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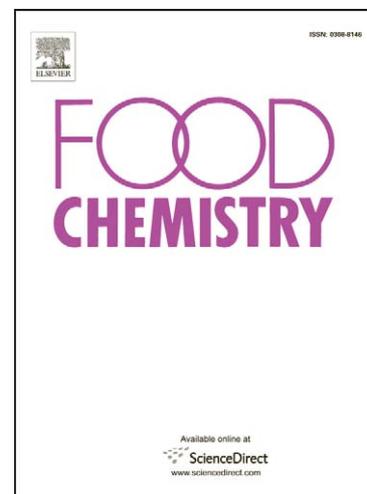
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1 **Manipulating the taste-related composition of strawberry fruits (*Fragaria x***
2 ***ananassa*) from different cultivars using deficit irrigation**

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9
10 **ABSTRACT**

11
12 Demand and, consequently, production of strawberry fruits has increased over the past few
13 years and, as a result, the water abstractions for cultivation of this fruit have risen considerably. To
14 limit the amounts of water used for several horticultural crops, water deficit irrigation (DI) has been
15 seen as a potential alternative for new cultivation systems. DI in strawberry fruits is generally
16 associated with reduction in berry size and yield; however, a recent study demonstrated that DI on
17 strawberry can increase the concentration of some taste- and health-related compounds in fruits from
18 cv. Elsanta. Hence, the aim of the present study was to further corroborate such findings and to assess
19 the response (and variability) among different strawberry cultivars (namely Christine, Elsanta,
20 Florence, Sonata and Symphony) to imposed water-DI conditions. Water-DI affected both fruit
21 physiology and biochemistry. Nevertheless, the response to drought stress was different for each of the
22 cultivars tested. Plants from cvs. Elsanta, Sonata and Symphony showed a greater reduction in berry
23 size, accompanied by a significant increase in dry matter content for fruit harvested from DI-treated
24 plants. Concomitant to this, and where dry matter was increased, the concentrations of sugars and some

25 acids were generally higher in DI-derived fruit. In contrast, cvs. Florence and Christine did not show
26 significant variations in berry weight or any of the target analytes measured when grown under the
27 conditions imposed in this study. The results presented herein suggest that reducing water irrigation
28 between flower initiation and fruit harvest may be a viable technique for increasing the concentrations
29 of taste-related compounds in cvs. Elsanta, Sonata and Symphony and it may not have a negative
30 impact on overall fruit size of cvs. Christine and Florence.

31

32 *Keywords: Berry size, dry matter, organic acids, sugars, sweetness*

33

34 **1. Introduction**

35 Demand for and availability of strawberries (*Fragaria x ananassa* Duch.) have increased
36 substantially during recent years, driven in part, by the highly desired taste of the fruit, along with its
37 known health-promoting properties (Wang, Feng, Lu, Bowman & Ding, 2005). To satisfy this demand,
38 over 250,000 ha are currently designated for strawberry cultivation worldwide (FAOSTAT, 2007).
39 Strawberry production is generally irrigated, as it is known that strawberry plants are very sensitive to
40 drought stress during flowering and fruit ripening (Krüger, Schmidt & Brückner, 1999). Nowadays,
41 however, concerns are arising due to the high water abstractions used for some horticultural purposes,
42 especially in some areas where water resources are already scarce or threatened. Growers are under
43 increasing pressure to demonstrate that their water abstractions for irrigation are reasonable, justified
44 and environmentally sustainable (Fereres & Soriano, 2007; Terry, Chope & Giné Bordonaba, 2007a;
45 Leathes, Knox, Kay, Trawick & Rodríguez-Díaz, 2008). To ease pressure on existing water resources,
46 water deficit irrigation (DI) has been seen as a potential alternative for new cultivation systems which
47 could not only considerably reduce water usage but also increase water use efficiency in several
48 horticultural crops (Topcu, Kirda, Dasgan, Kaman, Cetin, Yazici & Bacon, 2007). DI, also known as

49 regulated deficit irrigation (RDI), is an irrigation technique whereby crops are exposed to lower
50 amounts of water and the minor stress experienced by the plant is expected to have a minimal effect on
51 the yield (English & Raja, 1996). In strawberry plants, however, this technique (DI) is generally
52 associated with reduction in fruit size and yield (Blatt, 1984; Serrano, Carbonell, Savé, Marfà &
53 Peñuelas, 1992; Krüger et al., 1999; Liu, Savić, Jensen, Shahnazari, Jacobsen, Stikić & Andersen,
54 2007). Nevertheless, a recent study demonstrated that DI of strawberry cv. Elsanta plants can markedly
55 increase the concentration of some taste- and health-related compounds in both primary and secondary
56 ripe fruit (Terry *et al.*, 2007a). Indeed, despite berry size being detrimentally affected by DI,
57 monosaccharides, and more importantly the sugar/acid ratio, were generally much greater in DI-treated
58 fruits. In this context, the ratio between sugar and acids in strawberries and other berries can act as an
59 important indicator of fruit taste (Terry, White & Tigwell, 2005; Giné Bordonaba & Terry, 2008), fruit
60 ripeness (Pérez, Olías, Espada, Olías & Sanz, 1997) or even as an index of consumer acceptability
61 (Keutgen & Pawelzik, 2007a).

62 Most of the studies conducted thus far, which have endeavoured to elucidate the effect of DI on
63 strawberry fruit, have been focused on a single cultivar, rather than evaluating the response of different
64 genotypes to imposed water deficit conditions. It is known that different strawberry cultivars respond
65 differently to imposed stress conditions. For instance, cvs. Elsanta and Korona responded differently
66 when grown in enriched ozone atmospheres (Keutgen & Pawelzik, 2008a) or under long term salt
67 stress (Keutgen & Pawelzik, 2008b). It is therefore plausible to speculate that strawberry cultivars will
68 respond differently to imposed DI conditions. Hence, the aim of the present study was to assess the
69 response (and variability) among five different strawberry cultivars (namely Christine, Elsanta,
70 Florence, Sonata and Symphony) to imposed water-DI conditions. Specific emphasis was given to
71 quantifying sugars and organic acids as the main indicators of strawberry fruit quality and taste.

