as RRR- α -tocopherol, which presents the highest
291 bioavailability (Dersjant-Li & Peisker, 2010). It is obvious that the higher the
292 bioavailability the greater the deposition of α -tocopherol in the muscle. On the other

293 hand, natural vitamin E is located within vegetal lipids, which may facilitate its
294 absorption (Ponnampalam, Behrendt, Kerr, Raeside, McDonagh, 2018).

295 Synthetic vitamin E has a high cost, so optimizing the supplementation rate is a key
296 point to producers. The studies of Jose et al (2016), Turner et al. (2002) and
297 Ponnampalam et al. (2012a) showed that extensive systems based on forages provide a
298 concentration of tocopherol in muscle enough to maintain the quality of lamb
299 throughout the display period, without needing to provide extra synthetic vitamin E.
300 Nevertheless, most regions around the globe lack natural resources to grow lamb
301 extensively and farmers are constrained to feeding lambs with grain-based concentrate
302 enriched with synthetic vitamin E. Supplementing lamb diets with supra-nutritional
303 doses of synthetic vitamin E represents a significant cost to producers. Furthermore,
304 consumers concern about chemical additives continues to grow, so they would be more
305 keen towards natural sources of antioxidants. Recent studies have pointed out a great
306 number of natural sources of vitamin E that may be used to supplement grain-based
307 diets. Chesnutt, mimosa and tara extracts, dried tomato pomace, rosemary distillation
308 residues, dried citrus pulp and olive cake are some feasible examples of alternative
309 sources of vitamin E available in many regions where lambs grow intensively (Luciano
310 et al., 2013; Luciano et al., 2017; Valenti et al., 2018a; Valenti et al., 2018b; Yagoubi et
311 al., 2018). Moreover, these resources are cheaper and ecologically friendly, since they
312 are agro-industrial by-products. The development of strategies to reduce or even replace
313 synthetic vitamin E from lamb's diet seems to be an interesting area of research whose
314 results will be very useful for both producers and consumers.

315 On the other hand, vitamin E has been described to modify meat fatty acid profile by
316 acting at two different levels, ante-mortem and post-mortem. Vitamin E seems to play a
317 role in rumen metabolism although it is not completely clear the mechanism and the

318 specific modifications. Recent studies pointed at a modification of biohydrogenation
319 processes, which would involve ruminal fatty acid hydrogenation. The modification of
320 ruminal microbiota might be a possible mechanism by which vitamin E would affect
321 ruminal processes (Hou, Wang, Wang and Liu, 2013). The addition of supranutritional
322 doses of vitamin E to the feed could result in changes of specific fatty acids. Demirel et
323 al. (2014) observed an increase in the proportions of C18:2 *n*-6, C20:5 *n*-3 and C22:6 *n*-
324 3 together with a decrease of the percentages of C16:1 and C18:1 *n*-9, while Berthelot et
325 al. (2014) only registered an increase in the proportion of C18:1 10*t*. Similarly, Hou et
326 al. (2013) determined a higher percentage of C18:1 10*t* and C18:1 11*t* while the
327 proportions of C18:1 *n*-9, C18:2 *n*-6 and C18:3 *n*-3 were lower. Nevertheless, the effect
328 of vitamin E on modifying total percentage of saturated, monounsaturated or
329 polyunsaturated fatty acids in lamb tissue seems to be low (Chen, Mao, Lin, and Liu,
330 2008) or even inexistent (Demirel et al., 2014; Kasapidou et al., 2009; Berthelot et al.,
331 2014).

332 The post-mortem effects of vitamin E on fatty acid profile are related to lipid oxidation.
333 As it is widely known, PUFA are more prone to oxidation than monounsaturated and
334 saturated fatty acids due to their higher degree of **unsaturation, which can lead to their**
335 **decreased proportions during aerobic display** (Álvarez et al., 2009, Bellés et al., 2018).
336 Many studies focused on the effect of dietary vitamin E on fatty acid evolution through
337 display have registered a higher percentage of PUFA in meat from supplemented than
338 from control lambs after several days of aerobic display (Bellés et al. 2018, Alvarez et
339 al., 2009; Chen et al., 2008). Supranutritional dosages of vitamin E may increase the
340 deposition of tocopherol into cell membranes, where it offers an enhanced protection of
341 PUFA from oxidative degradation during display **and, therefore, it allows preservation**
342 **of lamb** nutritional value. In contrast, published data **suggest a lack of** effect of dietary

343 vitamin E on modifying the percentage of intramuscular fat (Bellés et al., 2018;
344 Kasapidou et al., 2012, Zhao et al. 2013).

