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RESEARCH PAPER

## Effect of crop load on the phenological, vegetative and reproductive behavior of the ‘Frantoio’ olive tree (*Olea europaea* L.)

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### Abstract

**V. Beyá-Marshall, and T. Fichet. 2017. Effect of crop load on the phenological, vegetative and reproductive behavior of the ‘Frantoio’ olive tree (*Olea europaea* L.). Cien. Inv. Agr. 44(1): 43-53.** The aim of this study was to characterize the phenological, vegetative and reproductive behavior variables of ‘Frantoio’ olive trees in an “off” year (with a low crop load) and an “on” year (with a high crop load). To do this, during the 2011–2012 and 2012–2013 seasons, “off” and “on”, respectively, phenological variables, plant growth (shoots and roots) and reproductive growth (type of flower, fruit set and growth), were monitored biweekly. In addition, the yield per tree was assessed, and the crop load was estimated. The main results showed that crop load strongly influenced these variables. The distribution and intensity of vegetative growth, both in the roots and aboveground, decreased more and had lower intensity in the high fruiting season, with a large part of this growth occurring prior to flowering. With respect to reproductive variables, a higher percentage of perfect flowers and fruit set in the low flowering season was observed compared to the high load season. These results suggest a partial crop load compensation mechanism under low flowering conditions. This mechanism, however, does not compensate for lower production in the “off” season. In terms of volume, fruit growth was similar between seasons until pit hardening, then the fruit growth rate dropped dramatically in the “on” season, indicating that fruit growth, until pit hardening, would not be affected by the presence of a higher number of fruits per tree.

**Keywords:** Alternate bearing, flowering, rhizotron, root growth dynamics, shoots, source-sink.

### Introduction

The olive (*Olea europaea* L.) is characterized as a species by strong fluctuations in its yield, going from a year with a high crop load to a year with a low crop load. This causes serious problems in production logistics and marketing, causing

uncertainty and instability in the olive grower’s returns (Goldschmidt, 2005; Lavee, 2007). Currently in Chile, there are commercial olive growers who can see their yield reduced from one year to the next by more than 90% in varieties such as Coratina, Frantoio, Koroneiki, Kalamata, and Barnea, among others (Fichet, 2013).

The first step in the study and development of strategies to mitigate this alternate bearing is to determine its effect on the phenology, vegetative

and reproductive cycles of olive trees (Lavee, 1986; Fichet and González, 2011). The vegetative and reproductive growth cycles occur simultaneously, which is why throughout the season a series of competitive interactions between sinks (shoots, fruits, roots and buds) occur that will affect the fruiting of the tree throughout its entire productive cycle (Rallo and Cuevas, 2008). In this respect, Lacointe (2000) describes an order of priority in the partitioning of photoassimilates among sinks, with the first being seeds, then fruits, growing apices, leaves, roots and finally storage organs. In addition, these cycles are not only affected by endogenous factors such as phytohormonal signals and demand for photoassimilates, nutrients and water but also by exogenous factors such as edaphoclimatic conditions and agronomic management (Lavee, 2007; Samach and Smith, 2013). Of these factors, crop load is one of the most influential in the phenomenon of alternate bearing, inducing a reduction in the vegetative growth and dry weight of shoots, leaves and roots under high fruiting conditions, which partly explains the biennial behavior of the species (Fernández *et al.*, 1992; Rallo and Cuevas, 2008; Dag *et al.*, 2010).