73 2. Materials and methods

74 2.1. Plant materials and experimental design

75 Five different maiden year cold-stored strawberry cultivars were grown in a glasshouse during
76 2007 (April to July) in 1 l capacity pots containing compost. The total nitrogen concentration of the
77 compost substrate was 8.88 g N kg⁻¹, as determined by Kjeldahl analysis. A completely randomised
78 design was adopted with each of 4 blocks containing 30 plants (5 cvs. x 3 replicates x 2 treatments = 30
79 x 4 blocks = 120). Water treatments started when most of the primary fruits from the primary truss
80 were at flower initiation stage. Plants were irrigated with either 50 or 200 ml day⁻¹ over an eight-week
81 periods, daily (*ca.* 09:00 h). Prior to commencing water treatments, plants were kept at or near field
82 capacity (*ca.* 0.8 m³ of water per m³ of soil) for approximately four weeks. Plants were treated to
83 prevent incidence of spider mites (*Tetranychus* spp.) and powdery mildew (*Podosphaera aphanis*,
84 formerly *Sphaerotheca macularis* (Wallr.: Fr) Jacz f sp. *fragariae* Peries), as described elsewhere
85 (Terry & Joyce, 2000; Terry *et al.*, 2007a). Flowers were hand-pollinated with a sable paintbrush to
86 minimise the occurrence of misshapen fruit.

87

88 2.2. Soil moisture content and environmental monitoring

89 Soil moisture content (m³ water per m³ of growing media) was measured daily (*ca.* 16.00h) by
90 time-domain-reflectometry (TDR), using a Thetaprobe (ThetaKit type TK3, Delta-T devices, Cambs.,
91 UK). The water-holding characteristics of the soil media were determined as described by Terry *et al.*
92 (2007a). Hourly temperatures within the glasshouse were recorded by means of four Tiny Tag Ultra 2
93 data loggers (Gemini Data Logger, Sussex, UK), each shielded from solar radiation by a polystyrene
94 cup and placed in each block. Mean temperature inside the glasshouse during the growing period was
95 21 °C.

96

97 *2.3. Fruit sampling*

98 From each plant, both of the secondary fruits from the primary truss were harvested according
99 to developmental stage. All fruits were harvested at the red stage, which was considered as optimum
100 ripeness. Days after anthesis (DAA) was monitored for primary and secondary fruits from the primary
101 truss by tagging of flowers (n = 360) at anthesis (Terry & Joyce, 2000). The objective colour of each
102 fruit was measured using a Minolta CR-400 colorimeter and a DP-400 data processor (Minolta Co.
103 Ltd., Japan) with an 8 mm light-path aperture. The instrument was calibrated with a Minolta standard
104 white tile CR-400 (Y = 93.5, x = 0.3114, y = 0.3190). The mean of three readings at 3 equidistant
105 points around the equatorial axis of the fruits were recorded and the lightness (L*), chroma (colour
106 saturation; C*) and hue angle (H°) automatically calculated (Terry, Ilkenhans, Poulston, Rowsell &
107 Smith, 2007b). Berry weight, with and without calyx, was measured and recorded. Strawberry
108 secondary fruits without calyces were cut in half vertically, immediately snap-frozen in liquid nitrogen
109 and stored briefly at -40°C before being freeze-dried in an Edwards Modulyo freeze-drier (W. Sussex,
110 UK) for 3 days at 0.015kPa. Lyophilized samples were then ground in a pestle and mortar, weighed and
111 returned to the freezer prior to use. All reagents were purchased from Sigma (Dorset, UK) unless
112 otherwise stated.

113

114 *2.4. Extraction and quantification of sugars*

115 Sugars were extracted using 62.5% (v/v) aqueous methanol, as described elsewhere (Terry et
116 al., 2007a). Sugar content in strawberry extracts was determined using an Agilent 1200 series HPLC
117 binary pump system (Agilent, Berks., UK), equipped with an Agilent refractive index detector (RID)
118 G1362A. Strawberry extracts (20 µl) were diluted (1:10), and injected into a Rezex RCM
119 monosaccharide Ca⁺ (8%) column of 300 mm x 7.8 mm diameter (Phenomenex, CA, USA; Part no.
120 00H-0130-K0) with a Carbo-Ca²⁺ guard column of 4 mm x 3 mm diameter (Phenomenex,; Part no.

121 AJ0-4493). Temperature of the column was set at 80°C, using a G1316A thermostatted column
122 compartment. The mobile phase used was HPLC grade water at a flow rate of 0.6 ml min⁻¹ (Terry et al.,
123 2007a; Giné Bordonaba & Terry, 2008). Temperature of the optical unit in the detector was set up at
124 30°C and temperature of the autosampler at 4°C using an Agilent cooled autosampler G1330B. The
125 presence and abundance of fructose, glucose and sucrose were automatically calculated by comparing
126 sample peak area to standards (0.025-2.5 mg ml⁻¹) using ChemStation Rev. B.02.01.

127

128 *2.5. Extraction and quantification of non-volatile organic acids*

129 Extracts for organic acids determination were prepared as described elsewhere (Terry et al.,
130 2007a; Giné Bordonaba & Terry, 2008). Briefly, freeze-dried strawberry extracts (50 mg) were
131 dissolved in 3 ml of HPLC grade water. Samples were kept at room temperature (25°C) for 10 min and
132 then filtered through a 0.2 µm syringe filter. L-ascorbic, citric, and malic acid contents in extracts were
133 detected at 210 nm, using the same HPLC system, as described above, equipped with an Agilent DAD
134 G1315B/G1365B photodiode array with multiple wavelength detector. Extracts (20 µl) were injected
135 into an Alltech Prevail Organic Acid column 250 mm x 4.6 mm diameter, 5 µm particle size (Alltech,
136 CA, USA; Part no. 88645) with an Alltech Prevail Organic Acid guard column of 7.5 mm x 4.6 mm
137 diameter (Alltech; Part no. 96429). The mobile phase was analytical grade degassed 0.2% (w/v)
138 metaphosphoric acid in H₂O (Giné Bordonaba and Terry, 2008). The flow rate of the mobile phase was
139 1.0 ml min⁻¹ under isocratic conditions and the column temperature was set at 35 °C. Temperature of
140 the autosampler was set at 4°C. The presence and quantity of each acid was calculated by comparing
141 the peak area obtained with standards (0.02-2.0 mg ml⁻¹), using ChemStation Rev. B.02.01.

