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Growth Is Inversely Correlated with Yield Efficiency across Cultivars in Young Olive (*Olea europaea* L.) Trees

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***Abstract*. The modern olive industry is increasingly interested in olive cultivars that start producing early and remain relatively small, because they are suitable for super high-density orchards. Some cultivars are better suited to this than others but it is not clear why. Understanding the mechanisms that lead to early production and reduced canopy size is therefore important. The object of this study was to investigate whether differences in vigor across olive cultivars are related to earliness and abundance of bearing. We analyzed tree growth and productivity in young coetaneous trees of 12 olive cultivars, grown together in the same orchard. Trunk diameter increased over the observation period, reaching significantly different values across cultivars. Canopy volume also increased, reaching 2-fold differences between the minimum and the maximum values. Cumulative yield increased, reaching up to 3-fold differences. When the cumulative yield at the end of the experiment was plotted against the final trunk diameter, no correlation was found. A significant correlation was found when cumulative yield was plotted against the increment in trunk diameter during the observation period for which yield data were collected. This relationship improved (i.e., R^2 rose from 0.57 to 0.83) when yield efficiency [i.e., cumulative yield per unit of final trunk cross-sectional area (TCSA) or per unit of canopy volume] was used instead of yield. These results clearly showed that trees that produced proportionally more (i.e., higher yield efficiencies) grew less. We conclude that, in young olive trees, vigor is inversely related to early bearing efficiency, which differs significantly across cultivars. The results support the hypothesis that early and abundant bearing is a major factor in explaining differences in vigor across olive cultivars.**

The olive industry requires canopy reduction to allow super high-density orchards which permit earlier production and continuous mechanical harvesting (Rallo et al., 2007; Tous et al., 1999). This has stimulated much research into reduced vigor or even dwarf cultivars (Barranco, 1997; León Moreno, 2007; Sonnoli, 2001) and dwarfing rootstocks (Baldoni and Fontanazza, 1990; Barranco, 1997; Pannelli et al., 1992, 2002; Troncoso et al., 1990). Some cultivars, such as Arbequina, Arbosana, and Koroneiki, are better suited than others for super high-density orchards which require small-canopy trees (Camposeo et al., 2008; Tous et al., 2006) but it is not clear why. Understanding the mechanisms that lead to early and high production and reduced canopy size is therefore very important.

It is generally assumed that such cultivars have an inherent low vigor, and that this trait is the key factor for their suitability to super high-density orchards. It has also been shown that these cultivars exhibit greater branching associated with smaller diameters of trunk, branches, and shoots, resulting in higher yield efficiency and a greater number of fruiting shoots in the small canopy volume allowed in super high-density systems (Rosati et al., 2013). Therefore, the lower tree size results, at least in part, from the different branching characteristics, which concentrate more shoots in a small canopy volume, without necessarily implying lower shoot growth. However, the low vigor of such cultivars is also associated with the ability to produce more and earlier (Camposeo et al., 2008; Tous et al., 2003, 2006). It is possible, therefore, that the low vigor (reduced growth) of early-bearing cultivars could derive from their higher early productivity. If a tree spends more of the available resources into producing fruits, it can only grow less as a result (Grossman and DeJong, 1994). Competition between vegetative and reproductive growth is well established in several tree 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; Fernández et al., 2015; Monselise and Goldschmidt, 1982; Rallo and Suárez, 1989). However, very few studies considered young trees and no relationship between tree initial growth and cumulative yield was found (Moutier, 2006). It is important to consider that absolute yield is a size-dependent parameter and it is possible that, if less productive young trees grow faster, they will eventually become bigger enough to outyield the smaller, albeit more yield-efficient, trees. A more thorough analysis of growth and productivity, the latter expressed as yield efficiency, might reveal a relationship between tree growth and yield.

In this article, we test the hypothesis that the initial growth of young olive trees is inversely related to their yield efficiency.

Materials and Methods

The trial was carried out in an olive orchard located at the experimental farm of the CREA-OLI, near Spoleto in central Italy (42°48′48″N, 12°39′15″E, 356 m above sea level). Self-rooted trees were planted in 1986 and measurements began in 1990 on five trees of each of 12 cultivars studied, namely 'Vocio', 'San Felice', 'Rosciola', 'Raio', 'Raia', 'Pocciolo', 'Marchigiana', 'Leccino', 'Frantoio', 'Dolce Agogia', 'Correggiolo', and 'Borgiona'. The cultivars were placed in rows (i.e., one row per cultivar) and border rows were not used. Along the row (20 trees), the five representative trees were sampled at random along the whole length of the row (excluding border trees), to avoid possible differences due to position, even though the soil was uniform. Tree spacing was 5 × 5 m and the trees were trained to a cone shape. In order not to interfere with tree growth, pruning was limited to the minimum necessary to train the trees to a cone shape. Other field practices were carried out as traditionally done in the area, including chemical fertilization with N, P, and K, and natural

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green mulch mowed two to three times per year.