Although many studies have reported on the effect of crop load on the aerial part of the plant (Dag *et al.*, 2010; Trentacoste *et al.*, 2010; Rapoport, 2011), few studies have examined the competition among the growth of roots, shoots and fruits (Rallo and Cuevas, 2008). These authors indicate that the distribution of photoassimilates between alternative sinks, such as roots, seems to play a relevant role in the plant's vegetative and reproductive growth processes. Connell and Catlin (2005) describe all the functions of the roots, among them storage and growth, as dependent on the supply of products of photosynthesis; therefore, any condition or cultural practice that negatively affects this supply is potentially detrimental to the functioning of the roots and thus the plant. Although root growth characteristics of different plant species are genetically determined, they are highly susceptible to modification by the environment in which they develop, varying in terms of

the physical, chemical and biological properties of the soil, the climate and the growing conditions. Of these, the most influential are crop load (Dichio *et al.*, 2002; Fichet and González, 2011) and water availability, the latter being the most important (Fernández *et al.*, 1992; Palese *et al.*, 2000; Dichio *et al.*, 2002). Polverigiani *et al.* (2012) indicate that knowing how environmental factors and the source-sink ratios affect root growth is crucial to understanding how plants adapt to climate conditions, and it is also essential to the efficient agronomic management of fruit orchards. Nevertheless, although adult olive groves are generally biennial in nature, few studies have assessed the influence of alternate bearing on the pattern of root growth and its relationship to the aerial part of the tree (Fichet and González, 2011). In fact, most studies have focused on the effect of water supply on root growth (Fernández *et al.*, 1992; Nuzzo *et al.*, 1997; Palese *et al.*, 2000). In turn, it is also worth noting that studying the growth period of the roots aids in understanding how the root system works and its relationship to the aerial part of the tree, as well as in identifying the periods when fruit trees absorb the greatest amount of water and mineral elements (Connell and Catlin, 2005). In this sense, the use of observation rooms, or rhizotrons, allows root growth to be examined under field conditions over a long period of time (Fernández *et al.*, 1992; Noordwijk *et al.*, 2000).

## Materials and methods

### *Study location*

The study was conducted between March 2011 and August 2013 in a polyvarietal olive orchard planted in 1998 in Cholqui, Melipilla, Chile (33°48' S and 71°05' W, 345 m.a.s.l.) owned by the Agrícola Valle Grande Ltda. company. The region has a semi-arid Mediterranean stenothermal mesothermal temperate climate, with temperatures that vary between a maximum mean in January of 28.7 °C and a minimum mean in July of 3.4 °C,

with an average annual precipitation of 330 mm, concentrated between mid-autumn and winter, and a dry period of 8 mo (Santibáñez and Uribe, 1990). The soil is sandy clay loam, alluvial and deep in origin (90–110 cm) (Reyes, 2013). The orchard has been under organic management since 2001, with drip irrigation composed of 2 L h<sup>-1</sup> drippers in each row every 50 cm, reaching a supply of 4000 m<sup>3</sup> ha<sup>-1</sup> year<sup>-1</sup>. The ‘Frantoio’ olive trees (self-rooted) were planted with 6 × 4 m spacing in a north-south orientation and were managed as wide-hedgerows using the central leader training system. Crop management, such as irrigation, fertilization and pruning, was carried out according to the criteria and management implemented by the company. The weather data were obtained from a WatchDog weather station (Spectrum Technologies Inc., Illinois, USA) located at the property.

#### *Olive tree selection and follow-up*

The study was conducted in nine trees of uniform development, vigor and height, and without nutritional or pathological issues. The olive trees presented strong alternate bearing. In the first season (2011–2012), they had a low crop load (“off” year: average 6.3 kg/tree), i.e., with few fruits; in the 2012–2013 season all trees had high fruiting (“on” year: average 28.2 kg/tree). In order to identify the vegetative and reproductive phenological stages in which the measurements were taken, the standardized BBCH scale system of Sanz-Cortés *et al.* (2002) was used. In this way, the phenophases winter rest, budbreak, full bloom, fruit set, pit hardening and veraison correspond, on this scale, to stages 00 in the development of the vegetative buds, 31 in shoot development, 65 and 69 in flowering, 75 in fruit development and 81 in fruit maturity, respectively. The harvest date was determined according to the commercial operation schedule of the orchard criteria.

