

Partitioning of Dry Matter into Fruit Explains Cultivar Differences in Vigor in Young Olive (*Olea europaea* L.) Trees

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Abstract. Low vigor and early and abundant production are desirable traits for modern tree crops. In olive, most cultivars are too vigorous and cannot be successfully constrained in the small volume allowed by the straddle harvester used in the so-called superhigh-density (SHD) orchards. Only few cultivars appear to have sufficiently low vigor to be suitable for this system. These cultivars combine low vigor with earlier and higher yield. This study investigated the hypothesis that differences in vigor between Arbequina, a low vigor and the most commonly used cultivar in SHD orchards, and Frantoio, a highly vigorous cultivar not suitable for such orchards, are related to their differences in early bearing and consequent differences in dry matter partitioning into fruit. Young trees of both cultivars were deflowered either in 2014, 2015, both years, or neither one, resulting in a range of cumulative yields over the 2 years. Tree trunk cross-sectional area (TCSA) was measured at the beginning of each year. This was closely related to total tree mass, as assessed at the beginning and at the end of the experiment. Cumulative yield, in terms of fruit dry matter, was also assessed. TCSA increased less in fruiting trees in both years. As expected, when not deflowered, 'Frantoio' was less productive and more vigorous than 'Arbequina'. However, there was no difference in TCSA increment when both cultivars were completely deflowered. TCSA increments were closely inversely related to yield across all treatments and cultivars ($R^2 = 0.90$). The regressions improved further when data from 2015 only were used ($R^2 = 0.99$). The results represent the first quantitative report showing that differences in vigor among cultivars can be completely explained in terms of different dry matter partitioning into fruit, supporting the hypothesis that early bearing is a major cause, rather than merely a consequence, of lower vigor in young 'Arbequina' trees. These results provide new understanding on vigor differences across cultivars, which will be useful for breeding and selection of new genotypes.

The higher productivity of modern fruit tree cultivars, compared with wild trees, is mostly related to their higher partitioning of dry matter into fruit [i.e., higher harvest index (HI)] (Patrick, 1988), rather than to differences in photosynthetic abilities (Loomis, 1983). In cultivated species, HI often reaches 75% (Cannell, 1985), whereas it is much lower in wild species. The increase in HI is obtained both by a shorter initial unproductive period (i.e., early bearing) and by maintaining

higher partitioning into fruit in the mature tree (more abundant yield, relative to tree size) to the detriment of vegetative growth (Archbold et al., 1987; Forshey and McKee, 1970). In fact, reproductive and vegetative growth are in competition for the available resources and one inhibits the other (Grossman and DeJong, 1995a, 1995b; Kramer and Kozlowski, 1979; Spurr and Barnes, 1980).

Because of this competition, it has long been assumed that reducing vegetative growth is essential to bring about early and abundant fruiting (Browning, 1985). Containing plant vigor, e.g., by controlled water stress (Mitchell et al., 1989); containing root volume with drip irrigation (Mitchell and Chalmers, 1983) or by root pruning (Geisler and Ferree, 1984); dwarfing rootstocks (Avery, 1970; Preston, 1958); and shoot removal, chemical control of vegetative growth, or both (Mulas et al., 2011; Rugini

and Pannelli, 1992; Williams et al., 1986), all result in enhanced yield.

However, the opposite is also true: once reproduction starts, the crop will compete with, and reduce, vegetative growth and, therefore, vigor, as shown also by modeling (Grossman and DeJong, 1994; Smith and Samach, 2013). This is the case for mature trees of many species (Berman and DeJong, 2003; Costes et al., 2000; Lauri and Térouanne, 1999; Salazar-García et al., 1998; Stevenson and Shackel, 1998), including olive (Castillo-Llanque and Rapoport, 2011; Connor and Fereres, 2005; Dag et al., 2010; Lavee, 2007; Monselise and Goldschmidt, 1982; Obeso, 2002; Rallo and Suárez, 1989). In young trees, the removal of all blossoms or fruits results in dramatic increases in growth relative to the fruiting trees (Chandler and Heinicke, 1926; Embree et al., 2007; Forshey and Elfving, 1989; Mochizuki, 1962; Verheij, 1972). Similarly, earlier and more abundant fruiting (i.e., higher partitioning into fruit) is at least one of the mechanisms involved in the effect of dwarfing rootstocks (Avery, 1970; Preston, 1958) and in some cases, the only mechanism (Lliso et al., 2004), although in other cases, it is probably not the only one. In fact, defruiting apple trees on dwarfing rootstocks allows tree vigor to increase dramatically, but still less than in trees with more vigorous rootstocks (Avery, 1969; Barlow, 1964). It could be argued, therefore, that early and abundant fruiting is not just a consequence of lower vigor, but once induced, it becomes a cause of the reduction in vigor.