345 **4.2 Oxidative reactions**

346 Meat oxidation comprises both lipid and protein oxidative reactions. Lipid oxidation
347 starts at the membrane level in the phospholipid fractions as a free-radical autocatalytic
348 **chain reaction mechanism** in which prooxidants interact with unsaturated fatty acids
349 leading to the release of free radicals and the propagation of the oxidative chain.
350 Regarding protein oxidation, it could be promoted by either the interaction with reactive
351 oxygen species or indirect reactions with secondary products of oxidative stress
352 (Faustman, Sun, Mancini, & Suman, 2010; Zhang, Xiao, & Ahn, 2013).

353 Vitamin E is a major *in vivo* antioxidant that protects tissues from oxidative damage,
354 and this **effect is carried through to meat after slaughter**. The effect of vitamin E on lipid
355 stability increases with dosage and, **therefore**, with its concentration in muscle (Jose et
356 al., 2016; Kasapidou et al., 2012; González-Calvo, Ripoll, Molino, Calvo, & Joy, 2015).
357 **Indeed, as strong correlation has been observed** (higher than -0.7) between the content
358 of α -tocopherol in muscle **and its ability to protect against oxidative reactions** (Álvarez
359 et al., 2008). Nevertheless, there is a threshold concentration above which any
360 improvement against lipid oxidation could be noted. Álvarez et al. (2008) evaluated the
361 effect of increasing dietary dosages of vitamin E (20, 270, 520 and 1020 mg vitamin
362 E/kg feed) on lamb oxidation, without registering any additional improvement in lipid
363 stability when α -tocopherol in muscle **surpassed** 2.26 mg/kg. Similarly, Lauzurica et al.
364 (2005) and De la Fuente et al. (2007) did not observe any further improvement by
365 increasing the concentration of α -tocopherol above 2.17 mg/kg meat. However, a lower
366 threshold has been proposed by González-Calvo et al. (2015) (0.61-0.90 mg α -
367 tocopherol/kg meat) and Kasapidou et al. (2012) (1.52 mg α -tocopherol/kg meat). By

368 contrast, Yagoubi et al. (2018) and Ponnaipalam et al. (2014) registered the
369 development of lipid oxidative reactions in lamb meat containing approximately 2.30
370 and 2.95 mg α -tocopherol/kg, respectively.

371 Disagreements in the target concentration may be related to differences in meat
372 susceptibility to oxidation, which depends on muscle composition (content of
373 unsaturated lipids, heme pigments, metal catalysts and a range of oxidizing compounds
374 in the muscle tissue) (Falowo, Fayemi, & Muchenje, 2014). In this regard, the study
375 carried out by Ponnaipalam et al. (2014) helps to understand the relationship between
376 meat biochemical components and the effect of vitamin E on inhibiting lipid oxidation.
377 It shows that when muscle tocopherol concentration is lower than 2.95 mg/kg muscle,
378 other variables such as heme iron or PUFA have a significant role in lipid oxidation
379 spread. Above this concentration, vitamin E is the major compound managing lipid
380 oxidation in meat. On the other hand, extrinsic variables like illumination and
381 atmosphere composition during display also influence lipid oxidation. Thus, it seems
382 difficult to establish a minimum concentration of muscle tocopherol to avoid completely
383 lipid oxidation, since there are numerous factors taking part on these reactions.