The monitoring of vegetative growth was done in one olive tree, selected in March 2011, with high crop load, where an observation chamber

(trench profile or rhizotron) was installed for root monitoring. Rhizotron dimensions were 84 cm wide, 84 cm long and 104 cm deep, and the rhizotron was placed 50 cm from the tree trunk. This chamber had a glass panel, 72 cm wide, 100 cm long and 8 mm thick, on the side next to the plant. Once the roots reached the glass (August 2011), biweekly measurements of new root interceptions (Noordwijk *et al.* 2000) and shoot length were recorded. Counting new root interceptions was done in a simple sampling grid of 5 × 5 cm drawn on the glass panel. New growth was recorded when new roots emerged from the soil in the observation plane or when old roots showed new growth. Two differently colored permanent markers were used to trace each observation in order to make chronological records of new growth. For shoot growth, 10 homogenous one-year-old shoots distributed around the entire canopy were marked at a height of 1.5 m.

To monitor the reproductive cycle, eight olive trees were selected in full bloom (November 2011). These were in similar conditions to those of the olive tree with the rhizotron, in terms of intensity of flowering and trunk cross-sectional area. In both seasons, the percentage of perfect and staminate flowers, percentage of fruit set, fruit growth, date of pit hardening, Ferreira’s coloration index and fruit yield were assessed. To determine the proportion of perfect flowers (with normal-length pistil) and staminate flowers (with atrophied pistil), a sample of 600 to 1000 flowers per tree in full bloom was collected from both the east and west sides. Then, for the fruit set percentage, 100 inflorescences were selected from a total of 10 branches and checked every 15 d, counting the flowers and then fruits from flower bud to harvest. Subsequently, to evaluate the fruit growth and pit hardening date, three fruit-bearing branches per tree were selected in the fruit set phase. Each branch had between 5 and 8 fruits, approximately, and fruit volume was estimated using the formula for a prolate spheroid, measuring the cross-sectional and longitudinal diameters of fruits with a digital caliper every

15 d. In addition, a follow-up was carried out to determine the date of pit hardening, by cutting cross-sections from 100 fruits at random per tree every 7 d starting January 15. The fruit maturity index (MI) was determined by Ferreira's coloration index (1979), which classifies fruits from 0 to 7 according to skin and pulp color (Beltrán *et al.*, 2008). In the 2011–2012 season, due to the low crop load, weekly monitoring of this variable was not possible since it would have required 100 fruits to be collected per tree, which is why it was evaluated only at harvest. Nevertheless, in the following season (2012–2013), which had a high crop load, a weekly follow-up of this variable was done from the last week of April until harvest. The oil concentration in the pulp at harvest was determined using the Soxhlet method (AOAC, 2000). Both harvests, 2012 (30–04–2012) and 2013 (22–05–2013), were conducted on the basis of the same number of accumulated degree-days from full bloom due to the strong temperature influence on the oil accumulation process (Trentacoste *et al.*, 2012). For the degree-day calculation, with a temperature threshold of 10 °C, González's (1995) formula was used.

### Statistical analysis

The statistical analysis was performed with a sample of nine olive trees, with the tree being the experimental unit. Consideration was given to whether there were statistically significant

differences for all the variables between the crop loads, high and low, between the two seasons, under the theoretical framework of mixed linear models. The yield per tree, high and low, was considered a fixed effect and the tree effects in each season, a random factor. In case of significant differences between the years, Fisher's LSD test for multiple comparisons was used ( $\alpha=0.05$ ). The statistical program used was InfoStat v. 2013 (Di Rienzo *et al.*, 2013).

### Results and discussion

The accumulated heat requirement (°Cd), from budbreak to pit hardening (September to January), was similar in both seasons, at 966 °Cd and 967 °Cd for 2011–2012 and 2012–2013, respectively. However, at the oil synthesis and accumulation stages (pit hardening to harvest), the accumulated temperature in 2012 was higher than that in 2013, at 1730 °Cd and 1722 °Cd, respectively. It should be remembered that the 2013 harvest was an “on” year, which, together with a lower rate of temperature accumulation, delayed harvest for almost a month (Table 1). The 2013 autumn and winter were not only colder but also drier, presenting accumulated precipitation of 160 mm between May and August compared to 283 millimeters in 2012 (data not shown).