Whether different partitioning into fruit (i.e., difference earliness and abundance of fruiting) could be the cause of differences in vigor among different cultivars has not been studied.

In olive, as for other fruit trees, vigor reduction and early and abundant production are also desirable traits (Rallo et al., 2007; Tous et al., 1999), but few cultivars possessing these traits have been identified, despite much research on reduced vigor or even dwarf cultivars (Barranco, 1997; León Moreno, 2007; Sonnoli, 2001). Nor has it been possible to successfully induce these traits in traditional olive cultivars by grafting, despite much research on olive rootstocks (Baldoni and Fontanazza, 1990; Barranco, 1997; Pannelli et al., 1992, 2002; Troncoso et al., 1990). Recently, the so-called SHD orchards have been developed, using the few cultivars found to have sufficiently low vigor and early yield. SHD olive orchards, if indeed technically and economically viable, are important for the olive industry because they allow continuous (i.e., straddle harvester) mechanical harvesting (Rallo et al., 2007; Tous et al., 1999), thus greatly reducing costs and hand labor requirements. However, the straddle harvester requires small-canopy trees (Camposo et al., 2008; Tous et al., 2006) and traditional cultivars tend to "escape" from the small volume allowed, thus requiring intense pruning, which stimulates vegetative growth and reduces fruiting (Jerie et al., 1988). SHD

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orchards also require early and abundant fruiting if they are to be economically viable (De Benedetto et al., 2003). It is important, therefore, to understand the mechanisms implicated in early and high production and reduced canopy size.

So far, the cultivars that proved most suitable for SHD olive orchards are Arbequina, Arbosana, and Koroneiki (Tous et al., 2006), three cultivars characterized by low vigor compared with most traditional cultivars (Rosati et al., 2013; Tous et al., 2006). However, they are also characterized by early and abundant bearing, as well as low alternate bearing (Caruso et al., 2012; Díez et al., 2016; Farinelli and Tombesi, 2015; Godini et al., 2011; Moutier, 2006; Moutier et al., 2008). Trees of these cultivars produce large crops, relative to their size, already in the second and third year after transplanting.

Given the competition between crop and vegetative growth, we hypothesize that early bearing is implicated in the difference in vigor between such cultivars and more traditional ones that do not fruit until much older. In a previous study (Rosati et al., 2017), we found that tree growth, in terms of both tree diameter and canopy volume increments, was inversely related to tree yield across 12 cultivars in young olive trees. Similarly, Di Vaio et al., (2013) found that across 20 cultivars, the least vigorous tended to have greater early yields. However, correlation does not prove causality and only by defruiting the trees it would be possible to test whether fruiting is indeed a cause, rather than a mere consequence, of reduced vigor in early-bearing low-vigor cultivars.

In this article, we test the hypothesis that earlier and more abundant bearing is the cause, or one of the causes, of reduced vigor. To test this hypothesis, we compared the initial growth of deflowered, partially deflowered (i.e., in alternate years), and control fruiting trees in Arbequina, the cultivar most used in SHD orchards, and in Frantoio, a traditional cultivar much more vigorous than Arbequina (Rosati et al., 2013; Vivaldi et al., 2015).