142

143

144

145 2.6. Estimation of strawberry taste parameters

146 Sweetness index (SI) for the different cultivars analysed was calculated as previously described
147 (Keutgen & Pawelzik, 2007a). Briefly, the contribution of each major sugar found in strawberry fruits
148 was calculated, considering that fructose and sucrose are 2.3 and 1.35 times sweeter than glucose,
149 respectively. Accordingly, $SI = 1.0 [\text{Glucose}] + 1.35 [\text{Sucrose}] + 2.3 [\text{fructose}]$.

150

151 2.7. Data analysis

152 All statistical analyses were carried out using Genstat for Windows, Version 10 (VSN
153 International Ltd., Herts., UK). Data were subjected to analysis of variance (ANOVA) tests, based on a
154 completely randomised design within blocks. Least significant difference values (LSD; $P = 0.05$) were
155 calculated for mean separations, using critical values of t for two-tailed tests. Correlations between
156 experimental variables were made using Spearman's rank correlations and, if required, presented as
157 Spearman's correlation coefficient (r) and P value, based on a two-tailed test. Unless otherwise stated,
158 significant differences were $P < 0.05$.

159

160 3. Results and discussion

161 3.1. Soil water status

162 Soil water content values of the growing media differed between treatments, but also between
163 cultivars when submitted to DI conditions, indicating the existence of genotypic differences in the
164 response of strawberry plants to drought stress, as well as differences in water usage between different
165 cultivars. Values for non-DI-treated plants were consistent between cultivars, ranging from 0.73 to 0.85
166 m^3 of water per m^3 of growing media (Figure 1). Similar water contents were observed by Terry et al.
167 (2007a) when assessing water deficit irrigation in cv. Elsanta fruits grown under comparable
168 conditions. Greater differences between water content of soils from water-stressed plants and plants

169 kept at or near field capacity were observed for cv. Elsanta during the whole duration of the study
170 (Figure 1). Elsanta plants grown under drought stress conditions used more water (up to 20% more)
171 from the growing medium during the first days after commencing water treatments than did the rest of
172 cultivars. Water usage of DI-treated plants for cvs. Sonata and Symphony were similar throughout the
173 trial as was also observed for cvs. Florence and Christine. Higher water uptake for Elsanta plants may
174 be the result of either the increase in root growth or root hydraulic conductivity or even greater water
175 usage as compared to other cvs. (Savić, Stikić, Radović, Bogičević, Jovanović & Šukalović, 2008).
176 Overall, water content in the growing media of DI-treated plants declined, following water-soil
177 dynamics similar to those previously described (Liu et al., 2007; Terry et al., 2007a; Savic et al., 2008).

179 *3.2. Effect of DI on fruit physiology*

180 The response of fruit physiology to water stress was dependent on the genotype. Differences in
181 fruit physiology among cultivars may be accounted for by differences in abscisic acid (ABA) or other
182 hormone metabolism in plants exposed to drought stress. For instance, the plant hormone ABA
183 regulates various physiological reactions in plants and its role in the response to drought stress is well
184 documented for many horticultural crops (Seki, Umezawa, Urano & Shinozaki, 2007). In strawberry
185 plants (cv. Elsanta), grown under comparable DI conditions, ABA was greater than that of fully
186 irrigated plants (Terry et al., 2007a). In the present study, berry weight from secondary strawberry
187 fruits was significantly reduced (approximately 1/3 lower) by DI in cvs. Symphony, Elsanta and Sonata
188 (Figure 2a). However, both cvs. Christine and Florence showed similar weights, for both water-stressed
189 and non water-stressed plants. Concomitant with this, and in those cultivars where berry size was
190 reduced, dry matter, as a proportion of fresh weight, was considerably greater in fruits from water-
191 stressed plants than from plants kept at or near field capacity (Figure 2b). Previous studies also showed
192 that fruit from strawberry plants that received full irrigation had a higher water content and greater

193 berry fresh weight than had fruit from plants grown under reduced irrigation (Blatt, 1984; Serrano *et*
194 *al.*, 1992; Krüger *et al.*, 1999; Kirnak, Kaya, Higgs & Gercek, 2001; Kirnak, Kaya, Higgs, Bolat,
195 Simsek & Ikinici, 2003; Liu *et al.*, 2007; Terry *et al.*, 2007a). Fruits from cv. Elsanta showed the
196 greatest increase (1.24-fold higher) in dry matter content as a proportion of fresh weight in response to
197 reduced water supply. These findings were in agreement with Terry *et al.* (2007a), since strawberry
198 fruits (cv. Elsanta) from DI-treated plants also showed 25% more dry matter than did non-water
199 stressed plants. Similarly, Kirnak *et al.* (2003) reported higher soluble dry matter contents for cvs. Oso
200 Grande and Camarosa fruits submitted to DI in trials conducted in the field. Plant responses to either
201 water or salt stress have been reported to have much in common (Munns, 2002). For instance, salinity
202 reduces the capacity of plants to take up water, which may result in reduced growth rate and metabolic
203 changes similar to those observed in plants grown under water stress. In this context, strawberry plants
204 grown under high salinity conditions had either higher (Awang & Atherton, 1995) or lower (Keutgen &
205 Pawelzik, 2008b) dry matter contents. The greater dry matter content observed in the results presented
206 herein suggests a concentration effect by either limitation of water uptake and/or enhanced import of
207 solutes into the fruit. In this study, dry matter content from other parts of the plants were not
208 investigated and therefore, it is difficult to conclude whether or not the increased dry matter may be
209 the result of a trade off in resource allocation within the plant (e.g. vegetative and root growth versus
210 fruit growth). This said, the dilution effect observed in plants that received more water was limited to
211 certain cultivars since fruits from cv. Christine and/or Florence showed similar dry matter contents
212 between DI-treated and non-water-stressed plants (Figure 2b).