Although there was a large difference in the crop loads between seasons, the degree-day accumu-

**Table 1.** Accumulated heat requirement in degree-days (°Cd) with a 10 °C base, from budbreak to fulfillment of each of the phenological stages and their related chronological date in ‘Frantoio’ olive trees during the 2011–2012 and 2012–2013 seasons.

Phenological stage	Accumulated °Cd /Date			
	2011-2012 (Off)		2012-2013 (On)	
	Accumulated °Cd	Date	Accumulated °Cd	Date
Budbreak	0000.0	31-08-2011	0000.0	12-09-2012
Bloom	0279.6	17-11-2011	0283.2	19-11-2012
Fruit set	0414.4	02-12-2011	0402.1	03-12-2012
Pit hardening	0966.1	27-01-2012	0967.2	31-01-2013
Beginning of veraison	1647.2	09-04-2012	1707.9	08-05-2013
Harvest	1730.4	30-04-2012	1722.3	22-05-2013

lation during the different phenophases until pit hardening (PH) was similar (Table 1), suggesting that crop load does not affect these phenophases. Corelli-Grappadelli and Lakso (2004) report that the beginning of PH is due mainly to environmental conditions (temperature and precipitation) and to the genetic traits of the variety. On the other hand, crop load indeed affected the thermal time that elapsed between PH and the beginning of fruit color change (Table 2), delaying the beginning of veraison in the “on” season (2012–2013). Although the harvest of the 2012–2013 season was conducted with a degree-day accumulation (Table 1) and a pulp oil concentration (Table 2) similar to that of the 2011–2012 season, the fruit presented a lower coloration index (1.8 versus 3.0) (Table 2). This result agrees with the studies by Tognetti *et al.* (2006) and Trentacoste *et al.* (2010) average fruit weight and fruit oil concentration, who describe the pigment synthesis rate as dependent on the crop load; hence, fruit color, as an index for harvest decisions, must include the production level of the orchard (Trentacoste *et al.*, 2010) average fruit weight and fruit oil concentration.

Root growth occurred practically throughout the year (Figure 1), as other researchers have indicated (Palese *et al.*, 2000; Polverigiani *et al.*, 2012) distribution, differentiation and mortality to be directly observed. Four olive trees were selected and a glass window for each tree (0.8 m deep by 1.3 m wide). However, this growth was strongly determined by the reproductive process, since during flowering and later fruit growth, the number

of root interceptions dropped dramatically, which was consistent with what Fichet and González (2011) and Polverigiani *et al.* (2012) distribution, differentiation and mortality to be directly observed. Four olive trees were selected and a glass window for each tree (0.8 m deep by 1.3 m wide) observed, with this decrease being greater during the “on” season. The growth, although lower in intensity, remained steady over the summer; then, a heavy reduction in the pre-harvest number of root interceptions (March-May) was observed in both seasons. Later, root growth reactivated during winter months (June-July) and was of greater intensity in the 2012 winter period, which has also been reported by other olive researchers (Palese *et al.*, 2000; Polverigiani *et al.*, 2012) distribution, differentiation and mortality to be directly observed. Four olive trees were selected and a glass window for each tree (0.8 m deep by 1.3 m wide). The number of roots produced varied considerably between seasons, with 33.3% fewer roots in the “on” year. This decrease may be due to the greater competition by photoassimilates among the different plant organs, particularly in the process of fruit growth and oil accumulation, demonstrating the priority of these over the other sinks, as has been indicated by other authors (Wright, 1989; Lacoïnte, 2000; Palese *et al.*, 2000). In the absence of any other sink, however, it is reasonable to think that photoassimilates produced by leaves can be assigned to root growth. In such conditions, the plant seeks to explore the greatest amount of soil volume possible through the emission of roots (Polverigiani *et al.*, 2012)

**Table 2.** Proportion of perfect and staminate flowers, fruit set, yield, maturity index and oil concentration in the fruit of olive trees in two consecutive seasons: “off” (2011–2012) and “on” (2012–2013).