384 Oxidation of meat lipids and proteins widely contribute to the deterioration in flavour of
385 meat products (Campo et al., 2006). TBARS has been described to be a good indicator
386 of the development of rancid off-flavours. Campo et al. (2006) have related TBARS
387 with human perception of rancid compounds, concluding that beef flavours were
388 overpowered when TBARS values exceeded a value of 2 mg/kg. The effect of vitamin
389 E on inhibiting lipid oxidation in lamb has been widely demonstrated. Ortuño, Serrano
390 and Bañón (2015) registered values under the proposed threshold in supplemented lamb
391 (600 mg synthetic vitamin E/kg feed) maintained in common retail conditions even after
392 18 days. The strong inhibition of oxidative reactions reduced the perception of rancid

393 odour in chops from supplemented lambs, registering also a more intense meaty odour
394 and as a result, a higher freshness. On the other hand, meat from grass fed lambs
395 containing between 3.3 and 5.88 mg tocopherol/kg meat have shown TBARS values
396 lower than 0.5 MDA at 96 h post-mortem (Ponnampalam et al., 2012a), while
397 Ponnampalam et al. (2017) reported a content of MDA lower than 3 mg in lambs
398 finished with ryegrass (approximately 3 mg vitamin E/kg meat) even after 9 weeks of
399 storage. Guerra-Rivas et al. (2016) and Muñio et al. (2014) also pointed out the great
400 effect of dietary vitamin E on preserving lamb sensory properties, since dietary vitamin
401 E was an effective tool to preserve freshness and overall liking of fresh lamb by
402 reducing the formation of rancid odours and flavours. Table 3 summarises the effect of
403 muscle α -tocopherol on inhibiting lipid and protein oxidation during display.

404 Dietary vitamin E also seems to exert a significant effect on delaying protein oxidation.
405 Protein oxidation involves amino acid destruction, a decrease in protein solubility, loss
406 of enzyme activity, and formation of carbonyls, resulting in a reduction of tenderness
407 and juiciness, flavour deterioration, and discoloration (Zhang et al., 2013). A great
408 reduction of carbonyl formation during storage in lamb chops containing 3.95 mg α -
409 tocopherol/kg (Ortuño et al., 2015) and a delay of protein oxidation in lamb meat with a
410 concentration of α -tocopherol of 2.42 mg/kg (Muñio et al., 2014) have been observed.
411 Nevertheless, these levels are not high enough to completely inhibit carbonyl formation
412 throughout display. Lipid and protein oxidation are cross linked reactions by which they
413 could exacerbate each other (Faustman et al., 2010); therefore, the target concentration
414 of α -tocopherol in muscle to completely inhibit oxidative reactions should be
415 determined taking into account both lipid and protein oxidation.

416 **4.3 Colour**

417 Meat colour mainly depends on the quantity and the chemical state of its principal
418 pigment, myoglobin. When this sarcoplasmic protein is associated with an oxygen
419 molecule it forms a complex called oxymyoglobin, which shows a bright red colour. In
420 the absence of oxygen, it remains as the deoxymyoglobin form, having a purplish red
421 colour (oxymyoglobin and deoxymyoglobin forms are interconvertible). Oxidation of
422 Fe^{2+} to Fe^{3+} implies the conversion of the pigment into metmyoglobin, resulting in the
423 change of a desirable red to a brown colour.

424 Myoglobin may be oxidised to metmyoglobin by different chemical pathways. Primary
425 and secondary products of lipid oxidation have been identified as major causes of
426 myoglobin oxidation, especially in muscles with high amounts of PUFA. Unsaturated
427 fatty acids are known to be more susceptible to oxidation, leading to the release of free
428 radicals that enhance meat discolouration. On the other hand, heme proteins could
429 favour lipid oxidation. Nevertheless, lipid and protein oxidation are not always tightly
430 interconnected. In low pO_2 atmospheres oxymyoglobin is rapidly converted to
431 metmyoglobin while these conditions provide a high stability to lipids (Faustman et al.,
432 2010). Therefore, myoglobin may oxidise either by interacting directly with reactive
433 oxygen species or indirectly with secondary products of lipid oxidation.

434 A better appearance of meat from supplemented lambs through display can be explained
435 by the effect of vitamin E on delaying the formation of metmyoglobin. The mechanism
436 by which vitamin E inhibits the conversion of myoglobin to its oxidised form is not
437 completely clear. The direct antioxidant action of α -tocopherol on protecting membrane
438 lipids would reduce the formation of primary and secondary compounds of lipid
439 oxidation, delaying indirectly myoglobin oxidation. On the other hand, vitamin E could
440 prevent the oxidation of myoglobin directly. In this sense, the conclusions obtained in

441 the study of Ponnampalam, Butler, McDonagh, Jacobs and Hopkins (2012b) highlighted
442 the key role of heme iron and tocopherol in overriding meat colour.