Materials and Methods

The study was carried out at the Department of Agricultural and Environmental Sciences of the University of Perugia. One-year-old plants, originated from rooted cuttings, were grown in 9.5-L pots. The trees were grown outdoors for two seasons (2014 and 2015). The trees were regularly fertigated using a drip irrigation system, avoiding any water and nutrient stress. A total of 48 'Arbequina' and 48 'Frantoio' trees were used. Initially, we planned to deflower half of the plants during the first season and then half of each treatment in the second season. 'Frantoio', however, had no flowers the first season and only 'Arbequina' could be deflowered. Therefore, only 24 'Frantoio' plants were retained in the experiment. In 2015, instead, both cultivars bore inflorescences and could be deflowered. To avoid

confusion, we, therefore, called the different treatments fruiting (Fr) and not fruiting (NF), whether naturally or because deflowered. Therefore, plants that fruited only in 2014, only in 2015, in both years, or in neither year were labeled, respectively, as Fr + NF, NF + Fr, Fr + Fr, and NF + NF. Deflowering treatments were carried out by removing inflorescences in May (white stage) of both years, when flowers were not yet open.

In November of both 2014 and 2015, fruits were harvested and oven-dried at 80 °C until reaching constant weight.

Trunk cross-sectional area was calculated from the trunk diameter measured on the main stem, 5 cm above its insertion on the original cutting wood. The diameter was measured at the beginning of each year (2014, 2015, and 2016), before vegetative growth started.

In Feb. 2016 (end of the experiment), three plants per treatment were removed from the pots, their roots washed in running water, and the whole plants were then oven-dried at 80 °C until reaching constant weight. Similarly, in Feb. 2014 (beginning of the experiment), six plants per cultivar were also sampled and treated as previously described.

Data are presented as means ± SE. Treatment and cultivar effects were analyzed by analysis of variance (ANOVA) using a completely randomized design, and averages were compared using the Student–Newman–Keuls test ($P < 0.05$). Regressions between parameters were evaluated using the statistical significance of the fits and the coefficients of determination (R^2).

Results

Yield in the two fruiting treatments for 'Arbequina' were low in 2014, whereas 'Frantoio' had no flowers and, therefore, no fruiting treatments were possible (Fig. 1). In the second year, yield was higher and cumulative yield reached about 150 g of fruit dry matter per tree in the highest fruiting treatment in 'Arbequina', and about 45 g in 'Frantoio'.

Trunk cross-sectional area increased in all treatments over the years, but the increase was clearly reduced in fruiting trees, compared with nonfruiting trees, in both years (Fig. 2). In the first year, 'Frantoio' did not flower and only the two non-deflowered 'Arbequina' treatments had fruit: both these fruiting treatments increased TCSA less than all other treatments with no fruit. Similarly, in the second year, TCSA increased less in all fruiting treatments, compared with the correspondent deflowered treatments.

The total increment in TCSA, from 2014 to 2016 (i.e., from the beginning to the end of the experiment) was significantly and inversely correlated with the cumulative yield, across all treatment and cultivars (Fig. 3). A single regression explained 90% of the variability across all treatments and cultivars.

When using data from 2015 only, both in terms of TCSA increments and yield, the

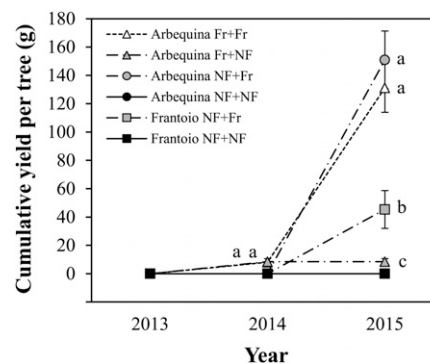


Fig. 1. Cumulative yield per tree (dry matter) over the 2 years (i.e., year 1 = 2014; year 2 = 2015), for the different treatments. Fr = fruiting treatment; NF = non-fruited treatment. Each point is the average of 12 trees. Bars denote standard errors. Different letters denote significant differences within each year (averages were compared using the Student–Newman–Keuls test, $P < 0.05$). Treatments with no fruits are excluded from the ANOVA. Where symbols are not visible, they are hidden behind other symbols, but the lines help locate them (except for 'Arbequina' NF + NF, for which both the symbol and the line are hidden behind those of 'Frantoio' NF + NF).