Season	Flower type		Fruit set	Yield	Harvest	
	Perfect (♀)	Staminate (♂)			MI†	d.w.b‡
	%			kg		%
2011-2012	96.5a	3.6a	7.6a	6.3a	3.0a	36.2 <sup>ns</sup>
2012-2013	69.2b	30.8b	3.5b	28.2b	1.8b	32.0

The adjusted average is presented in each column. Adjusted means with different letters in the same column indicate significant differences between crop loads according to Fisher’s LSD test for multiple comparisons ( $p < 0.05$ ). n.s.= No significant differences between crop loads.

† MI= Maturity index

‡ d.w.b= Dry weight base



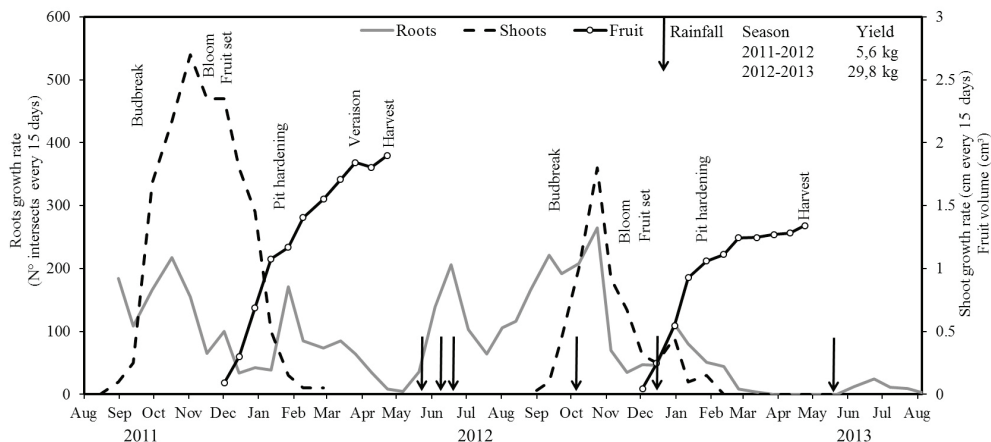
distribution, differentiation and mortality to be directly observed. Four olive trees were selected and a glass window for each tree (0.8 m deep by 1.3 m wide). This root reactivation occurred post-harvest and at the same time as the first winter rains. This could be attributed to the absence of fruit or to rains, which increased the water content in the soil, or to a combined effect.

In this study, a reduction was also observed in the number of pre-harvest root interceptions (Figure 1); this is likely due to the lower water availability in the soil as a result of the pre-harvest regulated deficit irrigation done by the company to improve oil extractability in both seasons. In this sense, water availability is needed for optimal root activity, because roots do not grow through dry soil and their exploration of the available resources is limited in these conditions of increased mechanical resistance (Fernández *et al.*, 1992; Connell and Catlin, 2005).