213 Anthesis occurred significantly ($P < 0.05$) later in water-stressed plants for cvs. Elsanta,
214 Florence and Christine and was generally reduced for the other cultivars investigated. In a similar
215 manner, fruit maturation was also slower for some water-stressed cvs. (*viz.* Elsanta and Christine)
216 taking 33 days after anthesis for plants treated with 50 ml of water per day in comparison to 31 days for

217 plants receiving 200 ml per day (data not shown). Time from anthesis to harvest for all other cvs. was
218 not affected by DI. Terry et al. (2007a) also found that fruit maturation was slower (not significantly) in
219 Elsanta fruit grown under drought stress conditions. Indeed, it has been shown that, for certain crops,
220 drought stress may result in considerable increase of the time to anthesis and to physiological maturity
221 (Geerts, Raes, Garcia, Mendoza & Huanca, 2008).

222

223 *3.3. Effect of DI on taste-related compounds and overall fruit quality*

224 Colour of strawberries is without doubt one of the main attributes which governs consumer
225 perception and therefore their acceptability (Francis, 1995). Objective colour of each fruit was
226 measured when fruit was adjudged to be at optimum ripeness (when fully red) and significant
227 differences were encountered between the different cultivars investigated (Table 1). Similarly,
228 significant differences in objective colour have been reported by others when studying different
229 cultivars (Sacks & Shaw, 1994; Capocasa, Scalzo, Mezzetti & Battino, 2008; Hernanz, Recamales,
230 Meléndez-Martínez, González-Miret & Heredia, 2008; Giné Bordonaba and Terry, 2009) or between
231 fruits from plants grown under different conditions (Hernanz et al., 2008). Generally, no significant
232 differences were observed for colour (L^* , C^* , H°) parameters among secondary fruits within a cultivar.
233 Nonetheless, even if all fruit were picked at the full red stage, significant differences were encountered
234 for C^* values among fruits from Elsanta. Accordingly, previous work carried out by Terry et al.
235 (2007a) also found significant differences in the objective colour of strawberry cv. Elsanta fruits when
236 picked at optimum harvest. Generally, DI had a considerable effect on objective fruit colour. Plants
237 receiving 50 ml of water per day showed lower C^* values than did non-water-stressed plants (Table 1).
238 These differences were especially highlighted for cvs. Elsanta, Sonata and Florence ($P < 0.05$). The
239 effect of DI on L^* and H° values was dependent on the cultivar. Some cultivars (namely Elsanta and
240 Symphony) showed higher values for lightness (L^*) and lower redness (higher H°) for

241 plants receiving 50 ml per day than did non-water-stressed plants. The remaining cultivars tended to
242 show lower L^* and H° values for DI-treated plants (Table 1). Likewise, Terry et al. (2007a) also found
243 higher Hue angles in cv. Elsanta fruits treated with 50 ml day⁻¹ than with plants receiving either 100 or
244 200 ml day⁻¹. Strawberry fruit colour is due, in part, to anthocyanins, which account for the red colour
245 of the fruits. It will be expected, therefore, that if lower red coloration (higher H°) is reported for water-
246 stressed plants, lower anthocyanin contents will also be encountered in the fruit. However, in the study
247 carried out by Terry et al. (2007a), DI resulted in lower redness but higher concentration of
248 pelargonidin-3-glucoside and derivatives of this anthocyanin on a FW basis. In view of that, the authors
249 suggested that the lower redness in smaller fruits was most probably an artefact of the objective
250 colorimeter measurement since shorter distances between achenes will exist in smaller fruits, resulting
251 in lower recorded redness.

252 Little information is available which describes the effect of DI on the taste-related attributes
253 (namely sugars and acids) of strawberries (Terry et al., 2007a). In contrast, ample data are available on
254 the effect of either cultivation practices or other stress conditions (namely ozone exposure, salinity) on
255 strawberry fruit quality (Wang, Zheng & Galletta, 2002; Davik, Bakken, Holte & Blomhoff, 2006;
256 Keutgen & Pawelzik, 2007a and 2007b; Hargreaves, Adl, Warman & Rupasinghe, 2008; Keutgen &
257 Pawelzik, 2008b; Hargreaves, Adl & Warman, 2009). In strawberry fruits, non-structural carbohydrates
258 are the main components of dry matter. Independent of the water treatment applied, results showed that
259 sugars accounted for 6 to 8% of the total fresh matter. Similar proportions have been reported by others
260 (Cordenunsi, do Nascimento, Genovese & Lajolo, 2002; Ménager, Jost & Aubert, 2004; Terry et al.,
261 2007a; Keutgen & Pawelzik, 2008b). Fructose, glucose and sucrose were the three main sugars found
262 in the different strawberry genotypes studied, and concentrations differed significantly among cultivars
263 and water treatments (Table 2). Variations in sugar content between different cultivars are not unusual
264 and have been extensively reported (Wang *et al.*, 2002; Skupien & Oszmiański, 2004; Davik *et al.*,

265 2006; Keutgen & Pawelzik, 2008a). The relative concentrations of sugars were similar between cvs.
266 (Table 2); however, fruit from cv. Sonata, had a greater sucrose content than had other cultivars
267 studied. Overall, values were in the range of previously reported studies (Wang *et al.*, 2002; Skupien &
268 Oszmiański, 2004; Davik *et al.*, 2006; Keutgen & Pawelzik, 2008; Giné Bordonaba and Terry, 2009).
269 This said, greater amounts of sucrose were encountered herein and can only really be comparable to the
270 results from Terry *et al.* (2007a), given that the same extraction method was used. Along these lines,
271 fructose and glucose or sucrose are nearly twice or three times more soluble in methanol-based solvents
272 than in aqueous-based solvents (Davis, Terry, Chope & Faul, 2007) and therefore the methanol-based
273 extraction used herein may have enhanced the solubility of these sugars, especially sucrose.
274 Consequently, it is clear that comparison of sugar contents in strawberry fruits from different studies
275 should be treated with some caution.