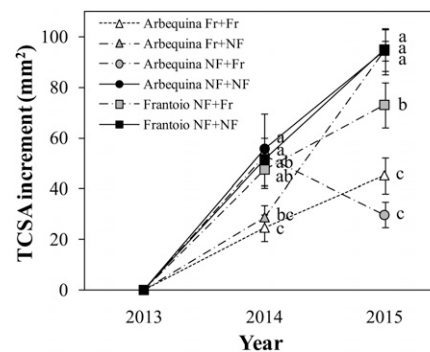


Fig. 2. Increment in trunk cross-sectional area (TCSA) over the 2 years (i.e., year 1 = 2014; year 2 = 2015), for the different treatments. Fr = fruiting treatment; NF = nonfruiting treatment. Each point is the average of 12 trees. Bars denote standard errors. Different letters denote significant differences within each year (averages were compared using the Student–Newman–Keuls test, for $P < 0.05$). Treatments with no fruits are excluded from the ANOVA. Where symbols are not visible, they are hidden behind other symbols, but the lines help locate them.

same regression improved, explaining 99% of the variability (Fig. 4).

Whole-tree biomass was strongly and linearly related to TCSA, across all data from 2014 and 2016 (Fig. 5).

Discussion

Arbequina produced up to 150 g of fruit dry matter, mostly in the second year after transplanting, which is similar to what has previously been found in this cultivar (Tous et al., 2003). Therefore, the precocious fruit

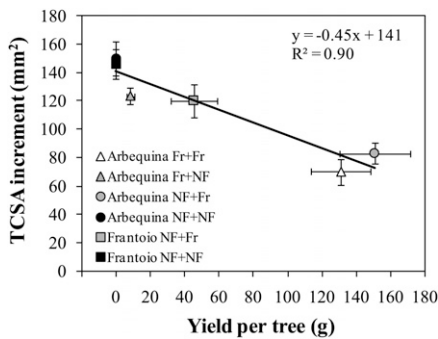


Fig. 3. Relationship between the total increments in trunk cross-sectional area (TCSA) and total yield over the 2 years, for the different treatments. Fr = fruiting treatment; NF = nonfruiting treatment. Each point is the average of 12 trees. Bars denote standard errors. The regression is statistically significant ($P < 0.01$).

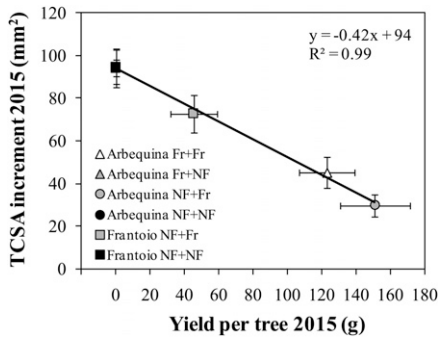


Fig. 4. Relationship between the increments in trunk cross-sectional area (TCSA) and yield for 2015 only, for the different treatments. Fr = fruiting treatment; NF = nonfruiting treatment. Each point is the average of 12 trees. The regression is statistically significant ($P < 0.01$).

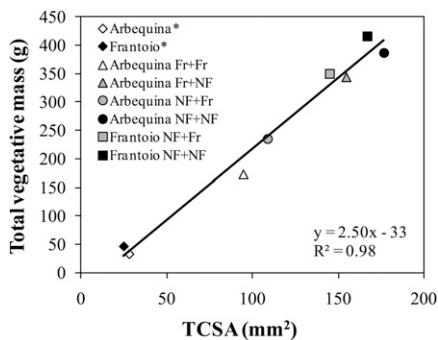


Fig. 5. Relationship between whole-tree vegetative mass and trunk cross-sectional area (TCSA) measured at the beginning (2014) and the end (2016) of the experiment. * denotes the plants sampled at the beginning of the experiment (i.e., beginning of 2014). All other plants were sampled at the end of the trial (beginning of 2016). Each point is the average of three trees (six trees for 2014 data). The regression is statistically significant ($P < 0.01$). Fr = fruiting treatment; NF = nonfruiting treatment.

bearing of Arbequina, higher than most other cultivars (Tous et al., 2003, 2008), can be considered high, especially for olive, representing a significant reproductive effort for the young plant.