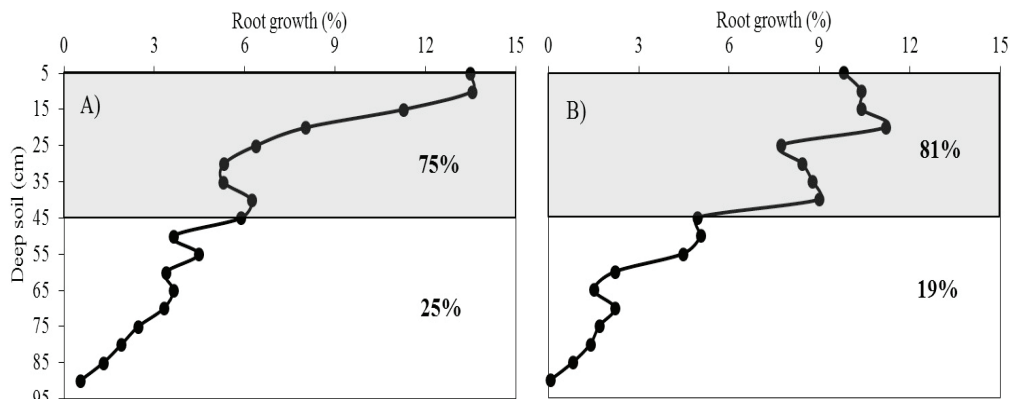
It was observed that most of the root growth occurred in the top 45 cm of soil (Figure 2), regardless of the current year’s crop load. This distribution is probably because olive trees were self-rooted, which is why the roots did not grow deeper. Knowledge of the soil volume explored by the roots is indispensable to managing irrigation

correctly, in terms of volume and frequency, as well as fertilization practices (Nuzzo *et al.*, 1997), thus contributing to a better use of water by the olive grower, and at the same time, enabling him to reduce electricity and fertilizer costs.

The current year’s vegetative growth is fundamental for the flowering and production of the following year and depends on the water availability in the soil and the number of fruits on the tree (Rallo and Cuevas, 2008). This is because crop load is a strong carbohydrate sink, receiving a greater amount of resources at the expense of shoot growth (Lavee, 2007). Therefore, it is important to know the stage at which this competition begins, mainly in “on” years, with the aim of maximizing shoot growth prior to this period, thereby attenuating the probable low yield of the following season. In relation to this, it was found that shoot growth began in both seasons at the beginning of September and stretched to the end of January (Figure 1). However, both the final shoot length and the duration of this vegetative growth were affected by crop load. Hence, in the “on” year, approximately 80% of the total shoot growth occurred between budbreak and flowering, i.e., the first 10 weeks after budbreak (Figure 3). Wright (1989) reports that at the beginning of the flowering period there is competition between flowers



**Figure 1.** Growth of shoots, roots (0–100 cm soil depth) and fruits of an olive tree, in two consecutive seasons: “off” (2011–2012) and “on” (2012–2013), in Cholqui, Chile. Highlighted precipitation is more than 20 mm.

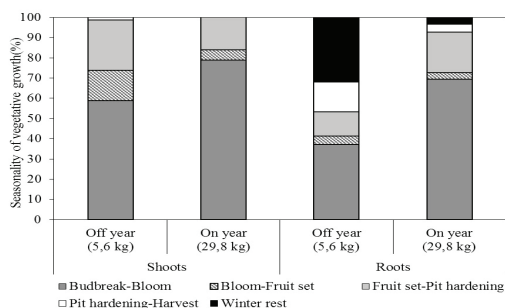


**Figure 2.** Distribution of root growth, expressed as the percentage of growth produced at different soil depths over the total of one season. A: 2011–2012 season; B: 2012–2013 season.

and growing apices, with the latter presenting greater sink strength, because the shoots are in a very active phase of development. Therefore, promoting shoot growth during the “on” year before flowering could be convenient given that, later on, competition between reproductive and vegetative growth is clearly very strong.

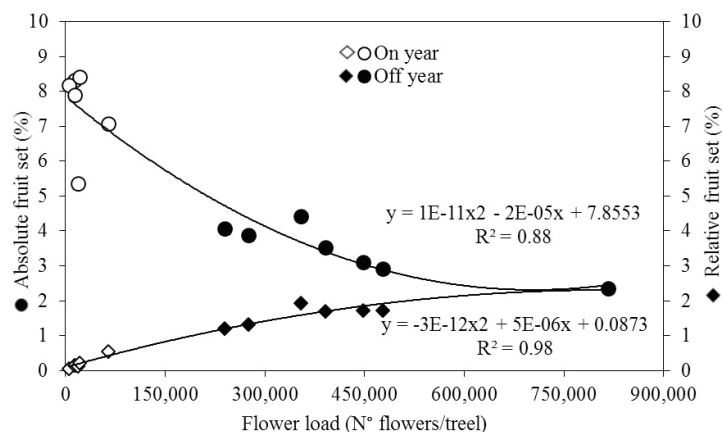
In the “off” season, the proportion of perfect flowers was higher than during the “on” season (Table 2), which agrees with what was found by Cuevas *et al.* (1994), possibly due to a lower level of competition by photoassimilates and mineral elements among the existing inflorescences (Cuevas *et al.*, 1994; De la Rosa *et al.*, 2000). In turn, fruit set not only depends on the competition within each inflorescence but also on the poten-