443 By both mechanisms, vitamin E has been demonstrated to reduce the conversion of
444 myoglobin to metmyoglobin and therefore to protect lamb from colour fading (Bellés et
445 al., 2018; Jose et al., 2016; Kerry et al., 2000; Lauzurica et al., 2005; Leal et al., 2018;
446 Ripoll et al., 2011). Table 4 summarises the effects of dietary vitamin E on meat colour.
447 Data from instrumental (Álvarez, et al., 2008; Bellés et al., 2018, Ripoll, Jose et al.,
448 2016; Joy and Muñoz, 2011, Kerry et al., 2000, Yagoubi et al., 2018) and sensory
449 (Muela, Alonso, Campo, Sañudo, & Beltrán, 2014) colour analyses indicate the
450 existence of a concentration-dependent effect; the higher the α -tocopherol concentration
451 in muscle, the higher colour stability. Nevertheless, there seems to exist a concentration
452 above which no improvement in meat colour could be expected. Recent studies
453 suggested a concentration of 3.5-4.0 mg α -tocopherol/kg tissue as the threshold for
454 obtaining an improvement in lamb colour (Jose et al. 2016; Hopkins, Lamb, Kerr, Van
455 der Ven, & Ponnampalam, 2013).

456 4.4 Aromatic compounds

457 The aroma of meat is the result of a very complex process. The primary reactions
458 involved in the formation of aroma compounds are the oxidation of lipids, the
459 degradation of thiamine, the Strecker reaction, and the Maillard reaction (Resconi,
460 Escudero, & Campo, 2013). The aroma of meat is mainly developed upon heat
461 treatment, where the precursors of aroma compounds (thiamine, glycogen,
462 glycoproteins, nucleotides, nucleosides, free sugars/phosphate, amino acids, peptides,
463 amines, organic acids and lipids) participate through those primary reactions in forming
464 intermediates, which can continue to react with other degradation products to form a

465 complex mixture of volatiles, including those that are responsible for the aroma of meat
466 (Imafidon & Spanier, 1994).

467 The action of vitamin E would indirectly affect the development of lamb aroma by
468 reducing protein and lipid oxidation. The inclusion in the diet of 300 IU (Rivas-Canedo
469 et al., 2013) is able to reduce the formation of 2-heptanone, 2-penten-1-ol, 2-octen-1-ol,
470 pentane and heptane, deriving from lipid oxidation, and ethylbenzaldehyde, deriving
471 from Strecker degradation. Aldehydes and ketones have a key impact in sensory
472 perception due to their lower threshold. As an example, 2-heptanone has been
473 associated to lamb flavour (Resconi et al., 2010).

474 The different ingredients in the diet have a clear effect in the fatty acid composition,
475 which further influences the formation of volatile and therefore meat aroma (Wood et
476 al., 2008). Together with a higher PUFA content, especially from *n*-3 PUFA, pasture
477 based diets show increased levels of antioxidants. The effect of antioxidants in these
478 diets is difficult to separate from the effect of the fatty acid composition, since the
479 different fatty acids are able to develop different volatile compounds, in increasing
480 number, as the unsaturation of the fatty acid increases (Elmore et al., 2002). This
481 increased number of aroma volatiles also implies a higher number of odour notes
482 (Campo et al., 2003), including fishy notes that only appear when *n*-3 PUFA are
483 involved.

484 4.5 Microbial growth

485 Microbial growth is one of the main causes of fresh meat spoilage. Commonly, bacteria
486 responsible of this process are *Brochotrix thermospacta*, *Carnobacterium*,
487 *Enterobacteriaceae*, *Lactobacillus* spp., *Leuconostoc* spp., *Pseudomonas* spp. and
488 *Shewanella putrefaciens*. Microbial growth involves the consumption of meat specific
489 compounds such as glycogen, glucose, lactic acid, amino acids or proteins and its

490 conversion into a wide variety of metabolites responsible of the characteristic off odours
491 and off flavours of spoiled meat. Moreover, other defects like discolouration, gas or
492 slime production tend to appear in fresh meat when microbial counts reach 10^{7-8} ufc/g
493 (Nychas, Skandamis, Tassou, & Koutsoumanis, 2008).

