**Fruit growth and sink strength in olive (*Olea europaea* L.)
are related to cell number, not to tissue size**

Abridged title: Cell number determines fruit growth

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Summary Text for the Table of Contents:

Whether tissue size or cell number determine fruit growth and sink strength is not known, because cell number and tissue size are strongly correlated. Using a diploid cultivar and its tetraploid (with larger ovaries made up of larger cells but in similar number) as a biological model we separated these effects and found that fruit growth and sink strength correlated to cell number across genotypes but not to tissue size. This is fundamental knowledge for fruit growth modeling and management.

32 **Abstract**

33 The relationship between tissue (mesocarp and endocarp) growth and either tissue
34 initial (i.e. in the ovary at bloom) size or cell number was studied using the olive
35 cultivar Leccino (L) and its mutated clone (LC), which produces tetraploid fruits. LC
36 ovaries were 2.7 times the volume of L ovaries, but contained an overall similar number
37 of much larger cells. This allowed decoupling cell number and ovary size, which are
38 normally closely correlated. With this decoupling, cell number in the ovary correlated
39 with tissue growth in the fruit while tissue size in the ovary did not. Cell size in the
40 ovary was inversely correlated with the tissue relative growth from bloom to harvest
41 (i.e. the ratio between final and initial tissue size). These results support the hypothesis
42 that cell number and not tissue size are related to fruit growth and sink strength, and that
43 cell size in the ovary tissues is a good predictor of tissue growth, across cultivars and
44 tissues, even when cell size is strongly affected by ploidy.

45

46 Additional keywords: activity, division, endocarp, expansion, mesocarp, ploidy, sink
47 strength, size.

48

49

50 **Introduction**

51

52 Fruit size is of both scientific and economic importance. Genetic differences in fruit size
53 among genotypes are mostly due to differences in cell number, as was found in many
54 species (Bohner and Bangerth 1988; Scorza *et al.* 1991; Cheng and Breen 1992;
55 Tuberosa *et al.* 1992; Cowan *et al.* 1997; Higashi *et al.* 1999; Jullien *et al.* 2001; Bertin
56 *et al.* 2003; Hamada *et al.* 2008; Quilot and Génard, 2008).

57 In olive, potential fruit size differs up to several fold among cultivars (Barranco 1999),
58 being determined by genetic control (Padula *et al.* 2008).

59 Fruit size across olive cultivars is related to ovary size at bloom (Rosati *et al.* 2009),
60 which, in turn, is mostly explained by differences in cell number, both for the mesocarp
61 and the endocarp (Rosati *et al.* 2011). Therefore tissue size in the fruit also correlates
62 with tissue cell number in the ovary at bloom in both tissues (Rosati *et al.* 2012). This