Parameters measured annually, from 1990 (year 1) to 1996 (year 7), included trunk diameter, from which TCSA was calculated, tree yield, and basal diameters and height of the canopy from which canopy volume was calculated, assuming a cone-shaped canopy. Yield efficiency was calculated as the cumulative yield over the studied period divided by the TCSA, or by the canopy volume, at the end of the period.

Cultivar differences in the various parameters measured were statistically analyzed by analysis of variance (ANOVA), according to a completely randomized design, and averages were compared by using the Student–Newman–Keuls test. Relationships between parameters were evaluated by calculating the coefficients of determination (R^2) and the statistical significance of the fits.

Results and Discussion

Tree diameter increased over time with large variation among cultivars (Fig. 1). Vocio, the cultivar reaching the largest diameter, had values about 45% greater than Borgiona, the smallest cultivar. Results of the ANOVA for the final diameter are reported in Table 1. The different tree growth here found is similar to what has been found in previous studies (Farinelli and Tombesi, 2015; Vivaldi et al., 2015).

Canopy volume increased over time with larger variations among cultivars than for trunk diameter (Fig. 2): 'Raio' reached the largest canopy volume, more than double that of 'Pocciolo', the smallest. Results of the ANOVA for the final canopy volume are reported in Table 1.

Cumulative yield increased over the observed period, reaching more than 3-fold differences between the most and the least productive cultivars (Fig. 3). Results of the ANOVA for the final cumulative yield are reported in Table 1.

To assess whether tree growth was affected by yield, we plotted the cumulative yield obtained over the 7-year observation period against the final trunk diameter and found no significant relationship (Fig. 4) as previously found (Moutier, 2006).

The lack of correlation was because trees were of dissimilar size at the start of the experiment, and the final diameter was not a good parameter to indicate tree growth during the period over which yield was evaluated. Final diameter represents tree growth from the beginning of the tree life, but yield data were not collected before 5 years from transplanting, when all cultivars had at least some fruits, although other cultivars had already produced more extensively. Therefore, to compare tree growth and yield over the same period, the diameter increment during the observed period was used in place of the final diameter. When cumulative yield was plotted against the diameter increment over the same observation period, a significant relationship was found (Fig. 5).

However, the relationship was much improved (i.e., $R^2 = 0.83$ instead of 0.57 and significance of the relationship was $P \leq 0.01$) when yield efficiency was used in place of yield, both when efficiency was expressed in terms of yield per unit cross-sectional area (Fig. 6) or unit of canopy volume (Fig. 7). This indicates that a poor (or lack of) relationship between growth and cumulative yield derives from growth dynamics. In fact, trees that initially produce less (i.e., lower yield efficiency) and grow more can eventually become bigger enough to outyield trees that initially produced more and thus remained smaller.

These results point at the importance of correctly evaluating growth and yield parameters. Because of the growth dynamics described above, yield alone does not represent a good parameter to evaluate whether tree growth is related to fruit production. In fact, the same yield represents a different effort depending on tree size (Avery, 1970). Yield efficiency is a better parameter because it is more independent of tree size, allowing the comparison of trees that grew more with those that remained smaller.

The strong negative correlation between yield efficiency and tree growth does not necessarily prove causality. It is possible that inherently low vigor reduces growth and sink demand for vegetation, leaving more sources available for fruit set and reproductive growth. In fact, 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), shoot removal and/or chemical control of vegetative growth (Mulas et al., 2011; Rugini and Pannelli, 1992; Williams et al., 1986), all result in enhanced yields.