tial fruiting of the tree (Lavee *et al.*, 1996). For this reason, the effect of reduced flowering also influenced the percentage of fruit set (Figure 4); it was observed that the final number of fruits was 7.6% when there was little flowering, and the final number of fruits can reach, on average, 3.5% in the “on” year. Similar results have been reported by Lavee (1986). Thus, when the two seasons are analyzed together (Figure 4), the trees with a low flower load have greater fruit set than those with a high load ( $P < 0.0001$ ), and the former also have a higher percentage of perfect flowers. However, if it is considered that the tree with the greatest number of flowers (“on” season) is the one that has the greatest fruiting potential, it is observed that this increase in fruit set does not compensate for the season’s yield ( $P < 0.0001$ ) (Figure 4). In spite of the fact that these mechanisms (increases in perfect flowers and fruit set in an “off” season) do not compensate for alternate bearing, other authors indicate that in the medium term, they would gradually regulate it (Rallo and Cuevas, 2008).



**Figure 3.** Distribution of shoot and root growth, expressed as the percentage of the growth among the different phenological stages over the total of the season, in two consecutive seasons: “off” (2011–2012) and “on” (2012–2013).

The literature reveals that the olive presents a double sigmoidal growth pattern (Lavee, 1986); however, this was not observed in this study. In both seasons, it was found that the fruit volume increased almost linearly between 3 and 11 weeks after total flowering (WAFB, fruit set-pit hardening) and then continued increasing, but at a slower rate, until 21 and 25 WAFB, for the “on”



**Figure 4.** Percentage of absolute fruit set and relative fruit set of olive trees in terms of their floral load, expressed in number of flowers/tree in two consecutive seasons: “off” (2011–2012) and “on” (2012–2013). Absolute fruit set = (N° of fruits/N° of flowers) \* 100; relative fruit set = (N° of total fruits / Maximum N° of flowers) \* 100.

and “off” years, respectively (Figure 5). This is consistent with recent studies on olive trees, in which no double sigmoidal pattern was found (Lavee, 2007; Trentacoste *et al.*, 2010). This may be because deceleration of growth at stage II of fruit growth would be associated with water availability in the soil. Different authors indicate that this deceleration can be clearly seen in olive fruits under drought conditions, whereas under irrigation, as was the case in this study, it is not observed, or if observed, it is very slight (Lavee, 2007; Gucci *et al.*, 2009).

In relation to fruit growth, expressed in volume, in the first phase, no great differences were seen between the seasons (Figure 5), because the pit occupies most of the fruit volume (Lavee, 1986). Morettini (1972), cited by Lavee and Wodner (2004), reported that fruit growth until pit hardening is less affected by crop load than the subsequent mesocarp growth. This is due to the pit having a higher priority as a sink than the mesocarp and competition for water and nutrients (Morales-Sillero *et al.*, 2008). Thus, the differences in growth between seasons were observed after this phenophase, when the mesocarp began to grow. In this sense, the oil biosynthesis rate increases from pit hardening (Lavee and Wodner, 2004) and,