63 also occurs in other species, such as peach (Scorza *et al.* 1991), tomato (Böhner and
 64 Bangerth 1988; Nesbitt and Tanksley 2001), kiwi (Cruz-Castillo *et al.* 1991),
 65 persimmons (Hamada *et al.* 2008), saskatoon (McGarry *et al.* 2001), apple (Harada *et*
 66 *al.* 2005; Denne 1960), and strawberry (Cheng and Breen 1992), where cell number in
 67 some parts of the ovary correlates with the cell number of the corresponding part in the
 68 fruit and with fruit size. In multi-seeded fruit, final fruit size also depends on seed
 69 number, and even in olive, presence and number of seeds per fruit affected fruit size on
 70 cv Hojiblanca, which had up to 14% biseeded fruits under open pollination Cuevas and
 71 Oller 2000). In previous work we found that the correlation between tissue size in the
 72 fruit and tissue cell number in the ovary applied to both the endocarp and the mesocarp,
 73 with a similar quantitative relationship (i.e. a single regression fit all data pooled for
 74 cultivars and tissues, see Fig. 3 in Rosati *et al.* 2012), despite different developmental
 75 patterns and timing between tissues (Hammami *et al.* 2011; Rapoport and Moreno-
 76 Alías, 2017), and different tissue characteristics in the ovary, the mesocarp having about
 77 twice as many cells of about half the size than the endocarp (Rosati *et al.* 2011). The
 78 finding of a strong correlation between tissue cell number in the ovary and tissue mass
 79 in the fruit, led to the hypothesis that cell number in the ovary is a good determinant of
 80 tissue growth and sink strength in olive fruits. In some species, such as cherry
 81 (Olmstead and Iezzoni 2007), pear (Zhang *et al.* 2006) and melon (Higashi *et al.* 1999)
 82 for instance, differences in fruit cell number are defined by different duration of cell
 83 division after bloom, but final fruit size is still related to fruit cell number. All of this
 84 agrees with the previous hypothesis that cell number is a good indication of sink size in
 85 fruits (Ho, 1988,1992; Génard *et al.* 2007).
 86 Within tissues, however, tissue size in the fruit also correlates well with tissue size in
 87 the ovary (see Fig. 4 in Rosati *et al.* 2012), therefore a possible causal relationship
 88 between tissue mass and tissue growth cannot be ruled out. Fruit mass has been
 89 extensively used as a basis to model potential fruit growth (i.e. sink strength) as the
 90 product of fruit mass (i.e. sink size) and relative growth rate (RGR) (i.e. sink activity),
 91 with RGR decreasing over time during fruit development (Grossman *et al.* 1995;
 92 Bangerth and Ho 1984; Marcelis 1992). While extensively used, such models are
 93 phenomenological, and not mechanistic, therefore they do not prove causality between

94 growth and mass. Other models use cell number as sink size and potential cell growth
95 rate as sink activity (Génard *et al.* 2007; Fanuowa *et al.* 2013), but the mechanisms
96 determining fruit growth and sink strength are still far from being understood.
97 The aim of this work was test the hypothesis that cell number (i.e. not tissue size) is
98 causally linked to fruit growth and sink strength. To do this, we used the olive cultivar
99 Leccino (L) and its mutated clone (LC), which produces tetraploid fruits, developed
100 from much larger ovaries, made up of much larger cells, but in similar numbers
101 (Caporali *et al.* 2014). This allowed us to decouple tissue size (i.e. much larger in LC
102 ovaries) from cell number (similar in both genotypes). The different cell size, due to the
103 different ploidy level, also allowed us to further test the hypothesis that initial (i.e. in the
104 ovary) cell size is inversely related to the tissue relative growth from bloom to harvest
105 (Rosati *et al.* 2012).

106

107 **Materials and methods**

108

109 *Plant material*

110 Leccino Compact (LC) and regular Leccino (L) 25-year-old trees were used. Trees are
111 part of a germplasm collection at the experimental farm of the CRA – OLI, near Spoleto
112 in central Italy (42° 48' 48''N, 12° 39' 15''E, 356 m above sea level). The trees were
113 not irrigated as is normally practiced for olive growing in the area.
114 Thirty inflorescences per genotype, 10 per each of three trees, with similar vigor and
115 flowering intensity, were collected at the beginning of bloom. The inflorescences were
116 sampled between two and three meters from ground level, from central positions of
117 flowering shoots located around the tree canopy when 20-40% of flowers had just
118 opened, in order to assure that the time of sampling was close to anthesis.

119

120 *Histological measurements of ovaries*

121 Inflorescences were immediately fixed in a mixture of formalin, acetic acid, 95%
122 ethanol and distilled water (10:5:50:35 v/v/v/v). Subsequent to fixation the
123 inflorescences were transferred to 70% ethanol until the histological preparation could
124 be carried out.