276 Both on a DW and FW basis, Florence and Sonata were the cvs. showing higher sugar content for non-
277 water-stressed plants (70.8 and 68.8 mg g⁻¹ FW, respectively). Nevertheless, cvs. Elsanta and Sonata
278 fruits had the greater sugar content (82.34 and 81.57 mg g⁻¹ FW, respectively) when subjected to DI.
279 Fructose contents in cvs. Elsanta and Sonata plants, as well as glucose content in Elsanta, were the only
280 sugar contents significantly greater in DI-treated plants than in plants kept at or near field capacity
281 (Table 2). Previous studies (Terry *et al.*, 2007a) also highlighted that, although sucrose was not affected
282 by DI, monosaccharide contents (glucose and fructose) were significantly higher in DI plants. The
283 authors concluded that lower concentrations of sugars in fruits that received more water were most
284 probably due to a dilution effect. Despite total soluble solids not always being well correlated with
285 sugar content in strawberry fruits (Perez *et al.*, 1997; Terry *et al.*, 2005), in the study by Awang *et al.*
286 (1995), higher soluble solids content in cv. Rapella, grown under salinity stress, was associated with
287 restricted vegetative growth and shift of photoassimilates to fruits. In both of these cases, the results
288 from this study may support such findings. Although no evidence exists for strawberry fruits, it is well

289 documented that plants grown under water stress undergo a process of osmotic adjustment (Mahajan &
290 Tuteja, 2005). Thereby, the greater sugar content in DI-treated plants may be an attempt by the plant to
291 reduce osmotic potential by the accumulation of solutes.

292
293 Sweetness of strawberry fruits is an important factor which can characterise the acceptance of
294 the fruits by consumers. Considering that fructose is *ca.* 1.8 times sweeter than sucrose, and the
295 sweetness of glucose is 60% that of sucrose, DI resulted in generally sweeter berries, as determined by
296 the sweetness index (Figure 3a). Fruits from Elsanta plants subjected to drought stress showed as much
297 as one third higher sweetness than fruits from plants kept at or near field capacity. A significant
298 increase in the sweetness index of Sonata was also observed for DI-treated plants.

299
300 Taste in strawberry fruits is not, however, only just influenced by sugars. Acids and volatile
301 compounds are also important contributors to strawberry taste and flavour (Cordenunsi et al., 2002). In
302 the present study, and in earlier reports (Perez et al., 1992; Keutgen & Pawelzik, 2007; Terry et al.,
303 2007a), three major acids were found within the cultivars, corresponding to citric, malic and ascorbic
304 acids. Citric acid was the major acid found in the different cultivars investigated herein, accounting for
305 approximately 1% of the total fresh matter, in agreement with that found in the literature (Terry et al.,
306 2007a; Keutgen & Pawelzik, 2008b; Giné Bordonaba & Terry, 2009). Malic and ascorbic acid were
307 also identified in all cultivars at lower concentrations, up to 4.49 and 0.78 mg g⁻¹ FW, respectively.
308 Drought stress also affected acid composition (Table 3). On a DW basis, plants kept at or near field
309 capacity tended to have greater acid contents than did those exposed to drought stress. Christine and
310 Florence were the only cvs. where DI resulted in higher acid contents. However, considering the results
311 on a FW basis, DI resulted in greater acid content for Symphony and Florence whilst it did not
312 significantly affect acid content for the rest of the cvs. In an earlier study, DI resulted in lower ascorbic,

313 citric and malic acid contents on a DW basis for Elsanta plants (Terry et al., 2007a); however, it is clear
314 that, in the present study, DI had a genotype-dependent effect on acid metabolism. As indicated by
315 differences in fruit physiology, it may be plausible to speculate that DI resulted in different respiratory
316 metabolisms among cultivars and hence different utilisations of respiratory substrates such as organic
317 acids. Strawberry fruits are an important source of ascorbic acid (AsA). This vitamin, in combination
318 with other phytochemicals (namely anthocyanins and phenolic acids) found in strawberry has been
319 reported to be responsible for the numerous health benefits associated with these berries. In this
320 context, strawberries were recently ranked as one of the most important sources of cellular antioxidant
321 activity in the North American diet (Wolfe, Kang, He, Dong, Zhang & Liu, 2008). In the present study,
322 the concentration of AsA ranged from 0.42 (DI treated cv. Elsanta) to 0.73 (DI treated cv. Florence) mg
323 g⁻¹ FW and was dependent on the water regime and cultivar. Values were in agreement with those
324 previously reported (Perez et al., 1992; Davik et al., 2006; Terry et al., 2007a). DI resulted in
325 significantly lower and higher concentration of AsA only for cultivars Elsanta and Florence (Table 3).
326 DI had the greatest effect in cultivar Florence which showed a 1.3-fold higher AsA concentration in
327 fruits from water stressed plants, and hence perhaps resulting in more healthful berries. This said,
328 Keutgen and Pawelzik (2007b), testing strawberry fruits from plants grown under other environmental
329 stress conditions, observed that the content of ascorbic acid was reduced in fruits from cvs. Elsanta and
330 Korona plants subjected to moderate salt stress.