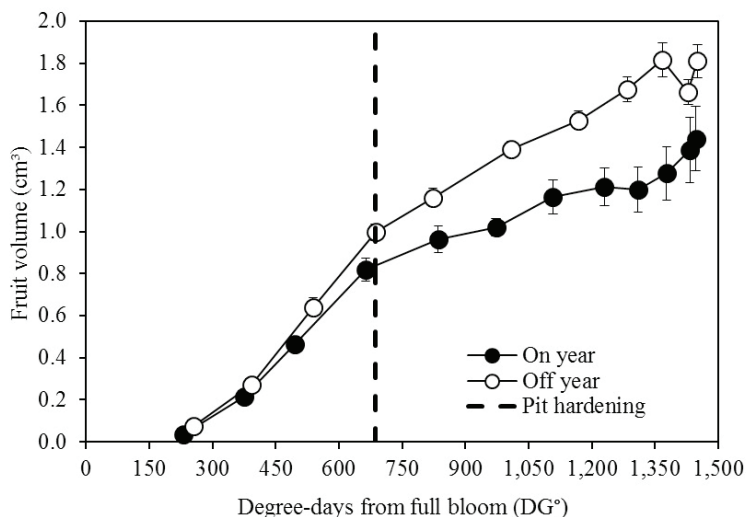
therefore, this difference in growth is related to the greater metabolic cost for lipid biosynthesis in the mesocarp (Poorter and Villar, 1997) and to the strong competition for photoassimilates that occur in high-yield trees (Lavee, 2007).

The number of fruits strongly affects the vegetative and reproductive cycles of the olive tree. In the “on” year, there is an early and prolonged negative effect of fruits on shoot and root growth. A low flower load favors a greater proportion of perfect flowers and fruit set; however, it does not compensate for the strong negative impact resulting from the previous year’s high crop load. Although there is less root growth in the “on” years, roots grow throughout the year, with most growth occurring in spring months.

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**Figure 5.** Fruit volume in  $\text{cm}^3$ , based on the accumulated degree-days from flowering, in two consecutive seasons: “off” (2011–2012) and “on” (2012–2013). Vertical bars indicate the standard error.

## Resumen

**V. Beyá-Marshall y T. Fichet. 2017. Efecto de la carga frutal sobre el comportamiento fenológico, vegetativo y reproductivo en olivo (*Olea europaea* L.) ‘Frantoio’.** *Cien. Inv. Agr.* 44(1): 43-53. El objetivo de esta investigación fue caracterizar el comportamiento fenológico, variables vegetativas y reproductivas de olivos ‘Frantoio’ en un año de baja “off” y uno de alta carga frutal “on”. Para ello, durante las temporadas 2011-2012 y 2012-2013, off y on, respectivamente, se realizó un seguimiento quincenal de variables fenológicas: crecimiento vegetativo (brotes y raíces) y reproductivo (tipo de flor, cuaja y crecimiento de fruto). Además, se evaluó la producción por árbol y se estimó la carga frutal. Los principales resultados muestran una fuerte influencia de la carga frutal en las variables evaluadas. La distribución e intensidad del crecimiento vegetativo, tanto radical como aéreo, fue más acotado y de menor intensidad en la temporada de alta fructificación, produciéndose, gran parte de este crecimiento, previo a la floración. Respecto a las variables reproductivas, se observó, en la temporada de baja floración, un mayor porcentaje de flores perfectas y cuaja respecto a la temporada de alta carga. Estos resultados sugieren un mecanismo parcial de compensación de carga frutal en condiciones de baja floración. Sin embargo, este mecanismo no alcanza a compensar la menor producción de la temporada de baja producción. El crecimiento de frutos, en cuanto a volumen, fue similar entre las dos temporadas hasta endurecimiento del endocarpo, luego en la temporada de alta carga, la tasa de crecimiento del fruto tuvo una fuerte disminución, indicando que esta variable, hasta endurecimiento de carozo, no se vería afectada por la presencia de un mayor número de frutos por árbol.

**Palabras claves:** Alternancia productiva, brotes, dinámica de crecimiento de raíces, floración, fuente-sumidero.

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