125 Afterwards pistils were selected from the inflorescences and dehydrated through a
 126 tertiary butyl alcohol series (Ruzin 1999), then infiltrated and embedded in Histosec®
 127 paraffin at melting point 56-58°C (Merck, Darmstadt, Germany). Transverse sections
 128 were cut at 12 µm with a rotary microtome, mounted on glass slides and stained with
 129 0.05% toluidine blue for 20 min prior to paraffin removal (Sakai 1973). Ovary and
 130 endocarp transverse areas were measured at the point of widest ovary diameter with an
 131 image analysis system (Leica QWIN 5001, Leica Imaging Systems Ltd., Cambridge
 132 UK) connected to a stereomicroscope (Leica MZ12). Mesocarp area was determined by
 133 subtracting endocarp area from ovary area.
 134 On 10 ovaries per genotype a field of 150 mesocarp cells was counted and its area was
 135 determined using the above-cited image analysis system connected to an ocular
 136 microscope (Nikon labophot, Nikon Microscope Systems, Amstelveen, Netherlands).
 137 The same procedure was used for 50 endocarp cells of 5 ovaries per genotype. Ovary
 138 sample numbers were determined by preliminary measurements and T test analysis of
 139 variability, and number of cells measured based on tissue thickness, structural
 140 variability and a preliminary T test.
 141 Cell and tissue volumes were calculated from their cross sectional areas assuming
 142 spherical ovary, endocarp and cell shape. Endocarp volume was calculated both as
 143 whole endocarp (i.e. including locules) and as true endocarp: whole endocarp volume
 144 subtracting locules' volume, assuming that both locules together have a spherical shape.
 145 While the assumption of spherical shape for the combined locules is based on both
 146 longitudinal and cross-sectional appearance of the ovary, some inaccuracy is possible;
 147 however, the locules' volume represented only 15 % of endocarp volume in L or 12% in
 148 LC (data not shown, but see difference in whole and true endocarp volume in table 1),
 149 so even a large error in the estimation of locules' volume, would have only a minor
 150 impact on true endocarp calculation. The total number of cells in the ovary tissues was
 151 calculated by dividing tissue volume (using both whole and true endocarp volumes) by
 152 cell volume. Whole endocarp was used when examining the ovary-to-fruit tissue
 153 relationships (Figs 1, 2, 3), as it most closely corresponds with the fruit pit (endocarp),
 154 and was also the parameter used in the cited previous studies,
 155

156 *Fruit tissue volumes*

157 At harvest, 30 fruits of representative size per tree, on three trees per genotype were
158 harvested at 50% veraison (i.e. fruits half green), which occurred at the end of October.
159 Fruit and pit (i.e. after pulp removal) length and diameter were measured and fruit and
160 pit volumes were calculated as:

161
$$\text{Volume} = 4/3 \pi (d/2)^2 (l/2), \quad \text{eq. 1}$$

162 where d is the fruit/pit transversal diameter, and l is the fruit/pit length.

163 Pulp volume was obtained as the difference between fruit volume and pit volume.

164

165 *Productivity measurements*

166 At harvest, 30 flowering shoots were randomly chosen for each genotype, from the
167 same trees as above, avoiding shoots used for the sampling of flower and fruit weight.
168 Shoot length and number of nodes and fruits on the one-year-old portion of the shoot
169 were recorded. To compare the fruit load, this was expressed as fruits per centimeter of
170 shoot length and per node, which is considered a way of measuring shoot production
171 efficiency (Suarez *et al.* 1984).

172

173 *Fruit thinning experiment*

174 On three other trees per genotype, two branches of five or more years of age were
175 chosen. On one of the two branches, all inflorescences but one per shoot were removed
176 as soon as visible before bloom. Two weeks after bloom, at initial fruit set, only one
177 fruit per fruiting shoot on only about 20–30 well-lit outer-canopy shoots were left, and
178 all other fruits were removed. Fruits were then collected at harvest (i.e. same date as for
179 the final sampling of fruits in the other experiment, described in the “*Productivity*
180 *measurements*” session, which served as control) and dried.