However, several previous findings also suggest that reduced growth might be indeed the consequence of early and abundant fruiting. In fact, in olive, it is well established that vegetative growth is more abundant in off (i.e., with low yield) years (Castillo-Llanque and Rapoport, 2011; Fernández et al., 2015; Lavee, 2007). Trees that spend more energy on production are expected to grow less vegetation because reproductive and vegetative growth compete for the same sources

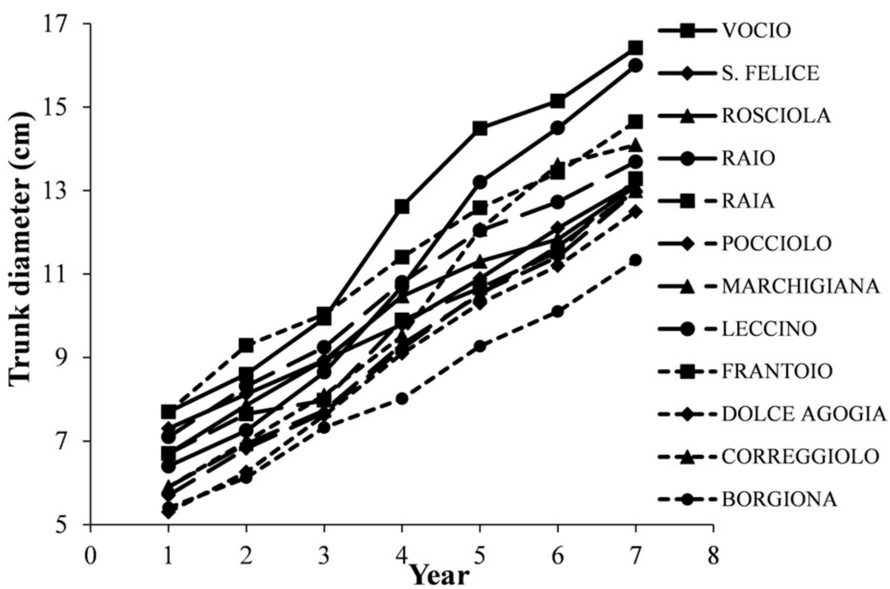

Fig. 1. Trunk diameter during the observation period. Each point is the average of five trees.

Table 1. Analysis of variance for final trunk diameter, canopy volume, and cumulative yield across 12 olive cultivars.

Cultivar	Trunk diam (cm)	Canopy volume (m^3)	Cumulative yield (kg/tree)
Borgiona	11.3 a	4.9 ab	56.9 cd
Correggiolo	14.1 de	9.6 cde	34.5 ab
Dolce Agogia	12.5 b	6.5 b	28.7 a
Frantoio	14.7 e	11.2 ef	92.8 f
Leccino	13.7 cd	10.8 def	77.8 e
Marchigiana	13.0 bc	6.4 b	33.4 ab
Pocciolo	13.0 bc	4.6 a	46.3 abc
Raia	13.3 bc	6.0 ab	52.7 bcd
Raio	16.0 f	11.5 f	29.0 a
Rosciola	13.1 bc	6.2 ab	65.4 cde
San Felice	13.2 bc	9.1 c	71.1 de
Vocio	16.4 f	9.2 cd	26.8 a

In each column, means followed by different letters are significantly different at $P \leq 0.05$.

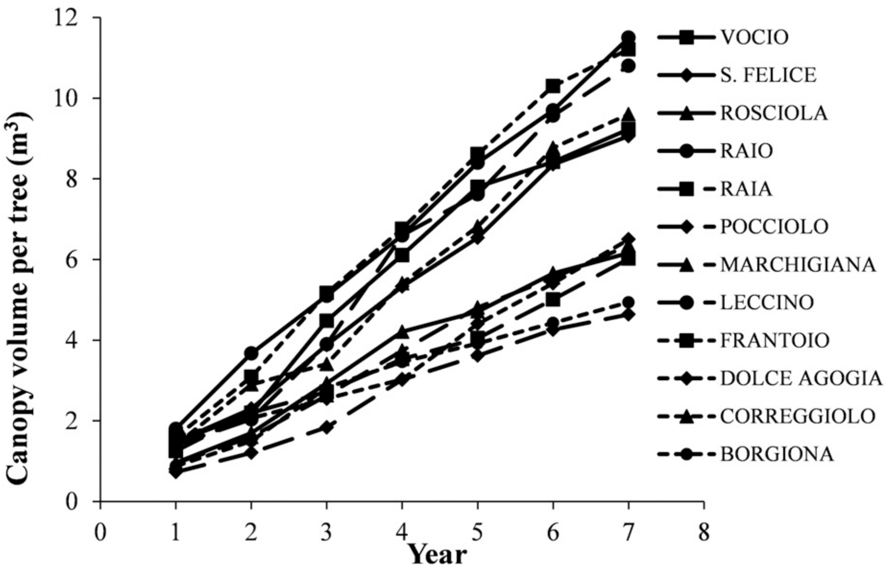

Fig. 2. Canopy volume during the observation period. Each point is the average of five trees.