494 Vitamin E is not likely to exert any effect against bacteria multiplication as no feasible
495 bacteriostatic or bactericide mechanism has been described. Neither the addition of α -
496 tocopherol directly on meat products (Georgantelis, Ambrosiadis, Katikou, Blekas, &
497 Georgakis, 2007) nor the supplementation of lamb diet with DL- α -tocopherol resulted
498 in lower total viable, *Enterobacteriaceae* or lactic acid bacteria counts trough display
499 (De la Fuente et al., 2007; Muno et al., 2014). Therefore, despite a limited number of
500 studies in which the effect of α -tocopherol on microbial growth has been evaluated, it
501 could be concluded that vitamin E lacks antimicrobial activity.

502 **5. Conclusions**

503 Vitamin E acts as a chain **breaking antioxidant, and its effects are perhaps most critical**
504 **at the PUFA-rich phospholipid bilayer of muscle cells.** This effect depends on
505 concentration, which may be increased by supplementation of natural or synthetic
506 sources. Increasing dietary vitamin E does not affect growth performance or carcass
507 characteristics if the minimum requirements for normal growth and health are already
508 satisfied. Nevertheless, it could produce modifications in ruminal processes which seem
509 to modify fatty acid hydrogenation, resulting in changes in the proportion of specific
510 fatty acids in tissue. Increasing the content of muscle tocopherol is an effective means to
511 protect PUFA and proteins from oxidation, therefore decreasing colour fading and off-
512 odour formation in lamb meat.

513 A key feature is to reach a minimum muscle concentration enough to effectively inhibit
514 oxidative reactions, which unfortunately depends on the different factors that affect the
515 balance between meat pro-oxidants and antioxidants such as muscle composition,
516 packaging or storage temperature.

517 **6. Conflict of interests**

518 None to declare

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820 **Figure 1.** Stereoisomers of α -tocopherol.

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823 **Figure 2.** Content of α -tocopherol in lamb *M. semimembranosus* after slaughter
824 obtained in different studies.

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832 **Table 1.** Chemical structure of vitamin E-like compounds

Trivial name	Chemical name	Ring position		
		R ¹	R ²	R ³
α -tocopherol	5,7,8 -Trimethyltocol	CH ₃	CH ₃	CH ₃
β -tocopherol	5,8-Dymethyltocol	CH ₃	H	CH ₃
γ -tocopherol	7,8-Dymethyltocol	H	CH ₃	CH ₃
δ -tocopherol	8-Methyltocol	H	H	CH ₃
α -tocotrienol	5,7,8 -Trimethyltocotrienol	CH ₃	CH ₃	CH ₃
β -tocotrienol	5,8-Dymethyltocotrienol	CH ₃	H	CH ₃
γ -tocotrienol	7,8-Dymethyltocotrienol	H	CH ₃	CH ₃
δ -tocotrienol	8-Methyltocotrienol	H	H	CH ₃

833 From: Fennema, Whitaker, Davidson, & Hartel (2004)

834

835

836 **Table 2.** Bioequivalence between RRR- α -tocopherol and all-rac- α -tocopherol in some
837 livestock species.

Species	Bio-availability RRR- α -tocopherol/ all-rac- α -Tocopherol	Reference
Dairy cows	2	Weiss, Hogan, & Wyatt (2009)
Piglets	2	Lauridsen et al. (2002)
Sows	1.5	Lauridsen et al. (2002)
Swine	2	Lauridsen et al. (2002)

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Muscle	Content of tocopherol (mg/kg)	MAP composition	Display	Effect on selected traits	Reference
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841 **Table 3.** Effect of muscle tocopherol on lipid and protein oxidation during display.