181

182 **Results and discussion**

183

184 *Tissue size, cell size and cell number in ovaries and fruits*

185 Ovaries of the tetraploid genotype LC were 2.73 times bigger (in volume) than L
186 ovaries; mesocarps were more than three-fold bigger while endocarps were 2.36 and

2.48 times bigger respectively for whole and true endocarp (Table 1). Similarly, cell volume was bigger in LC ovaries (2.27 times in the mesocarp and 3.07 in the endocarp). In the fruits the situation changed: despite the much larger ovaries, fruits were slightly smaller in LC than in L, though this was the result of slightly larger (1.2 times) mesocarps but considerably smaller endocarps (0.58 times) (Table 2). The number of cells in the ovary as a whole was relatively similar (1.23 times in LC) between genotypes, resulting from moderately higher (1.35 times) numbers in the mesocarp, and lower (0.76 times) numbers in the endocarp of LC ovaries (Table 3).

Tissue size in the ovary vs. tissue size in the fruit

Fruit size correlates with ovary size across cultivars of different fruit size, in olive (Rosati *et al.* 2009) and other species (Lai *et al.* 1990; Lawes *et al.* 1990; Cruz-Castillo *et al.* 1991; Scorza *et al.* 1991; Cheng and Breen 1992; Nesbitt and Tanksley 2001; Handley and Dill 2003). At least in olive, this is true also at the single tissue level, although with different relationships (i.e. slopes) for the two tissues (Rosati *et al.* 2012). However, when comparing L and LC ovaries and fruits, such correlation did not apply (Fig. 1). In fact, while LC mesocarp and endocarp in the ovary were respectively 3.15 and 2.36 times larger than in L (Table 1), in the fruit LC mesocarp and endocarp were only 1.2 and 0.58 times the volume of L tissues (Table 2). Overall, at the whole-ovary or fruit level, LC ovaries were 2.73 times larger than L ovaries (Table 1), while fruits were 0.94 times (Table 2), that is, slightly smaller than L fruits.

Tissue cell number in the ovary vs. tissue size in the fruit

Fruit mesocarp and endocarp volumes at harvest correlated with the initial tissue cell number in the ovary across tissues and genotypes (Fig. 2), suggesting that the growth potential of both tissues is a function of their initial number of cells. These results confirm previous finding that tissue cell number in the ovary correlates with tissue size in the fruit both across tissues and across a range of cultivars with different ovary/fruit size (Rosati *et al.* 2012). In fact, when those data were pooled with the present data on L and LC, a single linear model fit all data with an R^2 of 0.74 (see inset in Fig. 2). In that earlier work (Rosati *et al.* 2012) we discussed the meaning and implication of such

relationship, concluding that cell number in the ovary is a strong determinant of tissue growth in the fruit. This has remained true in the present study where ploidy affected cell and ovary size (Fig. 2).

In olive, cell size is usually similar across cultivars, both in the ovary (Rosati *et al.* 2011) and in the fruit (Rapoport *et al.* 2004), and cell number and tissue size correlate closely. In the present study, however, the large differences in ovary size between L and LC were mostly due to cell size (Table 1) while cell numbers were overall similar (Table 3). As a result, tissue volume in the ovary no longer correlated with tissue volumes in the fruit (i.e. larger ovaries developed into slightly smaller fruits), but cell numbers in the ovary still correlated with tissue volumes in the fruit (Fig. 2). This suggests that cell number is the driving factor affecting tissue growth and sink strength, independent of tissue size.

This hypothesis agrees with the suggestion that pre-anthesis cell division activity exerts an important control of potential fruit size (Ho 1996), even when a significant amount of cell division occurs after anthesis (Scorza *et al.* 1991) which is also the case in olive (Hammami *et al.* 2011).