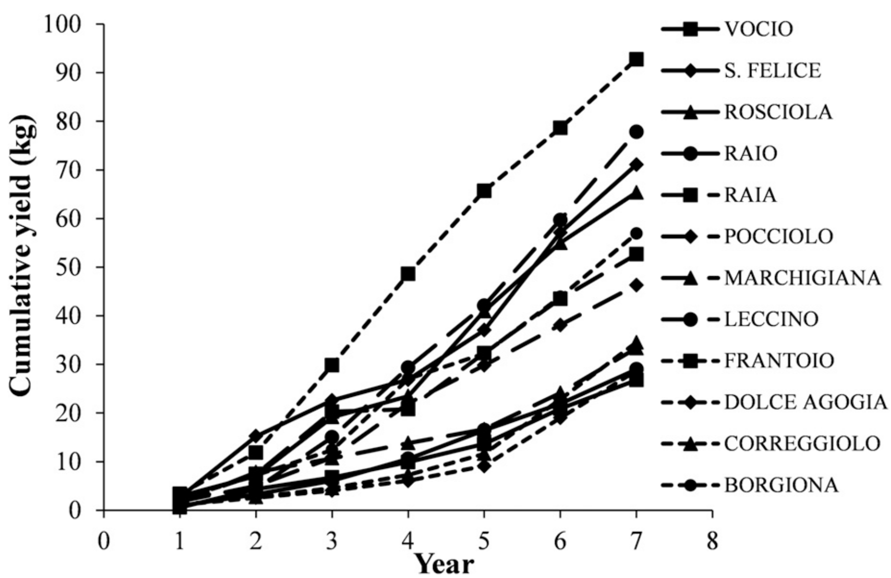

Fig. 3. Cumulative yield per tree during the observation period. Each point is the average of five trees.

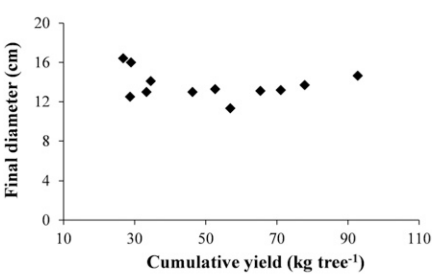

Fig. 4. Relationship between cumulative yield at the end of the observation period and the final trunk diameter. Each point is the average of five trees. The relationship was not significant.

within a tree (Grossman and DeJong, 1994). This competition is well established in several tree 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; Fernández et al., 2015; Monselise and Goldschmidt, 1982; Rallo and Suárez, 1989). Most of these studies have focused on mature trees during 1 year. In mature trees that reached their final size, reduced vegetative growth in 1 year makes little impact on tree size, which reflects accumulated growth over many years. In fact, in a mature tree, reduced vegetative growth in 1 year is likely to result in reduced removal of pruning materials and little or no difference in canopy volume after pruning. However, in young trees that have not reached the final size (as in our case), reduced vegetative growth, consequent to early bearing, will impact tree size (i.e., vigor) relatively more.

Fewer studies have been carried out on young trees. On young apple trees, defruiting increased tree growth and vigor (Chandler and Heinicke, 1926; Embree et al., 2007; Mochizuki, 1962; Verheij, 1972). Similarly, yield efficiency and vigor is inversely correlated across rootstocks in apple (Forshey and Elfving, 1989 and references therein). Studies on possible cultivar differences in early bearing and the consequent effect on tree vigor are scanty (Moore, 1978), and no studies have been published in olive, showing, or even suggesting, that differences in early bearing might explain (i.e., be the cause rather than the consequence of) differences in cultivar vigor. The present results show that genetic differences exist across olive cultivars in earliness and abundance of bearing and in yield efficiency, and that these differences are related to tree vigor. This agrees with findings by Lliso et al. (2004) who suggested that the dwarfing mechanism in citrus rootstock is related to the competition between vegetative and reproductive growth. 'Arbequina' and 'Arbosana', the two cultivars most frequently used in super high-density olive orchards, are known to have lower vigor than other cultivars; these cultivars also have higher early yields than most others (Camposeo et al., 2008; Tous et al., 2003, 2006). Data reported by Di Vaio et al. (2013) show that, across 20 cultivars, the least vigorous cultivars tended to have greater early yields.