As described in the introduction, it is well known that reproductive and vegetative growths compete for the available resources. In most studies in tree crops, however, this competition has not been investigated at a whole-plant level, because of the difficulties in measuring whole-tree growth. Most often, growth is measured only on some shoots (Acebedo et al., 2000; Rallo and Suárez, 1989), comparing their growth on fruiting and nonfruiting trees (Cimato and Fiorino, 1986; Proietti and Tombesi, 1996). Few articles report more comprehensive data on populations of modules within the canopy (Hasegawa and Takeda, 2001) or on entire branches (Castillo-Llanque and Rapoport, 2011). However, a completely quantitative description of the competition between vegetative and reproductive growth can be obtained only with a whole-tree approach. Such approaches are rare, mostly adopted in older studies on the effects of defruiting or of rootstocks (Chandler and Heinicke, 1926; Forshey and Elfving, 1989; Mochizuki, 1962; Verheij, 1972). No studies, however, investigated whether cultivar differences in vigor can be related to differences in early bearing. Furthermore, even in these old studies, trees were either completely defruited or fruits were left in high numbers, thus allowing to study the effects of “off” and “on” trees. In the present study, a whole range of fruit loads over the 2 years were obtained by deflowering trees in alternate years, both years, or not at all, across two cultivars with different productivity. This allowed for a regression between tree growth, expressed as increments in TCSA, and yield biomass (Fig. 3). Moreover, TCSA was closely ($R^2 = 0.98$) related to tree biomass (Fig. 5). Therefore, TCSA was a good proxy for total tree biomass, and the close regression shown in Fig. 3 implies that the increments in whole-tree vegetative biomass were also closely correlated with yield biomass.

The regression in Fig. 3 explained 90% of the variability; however, the regression was further improved when using data from 2015 only (99% of the variability). This was probably because producing fruit during the first year reduced vegetative growth over the 2 years not only via direct competition (i.e., by allocating dry matter to fruit) but also by indirect mechanisms. That is, fruiting in the first year reduced vegetative growth, and, therefore, leaf area and light interception, thus reducing potential growth in the second year, independent of fruiting. In fact, it may be observed that in Fig. 3, the two treatments fruiting in the first year were both well below the line, unlike all other points, implying that their growth was less than what could be expected from their cumulative yield. Omitting these treatments improves the regression in Fig. 3 ($R^2 = 0.98$, data not shown). Using data from 2015 only reduces the effect of these indirect reduction of canopy growth, and in fact, the regression was improved ($R^2 = 0.99$, Fig. 4).

The most relevant result is that a single regression fits very closely all points across cultivars and treatments (Figs. 3 and 4). To the best of our knowledge, this is the first report providing quantitative evidence that the variability in vigor between cultivars was almost entirely (i.e., $R^2 = 0.90$ in Fig. 3, and 0.99 in Fig. 4) explained by differences in dry matter partitioning due to earliness and abundance of fruiting.

These findings suggest that in the case of ‘Arbequina’ and ‘Frantoio’, differences in fruiting habits are the cause, rather than the effect of lower vigor, otherwise vigor should have been lower even in deflowered trees. In fact, if greater flowering and fruiting was the result of higher resource availability, because of lower resource use by vegetative growth (i.e., lower vigor), then these additional resources would be available only after a reduction in vegetative growth had taken place. Instead, deflowered ‘Arbequina’ trees had the same TCSA (and therefore biomass) increments as deflowered ‘Frantoio’ trees (Figs. 2–4). This suggests that compared with Frantoio and other traditional cultivars that do not fruit as easily as very young trees, Arbequina has an inherent ability to flower and set fruit early, independent of (additional) resource availability. Investigating the mechanisms that allow certain cultivars, such as Arbequina, to flower and set more fruit earlier and more abundantly and constantly is of great interest both to increase yield and to reduce alternate bearing, but also, in turn, to reduce tree vigor (as a consequence of more fruiting) and allow high-density planting.