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Lipid oxidation

<i>Semimembranosus</i>	3.91	70% O ₂ - 30% CO ₂	9 days at 4 °C	Vitamin E supplementation reduced at least half the content of MDA found in control samples (1.21 vs 2.83 mg MDA/kg)	Bellés et al. 2018
<i>Longissimus thoracis et lumborum</i>	3.95	70% O ₂ - 30% CO ₂	18 days at 2 °C	Tocopherol decreased TBARS values compared to control (1.03 vs 8.15 mg MDA/kg)	Ortuño et al., 2015
<i>Longissimus dorsi</i>	2.42	70 % O ₂ - 30% CO ₂	12 days at 2 °C	Dietary vitamin E inhibited MDA formation	Muiño et al., 2014
<i>Semimembranosus</i>	1.90	75% O ₂ - 25% CO ₂	6 days at 4 °C	This level seemed to be minimum to inhibit lipid oxidation	Kasapidou et al., 2012
<i>Semimembranosus</i>	0.90	75% O ₂ - 25% CO ₂	6 days at 4 °C	This concentration of tocopherol in muscle appeared inactive in preventing lipid oxidation	Kasapidou et al., 2012
<i>Longissimus dorsi</i>	2.17	70% O ₂ - 30% CO ₂	28 days at 2 °C	Muscle tocopherol reduced significantly lipid oxidation compared to control (1.5 vs 8 mg MDA/kg)	Lauzurica et al., 2005
<i>Longissimus dorsi</i>	3.57	70% O ₂ - 30% CO ₂	28 days at 2 °C	This concentration of tocopherol avoided lipid oxidation	Lauzurica et al., 2005
<i>Longissimus dorsi</i>	5.30	70% O ₂ - 30% CO ₂	10 days at 4 °C	Supplemented lamb had lower TBARS values than non-supplemented (3 vs 9 mg MDA/kg)	Kerry et al., 2000
<i>Longissimus dorsi + Semimembranosus</i>	≈ 3	Vacuum packaging + overwrapping	60 days aging + 4 days of display at 3 °C	Lambs fed with ryegrass had higher levels of tocopherol and showed lower levels of lipid oxidation	Ponnampalam et al., 2017
<i>Longissimus thoracis et lumborum</i>	6.64	Overwrapping	9 days at 4 °C	Rosemary supplemented lambs presented lower TBARS values	Yagoubi et al., 2018
Protein oxidation					
<i>Longissimus thoracis et lumborum</i>	3.95	70% O ₂ - 30% CO ₂	18 days at 2 °C	Muscle tocopherol prevented protein oxidation (3.16 vs 6.96 nmol carbonyl g ⁻¹ protein)	Ortuño et al., 2015
<i>Longissimus dorsi</i>	2.42	70% O ₂ - 30% CO ₂	12 days at 2 °C	Vitamin E samples showed lower carbonyl content than the controls	Muiño et al., 2014

843 MAP: Modified atmosphere packaging; MDA: Malondialdehyde; TBARS:

844 Thiobarbituric reactive substances.

845

846 **Table 4.** Effect of muscle tocopherol on meat colour during display.

Muscle	Content of tocopherol (mg/kg)	MAP composition	Display	Effect on selected traits	Reference
				Vitamin E decreased MMb formation (12 %), obtaining a higher value of the 630/580 ratio (1.41 vs 1.18)	
<i>Semimembranosus</i>	3.91	70% O ₂ -30% CO ₂	9 days at 4 °C		Bellés et al. 2018
<i>Longissimus thoracis et lumborum</i>	3.95	70% O ₂ -30% CO ₂	18 days at 2 °C	Supplemented sampled showed higher chroma values and a better appearance	Ortuño et al., 2015
<i>Semimembranosus</i>	3.73	75% O ₂ -25% CO ₂	6 days at 4 °C	Dietary vitamin E prevented meat from discolouration, resulting in higher chroma and a* values than control	Kasapidou et al., 2012
<i>Longissimus dorsi</i>	3.57	70% O ₂ -30% CO ₂	28 days at 2 °C	A dosage of 1000 mg α-tocopherol/kg feed reduced MMb formation by half	Lauzurica et al., 2005
<i>Longissimus dorsi</i>	5.30	70% O ₂ -30% CO ₂	10 days at 4 °C	Dietary vitamin E enhanced colour stability (lower proportions of MMb and higher a* values)	Kerry et al., 2000
<i>Semimembranosus</i>	3.5-4.0	Wrapping with chloride cling wrap	96 hours at 4 °C	No added benefit in meat colour was noted above this concentration	Jose et al., 2016
<i>Longissimus thoracis et lumborum</i>	6.64	Overwrapping	9 days at 4 °C	Rosemary supplemented lambs presented higher Chroma, Hue and oxymyoglobin values	Yagoubi et al., 2018

847

848 MAP: modified atmosphere packaging; MMb: metmyoglobin.

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852 **Highlights**

- 853 The deposition of tocopherol in the muscle depends on the supplementation rate.
- 854 The relationship between vitamin E dose and α -tocopherol deposition may be nonlinear.
- 855 Dietary vitamin E does not affect productive parameters.
- 856 Vitamin E reduces lipid oxidation, discolouration and protects PUFA from degradation.
- 857 Vitamin E would indirectly affect the development of lamb aroma.