Sink strength and cell number vs. tissue mass

Sink strength is the product of sink size and sink activity (Warren Wilson 1972), which can also be stated as the product of sink mass and relative growth rate (RGR) (Marcelis 1998). Ho (1988, 1992) and Génard *et al.* (2007) suggest instead that sink size reflects cell number while sink activity reflects the cell potential growth. The first approach (i.e. sink mass times RGR) is very practical, since mass is easier to measure than cell number, and has often been used for modeling of fruit growth (see for example Grossman and DeJong 1994). However, there is no evidence that mass is causally related to sink size, in fact there is evidence that it is not (Marcelis 1996). Starck and Ubysz (1974) concluded that the dry matter partitioning into an organ (i.e. function of sink strength) was determined by its growth rate rather than its size. Fruit RGR usually decreases exponentially over time as the fruit develops (Bangerth and Ho 1984; Marcelis 1992; Grossman and DeJong 1995) and there is no clear physiological

248 explanation for this. Models using this approach are phenomenological, and not able to
 249 explain fruit growth in terms of the physiological functioning of the plant.

250 The present results agree with the hypothesis that cell number, rather than tissue mass,
 251 is related to the sink strength of an organ (Ho 1992; Bertin 2005) even though this
 252 might be not always the case (Marcelis 1996), because cell number is only one factor
 253 determining sink strength (Gillaspy *et al.* 1993). The number of cells in the pre-anthesis
 254 ovary is considered a critical factor in determining the sink strength of the developing
 255 fruit and is genetically determined (reviewed in Coombe 1976). Therefore, the similar
 256 number of cells in the LC ovaries, compared to L (LC ovaries had only 23% more cells,
 257 Table 3), may confer similar sink strength and final fruit size to these genotypes, despite
 258 the very different initial tissue volume (2.73 times in LC ovaries) and cell size in the
 259 ovary (Table 1).

260 In previous work on many olive cultivars with varying fruit size, it was found that larger
 261 fruits derived from proportionally larger ovaries (Rosati *et al.* 2009; 2012), implying
 262 that, from bloom to harvest (i.e. same period duration for all CVs), the fruit relative
 263 growth (RG) was similar across cultivars. Considering that the initial mass of the ovary
 264 is negligible compared to the final fruit mass, these results also imply that the fruit
 265 absolute growth (AG) was proportional to final fruit mass, and thus AG correlates with
 266 ovary and fruit size. With the present data, this was no longer the case: much larger
 267 ovaries in LC produced slightly smaller fruits (over the same time period), implying that
 268 their RG was much reduced compared to L (this was true also at the single tissue level,
 269 see Fig. 3), while the AG was slightly lower (i.e. slightly lower final fruit size) rather
 270 than much greater as expected for much larger ovaries. Cell number seems to explain
 271 such different behavior. In fact, usually cultivars with larger ovaries have proportionally
 272 more cells, resulting in larger fruits with more cells, and proportionally greater AG.
 273 Even though LC ovaries were almost triple in size, they did not have proportionally
 274 more cells, but rather a similar number of cells as L ovaries (Table 3). This resulted in
 275 similar fruit size and AG (instead of proportionally greater values) and reduced RGR
 276 (instead of similar RGR). In other words, with similar cell numbers to L, LC ovaries
 277 behaved similarly to L ovaries in subsequent fruit size and AG (i.e. sink strength), thus

278 decreasing their RG, as a result of larger ovary size. This supports the hypothesis that
279 cell number and not tissue or organ mass is related to AG and sink strength.

280

281 *Further evidence for the dependence of sink strength on cell number*

282 In previous work, evidence was found that competition for resources among ovaries of
283 different mass (i.e. across cultivars of different ovary/fruit size) affects fruit set after
284 boom, and that larger ovaries (i.e. in larger fruited cultivars) compete more and set
285 fewer (but larger) fruits, resulting in a similar total mass of set fruits and, later,

286 harvested fruits (Rosati *et al.* 2010). Again, since ovary size and cell number usually
287 correlate across olive cultivars (Rosati *et al.* 2011) it is difficult to separate ovary size
288 and cell number effects on fruit set. The biological model used here (i.e. LC vs. L)

289 offered this possibility. We therefore investigated fruit set and total fruit mass, at
290 harvest, as well as shoot length and node number in L and LC shoots. No significant
291 differences were found between the two genotypes in shoot length, nodes per shoot,
292 fruits per shoot, fruits per node or fruits per centimeter of shoot (Table 4). These data
293 indicate that the impact of the ovary sink strength on fruit set, did not differ between L
294 and LC, despite the very different ovary size, suggesting that the similar cell number in
295 the ovaries may be linked to the similar fruit set.