These results are in line with previous finding that vegetative growth (i.e., vigor) is reduced by the presence of fruit, which compete for resources (Berman and DeJong, 2003; Castillo-Llanque and Rapoport, 2011; Chandler and Heinicke, 1926; Connor and Fereres, 2005; Costes et al., 2000; Dag et al., 2010; Embree et al., 2007; Forshey and Elfving, 1989; Lauri and Térouanne, 1999; Lavee, 2007; Mochizuki, 1962; Monselise and Goldschmidt, 1982; Obeso, 2002; Rallo and Suárez, 1989; Salazar-García et al., 1998; Stevenson and Shackel, 1998; Verheij, 1972). This is not to say, however, that more abundant fruiting cannot be a consequence, rather than the cause, of reduced vigor. Many studies show that reducing vigor by dwarfing rootstock (Avery, 1970; Preston, 1958); controlled water stress or regulated deficit irrigation (Mitchell et al., 1989); root pruning (Geisler and Ferree, 1984) or containing root volume with drip irrigation (Mitchell and Chalmers, 1983), and shoot removal, chemical control of vegetative growth, or both (Mulas et al., 2011; Rugini and Pannelli, 1992; Williams et al., 1986), all result in enhanced yield. With all probability, reducing vigor with any of these techniques would have similar effects also on ‘Arbequina’, making increased fruiting the result of reduced vigor. It appears, therefore, that vigor can be both the cause and the consequence, depending on the situation.

Although this article demonstrates that differences in early bearing and partitioning of biomass into fruit has a major role in the different vigor between the two cultivars tested, this is probably not the only mechanism. In fact, in this study, vigor was expressed in terms of increments in TCSA, which closely correlated with total biomass. Arbequina and other cultivars suitable for SHD orchards have higher branching than most other cultivars, implying a more compact canopy for an equal amount of biomass growth (Rosati et al., 2013, 2018) as previously found in other species (Forshey et al., 1992; Lauri, 2007; Lespinasse and Delort, 1986). Therefore, an equal amount of biomass increment results in a lower increment in canopy volume in more branched cultivars. This would eventually reduce canopy light interception and, therefore, reduce growth even in the absence of fruit, thus explaining an inherent lower vigor independent of fruiting. Other causes concurring to explain cultivar differences in vigor are also possible. Nonetheless, the initial differences in vigor (i.e., expressed as biomass increment) between 'Arbequina' and 'Frantoio' appeared to be almost entirely dictated by the difference in dry matter partitioning into fruit.

In a previous study (Rosati et al., 2017), we found that tree growth was inversely related to yield efficiency across 12 olive cultivars over a period of several years, thus including adult trees. In that article, causality was not proven, as no defruiting treatments were carried out. The present results suggest that the relationship is causal because defruited 'Arbequina' was as vigorous as 'Frantoio'. Even though only two cultivars were considered, the choice included a very vigorous cultivar (Frantoio) and a very low-vigor cultivar (Arbequina), thus encompassing the range of vigor across most cultivars. Because vigor across these two cultivars was quantitatively related to early yield, just as it was the case among the 12 cultivars in the previous study, the present results suggest that the finding that early fruiting explains differences in vigor across cultivars is probably a general phenomenon and not just a peculiarity of the two cultivars chosen. Further studies are needed to confirm this.

Conclusions

Vegetative and reproductive growth compete for the same resources and one can be affected and, in turn, affect the other. It can be difficult to ascertain whether earlier and more abundant fruiting is the cause of differences in vigor among cultivars or the consequence. In the present study, young trees of 'Arbequina' had the same vigor as those of 'Frantoio', when both were deflowered, suggesting that earlier and more abundant fruiting is a major cause of the reduced vigor usually observed in 'Arbequina'. The present findings provide the first quantitative report showing that differences in vigor among cultivars can be explained in terms of differences in dry matter partitioning into fruit.

These results provide new understanding of differences in vigor across cultivars and new avenues for the breeding and selection of new cultivars suitable for SHD olive orchards.

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