Plants that spend a greater fraction of resources in vegetative growth produce more leaf area and intercept more light per unit total dry matter, thus increasing their relative growth rate (RGR: growth per unit plant mass and time). This is especially true in small trees where self-shading is minimal so that canopy light interception (and photosynthesis) is proportional to the total leaf area. Poorter and Pothmann (1992) found that fast-growing grasses had greater leaf area ratio (plant leaf area per unit of plant biomass) than slow-growing grasses and this explained their greater RGR. In fact, no correlation was found between RGR and net assimilation rate (growth per unit leaf area) of 24 C3 species (Poorter and Remkes, 1990), suggesting that greater biomass partitioning into leaf area, and not higher photosynthetic rates, was the mechanism leading to higher RGR. Producing earlier and greater yields, as for some olive cultivars, reduces source availability for vegetative growth (i.e., new leaves), leading to lower light interception and therefore lower carbon assimilation and lower growth.

It may be argued that calculating yield efficiency with fresh fruit yield is physiologically incorrect because the competition for resources is likely determined by the energetic cost for the dry matter produced in the fruit. We therefore converted the yield into grams of glucose equivalents using the conversion factors (i.e., the amount of dry matter produced per gram of glucose, $g \cdot g^{-1}$) from Penning de Vries et al. (1974), as in Mariscal et al. (2000) and in Villalobos et al. (2006),

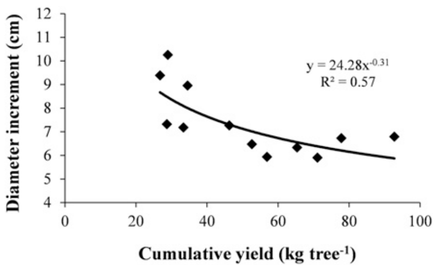

Fig. 5. Relationship between cumulative yield at the end of the observation period and the trunk diameter increment over the observation period. Each point is the average of five trees. The relationship was statistically significant ($P \leq 0.05$).

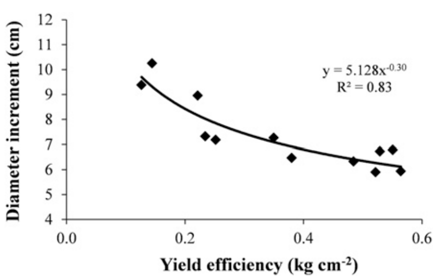

Fig. 6. Relationship between yield efficiency (i.e., cumulative yield per unit of trunk cross-sectional area) and the trunk diameter increment over the observation period. Each point is the average of five trees. The relationship was statistically significant ($P \leq 0.01$).

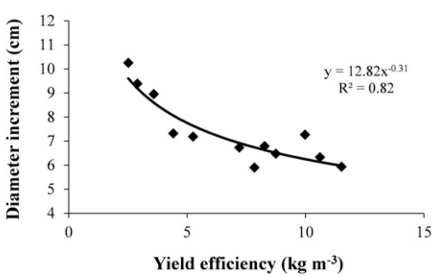

Fig. 7. Relationship between yield efficiency (i.e., cumulative yield per unit of canopy volume) and the trunk diameter increment during the observation period. Each point is the average of five trees. The relationship was statistically significant ($P \leq 0.01$).

using the actual oil content measured in the field for this experiment (data now shown). The results were nearly identical in terms of goodness of the fit (i.e., $R^2 = 0.81$ for both Figs. 6 and 7, instead of 0.83 for Fig. 6 and 0.82 for Fig. 7, using the same regression type, data not shown).

The correlations found between tree growth and yield or yield efficiency indicate that early and abundant yield is a major factor for differences in tree vigor across olive cultivars, explaining up to 83% (i.e., $R^2 = 0.83$) of the variance in tree growth (Figs. 6 and 7). However, this is probably not the only mechanism explaining the lower vigor of cultivars suitable for super high-density olive orchards, such as 'Arbequina' and 'Arbosana'. It has been shown that these cultivars also have higher branching, which reduces canopy volume at equal production of new shoots (Rosati et al., 2013) as found in other species (Forshey et al., 1992; Lauri, 2007; Lespinasse and Delort, 1986). Therefore, the low vigor of the cultivars suited to super high-density orchards may result from a combination of early and abundant bearing and higher branching (as well as shorter internodes that also mean more potential fruiting sites).

Clearly, the negative relationship between growth and yield efficiency does not necessarily hold true in every situation. When trees are stressed in any way (i.e., water, nutrient or temperature stress, pests and diseases, shading, etc.) they will both grow and produce less. It is only when light (i.e., assimilates) is the major limiting factor to growth that growth and yield will be inversely related.

Conclusion

The present results show that early and abundant bearing is strongly and negatively related to tree vigor, explaining most (about 83%) of the large variability in tree growth among cultivars. This suggests that early and abundant bearing is a major factor explaining differences in tree vigor across olive cultivars. Varieties characterized by early and abundant yield, along with a higher branching, may be the most suitable for super high-density olive orchards.

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