296 Since larger-fruited cultivars tend to set fewer fruits, thus adjusting fruit number to
297 produce similar fruit mass, and since this did not happen with the much larger ovaries of
298 LC, it may be argued that the similar number of set fruits between L and LC limited the
299 potential fruit growth in LC due to source limitation. In other words, if LC had set fewer
300 fruits, these would have grown much larger, as expected from larger ovaries. We tested
301 this hypothesis by heavily thinning both genotypes to increase the leaf-to-fruit ratio in
302 order to allow fruits to grow to their potential size (Grossman and DeJong 1995). The
303 results showed no significant difference in fruit parameters (fruit, pulp and pit, fresh and
304 dry weights) for either genotype, despite a tendency of larger fruits in thinned plants,
305 especially in L (Fig. 4). This indicates that fruit size in LC was not source limited, or
306 not more so than in L. The fact that larger ovaries turned into slightly smaller fruits,
307 instead of proportionally larger ones, appears therefore genetically determined and not

308 environmental. The similarities in fruit AG (and sink strength) between L and LC do
309 not appear biased by a different level of source limitation.

310

311 *Initial cell size and relative growth (RG)*

312 In previous work we found a strong negative exponential correlation, across cultivars
313 and tissues, between the relative growth (RG, the ratio between final volume in the fruit
314 and the initial volume in the ovary) and the initial average cell volume of that cultivar
315 and tissue in the ovary. The same relationship was found with L and LC tissues with a
316 good correlation ($R^2 = 0.78$, Fig. 3). When data from L and LC were pooled with data
317 from eight cultivars from previous work (Rosati *et al.* 2012), the overall fit had an R^2 of
318 0.65 (inset of Fig. 3). While the RG of L was within the range of the other cultivars, for
319 both tissues, the values for LC were below all other cultivars for both tissues. In the
320 mentioned previous work, we discussed the meaning of that relationship, suggesting
321 that cell size in the ovary tissues indicates how far that tissue is in the growth process:
322 the bigger the cells, the less relative growth remains to be carried out. This
323 interpretation appears plausible since it is known that cell size increases continuously
324 from bloom to harvest (Sinnott 1942; Jullien *et al.* 2001; Bertin 2005; Harada *et al.*
325 2005; Hammami *et al.* 2011). Sinnott (1942) stated that: "each pair of daughter cells,
326 before they divide again, evidently grow to a greater size than was reached by their
327 mother cell", which clearly implies that cell size can be indicative of tissue
328 developmental stage. The fact that the same regression also fit all data including L and
329 LC ovaries/fruits suggests that cell size might hold its predicting ability on the RG of
330 olive fruits, also when cell size is altered by ploidy, at least in olive fruits.

331

332

333 **Conclusions**

334 What determines sink strength and fruit growth is of great relevance for productive and
335 scientific reasons and it is at the base of mechanistic fruit growth models. Two
336 approaches are usually employed, one assuming that fruit growth is a function of
337 tissue/organ mass, the other based on cell number. Since tissue or organ size and cell
338 number are usually strongly correlated, separating their effects is difficult. In the present

339 study, for the first time we decoupled the effects of ovary tissue mass from those of cell
340 number, by using a cultivar and its mutated clone which produces tetraploid fruits,
341 originating from much larger ovaries but a similar number of larger cells. Cell number
342 in the ovary still correlated with fruit growth, but tissue size did not. These results
343 support the hypothesis that cell number, rather than tissue mass, may be causally linked
344 to the sink strength and growth of the fruit in olive.
345 Furthermore, cell size in the ovary at bloom appeared to be related to the fruit relative
346 growth from bloom to harvest (RG) even when cell size is altered by ploidy.