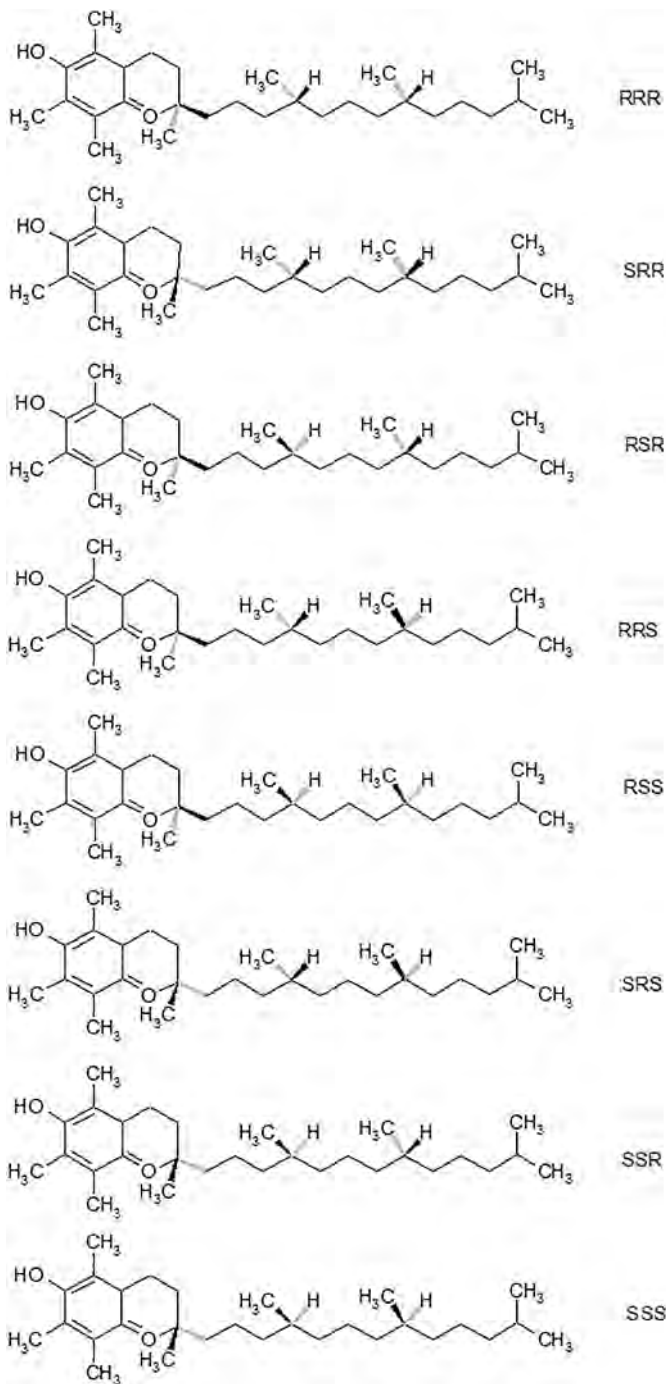


Figure 1

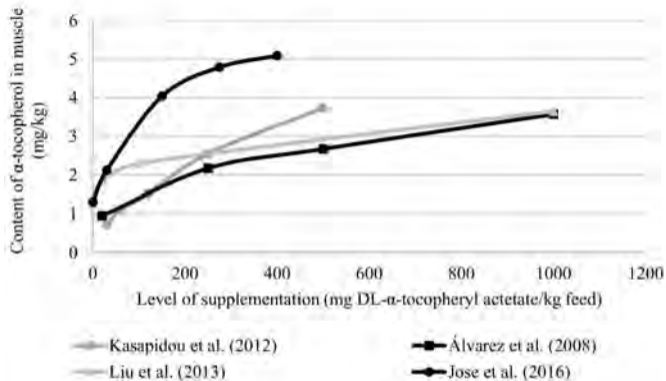


Figure 2