331

332 The balances between sugars and acids in strawberries and other berries are important
333 indicators of fruit taste (Terry et al., 2005 & 2007a; Giné Bordonaba & Terry, 2008). Additionally, the
334 ratio can be used as an indicator of fruit ripeness (Pérez et al., 1997) or even as an index of consumer
335 acceptability (Keutgen & Pawelzik, 2007a). Recently, Terry et al. (2007a) showed that sugar/ acid
336 ratios were significantly greater in DI-treated plants than in non-water-stressed plants. The results from

337 this study show that, although sugar/acid ratios for DI-treated were substantially higher in Symphony,
338 Elsanta and Sonata, significant differences between treatments ($P < 0.05$) were only encountered in
339 fruits from Sonata (Figure 3b). Water DI did not have a significant effect on the sugar / acid ratio of
340 either Christine or Florence, and comparable values were observed for both irrigation regimes.
341 Cordenunsi et al. (2002) reported that good quality strawberry fruits were those with a ratio higher than
342 5.3. However, such information must be accepted with caution as values will directly depend on the
343 nature of the measurements. Plants kept at or near field capacity (for all the cultivars except
344 Symphony) had sugar acid ratios higher than 5 (e.g. Elsanta and Christine with values of 5.9). As a
345 result of DI, the quality of strawberries was significantly and substantially higher in Sonata and Elsanta
346 with values of 6.2 and 6.9, respectively.

347

348 **4. Conclusions**

349 It is known that DI on strawberry plants can reduce berry size and yield. However, the results
350 presented herein, and previous findings by Terry et al. (2007a), showed that DI can have a considerable
351 effect on the concentrations of certain compounds linked to taste and consumer preference. This study
352 showed, for the first time, that differences exist in the way different cultivars respond to drought stress
353 resulting in different fruit compositions. Despite the detrimental effect that DI can have on berry size,
354 reducing water irrigation by a quarter from flower initiation to fruit harvest, resulted in better water use
355 efficiency, as well as enhanced fruit quality and taste (greater sweetness and sugar/acid ratio) in cvs.
356 Elsanta, Sonata and Symphony. In addition, results indicated that, for certain cultivars (namely
357 Christine and Florence), water savings by means of DI, can be achieved without having a negative
358 effect on overall strawberry fruit quality.

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479 **Table captions**

480

481 **Table 1** Effects of water deficit irrigation (DI: 50 ml day⁻¹) or full irrigation (FI: 200 ml day⁻¹) on
482 objective colour (L* is lightness, C* is chroma, and H° is the hue angle) of secondary strawberry fruits
483 from the primary trusses of five different cultivars. Cultivars are arranged in descending order of H°
484 values for fully irrigated plants

485

486 **Table 2** Effects of water deficit irrigation (DI: 50 ml day⁻¹) or full irrigation (FI: 200 ml day⁻¹) on
487 concentration of main sugars of secondary strawberry fruits from the primary trusses of five different
488 cultivars. Cultivars are arranged in descending order of total sugar concentrations for fully irrigated
489 plants on a DW basis

490

491 **Table 3** Effects of water deficit irrigation (DI: 50 ml day⁻¹) or full irrigation (FI: 200 ml day⁻¹) on main
492 non-volatile organic acids of secondary strawberry fruits from the primary trusses of five different
493 cultivars. Cultivars are arranged in descending order of total acid concentrations for fully irrigated
494 plants on a DW basis

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503 **Figure captions**

504

505 **Figure 1** Water volume of the growing medium of five different strawberry cultivars (Symphony (-○-),
506 Elsanta (-▼-), Sonata (-△-), Florence (-■-) and Christine (-□-)) grown under deficit irrigation (50 ml
507 day⁻¹) conditions. Water volumes of growing media from fully irrigated (-●- 200 ml day⁻¹) plants were
508 similar among cultivars and values are presented as the mean per day of the five cultivars. Error bars
509 indicate LSD (P < 0.05) values for the daily interaction cultivar*water treatment. LSD (P < 0.05) value
510 for the overall interaction days*cultivar*water treatment was 0.182

511

512 **Figure 2** Effects of water deficit irrigation (— DI; 50 ml day⁻¹) or full irrigation (— FI; 200 ml day⁻¹)
513 on weight characteristics of secondary fruits from the primary trusses of five different strawberry
514 cultivars; (A) Weight (g) and (B) Dry matter as a proportion of fresh weight (g 100 g⁻¹ FW). Cultivars
515 are arranged in descending order of berry weight for fully irrigated plants. Error bar indicates LSD
516 value (P < 0.05)

517

518 **Figure 3** Effects of water deficit irrigation (— DI; 50 ml day⁻¹) or full irrigation (— FI; 200 ml day⁻¹)
519 on taste-related attributes of secondary fruits from the primary trusses (A: Sugar/acid ratio; B:
520 calculated sweetness) of five different strawberry cultivars. Cultivars are arranged in descending order
521 for calculated sweetness of DI-treated plants. Error bar indicates LSD value (P < 0.05)

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529 **Table 1** Giné Bordonaba and Terry

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Cultivar	L*		C*		H°	
	DI	FI	DI	FI	DI	FI
Christine	44.85	46.87	51.92	52.78	42.6	43.09
Sonata	44.73	46.08	51.69	53.84	43.42	42.98
Elsanta	44.91	44.12	47.49	49.56	46.68	41.84
Symphony	41.76	39.89	46.21	46.65	43.2	38.15
Florence	36.49	40.77	38.06	44.27	36.22	37.12
LSD ($P < 0.05$)	1.857		2.486		2.310	

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Table 2 Giné Bordonaba and Terry

Cultivar	mg g ⁻¹ DW								mg g ⁻¹ FW							
	Sucrose		Fructose		Glucose		Total sugars		Sucrose		Fructose		Glucose		Total sugars	
	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI
Sonata	252	291	143	139	150	169	545	599	39.0	33.5	20.8	16.0	21.8	19.3	81.6	68.8
Florence	202	243	141	156	144	165	487	565	27.3	30.7	19.7	19.4	20.1	20.7	67.1	70.8
Elsanta	191	223	183	158	188	169	562	550	28.0	24.0	26.9	16.8	27.5	17.9	82.3	58.6
Symphony	187	173	145	154	150	171	482	497	23.3	16.7	17.6	14.7	18.3	16.2	59.3	47.6
Christine	188	161	158	148	168	150	514	458	22.9	19.6	19.3	18.2	20.4	18.3	62.5	56.1
LSD (P < 0.05)	49.3		21.1		24.2		50.8		7.20		3.78		4.26		8.74	