347

348 **Conflict of interest**

349 The authors declare no conflicts of interest

350

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352

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Table 1. Ovary, tissue, and cell volumes (mm³) in olive ovary at bloom in Leccino (L) and Leccino Compact (LC).

	Ovary	Mesocarp	Endocarp whole ²	Endocarp true ²	1 Cell-Meso	1 Cell-Endo
L	0.59 b	0.27 b	0.32 b	0.28 b	0.54 10 ⁻⁶ b	2.41 10 ⁻⁶ b
LC	1.61 a	0.85 a	0.76 a	0.68 a	1.22 10 ⁻⁶ a	7.40 10 ⁻⁶ a
LC/L¹	2.73	3.15	2.36	2.48	2.27	3.07
¹ LC/L represents the increment of change of "LC" with respect to "L"						
² Whole endocarp includes locules, true endocarp excludes locules. Details in materials and methods						
Different letters within columns indicate significant difference (P < 0.05).						

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Table 2. Fruit and tissue volumes (mm³) in olive fruits at harvest in Leccino (L) and Leccino Compact (LC).

	Whole-fruit	Mesocarp	Endocarp
L	1162 a	672 b	490 a
LC	1094 b	808 a	286 b
LC/L¹	0.94	1.20	0.58

¹LC/L represents the increment of change of "LC" with respect to "L"

Different letters within columns indicate significant difference ($P < 0.05$).

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Table 3. Total cell number in ovary tissues in Leccino (L) and Leccino Compact (LC).

	Whole-ovary	Mesocarp	Endocarp whole ²	Endocarp true ²
L	650110 b	513050 b	137061 a	116622 a
LC	798755 a	693413 a	105342 b	92776 b
LC/L¹	1.23	1.35	0.76	0.80

¹LC/L represents the increment of change of "LC" with respect to "L"²Whole endocarp includes locules, true endocarp excludes locules. Details in materials and methods

Different letters within columns indicate significant difference (P < 0.05).

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Table 4. Productive parameters of shoots. No parameters differed statistically between Leccino (L) and Leccino Compact (LC). Standard error in brackets.

	Shoot length	Nodes per shoot	Fruits per shoot	Fruits per node	Fruits per cm of shoot
L	16.7 (0.93)	8.2 (0.42)	6.6 (0.48)	0.83 (0.054)	0.41 (0.028)
LC	15.7 (0.86)	8.7 (0.36)	6.8 (0.48)	0.79 (0.042)	0.45 (0.024)

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513 Fig. 1

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516 FIG. 1. Relationship between the final (i.e. in the mature fruit) volume of the mesocarp
517 and the endocarp vs. the initial (i.e. in the ovary at bloom) volume in the same tissue.
518 Open symbols are for the mesocarp, closed symbols are for the endocarp. Diamonds are
519 for Leccino, circles are for Leccino Compact. No significant relationship was found.

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522 Fig.2

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FIG. 2. Relationship between the final (i.e. in the mature fruit) volume of the mesocarp and the endocarp vs. the initial (i.e. in the ovary at bloom) cell number in the same tissue. Symbols as in Fig. 1. Inset figure: same relationship pooling all data from this experiment and from 8 cultivars (Rosati *et al.* 2012).

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535 Fig. 3

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539 FIG. 3. Relationship between the relative growth (i.e. RG: the ratio between the final
 540 volume in the fruit and the initial volume in the ovary) of the mesocarp and the
 541 endocarp vs. the initial (i.e. in the ovary at bloom) cell volume in the same tissue.
 542 Symbols as in Fig. 1. Inset figure: same relationship pooling all data from this
 543 experiment and from 8 cultivars (Rosati *et al.* 2012).

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547 Fig. 4
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 553 FIG. 4. Fresh weight (FW) and dry weight (DW) of fruit, pulp, and pit in Leccino (top)
 554 and Leccino Compact (bottom), in thinned and control (unthinned) shoots. No
 555 significant differences were found for the thinning treatment in any variable.