Table 3: Giné Bordonaba and Terry

Cultivar	mg g ⁻¹ DW								mg g ⁻¹ FW							
	Ascorbic		Malic		Citric		Total Acids		Ascorbic		Malic		Citric		Total Acids	
	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI	DI	FI
Symphony	90.5	99.1	25.2	35.1	4.86	5.68	121	140	11.1	9.45	3.10	3.35	0.59	0.54	14.8	13.3
Sonata	62.1	83.6	29.5	39.0	3.50	4.13	95.1	127	8.59	9.67	4.13	4.49	0.47	0.47	13.2	14.6
Florence	82.4	80.3	21.4	23.4	5.33	4.31	109	108	11.4	10.1	2.91	2.97	0.73	0.54	15.1	13.6
Christine	80.4	66.2	29.1	21.5	5.09	5.10	115	92.8	9.63	7.87	3.46	2.55	0.60	0.61	13.7	11.0
Elsanta	64.7	63.6	16.4	22.2	3.07	5.22	84.2	91.0	9.22	6.88	2.36	2.43	0.42	0.57	12.0	9.88
LSD (P < 0.05)	1.26		7.11		17.0		20.3		0.143		0.876		2.12		2.81	

FIGURES

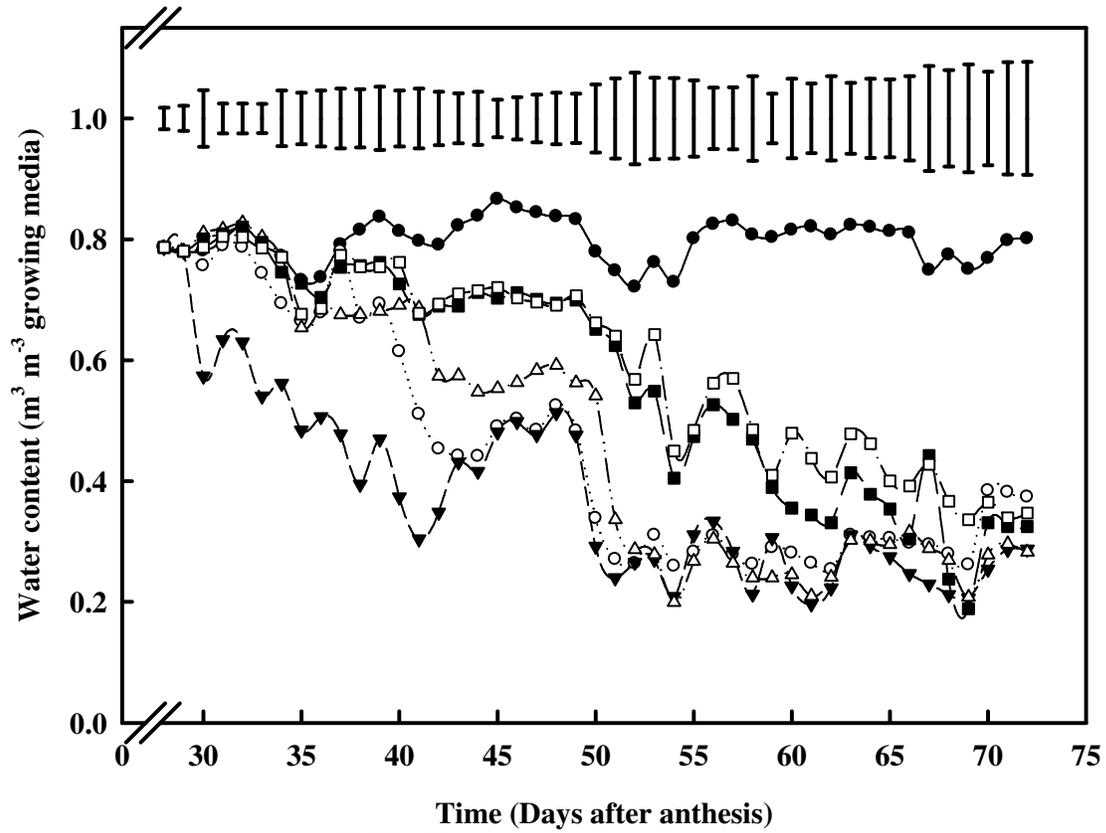


Figure 1 Giné Bordonaba and Terry

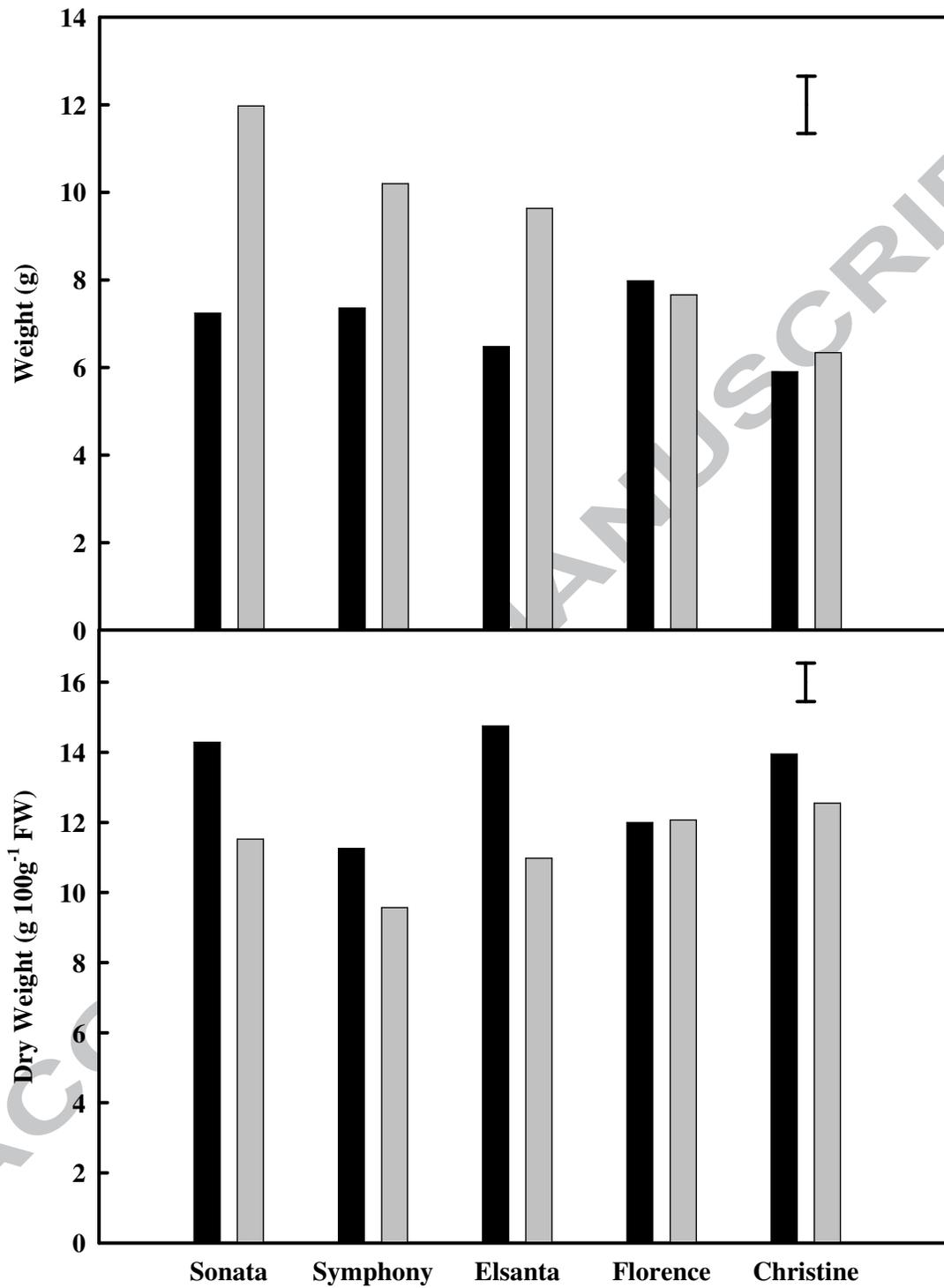


Figure 2 Giné Bordonaba and Terry

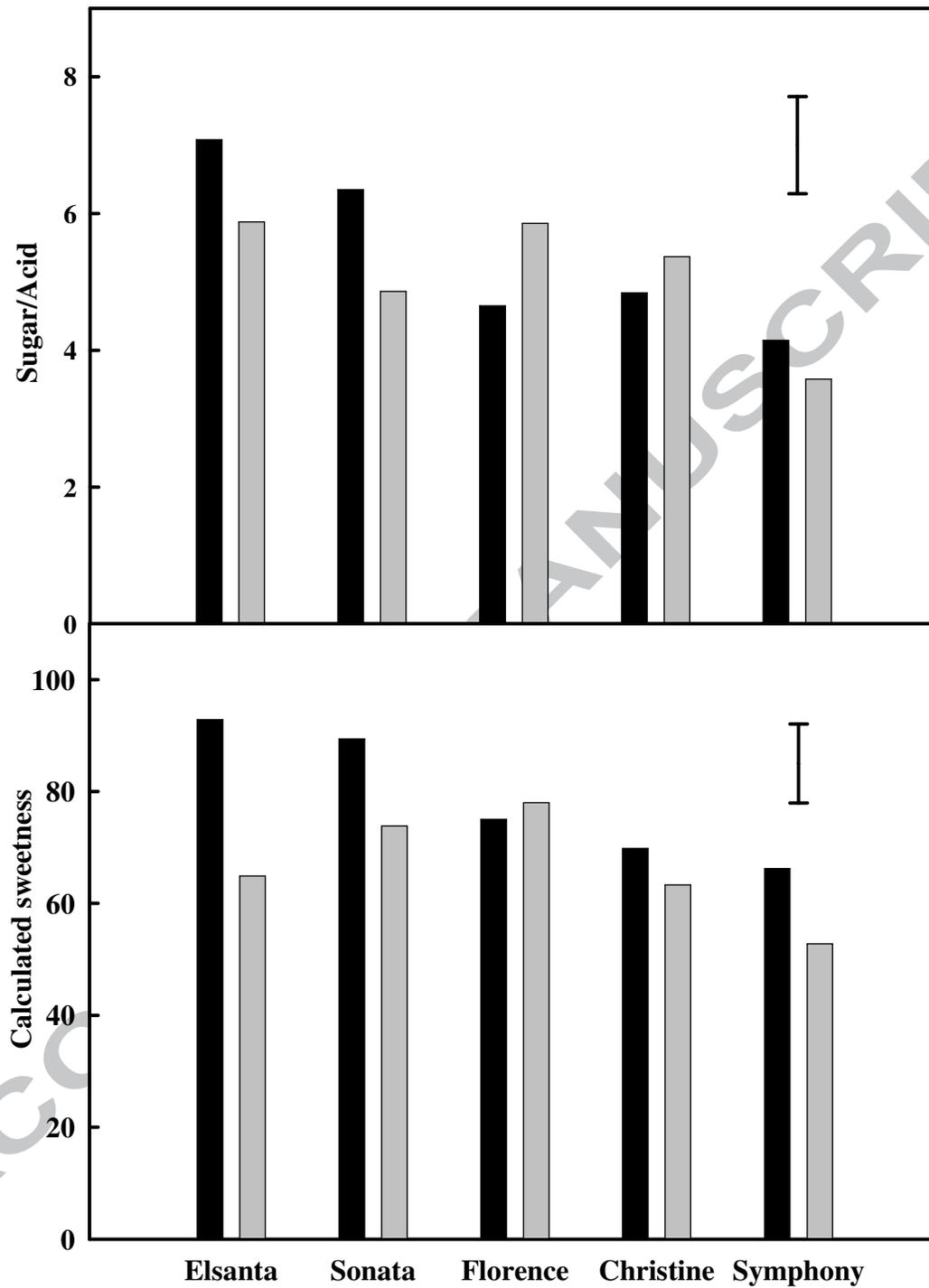


Figure 3 Giné Bordonaba and Terry